9-27-1996

Proceedings of the International Conference on Genetic Improvement of Sorghum and Pearl Millet

Darrell Rosenow
Texas A&M University

Gary Peterson
Texas A&M University

John Mullet
Texas A&M University

Henry Nguyen
Texas Tech University

Gebisa Ejeta
Purdue University

See next page for additional authors

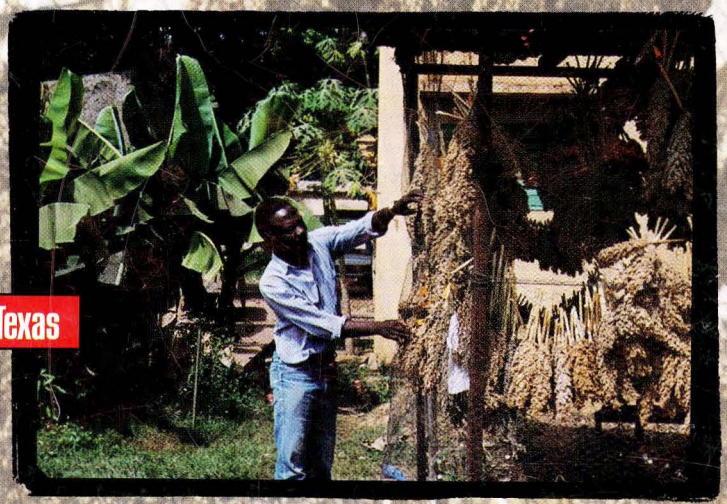
Proceedings of

The International Conference on Genetic Improvement of Sorghum and Pearl Millet

Sponsored by

INTSORMIL

ICRISAT



September 23–27, 1996–Lubbock, Texas

The conference sponsors, INTSORMIL and ICRISAT, gratefully acknowledge the contributions made to this conference by the following organizations.

The Rockefeller Foundation
Overseas Development Administration (ODA)
National Sorghum Producers Association
Texas Seed Trade Association
Texas Tech University
Texas A&M University

Members of the Organizing Committee

Proceedings
of the

International Conference on Genetic Improvement of Sorghum and Pearl Millet

September 22 - 27, 1996
Holiday Inn Plaza, Lubbock, Texas

Sponsored by
USAID Title XII Collaborative Research Support
Program on Sorghum and Pearl Millet
(INTSORMIL)

and

International Crops Research Institute for the Semi-Arid Tropics
(ICRISAT)

December 1997
Publication No. 97-5

Contents

Session IV - Breeding Techniques

Session V - Breeding for Resistance to Biotic Stress

Foreword

In 1971, an international symposium, "Sorghum in the Seventies", organized by the All India Coordinated Sorghum Improvement Project with support from the Indian Council of Agricultural Research and the Rockefeller Foundation was held in Hyderabad, India. The symposium reviewed the current knowledge base of the scientific, production and nutritional aspects of sorghum as a crop and as a human food. In 1981, ICRISAT, INTSORMIL, and the Indian Council of Agricultural Research (ICAR) sponsored "Sorghum in the Eighties", an international symposium at ICRISAT Center in India, to review the achievements accomplished in sorghum research during the preceding 10 years. They reviewed sorghum's role as an important cereal food, feed, construction material, and fuel in the developed and developing countries. In 1994, after discussion among INTSORMIL and ICRISAT scientists, it was recognized that an international meeting on the genetic improvement of grain sorghum and pearl millet was needed and would be strongly supported by the international sorghum and millet research community.

Those discussions led to the September 1996 International Conference on Genetic Improvement of Sorghum and Pearl Millet.

Grain sorghum and pearl millet are major food grains in the semiarid tropics of Africa, India, and South America. Sorghum ranks fifth among the world's cereals, following wheat, maize, rice, and barley. FAO includes all millets together in its production estimates. Current estimates indicate that annual world sorghum production is approximately 61 million metric tons and world millet production is approximately 20 million metric tons. The inaugural speaker of this 1996 conference, Dr. Leland House, indicated global population is projected to increase to nine billion people by the year 2030 and is projected to increase most rapidly in the developing world. This will create a growing demand for food, as well as potential new market opportunities for food products developed from these basic grains.

This conference brought together sorghum and millet research scientists from around the world to share and exchange information on the genetic improvement of these two crops. Papers were presented on genetic resources, yield and adaptation, breeding, breeding techniques, breeding for resistance to biotic stresses, abiotic stresses and *Striga*, breeding for improved grain quality and utilization, and the current and future use of biotechnology in genetic improvement. Mr. Dennis Avery, of the Hudson Institute, and closing keynote speaker to the conference, challenged the conferees with this concept: "Research is the largest component of agricultural sustainability under human control".

INTSORMIL and ICRISAT wish to thank the Rockefeller Foundation, the Overseas Development Administration (ODA), the National Grain Sorghum Producers Associa-

tion, the Texas Seed Trade Association, Texas Tech University, and Texas A&M University for their support of international participants and conference activities which made this meeting a special success. Special thanks go to the Texas A&M scientists who organized the field tours and to Cargill Seed Company, Crosbyton Seed Company, DeKalb Seed Company and the Pioneer Seed Company for hosting tours through their breeding nurseries and seed production facilities. Special thanks also goes to the organizing committee for pulling this program together and to the participants who prepared the papers appearing in this volume. The conference body applauded the INTSORMIL support staff, Joan Frederick, Marilyn McDonald, and Dottie Stoner, and Sheryl Smith of the Texas A&M Research Center, Lubbock, in appreciation for the outstanding manner in which logistics and conference details were handled.

A special award was presented at the Conference to Dr. Leland K. House who was honored for his many years of service to international sorghum research and for the many contributions he made to improving sorghum in developing countries. Dr. House was the leader in organizing and served as a symposium coordinator in the previous International Sorghum Conferences in 1971 and 1981. A summary of the professional career and accomplishments of Dr. House are printed on page 689 in these proceedings. It was fitting that Dr. House served as the keynote speaker at this conference. During the banquet Thursday evening, Dr. Ouendeba Botorou, Coordinator for the Pearl Millet Research Network in West Africa (ROCAFREMI), was also recognized for his years of service as INTSORMIL Host Country Coordinator and pearl millet research collaborator in Niger.

Participants came to this conference prepared to spend long hours in getting caught up on the most recent scientific advancements made in the field of genetic improvement in sorghum and millet. While we take our research very seriously, there were light moments as well. At the banquet, Dr. Aliya Kasakova, Deputy Director, All Russia Sorghum Research Institute, Rostov, Russia, dedicated a poem to the conference participants entitled "Sorghum and Millet That Need To Be Improved." The poem captures the spirit of the conference and is included in these proceedings.

This publication will be widely distributed throughout the world. We hope the information, poster abstracts and discussions appearing in this proceedings will be as stimulating to the reader as the actual presentations. I believe this meeting strengthened the collaboration between National Agricultural Research Organizations (NARs), scientists from the U.S., ICRISAT, ODA, and other international organizations.

John M. Yohe
INTSORMIL Program Director

Sorghum and Millet That Need to Be Improved

**by Aliya S. Kasakova, Deputy Director,
All Russia Sorghum Research Institute,
Rostov, Russia**

There are Sorghum and Millet that need to be improved.

And this is a conference that was organized because
Sorghum and Millet need to be improved.

And this is the Lubbock - city that has a conference
that was organized because Sorghum and Millet need
to be improved.

And there is our Organizing Committee that has done
everything and chosen the Lubbock - city
that has a conference which is organized because
Sorghum and Millet need to be improved.

And this is an international team of Sorghum and Millet scientists
that thanks an Organizing Committee,
that has done everything and chosen the Lubbock - city
that has the conference that was organized
because Sorghum and Millet need to be improved.

And those (in the field) are Sorghum and Millet varieties
that were created by plant breeders
that thank an Organizing Committee that has done everything
and chosen the Lubbock - city
that has the conference
because Sorghum and Millet need to be improved.

And this is the large Texas beef that like to eat new
forage Sorghum and Millet varieties,
that grow in the field
that were created by plant breeders
that thank an Organizing Committee that has done everything
and chosen the Lubbock - city
that has a conference
because Sorghum and Millet need to be improved.

And this is a good piece of real Texas meat
that was prepared from the large Texas Beef
that liked to eat new forage Sorghum and Millet varieties
that grow in the field
that were created by plant breeders
that thank an Organizing Committee
that has done everything and chosen the Lubbock - city
that has the conference
because Sorghum and Millet need to be improved.

And all that is a magic power of science
that gives us a good piece of real Texas meat
that was prepared from large Texas beef
that liked to eat new forage Sorghum and Millet varieties
that grow in the field
that were created by plant breeders
that thank an Organizing Committee
that has done everything and chosen the Lubbock - city
that has the conference
because Sorghum and Millet need to be improved.

Session I

Inaugural Session

Session Chair: Darrell Rosenow

Rapporteurs: A.M. El Ahmadi and John Axtell

Speakers:

L.R. House
J.L. Bennetzen

Inaugural Address

Leland R. House

I wish to thank the organizers of this conference for giving me the opportunity to give this inaugural address.

We are a group of agricultural scientists with a focus, or at least an interest, in sorghum and millets. Our interest in and approach to our science is varied, our expectations different, and our rewards individual; but being involved in agriculture, particularly with sorghum and pearl millet, which are important crops to some of the world's poorest people, carries a responsibility to address issues of concern to those who use the crop. I feel that for those of us involved in crop improvement, the end point is the user, not a publication or cultivar release. Advances in our science are made by people and for people, so we must be concerned about people. This meeting has a focus on the science; it is international in scope and wants projection into the future. I would like in recognizing these issues to consider several areas: our science, development, and the human resource with which we work. I believe that these topics are relevant to our concern about where we are going.

Changes in Sorghum and Millet Production

Before beginning these topics, I should mention something about significant trends in sorghum and millet production and projection of crop demand.

Leland R. House, Rt. 2, Box 136 A-1, Bakersville, NC 28705, USA

Sorghum ranks fifth among the world's cereals, following wheat, maize, rice, and barley. Production in the early 1960s was about 35 million tons but increased rapidly, reaching almost 70 million tons in 1978. Production then fluctuated substantially, reaching a peak of 77 million tons in 1985. Production declined and in 1993-94 was about 61 million tons. In the 1993-94 season, area sown and yield figures more or less followed production and declined as well, with about 44 million hectares sown and with an average yield of about 1420 kg ha^{-1} (FAO Production Year Books).

FAO includes all millets together in its estimates, so figures for Africa and India have been used to better represent changes for pearl millet. Comparing the averages for the years 1975-79 with the years 1990-94, area declined by 4.5 million hectares (35.0 and 30.5 million hectares, respectively), while yield increased by 115 kg ha^{-1} (565 compared to 680 kg ha^{-1}) so production was relatively constant during this period, with an increase of 800,000 tons (19.6 compared 20.4 million tons, respectively).

On a world basis, sorghum represents four percent of the total cereal production. While this figure is small, there are countries where sorghum production is of great importance: Burkina Faso (53%), Sudan (72%), Chad (41%), Cameroon (40%), Botswana (84%), Rwanda (52%). In Africa as a whole, sorghum represents 18 percent of the total (Dendy, 1995).

Averaging the production figures for 1987, 88, and 89, pearl millet represents about 1.1% of total world cereal production. In Africa as a whole (1989), the figure is 10%, and in India, 5% of total cereal production. The crop is very important in several African countries, accounting for the following percentages of cereal production: Niger 70%, Senegal 63%, Mali 40%, Chad 38%, Uganda 39%, Burkina Faso 25% (FAO Production Year Book, 1989). A concerned focus on pearl millet in a number of African countries is important.

It is worth noting that production of sorghum in Africa, with a low of eight million tons in 1973, increased to 17 million tons in 1988 and averaged about 15.5 million tons in the 1993-94 period (FAO Production Year Books).

The use of grain as animal feed has been an important stimulus for the global use of sorghum (Dendy, 1995). Feed use was relatively minor until the mid 1960s when it expanded rapidly, particularly in North America. Feed utilization overtook food use for the first time in 1966. Over the past 25 years, feed use has risen from 15 million to 40 million tons. This use, up to 97%, has occurred in developed countries, but also in some better-off developing countries, particularly in Latin America, where it accounts for about 80% of sorghum utilization.

I would like to comment about the situation in India, which I feel presents a significant lesson. In the 1960s, sorghum was grown on about 11.3 million hectares, producing about 5.8 million tons of grain. Yield was 400-450 kg ha^{-1}. In 1986-1990, area sown was about 9.1 million hectares, production around 8.0 million tons, and yield about 1048 kg ha^{-1} (Murty, 1992). This represents a decline of about 2.1 million hectares in area sown, but an increase in production of about 2.2 million tons of grain. This is a consequence of efforts made in the country to develop an All India Coordinated Sorghum Improvement Program, with a focus on hybrids, and the establishment of a seed industry to produce and market hybrid seed of a number of crops.

Area sown to sorghum in the U.S. began a decline in the last half of the 1980s, and in 1995 the area sown was approaching half of the area sown in 1986. As a consequence, some three to five years ago, several large seed companies undertook dramatic cutbacks in their sorghum programs. Recently, both Pioneer and Dekalb, which sell nearly 50% of the sorghum seed in the U.S., also began substantial cutbacks. This reaction is cause for concern because it jeopardizes the private sector's contribution to product development and marketing; research that addresses the issue of genetic vulnerability; and country-wide, even international, testing leading to hybrids with broad adaptability. Private sector research also addresses such issues as drought and pest resistance, having a more fundamental as well as applied outlook. Part of this problem was created by allocation of acreage for maize. Farmers would sow maize to retain their allotment, thus leading to a negative impact on the area sown to sorghum. The recent change in the U.S. Farm Bill permits farmers to sow as they choose, and, with dry weather this past year, the area sown to sorghum in 1996 is

12.5 million acres, up from 9.5 million acres in 1995. This is encouraging and I hope helps address this issue.

In the U.S., during most of its history, agricultural production was intended for domestic consumption. However, during the last several decades, export demand has grown faster than domestic demand. This reflects a decline in the rate of population growth and a declining percentage of income spent on food. By contrast, much of the rest of the world, particularly developing countries, have experienced a more rapid rise in both population and income growth. This has stimulated a market to which U.S. agriculture has responded.

Looking to 2030, based on the U.S. Census and United Nations base line projections, the U.S. population is expected to grow about 20-25 percent, while in other areas, particularly developing countries, the rate is projected to be around 80 percent. Global population will increase from about 5 billion in 1990 to about 9 billion in 2030. This population increase will create a rising demand for food as well as a market for produce.

With rising income in the lesser developed countries (LDCs), it is projected that a greater portion of income will be spent on food and increasingly on animal products, raising the demand for feed.

Combining various population and per capita income data, Figure 1 was developed. It compares data for the period 1985-1988 with projected data for 2030. The coarse grains include corn, sorghum, barley, and oats. This projection indicates a substantial increase in demand in less

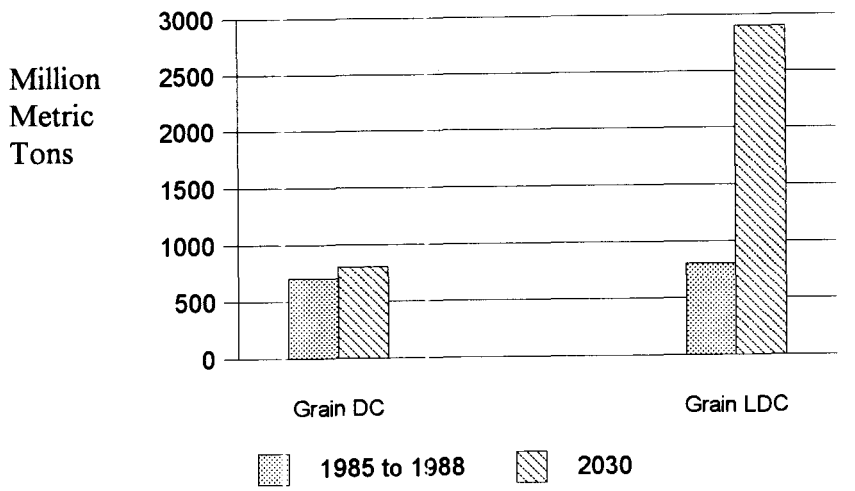


Figure 1. Demand for Grain in Developed (DC) and Less Developed Countries (LDC), 1985-88 and 2030 (Projected).

developed countries and adds relevance to the international scope of this meeting. (CAST, 1992).

The Science

A Glimpse of History

We now have a pretty good understanding of where our crops came from and evidence that humans began domestication of sorghum about 8,000 years ago. Sorghum was moving in trade channels eastward over the Arabian Peninsula and across the Indian Ocean some 3,500 years ago. Over centuries, farmer breeders adapted the crop to an array of conditions. They did a good job in selecting cultivars they could rely on to give them food every year, but with a narrowing genetic base, they frequently had to be content with modest yields.

Our Germplasm Resource

Today, we are active in the collection, preservation, and understanding of our germplasm. Countries have been willing to share their resources and to benefit from the developments of their colleagues. Germplasm accessions, breeding stock, and sources of resistance and quality traits have moved extensively in the last 30-50 years. In an effort to capitalize on tropical cultivars in the temperate region, where some tropical types did not flower during the growing season or did so extremely late, the USDA and Texas A&M, since 1962, have undertaken a backcrossing program to convert tropical materials to temperately adapted lines. Selections from this program have, for many years, been used worldwide. This flow of material has been free and frequent and has been significant to our efforts and achievements. Many have given and many have received and the process has no end.

The issue of proprietary rights looms larger and larger on the horizon and may impact the way germplasm exchange occurs. The basic concept in the minds of us all is that the exchange process is valuable and we need to ensure that it continues.

Crop Improvement

We have developed an array of techniques for breeders: pedigree breeding, populations, hybridization, and gene movement via backcrossing, to mention some. Our pathologists, entomologists, and physiologists have identified economically important traits, prioritized them in different environments, developed techniques for their systematic evaluation, and formed teams with breeders to bring together traits for yield, response to biotic and abiotic stresses, and improvement in grain and forage quality.

As a consequence, significant contributions to production have occurred in many places: change in the grain-straw ratio (i.e., shorter, generally earlier plants more responsive to management); commercial exploitation of heterosis; effective use of resistance and quality traits; interaction of disciplines to support integrated pest management; and crop management contributions, including stand establishment, weed control, and response to fertilization and irrigation. While in many of the sorghum and millet growing areas of the world, these changes have made a significant difference, there

are some exceptions. Guinea sorghum has been difficult to improve, as well as the long season cultivars along the high rainfall coast of tropical Africa. While improvement in rainy-season sorghum in India was readily made, the development of sorghum cultivars for the post-rainy season has been slower. These more difficult situations present an interesting challenge.

Great strides have been made for some traits: grain quality, plant color, maturity, and resistance to greenbug, downy mildew, midge, *Striga,* and milo disease. Others have been less successful, in developing, for example, resistance to stem borers and headbugs. Traits like drought resistance and yield are poorly understood. New traits come forward; for example, improved nutritive value of food from our crops and bird resistance in sorghum not involving tannin. A lot of our work is empirical and complicated by the number of traits we can manage. How many components of resistance to stem borer are known and how many of these components are actually selected for in the crop improvement process? The genetics of many traits are poorly understood, and seem variable with cultivar and location. How much do practicing breeders make use of known genetics of the traits with which they deal? For me, as a breeder addressing quantitative traits, it is more a general idea based on observation over time than an appreciation of a determined nature of inheritance. No wonder crop improvement has been recognized as both an art and a science. Improvement in yield-limiting traits has made a significant contribution to increased production; what contribution can come from a better ability to utilize the genetics of the traits of interest?

Can we do more? The green revolution was made possible by a change in plant design, most frequently where irrigation was involved. We can still exploit improved plant design in places where traditional varieties are grown, particularly on rainfed land; for example, traditional cultivars are in use on about 50 percent of the hectarage in India, on most of the area sown to our crops in countries of southern and western Africa, and in higher rainfall areas of central Africa. Hybridization has certainly contributed in the Americas, the Sudan and India, and with corn in a number of African countries. Yet there are many places, particularly in Africa, where hybrids can contribute. This is somewhat more difficult because of problems of seed production and distribution, but hybridization deserves the effort, not only because of the yield gain of hybrids, but because of the creation of an industry that contributes adequate quantities of good quality seed on a timely basis and, as it grows, research and development. Hybridization, I believe, can be a very important contributor to a second green revolution, particularly in Africa. Looking to the future, we should encourage its consideration.

I was impressed ten or more years ago with the thesis work of Stan Cox, a student of Dr. Kenneth Frey, undertaken at the ICRISAT Center, who transferred just a few genes from wild sorghum into the cultivated types. In some cases, results were striking, and they raise the question whether we have done enough to work

with fewer numbers of genes focused on traits of interest.

Although I believe the situation is improving, we can do more in terms of crop utilization. To be readily accepted for traditional use, a new cultivar must satisfy the taste and texture qualities preferred.

Changes in traits of the grain to improve food taste and texture and nutrition, and to reduce cooking time and equipment to reduce the labor to prepare food, are all recognized and at times available (sorghum flour on the grocery store shelf in Botswana is an example). As high-yielding cultivars become available, it is important to explore uses for increased grain produced to avoid a drop in grain price, which can have an adverse impact on new projects.

We have examples, as with Hageen Dura-1 in the Sudan in 1986, when over production resulted in a drop in price and slowed a rapidly growing interest in hybrid seed. As production of grain sorghum and pearl millet increased in India, the area sown declined as higher value crops were used. Grain went to livestock, particularly poultry.

The All India Coordinated Sorghum Improvement Program now has an objective of forage improvement, and the sorghum improvement program in Zambia includes dual purpose and forage sorghum. The SADC/ICRISAT program is incorporating the brown mid-rib gene, and the cross between pearl millet and elephant grass is rapidly gaining popularity. It is not uncommon these days to hear people talking about sorghum for feed to free maize for food. Looking to the future in areas where sorghum has been traditionally grown for food, the use of both grain and stover for animal feed should likely become a more prominent part of our crop improvement effort.

The increased availability of good malting sorghum in Zambia has resulted in increased use of sorghum by national brewers. Progress has been made in blending sorghum and millet flour with flour from wheat and maize. Frequently, in Africa, these efforts have been hampered by the availability of inexpensive imported wheat and rice. As an example of the influence of wheat and rice availability, when Nigeria stopped the import of wheat and rice in 1985, sorghum production increased from 7.9 million metric tons on seven million hectares in 1979-1981 to 11 million metric tons on ten million hectares in 1989 (Dendy 1995).

Biotechnology is of rising significance, is exciting, and holds much promise. Without stealing from Dr. Bennetzen, the next speaker, let me make a few comments. The promise to better relate genes to function, to track genes in the breeding process, to transfer useful genes across infertility barriers, to recognize similarities and differences, and to hasten the rate of progress have been demonstrated in our crops. It is not so much a question of possibility as of cost, of prioritizing traits and their components, and of increasingly bringing the use of the techniques into the hands of crop improvement scientists. Collaboration between the biotechnologist and the more traditional scientist is important. The promise for the future is great.

For younger people, in particular, the array of opportunities is large. There is need for the theoretical in understanding basic principles, and there is need for the applied in making better food, feed, and industrial products, enhancing resistances, improving yield, and working in one's parent society or a distant one. I believe that all aspects are important and that individuals will be the most creative and find life most rewarding doing what they enjoy the most. Many of us may need some missionary spirit, but more importantly we must be skillful in our effort, and we should leave the place better than we found it. As scientists, we should have the imagination to make relevant changes. It is not that the farmer will not or cannot change; we must create situations where he will change to an opportunity that he could not visualize. This is a challenge without an end point and we are privileged to be the best equipped to do something about it. We should not be so swept along by our interests in the science that we lose sight of those who can benefit; as Dean Rusk told me when I first joined the Rockefeller Foundation in 1959, "don't miss the forest for the trees."

Development

What is development? I define it, for our purposes, as the application of the findings of research into socially beneficial enterprise. Research and development are closely coupled, and I will always respect the program of the Rockefeller Foundation in India, which I perceive as a development program based on research. As new hybrids came from research, the Foundation expanded its program to participate in the development of a seed industry; and as new agricultural universities were established, the Foundation provided expertise in experiment station development and management. In my experience, research and development have frequently been separated. For example, the international institutions are involved primarily with research and training, not development activities. This situation, however, may be changing. In many countries, the functions of research and extension reside in different departments, complicating communication between the two. As a consequence, focus (and, hence, resource allocation) has been on research, and development (frequently extension) has been left for somebody else without adequate concern for who that somebody is and the problems he or she may have. Land-grant universities in the U.S. have, to a substantial degree, solved this dilemma by housing research, extension, and education within the same institutions and permitting staff to divide their time among the three.

There are dramatic situations where research accomplishments have greatly benefited the farmer and the community. But there are a number of situations where good research has been and is being done, but it is not adequately realized in the user community. During the last few years, the question of why has been more loudly raised; some even question if supporting agricultural research is worthwhile. Surely this has raised concerns that support for research will decrease unless accomplishment is measured, not so much by how many varieties have been released or publications written, as by what change has taken place on farm or by the user of the research accomplishment.

My comments will focus primarily on India and Africa, where I have experience. Problems in many of the countries in which we have concern are very complicated, and the resources to generate change are limited. To me, the basic means of causing change from our research is to generate a technique or cultivar that will contribute. In my experience, as we try to initiate change in a traditional society, a new cultivar should contribute a 40 to 50% yield increase over the local varieties in the areas in which it is adapted (recommended). This level of change is sufficient for the farmer and others involved (for example, government officers) to sit up and take notice, encouraging necessary changes.

Going into the 1950s, India was facing a food problem with large imports of food grain. The Rockefeller Foundation was invited to participate in cereal crop improvement, initially maize. Negotiations began in 1954 and the first three members of the Rockefeller Foundation Indian Agricultural Program arrived in 1957. The strategy was to establish All India Coordinated Programs. Foundation staff were participants in, not advisors to, the crop improvement program. This provided the opportunity for a shared experience with colleagues. Staff numbers increased during the last few years of the 1950s and early 1960s, reaching a maximum of fourteen in the period 1967-70, and then declined, phasing out about 1975. Interestingly, of the fourteen staff members, three were devoted full time to quality seed production and marketing and one to experiment station development and management.

Four hybrids of maize were released by the All India Coordinated Maize Program in 1962, and the government established All India Coordinated Programs for sorghum and pearl millet; in the 1964-66 period the government established similar programs for wheat and rice. In the years that followed, some 25 All India Coordinated Programs were established. The Rockefeller Foundation was involved only with maize, sorghum, millet, wheat, and rice.

There are several significant aspects of the Foundation's involvement in India. The program was carefully planned with Indian authority. Foundation staff were participants in the programs. Development was an important component of the program; the objective was to stabilize accomplishments and then depart. The period required was about 20 years.

As part of the technology transfer effort in the mid 1960s, the government developed the high-yielding varieties program, in which for two years scientists were responsible for national demonstrations and were involved with training extension trainers.

Based on research accomplishments, the government took steps to establish a seed industry, to enhance rural credit, and to encourage the use of inputs such as fertilizer. With this determination, now some 35 years later, the agricultural situation has dramatically changed. The following comment is a brief indicator of what happened.

"For sorghum in the 1989-90 period, approximately 7.4 million hectares were

sown to high-yielding hybrids and varieties (about 50% of the total hectarage). By 1988, the total seed production capacity in the country was 667,853 tons and processed in 504 processing plants. By 1990, private companies had developed 122 varieties and hybrids of different crops, about 70% of these being hybrids. At this time about 500 companies emerged of which 35 are large, most of them including research. During the last five years the input into research by the private sector has greatly increased" (Singh et al., 1990).

During 1962 and 1963, India imported 10 and 14 million tons of food grain. By the mid 1970s, India was exporting food grain, and a few years later its agriculture was no longer dependent on monetary aid. This was made possible by a solution to the agricultural problem — and others can do this. The situation in every country has its level of uniqueness. But I feel it is essential that the results of the research I have been involved with are made available to the farmer in adequate quantities (tons of seed) and for a long enough time (3-8 years) to verify the research findings, generate farmer interest, generate interest and understanding by others such as government officials, and develop a mechanism (seed production and distribution) to support and encourage the new development in the hands of the user. After all, who other than the originating scientist is going to know the development better and take the initial steps to fit it into a community? It is important that the originating researcher help colleagues understand all that is involved.

Several years ago, staff of the Zambian Sorghum Improvement Program visited a farmer in the Gwembe Valley where she had just harvested two tons of grain of the variety Kuyuma (the seed was sold to her by the research program). Her annual requirement is 800 kg. Asked what she was going to do with the excess, she said she wanted money. I use this as an example of the quantum jump in yield, resulting in almost immediate increase in production. Production of grain from Hageen Dura-1 in the Sudan expanded at almost an explosive rate, resulting in over-production, a drop in grain price, and a temporary setback for the program. Norm Borloug in Pakistan advocated a floor price that would hold up farmer enthusiasm. This is fine for a modest time period, but sorghum in storage from over-production in Zimbabwe was very expensive, quality was lost, and seed sold at a loss. Opportunities for commercial uses of our crops have been mentioned earlier in this paper. Like the establishment of the seed industry, the uptake of these commercial activities requires a determined effort.

The Human Resource

Our Farmer Clientele in Developing Countries

For many of us, the end user is the farmer, and we are fond of referring to the "poor farmer" and "the poorest of the poor." Sometimes I feel we do this so frequently it becomes a universal kind of category into which all farmers in developing countries fit. Saying this, I am sure we all recognize variability among people, including farmers. My experience indicates that among the so-called "poor" farmers are those who are more capable, willing to take risk, entrepreneurial in outlook, and frequently exemplary members

of their communities. There are those at the other end of the scale who will not or are slow to respond. Everywhere I have been there are business people in the agriculture community. Also, in my experience, farmers will pay for seed if they are convinced that the cultivar is worthwhile. We should not use a common label, but address those who understand and will take risk and demonstrate the technology to others.

Education and Training

Many of the colleagues with whom I have interacted in the countries in which I have worked feel the most important thing we did was educate and train — to strengthen their people for the future development of their countries. The contributions of universities everywhere to educate and train have been outstanding and generate a backbone for development. This opportunity to provide education and training should continue at the same or increasing rate.

Education and training, I feel, should include more than a focus on a specific discipline or problem. After receiving their degrees and returning home, scientists do not know what lies in front of them; some will be practicing scientists, some will be educators, some will go into administration, some into private businesses, some will be experiment station managers. If the total focus of an individual's education is on his/her discipline/research project, he/she is left poorly prepared for other activities. Let me ask how many of your graduate students know why they are on field B-3 of the experiment station and what steps were taken to prepare the field for sowing. Exposure of the user scientist to the station manager and the management of the station all too frequently does not occur. Students are not exposed to the ramifications of the seed industry and, where relevant, the management of irrigation water, etc. I feel we can greatly enrich the opportunities for students by planning time for them to participate in those activities to the point that they can usefully conceptualize them. This can be important for the quality of our research and the efficiency with which provided resources are used. I encourage paying more attention to some of these activities in our educational systems than we have paid in the past.

In some cases, students return home after completing their education to a situation where they find it difficult to be productive. The idea of providing resources to help overcome this problem is worthy of consideration. Support for such resources could be part of the grant for education or part of a program in their home country.

The Scientific Community

We generally find more breeders and agronomists than entomologists, pathologists, and food technologists. One advantage of regional and international centers is to bring together a critical mass of scientific talent that can be broad based in its research accomplishment and catalytic to many in other situations.

I feel another significant development has been the tremendously increased interaction between sorghum and millet scientists nationally, regionally, and interna-

tionally. We have become a community of scientists working together. This sense of community has led to greater understanding of problems (hence relevance to research), to interpersonal relationships encouraging openness and appreciation, and to a more rapid mobilization of ideas and products of research. This has been encouraged by meetings such as this and, institutionally, by agencies such as INTSORMIL, IRAT, FAO, and ICRISAT. This is an extremely valuable development that will no doubt be continued and should be ensured.

Donor Assistance

The strengthening of national research systems in a number of developing countries is often difficult because of a low, inadequate resource base. Donor contribution becomes an important component of support, which helps, but also subjects the system to the uncertainties of changes in the donor organizations. Today we hear about donor fatigue, government debt in donor countries, changes in demand for donor resources, particularly in Eastern Europe. Indications are that, in the future, support for research and development from donor sources will gradually diminish. The response to the problem is anything but easy; but clearly if the donor source declines, more of the burden will need to be picked up locally.

The need for donor funds in too many places becomes an accepted norm, but it should not, and I encourage us to see it more as a stepping stone — but a stepping stone that is effectively there to stabilize accomplishment in the local situation. Again, I refer to the Rockefeller Foundation involvement in India where objectives were carefully defined, activities were jointly undertaken, development was included to stabilize accomplishment, and the Foundation departed. By going beyond research to ensure utilization effective to the community, contribution can be made to help recipient countries reduce their need for donor support. This can be an objective of our work.

In recent years USAID has been placing increasing emphasis on private sector activity, and this, I believe, is a logical thing to do. Sorghum and millet are involved in the seed industry, the feed industry, in foods and beverages. We are aware of all of these, but how effective have we been in seeing them make a significant impact on their respective societies?

Conclusion

A successful response to our endeavors will compromise our time on research. As I look to the future, I hope we will recognize the contribution we should make: to play our role in strengthening people and institutions. Our own interests and those of the institutions to which we are responsible should not only permit us, but encourage us, to respond to this need. We are not without example.

Consideration has been given to research, development, and the human resource. Focus generally is on research and much is being done toward personnel development. It is my concern that there is a greater need for development and education. This conference is international in scope and, I believe, should recognize that these three components need strengthening in many countries. They are interre-

lated and mutually supporting. Good research and its contribution to the community is not going to happen without consideration of all aspects.

I wish the conference well and hope that research and development will benefit from it. Again, thank you so much for giving me the opportunity to make the inaugural statement.

References

CAST. 1992, June. The backdrop for farming, including climatic scenarios. Council for Agricultural Science and Technology Report 119:8-17.

Cox, T.S., L.R. House, and K.J. Frey. 1984. Potential of wild germplasm for increasing yield of grain sorghum. Euphytica 33:673-684.

Dendy, D.A.V. 1995. Sorghum and the millets: Production and importance. p. 11-25. *In* D.A.V. Dendy (ed.) Sorghum and millets chemistry and technology. American Association of Cereal Chemists, Inc., St. Paul, MN, USA.

Ejeta, G. 1986. Breeding sorghum hybrids for irrigated and rainfed conditions in the Sudan. Presentation at the international drought symposium on food grain production in semi-arid food grain research and development project, 19-23 May 1986, Nairobi, Kenya.

FAO. 1964-1994. Production yearbook. Food and Agriculture Organization of the United Nations, Rome.

Hamaker, B. 1995. Digestible protein may make sorghum a better food source. Agricultural Communication Service, Agronomy Dept., Purdue University, West Lafayette, IN, USA.

House, L.R. 1988. Sorghum improvement in the third world: Successes and failures. Presentation to the international workshop on maicillos criollos and other sorghum in middle America, 7-11 December 1987, Tegucigalpa, Honduras. CEIBA 29(2):151-159.

House, L.R. 1995. Problems and opportunities for seed production and distribution in developing countries: A breeders experience. Paper presented at the INTERCRISP meeting, Sept. 1995, Niamey, Niger.

Murty, U.R. 1992. Sorghum production and utilization in India: The present and the future. Agricultural Situation in India. Directorate of Economics and Statistics, Dept. of Agriculture and Cooperation, Ministry of Agriculture, New Delhi, India.

Singh, G., S.R. Asokan, and J.N. Asapa. 1990. Seed industry in India: A management perspective. Oxford and IBH Publishing Co. Pvt. Ltd., New Delhi, India.

The Potential of Biotechnology for the Improvement of Sorghum and Pearl Millet

Jeffrey L. Bennetzen

Abstract

Plant biotechnology focuses on the modification of a crop's genetic complement to provide improved agronomic properties. In both its goals and basic rationale, biotechnological enhancement of crops is no different from the traditional processes of crop improvement by targeted breeding. However, biotechnology brings a powerful set of new molecular tools to the plant breeder's assistance. Marker-assisted breeding and gene transfer will open new horizons in the rate, quality, and quantity of improvements. Crops will produce higher yields of higher quality food and feed, with fewer chemical inputs. In the longer term, the genetically engineered synthesis of specialty products in farmers' fields may replace chemical and pharmaceutical production plants. With increased opportunity will come increased competition. Sorghum and pearl millet have significant advantages, particularly their tolerance to arid environments and poor soils, that could permit their survival or expansion in this new pan-crop competition. Other crop species could displace sorghum and millet, however, if they continue to receive disproportionately low levels of research attention.

The last twenty years have witnessed remarkable changes in the rate and range of potential modifications to the genetic composition of plants. DNA markers allow geneticists and plant breeders to unambiguously map and follow the numerous interacting genes that determine complex traits like drought tolerance. Crops can now receive and express genes from any eukaryotic or prokaryotic source. In a broad sense, these plant breeding skills are merely amplifications of the classical (and highly successful) efforts to rearrange genetic composition and to introduce new genes into a crop by wide crosses and selective breeding.

Jeffrey L. Bennetzen, Department of Biological Sciences, Purdue University, West Lafayette, IN 47907-1392

The high-yielding varieties developed by traditional plant breeders have been essential to maintaining adequate food supplies for the ever-expanding world population. These routine approaches will not be adequate, however, to meet the great increase in food production necessitated by population growth and the higher standards of living deservedly desired in developing countries. If we are to avoid catastrophic famine and the loss of our remaining wild spaces to agricultural production, then biotechnology will need to provide a quantum increase in the rate of crop improvement.

Marker-Assisted Plant Breeding

The use of DNA markers has greatly increased the number of traits that can be

definitively followed in a breeding program. As this process continues to be automated, an individual breeder could foreseeably monitor thousands of traits in vast populations in a single season's program. To date, association of agriculturally significant characteristics with DNA markers is still in its infancy, but this area is currently receiving much emphasis. At this early stage, full sets of participating genes should be identified without the distraction of efforts to understand the physiological contributions of the gene products. A tremendous strength of genetics (and its traditional application by plant breeders) is that one does not need to know the molecular nature of a gene's contribution in order to use the phenotype it conditions. Breeders will need to expand their analytic and computational capabilities to deal with this great surge of genetic information.

Once co-segregating DNA markers are identified for a particular trait, analysis of these same mapping populations will indicate the genotype × environment effects and whether specific polygenic interactions are synergistic or antagonistic. Molecular marker analysis is so easy that the number of quantitative trait loci (QTL) that need to be followed becomes relatively unimportant. The breeder can follow, for instance, fifteen (or fifty or five hundred, whatever the mapping results indicate) different DNA segments known to positively influence drought tolerance. These traits could all be backcrossed into a preferred inbred, perhaps from one or several non-recurrent backgrounds. Testing for the drought tolerance trait in the intermediate generations would be largely superfluous, thereby saving tremendous amounts of time and money. At each backcross generation, the lines with all fifteen introduced segments and as few other introduced (non-recurrent) DNA segments as possible are selected, and at the end of a relatively few backcross generations, one has converted this inbred to drought tolerance.

Another powerful use of DNA markers will be to identify novel sources of germplasm. Despite the existence of extensive varietal collections and their partial characterization (see Dahlberg et al. and Eberhart et al. elsewhere in these proceedings), very limited concrete information exists indicating which of the collected materials will be the source of useful genes. In sorghum, for instance, some of the wild sorghum relatives do not appear to have many alleles of genes not found in the cultivated sorghums, probably due to gene flow from the preponderant agronomic varieties that grow in the same regions (Oliveira et al., 1996). Characterization of sorghum genotypes at the DNA level indicates fairly unambiguously overall relatedness and allelic novelty. This will allow germplasm collections to be pruned to their truly novel accessions. Moreover, core subcollections (see Dahlberg et al. and Eberhart et al. elsewhere in these proceedings) can then be identified that contain the majority of the diversity in a species, permitting a more detailed and cost-effective characterization of the potentially useful agronomic traits in this manageable core. Pedigree analysis with DNA markers also will be used to identify the DNA segments that are the source of important traits currently used in improved varieties and landraces (Lee, 1995). This "segmental pedi-

gree" information would indicate both sources of genetic improvement that are consistently effective and sources that are novel or under-utilized.

The final outcome of marker-assisted crop breeding will be the increasingly rapid production of improved varieties generated at far lower costs. Genetic engineering, although not likely to soon be rapid or inexpensive, holds out the promise of truly novel improvements in crop productivity.

A Need for the Genetic Engineering of Crop Plants

Much of the success of the green revolution in increasing world food production was due to improved agronomic practices and higher inputs on irrigated farmlands. Agricultural productivity in dryland subsistence environments was not greatly enhanced. Severe and increasing water limitations are such that net expansion of irrigated acreage worldwide does not appear to be feasible; therefore, future increases in world food production will require improvements in the performance of unirrigated lands. Given the many varied environments and low input potential, there will be no silver bullet to cure the deficiencies of subsistence agriculture, and traditional plant breeding strategies are likely to be too slow and inefficient to generate the three- to four-fold increase in food production necessary in the next fifty years.

Plant genetic engineering has the potential to bring totally novel traits into any crop species. We have already seen improved pest or pathogen tolerances provided by bacterial or fungal genes. These changes can be tailored for any given agricultural milieu, and for any given need (low cost, environmental protection, etc.). For instance, the improved insect resistances provided by transgenic crystal proteins from *Bacillus thuringensis* are both less expensive and less damaging to the environment than broad insecticide application. Moreover, the cost of a comprehensive set of crop improvements by traditional methods often can only be justified for seed that will be grown across extensive acreages, usually in the seed-buying developed countries. However, as plant genetic engineering becomes less costly to perform, crops will be inexpensively engineered with an array of traits specifically targeted to each of the microenvironments common to tropical agriculture.

Opposition to Plant Genetic Engineering

Current opposition to genetic engineering is not likely to withstand the growing understanding among agricultural producers and consumers that this technology can be safer and less environmentally damaging than our present food production system. Opponents of genetic engineering belong to two non-exclusive groups: those who fear there may be unknown dangers in this new technology, and those fundamentally opposed to any new technology.

The possibility that genetic engineering might have unexpected hazards was responsible for the unprecedented experimental moratorium initiated by the scientific community in the 1970s. Subsequent experimentation and experience have convinced the vast majority of biological

scientists that there are few, if any, hidden dangers to this research. Hazards there may be, and review processes taking this possibility into account have been developed and followed in all of the nations with major biotechnology programs. However, the possible hazards in transferring a characterized single gene (for instance) from one plant to another are certainly more easily predicted and less likely to be problematic than is the classical agronomic procedure of crossing the entire genome from one species into that of another. Although these wide-crosses have produced the rare notable negative outcome (for instance, Africanized European honey bees), they also have been the foundation of the improved varieties that currently feed the world. It seems odd that the more dangerous traditional breeding process is much less regulated than is single-gene engineering of crops.

Some opponents of plant and animal genetic engineering believe that technology *per se* is responsible for most of the problems on our planet and that return to an idealized low-technology lifestyle would be a panacea. This Luddite view is obviously ludicrous in its most extreme forms, as these opponents are not willing to abandon our most dangerous technologies (fire, the wheel) or our most technology-dependent activities (modern medicine, worldwide communication). At a more moderate level, though, this argument is equally incorrect and more dangerous. Current life expectancies and populations would not be sustainable without modern advances in food production technology. If we return to the landraces and low input agricultural practices of sixty years ago, then we have to face the fact that at least half the current world's population will die of starvation almost immediately. This disaster could be partly ameliorated by bringing the rest of the world's farmable wildlands into production, but at a great cost to the environment and biodiversity.

A major point of plant biotechnology is that crops can be grown on fewer acres, due to higher yields, thereby allowing more land to be set aside for environmental and biodiversity preservation. Moreover, one of the goals of plant genetic engineering is to use genetic modification to replace the numerous chemical additives now used in high-yield agriculture. Crops that provide their own fertilizers or are resistant to pathogens and pests without chemical treatment would provide a much cleaner environment. For these reasons, the international environmental movement should be the strongest proponent of agricultural biotechnology rather than its intermittent opponent.

Current and Future Limitations on Crop Biotechnology

As general arguments against plant genetic engineering fade into irrelevance, the chief limitation upon this technology will be our basic understanding of plant biology. Both the nature of and most efficient route to valuable crop modifications are generally not clear. Most of the simple modifications targeted so far — such as pest, pathogen, or herbicide resistance — may appear obvious, but they were founded on extensive backlogs of basic research. For more complex alterations in crop stress tolerance, secondary product production, or growth habit, most of the appropriate genes have not been identi-

fied, and a basic understanding of their biology is lacking.

In the long term, particularly in industrialized nations, much of the cash value from agriculture could come from the production of value-added secondary products, chemicals, and pharmaceuticals (Moffat, 1995). In this environment, those physiological processes that have received the most research attention are likely to dominate, whether or not they would be the most preferred routes from a basic perspective. The same is true for individual crop species. Sorghum and pearl millet are particularly well-suited to semi-arid agriculture, but if a better-studied species (e.g., maize) were easier to engineer to a new high-value use, then the engineered species might justify the increased inputs that would allow it to supplant sorghum or pearl millet, even in their current agronomic niches. Hence, basic understanding and investigation of both specific biological processes and particular crops may be their only hope to contribute to an increasingly competitive agricultural milieu.

Genome Synteny as a Tool for the Study and Improvement of Grasses

Beyond their superior dryland adaptation, sorghum and pearl millet also can offer the advantages obtained from a "unified grass genome" (Bennetzen and Freeling, 1993) approach to crop study and improvement. Molecular mapping and gene discovery studies have shown that all grasses have great similarity in gene content and in the order of those genes on their genetic maps. This phenomenon of interspecies "synteny" indicates that the grasses differ more by their allelic composition than by their genic composition.

One can now use map synteny as a mechanism to determine whether two genetic processes in two different species are due to different alleles of the same genes. For instance, it is now possible to determine whether genes that provide improved drought tolerance in sorghum might be the same genes that specify this trait (to a less-effective degree) in maize. If so, then these genes could be transferred from one species to the other with a reasonable assurance that they will function in the transgenic host. Moreover, information gained from the study of these syntenous genes and their physiological processes can now be used to inform studies in either species. Hence, the traditional dilution of plant science studies across a broad range of species could now become a strength rather than a weakness, as crop scientists would have at their disposal broader allelic variation than possible within any single species.

For any crop that has received relatively little basic research attention, like sorghum and pearl millet, the "unified grass genome" approach will allow the more rapid application of tools developed in better-studied systems. Hence, given an increase in current efforts, sorghum and millet could use this new tool to efficiently achieve parity with maize, rice, barley or wheat as targets for molecular crop improvement.

Sorghum as a Model for Plant Genetics and Genetic Engineering

Beyond the possible enhancements that sorghum and pearl millet could achieve

through the use of pan-grass tools and information, sorghum has the potential to become a model system for the understanding of C4 plants. Sorghum has a relatively small genome for a grass (Arumuganathan and Earle, 1991), and has the expected smaller distance between individual genes than its larger genome relative, maize (Avramova et al., 1996; Chen et al., 1996). Hence, map-based gene cloning and the development of a contiguous physical map are both reasonable options in sorghum, as opposed to most other grasses. Several laboratories are now using sorghum as a model organism to identify, clone and understand genes from maize.

Despite the relatively few attempts made at sorghum transformation, transgenic sorghum plants have been produced (Casas et al., 1993). Further efforts are needed on transformation technology, but the current status indicates that sorghum can be genetically engineered and that basic studies of transgene expression could (and should) be performed in sorghum.

Given its small genome and transformation competence, sorghum should become a model for understanding other members of the tribe Andropogonae, like maize and sugarcane. Along with a C3 grass, like rice, the C4 grass sorghum could become a model for understanding the molecular genetics of all grass species. Sorghum itself would benefit tremendously from its possible status as a model organism. As stated earlier, those organisms that are best understood at a very basic level will usually be the hosts for the modifications brought about by genetic engineers. For example, many genetic engineering companies now produce recombinant proteins in *Escherichia coli*, despite its severe deficiencies as a fermenting organism, largely because they know how to easily engineer genes for expression in *E. coli*. Similarly, any cereal that is well-characterized genetically will have a better chance of being used as host for genetic engineering in the industrial sector.

Targets for Biotechnological Improvement in Sorghum and Pearl Millet

Although priorities are always arguable, it is clear that some applications of biotechnology could immediately be applied to sorghum and pearl millet, while others remain on the horizon. With current technology, marker-assisted breeding could rapidly be applied to any crop, while most other significant crop genetic engineering applications will not come to fruition in the short term.

Both sorghum and pearl millet need assessment of the genes — commonly called quantitative trait loci (QTL) — that contribute to important agronomic traits. Once these traits are identified and mapped to reasonably small chromosome segments, marker-assisted breeding could be used to introduce them into a wide variety of populations. Marker-assisted breeding can greatly reduce breeding population sizes, the need for (and therefore cost of) continuous recurrent testing, and the number of generations to develop a superior inbred. This technology is now being directly applied in the private sector, but seems to be surprisingly underutilized in the public sector. However, in the immediate short term, sorghum and

pearl millet require the detailed genetic mapping studies that would identify and position agronomically important genetic traits, determine their variability across environments, and characterize their synergy or antagonism with other genes.

Studies of genetic diversity are also appropriate and technically simple at this time (Lee, 1993; Oliveira et al., 1996). These studies will show from what germplasm (and chromosomal segments) previous crop improvements have arisen and will indicate what sources of genetic novelty have not been extensively utilized.

Genomics, the characterization of the entire genetic composition of a species, could and should be initiated with sorghum at this time. On the grounds of small genome size and relatedness to maize and other important grasses, sorghum could assert a role as a model for understanding plant biology pertinent to crop improvement. The development of a contiguous physical map (contig) of sorghum, using an already-existent bacterial artificial chromosome (BAC) library (Woo et al., 1994), and its anchoring with genes positioned on the recombinational map, would provide an invaluable tool to all plant scientists. Sorghum, of course, would benefit the most from this contig and would thereby position itself as a central organism for additional molecular genetics.

The genetic engineering of a few traits, like insect tolerance or pathogen resistance, could be initiated at this time for sorghum. This will also be true for pearl millet, of course, once transformation technologies have been worked out. As in other crops, some of these simple changes will prove quite (perhaps spectacularly) valuable and others (probably most) will be of limited or no sustainable significance. This is, of course, true of all technologies, particularly at their early stages. (It took many decades of automotive improvements before any car was nearly as useful as a horse and buggy.) Nevertheless, it is a good time to begin the genetic engineering process so we can see what specific advantages and disadvantages sorghum can bring to the table. However, the more subtle, durable, and significant changes to the quality and quantity of crop yields will require a greater basic knowledge of plant biology that will most easily come from basic studies involving the interaction of physiologists, geneticists, molecular biologists, and other plant biologists.

Will the Future Approach The Potential of Biotechnology in Sorghum and Pearl Millet Improvement?

Sorghum and pearl millet could both be major beneficiaries of biotechnological enhancement, due to their hardiness in arid environments and, in sorghum's case, because of its advantages as a possible model grass. Higher-yielding varieties, with a broader genetic base, requiring lower inputs and causing less environmental degradation are all fully feasible. The impressive production of biomass on hot and dry lands could justify the choice of these species for production of food, forage, and engineered specialty products on poor soils all over the world. However, because neither of these crop species is central to the agricultural economy of any developed country, they are likely to con-

tinue to be relatively ignored as targets of study and improvement.

In a crop improvement system where any trait can be acquired from any other species, the most competitive crops will be those that are best understood. Sorghum and pearl millet need attention and resources commensurate with their obvious agronomic advantages in order to compete with maize, rice, or barley. With these enhanced characterizations, sorghum and pearl millet could maintain or increase their contribution to world agriculture. Without this added attention, these two species could become little more than historical novelty crops.

References

Arumuganathan, K., and E.D. Earle. 1991. Nuclear DNA content of some important plant species. Plant Mol. Biol. Rep. 9:208-218.

Avramova, Z., A. Tikhonov, P. SanMiguel, Y.-K. Jin, C. Liu, S.-S. Woo, R.A. Wing, and J.L. Bennetzen. 1996. Gene identification in a complex chromosomal continuum by local genomic cross-referencing. Plant J. 10:1163-1168.

Bennetzen, J.L., and M. Freeling. 1993. Grasses as a single genetic system: Genome composition, collinearity and compatability. Trends Genet. 9:259-261.

Casas, A.M., A.E. Kononowicz, U.B. Zehr, D.T. Tomes, J.D. Axtell, L.G. Butler, R.A. Bressan, and P.M. Hasegawa. 1993. Transgenic sorghum plants via microprojectile bombardment. Proc. Natl. Acad. Sci. USA 90:11212-11216.

Chen, M., P. SanMiguel, A.C. Oliveira, S.-S. Woo, H. Zhang, R.A. Wing, and J.L. Bennetzen. 1990. Microcolinearity in *sh2*-homologous regions of the maize, rice and sorghum genomes. Proc. Natl. Acad. Sci. USA 94:3431-3435.

Lee, M. 1995. DNA markers and plant breeding programs. Adv. Agron. 55:265-344.

Moffat, A.S. 1995. Exploring transgenic plants as a new vaccine source and plants as chemical factories. Science 268:658-660.

Oliveira, A.C., T. Richter, and J.L. Bennetzen. 1996. Regional and racial specificities in sorghum germplasm assessed with DNA markers. Genome 39:579-587.

Woo, S.-S., J. Jiang, B.S. Gill, A.H. Paterson, and R.A. Wing. 1994. Construction and characterization of a bacterial artificial chromosome library for Sorghum bicolor. Nucl. Acids Res. 22:4922-4931.

Discussion

Session 1 - Inaugural Session
Session Chair, Darrell Rosenow
Rapporteurs - John Axtell and Abdelmoneim B. El Ahmadi

Bob Schaffert - Biotechnology and molecular tools may be more important in developing countries than in developed countries because the problems in many of these countries are very difficult.

J.L. Bennetzen - This is quite true. Biotechnology is very cash intensive but could give rise to great breakthroughs. Progress will depend on the availability of financial resources. Biotechnology will make it possible to custom design crops for each situation, since each developing country location will have unique requirements.

David Andrews - Progress in biotechnology has been very rapid for crop protection characters. To solve problems such as yield potential and adaptation, we must look at fundamental physiological processes if we are to make progress.

J.L. Bennetzen - I agree. Biotechnologists now doing targeting relatively simple improvements that are relatively narrow in scope. The tools are equally applicable for more complex traits. We need an interdisciplinary approach which will lead to an understanding of correlates between genetics and physical traits.

B.S. Rana - Where absolute resistances are not available in the germplasm and conventional breeding approach could not make a significant progress, biotechnology could be very important to solve such difficult problems such as the shoot fly problem in sorghum.

Hector Quemada - With the advent of biotechnology, sorghum researchers need to be more sensitive to issues of regulation. They must be more aware of these issues, so that they can ensure that the benefits of biotechnology in sorghum can be applied. This is especially critical in developing countries.

Darrell Rosenow - In developing countries, government policies on seeds are difficult to overcome. How do we help them to change priorities to overcome these difficulties?

Lee House - The first step is to make sure the new technology is really significant and will effect real change. Scientists must address issues of development so that the end users will recognize the usefulness of the new technology. For example, when sorghum hybrids became available in India, there was farmer pressure contributing to change in policy so that seed could be produced and made available. It is also important that changes must address important problems in the country. India was, at that time, importing large quantities of grains so had a difficult problem to solve. In Zambia, following the removal of maize subsidies, there is greater farmer interest in growing sorghum. This, in part, was stimulated by a clear on farm demonstration of the contribution of new sorghum cultivars.

Osman O. El Nagouly - In Egypt, sorghum acreage is declining while that of maize is increasing. This is happening in many other countries. Can you give some reasons for sorghum decline? How can we increase sorghum areas in those countries? Our country is facing water shortage but the area of maize is increasing anyway. Why?

Lee House - I would like to make two comments. First, it is logical that maize moves into traditional areas of sorghum where it is well adapted. Also, visa versa, sorghum has moved into many traditional maize areas in Mexico and several Latin American countries. Second, how is investment in research being placed? Sorghum and millet are often left on the sidelines as lower priority crops. In Southern Africa, following years of drought, diversification to other crops than maize was wanted. If we can develop cultivars of sorghum with a yield potential that can compete with maize, particularly in drier environments, we will begin to see some changes and perhaps increases in sorghum acreage.

Bruce Maunder - Sometimes profits from sorghum are put into maize research.

Session II

Genetic Resources

Session Chair: Bhola Nath Verma

Rapporteurs: Yu Li and Kay Porter

Speakers

S.A. Eberhart
J.A. Dahlberg

Preserving Genetic Resources

S. A. Eberhart*, P.J. Bramel-Cox, and K.E. Prasada Rao

Abstract

The mission of the U.S. National Plant Germplasm System (NPGS) is to effectively collect, document, preserve, evaluate, enhance, and distribute plant genetic resources for continued improvement in the quality and production of economic crops important to U.S. and world agriculture. Plant genetic resources in the NPGS are made freely available to all bona fide users for the benefit of humankind. The active collection is maintained and distributed by 19 national repositories, and the base collection is preserved at the National Seed Storage Laboratory (NSSL), U.S. Department of Agriculture, Fort Collins, Colorado. The NPGS collections include 40,477 sorghum and 1,507 pearl millet accessions. Of the 20,169 sorghum accessions in the base collection at NSSL, 80% are in conventional storage at about -18°C and 20% are in cryostorage in vapor phase above liquid nitrogen at about -160°C; the pearl millet collection is in conventional storage.

The International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) located at Patancheru, near Hyderabad, India, has assembled a collection of 35,643 sorghum and 21,195 pearl millet accessions, both ICRISAT mandate crops. All these accessions are maintained and preserved in aluminum cans in the medium-term storage facility at about 4°C and 20% relative humidity. Freshly rejuvenated accessions with at least 90% viability and about 5% seed moisture content are being placed in moisture proof aluminum foil packets that are vacuum sealed and stored in long-term storage at -20°C. For these crops, 17% of the sorghum collection and 23% of the pearl millet collection have been transferred to long-term storage.

Landraces and wild relatives of crops from centers of diversity have been rich sources of resistance to new pathogens, insect pests, and other stresses, as well as sources of traits to improve food and fiber quality, animal feed, and industrial products. But, as farmers in centers of diversity switch to new stress-tolerant, higher yielding cultivars, these valuable sources of useful genes will be lost forever unless they have been collected and preserved *ex situ* in gene banks.

No country has all the plant genetic resources required to develop and maintain a high level of agricultural productivity. The U.S. has an extremely limited number of native agricultural crop species of economic importance. As with many countries, our exceptionally productive agricultural systems were founded on introduced plant genetic resources, including sorghum [*Sorghum bicolor* (L.)

S.A. Eberhart, Director, National Seed Storage Laboratory, USDA, ARS, 1111 South Mason Street, Fort Collins, CO 80521-4500, USA; P.J. Bramel-Cox and K.E. Prasada Rao, Genetic Resource Division, ICRISAT, Patancheru P O, Andhra Pradesh 502 324, Hyderabad, India. *Corresponding author

Moench] and pearl millet [*Pennisetum glaucum* (L.) R. Br.].

Mann et al. (1983) hypothesized that sorghum probably originated and was subjected to domestication more than 5,000 years ago in northeastern Africa. More recently, Wendorf et al. (1992) reported that carbonized seeds of sorghum, evacuated at Nabta Playa near the Egyptian-Sudanese border, appear to be about 8,000 years old.

Duncan et al. (1991) summarized known introductions of sorghum into the U.S., including broomcorn by Benjamin Franklin in 1725, 'Chinese Amber' sweet sorgo in 1851, milo in 1879, 'Blackhull Kafir' in 1886, 'Feterita' in 1906, and 'Hegari' in 1908. They indicate that the first mention of the value of a guinea kafir corn from West Africa occurred at the Philadelphia Agricultural Society in 1810. As the value of sorghum in low rainfall areas of the Great Plains was recognized, breeders in state agricultural experiment stations and in the Agricultural Research Service began sorghum improvement in the 1920s. Introduction of additional materials was important to their programs, and by 1957, more than 13,000 accessions (many of which were landrace collections from Africa) had been introduced (Duncan et al., 1991).

Pearl millet has been used in Central Africa for many centuries by nomads and hunters (Rachie and Majmudar, 1980). Ball (1903) reported that pearl millet has been "known in cultivation as a forage or cereal crop for at least 3,000 years" in India, Arabia, and Africa. He indicates that pearl millet was widely cultivated in the southeastern U.S. by 1873, and he speculates that it probably arrived along with sorghum in the early 1850s. Extensive research by Burton (1980, 1995) and Hanna et al. (1987) at Tifton, Georgia, has concentrated on developing improved pearl millet cultivars for forage production, but their parental lines also have been used in hybrids developed for grain production. More recently, breeding research programs at Tifton; Hays, Kansas; and Lincoln, Nebraska, have included grain types (Hanna, 1995; Stegmeier, 1994; Rajewski and Andrews, 1995).

The Organic Act of 1862, establishing the Department of Agriculture, directed the first Commissioner of Agriculture, Isaac Newton, "to collect, as he may be able, new and valuable seeds and plants; to test, by cultivation the value of such of them as may require such tests; to propagate such as may be worthy of propagation, and to distribute them among agriculturists." In 1898, the Seed and Plant Introduction Section, which later became the Plant Introduction Office, was established to manage plant explorations and introductions. Before the late 1940s, introductions were sent directly to interested scientists without any requirement that they be maintained. Adequate preservation methodologies and facilities were not available, and many accessions were lost.

The U.S. National Plant Germplasm System

Ex situ preservation of plant genetic resources is extremely important to U.S. agriculture. The Research and Marketing Act of 1946 (Public Law 733) authorized the creation of four Regional Plant Introduction Stations (Ames, Iowa; Pullman,

Washington; Geneva, New York; and Griffin, Georgia) with the mission to acquire, maintain, evaluate, and distribute germplasm to scientists to be used for crop improvement. The Inter-Regional Potato Introduction Station at Sturgeon Bay, Wisconsin, was established in 1947. National Clonal Germplasm Repositories were established in the mid-1980s to provide more systematic maintenance of vegetatively propagated germplasm. The National Small Grains Collection (NSGC), now in Aberdeen, Idaho, began in 1894 as a breeders' collection in Beltsville, Maryland. These repositories grow and maintain the active collections and distribute samples to scientists worldwide. The National Seed Storage Laboratory (NSSL), Fort Collins, Colorado, was dedicated in 1958 as a long-term storage facility to preserve the base collection for backup of the active collections. These units have been integrated into the National Plant Germplasm System (NPGS) (ARS Information Service, 1990; Shands et al., 1989).

The mission of the NPGS is "to effectively collect, document, preserve, evaluate, enhance, and distribute plant genetic resources for continued improvement in the quality and production of economic crops important to U.S. and world agriculture. This is achieved through a coordinated effort by the U.S. Department of Agriculture in cooperation with other public and private U.S. and international organizations. Plant genetic resources in the NPGS are made freely available to all *bona fide* users for the benefit of humankind."

New acquisitions must be increased, characterized, and preserved as part of the active collections. Each repository conducts a systematic evaluation program to obtain specific information on disease and insect resistance, nutritional quality, agronomic and physiological attributes, and other traits of interest. Information on the collection and characterization (passport data) and evaluation data are entered in the Germplasm Resources Information Network (GRIN) database. When requested, samples are distributed to scientists worldwide at no cost for use in crop improvement and basic research. Research relating to improved methods of collection, regeneration, propagation, preservation, evaluation, and distribution is conducted, and the results are published.

The National Germplasm Resources Laboratory (NGRL), located at the Beltsville Agricultural Research Center (BARC) in Beltsville, Maryland, is responsible for a number of activities that support the entire NPGS. The Plant Exchange Office (PEO), the Germplasm Resources Information Network Database Management Unit (GRIN/DBMU), and the Plant Germplasm Quarantine Office (PGQO) are components of the NGRL.

The Plant Exchange Office coordinates the acquisition and exchange of plant germplasm, documents passport data and descriptive information for newly acquired material, assigns unique Plant Introduction (PI) numbers, and serves as a liaison on quarantine matters. Strategies are developed for increasing the genetic diversity of U.S. collections. Based on these strategies, gaps in current germplasm collections are identified and communicated to the appropriate Crop Germplasm Committee (CGC) or to other

crop specialists for their concurrence. The NGRL facilitates the activities of the CGCs. The public and private scientists on these committees represent the germplasm user community for a particular crop or group of crops. These committees provide crop-specific expert guidance on germplasm needs, collection gaps, descriptors, documentation, regeneration, evaluation, and research goals to various components of the NPGS.

The GRIN is the computerized database for the NPGS. Information in GRIN is available to any plant scientist or researcher worldwide through a variety of avenues: direct connection to the database, PC GRIN, World Wide Web (http://www.ars-grin.gov), or contact with the curator for the active collection of the crop of interest. GRIN contains data on taxonomy, origin, evaluation, and characterization for plant germplasm preserved in the NPGS.

All plant germplasm entering the NPGS from outside the U.S. must comply with federal quarantine regulations, which are designed to facilitate the exchange of plant germplasm while limiting/ preventing the movement of pathogens. Regulations are written, interpreted, and enforced by the USDA Animal and Plant Health Inspection Service (APHIS).

Although the ARS components of the NPGS are administered by the area director for the geographic location of that component, the Associate Deputy Administrator for Genetic Resources and the National Program Leader for Plant Germplasm on the national program staff provide leadership and coordinate activities for the NPGS. They also provide administrative support to the various advisory councils and committees for plant genetic resources.

The NPGS maintains one of the largest *ex situ* collections of plant genetic resources in the world. A detailed report of the NPGS history, policies, and architecture is given in *Plant Breeding Reviews* (ed. by J. Janick, 1989). Since 1898, about 575,000 accessions with real or potential economic importance to U.S. agriculture have been acquired through the former Plant Introduction Office. Many of these are among the more than 433,000 accessions, representing over 9,000 plant species, that are now preserved in the NPGS. Between 1986 and 1995, the NPGS distributed an average of 161,358 samples each year to U.S. public scientists (64%), U.S. private industry scientists (13%), foreign public scientists (8%), foreign private industry scientists (13%), and international centers and USAID (2%).

The principal mission of NSSL is to preserve the base collection of the NPGS and conduct research to develop new and improved technologies for the preservation of seed and other plant propagules. NSSL also provides long-term storage for plant materials not in the NPGS that are not to be distributed: 1) voucher samples of cultivars and parental lines licensed by the U.S. Plant Variety Protection Office, 2) accessions of endangered species maintained by botanical gardens, 3) quarantined samples queued for regeneration under APHIS inspection, and 4) security backup materials from international centers and other gene banks.

Physical facilities of NSSL were modernized and expanded fourfold in 1992.

High security storage vaults have the capacity to provide protection from natural disasters, including floods, tornadoes, fires, and earthquakes, for nearly one and a half million samples. The insulated walls, ceiling, and floor of the cold vault environmental chambers are 15.2 cm (6") thick, and movable shelves increase capacity. Energy requirements are much less with 15.2 cm insulation and movable shelves (Walters et al., 1997).

Minimizing genetic change during *ex situ* preservation is paramount to retain as much genetic variation as possible for future use (Crossa et al., 1994). A key first step to minimize genetic change is to preserve the initial regenerated sample in the base collection. This regeneration should be done with an appropriate number of plants, with the required pollen control, and under optimum growing conditions to produce high quality seed. Careful processing and drying are required to maintain high viability. Storage of dry, high quality seed at sub-zero temperatures can extend viability for many years before a second regeneration of the base collection is necessary. When continuing demand on the active collection occurs, seed from the base collection should be used for every second or third regeneration.

Scientists in the Plant Germplasm Preservation Research Unit (PGPRU) at NSSL focus on the development of new and improved technologies for the long-term preservation of all forms of plant germplasm. This research is expected to increase the number of species that can be stored at NSSL, the longevity of the various accessions, and the efficiency of viability testing of accessions. Longer storage periods and reduced number of field and/or greenhouse regeneration cycles will result in lower costs and greater genetic integrity of the germplasm.

Preservation of Orthodox Seeds

The technologies for preserving orthodox seeds are well understood. Seeds should be dried and stored at a low temperature (Justice and Bass, 1978; Roos, 1986, 1989). Research by Justice and Bass (1978), Bass (1980), and Bass and Stanwood (1978) showed that reducing the storage temperature from 5°C to sub-zero temperatures increased seed longevity from less than 10 years for some species to several decades for most species.

The ultra-low temperature of liquid nitrogen (LN) used in cryogenic storage should extend seed longevity (Stanwood, 1980, 1985; Stanwood and Bass, 1981). Stanwood and Sowa (1995) reported that after 10 years of storage, oxygen uptake rates and average seedling root lengths were greater for onion samples stored in the vapor phase above LN (approximately -160°C), compared to samples stored at -18°C. Germination percent did not change during 10 years of storage at either of these temperatures. However, major differences in germination were observed between 5°C and the sub-zero temperatures.

Although seed drying extends longevity, there are limits to the beneficial effects, and the optimum moisture content varies with the chemical composition of the seed (Vertucci and Roos, 1990, 1993; Vertucci et al., 1994; Walters-Vertucci and Roos (1996); Ellis et al., 1989, 1990). Drying seeds beyond a critical moisture

content can result in accelerated deterioration at above zero temperatures. Using basic thermodynamic principles, scientists at the NSSL (Vertucci, 1989; Vertucci and Roos, 1990, 1993; Vertucci et al., 1994) have established that, contrary to the viability equations (Ellis and Roberts, 1980; Ellis et al., 1989), the effects of storage temperature and water content of seeds are not independent. Consequently, the optimum water content for seed storage varies with both the species and the storage temperature. The thermodynamic principles used by Vertucci and Roos (1990, 1993) and Vertucci et al. (1994) can be used to predict optimum moisture levels for all orthodox seeds at all storage temperatures. Equilibration at about 25% RH at a specified temperature provides the optimum seed moisture for storage at that temperature for all orthodox seeds studied. Seed moisture at equilibrium will be less in seed with a greater lipid content (Walters-Vertucci and Roos, 1996). The procedure of drying to equilibrium at an appropriate relative humidity (RH) and temperature eliminates the requirement of determining the moisture content of each accession and saves processing time. When high quality seed is dried to the optimum moisture content and stored at sub-zero temperatures, longevity of several decades can be expected (Walters et al., 1997).

Preservation of Sorghum and Pearl Millet in the NPGS

The NPGS active collections of sorghum and pearl millet are maintained and distributed by staff of the Plant Genetic Resources Conservation Unit (PGRCU) at Griffin, Georgia, in cooperation with the sorghum curator at the Tropical Agricultural Research Station (TARS) in Mayaguez, Puerto Rico, and the pearl millet curator at Tifton, Georgia. Accessions of both crops are regenerated at the TARS. About 100 plants are established and selfed by bagging at least one panicle per plant. Panicles are harvested and equal seed quantities from all selfed panicles are bulked. These bulked seed samples are then divided, with part staying in the active collection and the other part deposited in the NSSL base collection. Sorghum and pearl millet samples at the Griffin PGRCU are maintained in cold vaults at about 5°C and 25% RH.

Seed samples received at NSSL are dried initially to equilibrium at about 10°C and 30% RH, to obtain near optimum seed moisture for long-term storage. At this temperature, the dehumidifier seldom runs to achieve 30% RH, whereas at 15°C the RH drops below the desired 35% for this temperature because of the naturally low RH of the ambient air at Fort Collins. Either of these combinations gives the same seed moisture as 5°C and 25% RH (Vertucci and Roos, 1993). Seed quality is normally evaluated by germination tests with four replications of 50 seeds each, using standard Association of Official Seed Analysts procedures. For cryopreservation, two replications of 50 seeds are tested as usual (control), and two replications are stored for 24 hours over LN before the germination tests are conducted. As the seed counts and germination tests are being conducted, a final equilibration is done at about 5°C and 25% RH (seed moisture of sorghum samples stored at NSSL ranges from 6 to 9%,

depending on lipid content). These equilibrium procedures are predicted to result in seed moistures corresponding to those obtained with 20% RH at -18°C.

After seed counts have been made, samples are packaged in moisture-resistant aluminum foil envelopes and stored in the cold vault at about -18°C or placed in polyolefin tubes and stored in the vapor phase above LN at about -160°C in cryotanks. Samples that are substandard for germination (below 65%, or LN-treated samples that deviate from the control by 10% or more) or are substandard for seed number (below 1,000 seeds) are stored in cold vaults while the accessions are queued for regeneration. Operating costs at NSSL to maintain samples at -18°C are estimated to be about $.04 per sample per year and about $0.14 per sample in cryotanks.

The seed quality data for accessions in the NPGS active and base collections are entered in GRIN. Viability is monitored periodically at NSSL depending on initial viability (about every 15 years, except for accessions with poorer initial quality that are tested more often). Substandard samples of sorghum and pearl millet are identified for regeneration by the Mayaguez TARS.

The NPGS collections include 40,477 accessions of sorghum (Table 1). Of the 20,169 accessions now in the base collection at NSSL, 80% are in conventional storage and 20% are in cryostorage. Seed quality is fair, with 79% of the accessions having samples with germination above 64%. The NPGS collections include 1,507 accessions of pearl millet and related species (Table 2). Only 102 *Pennisetum* accessions are backed up in the NSSL base collection. Seed quality is fair, with 79% of the accessions having samples with germination above 64%. Countries of origin of NPGS accessions, as listed in GRIN, are shown in Table 3.

U.S. quarantine regulations require that sorghum and pearl millet accessions from Africa and Asia be grown under controlled conditions and inspected by the Animal Plant and Animal Health Inspection Service (APHIS). In the past seven years, 10,893 quarantined sorghum introductions have been regenerated in St. Croix, Virgin Islands, inspected, and added to the NPGS sorghum collection, with only 278 remaining in quarantine for regeneration. Pearl millet accessions have been regenerated under quarantine restrictions in greenhouses in Tifton, but 724 introductions are backlogged. Authorization to re-

Table 1. Status of *Sorghum* accessions in NPGS.

	Number	Per Cent
Plant variety protection voucher samples	48	
Accessions in quarantine status	278	
Accessions in NPGS	40,477	
Accessions in NSSL base collection	20,169	50
Tested for germination	19,803	99
85 to 100%	9,131	46
65 to 84%	6,479	33
1 to 64%	4,193	21

Table 2. Status of *Pennisetum* accessions in NPGS.

	Number	Per Cent
Plant variety protection voucher samples	5	
Accessions in quarantine status	724	
Accessions in NPGS	1,507	
Accessions in NSSL base collection	102	7
Tested for germination	77	77
85 to 100%	32	42
65 to 84%	29	37
1 to 64%	16	21

Table 3. Source of *Sorghum* and *Pennisetum* accessions in the NPGS and ICRISAT.

	NPGS		ICRISAT	
Country	*Sorghum*	*Pennisetum*	Sorghum	*Pennisetum*
Africa	3			
Algeria	41	52	23	5
Angola			44	
Benin	417		199	46
Botswana	153	2	219	82
Burkina Faso	334	117	549	868
Burundi	154	8	140	
Cameroon	229	41	2486	998
Cape Verde Islands			1	2
Central African Republic	4		249	156
Chad	111		192	136
Congo			1	8
Cote D'Ivoire	1		7	
Egypt	16	1	35	
Ethiopia	7080	42	4401	2
French Equatorial Africa	5			
Gambia	67		57	15
Ghana	46	9	147	283
Guinea	1			
Kenya	723	50	988	98
Lesotho	10	12	271	4
Liberia	3			
Libya	22			
Madagascar	10		14	
Malawi	550	15	423	312
Mali	1016	18	701	1178
Mauritania	15		9	37
Morocco	1	4	27	4
Mozambique	23	13	48	33
Namibia			182	1126
Niger	515	37	412	1270
Nigeria	460	188	1672	1917
Rwanda	86		291	
Senegal	347	4	241	415

(Continued on Next Page)

Table 2. Status of *Pennisetum* accessions in NPGS.

	Number	Per Cent
Plant variety protection voucher samples	5	
Accessions in quarantine status	724	
Accessions in NPGS	1,507	
Accessions in NSSL base collection	102	7
Tested for germination	77	77
85 to 100%	32	42
65 to 84%	29	37
1 to 64%	16	21

Table 3. Source of *Sorghum* and *Pennisetum* accessions in the NPGS and ICRISAT.

	NPGS		ICRISAT	
Country	*Sorghum*	*Pennisetum*	Sorghum	*Pennisetum*
Africa	3			
Algeria	41	52	23	5
Angola			44	
Benin	417		199	46
Botswana	153	2	219	82
Burkina Faso	334	117	549	868
Burundi	154	8	140	
Cameroon	229	41	2486	998
Cape Verde Islands			1	2
Central African Republic	4		249	156
Chad	111		192	136
Congo			1	8
Cote D'Ivoire	1		7	
Egypt	16	1	35	
Ethiopia	7080	42	4401	2
French Equatorial Africa	5			
Gambia	67		57	15
Ghana	46	9	147	283
Guinea	1			
Kenya	723	50	988	98
Lesotho	10	12	271	4
Liberia	3			
Libya	22			
Madagascar	10		14	
Malawi	550	15	423	312
Mali	1016	18	701	1178
Mauritania	15		9	37
Morocco	1	4	27	4
Mozambique	23	13	48	33
Namibia			182	1126
Niger	515	37	412	1270
Nigeria	460	188	1672	1917
Rwanda	86		291	
Senegal	347	4	241	415

(Continued on Next Page)

Table 3. Source of *Sorghum* and *Pennisetum* accessions in the NPGS and ICRISAT, continued.

	NPGS		ICRISAT	
Country	*Sorghum*	*Pennisetum*	Sorghum	*Pennisetum*
Sierra Leone	26		108	60
Somalia	102		446	4
South Africa	807	65	935	162
Sudan	3813	31	2494	614
Swaziland	11		202	
Tanzania	86		718	503
Togo	565	23	294	515
Tunisia		6		
Uganda	682	7	1759	124
Zaire	40	22	52	11
Zambia	580	31	341	157
Zimbabwe	1237	385	1607	1386
Africa sub-total	20,392	1,183	22,985	12,531
Afghanistan	10	3	5	
Bangladesh		1	9	
China	1122	5	380	
India	1083	120	6106	7775
Indonesia	20		33	
Iraq	5		3	
Iran	420	3	7	
Kazakhstan	3			
Korea	40		78	1
Lebanon	32		360	108
Nepal	3		8	
Oman	54	7		
Pakistan	24	15	70	160
Saudi Arabia	23	3	22	
Turkey	111		50	2
Yemen	4635	62	2130	290
Asia, other	83	2	242	2
Asia sub-total	7668	221	9503	8338
Oceania sub-total	239	9	64	8
Caribbean sub-total	134	0	84	0
Europe sub-total	501	25	526	61
North America sub-total	2642	58	2226	245
South America sub-total	132	11	192	2
Unknown	8769		63	10
Total	40,477	1507	35,643	21,195

generate these accessions in St. Croix has been requested.

A total of 1,596 sorghum landrace collections have been submitted for conversion from photoperiod-sensitive to adapted insensitive versions in the TAES-USDA Sorghum Conversion Program, and 623 fully converted lines have been released and are available in the NPGS sorghum collection (Duncan et al., 1995; Rosenow et al., 1995; J.A. Dahlberg, personal communication). Most accessions available from the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India, are in the NPGS sorghum collection.

The International Crops Research Institute for the Semi-Arid Tropics

Within the Consultative Group for International Agricultural Research (CGIAR), ICRISAT has responsibility for the world sorghum and pearl millet collections, as well as their wild relatives. The policy of the CGIAR centers is to conserve, maintain, improve, and distribute germplasm world-wide for use in agricultural research and development. In 1983, the FAO member countries adopted the International Undertaking on Plant Genetic Resources and established the Commission on Plant Genetic Resources. Under the framework of the International Undertaking, a Global System for Plant Genetic Resources has been proposed. As part of this system, the FAO International Network of *Ex Situ* Collections aims to ensure safe conservation and to provide an equitable means whereby all countries have access to plant genetic resources to enhance their agricultural stability, productivity, and well-being, while they share equally and fairly in the benefits accruing from the utilization of such resources. Under this agreement, ICRISAT has designated 80% of the sorghum collection and 98% of the pearl millet collection to the auspices of the FAO/CGIAR agreement, where these collections will be held in trust for the benefit of humankind. This agreement covers collections held by ICRISAT prior to December 1993 when the Convention of Biological Diversity, which affirmed the sovereign rights of national governments over their national resources, came into effect. The agreement states that ICRISAT's designated germplasm will continue to be readily available to all, since ICRISAT will not claim ownership nor apply intellectual property protection to the germplasm they hold in trust and will ensure that recipients will not apply for intellectual property rights to the germplasm. Germplasm acquired after December 1993 will be subject to conditions imposed by the source country and may be very specific for each accession until a more global system for plant genetic resources can be developed. To meet their responsibilities, ICRISAT requires every recipient of designated germplasm to sign a material transfer agreement. The availability and status of germplasm acquired by ICRISAT after December 1993 will depend on individual agreements.

Chapter 14G of Agenda 21 of the United Nations Conference on the Environment and Diversity (UNCED) recommends that all gene banks duplicate their collections of germplasm for safety. ICRISAT's agreement with FAO also requires a safety duplication. The designation of sites for safety duplication and storage is being investigated for both sor-

ghum and pearl millet. Once sites are identified, an agreement will be arranged to facilitate transfer and ensure safe storage for the duplicate collection. At this time, various options are being investigated, including an arrangement with NSSL, regional gene banks, other CGIAR Centers, and specific national gene banks.

The first major effort to assemble a world collection of sorghum was made in the 1960s by the Rockefeller Foundation in the Indian Agricultural Research Program (House, 1980, 1985; Murty et al., 1967; Rockefeller Foundation, 1970). A total of 16,138 accessions were assembled from different countries, and International Sorghum (IS) numbers were assigned to them. In 1976, ICRISAT was given the responsibility to add sorghum germplasm to the world collection in accordance with the recommendation made by the Advisory Committee on Sorghum and Millet Germplasm sponsored by the International Board for Plant Genetic Resources (now IPGRI, the International Plant Genetic Resources Institute) (IBPGR, 1976; Mengesha and Prasada Rao, 1982). At present, ICRISAT Asia Center (IAC) is a major repository for the world sorghum and pearl millet germplasm collection, with a total of 35,643 sorghum accessions from 90 countries and 21,195 pearl millet accessions from 48 countries. The existing collections of these two crops conserved at ICRISAT have been estimated to represent about 80% of the variability present in the crop. Despite this, germplasm still remains to be collected from a number of specific areas where a high degree of genetic diversity still exists in either the crop or its wild relatives. In the future, collection activities will be targeted to fill these gaps for both ICRISAT and the specific country. These collections will occur in cooperation with the specific country and will be based on a clearly defined agreement on the collection and receipt of the germplasm.

Greater research effort will be expended on assessing the adequacy of the existing collections both within national government programs and at ICRISAT, eliminating redundancy, and characterizing the degree of diversity. These assessments will be conducted in cooperation with specific countries and will hopefully involve a repatriation of collections held by ICRISAT and other gene banks, in-country evaluations using descriptors of value to the national programs as well as ICRISAT, and an opportunity to enhance the training of national scientists to assume responsibility for their genetic resources and to benefit more directly from their use. This increased national control over their own natural resources is affirmed by the Convention of Biological Diversity and will be an objective of any global genetic resource system. In the future, research emphasis will use *in situ* conservation of both the crop and the wild relatives in their natural habitats.

The accessions of both sorghum and pearl millet held by ICRISAT are listed in Table 3 according to their origins. These collections contain material donated by governments and private institutions over the past two decades or collected by ICRISAT in cooperation with national genetic resource programs in various countries. Thus, 90% of the sorghum collection and 98% of the pearl millet collection have come from developing countries in the semi-arid tropics. About 49% of the sor-

ghum collection is from five countries: India, Ethiopia, Sudan, Cameroon, and Yemen. Thirty-seven percent of the accessions in the pearl millet collection are from India. Within Africa, 33% of the accessions are from West Africa, while 18% are from Southern Africa. Besides India, the other main contributors to the pearl millet collection are Nigeria, Zimbabwe, Niger, Mali, and Namibia.

ICRISAT has maintained and continues to conserve 473 wild sorghum accessions from 23 taxa and 688 accessions from 38 taxa for the wild relatives of pearl millet. The sorghum accessions have been screened for downy mildew and shoot fly resistance at IAC. Some of the accessions of diploid wild races of *S. verticilliflorum, S. virgatum*, and *S. arundinaceum* were collected in their natural habitats in Sudan, near the Ethiopian border where sorghum is considered to have been domesticated (Doggett, 1970; de Wet, 1976). Harlan and de Wet's collection of wild sorghum, consisting of 188 accessions from the early 1960s, was obtained from Mayaguez, Puerto Rico, U.S.A., in 1979. A collaborative effort with the Department of Primary Industries, Central Region, Queensland, Australia, has resulted in the recent collection of 162 samples of wild sorghum belonging to the sections *Parasorghum, Stiposorghum, Heterosorghum*, and *Chaetosorghum*. The Australian collection, after being released from plant quarantine at IAC, will be added to ICRISAT's collection and will bring the total number of wild sorghum accessions at IAC to 635 (Prasada Rao et al., 1995). Fifty-five percent of the collection of wild relatives of pearl millet consists of 382 accessions of ssp. *monodii* from 13 countries. The other species represented include *P. pedicellatum* (132 accessions), *P. polystachyon* (79 accessions), *P. orientale* (20 accessions), and *P. purpureum* (16 accessions).

A separately-maintained genetic stock collection includes accessions identified as sources of resistance (to major diseases, insect pests, and *Striga)*, stocks with genes for specific morphological and agronomic characteristics, and cytoplasmic male-sterile lines (Prasada Rao and Mengesha, 1988). For pearl millet, four trait-specific gene pool populations have been developed at ICRISAT. These gene pools include an early maturity gene pool (EGP) with 1,143 accessions from 24 countries, a high-tillering gene pool (HTGP) with 1,093 accessions from 28 countries, a large-grain gene pool (LGGP) with 887 accessions from 19 countries, and a large-panicle gene pool with 804 accessions from 22 countries. These all have been random-mated at least four times.

All sorghum collections are regenerated during the post-rainy season at ICRISAT by selfing about 20 representative panicles from each line. Seeds harvested in equal quantities from these panicles are mixed. Landraces of pearl millet are maintained using cluster bagging. This method involves planting 120 plants of each accession. At the time of panicle emergence, five panicles, one from each of five adjoining plants, are clustered into a bag. At harvest, each accession will have 24 of these cluster bags, and an equal quantity of seed will be bulked from each panicle to reconstitute the accession. Breeding lines and genetic stocks are maintained with sibbing and selfing. The cluster bag technique has been used for a

number of years, but phenotypic evidence indicates that the technique may be inadequate to maintain the variability of an original accession. Thus, studies have been initiated at ICRISAT to evaluate the adequacy of this procedure. At harvest, the moisture content of the seeds of both sorghum and pearl millet is about 8-10%, so no additional drying is needed for medium-term storage. A bulk sample of about 500 g of each sorghum and pearl millet accession is preserved in an aluminum can in the medium-term storage facility (at about 4°C and 20% relative humidity). An initial moisture test is conducted on the seeds in medium-term storage, and any of those with viabilities above 95% are dried to 6-7% moisture content in a dryer at 15°C and 15% RH. These accessions are placed in moisture proof aluminum foil packets that are vacuum sealed and stored in long-term storage (-20°C). The exact requirements for the initial viability test to move an accession into long-term storage has been changed to 90% as of 1996. Specifically, 17% of the sorghum collection and 23% of the pearl millet collection have been put into long-term storage (Tables 4 and 5). A higher percentage of the two collections has been tested for viability, 44% for sorghum and 31% for pearl millet. Of those accessions tested for both crops, about 90% had viabilities of 85-100%.

Another important aspect of the ICRISAT genetic resource effort is the distribution of samples of requested accessions. Across all mandate crops since 1992, about 49% of the requests have come from within ICRISAT or other CGIAR Centers; about 43% come from national program scientists in developing countries, and about 1% come from scientists in developed countries. The majority of the germplasm sent from ICRISAT goes to international and national programs; only 2% of all requests have been from the private sector, and none of these were from developed countries. This dis-

Table 4. Status of *Sorghum* Accessions at ICRISAT.

	Number	Per Cent
Accessions in ICRISAT	35,643	
Accessions in long-term storage	5,955	17
Tested for germination	15,574	44
85 to 100%	14,080	90
51 to 84%	1,360	9
1 to 50%	134	1

Table 5. Status of *Pennisetum* accessions at ICRISAT.

	Number	Per Cent
Accessions in ICRISAT	21,195	
Accessions in long-term storage	4,866	23
Tested for germination	6,579	32
85 to 100%	5,934	90
51 to 84%	572	9
1 to 50%	73	1

tribution of requests may change in the future if the role of the private sector increases in the area of basic germplasm enhancement. At this time, research is being conducted primarily by public programs.

The greater utilization of the genetic diversity in developing sustainable solutions to basic crop constraints or enhancing productivity will be critical in the future. Increasing both the utilization of the sorghum and pearl millet collection and access to the information available on the collections will greatly contribute to this effort. ICRISAT has been involved with a CGIAR System-Wide Research Program (SGRP) to enhance the availability of the databases on the collections. The SINGER (System-wide Information Network for Genetic Resources) Program has resulted in the consolidation and entry of passport and a limited amount of characterization data for the sorghum and pearl millet collections. The primary objective of SINGER has been to develop an effective way to link the databases of the CGIAR Centers and allow searching across the Centers through a common user interface for data on specific collections, their transfer to collaborators, and access to the characterization data. SINGER will result in a more compatible and user-friendly format for managing these data at ICRISAT. This objective is being addressed, and the databases for these two collections should be available through a number of different means. This effort also will depend on a continuing effort to collect characterization data at ICRISAT or from specific country evaluations, and to consolidate information about specific accessions. The databases will need to be continually updated by both ICRISAT scientists and other users in the scientific community. This ability to easily and rapidly share information on the potential benefit of an accession is critical to the greater utilization of sorghum and pearl millet germplasm. These databases also will need to be compatible with other information systems, such as GIS databases, and other germplasm databases, such as GRIN or plant genome databases that have information for sorghum and pearl millet.

Core Subsets

When a scientist determines that genetic variation for a desired trait is inadequate in the available germplasm, new accessions are needed that will provide the highest probability of identifying useful source materials with minimum screening. Sometimes this can be achieved by obtaining accessions from an area where the problem has been endemic for many years, e.g., low soil pH. A list of candidate accessions often can be generated when appropriate information is in the database.

In other cases, especially for new pathogen strains or insect biotypes, searching database information is of little or no value. When the scientist must search within the crop collection for the desired trait, an initial screening of a diverse but smaller subset may reduce time and costs. The idea of developing such a subset was proposed by Frankel (1984) and further developed by Brown (1989a, b; 1995). They suggest that "a core collection consists of a limited set of accessions derived from an existing germplasm collection, chosen to represent the genetic spectrum of the whole collection. The

core should include as much as possible of its genetic diversity." The core subset is suggested to be about 10% of the crop collection, but may vary from 5% for very large collections to 50% or more for very small collections, with about 3,000 suggested as a maximum number.

Brown (1989a) recommended stratified sampling methods when establishing core collections. Grouping begins with taxonomic affinity (e.g., species, subspecies, cytological races). Accessions within each taxon can then be assigned to strata based on ecogeographic zones and genetic characteristics (e.g., ploidy level, photoperiod response, races). In some crops, country of origin (or region of adjacent countries) may be the only available means for developing preliminary groups.

Development of a useful core subset may involve the following steps: 1) assembling and reviewing passport data and other information for establishing nonoverlapping groups, 2) assigning accessions to appropriate groups, 3) choosing accessions for the preliminary core subset from each group, and 4) collecting data on phenotypic and genetic traits for accessions in the preliminary core and using multivariate analytical methods to construct clusters and dendrograms to elucidate systematic and statistical genetic relations for further refinement of the core subset.

Proportional sampling within each group may provide a more representative sample of the total genetic diversity in the core subset than would a completely random sampling from the crop collection. Once the number needed from each group has been determined, accessions for the core subset are usually chosen randomly within each group. However, some curators are choosing accessions with more desirable agronomic traits within each group. Clusters generated by multivariate analyses of morphological traits and molecular data may provide a better understanding of patterns of genetic divergence and diversity and will often identify ecogeographic regions that have not been adequately sampled, especially when the origin of each accession in the core is plotted geographically. This information may be valuable in planning future acquisitions.

The core collection concept has gained wide acceptance and core collections are being developed in many countries (Hodgkin et al., 1995; Knupffer and van Hintum, 1995). The NPGS is developing a core subset for each of the major crop collections (Erskine and Muehlbauer, 1991; Holbrook et al., 1993; Diwan et al., 1994).

A sorghum core collection has been established at ICRISAT (Prasada Rao and Ramanatha Rao, 1995) by stratifying the total world collection geographically and taxonomically into subgroups. Accessions in each subgroup were then clustered into closely related groups based on characterization data, using principle components analysis. Representative accessions from each cluster were drawn in proportion to the total number of accessions present in that subgroup to form a sorghum core collection of 3,475 accessions (approximately 10% of the total world collection). Designation of this core subset will not affect the conservation of the total world collection of sorghum germplasm at ICRISAT and at other centers where duplicate sets are conserved.

References

ARS Information Service. 1990. Seeds for our future. Program Aid 1470. Agricultural Research Service, U.S. Department of Agriculture.

Ball, C.R. 1903. Pearl millet. USDA Farmers Bulletin 168.

Bass, L.N. 1980. Seed viability during long-term storage. p. 117-141. *In* J. Janick (ed.) Horticulture reviews. AVI, Westport, Connecticut.

Bass, L.N., and P.C. Stanwood. 1978. Long-term preservation of sorghum seed as affected by seed moisture, temperature, and atmospheric environment. Crop Sci. 18:575-577.

Brown, A.H.D. 1989a. The case for core collections. p. 136-156. *In* A.H.D. Brown et al. (eds.) The use of plant genetic resources. Cambridge Univ. Press, Cambridge.

Brown, A.H.D. 1989b. Core collections: A practical approach to genetic resources management. Genome 31(2):818-824.

Brown, A.H.D. 1995. The core collection at the crossroads. p. 3-19. *In* T. Hodgkin, A.H.D. Brown, Th.J.L. van Hintum, and E.A.V. Morales (eds.) Core collections of plant genetic resources. IBPGRI, Sayce Publishing, and John Wiley and Sons, Chichester.

Burton, G.W. 1980. Registration of pearl millet inbred Tift 383 and Tifleaf 1 pearl millet. Crop Sci. 20:292.

Burton, G.W. 1995. History of hybrid development in pearl millet in Tifton. p. 5-8. *In* I.D. Teare (ed.) Proceedings of first national grain pearl millet symposium, Tifton, GA.

Crossa, J., S. Taba, S.A. Eberhart, P. Bretting, and R. Vencovsky. 1994. Practical considerations for maintaining germplasm in maize. Theor. Appl. Genet. 89:89-95.

de Wet, J.M.J. 1976. Variability in *Sorghum bicolor*. p. 453-463. *In* J.R. Harlan et al. (eds.) Origins of African plant domestication. Mouton Publ., Hague, the Netherlands.

Diwan, N., G.R. Bauchan, and M.S. McIntosh. 1994. A core collection for the United States annual *Medicago* germplasm collection. Crop Sci. 34:279-285.

Doggett, H. 1970. Sorghum. Longmans, Green, London.

Duncan, R.R., P.J. Bramel-Cox, and F.R. Miller. 1991. Contributions of introduced sorghum germplasm to hybrid development in the USA. p. 69-102. *In* H.L. Shands and L.E. Wiesner (eds.) Use of plant introductions in cultivar development. Part 1. CSSA Spec. Publ. 17. CSSA, Madison, WI.

Duncan, R.R., J. Dahlberg, and M. Spinks. 1995. International activities in sorghum germplasm acquisition during the past thirty-five years. p. 117-134. *In* R. Duncan (ed.) International germplasm transfer: Past and present. CSSA Spec. Publ. 23. CSSA, Madison, WI.

Ellis, R.H., T.D. Hong, and E.H. Roberts. 1989. A comparison of the low-moisture-content limit to the logarithmic relation between seed moisture and longevity in twelve species. Ann. Bot. 63: 601-611.

Ellis, R.H., T.D. Hong, E.H. Roberts, and K.L. Tao. 1990. Low moisture content limits to relations between seed longevity and moisture. Ann. Bot. 65: 493-504.

Ellis, R.H., and E.H. Roberts. 1980. Improved equations for the prediction of seed longevity. Ann. Bot. 45:13-30.

Erskine, W., and F.J. Muehlbauer. 1991. Allozyme and morphological variability: Outcrossing rate and core collection formation in lentil germplasm. Theor. Appl. Genet. 83:119-125.

Frankel, O.H. 1984. Genetic perspectives of germplasm conservation. p. 161-170. *In* W.K. Arber et al. (eds.) Genetic manipulation: Impact on man and society. Cambridge Univ. Press, Cambridge.

Hanna, W.W., H.D. Wells, and G. W. Burton. 1987. Registration of pearl millet inbreds Tift $85D_2A_1$ and $85D_2B_1$. Crop Sci. 27:1324-1325.

Hanna, W.W. 1995. Breeding pearl millet for grain production. p. 8-12. *In* I.D. Teare (ed.) Proceedings of first national grain pearl millet symposium, Tifton, GA.

Hodgkin, T., A.H.D. Brown, Th.J.L. van Hintum, and E.A.V. Morales (eds.) 1995. Core collections of plant genetic resources. IBPGRI, Sayce Publishing, and John Wiley and Sons, Chichester.

Holbrook, C.C., W.F. Anderson, and R.N. Pittman. 1993. Selection of a core collection from the U.S. germplasm collection of peanut. Crop Sci. 33:859-861.

House, L.R. 1980. A guide to sorghum breeding. ICRISAT, Patancheru, India.

House, L.R. 1985. A guide to sorghum breeding (2nd edition). ICRISAT, Patancheru, India.

IBPGR (International Board for Plant Genetic Resources). 1976. Proc. of the meeting of the advisory committee on sorghum and millets germplasm, 3-7 Oct. ICRISAT, Hyderabad, India.

Janick, J. (ed.). 1989. The national germplasm system of the United States. Plant breeding reviews. Volume 7. Timber Press, Portland, Oregon.

Justice, O.L., and L.N. Bass. 1978. Principles and practices of seed storage. Agriculture Handbook No. 506. U.S. Government Printing Office, Washington, D.C.

Knupffer, H., and Th.J.L. van Hintum, 1995. The barley core collection - an international effort.

p. 171-178. *In* T. Hodgkin, A.H.D. Brown, Th.J.L. van Hintum, and E.A.V. Morales (eds.) Core collections of plant genetic resources. IBPGRI, Sayce Publishing, and John Wiley and Sons, Chichester.

Mann, J.A., C.T. Kimber, and F.R. Miller. 1983. The origin and early cultivation of sorghums in Africa. Texas Agric. Exp. Stn. Bull. 1454.Texas A&M Univ., College Station.

Mengesha, M.H., and K.E. Prasada Rao. 1982. Current situation and future of sorghum germplasm. p. 323-333. *In* L.R. House et al. (ed.) Sorghum in the Eighties. Proc. int. symp. on sorghum, 2-7 Nov. 1981, Patancheru, India. ICRISAT, Patancheru, India.

Murty, B.R., V. Arunachalam, and M.B.L. Saxena. 1967. Classification and catalogue of a world collection of cultivated sorghums and *Pennisetums*. Indian Journal of Genetics and Plant Breeding 27:1-74.

Prasada Rao, K.E., and M.H. Mengesha. 1988. Sorghum genetic resources-synthesis of available diversity and its utilization. p. 159-179. *In* R.S. Paroda, R.K. Arora, and K.P.S Chandel (eds.) Plant genetic resources-Indian perspective. National Bureau of Plant Genetic Resources, New Delhi, India.

Prasada Rao, K.E., and V. Ramanatha Rao. 1995. Use of characterization data in developing a core collection of sorghum. p. 109-115. *In* T. Hodgkin, A.H.D. Brown, Th.J.L. van Hinthum, and E.A.V. Morales (eds.) Core collection of plant genetic resources. John Wiley and Sons, UK.

Prasada Rao, K.E., V. Gopal Reddy, and J.W. Stenhouse. 1995. Sorghum genetic resources at ICRISAT Asia Center. International Sorghum and Millets Newsletter 36: 15-18.

Rachie, K.O., and J.V. Majmudar. 1980. Pearl Millet. The Pennsylvania State University Press, University Park, PA.

Rajewski, J.F., and D.J. Andrews. 1995. Grain pearl millet performance and adaptability in six years of regional trials. p. 14-17. *In* Teare, I.D. (ed.) Proceedings of first national grain pearl millet symposium, Tifton, GA.

Rockefeller Foundation. 1970. Annual report. New York.

Roos, E.E. 1986. Precepts of successful seed storage. p. 1-25. *In* M.B. McDonald and C.J. Nelson (eds.) Physiology of seed deterioration. CSSA Special Pub #11. CSSA, Madison, WI.

Roos, E.E. 1989. Long-term seed storage. Plant Breeding Reviews 7:129-158.

Rosenow, D.T., J.A. Dahlberg, G.C. Peterson, L.E. Clark, A. Sotomayor-Rios, F.R. Miller, A.J. Hamburger, P. Madera-Torres, A. Quiles-Belen, and C.A. Woodfin. 1995. Release of 50 converted sorghum lines and 253 partially converted sorghum bulks. International Sorghum and Millets Newsl. 36:19-34.

Shands, H.L., P.J. Fitzgerald, and S.A. Eberhart. 1989. Program for plant germplasm preservation in the United States: The U.S. National Plant Germplasm System. p. 97-115. *In* L. Knutson and A.K. Stoner (eds.) Biotic diversity and germplasm preservation, global imperatives. Kluwer Academic Press, Dordrecht, the Netherlands.

Stanwood, P.C. 1980. Tolerance of crop seeds to cooling and storage in liquid nitrogen (-196°C). J. Seed Technol. 526-31.

Stanwood, P.C. 1985. Cryopreservation of seed germplasm for genetic conservation. p. 199-226. *In* K.K. Kartha (ed.) Cryopreservation of plant cells and organs. CRC Press, Inc., Boca Raton, Florida.

Stanwood, P.C., and L.N. Bass. 1981. Seed germplasm preservation using liquid nitrogen. Seed Sci. Technol. 9:423-437.

Stanwood, P.C., and S. Sowa. 1995. Evaluation of onion (*Allium cepa* L.) seed after 10 years of storage at 5, -18 and -196°C. Crop Sci. 35:852-856.

Stegmeier, W.D. 1994. Pearl millet germplasm enhancement for semi-arid regions. p. 80-85. *In* INTSORMIL annual report 1994. Lincoln, Nebraska.

Vertucci, C.W. 1989. Relationship between thermal transitions and freezing injury in pea and soybean seeds. Plant Physiol. 90:1121-1128.

Vertucci, C.W., and E.E. Roos. 1990. Theoretical basis of protocols for seed storage. Plant Physiol. 94:1019-1023.

Vertucci, C.W., and E.E. Roos. 1993. Theoretical basis of protocols for seed storage II. The influence of temperature on optimal moisture levels. Seed Sci. Res. 3: 201-213.

Vertucci, C.W., E.E. Roos, and J. Crane. 1994. Theoretical basis of protocols for seed storage III. Optimum moisture contents for pea seeds stored at different temperatures. Ann. Bot. 74:531-540.

Walters, C.T., E.E. Roos, and S.A. Eberhart. 1997. Cost-benefit analyses of various seed storage practices. Crop Sci. (in press)

Walters-Vertucci, C., and E.E. Roos. 1996. Seed moisture, seed drying and energy costs of a seed bank. p. 243-255. *In* Proc. 50th ann. corn & sorghum res. conf. Amer. Seed Trade Assoc., Washington, D.C.

Wendorf, F., A.E. Close, R. Schild, K. Wasylikowa, R.A. Housley, J.R. Harlan, and H. Krolik. 1992. Saharan exploitation of plants 8,000 bp. Nature 359:721-724.

Sorghum and Pearl Millet Genetic Resources Utilization

J. A. Dahlberg*, C.T. Hash, S. Kresovich, B. Maunder, and M. Gilbert

Abstract

Sorghum and pearl millet are unique in size and diversity. The largest collections contain 40,570 (U.S. sorghum collection) and 21,191 (ICRISAT pearl millet collection) accessions. Less than three percent of these accessions have been used in crop improvement. Curation — or acquisition, maintenance, characterization, and utilization — plays a role in exploitation of the genetic variation within these collections.

Cultivation of sorghum and pearl millet is increasing the use of marginal agricultural land. Future utilization will depend on increased research on abiotic and biotic stress tolerance. To facilitate exploitation of this vast germplasm, traditional and biotechnical methods must be combined to provide better understanding of the genetic variation available, which then can be used in crop enhancement. This can only be accomplished through sharing of ideas, particularly through creation of an arena where information is globally accessible.

Sorghum [*Sorghum bicolor* (L.) Moench] and millet (pearl millet [*Pennisetum glaucum* (L.) R. Br.] and several other small-seeded grasses grown as grain and fodder crops) are some of the most important cereals globally. In 1995, the FAO estimated sorghum was harvested on 43 million ha, with a production of 53 million MT, and an average yield of 1544 kg ha^{-1}. Millet was harvested on 37 million ha, producing 26 million MT, with an average yield of 1070 kg ha^{-1} (FAOSTAT database, 1996). Despite their importance as food and feed crops, literature on their curation is limited. As demand for food production — with fewer inputs based on a more balanced ecological scale — increases, information on more effective methods of identifying, maintaining, and using exotic germplasm within both crops is needed.

World collections are unique, not only in size, but also in diversity (Dahlberg and Spinks, 1995; Hanna and Lovell, 1995; Lawrence and Rettke, 1995; Prasada Rao et al., 1995; Wenzel, 1995). The diversity and availability of these resources has led to steady improvement in sorghum and millet. Sorghum improvement has been characterized by long-term increase of hybrid yields (Miller and Kebede, 1984; Doggett, 1988). Early work on utilization of sorghum germplasm was confined to pure line selection within cultivated landrace populations in Africa and India that

J.A. Dahlberg, USDA-ARS-TARS, Box 70, Mayagüez, PR 00681, USA; C.T. Hash, ICRISAT, Patancheru, AP 502 324, India; S. Kresovich, USDA-ARS-PGRCU, Georgia Agricultural Experiment Station, Georgia Station, Griffin, GA 30212; B. Maunder, 4511 Ninth St., Lubbock, TX 79416; M. Gilbert, Cargill Seed Co., P.O. Box 5645, MS16, Minneapolis, MN 55440-5645. *Corresponding author.

resulted in somewhat improved cultivars, some of which continue to be widely grown. Selection within dwarf populations was then taken up, followed by exploitation of cytoplasmic male-sterility, which permitted the production of commercial hybrids. Crossing and/or backcrossing between adapted introductions and local germplasm has been used to derive improved self-pollinated varieties and parental lines (Prasada Rao et al., 1989). Sorghum yields have increased by over 30% within the last 30 years and much of this gain can be attributed to genetic diversity found within the species. Useful traits such as increased seed number, larger panicles, greater total plant weight, drought tolerance, disease resistance, greater plant height, longer maturity, greater leaf area indices, increased green leaf retention, and greater partitioning of dry matter have contributed to increased yields (Miller and Kebede, 1984).

Utilization has been primarily limited to agronomically important and, in some cases, wild sources of germplasm. For example, use of Zerazera sorghum has become widespread in the development of new, superior hybrids because of superior yield potential and grain quality (Duncan et al., 1991). Restricted utilization of extensive germplasm collections has occurred because of several characteristics inherent to the collections themselves. The size of many collections has made it difficult to adequately screen them for useful traits. Most breeders rely on a one-time, one-environment evaluation of germplasm to make selections for use in breeding programs. Passport data is limited and, in many cases, missing. Information from donor countries on use, unique characteristics, and importance of individual accessions does not exist. Consequently, utilization of the total collection has not been realized.

This is not to say that we have not been successful in making use of available exotic germplasm. Examples of the importance of germplasm utilization have been cited in sorghum (Duncan et al., 1991) and millet (Andrews and Bramel-Cox, 1993). In 1968, greenbugs (*Schizaphis graminum* Rondani) were observed on sorghum in Wall, Texas. Hackerott and Harvey, working at the Kansas State University Agricultural Research Center in Hays, Kansas, planted their available collection of germplasm and found KS-30, tunisgrass, to have resistance to the new C-biotype. Cooperation between public and private sector scientists made this germplasm quickly available, resulting in enough seed of resistant hybrids to plant 1.6 million ha in 1976. The classic example of germplasm utilization in sorghum has been the Texas A&M-USDA Sorghum Conversion Program. For a review of the program and its impact, see Duncan et al. (1991). Currently 623 converted lines have been released; 533 lines are listed in Duncan and Dahlberg (1993); 50 are listed in Rosenow et al. (1995); and 40 new lines have been released by TAES & USDA (1996).

The successful introgression of resistance to midge (*Stenodiplosis sorghicola* Coq.) and downy mildew [*Peronosclerospora sorghi* (Weston & Uppal)] C. G. Shaw] has greatly stabilized sorghum production in Australia and Argentina. Considerable opportunities remain for exploiting the collections to improve sorghum production globally. For example,

over 340 accessions of the genus sorghum belonging to sections *Chaetosorghum*, *Heterosorghum*, *Stiposorghum*, *Parasorghum*, and *Sorghum* were recently evaluated for resistance to shootfly (*Atherigona soccata* Rondani) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Asia Center. Seven accessions with very high levels of resistance — in some cases close to immunity — were found (Nwanze et al., 1995). Transfer of this high level of resistance to cultivated sorghum could greatly improve productivity of late-sown crops in Africa and Asia, where shootfly is a major production constraint.

The pearl millet landrace 'Iniadi' has had widespread impact on the improvement of that crop globally over the last 25 years (Andrews and Anand Kumar, 1996). Large Grain Populations (LaGraP) and the Bold Seeded Early Composite (BSEC), which have excellent grain yield, grain size, and disease resistance, have been developed from this landrace at ICRISAT Asia Center. CZP-IC 923 was developed from a cross between a smut-resistant dual-purpose variety (ICMV 82132) and a mass-selected experimental variety from BSEC (ICMV 87901). GB 8735, ICMV 221, ICTP 8203, and Okashana 1 are examples of improved open-pollinated cultivars, based largely on this landrace, that have been widely accepted by farmers. Iniadi has also been used extensively in developing hybrid parents for India and the USA. Many of the popular early-maturing pearl millet hybrids in India are based on male-sterile lines developed in Kansas from crosses involving a sample of Iniadi (PI 185642) collected from a local market in Kumasi, Ghana, in 1949. Extensive evaluations of the potential utility of wild relatives of pearl millet in improving forage and grain cultivars over the past 20 years have taken place at the Coastal Plain Experiment Station, Tifton, Georgia, and in Francophone West Africa (Andrews and Bramel-Cox, 1993; Burton, 1995; Hanna, 1990, 1993; Hanna and Burton 1987; Marchais and Pernes, 1985; Wilson and Hanna, 1992).

Although these are impressive examples of the impact that can be achieved using exotic germplasm, the number of accessions used in crop improvement is very small given the size of collections maintained around the world. For example, the sorghum and millet collections in the United States stand at 40,477 and 1,507 respectively. At ICRISAT, the sorghum collection contains 35,643 accessions, while the millet collection, the largest in the world, contains 21,191 accessions (see Eberhart et al., 1996, for a country-wide breakdown of each collection). The Sorghum Conversion Program, which has released 623 converted lines, has tapped into less than 4% of the overall collection. Given these numbers, the question arises as to whether we have created collections that are too large and poorly characterized to effectively manage and utilize them for the benefit of global crop production.

One approach to addressing this question is to critically evaluate the utilization or "curation" of major agricultural collections. The overall goal of preserving genetic resources in an agricultural setting is the future safety of food and fiber production world-wide. This requires a long-term strategy based on the overall curation of each crop. A curator is defined by Webster (1979) as "one that has the care

and superintendence of something." The role of curation and curators of plants has traditionally been associated with herbariums, natural history collections, and/or botanical gardens. In fact, most writing dealing with preservation and curation of plants has concentrated on natural history collections or botanical gardens (Callery, 1995; Dessauer et al., 1990; Hawks, 1990; Hicks and Hicks, 1978; Howie, 1986; Spongberg, 1984). *Conservation Biology: A Training Manual for Biological Diversity and Genetic Resources* (1992) explored much of the theoretical background that encompasses curation from the standpoint of collecting, maintaining, and evaluating collections. Though a training manual for plant biodiversity, many of the principles are relevant to us within an agricultural context. The primary tasks of curation can be divided into four categories: acquisition, maintenance, characterization and evaluation, and utilization (Committee on Managing Global Genetic Resources, 1991).

Acquisition

Acquisition of germplasm has been a strong point within the sorghum and millet programs. Both ICRISAT and the U.S. National Plant Germplasm System (NPGS) have developed large germplasm collections from around the world (Eberhart et al., 1996). Unfortunately, in both collections, passport data available online is limited to date collected, collector, pedigree, country, state/province, location, and secondary identification. The lack of meaningful passport data makes the evaluation of accessions based on geographical diversity difficult. Oliveira et al. (1996) pointed out that geographical origin was found to be correlated with relatedness and that in some cases, the region of origin was a more significant factor than race in establishing how variation is partitioned.

Descriptors for Sorghum [Sorghum bicolor *(L.) Moench*] by IBPGR and ICRISAT (1993) lists over 50 variables critical to valid and informative passport data. Complete and thorough data is required for planning acquisition strategies. Even without full passport data and limited morphological traits, molecular techniques can provide useful information for further collection needs. Calculations of genetic distances will identify divergent subpopulations that could harbor valuable genetic variations not apparent in current holdings.

Genetic conservation, and therefore germplasm utilization, depends on effective sampling techniques used in the original collection. Snaydon (1992) observed that "collections may be made (a) to conserve, as accurately as possible, a particular population perhaps in danger of extinction; (b) to conserve, as accurately as possible, the overall pattern of genetic variation in a particular species, perhaps again in danger of extinction; (c) to conserve, or perhaps maintain temporarily, a wide range of useful variation for a breeding program; (d) to conserve, or maintain temporally, variation in some specific attribute (e.g. cold tolerance or disease resistance) for a breeding programme." In the case of sorghum and millet, we strive to conserve the overall pattern of genetic variation for future use in evaluation and enhancement. To ensure that future collections are made to maximize genetic diversity, collection strategies should be coordinated through their curators, and

strategies should be based on sound scientific theory (Snaydon, 1992; Usher, 1992).

Two areas of need for acquisition in both millet and sorghum are in genetic stocks and wild species or relatives. Genetic stocks are becoming increasingly important in crop improvement. The use of molecular approaches has emphasized studies of gene loci that control traits described in germplasm accessions and for which breeders select. Although genetic and cytogenetic stocks have been used in many ways, including cultivar development, their main use in sorghum and millet has been for research. Studies have been conducted on their inheritance, allelism, linkage, penetrance, and introgression, but their direct use in breeding programs has been limited. Most breeders have chosen to use the original germplasm accession or derived line as a source of an allele of interest. In other species, notably tomato, genetic stocks have been used for more practical purposes (Tomato Genetic Stock Center Task Force, 1988), because, in part, a wider array of stocks is available, they are more thoroughly described, and the potential user community is large and diverse.

With the availability of molecular approaches in sorghum and millet improvement, genetic and cytogenetic stocks should play a more important role. Indeed, the requests for genetic stocks have increased considerably during the last few years. Sorghum and millet scientific communities need to make the acquisition of genetic stock germplasm a priority for future enhancement and research.

Collection and preservation of wild relatives has been a major weakness in our acquisition policy. Currently, less than 1.5% of either the ICRISAT or the NPGS collections contain wild relatives. The collections' deficiencies in representation of wild relatives become more critical as native habitats come under increasing pressure from human and livestock populations, thus threatening some wild species — or at least local populations of them — with extinction. Both ICRISAT and Australian scientists have recognized the need to strengthen this area of germplasm acquisition and major collection trips are scheduled. The U.S. wild sorghum collection is being reevaluated for authenticity, and status of this collection should be available by the end of 1996. Australian scientists have undertaken a collection of indigenous sorghum (Lawrence and Corfield, 1995), which has been sent to both ICRISAT and NPGS for inclusion in their respective programs. The first set received by ICRISAT contained wild sorghum species belonging to the sections *Parasorghum, Stiposorghum, Heterosorghum, and Chaetosorghum* (Prasada Rao et al., 1995). These are being studied at ICRISAT Asia Center for taxonomic classification and species identification.

Maintenance

Sites for preservation and maintenance of the largest sorghum and millet accessions are located at: ICRISAT, Andhra Pradesh, India; the National Seed Storage Laboratory, Fort Collins, Colorado, U.S.; and the USDA-ARS Plant Genetic Resources Conservation Unit (PGRCU), Griffin, Georgia, U.S. Several countries also maintain their own collections within

their national collections. Major growouts and regenerations take place at the ICRISAT Center in India and at the USDA-ARS Tropical Agriculture Research Station, Mayagüez, Puerto Rico.

The number of plants required to maintain genetic variability within a sorghum or millet accession has not been determined scientifically. In self-pollinated crops, the population structure can be variable, depending on the percentage of outcrossing. Burton (1951) reported that wild-grass sorghum may outcross between 18 and 30% while Jones and Sieglinger (1951) indicated that cultivated sorghum may outcross between 5 and 10%. With no outcrossing, landrace collections will be primarily a mixture of pure lines. Theoretically, sorghum accessions collected from small plots in farmers' fields could contain a mixture of pure lines of cultivated, wild ɔ cultivated, and wild sorghum. In this case, the number of plants to be regenerated becomes a function of maintaining as many pure lines within the accession as possible. Ideally, a sorghum accession should be separated into its separate pure lines; realistically, however, this is not feasible. Therefore, maintenance of an accession must be divided into: 1) saving an equal number of seeds from each plant harvested from the first increase during the quarantine growout, and 2) bulking the accession to be used in distribution. Returning a balanced sample of the first increase for long-term storage will help preserve rare genes.

In cross-pollinated crops such as pearl millet, population structure can be more complex, depending on the percentage of selfing that takes place (Crossa et al., 1994). Ideally, an accession would be based on nearly 200 plants and would be regenerated by random mating, in isolation, a balanced bulk of the descendants. This strategy is almost never practical, except in the case of released open-pollinated cultivars where regeneration and breeder seed multiplication can occur simultaneously. Regenerating an accession by harvesting open-pollinated panicles from non-isolated plants is not acceptable, as most seeds will be hybrids of unknown male parentage. Intercrossing by hand is the next best option for maintaining the original population structure. Although laborious, the risk of cross-contamination between accessions is low. Selfing to produce S_1 seed has been recommended by Burton (1979) as a method for increasing seed of pearl millet accessions for distribution and evaluation. This is less laborious than intercrossing, and has a lower risk of cross-contamination. It has the added advantage of producing a population with a known genetic structure. However, many pearl millet accessions are not adapted to selfing and set little or no seed when panicles are bagged. Because of this, the ICRISAT pearl millet collection is maintained by cluster-bagging, in which several panicles of a given accession are enclosed in a single large selfing bag. The seed harvested has an unknown genetic structure, being composed of a mixture of selves and crosses within each bag used in multiplying seed of the accession. Seed from accessions that have been maintained in this manner should be random-mated several times, or crossed to a tester, to overcome inbreeding depression, before being assessed for traits related to grain and stover yield. Trait-specific gene pools, formed by random-mating many accessions, have been developed as an alternative strategy for

more efficiently maintaining and distributing pearl millet germplasm (Rai et al., 1997).

Genetic markers can play a crucial role in monitoring heterogeneity and heterozygosity as accessions are regenerated. Their use will provide guidelines in the refinement of regeneration strategies to ensure the long term maintenance of genetic diversity. Molecular markers will also assist identification of duplicate accessions, a problem within large collections that has never been fully addressed.

Accessions are probably most vulnerable to genetic drift or loss due to mishandling, labeling problems, growouts and regenerations, and storage. Therefore, proper maintenance of collections is critical in preserving the integrity of each accession. Both ICRISAT and the USDA have established guidelines for properly maintaining and regenerating accessions (Dahlberg, 1995; Prasada Rao et al., 1995; Roberts, 1992). Improper handling of the collection at this stage can minimize the potential utility of the germplasm and potentially lose valuable genes needed for future enhancement.

Characterization and Evaluation

Estimates of genotypic and phenotypic variation allow for the inference of genetic structures of individual germplasm accessions. This structure provides the framework in which utilization takes place. Phenotypic variation has been the primary evaluation tool utilized in millet and sorghum, and inference based on phenotypic variability has distinct advantages over that based on genetic variability. It is relatively easy to measure in the field and often provides assessment of a sample of many genetic loci (Huenneke et al., 1992).

Several collections have been evaluated for phenotypic or morphological traits (Table 1). Descriptor lists for evaluation purposes are available from ICRISAT and the USDA (Dahlberg and Spinks, 1995). Sorghum accessions have been identified with resistance to aluminum toxicity, shoot fly, stem borer (*Chilo partellus* Swinhoe), *Striga*, midge (*Stenodiplosis sorghicola* Coq.), rust (*Puccinea purpurea* Cooke), and downy mildew. Sources of twin seededness, cytoplasmic male-sterile systems, brown mid-rib, and other traits also have been identified (see both ICRISAT and USDA databases).

ICRISAT is developing improved screening systems in pearl millet to evaluate tolerance or resistance to witchweed [*Striga hermonthica* (Del.) Benth], head miner (*Heliocheilus albipunctella* de Joannis), stem borer (*Coniesta ignefusalis* Hampson), and several other biotic constraints. Pearl millet germplasm evaluation has identified sources of increased grain yield potential, cytogenic male-sterile systems (Hanna, 1990, 1993), disease resistance to rust (*Puccinia* sp.) and *Pyricularia* leaf blast (Hanna and Burton, 1987; Singh, 1990; Wilson and Hanna, 1992), and apomixis in several species and wild relatives (Hanna, 1995). Sources of resistance to important panicle diseases such as downy mildew [*Sclerospora graminicola* (Sacc.) Schroet], smut [*Moeziomyces penicillariae* (Bref.) Vanky] and ergot (*Claviceps fusiformis* Lov.) also have been identified (Thakur and King, 1988a, 1988b; Singh et al., 1993).

Table 1. Approximate number off accessions evaluated for abiotic and biotic stresses within the U.S. National Plant Germplasm System for sorghum (updated and modified from Duncan et al. 1995).

Characteristic	Causal organism	Approx. # of accessions evaluated	% of total collection
Al toxicity		8955	22.1
Mn toxicity		5910	14.6
Lodging		1186	2.9
Chinch bug	*Blissus leucopterus* (Say)	1000[†]	2.5
Fall Armyworm	*Spodoptera frugiperda* (J.E. Smith)	8503	21.0
Yellow sugarcane aphid	*Sipha flava* (Forbes)	5564	13.7
Greenbug (E, I)	*Schizaphis graminum* (Rondani)	19,000[†]	46.9
Midge	*Stenodiplosis sorghicola* (Coquillett)	10,000[†]	24.7
Head smut	*Sporisorium reilianum*	10,000[†]	24.7
Anthracnose	*Colletotrichum graminicola* (Cesati) Wilson	357	0.9
Striga	*S. Hermonthica, S. Asiatica, S. densiflora*	5000[†]	12.4
Downy mildew	*Peronosclerospora sorghi* (Weston & Uppal) C.G. Shaw	6214	15.4
Rust	*Puccinia purpurea* Cooke	877	2.2
Charcoal rot	*Macrophomina phaseolina* (Maulb.) Ashby	5000	12.4
Maize dwarf mosaic virus	Aphid-vectored Poty virus	500	1.2
Grain mold complex	*Fusarium, Curvularia, Aschocyta*	1000[1]	2.5

[1]These are approximations and totals are not currently available on GRIN.

Although these evaluations have identified several important sources of genes, assessment based on phenotypic variability is limited. It often is difficult to determine whether phenotypic variability is due to genetic or environmental effects, particularly when screenings are done only once at a single location. In contrast, molecular markers allow for assessment based on gene, genotype, and genome, and provide a more accurate and detailed outline of the genetic diversity within an accession. Molecular markers also provide a way to measure genetic variability in the absence of environmental influences. Markers must, however, be heritable, discriminate between accessions, populations, and taxa, easy (cost effective) to measure and evaluate, and provide reliable, repeatable results (Hillis and Moritz, 1990).

Future evaluations will require merging of traditional phenotypic screening with molecular markers to ensure a more complete and informative evaluation. One area in which merging of morphological and molecular data should be used is in designating core collections. Core collections are a subset of the total collection that can be effectively evaluated in times of particular need. Ideally they are rationalized, refined and structured around a small, well-defined and representative 'core' (Brown, 1988). Thus, a core represents the genetic diversity of a

crop and its relatives with minimal repetitiveness (Frankel, 1984). Development of core collections and the concept of their use has gained acceptance globally (Hodgkins et al., 1995; Knüpffer and van Hintum, 1995). Using geographic and taxonomic diversity and traditional evaluation, a representative core sorghum collection was set up at ICRISAT containing about 10% of the total collection (Prasada Rao and Ramanatha Rao, 1995). Using both traditional morphological evaluations and molecular markers, a more effective core subset can be developed which will optimize sources of genetic variation.

Utilization

Dudal (1976) points out that drought, shallow soil, and mineral deficiencies or toxicities account for 75% of the agricultural limitations from the soil (Table 2). Sorghum and millet have historically encountered higher levels of abiotic stress than other primary crops. They are primarily relegated to marginal land, accounting for roughly 80% yield loss in U.S. sorghum due to climatic/nutritional factors (Table 3, Kramer and Boyer, 1995). In the near future, sorghum and millet will remain the primary crops of poor soils and agricultural conditions. Therefore, utilization and improvement of yield stability will depend on increased research efforts on abiotic stress tolerance to drought, temperature, and adverse soil composition. Greater use of local landraces in crosses with agronomically elite material will be needed to combine higher grain yield with resistance/tolerance to locally important biotic and abiotic stresses (Andrews and Bramel-Cox, 1993). Improved selection methods of accessions that enhance combining ability for grain and biomass yield, along with better information on heterotic patterns between germplasm accessions is essential to increase sorghum and millet acreage worldwide.

Table 2. Area of total world land surface subject to environmental limitation of various types (Dudal, 1976).

Environmental limitation	Area of world soil subject to limitation (%)
Drought	27.9
Shallow soil	24.2
Mineral (excess vs. deficiency)	22.5
Flood	12.2
Miscellaneous	3.1
None	10.1
Total	100.0
Temperature*	14.8

*Note area affected by unfavorable temperatures overlaps with other classifications and is shown separately.

Breeders view utilization as the ability to place a specific gene(s) or special trait(s) in adapted cultivars. Utilization encompasses the capability to move identified genes into superior lines or cultivars that provide farmers with improved yield, disease resistance, tolerance to abiotic and biotic stress, and improved quality. Traditional breeding programs will continue to benefit from rapid identification and insertion of genes into elite material. Biotechnology offers many tools by which this process may be enhanced. Transgenic plants offer the potential for fast genetic solutions to serious problems. Insertion of Bt genes, incompatibility genes to prevent outcrossing with Johnsongrass (*Sorghum halepense*), and protein genes to enhance the nutritional value of sorghum and millet are just some of the examples in which both crops could benefit from biotechnology and genetic

Table 3. Record yields, average yields, and yield losses for major U.S. Crops in kg ha^{-1} (Kramer and Boyer, 1995).

Crop	Record yield	Average yield	Average losses			
			Disease	Insect	Weeds	Climatic/nutritional
Maize	19,300	4,600	836	836	697	12,300
Wheat	14,500	1,880	387	166	332	11,700
Soybean	7,390	1,610	342	73	415	4,950
Sorghum	20,100	2,830	369	369	533	16,000
Oat	10,600	1,720	623	119	504	7,630
Barley	11,400	2,050	416	149	356	8,430
Potato	94,100	28,200	8,370	6,170	1,322	50,000
Sugar beet	121,000	52,600	10,650	7,990	5,330	54,400
Mean % of record yield	100.0	21.5	5.1	3.0	3.5	66.9

transformation (Bennetzen, 1995; Kononowicz et al., 1995). Marker-assisted selection (Lande, 1992; Oh et al., 1994) could potentially halve the development time of improved cultivars and greatly assist the conversion of photoperiod-sensitive accessions to day-neutral forms.

Future Vision for Sorghum and Pearl Millet Genetic Resources Utilization

Without an effective, long-term curation strategy based on input from crop curators and other scientists, efficient use of germplasm resources currently available will continue to be limited. Plant breeders will continue to make use of genetic resources as a pool from which to identify specific sources of resistance to diseases, insects, and parasitic weeds. Curatorial needs will be broader: identity — the determination that an accession is catalogued correctly, is true to type, and maintained properly; relationships—the degree of relatedness to individual accessions or groups of accessions within a collection; structure — the partitioning of variation among individuals, accessions, populations, and species; and location — the presence of a desired gene or gene complex in a specific accession, as well as the mapped site of a desired DNA sequence on a particular chromosome in an individual or cloned DNA segment. The greater utilization of both sorghum and millet germplasm can be realized only through a strategic, forward looking plan that integrates the roles of scientists, breeders, and curators with traditional and biotechnological tools. Such a plan will provide a more complete and thorough understanding of available accessions in our collections and future acquisitions.

Sorghum and millet genetic resource utilization, as defined by curators and overseers of international and national collections, involves the integration of several disciplines. Curators strive to provide collections that are of the greatest use for scientists throughout the world. This encompasses the integration of acquisition, maintenance, evaluation and characterization, and utilization. Curators must provide collections that are easily accessible and readily available, with current and thorough information. They must strive to increase utilization of millet and sorghum germplasm through enhanced

scientific and management strategies. This integration can be accomplished through strategic planning of traditional methods of curation, such as field evaluations, data acquisition, and maintenance, with the integration of biotechnology. Core subsets for each crop will be an important part of this service. Integration of these technologies will fundamentally change how we utilize large collections by identifying new and useful genes and transferring these genes into superior, adapted cultivars.

Acknowledgment

The authors would like to thank Dr. Keith Schertz for his contribution to the genetic stocks section and Dr. K. E. Prasada Rao for his helpful suggestions on the manuscript.

References

Andrews, D.J., and K. Anand Kumar. 1996. Use of the West African pearl millet landrace Iniadi in cultivar development. Plant Genetic Resources Newsl. 105:15-22.

Andrews, D. J., and P.J. Bramel-Cox. 1993. Breeding cultivars for sustainable crop production in low input dryland agriculture in the tropics. p. 211-223. *In* International Crop Science I. CSSA, Madison, WI, USA.

Bennetzen, J.L. 1995. Biotechnology for sorghum improvement. African Crop Sci. J. 3:161-170.

Brown, A.H.D. 1988. Core collections: A practical approach to genetic resources management. CSIRO, Div. Plant Industry, Canberra, Australia.

Burton, G.W. 1951. The adaptability and breeding of suitable grasses for the Southeastern States. Adv. Agron. 3:197-241.

Burton, G.W. 1979. Handling cross-pollinated germplasm efficiently. Crop Sci. 19:685-690.

Burton, G.W. 1995. History of hybrid development in pearl millet in Tifton. p. 5-8. *In* I.D. Teare (ed.) Proceedings of first national grain pearl millet symposium, Tifton, GA, USA.

Callery, B.G. 1995. Collecting collections: Building the library of The New York Botanical Garden. Brittonia. 47:44-56.

Committee on Managing Global Genetic Resources: Agricultural Imperatives, Nat. Acad. Sci.1991. Managing global genetic resources: The U.S. national plant germplasm system. National Academy Press, Washington, D.C.

Crossa, J., S. Taba, S.A. Eberhart, P. Bretting, and R. Vencovsky. 1994. Practical considerations for maintaining germplasm in maize. TAG 89:89-95.

Dahlberg, J.A. 1995. Operations handbook for sorghum germplasm maintenance. ARS Special Publication, Beltsville, MD, USA.

Dahlberg, J.A., and M.S. Spinks. 1995. Current status of the U.S. sorghum germplasm collection. Int'l Sorghum and Millets Newsl. 36:4-12.

Dessauer, H.C., C.J. Cole, and M.S. Hafner. 1990. Collection and storage of tissues. p. 25-41. *In* D.M. Hillis and C. Moritz (eds.) Molecular systematics. Sinauer Associates, Inc., Sunderland, Massachusetts.

Doggett, H. 1988. Sorghum. John Wiley & Sons, Inc., New York.

Dudal, R. 1976. Inventory of the major soils of the world with special reference to mineral stress hazard. p. 314. *In* M.J. Wright (ed.) Plant adaptation to mineral stress in problem soils. Cornell Univ. Ag. Exp. Stat., Ithaca, NY.

Duncan, R.R., and J.A. Dahlberg. 1993. Cross-reference of PI/IS/SC numbers from the U. S. conversion program. Sorghum Newsl. 34:72-80.

Duncan, R.R., P.J. Bramel-Cox, and F.R. Miller. 1991. Contributions of introduced sorghum germplasm to hybrid development in the USA. p. 69-102. *In* H. L. Shands and L. E. Wiesner (eds.) Use of plant introductions in cultivar development: Part 1. CSSA Spec. Publ. No. 17., CSSA, Madison, WI.

Duncan, R.R., J.A. Dahlberg, and M. Spinks. 1995. International activities in sorghum germplasm acquisition during the past thirty-five years. p. 117-134. *In* R.R. Duncan, D.M. Kral, and M.K. Viney (eds.) International germplasm transfer: Past and present. CSSA Spec. Publ. No. 23., CSSA, Madison, WI.

Food and Agriculture Organization of the United Nations. 1996. WAICENT. FAOSTAT Database. FAO, Rome, Italy (http://www.fao.org/WAICENT/waicent.htm).

Frankel, O.H. 1984. Genetic perspectives of germplasm conservation. p. 161-170. *In* W. Arber, K. Llimensee, W.J. Peacock, and P. Starlinger (eds.) Genetic manipulation: Impact on man and society. Cambridge Univ. Press, Cambridge, England.

Hanna, W.W. 1990. Transfer of germplasm from the secondary to the primary gene pool in *Pennisetum*. TAG 80:200-204.

Hanna, W.W. 1993. Registration of pearl millet parental lines Tift 8677 and A_1/B_1 Tift $90D_2$ E_1. Crop Sci. 33:1119.

Hanna, W.W. 1995. Use of apomixis in cultivar development. Advances in Agronomy 54:333-350.

Hanna, W.W., and G.W. Burton. 1987. Registration of pearl millet inbred parental lines, Tift $85D_2A_1$ and Tift $85D_2B_1$. Crop Sci. 27:1324-1325.

Hanna, W.W., and G. Lovell. 1995. *Pennisetum* germplasm in USA. Int'l Sorghum and Millets Newsl. 36:1-3.

Hawks, C.A. 1990. Recent advances in the conservation of natural science collections. p. 53- 60. *In* E.M. Herholdt (ed.) Natural history collections: Their management and value. Spec. Publ. No. 1. Transvaal Museum, Pretoria, S. Africa.

Hicks, A.J., and P.M. Hicks. 1978. A selected bibliography of plant collection and herbarium curation. Taxon. 27:63-99.

Hillis, D.M., and C. Moritz. 1990. Molecular systematics, Sinauer Associates, Inc., Sunderland, MA.

Hodgkin, T., A.H D. Brown, Th.J.L. van Hintum, and E.A.V. Morales. 1995. Core collection of plant genetic resources. IBPGRI, Sayce Publ. and John Wiley and Sons, Chichester.

Howie, F.M.P. 1986. Conserving natural history collections: Some present problems and strategies for the future. p. 1-6. *In* J. Waddington and D. M. Rudkin (eds.) Proc. 1985 workshop on care and maintenance of natural history collections. Life Sci. Misc. Publ., Royal Ontario Museum, Canada.

Huenneke, L.F., K. Holsinger, and M.E. Palmer. 1992. Plant population biology and the management of viable plant populations. *In* P. Kapoor-Vijay and J. White (eds.) Conservation biology: A training manual for biological diversity and genetic resources. Commonwealth Secretariat.

IBPGR and ICRISAT. 1993. Descriptors for sorghum [*Sorghum bicolor* (L.) Moench]. International Board for Plant Genetic Resources, Rome, Italy; International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Jones, M.D. and J.B. Sieglinger. 1951. Effect of wind direction on natural crossing in sorghum *Sorghum vulgare* Pers. Agron. J. 43:571-572.

Kapoor-Vijay, P., and J. White (eds.). 1992. Conservation biology: A training manual for biological diversity and genetic resources. Commonwealth Secretariat.

Kramer, P.J., and J.S. Boyer. 1995. Water relations of plants and soils. Academic Press, New York.

Knüpffer, H., and Th.J.L. van Hintum. 1995. The Barley Core Collection—An international effort. p. 171-178. *In* T. Hodgkin, A. H. D. Brown, Th. J. L. van Hintum, and E. A. V. Morales (eds.) Core collection of plant genetic resources. IBPGRI, Sayce Publ. and John Wiley and Sons, Chichester.

Kononowicz, A.K., A.M. Casas, D.T. Tomes, R.A. Bressan, and P.M. Hasegawa. 1995. New vistas are opened for sorghum improvement by genetic transformation. African Crop Sci. J. 3:171-180.

Lande, R. 1992. Marker-assisted selection in relation to traditional methods of plant breeding. p. 437-451. *In* H.T. Stalker and J.P. Murphy (eds.) Plant breeding in the 1990s. C.A.B. Int'l., Wallingford, U. K.

Lawrence, P., and J. Corfield. 1995. Collecting Australian indigenous sorghums. Int'l Sorghum and Millets Newsl. 36:14-15.

Lawrence, P., and M. Rettke. 1995. Sorghum germplasm in Australia. Int'l Sorghum and Millets Newsl. 36:13-14.

Marchais, L., and J. Pernes. 1985. Genetic divergence between wild and cultivated pearl millets (*Pennisetum typhoides*). I. Male sterility. Zeitschrift fhr Pflanzenzhchtung. 95:103-112.

Miller, F. R., and Y. Kebede. 1984. Genetic contributions to yield gains in sorghum, 1950 to 1980. p. 1–14. *In* W.R. Fehr (ed.) Genetic contributions to yield gains of five major crop plants. CSSA Spec. Publ. No. 7., CSSA, ASA, Madison, W.I.

Nwanze, K.F., N. Seetharama, H.C. Sharma, and J.W. Stenhouse. 1995. Biotechnology in pest management: Improving resistance in sorghum to insect pests. African Crop Sci. J. 2:209-215.

Oh, B.J., R.A. Frederiksen, and C.W. Magill. 1994. Identification of molecular markers linked to head smut resistance gene (Shs) in sorghum by RFLP and RAPD analyses. Genetics 84:830-833.

Oliveira, A.C., T. Richter, and J.L. Bennetzen. 1996. Regional and racial specificities in sorghum germplasm assessed with DNA markers. Genome 39:579-587.

Prasada Rao, K.E, and V. Ramanatha Rao. 1995. The use of characterization data in developing a core collection of sorghum. p. 109-115. *In* T. Hodgkin, A.H.D. Brown, Th.J.L. van Hintum, and E.A.V. Morales (eds.) Core collections of plant genetic resources. Int'l Plant Genetic Resources Institute, Sayce Publ. and John Wiley and Sons, Chichester, England

Prasada Rao, K.E., V. Gopal Reddy, and J.W. Stenhouse. 1995. Sorghum genetic resources at ICRISAT Asia Center. Int'l Sorghum and Millets Newsl. 36:15-19.

Prasada Rao, K.E., M.E. Mengesha, and V. Gopal Reddy. 1989. International use of sorghum germplasm collection. p. 49-67. *In* A.D.H. Brown, O.H. Frankel, D.R. Marshall, and J.T.

Williams (eds.) The use of plant genetic resources. Cambridge University Press, Cambridge, England.

Rai, K.N., S. Appa Rao, and K.N. Reddy. 1997. Pearl millet. Chapter 18 in Diversity in trust: Conservation and use of plant genetic resources in CGIAR centers. CGIAR/Cambridge University Press.

Roberts, E. H. 1992. Physiological aspects of *ex situ* seed conservation. p. 171-177. *In* P. Kapoor-Vijay and J. White (eds.) Conservation biology: A training manual for biological diversity and genetic resources. Commonwealth Secretariat.

Rosenow, D.T., J.A. Dahlberg, G.C. Peterson, L.E. Clark, A. Sotomayor-R'os, F.R. Miller, A.J. Hamburger, P. Madera-Torres, A. Quiles-Belen, and C.A. Woodfin. Release of 50 converted sorghum lines and 253 partially converted sorghum bulks. Int'l Sorghum and Millets Newsl. 36:19-31.

Singh, S.D. 1990. Sources of resistance to downy mildew and rust in pearl millet. Plant Disease 74:871 – 874.

Singh, S.D., S.B. King, and J. Werder. 1993. Downy mildew disease of pearl millet. Information Bulletin no. 37. Patancheru A. P. 502 324, India: International Crops Research Institute for the Semi-Arid Tropics.

Snaydon, R.W. 1992. Sampling plant populations for genetic conservation. p. 87-92. *In* P. Kapoor-Vijay and J. White (eds.) Conservation biology: A training manual for biological diversity and genetic resources. Commonwealth Secretariat.

Spongberg, S.A. 1984. The value of herbaria for horticulture and the curation of living collections. Longwood Program Seminar. 16:33-38.

Texas Agricultural Experiment Station (TAES) and United States Department of Agriculture, Agricultural Research Service (USDA-ARS). 1996. Release of converted exotic lines from the world sorghum collection.

Thakur, R.P., and S.B. King. 1988a. Ergot disease of pearl millet. Information Bulletin no. 24. Patancheru A.P. 502 324, India: International Crops Research Institute for the Semi-Arid Tropics.

Thakur, R.P., and S.B. King. 1988b. Smut disease of pearl millet. Information Bulletin no. 25. Patancheru A.P. 502 324, India: International Crops Research Institute for the Semi-Arid Tropics.

The Tomato Genetics Stock Center Task Force. 1988. Evaluation of the University of California tomato genetics stock center: Recommendations for its long-term management, funding, and facilities. Genetic Resources Conservation Program, University of California, Davis, CA 95616, U.S.

Usher, M.B. 1992. Quantitative aspects of the collection and analysis of inventory data. p. 71-86. *In* P. Kapoor-Vijay and J. White (eds.) Conservation biology: A training manual for biological diversity and genetic resources. Commonwealth Secretariat.

Webster's New Collegiate Dictionary. 1979. G&C Merriam Co., USA.

Wenzel, W. G. 1995. The South African sorghum germplasm collection. Int'l Sorghum and Millets Newsl. 36: 12-13.

Wilson, J.P., and W.W. Hanna. 1992. Disease resistance in wild *Pennisetum* species. Plant Disease 76:1171-1175.

Discussion

Session II - Genetic Resources
Session Chair - Bhola Nath Verma
Rapporteurs - Yu Li and Kay Porter

Abdelmoneim B. El Ahmadi - I would like to point out that characterization of sorghums with respect to simply inherited characters especially those associated with grain quality such as the B_1, B_2, spreader genes, etc., i.e., which varieties have what genes is very important in countries where sorghum is used as food for humans.

Steve Eberhart - A very good point, and breeder must give priority to these traits when breeding sorghum cultivars for use as food.

Fred Miller - Please define "Core Collection" concept.

Steve Eberhart - The written version has a full definition with references.

Ndjekounkosse Djool Yagoua - What are the possibilities for *in situ* preservation? Because we are talking about *ex situ* preservation and there are limitations to that: cultivars do not evolve with the change of environment.

Steve Eberhart - Genetic changes occur in much more time than the time of *ex situ* conservation. Conservation *in situ* costs more than conservation *ex situ*. Evolution requires centuries *in situ* for much diversity to occur. Modern plant breeding is much more efficient. *In situ* conservation is very difficult to manage and often very expensive to make it effective.

Ranajit Bandyopadhyay - During the eighties, a lot of effort was put into screening sorghum germplasm to identify sources of resistance to biotic stresses such as downy mildew, grain mold, anthracnose, midge, shootfly, etc. Several sources of resistance have been identified and are utilized by breeders. Future need lies in characterizing the resistance genes in the sources to find if they are similar or dissimilar.

J.A. Dahlberg - Work needs to continue in evaluation and characterization, however, this work needs to be better focused on characterization of these genes that are identified, primarily on a molecular basis. Molecular tools will provide a tool by which we can identify similar or dissimilar alleles which will assist in greater utilization of these identified genes.

Fred Rattunde - What research is being conducted on the use of molecular tools for characterization of genetic resources? Also, with such large collections, how can these techniques be applied to the entire collection.

J.A. Dahlberg - Several groups are working on the development of RAPD and SSR markers for use in evaluating genetic diversity. Groups within the USDA, Purdue University, and Texas A&M are all evaluating molecular tools for use in genetic identification and diversity. The primary limiting factor to the use of these tools is DNA extraction, however, several groups are currently working on creating more efficient techniques for DNA extraction and in the near future, they will not be a major factor in using these markers.

Session III

Yield and Adaptation Breeding

Session Chair: Wayne Hanna

Rapporteurs: Ouendeba Botorou and James Osborne

Speakers

F.R. Miller
F. Gomez
K.N. Rai
L.R. House
O.P. Govila
A.B. Obilana
B.S. Rana

Breeding Photoperiod Insensitive Sorghums for Adaptation and Yield

Fred Miller*, Neil Muller, Roger Monk,
D. S. Murty, and A. Babatunde Obilana

Abstract

Photoperiod insensitivity in Sorghum bicolor *(L.) Moench has allowed the breeding and development of cultivars to fit defined target environments. By removing confounding variation created by photoperiod sensitivity, yield and its stability could be enhanced through critical selection of yield components. Maturity genes Ma1 and the Ma5/*Ma6 *interaction are responsible for the bulk of the sensitivity to photoperiod. Other biochemical reactions are driven by temperature and influence adaptation. As an adaptive trait, manipulation of maturity has provided highest yields in widely different regions of the world, i.e., early sorghums in drought-prone or short-duration seasons vs. late-maturing sorghums in well-watered, longer duration seasons. Once photoperiod insensitivity is established, responses to biotic and abiotic stresses are exposed. Solutions can be devised that target each of the stresses. Furthermore, research can be focused in areas of physiologic growth and development when the overwhelming impact of photoperiod response has been removed. Photoperiod insensitivity has allowed for continuous improvement of yield and adaptation in sorghum.*

Adaptation is the measure of a cultivar's ability to survive in and respond to a defined target environment. The ability of the cultivar to maintain high production depends on the degree and range of its adaptive traits, which allow continued growth and production in the presence of stresses. The achievement of adaptation can be expressed via mechanisms such as escape, tolerance, and resistance. Other adaptation responses include avoidance traits (such as early maturity/late maturity) and resistance traits and tolerance characteristics, which may be physiologic and/or physiochemical. Resistance traits are usually genetic, while avoidance traits are environmental/genetic.

Adaptation can be manifested in different ways (e.g., wide/ narrow or broad/specific). Breeders often relate adaptation to other disciplines. For example, specific adaptation can be described as vertical resistance, whereas broad adaptation can be described as horizontal resistance, tolerance, or avoidance. The following discussion will attempt to characterize and summarize some traits that affect adaptation.

Yield

Economic yield is the production of economically desirable plant parts per unit area (e.g., seeds, grains, forage, oil,

Fred Miller, M.M.R. Genetics, 6417 Zak Road, Bryan, TX 77808; Neil Muller, Pacific Seeds (Australia); Roger Monk, Pioneer Hi-Bred International (U.S.); D.S. Murty, ICRISAT (Mali); A. Babatunde Obilana, ICRISAT (Zimbabwe). *Corresponding author.

temperatures of the plains promote more rapid growth and development.

Second, the characteristic of tropical vs. temperate adaptation is basically a temperature response. Sorghum planted at Weslaco, Texas, on March 1 grows under cool soil and environmental conditions early in GS 1. Afterward, day and night temperatures increase rapidly throughout the life of the plant. In contrast, at Halfway, Texas, seeding occurs in warm soils and cool nights. By GS 2, daytime temperatures increase, but nighttime temperatures begin to drop. GS 3 is characterized by warm days and cool nights. Yields are significantly higher in this latter situation. However, there are differences between cultivars, and these differences have been used to separate more tropical and temperate adaptive types.

Maturity

Maturity differences in sorghum have been previously described by Quinby (1974). These differences are associated with four specific genes and the allelic series at each. Breeders working with photoperiod-insensitive sorghum quickly learn that some maturity genes form only the template within an acceptable range of production. The relationship of later maturity and higher yield is well-established. However, lateness in itself does not allow growers to obtain maximum yield. Breeders have established limits of environments and/or climatic regions within which a range of maturity will, over time, produce the largest consistent yield. These broad ranges of maturity are for early, medium, and full season hybrids. It is not appropriate to describe a range of days to anthesis to universally classify these types, since each major production region is different from the others. For example, an early sorghum in Argentina takes at least 10 days longer to reach maturity than an early sorghum in North or South Dakota (U.S.)

Manipulation of maturity as an adaptive trait has provided for higher and more stable yields in many areas. For example, high-yielding environments in Australia are limited, and the largest sorghum production areas have lower rainfall, higher temperatures, and poor moisture-holding capacity soils. In these areas, utilization of early and medium-early hybrids has been very effective to prevent moisture stress in GS 3. With the identification of non-senescence and other drought-related traits, there is a slow shift toward slightly later hybrids with higher yield (i.e., medium-early to medium maturity hybrids). The same situation describes the types of hybrid/variety maturities in PS 13 - 19 zones used by ICRISAT and the hybrid industry in the U.S. In the early 1970s the coastal plains of south Texas grew primarily medium-early hybrids; however, today only medium maturing hybrids are grown in the area. Some growers are even using near-full season hybrids to obtain highest yields, even though their input costs may increase.

To summarize, growers tend to use hybrids that mature as late as environmental conditions permit in order to maximize yields. It then becomes the responsibility of breeders to include in yield-maximizing hybrids those adaptive traits that increase stability. Disease and insect resistance, lodging resistance, and harvest traits must be part of the package as ma-

turity pushes the outer edges of production conditions and zones.

Drought and Other Abiotic Stresses

Drought remains the single most important threat to food security, especially in areas where sorghum and pearl millet are cultivated. Drought manifests itself in different forms, in different places, at different times in the growing season. Its periodic nature, therefore, makes it a significant factor in any strategy for genetic crop improvement.

In photoperiod-insensitive sorghum, the three main mechanisms for response to drought must be considered at the onset of a breeding program: escape, tolerance, and resistance. These and other physiologic responses to abiotic stresses enhance the stability of production in adaptive breeding programs. Some of those abiotic stresses include:

- Drought - escape and tolerance mechanisms/phenologic targets
- Temperature - (cold) emergence and early stage growth; (heat) blasting; evapotranspiration; desiccation
- pH soils - (high) iron chlorosis and nutrient use; (low) microflora interactions/nutrient release and utilization/toxicities
- Fertility - (low) nutrient availability

Biotic Stresses

Sorghum is host to a large number of insects and diseases that attack the seed, roots, stems, leaves, panicles, and grain. One or more of these in any one season can have a disastrous effect on final harvest yield. Fortunately, all are not present in every environmental situation. Germplasm resources have been exploited to incorporate resistance or tolerance to many of these economically important biotic stresses. Every hybrid or cultivar need not have every resistance to every disease or insect to be of benefit. Breeding for those biotic constraints in targeted production zones increases both the time to release of superior materials as well as the ability to concentrate on "next-limiting" traits.

Working with photoperiod-insensitive sorghum, it is essential to understand the genetics of insect and disease organisms. As we recognize the role of integrated pest management (IPM), the deployment of resistance genes must be fully understood. We cannot afford to carelessly spend a gene if we have alternative controls available. It is important to work closely with other professionals to protect the crop's productivity, the environment, and germplasm resources.

Growth and Development

The analysis of growth and development of photoperiod-insensitive sorghum is extremely important. The harvest index (ratio of total plant weight/grain weight) must be critically balanced. As panicle size, kernel number, and kernel size are viewed with regard to photosynthetic capacity, leaf area, green leaf area retention, and nonsenescence become important. Leaf area alone (in some types of hybrids) may not be as important to the production of grain as is the total leaf area available to intercept light. The greater the light interception, the higher the photosynthetic capacity (which may be affected by

genetic control mechanisms), leading to increased carbohydrate accumulation and opportunity to maximize grain yield. On the other hand, greater leaf area in later maturing cultivars leads to increased carbohydrate production over a longer period, and greater yield potential.

Retention of effective photosynthetic leaf area is essential for continued carbohydrate accumulation and maximization of yield. Adaptive breeding programs, therefore, must address senescence traits (pre- and post-flowering) and cultivar reaction to omnipresent leaf diseases, both of which reduce effective leaf area.

It is not possible in this paper to fully explore all ramifications of nonsenescence. Therefore, we address some of the broad aspects of nonsenescence in progressive breeding programs. Lodging is associated with severe moisture stress in GS 3 in a fairly large portion of the sorghum production areas of Australia, the United States, Argentina, and South Africa. Cultivars that maintain green leaf area, healthy green stems, and green panicles until maturity will have increased adaptation and yield. Although pre-flowering stress resistance is important in pre-yield formation, post-flowering stress resistance is more important, since it aims not only at lodging resistance but also at maximizing yield in stressful environments.

Highly senescent types of sorghum under moisture deficit situations mobilize carbohydrates from lower leaves and stems to the developing grain. These types sacrifice basic plant well-being to insure grain fill, in effect committing "physiological suicide." In situations like this, even moderate levels of nonsenescence can play a major role in reducing lodging and increasing harvestable yield. Other traits such as osmotic adjustment, water use efficiency, and nutrient use efficiency are most likely actively involved. These traits are more difficult to select for, except as they are expressed in stability of performance.

The incorporation of high levels of nonsenescence can lead to undesirable side effects, such as delayed maturity under stress, increased nodal and basal tillering, and some loss of yield. Control of apical dominance has been found and is easily manipulated to control tillering problems. Moderation seems to be the key to the usefulness of the nonsenescence traits in adaptive breeding.

High and useful levels of nonsenescence, which are now available, offer a great opportunity to improve both potential and harvestable yield by the development of later maturing hybrids for areas where early maturity has been traditionally used as a drought avoidance mechanism.

Physiological Parameters

Yield of grain is the final product of the factory (sorghum plant) that we have built. Significant progress has been made in characterizing the traits visible above the soil line that affect yield, but the root system has received little attention. We know there are different types of root systems — deep rooting, shallow rooting, sparsely branched, and profusely branched — but we need to know much more about how root systems function,

their role in lodging resistance, and the potential of genetic manipulation.

Likewise, only limited information is available to describe the genetic and physiologic systems operating within the plant. Some information is available on differences in photosynthetic rates, but it does not reflect whole plant or whole-plant-in-field values. Indirect yield measurements are the best estimates we have to use in adaptive change. Some cultivars store sucrose in much higher concentrations in leaves and stems than others. What controls feedback mechanisms? Why are caryopses allowed to reach only certain size? What are phloem flow rates and what controls those rates? What controls loading and unloading of the photosynthate transport system? How can breeders select for successive "bottle necks" in the photosynthate system? There is a great need for physiologic information that breeding programs can use to improve productivity.

In 1986, at the First Australian Sorghum Conference, this question was asked: " How do we raise the yield plateau without putting all our efforts into 'fire fighting'?" We offer these comments. Sorghum breeders are not just "fire fighting" in identifying, developing, and utilizing adaptive traits. Every breeder wants to improve productivity. The use of adaptive trait breeding has been successful in achieving a stable and productive commodity. The identification and utilization of such traits as nonsenescence, control of apical dominance, greenbug and midge resistance, lodging resistance, tillering control, resistance to downy mildew, head smut, foliar, and other diseases, have led to further improvement in yield and yield stability in many sorghum production areas.

Figures 1 and 2 offer a visual perspective of the sum of adaptation and its impact upon yield and stability of sorghum. The yield plateau of sorghum has been raised significantly by the identification, development, and use of sound and environmentally friendly adaptive traits.

References

Quinby, J.R. 1974. Sorghum improvement and the genetics of growth. Texas A&M University Press, College Station, Texas

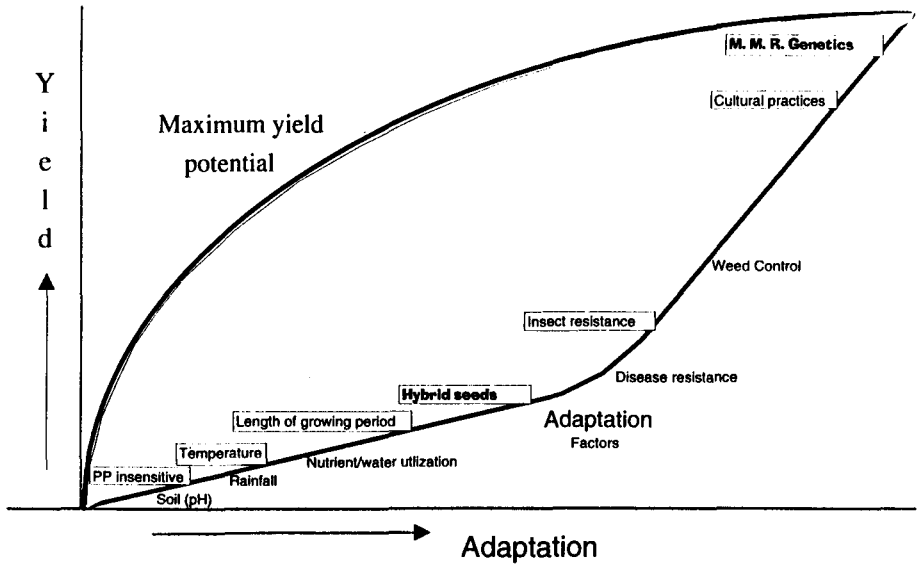


Figure 1. Yield potential of photoperiod-insensitive cultivars and constraints to reaching full potential.

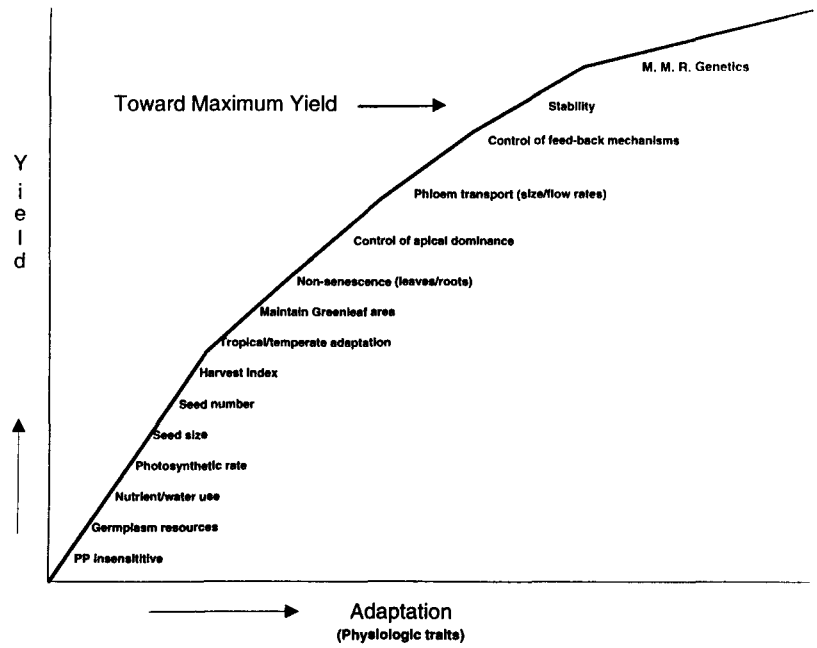


Figure 2. Progressive steps necessary to maximizing yield in an adaptive trait breeding program (physiologic traits).

Breeding Photoperiod Sensitive Sorghums

F. Gómez* and J. Chanterau

Abstract

Physiological mechanisms in the sorghum flowering system are capable of sensing differences in daylength. Sorghum breeders have recently started to manipulate this characteristic to develop specific maturity genotypes. In tropical regions of Africa and Central America, farmers have informally selected sorghum with specific daylength requirements that match local environmental conditions to ensure grain production. Daylength requirements for different sorghum genotypes have been determined and studied from several disciplines. Conventional breeding methodology and efforts from several institutions such us INTSORMIL and ICRISAT have been rewarding. New combinations of local and exotic enhanced germplasm have been developed that maximize grain and biomass production.

Dwarf Maicillos Varieties (DMVs) are new sorghum genetic combinations bred in Central America, that express an outstanding adaptation to the local sorghum-maicillos agroecosystem, superior yield potential, defensive capacity and grain quality. These DMVs also show a substantial variability in height and response to photoperiod, indicating perhaps new allelic combinations or new maturity loci involved. Some superior DMVs have been extensively tested in farmers' fields, where they have outyielded the original maicillos ecotypes. Further studies on the nature of the photoperiod response shall be supported to custom tailor sorghum genotypes for tropical environments.

The initiation of flowering in many tropical crops is sensitive to daylength or photoperiod (Norman, et al., 1984). Sorghum [*Sorghum bicolor* (L.) Moench] was classified as a short-day species by Garner and Allard as early as 1923. Physiological mechanisms in the sorghum flowering system are capable of sensing differences in daylength from the time of sunrise to sunset. Daylength is 12.1 hours throughout the year at the equator, and ranges from 10.6 to 13.7 hours at 25° latitude and from 8.7 to 15.7 hours at 45° latitude (Norman et al., 1984).

In tropical regions, farmers have informally selected sorghum with specific daylength requirements that match local environmental conditions to ensure grain production. In West Africa, for example, informal selection by farmers for daylength sensitivity has resulted in sorghum that matures as available soil water is exhausted in the early part of the dry season, thereby ensuring that the crop fully utilizes the growing season while avoiding diseases associated with high humidity during grain maturation.

F. Gomez, Escuela Agricola Panamericana, P.O. Box 93, Tegucigalpa, Honduras and J. Chanterau, ICRISAT/CIRAD, Bamako, Mali. *Corresponding author.

Similar outcomes have been achieved by Central American farmers where sorghum is a newcomer. Around 200 years ago, sorghum varieties sensitive to photoperiod were introduced from Africa to an area exhibiting distinctive climatological conditions, such as a bimodal rainfall pattern. There, sorghum readily adapted to local farming practices. Continuous selection by farmers has produced a unique group of sorghum, colloquially named *maicillos* or little corn. Acute photoperiod sensitivity was a key characteristic that enabled maicillos to become intercropped with early maize landraces.

Quinby (1974) described the genetic response of sorghum to daylength for flower initiation. Four maturity genes, designated Ma1, Ma2, Ma3, and Ma4, were found to control sensitivity to daylength. Recent studies point to the possibility that floral initiation in sorghum is controlled by more than four genes. Aydin and Rooney (personal communication) presented data on the inheritance of two new maturity genes in crosses of an Argentinian line derivative, 90T190, and Tx430. The authors have designated these new maturity genes as Ma5 and Ma6. Chanterau and collaborators (personal communication) are evaluating crosses between the landrace Guinea 1075 and IS 2807. A frequency distribution of F5 progenies also suggests that the genetic control of photoperiodism in these lines could involve more than the classical maturity genes.

These findings enable tropical plant breeders to tailor sorghum genotypes based on photoperiod requirements. As a result, breeders in temperate climates have developed sorghum cultivars with specific flowering requirements that fully exploit local daylength. Likewise in the tropics, attempts to breed for custom-tailored photoperiod-sensitive sorghum utilizing local ecotypes are under way.

Methodology

Sorghum scientists reponsible for manipulating tropical germplasm in the United States and India have explored many aspects of the photoperiod response in sorghums. Consequently, there is a significant understanding of the genetics, physiology, and breeding methodologies of photoperiod-sensitive sorghum.

Early genetic studies on sorghum flowering helped to establish the Sorghum Conversion Program (SCP), the foundation for bringing tropical germplasm to U.S. sorghum (Miller, 1979). Similar approaches have been utilized to a lesser extent by sorghum breeders in Central America and Africa to introduce elite temperate germplasm into tropical photosensitive sorghums.

A classic study of the effect of tropical photoperiods on the growth of sorghum was conducted by Miller et al. in 1968. They concluded that tropical sorghum has lower critical photoperiods than most U.S. sorghum when planted from January to July in Puerto Rico, but the same varieties nonetheless flower in about the same time when planted under daylength conditions of 12.2-11.3 hours (mid-September through mid-November).

Enhanced germplasm derived from crosses between elite exotic U.S. and Indian sorghum and tropical landraces has been developed in Central America and on several occasions in Africa. This germplasm contains the specific adaptation of landraces and superior alleles for yield, quality, and defensive capacity against biotic and abiotic stresses (Meckenstock et al., 1988). Conventional breeding schemes are used to introgress exotic germplasm into tropical sorghum. Pedigree methodology is the most common, but some population enhancement also has been attempted.

In 1981, Meckenstock (1991) began an ambitious breeding program while working in Honduras in collaboration with Central American and U.S. sorghum breeders. These efforts centered on enhancing the tall, photoperiod-sensitive, low-yielding white sorghum ecotype (maicillos) of Central America. Maicillos is a staple food of low income farmers in the hillsides of Central America. In this region, the cropping system (maize-sorghum) does not allow use of directly introduced photoperiod-insensitive sorghum cultivars. Improvement of maicillos must be made *in situ* due to its specific photoperiodic response (14° N) (Meckenstock, 1991).

In the early 1980s, crosses were made between selected maicillos and elite germplasm from Texas A&M and ICRISAT. At the same time, studies on photoperiodic response of several sorghum cultivars were conducted (Meckenstock, 1984). These studies concluded that maicillos is highly sensitive to photoperiod due to the presence of dominant alleles at the Ma1 and probably the Ma2 loci. These loci accounted for lateness in 100M and 90M growing in the tropical environments in Puerto Rico (Miller et al., 1968). 100M and 90M refer to the floral characteristics of milo genotypes described by Quinby (1972).

Segregant families of these crosses were subjected to several cycles of selection in multiple environments in subsequent years. Exposing these families to different biotic and abiotic stresses resulted in an ideal selection pressure to select a new enhanced photosensitive germplasm, combining excellent adaptation, better yield potential, and superior grain quality. In addition to maintaining the photoperiodic response, these segregant populations of enhanced maicillos are selected for short stature (2 and 3 dw), longer panicles and exsertion, and resistance to predominant pathogens causing diseases such as anthracnose, rust, gray leaf spot, downy mildew, and tan plant color (Gómez, 1995).

Results and Discussion

The germplasm developed in Central America has been named "Dwarf Maicillos Varieties" (DMV) because of its ancestors. Two hundred forty-one lines have been developed and are available as DMV-germplasm. These lines have been crossed among themselves to concentrate elite genes in new (maicillos × exotic) × (maicillos × exotic) germplasm. Table 1 presents yield data, days to bloom, and plant height of some elite DMV sorghum.

Based on plant height, four distinct groups of maicillos are identified. The MC group corresponds to the original

Table 1. Days to bloom, plant height (cm), and grain yield (kg ha^{-1}) of some photosensitive sorghum planted in Honduras (14° 5' N) on June 13, 1995, at 800 meters above sea level.

DMV	Grain/ plant color	Pedigree	Days to bloom	Plant	Grain yield kg ha^{-1}
219	whT/T	{[SPV346 (81LL691*Billy)]*(SC414*P.N.)}-25-3-4	143	177	2563
236	wh/T	{[(SC326-6*SC103-12)Liberal-40]*SC1207-2}-10-2-1-5-1	155	138	1935
228	whT/T	{[SPV346 (81LL691*Billy)]*(SC414*P.N.)}-41-1-2-2	144	165	1914
		Average	147	160	2138
137	whT/R	(TAM428*Porvenir)-29-2-3-b-b	140	228	4000
238	wh/R	[(Sepon 77*Santa Isabel)-6*ICSV-151}-6-2-1-2-4-1	145	217	3591
240	whT/P	[(Sepon 77*Santa Isabel)-6*ICSV-151}-6-2-1-2-4-8	142	213	3128
237	wh/T	[(Sepon 77*Santa Isabel)-6*ICSV-151}-6-2-1-2-1-1	143	218	3105
239	wh/T	[(Sepon 77*Santa Isabel)-6*ICSV-151}-6-2-1-2-4-4	145	210	3039
241	wh/T	{[(TAM428*77CS3)GPR148*Billy]-24*(SPV346(81LL691*Billy-7]-36}	148	222	2972
		Average	144	218	3306
179	whT/T	(SPV346*Gigante Pavana)-1-1-2	143	290	3780
221	wh/T	(Sureño*Caturra 68)-3-3-2-1	133	285	3580
198	wh/T	(TAM428*Porvenir)-29-1-1-b-b-1-b	142	267	3254
235	wh/T	[(TAM428*S.B.III)-17*(CS 3541*Lib)-6]-19-1-2	132	260	3057
213	whT/R	{[SPV346 (81LL691*Billy)]*(SC414*P.N.)}-7-1-b	146	247	2978
234	whT/T	[(TAM 428*S.B.III)-17*(CS 3541*Lib.)-6]-19-1-2	132	278	2957
210	whT/T	(TAM428*MC100)-2-2	140	278	2939
218	whT/R	{[SPV346 (81LL691*Billy)]*(SC414*P.N.)}-4-1-1	142	275	2557
		Average	139	273	3138
MC	wh/P	Peloton	149	388	3316
MC	wh/P	Porvenir	148	398	3247
MC	whT/P	San Bernardo III	142	397	3171
		Average	146	394	3248

MC = maicillos criollo DMV = Dwarf maicillos variety
wh=white, T=translucid pericarp, /P=purple plant color, /R=red plant color, /T=tan plant color

elite maicillos ecotype and averages 3.9 m in height (0 dw). The second group consists of DMVs averaging 2.7 m in plant height (1 dw). The third group includes DMV genotypes that average 2.2 m in height (2 dw), and the last group is composed DMVs that average 1.5 m in height (3 dw).

After several attempts to recover the daylength response from the original maicillos, these groups of enhanced maicillos exhibit photoperiod requirements similar to those of their maicillos counterparts. We have been able to recover genotypes with almost the same maturity as the maicillos (-3 days on the average).

Two elite lines that have exhibited outstanding performance and excellent combining ability are derivatives of crosses between the ICRISAT line SPV346 and the maicillos Gigante and between the U.S. line RTAM428 and the maicillos Porvenir. These lines are the first vehicles to introduce superior alleles for grain yield and quality into the maicillos population by means of natural introgression and farmers' selection.

On-farm data from these two enhanced DMVs show a substantial increase in grain yield (Table 2) under different technological levels. Data show that enhanced maicillos are capable of double grain production without sacrificing forage production due to reduction in plant height.

Table 2. Average yield of grain and forage of two enhanced maicillos cultivars grown at 59 locations in Honduras, 1993-1995.

Technological level	Grain yield kg ha^{-1}	Forage yield t ha^{-1}
Gigante Mejorado (DMV 179)		
Maicillos landrace	764	55
Enhanced maicillos	1056	54
Enhanced maicillos + soil insect control	2413	61
Enhanced maicillos + soil insect control + 60 k ha^{-1} of Nitrogen	2960	66
Porvenir Mejorado (DMV 197)		
Maicillos landrace	922	54
Enhanced maicillos	1396	
Enhanced maicillos + soil insect control	1510	
Enhanced maicillos + soil insect control + 60 k ha^{-1} of Nitrogen	2185	

New lines are continuosly being produced and deployed in farmers' fields with the objective of enhancing the local ecotypes and *in situ* conservation. Because we are mostly interested in lines that exhibit photoperiod response, until recently no attempt was made to select photoperiod insensitive lines. These efforts offer important new genetic combinations that can be utilized for developing photoperiod-insensitive tropical sorghum.

Conclusions

Breeding photosensitive sorghum for specific tropical environments offers opportunities to increase productivity, enhance grain quality, and maximize agricultural input utilization. Small farmers can benefit tremendously because no change in daylength requirements is needed; thus, there is no need to alter their cropping systems.

References

Chanterau, J., M. Ag Hamada, M.Diondel Maiga. 1996. Personal communication.

Garner, W.W., and H.A. Allard. 1923. Further studies on photoperiodism. The response of the plant to relative length of day and night. J. Agr. Res. 23:871-920.

Gomez, F. 1995. Tropical sorghum conservation and enhancement in Honduras and Central America. p. 135-145. *In* Sorghum/Millet Collaborative Research Support Program (CRSP) Annual Report 1995.

Meckenstock, D.H. 1991. Tropical sorghum conservation and enhancement in Honduras and Central America. *In* Sorghum/Millet Collaborative Research Support Program (CRSP) Annual Report 1991.

Meckenstock, D.H., A. Palma, and F. Gomez. 1988. Mejoramiento de sorgo en Honduras, 1987. *En* Memoria del VI Taller de la Comisión Latinoamericana de Investigadores en Sorgo "Uso de la Semilla Mejorada de Sorgo para los Agricultores de Mesoamerica." San Salvador, El Salvador, 6-9 de diciembre de 1988.

Meckenstock, D.H., G.C. Wall, and R. Nolasco. 1985. Aspectos de mejoramiento genético en la investigación sobre sistemas de cultivo en Honduras. p. 68-75. *In* C.L. Paul and B.R. DeWalt, (eds.). El sorgo en Sistemas de Producción en America Latina. Proc. Workshop INTSORMIL and CIMMYT, El Batán, Mex. Sep 16-22, 1984. Mexico, D.F..

Miller, F. 1979. Breeding of sorghum. p. 128-136. *In* Biology and Breeding Resistance to Arthropods and Pathogens in Agricultural Plants. College Station, Texas.

Miller, F. R., D.K. Barnes and H.J. Cruzado. 1968. Effect of tropical photoperiods on the growth of sorghum when grown in 12 monthly plantings. Crop Science 8:499-502.

Norman, M.J.T., C.J. Pearson, and P.G.E. Searle. 1984. The ecology of tropical food crops. Cambridge University Press, Cambridge.

Quinby, J.R. 1972. Influence on maturity genes on plant growth in sorghums. Crop Sci. 12:690-692.

Quinby, J.R. 1974. Sorghum improvement and the genetics of growth. Texas A&M University Press, College Station TX.

Breeding Pearl Millet for Grain Yield and Stability

K.N. Rai*, K. Anand Kumar, D.J. Andrews,
S.C. Gupta, and B. Ouendeba

Abstract

*Pearl millet [*Pennisetum glaucum *(L.) R. Br.] is traditionally grown in the arid to semi-arid tropical regions of the Indian subcontinent and Africa where sorghum and maize grain yields are low and unreliable due to drought and sandy soils of low fertility. Low harvest index (<20%) of landrace cultivars, combined with numerous biotic and abiotic constraints, results in low and unstable grain yields of pearl millet (500-600 kg ha^{-1}) in these environments. Breeding efforts addressing these constraints have taken into account their relative global and regional importance and probability of success. Thus, breeding for high grain yield potential has been accorded highest priority, followed by resistance to downy mildew. This strategy has resulted in impressive genetic gains and visible cultivar impacts in India, and just recently in Africa.*

For more rapid progress to occur in Africa, it is necessary to define clear research targets and foster effective inter-institutional research and development partnerships. Exploitation of the enormous genetic variability available in pearl millet germplasm, for both yield components and resistance to major diseases, will continue to be emphasized in cultivar development. Concentrated efforts are required to develop and validate effective screening techniques; to identify good sources of resistance/tolerance to drought, high soil temperatures at seedling emergence, Striga, *stem borer and head miner; and to understand the nature of their inheritance. The extent of integration of resistance to these constraints as selection criteria in breeding can then be examined. Opportunities exist for testing the utility and commercial viability of pearl millet top cross hybrids (made with and without CMS) and inter-population hybrids, in addition to open-pollinated varieties (OPVs) and CMS-based single-cross hybrids, and for realizing about 5 t ha^{-1} of grain yield in less than 90 days in intensive agriculture.*

Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important food grain cereal, grown annually on about 26 million ha in the arid to semi-arid tropical environments of Asia and Africa. Of the 12 million ha grown in Asia, the lion's share of about 10 million ha are found in India. Thirteen countries in western and central Africa grow this crop on 12 million ha, but five countries (Niger, Nigeria, Mali, Burkina Faso, and Senegal) account for 85% of the total area in this region. Sixteen countries in southern and eastern Africa grow pearl millet on about 2.5 million ha, with Sudan accounting for more than 50% of this area and Tanzania, Zimbabwe, and Angola together accounting for another 25%.

K.N. Rai and K. Anand Kumar, ICRISAT Asia Center (IAC), Patancheru 502 324, Andhra Pradesh, India; D.J. Andrews, Dept. of Agronomy, University of Nebraska, Lincoln, NE 68583-0915; S.C. Gupta, ICRISAT Western and Central Africa Region, PMB 3491, Kano, Nigeria; B. Ouendeba, RO-CAFREMI, ICRISAT Sahelian Center, BP 12404, Niamey, Niger. *Corresponding author.

Pearl millet is traditionally grown in low rainfall regions on sandy soils with low fertility where other coarse grain cereals such as sorghum and maize fail to give assured yields. The average grain yield of pearl millet in these environments is very low (500-600 kg ha^{-1}), although hybrid grain yields in excess of 5 t ha^{-1} with a harvest index of more than 40% have been obtained in India under optimal conditions (Rachie and Majmudar, 1980).

Pearl millet will continue to be a dominant cereal crop, mainly grown for grain production in the arid to semi-arid tropical environments of Asia and Africa. Therefore, this paper will largely address breeding for grain yield and stability in these environments. We shall present a comprehensive account of approaches followed in breeding high-yielding cultivars for high and stable grain production. We begin by describing production constraints and the rationale behind varying levels of integration of these approaches in the breeding programs, then illustrate the impact of these approaches with various categories of outputs. This paper draws heavily from, but is not limited to, the experience and research results of ICRISAT's and INTSORMIL's pearl millet breeding programs.

Pearl millet is a highly versatile and high quality cereal with great potential to become a valuable component of non-traditional agriculture. We shall briefly examine emerging opportunities for pearl millet cultivation under such systems.

Production Constraints and Breeding Priority

Several factors contribute to low grain yield and yield instability in pearl millet: a) low yield potential associated with the plant architecture of traditional landraces; b) biotic stresses such as diseases, insect pests, and a parasitic weed (*Striga* sp.); c) abiotic factors such as low soil fertility, heat, and drought; d) lack of management input; and e) policy factors that do not encourage labor and material investment in pearl millet production. The objective of this section is not to produce a detailed analysis of all factors that contribute to low grain yield and yield instability, but to briefly present an assessment and prioritization of those that can be addressed by breeding.

Plant Architecture

Pearl millet is a C_4 plant with highly efficient photosynthetic machinery and dry matter production ability. A study in northern Nigeria showed that a traditional open-pollinated variety maturing in 90 days produced dry biomass yield of 22 t ha^{-1} under low-resource farming conditions, but much of this was locked up in vegetative parts, leading to a low harvest index of 14.5% (Kassam and Kowal, 1975). Enormous genetic variability for yield components exists in the pearl millet germplasm (Table 1), but the natural character combinations in the landraces are largely unfavorable. For instance, large panicles are found in excessively tall and late-maturing backgrounds, while good-tillering germplasm exhibits mostly small panicles and small seed size. The direction of these combinations cannot be reversed by breeding; however, a much more favorable combination of yield components with higher harvest index and grain yields can be developed. Most of the yield components have high heritability, and they can be reliably assessed by simple measurements and visual scoring.

Table 1. Diversity for time to flowering, plant height, and grain yield components in the world collection of pearl millet germplasm, postrainy season, ICRISAT Asia Center, India.

Character	Accessions (number)	Range		
		Mean ± SE	Minimum (IP no.)	Maximum (IP no.)
Days to flowering	16 259	75.4±0.18	33 (IP 4021)	159 (IP 11945)
Plant height (cm)	16 128	160.4±0.30	25 (IP10401)	425 (IP 13016)
Productive tillers	16 115	2.1±0.01	1 (IP 3035)	19 (IP 3110)
Panicle length (cm)	16 123	25.6±0.09	4 (IP 15625)	125 (IP 10379)
Panicle thickness (cm)	16 125	23.3±0.04	9 (IP 10402)	61 (IP 14070)
1000-grain mass (g)	16 408	8.6±0.01	1.5 (IP 15352)	21.3 (IP 11407)

Thus, genetic manipulation of yield components for high grain yield has received highest priority in all breeding programs.

Biotic Stresses

Downy mildew [*Sclerospora graminicola* (Sacc.) Schröet] is the most widespread and serious disease of pearl millet in Asia and Africa. Its importance has substantially increased with the occurrence in India of three epidemics during the last 25 years on the most widely used single-cross hybrids. Effective screening techniques for large-scale application in both the field and the greenhouse have been developed (Williams et al., 1981; Singh and Gopinath, 1985), diverse sources with high resistance levels have been identified (Singh et al., 1990; Singh, 1992), and the inheritance of resistance has been found to be relatively simple. Based on these considerations, breeding for downy mildew resistance has been accorded highest priority among not only the biotic stress factors, but among all yield-reducing stress factors.

Smut (*Tolyposporium penicillariae* Bref.), ergot (*Claviceps fusiformis* Loveless) and rust (*Puccinia substriata* Ell. & Barth. var *indica* Ramachar & Cumm.) are also economically important diseases, but are much more localized and of less importance than downy mildew in these regions. Therefore, resistance breeding for them has received less priority in India and Africa, although effective screening techniques and resistance sources have been developed (Singh, 1990; Thakur et al., 1992, 1993). Rust is the most serious disease in the southeastern United States and is receiving considerable breeding attention.

Pearl millet is reputed to have fewer enemies in insect pests than sorghum and maize, and insect pest problems are largely confined to western Africa. Head miner (*Heliocheilus albipunctella* de Joannis) and stem borer (*Coniesta ignefusalis* Hampson) have been identified as the two major insect pests of pearl millet (Nwanze and Harris, 1992). *Striga* remains the most serious biotic constraint in this region, especially in low fertility fields most characteristic of pearl millet cultivation. In the absence of effective screening techniques and confirmed resistance sources, breeding for resistance to insect pests and *Striga* has received negligible attention.

Abiotic Stresses

Low soil fertility (mainly lack of nitrogen and phosphorous) and drought are the two most important abiotic factors limit-

ing pearl millet productivity. Poor plant stand, mainly caused by high soil temperatures and soil surface crusting, is another abiotic constraint. Researchers report significant genetic variability for seedling emergence and survival at high temperatures (Soman et al., 1987; Peacock et al., 1993) and for grain-filling and threshing percentage (a measure of terminal drought tolerance) (Bidinger and Mahalakshmi, 1993). Information available on the nature of inheritance of these traits and the effectiveness of screening techniques to select for resistance in segregating populations has not been established. As a consequence, breeding for these abiotic stress traits has not yet become an integral part of planned breeding. Breeding in the target environments, depending on the extent of the natural occurrence of these abiotic stresses, takes them into account by discarding progenies that have poor plant stand and do not yield well.

Breeding Approaches

Base Population

The base populations most extensively used for pearl millet breeding are developed by hybridization of parents with complementary traits, or by formation of composites. Individual landraces also have been used as base populations. Open-pollinated varieties (OPVs) developed from selection within individual landraces have not been successful with farmers, because the yield advantages of such varieties compared with the parental populations have been marginal (Niangado and Ouendeba, 1987), and they have not offered anything new in terms of character combination and quality.

Composites provide the best option for broad-based populations with greater scope for genetic gains and production of OPVs with wider adaptation. The composite approach also is quite relevant to breeding hybrid parents, provided the traits considered important for hybrid parents have been taken into account while selecting the parents for their constitution. The extent to which this approach is followed by various programs depends on their geographical mandate, access to diverse germplasm (raw and improved), target cultivars, and availability of testing facilities and manpower resources. Thus, ICRISAT and INTSORMIL (at Lincoln, Nebraska, and Hays, Kansas) have the largest programs on composites and population improvement. Most ICRISAT composites incorporate a large proportion of African germplasm and breeding materials, have substantial diversity, and are primarily intended for the development of OPVs. In contrast, most INTSORMIL composites are intended for the development of hybrid parents and have a relatively narrower genetic base.

The most commonly used populations, especially for breeding hybrid parents, are derived from hybridization. Inbred lines developed from such diverse populations also are used for breeding synthetics. About 2,000 inbred lines, most of them initially produced as restorers of the A_1 CMS system, have been assembled at IAC. A majority of these are of medium to tall height and medium to late maturity, have good downy mildew resistance levels, and represent tremendous diversity for other agronomic traits. National programs elsewhere, especially in India, also have developed a large number of inbred lines from such populations, which collectively represent a wide range of diversity.

Target Traits

Grain yield (measurements or visual scores), appropriate maturity, and downy mildew resistance are the key target traits for genetic enhancement both in Asia and Africa. Stover yield and quality are generally of secondary importance. Attention also is paid to stalk strength, tillering, grain size, grain color, and panicle length, to meet farmers' requirements in various regions. Large grain size (greater than 10 g 1000^{-1}) is now widely emerging as the most preferred grain trait. Grain traits related to better processing (hard and large grains) and better food quality (vitreous endosperm) also are taken into account in breeding programs in the African regions.

On the cytoplasm side, two more stable sources (A_4 and A_5) have recently been identified (Hanna, 1989; Rai, 1995). These sources substantially increase the option for genetic and cytoplasmic diversification of both inbred and population seed parents, opening up the possibility for breeding hybrids with higher grain yield and stability. In the improved germplasm, the frequency of restorers for the A_4 CMS system is less than for the A_1 CMS system, and almost non-existent for the A_5 CMS system. Thus, the use of these new CMS systems may appear to require greater efforts in breeding their restorers. However, the greater stability of male sterility of the A_4 CMS system, and perhaps relatively fewer complications arising from modifiers, may mean less effort in breeding its restorers (Andrews and Rajewski, 1994). Male sterility of the A_5 CMS system also is as highly stable as that of the A_4 CMS system, and its restorer gene(s) have been found in four trait-specific genepools based on diverse germplasm and in six *P. glaucum* subsp. *monodii* accessions originating from Mauritania and Sudan (2 each), Chad and Senegal (1 each) (Rai and Rao, 1996).

Selection Environment

Selection for grain yield and adaptation is done under rainfed conditions at fertility levels (20-60 kg N ha^{-1}) higher than where the cultivar will actually be grown (generally no more than an equivalent of 10-20 kg N ha^{-1}). The philosophy behind selecting at this higher fertility level is two-fold: 1) the heterogeneity in soil fertility is reduced, allowing more effective selection of plants and progenies, and 2) the goal of higher productivity has to be achieved by a combination of improved cultivars and improved management, including external input. Early generation progenies (S_1 and half-sibs in recurrent selection and F_3-F_5 in pedigree breeding) are generally evaluated at one location, and infrequently at two locations, owing to their large numbers. The collaborative research programs with NARS allow for progeny testing at later stages at two or three locations for some populations. National testing networks allow for extensive testing of finished products at varying productivity levels in both India and Africa.

Selection for downy mildew resistance in population progenies and early generation breeding lines is based on field evaluation in African regions where the disease pressure is generally high. Increasing use is being made of field disease nurseries. At IAC, the greenhouse inoculation technique is used most intensively. Open-pollinated varieties and advanced breeding lines are evaluated in field disease nurseries in all three regions.

Breeding Procedures

Recurrent selection in composites intended primarily for breeding OPVs and pedigree selection in mostly hybridization-derived populations intended primarily for breeding hybrid parents are the two most common breeding procedures. Backcross breeding also has been used to a limited extent to transfer major genes into elite genetic backgrounds or to convert composite populations.

A detailed comparative study of various recurrent selection procedures in pearl millet concluded that the choice of a selection procedure depends not so much on its relative efficiency, but more on the breeding objective and how it fits into the overall goal of the program and available resources (Singh et al., 1988). Thus, a range of selection procedures, including mass selection, half-sib and full-sib, and S_1/S_2 progeny selection, often are used in combination. Rattunde and Witcombe (1993) evaluated, in nine location × year environments, various cycle bulks of four composites improved for four to five cycles by different progeny testing methods. Results showed good per cycle gains for grain yield, ranging from 3.6% for Medium Composite (MC) to 4.9% for Early Composite (EC), with a minimum of 0.9% for New Elite Composite (NELC) (Fig. 1). These gains are comparable to genetic gains documented for maize. It is significant to note that these yield gains were accompanied by either significant changes for plant height and earlier maturity or no changes in plant height in two composites.

Hybrid parent research follows mostly pedigree and pedigree bulk breeding in populations derived from hybridization between two inbred lines or between an inbred line and a population, of which at least one parent must have local adaptation. Where both parents are inbred lines, three-way and complex crosses (albeit in low frequency) are made. Pedigree breeding also is done in progenies derived from composite populations, especially developed for their use in hybrid parent development.

Backcross breeding also is employed on a limited scale to transfer simply inherited traits (e.g., dwarf height, earliness, grain color, and brown midrib) in OPVs and hybrid parents. Molecular marker-assisted backcross transfer of downy mildew resistance genes in commercial hybrid parents is underway at IAC.

Cultivar Options

Both open-pollinated varieties and single-cross hybrids have been widely accepted and are multiplied on large scales in India. The adoption patterns over the years, however, reveal several factors working in favor of hybrids: 1) hybrids have 15-20% grain yield advantage over OPVs; 2) private sector investment in pearl millet is as high as public sector investment, and the private sector favors hybrid research and development of better quality seed with more aggressive publicity; 3) due to various seed malpractices, the morphological uniformity of hybrids makes farmers more confident in the genuine seed quality; 4) a large-scale institutional set up has been created to certify and monitor seed quality; 5) although hybrids to date have less stable resistance to downy mildew, the research infrastructure is geared for developing resistant hy-

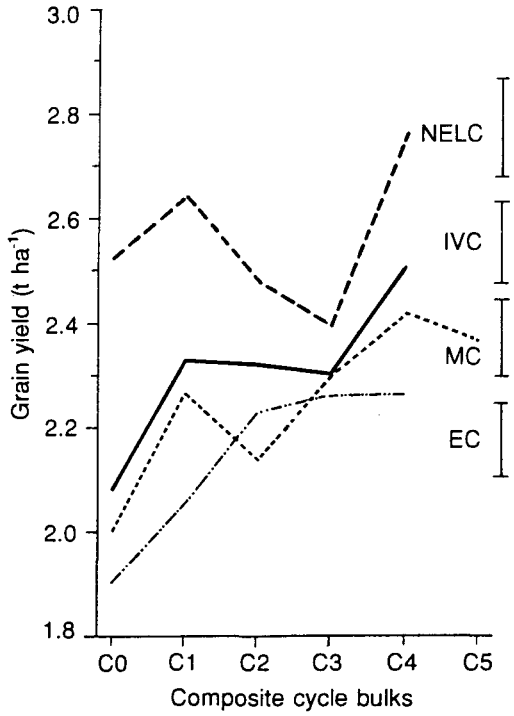


Figure 1. Grain yield improvement by recurrent selection in four pearl millet composites. Source: H.F. Rattunde and J.R. Witcombe, (1993) Plant Breeding 110:63-72.

brids with equally high or even higher yield levels; and 6) hybrids have no significantly greater disadvantage over OPVs with respect to any other biotic and abiotic constraints, except for significantly greater susceptibility to ergot and smut.

Hybrid adoption in India is fairly uneven — with more than 90% coverage, for instance, in Gujarat and Maharashtra and less than 25% in Rajasthan. Four factors influence these vastly different adoption scales: 1) differences in the availability of suitable hybrids with demonstrated significant yield advantage over OPVs; 2) productivity levels of the environments in terms of production constraints and use of external inputs; 3) the attitude and attention of private and public sector research and development toward hybrid development for these environments; and 4) the probability of crop failure and multiple planting needs in the drought stress environments of Rajasthan.

The foregoing has considerable implications for present and future cultivar options in African regions. OPVs will continue to be the only credible option until downy mildew-resistant hybrids are developed with at least 30% grain yield advantage over OPVs. Even with OPVs, seed production has proven to be a real bottleneck in their adoption, as reflected in sporadic adoption successes that are proportional to the seed production efforts. Hybrid research effort in Africa has been limited. Results available so far indicate that top cross hybrids, based either on male-sterile or male-fertile inbred seed parents, may outyield the best OPVs by

40-50% (Table 2). The use of locally adapted landraces in breeding top cross hybrids on high-yielding male-sterile lines may provide an opportunity to produce top cross hybrid cultivars with high grain yield and downy mildew resistance without any apparent loss of adaptation to marginal environments in which the landrace had evolved (Bidinger et al., 1994). More extensive evaluation is needed to determine the yield advantages of top cross hybrids, including evaluation in on-farm trials. The A_4 CMS system has made it feasible to breed male-sterile population seed parents with stable male sterility (Rai and Rao, 1995), permitting the breeding of inter-population hybrids. Limited research results from western Africa show that inter-population hybrids also may have yield advantages over the popular OPVs similar to those of the top cross hybrid. Further, male-sterile populations used as seed parents in such hybrids will have higher seed yield (reducing the cost of seed) and provide greater stability against downy mildew. The yield advantages of inter-population hybrids also need verification in extensive trials, including on-farm trials.

Output and Impact

Breeding for higher grain yield potential and stability has led to various outputs, including finished products and improved germplasm, whose visible impact has occurred both within and outside the region where they were developed.

Finished Products

The finished products (both OPVs and single-cross hybrids in India and OPVs in Africa) have the most visible impact. In the 1970s no more than two hybrids of 75 days maturity (both made on the same seed parent) were available for country-wide cultivation in India. In 1994, 18 hybrids and two open-pollinated varieties were grown on varying scales in Maharashtra state alone. The cultivar diversity in 1996 has been reported to be even greater than it was in 1994, in Maharashtra as well as the rest of the country, with about 50 hybrids in the market (see Govila et al., in these proceedings). Open-pollinated varieties, which gained popularity due to a paucity of suitable hybrids, continue to occupy their own niches.

Table 2. Grain yield advantages of four top-ranking top cross and interpopulation hybrids over open-pollinated varieties (OPVs) in pearl millet.

Location	No. of hybrids in trial	Percentage yield advantage of top four hybrids over OPV	Reference
Top cross hybrid			
Cinzana, Kolo, Sadoré, Tara	4	14-38 (CIVT)	ICRISAT West African Programs Annual Report, 1992
Lucydale, Makoholi	100	38-52 (ICMV F86415)	ICRISAT Southern and Eastern Africa Annual Report, 1993
Interpopulation hybrid			
Bambey (2 years)	35	27-59 (Souna II)	Lambert, 1983
Sadore, Bengou (2 years)	10	32-45 (P_3 Kolo)	Ouendeba et al., 1994

Today, more than 70 large and small seed companies are involved in the pearl millet seed business, several of them having developed their own hybrids. The extent of adoption of high-yielding varieties (both hybrids and OPVs) in India was about 55% during 1990-92, up from 5% during 1965-69 (Fig. 2). During the same period, grain yield increased from 360 kg ha^{-1} to 650 kg ha^{-1} (by 80% or at the rate of 3% $year^{-1}$).

A large number of OPVs with demonstrated superiority over locals for grain yield and downy mildew resistance have been developed in Africa. For instance, 23 OPVs already have been released or are in pre-release and on-farm trials in several countries of western and central Africa (Table 3). Inadequate seed production of these varieties has been the major bottleneck in their adoption. Where this problem has been overcome (e.g., Namibia), the impact has been highly visible.

Improved Germplasm

Improved germplasm targeted for high grain yield and stability consists of a wide range of materials, including improved trait-specific composites (e.g., wide maturity range, large seed size, large panicle size, high tillering, dwarf height, high plant growth rate, white grain, etc.). Rai and Anand Kumar (1994) have listed a diverse range of composites developed by ICRISAT. Valuable sources of improved germplasm include OPVs found promising but not released for cultivation, a range of inbreds with morphological di-

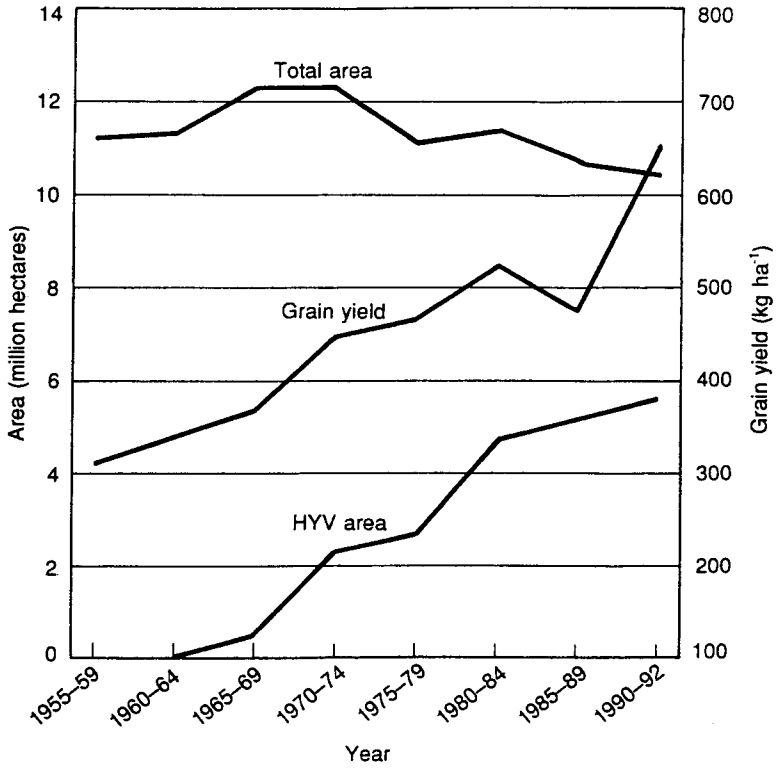


Figure 2. Five-year means of pearl millet area and grain yield in India.

versity and sources of yield components (large seed size, medium to large panicle size, and medium to high tillering), with resistance to abiotic and biotic stresses and fertility restoration, and diverse CMS sources with more stable male sterility.

Future Outlook

Sustained improvements in grain yield of both OPVs and single-cross hybrids are envisioned for India. With the private sector playing an increasingly greater role in hybrid promotion, cultivated areas under single-cross hybrids will increase. With an increasing number of hybrids under cultivation and greater replacement options, a repeat of downy mildew impact on production is unlikely. This will be further ensured by increasing use of diverse resistance sources in downy mildew resistance breeding. OPVs will continue to have their own niches in relatively less favorable environments. They will remain the only credible cultivar option for Africa for the near future, but strategic research on hybrids should be accorded highest priority as the possibility of a breakthrough in production is more likely through the hybrid option.

Table 3. Promising OPVs of pearl millet, released or in pre-release and on-farm trials in West African countries.

	Status in West African countries		
OPV	Released	Pre-released	On-farm test
GB 8735	Mauritania, Chad	—	Benin
ITMV 8001	Chad	—	—
ICMV 85327	Chad	—	—
ICMV 85333	Chad	—	Mali
ICMV 84400	Chad	—	—
ICMV-IS 88102	Burkina Faso, Mali	—	Gambia
Toroniou C1	Mali	—	—
SOSAT-C88	Mali, Mauritania	—	—
IBMV 8001	Senegal, Mali	—	—
IBMV 8004	Senegal	—	—
IKMV 8201	Burkina Faso, Mali	Cameroon	—
IKMP 1	Burkina Faso	—	Mali
IKMP 2	Burkina Faso	—	—
IKMP 1	—	Burkina Faso	—
IKMP 3	—	Burkina Faso	Mali
IKMP 5	—	Burkina Faso	—
3/4 HK-B78	—	Mauritania	—
ICMV-IS 88101	—	—	Burkina Faso
ICMV-IS 89102	—	—	Burkina Faso
ICMV-IS 89107	—	—	Burkina Faso
ICMV-IS 91116	—	—	Burkina Faso
ICMV-IS 89305	—	—	Burkina Faso
ICMV-IS 88103	—	—	Benin

Incorporation of resistance/tolerance to drought, seedling heat, *Striga*, stem borer, and head miner in high-yielding cultivars remains a challenge. Concerted efforts will be required to develop and validate effective screening techniques, develop enhanced resistance sources, and determine nature of inheritance. Positive results of applied value leading to successful cultivars with readily visible resistance/tolerance levels to these constraints are not likely to come easily.

Like many other crops, only a fraction of cultivated pearl millet germplasm has been utilized in breeding. The Iniadi group of germplasm from Ghana-Togo-Burkina Faso has proved most useful globally (Andrews and Anand Kumar, 1996). Other sources of useful variability in the landraces should be sought. Focused evaluation and utilization of other *Pennisetum* species for novel traits, e.g., stalk strength, disease resistance, fertility restoration and apomixis, etc. (Hanna, 1992), may further enhance the ability to breed for high grain yield and stability. Origin and key traits of improved germplasm available globally should be summarized as part of the International Crop Information System for efficient access to and greater utilization of this valuable genetic resource.

A diverse range of improved materials that can be of direct use has been produced globally. Most of them remain undocumented and hence unexploited. Introduction and proper evaluation of these materials may have considerable spill-over advantage as revealed in a few cases. For instance, the introduction and direct use of the male-sterile line Tift 23A in the early 1960s and of 842A (AKM 2021) and 843A (AKM 2068) in the early 1980s from the United States had tremendous effect on the pearl millet hybrid industry in India (Andrews and Bramel-Cox, 1993). Similarly, the introduction of ICTP 8203 and ICMV 88908 (Okashana 1) and ICMV 82132 (Kaufela) from ICRISAT Asia Center to Namibia and Zambia, respectively, had substantial impact on pearl millet productivity in these countries.

Results from the application of existing knowledge to pearl millet breeding indicate that pearl millet may play a potentially larger role in world agriculture, both in low-resource traditional environments of the tropics and non-traditional environments of the tropics and warm-temperate zones (Andrews and Kumar, 1992). For instance, a summer crop of pearl millet following wheat and *Brassica* in the Gujarat state of India has been reported to give 2.5-3.5 t ha^{-1}, double the yield in the main (rainy) season. Hybrid yields of about 3.5 t ha^{-1} have been reported in the southeast and midwest regions of the United States. Hybrids and populations maturing in 65 days under 14-15 hour daylength have been identified. These hybrids can be useful in multiple cropping systems and can help stabilize production by producing higher grain yield than medium-maturing hybrids under late planting conditions. An experiment with three hybrids produced by Haryana Agricultural University in India showed that an early-maturing hybrid HHB 67 (61 days to mature) yielded 12-15% less than HHB 50 and HHB 60 (75-79 days to mature) at normal planting time, but 45-72% more under late planting (Table 4). Cultivation of pearl millet in non-traditional environments may bring new challenges, includ-

ing greater impact of ergot and rust, and new requirements, such as resistance to herbicides, nematodes, and chinch bug (*Blissus leucopterus* Say).

Shrinking financial allocations for research and development and a growing need to address complex research issues related to greater crop productivity, biodiversity, and environmental quality call for enhanced inter-institutional partnership for the exploitation of comparative advantages and spill-over effects. This is especially so for pearl millet, which is grown in poorer environments, and has fewer funding sources and only a handful of well-established research centers. Some existing formal linkages for pearl millet breeding have proved immensely productive (e.g., partnerships between NARS in both Asia and Africa with ICRISAT and INTSORMIL, and between the John Innes Institute and University of Wales in the UK and ICRISAT). Partnership with NARS should be further strengthened, and the private sector and NGOs should be involved in more extensive and coordinated multilocational testing and seed production. Partnership involving international research centers and advanced research institutes should be worked out to address complex problems of long-term benefits — e.g., application of biotechnology to biotic and abiotic problems, utilization of novel traits from wild species, and evaluation of the potential of pearl millet in non-traditional environments, both for productivity and grain utilization. ICRISAT and INTSORMIL are suitably placed for developing and strengthening these partnerships.

Table 4. Effect of sowing time on grain yield of pearl millet hybrids, Hisar, Haryana (mean of 1987 and 1988)[1].

Hybrid	Grain yield (t ha^{-1}) at sowing[2]		Days to maturity[3]
	Normal	Late	
HHB 50	3.09	0.93	79
HHB 60	3.21	1.10	75
HHB 67	2.72	1.60	61

[1]Source: Haryana Farming (1989): 18(5), 5.
[2]Early sowing (during July); Late sowing (late July to mid-August).
[3]Source: Haryana Farming (1989): 1(6),15.

References

Andrews, D.J., and K. Anand Kumar. 1996. Use of the West African pearl millet landrace Iniadi in cultivar development. Plant Genetic Resources Newsletter 105:15-22.

Andrews, D.J., and P.J. Bramel-Cox. 1993. Breeding cultivars for sustainable crop production in low input dryland agriculture in the tropics. p. 211-224. *In* D.R. Buxton, R. Shibles, R.A. Forsberg, B.L. Blad, K.H. Asay, G.M. Paulsen, and R.F. Wilson (eds.) International crop science I. Crop Science Society of America, Inc., Madison, Wisconsin, USA.

Andrews, D.J., and K. Anand Kumar. 1992. Pearl millet for food, feed, and forage. Adv. Agron. 48:89-138.

Andrews, D.J., and J.F. Rajewski. 1994. Male fertility restoration and attributes of the A_4 cytoplasmic-nuclear male-sterile system for grain production in pearl millet. Int. Sorghum and Millets Newsletter 35:64.

Bidinger, F.R., and V. Mahalakshmi. 1993. Selection for drought tolerance. p. 57-59. *In* Cereals program, ICRISAT 1993, Annual Report 1992. Patancheru, A.P. 502 324, India (limited distribution).

Bidinger, F.R., E. Weltzien R., V. Mahalakshmi, S.D. Singh, and K.P. Rao. 1994. Evaluation of landrace top cross hybrids of pearl millet for arid zone environments. Euphytica 76:215-226.

Hanna, W.W. 1989. Characteristics and stability of a new cytoplasmic-nuclear male-sterile source in pearl millet. Crop Sci. 29:1457-1459.

Hanna, W.W. 1992. Utilization of germplasm from wild species. p. 251-257. *In* Desertified grasslands: Their biology and management. Academic Press, London, UK.

Kassam, A.H., and J.M. Kowal. 1975. Water use, energy balance and growth of gero millet at Samaru, Northern Nigeria. Agr. Met. 15:333-342.

Lambert, C. 1983. L'IRAT et l'amelioration du mil. Agronomie Tropicale 38:78-88.

Niangado, O., and B. Ouendeba. 1987. Varietal improvement of pearl millet in West Africa. p.

95-106. *In* Proceedings of the international pearl millet workshop, 7-11 April 1986, ICRISAT Center, Patancheru, A.P. 502 324, India, ICRISAT.

Nwanze, K.F, and K.M. Harris. 1992. Insect pests of pearl millet in West Africa. Review of Agricultural Entomology 80:1133-1155.

Ouendeba, B., G. Ejeta, W.E. Nyauist, W.W. Hanna, and K. Kumar. 1993. Heterosis and combining ability among African pearl millet landraces. Crop Sci. 33:735-739.

Peacock, J.M., P. Soman, R. Jayachandran, A.U. Rani, C.J. Howarth, and A. Thomas. 1993. Effects of high soil surface temperature on seedling survival in pearl millet. Experimental Agriculture 29:215-225.

Rachie, K.O., and J.V. Majmudar. 1980. Pearl millet. Pennsylvania University Press, University Park, USA.

Rai, K.N. 1995. A new cytoplasmic-nuclear male sterility system in pearl millet. Plant Breeding 114:445-447.

Rai, K.N., and K. Anand Kumar. 1994. Pearl millet improvement at ICRISAT — An update. Int. Sorghum and Millets Newsletter 35:1-29.

Rai, K.N., and A.S. Rao. 1995. Commercial feasibility of growing interpopulation hybrids in pearl millet. Int. Sorghum and Millets Newsletter 36:49-50.

Rai, K.N., and A.S. Rao. 1996. A new cytoplasmic-nuclear male sterility (CMS) system and its restorers in pearl millet. Abstract. Int. Crop Sci. Congr., New Delhi, 17-23 Nov. 1996.

Rattunde, H.F., and J.R. Witcombe. 1993. Recurrent selection for increased grain yield and resistance to downy mildew in pearl millet. Plant Breeding 110:63-72.

Singh, P., K.N. Rai, J.R. Witcombe, and D.J. Andrews. 1988. Population breeding methods in pearl millet improvement. L'Agronomie Tropicale 43:185-193.

Singh, S.D. 1990. Sources of resistance to downy mildew and rust in pearl millet. Plant Diseases 74:871-874.

Singh, S.D. 1992. New sources of resistance. p. 33. *In* Cereals program, ICRISAT 1992, Annual Report 1991. Patancheru, A.P. 502 324, India.

Singh, S.D., and R. Gopinath. 1985. A seedling inoculation technique for detecting downy mildew resistance in pearl millet. Plant Disease 69:582-584.

Singh, S.D., S.B. King, and P. Malla Reddy. 1990. Registration of five pearl millet germplasm sources with stable resistance to downy mildew. Crop Sci. 30:1164.

Soman, P., T.J. Somph, F.R. Bidinger, and L.K. Fussell. 1987. Improvement in stand establishment in pearl millet. p. 159-171. *In* J.M. Menyonga, T. Bezuneh, and A. Youdeowei (eds.) Food grain production in the semi-arid Africa. OAF/SSRC-SAFGRAD, Semi-Arid Food Grain Research and Development. Ouagadougou, Burkina Faso.

Thakur, R.P., S.B. King, K.N. Rai, and V.P. Rao. 1992. Identification and utilization of smut resistance in pearl millet. Research Bulletin No. 16. ICRISAT, Patancheru, A.P. 502 324, India.

Thakur, R.P., K.N. Rai, S.B. King, and V.P. Rao. 1993. Identification and utilization of ergot resistance in pearl millet. Research Bulletin No. 17. ICRISAT, Patancheru, A.P. 502 324, India.

Williams, R.J., S.D. Singh, and M.N. Pawar. 1981. An improved field screening technique for downy mildew resistance in pearl millet. Plant Disease 65:239-241.

Developing Countries Breeding and Potential of Hybrid Sorghum

L.R. House*, B.N. Verma, G. Ejeta,
B.S. Rana, I. Kapran, A.B. Obilana, B.V.S. Reddy

Abstract

Virtually everywhere that hybrids have been compared to improved and landrace varieties, there has been a yield advantage, commonly on the order of 20 to 60%. As growing conditions become stressed, the yields of both decline, but the yield difference between hybrids and varieties becomes larger, favoring the hybrid. The single biggest problem with hybrids in many developing countries is the production and marketing of hybrid seed. Where a seed industry does exist, it provides an important service in the timely supply of good quality seed and, for the larger companies, research. The availability of high-yielding hybrids paves the way for establishing a seed industry. There are many similarities in the breeding procedures and methods of evaluating resistance and quality traits in different countries. Yet there are differences between countries, particularly as the issue of seeds is addressed. This paper identifies some of these similarities and differences, not only to provide information, but also to help those working with hybrids in developing countries appreciate the opportunities and the potential.

The greater contribution of hybrids to yield, compared to improved and landrace varieties, has been demonstrated in almost every situation in which they have been evaluated. As growing conditions become stressed, the yields of both hybrids and varieties decline, but frequently the magnitude of difference, percentage wise, is greater for hybrids compared to the situation when growing conditions are good. Hybrids not only have yield superiority over open-pollinated varieties, but they are more stable across different environments. For example, local varieties in India were adapted to fairly narrow specific environmental niches, but the first hybrid, CSH-1, spread over much of the rainy season (kharif) sorghum area. Pest and quality problems frequently need resolution; however, the absence of a mechanism for the production and distribution of seed has been a major hurdle and a discouraging factor in a number of countries, despite the immense contribution to agriculture a seed industry can make.

Although the development and use of hybrids has occurred in many developing countries, this paper will focus on India and several countries in Africa. I hope to give adequate insight in the use of hybrids to indicate the problems and successes and help others relate to the issues involved.

L.R. House, Rt. 2, Box 136 A-1, Bakersville, NC 28705; B.N. Verma, Mt. Makulu Research Station, Chilanga, Zambia; G. Ejeta, Department of Agronomy, Purdue University, West Lafayette, IN 47907; B.S. Rana, National Research Center for Sorghum, Rajendranagar, Hyderabad, India; I. Kapran, INRAN, B.P. 429, Niamey, Niger; A.B. Obilana, Bulawayo, Zimbabwe; B.V.S. Reddy, ICRISAT, Patancheru, India. *Corresponding author.

Breeding

Common Considerations

There are two major aspects of breeding: generating diversity and exploiting the diversity by selection. In some situations, introduced varieties and hybrids have performed well, but locally developed cultivars have been superior. In my experience, the breeding procedures have been traditional; the problem has been related more to efficient application than to the development of new techniques.

In breeding, one cannot begin at the end. The first hybrid (CSH-1) released in India had a less desirable grain quality than locals, which I believe affected its acceptance. Because of other significant contributions, it was released and extensively used by farmers. The grain quality problem was overcome with CSH-5. Improvement is a continuing process, and it is important to keep a significant crop improvement activity over time.

Diversification of The Genetic Base

In those countries where I have been involved with developing crop improvement programs that included hybrids, introduction of substantial breeding stock and collection accessions to diversify the genetic base has been an important first step. Many cultivars introduced to begin the program for sorghum and pearl millet in India continued, becoming world collections. Entries from these collections for years have been distributed worldwide. Selection has generally been first from breeding stock, but landrace cultivars have been used to broaden the genetic base of traits of interest, particularly for quantitative traits. Landrace material is frequently poorly-adapted because of height and photoperiod sensitivity, hence more difficult to use, so programs of conversion to temperate adaptation and germplasm enhancement have been contributing.

During the last twenty years, a wealth of elite germplasm has been developed, mobilized, and distributed around the world. Today, elite germplasm for both "feed" and "food" grain types is readily available to any research program that wants it. The seed industry in developed countries has accumulated elite germplasm for feed grain hybrids. Public and international research programs have generated a diverse and elite array of food grain sorghum. As a result, elite hybrids of both food and feed grain hybrids can be developed without lengthy effort in developing parental lines. Many of these parental stocks have defensive traits against pests, disease, and parasitic infection.

Breeding Procedures

Good parents come from good varieties, but the best parents generally do not come from the best varieties. The breeding procedures to develop both varieties and parents of hybrids have much in common. In my experience, pedigree breeding has been the most common technique. Crosses of exotic × exotic parents have generally been the most rewarding, followed by exotic × local crosses; least rewarding have been selections from local × local crosses. This is not always true, however. Several cultivars from the Zerazera landrace, for example, (such as Sima in Zambia) have been selected and

released. Backcrossing has been used to transfer traits and develop new A-lines.

Important contribution to increasing yield has been made from the incorporation of resistance traits and to crop utilization because of the inclusion of traits for good quality. Significant in southern Africa was the effort over several years to identify locations for evaluating resistance to diseases, insects, and *Striga.* Facilities were established to rear and infest with stemborers, and to screen for resistance to nematodes. The program in Zambia focused on acid soils, and the food technology lab of the SADC/ ICRISAT program developed and applied a technique to evaluate diastatic power. These examples illustrate the range of traits evaluated. Evaluation contributed to national programs in the region.

Some sources of traits have been more difficult to use than others; for example S-GIRL was a potential source of midge resistance, but the recovery of good progeny from crosses was much less than when other sources were used. The Guineas have been difficult to improve and, while heterotic in crosses, have had other limiting traits, such as high levels of lodging.

The difference between varietal improvement and hybrid development occurs when promising cultivars are identified. In hybrid development, this has involved test-crossing to evaluate parents in hybrid performance. In India and African countries where I have worked, off-season nurseries have been established to make hybrids for test-crossing preliminary, advanced, and regional yield trials. This opportunity speeds breeding progress.

Once useful lines have been selected, more progress generally results from selection in advanced generations from crosses than from continued selection within the line. The utilization of populations, in my experience, has occurred only at the ICRISAT Center. Seeds of promising plants in populations were sown as head rows for selection and crossed with existing good breeding stock for further selection. This approach was effective.

Hybrids of sorghum generally involve two parents. The important consideration is the phenotype of the hybrid, so this must be kept in mind in selecting parents. The availability of a broad genetic base facilitates application of a high selection pressure for wanted traits. Evaluation in test crosses is important to be sure the hybrid has the desired traits. Nurseries frequently are grown in more than one environment to identify broad adaptability.

Compared to varietal development, the crossing of two parents can result in changes in maturity and plant height, but also in grain quality, which is generally less desirable than in local varieties, and in reduced effectiveness of resistance traits. These possibilities increase the need for greater evaluation and development of seed parents that contribute desired traits, particularly for grain quality traits whose A-lines are useful as testers for an array of potential pollinator parents.

The most common method for transferring traits is backcrossing. The technique is most effective for simply inherited traits, but with quantitative traits, one or two backcrosses are possible; then new parents are selected by pedigree breeding. While recessive traits must be incorpo-

rated in both parents, dominant traits need be present in only one parent and are worth watching for.

Test crosses in India were evaluated for restoration of male fertility in the hybrids by bagging heads before flowering and subsequently observing seed set. At the off-season nursery at Coimbatore, promising non-restorers were backcrossed to form new seed parents. Plants involved in backcrossing were numbered, each cross leading to a pair of head rows, and evaluated for non-restoration in the male-sterile row; this process of numbered crosses and evaluation of non-restoration continued to prevent problems of partial fertility. Most of my experience has been on A1 cytoplasm, although A2 has been increasingly used. Significant success has been achieved in India to identify new CMS systems. Good reviews of this work are included in the Proceedings of Sorghum in the Seventies (Rao, 1972) and Sorghum in the Eighties (Schertz et al., 1982).

Despite higher hybrid yields, some circumstances favor varieties. Because it is necessary to breed recessive traits into both parents, the time required to develop a hybrid can be longer than the time required to develop a variety. In India, varieties with resistance to midge and to *Striga* have outyielded hybrids in areas endemic for these problems when the problems are severe. The variety Kuyuma, while lower-yielding than hybrids, has been widely used in Zambia because of its drought tolerance and because of initial concerns related to seed production.

When the farmer first uses hybrids, there are several important considerations. The increase in yield over the locals should be significant (40% or more). There should be a nick in flowering when the two parents are sown at the same time to facilitate new seed producers. The hybrid should not be more susceptible to insect and disease pests than the locals, and it should have an acceptable grain/forage quality for its intended use. The hybrid should be grown on farm to generate farmer enthusiasm and interest of government officials and potential seed producers.

Hybrids are developed by researchers whose primary responsibility continues to be research. It is essential to identify and fund individuals whose primary responsibility is development of a seed industry. Collaboration with people from other countries with an established seed industry is invaluable. The research scientist needs to remain involved.

Why Hybrids

Table 1 has been organized from a number of sources to provide examples of hybrid/variety performance in India and several countries of Africa and Latin America.

Percentage increase in yield of hybrids over improved varieties ranges from 15 to 66 percent, and over locals from 7 to 131 percent (Table 1). Generally, improved varieties do not yield as well as hybrids, but the difference is generally not as great as when compared with traditional landrace varieties. In terms of crop improvement, I feel that the exploitation of heterosis is one of our strongest tools. The development of sorghum hybrids in India and several African countries is briefly outlined in the following paragraphs.

Table 1. Comparative performance of hybrids, improved varieties, and land race cultivars.

Country	Years of testing	Number of trials	No. of entries			Yield kg ha^{-1}			% increase over		Type of test	Authority
			Hybrid	Var.	Local	Hybrid	Var.	Local	Var.	Local		
India												
Kharif	1985-90	-	7	4		3665	3189		14.9		Regional	Murty, U.R. 1992
Rabi	1981-87	13	15-100	1		2400	2900		-17.2		Station	Reddy, B.V.S.
	1983-87	5	31-100	1		2400	4300		-44			1994
Zambia	1989-90		3	3		3977	3238		22.8		Demon.	Verma, B.N.
	1990-91		3	3		4162	3091		34.6		"	"Pers. Com.
	1991-92		3	3		2741	1928		42.2		"	"
Sudan	1985-irr		1	1		5189	3010		72.3		Regional	Ejeta, G., 1985
	1985-dry		1	1		2968	1543		92.3		"	
	1986	2	1	1		4152	2700		53.7		"	Ejeta, G.. 1985
		2	1	1		2670	2483		7.5		"	
		2	1	1		3891	3113		24.9		"	
		9	6	1		4573	3109		47.0		"	
Niger	1988-irr		90	33	2	2582	1779	1605	45	61	Station	Kapran, I.
	1988-dry		90	33	2	1799	1081	1204	66	49	"	1988
West Central Africa*	1986	87	10-34	1		2970	1770		67.7		Regional	Murty, D.S.
	1995					4340	3120		39.1		"	Pers. Comm.
Burkina Faso												
Farako Ba		1	21	2	1	2258-4241	2795-3236	1345	-19 31	67	Regional	Murty, D.S. Pers. Comm.
Kamboinse		1	21	2	1	945-1904	0-679	331	180	185	"	"
Ouahigouya		1	21	2	1	687-2302	1031-1490	271	-33 54	154	"	"
India			14	15		3254	2336		39		Intl.	ICRISAT
Pakistan			14	15		1663	1535		8		"	Annual
Thailand			14	15		3007	4775		-37		"	Report
Philippines			14	15		5394	2327		131		"	
El Salvador			14	15		6196	3549		75		"	
Venezuela			14	15		6826	4707		45		"	

*Benin, Burkina Faso, Cameroon, Cote d'Ivoire, Ghana, Mali, Niger, Nigeria, Senegal, Togo.

India

The sorghum situation in India has changed dramatically since the early 1960s. Hybrids of maize, sorghum, and pearl millet were released between 1962 and 1965 and provided a base for a seed industry that has grown significantly. Many introductions were used to create hybrids earlier than the locals by two to five weeks and with an improved grain/straw ratio of 1:1 to 1:2.5. These earlier hybrids avoided drought stress when late season rains failed to occur, and they were more management-responsive. I recall some early agronomic work indicating that locals were yielding six to ten kg of grain per kg of nitrogen applied, while high-yielding hybrids were producing 20-45 kg of grain per kg of nitrogen applied. Fourteen hybrids and eleven varieties have been released by the All India Coordinated Sorghum Improvement Program, offering farmers broader choices and preventing genetic vulnerability.

The research program of the All India Coordinated Sorghum Improvement Program has been broad-based, involving a range of management practices that focus on insect pests (shootfly, stemborer, midge, shootbug, and earhead bugs); diseases (downy mildew, grain molds, ergot, charcoal rot, and rust); grain and forage quality, involving a range of relevant tests; and development of dual purpose hybrids and forage hybrids involving sudangrass (Murty, 1992).

In the future, the All India Program plans to intensify efforts on post-rainy season (rabi) sorghum. Efforts will continue on kharif hybrids and new male-sterile seed parents with resistance and improved qualities, including exploitation of different sources of cytoplasm male sterility. Further efforts will be directed toward continued use of germplasm, a search for alternate uses of sorghum, development of multicut forage hybrids, continued responsibility for breeder seed, and a search for economical management practices (B.S. Rana, 1996, personal communication).

Results in the rainy (kharif) season have been spectacular. Nationally, the yield has increased from around 400-450 kg ha^{-1} in the 1960s to 1048 kg ha^{-1} in 1989-90. During 1962-67, the area sown covered 11,216,400 hectares; in 1986-90, the area sown covered 9,129,000 hectares, a drop of 2,097,400 hectares. However, during this same period, average production increased by 2,189,000 tons — from 5,779,000 tons in 1962-67 to 7,968,000 tons in 1986-90 (Murty, 1992). In 1988, 667,853 tons of seed of all crops — 70% hybrid — were produced and processed in 504 processing plants (Singh et al., 1990). This is an outstanding example and should encourage other countries to venture into hybrids.

While there have been some gains in the post-rainy (rabi) season, they have been modest and more difficult to achieve. A number of hybrids were released for the rabi season but their acceptance was low. Increasing effort over the years has been put forth to resolve this problem and develop hybrids for the post-rainy season. At the ICRISAT Asian Center an effort is being made to use landrace rabi varieties to bring in desired traits. Seed set is part of the study. A1 and A2 cytoplasms in Durra and Zerazera with landrace pollinators were evaluated for

seed set at low temperatures (10°C for several days) as part of the effort. Both A1 and A2 were found to have better seed set in the Zerazera than Durra backgrounds. Besides seed set, hybrids were evaluated for grain and fodder yield, lodging, stay-green, and pearly, bold, round grain. Resistance to shootfly and improved grain luster are still areas of concern. In India, the best quality sorghum comes from rabi varieties, so good grain quality will be required in the hybrids if they are to be accepted. Selection for seed set has been rewarding (Reddy and Stenhouse, 1994).

Zambia

Sorghum and millet are traditional crops in Zambia as in other countries of southern Africa. Over 40 years ago maize began to replace sorghum, extending even into areas poorly adapted for the crop. The maize hybrid SR-52 was introduced from Rhodesia (now Zimbabwe) prior to formation of the Zambia Seed Company (Zamseed) in 1980. It has been estimated that more than 70% of Zambian farmers use hybrid maize seed. At one time, 80% of Zamseed's revenue came from sale of hybrid maize seed and 10% from vegetable seeds.

The interest in maize encouraged a research focus on this crop, and research on sorghum and millet was neglected. However, frequent droughts, higher cost of agricultural inputs, and recurring food deficits leading to the need for substantial food imports led the government to consider increased crop diversification in the 1980s — not only in Zambia but in the SADC region as a whole. In Zambia, the Swedish International Development Agency (SIDA) provided expertise and financial assistance for several activities, including Zamseed and the research program.

To strengthen sorghum improvement, ICRISAT organized an introduction nursery of some 6000 accessions from 25 stations around the world. Two of the nurseries were sown in Zambia and provided a broad genetic base from which to develop the program. The process was not unique: pedigree selection among promising introductions, selection in advanced generations from crosses, and test-crossing of potential pollen parents to several A-lines. Selection pressure could be high because of opportunity provided by extensive introductions. The first off-season activity took place at Muzarabani in Zimbabwe and later in Zambia. Promising varieties and hybrids were organized into preliminary and advanced trials and evaluated at several locations in each of the three identified environmental regions of the country. The best entries were entered into SADC regional trials.

Concern developed about a virus disease, found primarily around Lusaka, and several leaf diseases occurring on the crop. An isolated field was established at the Golden Valley Station for systematic evaluation of susceptibility to downy mildew, and the breeding nursery was routinely evaluated for response to leaf blight and sooty stripe. Response to stemborers also was scored. Lusitu was selected as a site to evaluate crop response to high heat and moisture stress; Mount Makulu, to test not only for response to virus, but for crop potential in a climate with cool night temperatures; and Mansa, to evaluate the crop for anthracnose and soil acidity. Scientists from the SADC/ICRISAT pro-

gram participated in these evaluations with Zambian scientists.

From the outset, concern about crop utilization was reflected in the program where breeding was undertaken for food quality, milling, malting, and forage quality. Initially SVALOF AB tested entries in yield trials for grain quality parameters such as grain hardness, tannin content, diastatic power, protein content, and amino acid composition. Later, testing for some of these traits plus milling quality was undertaken by the SADC/ICRISAT program. Also, the HCN content of the regrowth of forage types was evaluated at SVALOF AB, and protein content of stems and leaves was evaluated at the Mount Makulu station near Lusaka.

Progress in the program, which began in 1983/84, was rapid. The hybrid WSH287 and two varieties, WSV387 and WSV187, were prereleased in 1987. All three had good quality white grain. The parents of WSH287 did not nick well in the main season, so it was dropped; but in 1989 the two varieties were released, WSV387 as Kuyuma and WSV187 as Sima. Also in 1989 two hybrids, MMSH375 and MMSH413, with brown grain and good malting quality for brewing, were pre-released and then released in 1991. A white-grained, drought-resistant hybrid, MMSH928, was pre-released in 1993. From the evaluation of 200 hybrids involving a grain sorghum seed parent and sudan grass pollinator, the forage hybrid FSH-22 was pre-released in 1993. This hybrid was found to have good forage yield, low HCN content, ease of seed production, and high protein content (Verma, 1992).

Two improved sorghum varieties, ZSV-1 and Framida, had been released earlier. In 1980 Zamseed began producing small quantities (10-20 tons) of these cultivars, plus a brown-seeded variety grown for malting purposes, Red Swazi. Production was undertaken by commercial farmers in Region II around Lusaka where the cultivars were not well adapted. Leaf diseases, low yield, and residual variability in ZSV-1 made certification difficult. Zamseed was discouraged and reluctant to become involved with production of sorghum seed again. Extension programs also responded negatively based on their concepts of existing and new cultivars for subsistence farmers.

To overcome these obstacles, the research team began to conduct preplanting meetings, carrying seeds to farmers at local schools in two target areas where sorghum is important (Lusitu and Chiawa). Farmers aware of the variety Kuyuma from on-farm demonstrations were interested in the seed. 1.4 tons of seed were sold in the first year, and 8 tons in the second; in the third year, 20 tons of seed were sold cash out of pocket at 2.5 times the grain price. At this point a GTZ program in the area took over the seed production project. Enthusiasm rapidly increased and received a boost from visits by the country's president and minister of agriculture.

With rising pressure for seed, the research team worked with Zamseed to begin large scale seed production during the off-season, beginning in the drought year of 1987 until 1992, on a privately operated irrigated farm at the edge of Lake Kariba.

In 1987, 120 tons of Kuyuma were produced on 80 hectares. In 1988, seed of WSH287 was produced on 40 hectares. In 1991, 50 tons of Kuyuma were produced on 16 hectares. In 1992, 374 tons of seed were produced, primarily of Kuyuma, but also Sima and the two hybrids MMSH375 and MMSH413. In 1994, 594 tons of seed were produced on 300 hectares (160 ha of Kuyuma, 80 ha of Sima, 40 ha of MMSH413, and 40 ha of MMSH375).

Through this process, Zamseed became more involved with sorghum as a profit-making crop, as reflected in the increased volume of the company's seed production after 1990. Seed sales increased from 21.9 tons in 1990/91 to 852 tons in 1995/96.

The involvement of the utilization industry has been slow. National breweries have begun to purchase sorghum grain. Three meetings have been held among representatives of the industry, Zamseed, and the research program. Export has been encouraging. Zamseed exports 200-300 tons of seed annually primarily to Mozambique, Malawi, Zimbabwe, and Botswana. Zimbabwe is interested in the hybrids for malting, Foods Botswana now wants annually 10,000 tons or more of white grain for milling and 5000 tons of brown grain from hybrids for brewing (B.N. Verma, 1996, personal communication).

A change in government policies toward economic liberalization and removal of controls and subsidies focused primarily on maize has created increasing interest of larger (commercial) farmers in hybrid sorghum. These farmers are predominantly on the plateaus where the environment is conducive to high yields. Hybrids with yields of eight to nine t ha^{-1} will be competitive with maize in years of good rainfall and will have higher yield when rains are poor. With this level of yield and appropriate grain/forage quality, hybrid sorghum would be a reliable commodity at favorable prices and would be competitive with maize in the utilization industry. Two high potential full season hybrids, MMSH1257 and MMSH1324, were pre-released in 1995.

Had the crop improvement team not developed varieties and hybrids to satisfy different uses, and had they not devoted so much effort and resource in establishing the value of the new cultivars and insuring availability of seeds, the new cultivars would have contributed much less and a much longer period of time would have been required. This is a significant example of a development activity growing out of a research program and carries valuable lessons for others.

South Africa

In South Africa, the commercial use of hybrid sorghum is well-established. The government sponsors a research program, and private seed companies are engaged in research activities. The food technology unit of the Council of Scientific and Industrial Research (CSIR) has long been involved with sorghum and has done pioneering work on fermentation of sorghum for food and beverage. Commercial companies that utilize sorghum not only provide products on the market but are involved in product development. A seed law, a certification program, a sorghum growers association, and plant breeders rights are in place. This industry has all

the components and hopefully will increasingly serve as an example and a place where other countries interested in hybrid seed and the seed industry can gain experience.

Sudan

Agricultural research in the Sudan goes back many years. The Gezira Research Farm was established in 1918; while the primary focus was on cotton, some work was done with sorghum. Local sorghums were collected and evaluated, and germplasm was introduced into the country by the 1930s. A full-fledged sorghum improvement program came into existence in 1952, and selection began in local types for earliness and shorter plant stature. Mechanized farming was increasing and with it the need for shorter plants. Exotic types brought in did not adapt well. In the 1960s, effort to develop hybrid sorghum met with only limited success and was discontinued. Around 1973, the Arid Lands Agricultural Development Program (ALAD) of the Ford Foundation initiated efforts to develop hybrid sorghum; these efforts were continued by the ICRISAT/Sudan Cooperative Program for Sorghum and Millet Improvement in 1977.

Via the ALAD program, large collections of germplasm were introduced and evaluated along with locally developed cultivars. Significant among the introductions were yellow endosperm lines selected from the nursery of the late Dr. Karper. Introductions were evaluated at the station at Wad Medani, an off-season crossing block was established, selected parents were crossed to introduced A-lines, and the hybrids were evaluated. When ICRISAT became involved, a multidisciplinary base was established among the scientists at the station. Because *Striga* was a severe problem, it received added attention. Over four seasons (1979-82), 3000 experimental hybrids were evaluated in both irrigated and dryland conditions.

Three elite experimental hybrids were identified from 21 yield trials over four seasons at several locations on the central clay plains of the country. While this testing was underway, experimental production of seeds of these three hybrids was undertaken on separate one-acre fields. The purpose was to check nicking of the two parents and to demonstrate that the hybrids were readily produceable — an important consideration for the first hybrid. Nicking was good in two of the three hybrids. The hybrid grain was evaluated at the Food Technology Center at Shambat near Khartoum, and the food products made from the grain were found to be good.

One of the experimental hybrids (EEH-3, Tx623A × YE1592) was released in 1983 with the name Hageen-Dura-1, or sorghum hybrid number 1. The A-line (Tx623A) is from the Texas Experiment Station and yellow endosperm YE1592 was selected from an introduction from the nursery of Dr. Karper, a good example of shared germplasm. Results indicated that Hageen Dura-1 had an average yield of 5189 kg/ha, or 58% greater than the local under irrigation, and 2968 kg/ha, or 52% greater than the local under rainfed conditions (Ejeta, 1983, 1985).

Following Hageen Dura-1's release, a proposal was submitted and accepted by USAID for a pilot project to produce hybrid seed. A meeting also was organized involving Sudanese authority, private seed producers, and individuals from the U.S. and India with experience in the seed industry. One purpose of this meeting was to describe the differences in the production of varietal and hybrid seed and to encourage production in the private sector.

In 1985, two years after its release, Hageen Dura-1 was planted on 29,000 ha; seed available for the 1986 season was sufficient for 250,000 hectares. Yields on farmers' fields far surpassed the 50% increase over locals indicated in yield trials. During the drought year of 1984, the hybrid had an 85% increase over locals on dry land and a 300-400% increase in irrigated conditions. (Ejeta, 1986).

Some concern developed because the large harvests of 1985 and 1986 resulted in a drop in sorghum grain price, temporarily slowing further development of seed production. The area under seed production dropped from 1080 hectares in 1985 to under 400 hectares in 1986. Such an experience as this highlights the need to consider how the crop can be utilized and marketed to avoid the problem. Production continued, however, and reached 5,850 hectares in 1988-1989 (Ejeta, 1993). While no seed industry has developed in the Sudan, there is a significant private sector seed sales operation today. There is some concern that Hageen Dura-1 is still the only hybrid available. Hopefully, in the not too distant future, other hybrids will be released.

Nigeria

Interest in hybrid sorghum in Nigeria began before 1980 and was encouraged by an Action Committee for a Hybrid Sorghum Project (Obilana, 1982). Five sorghum hybrids were released in 1985, and breeder seed was provided to the National Seed Service and the private company AGSEED. Seed production was slow and finally stopped with interest in the variety SK5912 used in commercial malting in the production of lager beer. Four hybrids developed by ICRISAT and the Institute for Agricultural Research (IAR) are soon to be released. However, Premier Seed Company already has been producing seed of one hybrid, ICSH 89002 NG — 717 kg in 1992-93, 9828 kg in 1993/94, 10,000 kg in 1994/95 and again in 1995/96.

Niger

In 1975, the Government of Niger and USAID organized a program to strengthen activities for developing and utilizing crops and advancing agricultural inputs, including seeds. After ten years the program was stopped. One recognized problem was the need for a high-yielding hybrid to generate seed activity. Out of this experience the government wants to establish a seed industry in the private sector.

INTSORMIL-INRAN collaboration for sorghum improvement began in the early 1980s. Collections were made of landraces, particularly the 'dune' sorghums specific to Niger. These were incorporated into a random-mating population, providing a broad-based source of local germplasm. Introductions also came

from outside, particularly from countries like the Sudan that were environmentally similar to Niger. These were evaluated and advanced by pedigree selection, crosses were made, and selection was undertaken in advanced generations. Hybrids had been introduced into the country in the 1960s, but were discontinued because of grain quality problems and the perception that they required good growing conditions (inputs).

Beginning in 1986, two students supervised by INTSORMIL conducted their masters theses in Niger. Kapran (1988) compared 90 hybrids with their parents and local checks in several environments. The parents and checks had similar yield under irrigation, but hybrids were better yielding than both under rainfed and irrigated conditions (see Table l). The second student, Tyler (1988), evaluated 40 hybrids where male parental lines were grouped as exotic, intermediate (from crosses of exotic × locals), and locals. Grain yield heterosis over male parents was 127% for exotics, 83% for intermediates, and 66% for local pollinator parents (the seed parent was exotic).

From these studies, seed of the best hybrids was increased, and the hybrids were evaluated in trials in sorghum growing areas of the country. Food quality tests were conducted to determine the acceptability of the grain to make Tuwo. The hybrid Tx623A × MR732 was found to be the best yielder with good food quality and was released as NAD-1. NAD-1 was included in Regional Trials in West Africa, where in 1989 it ranked third among twenty entries.

Experimental seed production began at Maradi in 1989, demonstrating producability of the hybrid. Since that time, modest amounts of seed have been produced in the country and at Purdue to support on-farm demonstrations (Kapran et al., 1995).

An effort is currently underway to identify individuals interested in seed production and to sell hybrid seed at eight times the grain price. For the current season, the breeder used the radio to inform farmers of the availability of seed, which was completely sold. Posters displaying NAD-1 have been given to the country's president and to the governor of Maradi. Most of the NAD-1 seed continues to be produced by INRAN, but steps are being taken to shift seed production to private interests.

Assistance

Assistance in supporting research, education, and training from many donors, universities, agencies such as ICRISAT, INTSORMIL, USAID, IRAT, FAO, and others needs thankful recognition.

Conclusion

The idea is fairly prevalent that hybrids are suitable only for the better watered areas where fertilizer is used and not for the poor farmer working in harsh growing conditions. In my experience, however, all farmers, given the chance, have benefited from hybrids. Binswanger and colleagues (1979) undertook a study of risk among farmers in India and nicely summarized the situation. "Economic analysis justified that the technology developed is compatible with the needs and capabilities of the small farmer; in fact, more suited to him; that it is economically

sound and viable and that there is no need or justification for the development of separate technologies for the small and large farmer."

In my experience, the breeding techniques have been traditional, but efforts have been made to use them efficiently. The importance of resistance and traits for crop utilization have been part of the crop improvement process in the countries mentioned. We are experiencing and can expect an increasing contribution from biotechnology. An important challenge comes when the opportunity arises to move hybrids to farmers. Where this has gone well, it involved a sustained contribution from the originating scientists and/or their institutions over a three to ten year period. India, for example, went in a relatively few years from a major food importing country depending heavily on foreign donor support to one that exported food grain and no longer needed outside support. It serves as an example for others that with determination it can be done.

References

Binswanger, H.P., N.S. Jodha, and B.C. Barah. 1979. The nature and significance of risk in semi-arid tropics. p. 303-16. *In* Proc. international workshop on socioeconomic constraints in development of semi-arid tropical agriculture. ICRISAT, Hyderabad.

Ejeta, G. 1983. Pilot project for hybrid sorghum seed production, distribution and utilization: A proposal. Ministry of Agriculture and Irrigation, Democractic Republic of the Sudan.

Ejeta, G. 1985. Overcoming problems encountered in production, distribution and adoption of hybrid sorghum seed in the Sudan. *In* V. Guiragossian, C. Paul, G. Peterson (eds.) La produccion de la semilla de sorgo en America Latina, CIMMYT Londres 90, Apdo 6-641, Mexico CP 06600 D.F. Mexico.

Ejeta, G. 1986. Breeding sorghum hybrids for irrigated and rainfed conditions in the Sudan. Presented at the International Drought Symposium on Food Grain Production in Semi-Arid Regions of Sub-Saharan Africa. Semi-Arid Food Grain Research and Development Project, Nairobi, Kenya, 19-23 May 1986.

Ejeta, G. 1993. Sudan annual report 1993. INTSORMIL Publication 94-4, University of Nebraska, Lincoln, Nebraska.

Kapran, I. 1988. Evaluation of the agronomic performance and food quality characteristics of experimental sorghum hybrids in Niger, West Africa. M.S. thesis, Purdue University, West Lafayette, Indiana.

Kapran, I., J.D. Axtell, and G. Ejeta, 1995. Sorghum hybrids: A viable technology for sustaining Sahelian agriculture. Workshop on Technology Development and Transfer to Improve Natural Resource Management in West Africa, Niamey, Niger, September 18-22, 1995.

Murty, U.R. 1992. Sorghum production and utilization in India. The present and the future. An information paper. National Research Center for Sorghum, Rajendranagar, Hyderabad.

Obilana, A.B. 1982. A report of the action committee on hybrid sorghum project for the technical sub-committee of the national sorghum project for committee on green revolution, Mar. 1982. Federal Dept. of Agriculture, Lagos, Nigeria.

Rao, N.G.P. 1972. Sorghum breeding in India: Recent developments. p. 101-140. *In* N.G.P. Rao and L.R. House (eds.) Sorghum in the seventies. Oxford and IBH Publishing Co., New Delhi.

Reddy, B.V.S., and J.W. Stenhouse. 1994. Improving post-rainy season sorghum, *Sorghum bicolor* (L.) Moench: A case for landrace hybrids breeding approach. Presented at AICIP workshop, GBPUAT, Pantnagar, U.P. India, April 18-20, 1994. ICRISAT Conference Paper #913.

Schertz, D.F., and D.R. Pring. 1982. Cytoplasmic sterility systems in sorghum. *In* L.R. House, L.K. Mughogho, and J.M. Peacock (eds.) Sorghum in the eighties: Proceedings of the international symposium on sorghum, 2-7 Nov. 1981. ICRISAT, Patancheru, A.P., 502 324, India.

Singh, G., S.R. Asokan, and V.N. Asopa. 1990. Seed industry in India. A management perspective. Oxford and IBH Publishing Co. Pvt. Ltd, 66 Janpath, New Delhi, India.

Tyler, T.A. 1988. Heterotic pattern and combining ability for agronomic and food quality traits in Exotic x Exotic, Exotic x Intermediate, and Exotic x Local sorghum hybrids in Niger. M.S. thesis, Purdue University, West Lafayette, Indiana.

Verma, B.N. 1992. Release proposals. GTZ/SIDA/SVALOF Weibull, Mt. Makulu Res. Station, P/Bag 7, Chilanga, Zambia.

Breeding Pearl Millet Hybrids for Developing Countries: Indian Experience

O.P. Govila*, K.N. Rai, K.R. Chopra,
D.J. Andrews, and W.D. Stegmeier

Abstract

*Pearl millet [*Pennisetum glaucum *(L.) R. Br.] is mainly grown in India and Africa. In India, the production and productivity is steadily on the rise mainly due to the widespread adoption and cultivation of single cross hybrids based on cytoplasmic nuclear male sterility. On the contrary, in Africa the hybrid development program has not been successful due to nonavailability of suitable parental lines possessing downy mildew [*Sclerospora graminicola *(Sacc.) J. Schroet] and ergot [*Claviceps fusiformis*] (Loveless) resistance.*

The first hybrid (HB 1) was released in India in 1965 using A_1 cytoplasmic male sterile line Tift 23. In this paper, history of the hybrid development program in India has been discussed. HB 4, BJ 104, BK 560, ICMH 451, Pusa 23, HBH 110, MLBH 104 and HHB 67, are among the most widely cultivated past and present hybrids. The pearl millet hybrid program in India has occasional setbacks due to downy mildew epidemics. At present, India has a very strong research and development program, testing network and seed production for pearl millet hybrids. Further progress is continuing with the active participation of National Agricultural Research System, private sector and ICRISAT Asia Center. Male sterile lines with A_1 cytoplasm incorporating downy mildew resistance have been bred in the National program and at ICRISAT Asia Center. A great deal of genetic diversification of CMS lines has been achieved in A_1 cytoplasm background. As a result of this about 50 single cross hybrids in different maturity groups are now available. However, fewer than twelve are popular among the farmers. It has been focused in the paper that lack of genetic diversity led to outbreaks of downy mildew. The reasons for high rate of adoption of hybrids in India, and successful hybrid seed production and distribution have also been discussed.

In Africa, the hybrids developed in India have not been successful mainly due to their undesirable maturity and high susceptibility to downy mildew and ergot. Heterosis has been identified in many combinations involving local material. Strategies for development of hybrids in Africa have been discussed. The Indian experience can be considerably useful to Africa and other developing countries in hybrid research and enhancement of pearl millet productivity and stability.

O.P. Govila, Division of Genetics, Indian Agricultural Research Institute, New Delhi 110 012, India; K.N. Rai, Genetic Enhancement Division, ICRISAT Asia Center, Patancheru; 502 324, Andhra Pradesh, India; K.R. Chopra, Mahendra Hybrid Seeds Company, Post Box No. 52, Jalna 431 023, Maharashtra, India; D.J. Andrews, Department of Agronomy, University of Nebraska, Lincoln, NE 68583, U.S.; and W.D. Stegmeier, Fort Hays Branch Agricultural Experiment Station, Kansas State University, Hays, KS 67601, U.S. *Corresponding author.

Pearl millet. *[Pennisetum glaucum* (L.) R. Br.] is grown predominantly in Africa and India, primarily as a grain crop, but also for its stover and fodder. It is generally cultivated in areas with rainfall varying from 150 to 600 mm. It can withstand drought to a great extent, but responds well to good management and higher fertility levels (Nirwal and Upadhyaya, 1979; Singh and Maurya, 1969).

Pearl millet is an excellent forage crop because of its comparatively low hydrocyanic acid content. The green fodder is rich in protein, calcium, phosphorus, and other minerals, with oxalic acid within safe limits (Athwal and Gupta, 1966; Gupta, 1975). It is more digestible when fed green to animals rather than as chaffed straw.

Production and productivity of pearl millet in India are increasing in spite of the reduction in area planted to pearl millet (Table 1). The same is not true for Africa, where production is more or less stagnant (Table 2). The increase of production and productivity in India is related to the widespread use of single cross hybrids based on cytoplasmic-nuclear male sterility (CMS) and to abundant hybrid seed production and supply. Nearly 55% of the total pearl millet area in India is under hybrids and improved open-pollinated varieties (OPVs) (see Rai et al., these proceedings). In comparison, there are no hybrids and relatively little adoption of improved OPVs in African countries.

Pearl millet is a highly cross-pollinated crop, with outcrossing rates in excess of 85 percent (Burton, 1974). It also displays a high degree of heterosis for grain and fodder yields. These two features of pearl millet meet some key biological requirements for exploitation of heterosis in high-yielding cultivars. Work on exploitation of heterosis first started in India in the 1950s (Rao et al., 1951; Chavan et al., 1955) utilizing the protogynous flowering habit of the crop. The discovery of cytoplasmic male sterility by Burton (1958, 1965) fulfilled the need for a viable and economic method of producing pure hybrid seed on a commercial scale.

The pearl millet hybrid program for grain production is a great success story in India, resulting from the gradual evolution of a research and development infrastructure and close interaction between the National Agricultural Research System (in both the public and private sectors) and the International Research Centers with their varying roles and responsibilities. Implications are positive for

Table 1. All India area, production and productivity of pearl millet on triennium basis.

Triennium ending	Area (m. ha)	Production (m.t.)	Productivity (kg ha^{-1})
1977	11.20	4.95	443
1980	11.02	4.75	429
1983	11.46	5.33	465
1986	11.03	5.81	522
1989	10.67	5.19	475
1992	10.47	6.06	577
1995	10.08	7.01	684

Source: Directorate of Economics and Statistics, Government of India

Table 2. Area, production and productivity of pearl millet in Africa on triennium basis.

Triennium ending	Area (m. ha)	Production (m.t.)	Productivity (kg ha^{-1})
1977	16.06	9.88	614
1984	15.52	9.30	598
1991	14.92	10.53	707
1994	16.51	10.07	598

Source: FAO Production Bulletin.

hybrid research and development programs in other developing countries, not only for breeding hybrids but also for seed production and impact generation. This paper reviews the historical aspects and present status of hybrid breeding, testing, and seed production in India and the role of the private sector. Other developing countries can greatly benefit from information about the way hybrids were developed in India for adoption by small scale farmers.

Table 3. Average statewide area, production and yield of pearl millet. Mean of 1992-93 and 1994-95.

State	Area (m. ha)	Production (m.t.)	Productivity (kg ha^{-1})
Rajasthan	4.78	2.17	445
Maharashtra	1.82	1.37	746
Gujarat	1.23	1.23	996
Uttar Pradesh	0.80	0.92	1146
Haryana	0.58	0.60	1024
Karnataka	0.33	0.17	532
Tamil Nadu	0.21	0.26	1201
Madhya Pradesh	0.15	0.13	872
Andhra Pradesh	0.15	0.11	759
All India	10.09	7.00	688

Source: Directorate of Economics and Statistics, Government of India.

Pearl Millet Hybrids in India

In India from 1993 to 1995, pearl millet was grown on an average of ten million hectares with an average grain production level of seven million tons (Table 1). It is the fourth most important food crop, mostly grown in the arid and semi-arid regions, particularly in the northwest parts of the country in the states of Rajasthan, Maharashtra, Gujarat, Uttar Pradesh, and Haryana, which account for nearly 95% of the total pearl millet area (Table 3). The crop is grown in varying ecological environments from very low to high productivity levels.

The first pearl millet hybrid, HB 1, was released in 1965 (Athwal, 1965, 1966). The seed parent was the A_1 cytoplasmic-nuclear male-sterile line Tift 23A, bred in the U.S.(Burton, 1958, 1965). Since then 45 hybrids have been officially released (Table 4) and a similar number developed by the private sector (Table 5). Thus a large number of genetically diverse hybrids are currently available to farmers. Private companies have popularized their hybrids in specific areas of adaptation, further increasing the production of pearl millet.

In spite of their overall success, the pearl millet hybrid programs in India have had occasional setbacks due to downy mildew [*Sclerospora graminicola* (Sacc.) J. Schroet.] epidemics and the potential threat posed by smut [*Moesziomyces penicillariae* (Bref.) K. Vánky; syn. *Tolyposporium pencillariae* Bref.] and ergot [*Claviceps fusiformis* (Loveless)] to single cross hybrids. The hybrids HB 3 and HB 4 were very popular during 1968-74. However, when the seed parent of these hybrids (Tift 23A) became susceptible to downy mildew in 1975, multiplication of hybrids on Tift 23A was discontinued. Two new hybrids produced on seed parent 5141A, BJ 104 and BK 560 (Pokhriyal et al., 1976), became common in pearl millet growing areas in India. The entire hybrid area was occupied by just these two hybrids. BJ 104 was adapted to low rainfall areas but also gave high yields under good management conditions, while BK 560 was adapted to good rainfall areas of the country. Due again to an increase in the downy mildew susceptibility of both parents (5141A and restorer line J 104), hybrid BJ 104 was completely withdrawn from seed multiplication. However, hybrid BK 560 (5141A × K 560-230) is still

Table 4. Pearl millet hybrids released and notified in India as of 1995.

Hybrid	Source	Year of release	Pedigree	Remarks
Hybrids predominantly bred on Tift 23A				
HB 1	Ludhiana	1965	Tift 23A x Bil 3B	
HB 2	Jamnagar	1966	Tift 23A x J 88	
HB 3	Jamnagar	1968	Tift 23A x J 104	Highly popular
HB 4	Kanpur (IARI)	1968	Tift 23A x K 560	Highly popular
HB 5	Kanpur (IARI)	1969	Tift 23A x K 559	
NHB 3	Delhi (IARI)	1975	5071A x J 104	
NHB 4	Delhi (IARI)	1975	5071A x K 560-230	
NHB 5	Delhi (IARI)	1975	5071A x K 559	
PHB 10	Ludhiana	1975	Pb 111A x PIB 155	
PHB 14	Ludhiana	1975	Pb 111A x PIB 228	
GHB 1399	Jamnagar	1975	126 D_2A x J 1399	
Hybrids predominantly bred on 5141A				
BJ 104	Delhi (IARI)	1977	5141A x J 104	Highly popular
BK 560	Delhi (IARI)	1977	5141A x K 560-230	Highly popular
CJ 104	Delhi (IARI)	1977	5054A x J 104	Moderately popular
BD 111	Delhi (IARI)	1977	5141A x D 111	
GHB 27	Jamnagar	1981	5141A x J 2002	
BD 763	Delhi (IARI)	1982	5141A x D 763	
GHB 32	Jamnagar	1983	5141A x J 1188	
HHB 45	Hisar	1984	5141A x H90/4-5	
COH 2	Coimbatore	1984	5141A x PT 1921	
Hybrids on genetically diversified male sterile lines				
CM 46	Delhi (IARI)	1981	5054A x M 46	
MBH 110	MAHYCO	1981	MS 2 x PL 2	Highly popular
PHB 47	Ludhiana	1983	Pb 111A x PIB 1234	
X_5	Coimbatore	1984	Pb 111A x PT 1921	
MBH 118	MAHYCO	1984	MS 2 x PL 3	
ICMH 451	ICRISAT	1986	81A x ICMP 451	Highly popular
ICMH 501	ICRISAT	1986	834A x ICMP 501	
MH 182	Pune	1986	PT 732A x PNBM 83099	
GHB 32	Jamnagar	1986	5054A x J 2002	
Pusa 23	Delhi (IARI)	1987	841A x D 23	Highly popular
HHB 50	Hisar	1987	81A x H 90/4-5	
MBH 130	MAHYCO	1987	MS 2 x PL 4	Moderately popular
HHB 60	Hisar	1988	81A x H 77/833-2	Moderately popular
ICMH 423	ICRISAT	1988	841A x ICMP 423	
MBH 136	MAHYCO	1989	MS 2 x P 16	
HHB 67	Hisar	1990	843A x H 77/833-2	Highly popular
VBH 4	Vijay seeds	1990	VBMS 1A x BBR 19	Moderately popular
EKNATH 301	Nath seeds	1991	NBH5 13A x NB 37	Moderately popular
Current hybrids				
MLBH-104	Mahendra	1991	3A x 13	Highly popular
ICMH 356	ICRISAT	1993	ICMA 88004 x ICMR 356	Moderately popular
Pusa 322	Delhi (IARI)	1993	841A x PPMI 301	Moderately popular
HHB 68	Hisar	1993	842A x H 77/833-2	
Pusa 444	Delhi (IARI)	1994	189A x PPMI-301	Moderately popular
MLBH-267	Mahendra	1995		Highly popular
Pusa 325*	Delhi (IARI)	1995	490A x PPMI-303	

*Identified by AICPMIP workshop

Table 5. Pearl millet hybrids bred by private sector* in India as of 1995.

Name of the Company	Hybrids available
Nath Seeds	EKNATH-201, 301, 302, 2011
	SWAMINATH-10, 12, 16, 20, 401, 1024 and 1038
Ajeet Seeds	AJEET- 11 and AJEET-21
J.K. Seeds	JKBH-26
Hindustan Lever Ltd.	PBH-13, 22, 24, 35
Kalyani Agro Corpn. Ltd.	KBH-1
Ganga Agri Seeds Ltd.	GK-1004, GK-1006
M.S.S.C., Akola	RHRBH-8609, (Shraddha)
MAHYCO	MBH-163, 151, 183, 1101, 191, 118 and 188
ITC Zeneca Ltd.	AH-903, AH-931
ProAgro Seeds	7701, 7601, 9401 and 9402
Mahendra Hybrid Seeds	MLBH-104, 267, 285, 287, 298 and 305

*The pedigree of the hybrids is not known. Most of the hybrids are not tested in the National Program. The seed is sold as truthfully labelled.

cultivated on large areas due to its high grain and fodder yields and farmer demand. Though 5141A is susceptible to downy mildew, its restorer K 560-230 is fairly resistant. Due to the dominant nature of downy mildew resistance, the hybrid does not pose any problems for farmers. During 1981, MAHYCO, a private seed company, released MBH 110, which was very popular in the state of Maharashtra. Again, due to an increase in downy mildew susceptibility, this hybrid was withdrawn by the company after about ten years of successful cultivation.

Since 1986, a large number of hybrids have been released, some of which (ICMH 451, Pusa 23, HHB 67, MLBH 104) are very popular with farmers. Characteristics of some of the hybrids are given in Table 6. Almost all these hybrids were bred from downy mildew-resistant parental lines. Significantly, in all these hybrids, the A_1 CMS system has been utilized, but there is no evidence that A_1 CMS is associated with downy mildew resistance. At this stage, genetically diverse A-lines were utilized in the breeding program in India. Characteristics of some of the A-lines are given in Table 7. Considerable efforts have gone into the development of these A-lines at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru; the Indian Agricultural Research Institute (IARI), New Delhi; other institutions in the National Agricultural Research System (NARS) in India; and the Fort Hays Branch Experiment Station of Kansas State University, in the U.S.

An evaluation of some newly developed, downy mildew-resistant A-lines (Table 8) was carried out at IARI, New Delhi (Madhusudhana, 1996; Venkatachalam, 1996) to assess the diversity available among them for their per se performance and hybrid performance. The range and variance for characters (Table 9) clearly indicated adequate diversity among the new A-lines in terms of their performance per se. Flowering time ranged from 47 to 61 days, and height ranged from 106 to 168 cm. Similarly, the range and variance for effective tiller number, panicle length, and panicle width indicated adequate variability among these parental lines. In case of grain yield

Table 6. Characteristics of some of the popular hybrids released in India.

Hybrid	Parentage	Average grain yield (kg ha^{-1})	Days to 50% flowering	Maturity (days)	Average plant height (cm)	Tillering	Adaptation	Remarks
HB 3	Tift 23A x J-104	2250	45-48	75	165	Profuse	All India dry tract	Fair degree of resistance to downy mildew.
HB 4	Tift 23A x K-560	2298	50-55	85	175	Profuse	All India	Suited to both rainfed and irrigated areas but susceptible to downy mildew.
BJ 104	5141A x J-104	2110	45-50	75-80	150	Profuse	All India	Suited to both rainfed and irrigated areas, fertilizer responsive.
BK 560	5141A x K 560-230	2200	50-55	85-90	180	Profuse	All India	Resistant to downy mildew.
Pusa 23	841A x D 23	2312	47-52	77-82	160	2-4	All India	Drought tolerant, downy mildew resistant.
Pusa 322	841A x PPMI-301	2463	48-52	75-80	160	2-4	All India	Resistant to downy mildew, lodging.
ICMH 451	81A x ICMP 451	2400	50-55	85-90	175	2-3	All India	Resistant to downy mildew and lodging, drought and salinity.
HHB 60	81A x H 77/833-2	2400	44-47	74-76	190	High	Haryana state	Downy mildew resistant, suited to early and late sowing.
HHB 67	843A x H 77/833-2	2135	40-42	62-68	150	High	Haryana and adjoining drought prone areas	Downy mildew resistant, suited to early and late sowing.
ICMH 356	ICMA 88004 x ICMR 356	2450	45-50	75-80	160	1-4	All India	Resistant to downy mildew.

Table 7. Morphological features of some important pearl millet male sterile lines.

A-line	Days to 50% flowering	Plant height (cm)	No. of tillers/ plant	Panicle width (cm)	Panicle length (cm)	1000-grain weight (g)	Downy mildew reaction	Remarks
5141A	58	155	3.4	1.49	18.9	6.0	Susceptible	Good for high & low input conditions
5054A	53	150	5.1	1.30	17.54	5.3	Resistant	Good for drought prone areas
81A	60	75	2.3	1.40	20	7.6	Resistant	Good for high input conditions
841A	50	165	2.6	1.95	15.20	6.4	Resistant	Good for medium maturity hybrids
843A	42	105	4.2	2.05	16.50	10.5	Susceptible	Good for early hybrids
842A	49	102	2.1	1.8	16.00	11.7	Susceptible	Good for early hybrids
189A	53	160	2.1	2.06	18.3	6.8	Highly resistant	Good for medium maturity
ICMA 88004	45	141	4.0	1.2	13.16	12.3	Highly resistant	Good for early hybrids

Ref.: AICPMIP trial IIIA

Table 8. CMS lines (A_1) utilized for heterosis study.

Study - 1[1]	Study - 2[2]
843A	1049A
81A	1023A
863A	1139A
123A	1161A
Tift 23A	1109A
5141A	ICMA 91333
841A	ICMA 91444
189A	ICMA 91777
480A	ICMA 92444
393A	ICMA 92777
267A	ICMA 92888
278A	841A (control)
	843A (control)
	5141A (control)

[1]Venkatachalam S.R. (1996)
[2]Madhusudhana R. (1996)

per plant, the range (27.3 to 40.5 g) and variance (9.8) indicated greater genetic differences for their potentiality. The diversity among these A-lines was further reflected in the performance of their hybrids (Table 9). Individual plant grain yields of the hybrids ranged from 36.6 g (56.5% below Pusa-23) to 143.9 g (71.4% over Pusa 23), and variance (389) was high. Nine of the hybrids had significantly positive economic heterosis for this character. Similarly, a good amount of diversity in the performance of hybrids was observed for various other characters. Thus, it is apparent there is sufficient variability among available A_1 cytoplasmic male-sterile lines to permit generation of a wide range of genetically diverse hybrids with high grain yield.

Based on the history of hybrid development in India, it is evident that some popular hybrids — most importantly, HB 3, HB 4, BJ 104 and MBH 110 (Dave, 1987; Govila, 1988) — had to be withdrawn from farmers' fields because of an increase in their susceptibility to downy mildew. A critical appraisal of the situation may now reveal that failure of these hybrids was mainly due to lack of diversity in the parental lines, as all hybrids were first based on Tift 23A, then on 5141A. Out of 20 hybrids available then, 16 were based on three male-sterile lines [5141A (8), Tift 23A (5) and 5054A (3)]; three restorers were male parents of nine commercial hybrids [J 104 (4), K 560-230 (3) and K 559 (2)]. These facts indicate that outbreaks of downy mildew were merely due to a narrow genetic base among CMS lines and restorers (and thus their hybrids) and their subsequently evident lack of durable genetic resistance to downy mildew, rather than to any deleterious effects of A_1 cytoplasm.

Hybrid Research and Testing Network

Prior to 1993, the entire pearl millet growing area in India was treated as one unit for multilocational testing, although in the state breeding programs, requirements for local adaptation were attempted to be catered for. However, now the country has been divided into three zones (see Fig. 1).

Zone A1 is composed of parts of the states of Rajasthan, Gujarat, and Haryana. The zone is drought-prone with annual rainfall of less than 400 mm, light sandy soils, and high temperatures.

Zone A is composed of the remaining parts of the states of Rajasthan, Gujarat, and Haryana and the entire pearl millet growing areas of other northern states like Uttar Pradesh, northern Madhya Pradesh, and Delhi. The zone has sandy to sandy loam soils and an annual rainfall of greater

Table 9. Performance per se of male sterile lines and heterosis of their hybrids.

Character	CMS lines: Per se performance range	CMS lines: Per se performance variance	Hybrids: Performance (range)	Hybrids: Heterosis (%)* (range)
Study I				
Days to 50% flowering	43.0-57.0	14.8	43.00-59.00	-14.0-18.0
Plant height (cm)	108-182	582	160-250	-25.5-21.10
Productive tillers	1.0-2.8	1.14	1.0-3.5	-20.0-180.0
Panicle length (cm)	16.4-25.5	8.0	17.4-28.3	-29.58-14.48
Panicle width (cm)	1.5-2.6	0.1	1.7-2.8	-19.32-33.8
1000-grain weight (g)	4.2-11.0	5.0	6.0-13.2	-50.3-9.8
Grain yield/plant (g)	10.8-42.5	19.6	20.4-60.0	-49.0-50.0
Study II				
Days to 50% flowering	47.0-61.0	10.1	41.0-60.0	-21.0-14.0
Plant height (cm)	106-169	417	155-269	-18.2-41.4
Productive tillers	1.9-3.2	0.2	1.6-5.0	-50.0-58.0
Panicle length (cm)	16.6-24.5	5.0	19.0-29.0	-27.0-12.8
Panicle width (cm)	1.5-2.6	0.1	1.7-2.9	-20.5-32.1
1000-grain weight (g)	18.1-30.6	2.5	17.6-42.1	-17.3-97.4
Grain yield/plant (g)	27.3-40.5	9.8	36.4-143.9	-56.6-71.5

*over Pusa 23

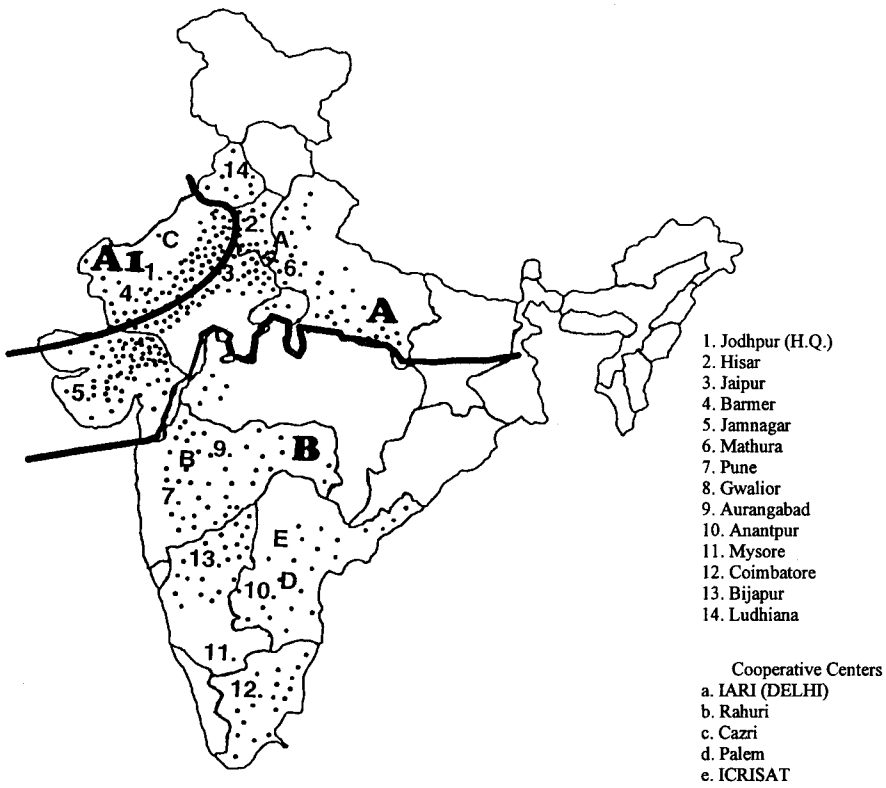


Figure 1. Pearl millet production zones and distribution of pearl millet research centers in India.

than 400 mm; irrigation facilities are available in some areas.

Zone B is comprised of the southern states of Maharashtra, Karnataka, Tamil Nadu, and Andhra Pradesh with greater than 400 mm rainfall, heavy soils, and mild temperature conditions. The zone has shorter days compared to Zones A1 and A.

Even this zone designation is not adequate since the following facts pivotal to further zoning merit serious attention:

- Pearl millet is a quantitative short day plant. As one moves its cultivation to northern latitudes, the flowering behavior is conditioned by this photoperiodic requirement.
- Pearl millet is predominantly a rainfed crop. Its planting is critically conditioned by the onset and quantity of southwest monsoon rains, which vary according to geographical location. Thus "maturity" becomes a vague and relative term and does not have the same implication even within one zone.
- Within each zone, areas of advanced agronomy with input-intensive conditions and areas of intensive stress conditions should be recognized.

Testing of hybrids is carried out through the Indian Council of Agricultural Research, administered by the All India Coordinated Pearl Millet Improvement Project (AICPMIP). The project has 14 research centers and four voluntary centers (not funded through AICPMIP) (Fig. 1). Both public and private research organizations contribute hybrids for testing in national trials conducted at sites located in different agroclimatic zones of the country (Fig. 2). ICRISAT works in close collaboration with the entire NARS. Table 10 lists the state-wide hybrid trials conducted through AICPMIP during 1991-95. Although Rajasthan represents 47% of the total pearl millet-growing area in the country, results from only 26 effective trials were reported from this state during these five years of testing. Andhra Pradesh, on the other hand, represents only 1.5% of the total pearl millet area in the country, but results from 65 effective trials were reported from this state during the same period. Similarly, a comparison of A and B Zone trials revealed that the testing system in India needed reorientation for identifying promising location-specific hybrids within the states. Keeping this situation in view, the Indian Council of Agricultural Research has shifted the AICPMIP headquarters from Pune in Maharashtra to Jodhpur in Rajasthan, which falls in the A1 Zone. As a result, research priorities and testing sites for hybrids are being reoriented in the A and A1 Zones.

Hybrid testing starts when the cooperating centers (ICAR Institutes, State Agricultural Universities, and private companies) nominate their promising hybrids for the Initial Hybrid Trial (IHT) (Fig. 3). The hybrids found promising for grain yield and downy mildew resistance are promoted to the Advance Hybrid Trials (AHTs). AHTs are conducted on a zonal basis for two years. Similarly, agronomic data and information on downy mildew resistance and pests are recorded on the hybrids under testing. On-farm trials are conducted simultaneously by the extension staff of ICAR Institutes, state agricul-

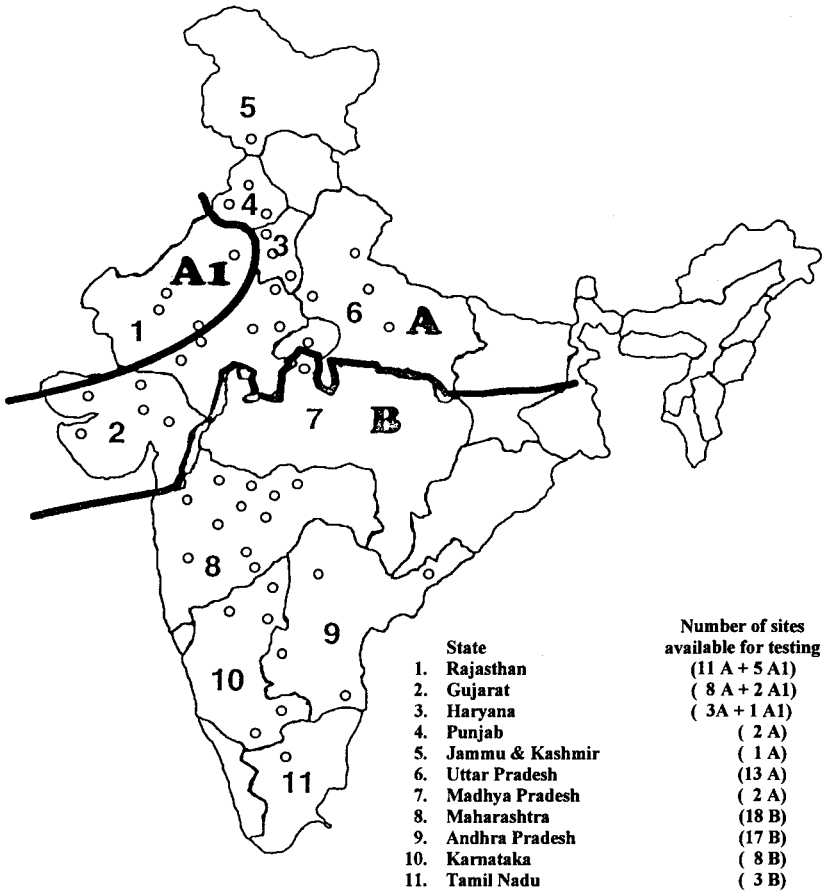


Figure 2. Testing network for pearl millet hybrids in India.

tural universities (SAUs) and private companies. Normally it takes three years of testing to identify a promising hybrid. The originating breeder has to submit to the annual pearl millet workshop a proposal for identification of hybrids for release. After agreement of the workshop, the proposal is sent to the Government of India for notification and release by the Central Varietal Release Committee. The seed multiplication chain (Breeder-Foundation-Certified) starts after notification of the hybrid.

Apart from grain yield, major emphasis during testing is placed on downy mildew incidence, both on hybrids and parental lines. Hybrids showing more than 10% of the downy mildew incidence on suscepti-

Table 10. Hybrid trials conducted through AICPMIP in different states of India during 1991-95.

States	Pearl millet area (m. ha)	% of area	Number of trials		
			Conducted	Rejected	Effective
Zone A					
Rajasthan	4.77	47.60	30	4	26
Gujarat	1.22	12.18	75	13	62
Uttar Pradesh	0.80	7.96	21	3	18
Haryana	0.57	5.69	26	1	25
Madhya Pradesh	0.15	1.50	13	-	13
Total	7.51	74.93	165	21	144
Zone B					
Maharashtra	1.82	18.16	82	6	76
Karnataka	0.33	3.29	30	1	29
Tamil Nadu	0.21	2.01	21	6	15
Andhra Pradesh	0.15	1.50	72	7	65
Total	2.51	24.96	205	20	185
All India	10.02		370	41	329

Source: All India Coordinated Pearl Millet Improvement Project Annual Reports 1991 to 1995.

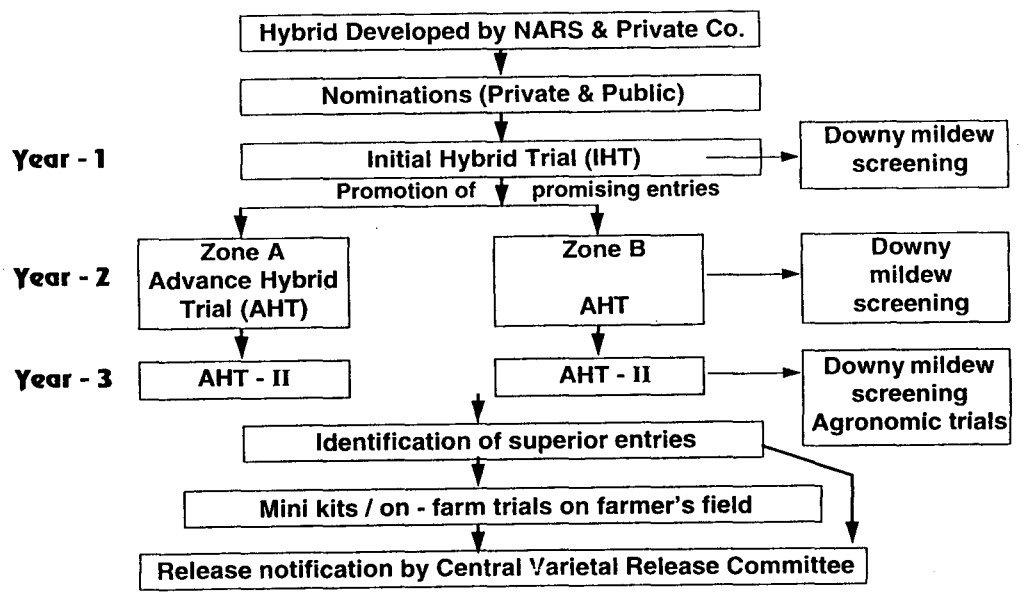


Figure 3. Procedure for hybrid testing and release through All India Coordinated Pearl Millet Improvement Project.

ble check HB 3 are rejected from the first year onward. Three years of testing for downy mildew resistance reduce the risk of releasing a susceptible hybrid. This procedure was not adopted in India when the first popular hybrids, HB 3 and HB 4, were released. Similarly, no information on downy mildew resistance was available on the seed parents of hybrids BJ 104 and BK 560. Presently, parental lines of hybrids also are subjected to downy mildew testing from the second year onward. Downy mildew sick plots have been developed at many locations in the country (ICRISAT Asia Center, Mysore, Pune, Hisar, Jaipur, etc.). Some of the recently bred male-sterile lines that have been widely tested and found resistant to downy mildew are 863A, ICMA 88004, ICMA 89111, 189A, and 490A. It is evident that India now has a very strong research/development and testing network for pearl millet hybrids. Further refinement of the system is continuing. It may be incorrect to conclude that parental lines Tift 23A, 5141A, 5071A, and J 104 of the first released hybrids were cases of breakdown of downy mildew resistance. These lines probably did not have rigorous evaluation against downy mildew before their hybrids were released. Extensive downy mildew in the earlier released hybrids was due to lack of diversity in the breeding material, as the hybrids were all based first on Tift 23A and then on 5141A.

Seed Production Network

With a view to providing quality seed for the farmers in India, the National Seed Corporation (NSC) was established in 1963 at the central level. Subsequently, State Farms Corporation of India (SFCI) came into existence in 1969. Later, an urgent need for the establishment of seed corporations in each state was felt. Thus in the early 1980s, state seed corporations were established in Andhra Pradesh, Assam, Bihar, Haryana, Karnataka, Maharashtra, and Madhya Pradesh.

The Government of India declared seed an essential commodity in 1955, and, anticipating the likely growth of the Indian seed industry and the need for quality control, enacted the Seeds Act in 1966. The seed rules framed under the Seeds Act were established in 1968 and amended as needed from time to time. A seed control order was issued in 1983. Under the Seeds Act, the Central Seed Committee and Central and State Seed Testing Laboratories were established, with power to notify varieties, fix minimum limits of germination and purity, and regulate sale of seeds. A seed certification mechanism was devised, which covered certification of seeds of foreign origin as well. By-laws for the export and import of seeds also were formulated.

The National Research Centers, AICPMIP, SAUs, NSC, SFCI and some seed companies are producing breeder and foundation seeds of parental lines of pearl millet hybrids. ICRISAT Asia Center produces breeder seed, and the private sector in India also is involved in large scale production of foundation and certified seeds of publicly bred hybrids, as well as their own proprietary hybrids. The certified seed production program is organized primarily in farmers' fields by various seed corporations and private companies.

The following procedure has been adopted to produce breeder seed (Rai, 1992).

1. The Directors of Agriculture, NSC, SFCI and other central agencies submit indents—indications of their likely requirements—for breeder seed directly to the Department of Cooperation (DC)-Seeds, Ministry of Agriculture, Government of India (GOI). Private companies submit their indents to the DC-Seeds through the Seed Association of India.

2. The DC-Seeds communicates compiled indents to the Assistant Director General-Seeds, Indian Council of Agricultural Research, who, in turn, passes on the indents to the Pearl Millet Project Coordinator (PC).

3. In BSP-1, the PC communicates the Breeder Seed Production Plan (BSP) to all those mentioned in steps one and two above, as well as to agencies responsible for breeder seed production.

4. In BSP-2, after actually sowing nucleus seed for breeder seed production, the concerned breeder communicates the sowing date, area, expected production, and location to a monitoring team nominated by the PC.

5. In BSP-3, a joint monitoring team inspects the breeder seed crop and presents a report about its conformity to genotype description, adequacy of isolation, etc.

6. In BSP-4, the breeder seed is harvested and production figures are recorded.

7. In BSP-5, results of grow out tests are recorded and the DC-Seeds communicates the allocation of breeder seeds to all concerned.

8. In BSP-6, the breeder seed distribution plan is communicated by the DC-Seeds to all indentors who take the delivery of seeds from the concerned breeder.

9. In BSP-7, the DC-Seeds communicates availability of foundation seed produced from supplies of breeders seed.

The Government of India also assesses certified seed demand every year for all states and allocates certified seed production programs to various seed-producing organizations.

Certified Seed Production

In both the public and private sectors, large scale certified seed production of released and notified hybrids occurs in Gujarat, Andhra Pradesh, Maharashtra, Karnataka, and Tamil Nadu during the dry season from January to April every year. In compliance with the Seeds Act of 1968, seed growers must register the area under seed production with their state's seed certification agency, which is empowered to control the quality of seed and assess the quantities produced every year. The certified seed production of pearl millet hybrids and OPVs from 1988 to 1996 is given in Table 11. Popularity of public-bred hybrids can also be judged from these seed production trends.

In India, the private sector has recently started producing large quantities of "truthfully labeled seed," which need not

be certified by the seed certification agencies. It is difficult to assess the quantity of such seeds produced and marketed by the private sector.

Adoption of Hybrids in India

The extent of adoption and impact of hybrids in India continues to be fairly uneven, with greater impact in areas presenting relatively more favorable climate and soil conditions and better developed state agricultural and extension services, and, more recently, those with well-placed private research and development agencies.

HB 3, HB 4, BJ 104, BK 560, ICMH 451, Pusa 23, MBH 110, MLBH 104, and HHB 67 are among the most widely cultivated past and present pearl millet hybrids. Adoption of hybrids in India has been rapid since the release of hybrid HB 3 (Tift 23A × J 104). Hybrids and improved OPVs presently cover about 55% of the total pearl millet area in India. The proportion of fresh seed usage varies from state to state. Andhra Pradesh and Gujarat rank highest in fresh seed usage, followed by Haryana, Maharashtra, and Karnataka (Table 12).

Over 50% of the pearl millet hybrid seeds produced are sold in Maharashtra and Gujarat, indicating that the area under hybrids is greater in these states than in others. Although Rajasthan has the largest area under pearl millet, adoption of hybrids in this state has been very low, primarily due to the unavailability of suitable hybrids for areas characterized by adverse agroclimatic conditions and moisture stress. The AICPMIP and private companies with well-organized research and development infrastructures are now targeting Rajasthan as a major market and breeding hybrids to withstand harsh growing conditions and moisture stress. Thus, the area under hybrids in Rajasthan is likely to increase by the end of this century. The adoption of hybrids has been mainly affected by the following factors.

Stable grain and fodder yields

Hybrids offer stable yields of grain and fodder, provided they are of desirable maturity. Adoption has been very high in the states of Gujarat and Andhra Pradesh, moderate in Maharashtra, Karnataka, and Haryana, and poor in Rajasthan and Uttar Pradesh. The rate and level of adoption also has been influenced by research, extension activity, and seed production programs of the individual states.

Desirable maturity

The most desirable maturity period for hybrids to be widely adopted under Indian conditions is around 70-75 days. The popular hybrids HB 3 and BJ 104 were in this maturity range. Hybrids with maturity of more than 75 days tend to experience terminal drought stress. Among the most recent hybrids, Pusa 23, HHB 67, and MLBH 104 have been adopted by farmers because of early maturity. Pusa 23 has an added advantage of high biomass production. A medium maturity and high-yielding hybrid, ICMH 451 (85 days), also is popular in areas with good rainfall and under better management. Earliness also is useful because it allows pearl millet to be grown in multiple cropping systems. In Haryana, HHB 67 is preferred by the farmers because it allows convenient double cropping of pearl mil-

Table 11. Certified seed production of public sector pearl millet hybrids and OPVs (tons).

Cultivar	Institute	1988	1989	1990	1991	1992	1993	1994	1995	1996
Hybrids										
BK 560	IARI	3774	4761	4351	1557	2966	2509	1448	858	1466
Pusa 23	IARI	-	299	688	1407	1950	2245	1687	2204	2272
CJ 104	IARI	138	227	16	40	185	184	81	45	14
Pusa 322	IARI	-	-	-	-	-	-	98	110	-
ICMH 451	ICRISAT	4985	6575	475	1053	245	2846	1273	794	1022
ICMH 356	ICRISAT	-	-	-	-	-	-	0.4	113	-
HHB 50	HAU	733	322	240	96	264	-	77	45	28
HHB 60	HAU	-	26	22	11	175	156	102	125	91
HHB 67	HAU	-	-	74	279	149	540	1029	919	1314
GHB 30	GAU	809	393	146	157	119	-	19	-	-
GHB 235	GAU	-	-	-	-	-	-	21	-	-
OPV										
WC-C75	ICRISAT	1668	2603	608	556	587	263	268	202	329
ICTP 8203	ICRISAT	-	900	3335	1545	2960	2446	1263	2216	1731
ICMS 77003	ICRISAT	319	308	225	165	240	-	-	151	3
ICMV 221	ICRISAT	-	-	-	-	-	-	3	-	56
ICMV 155	ICRISAT	-	-	-	-	-	-	4	2	23
Total		12426	16414	10180	6066	12048	11189	7373	7784	8358
% contribution of	IARI	31.48	32.21	49.65	44.39	42.33	44.13	44.94	41.32	44.89
% contribution of	ICRISAT	56.10	63.27	45.60	49.05	33.46	49.64	39.17	44.68	37.85
% contribution of	Others	12.42	4.52	4.75	6.56	24.21	6.23	15.89	14.00	17.26

Source: 1) Seed Certification Agencies of the states of Gujarat, Andhra Pradesh, Maharashtra, Tamil Nadu and Karnataka.
2) The figures were obtained as area offered for certification (acres) and have been extrapolated to tons @ 400 kg seed production per acre.
3) Figures do not include truthfully labelled seed produced by private companies.

Table 12. Statewide seed requirement, availability and percentage of area covered.

State	Total area (m ha)	Total seed requirement (000 tons)	C/S & TL seed availability during 1991-92 (000 tons)	% of pearl millet under high-yielding varieties
Rajasthan	4.85	19.4	4.1	21.13
Gujarat	1.15	4.6	5.5	100.00
Haryana	0.61	2.4	1.3	54.17
Maharashtra	1.93	7.7	4.1	53.25
Uttar Pradesh	0.77	3.1	0.5	16.13
Tamil Nadu	0.26	1.0	0.4	40.00
Karnataka	0.42	1.7	0.8	47.06
Andhra Pradesh	0.23	0.9	1.5	100.00
Madhya Pradesh	0.17	0.7	0.2	28.57
Others	0.06	0.3	-	-
All India	10.45	41.8	18.4	44.02

Source: National Conference on Seeds Agra.

let with *Brassica* or chickpea (*Cicer arietinum* L.).

Resistance to downy mildew

The main reason for decline in grain yield of the hybrids HB 3 and HB 4 in India during the 1970s was downy mildew. Later, two more popular hybrids, BJ 104 and BK 560, succumbed to downy mildew during 1982-83. A hybrid from the private sector, MBH 110, also met the same fate. Thus, breeding of downy mildew-resistant male-sterile and restorer lines gained high priority in India, contributing to greater adoption of hybrids. Several hybrids with resistance to downy mildew (such as ICMH 451, Pusa 23, HHB 67, ICMH 356, Pusa 322, Pusa 444, and MLBH 267) have been released in India since 1985 and are under moderate to large scale cultivation.

Economical seed production

Public sector seed-producing organizations in India are required to produce and sell certified hybrid seed to farmers at a specified controlled rate. Thus, certified seed production per unit area becomes very important. One of the main factors for the fast adoption of the hybrid Pusa 23 is high productivity of the female parent, 841A (Table 13), leading to higher monetary returns to seed producers. A seed-producing farmer gets 20% higher profits from multiplying Pusa 23 than from ICMH 451. Good synchronization between male-sterile and restorer lines, and high fodder and seed yield from the parental line in the certified seed production plot also contribute to high seed production profits and quick adoption (as was the case with hybrid Pusa 23). It is implied that along with economical seed production, the hybrid should be acceptable to farmers.

Role of the Private Sector

Private research to develop superior hybrids was initiated by a few seed companies in the mid-sixties. Persistent efforts by MAHYCO's pearl millet research team led to the development of MBH 110, the first private sector pearl millet hybrid released by the Central Variety Release Committee in 1981. Because of its short duration, resistance to downy mildew,

Table 13. Certified seed production of Pusa 23 and ICMH 451.

Hybrid	A-line	Area (ha)	Seed production (tons)	Average seed yield (kg ha^{-1})
ICMH 451	81A	496	488	983
Pusa 23	841A	467	552	1183

Source: Gujarat Cooperative Marketing Federation, 1992.

and large grains, and in the absence of downy mildew-resistant publicly-bred hybrids, MBH 110 nearly monopolized the pearl millet hybrid market in Maharashtra until it suddenly succumbed to downy mildew in 1988-89.

The number of companies with private research and development, including multinationals, has steadily increased from about 12 in 1987-88 to over 30 by 1995, largely due to the GOI's recognition of the private sector's performance capabilities and announcement of a New Seed Policy in 1988. Established domestic companies like Mahendra Hybrid Seeds Company, which initiated a pearl millet breeding program in 1986, obtained a wide range of germplasm from national and international research centers, and concentrated on developing superior pearl millet hybrids with early maturity and wide adaptability. Their first hybrid, MLBH 104, was released by the Central Variety Release Committee in 1991. This company also conducted large scale demonstrations in farmers' fields in major pearl millet growing areas during 1990-91. Because of its short duration, medium height, synchronous tillering, and bold grayish grains, this hybrid was widely accepted by farmers and filled the gap created by withdrawal of MHB 110. The company is promoting another hybrid, MLBH 267, released in 1995. Several additional hybrids bred by the private sector have been released by the Central Variety Release Committee (Table 4).

About 50 single cross hybrids of pearl millet are now on the market. Only a few of these hybrids were entered in AICPMIP trials. Many companies do not even conduct multilocational trials through AICPMIP before entering their product in the market; therefore, most hybrids have a short market life because of the rapid breakdown of their downy mildew resistance. However, of these 50 hybrids, fewer than ten are popular among farmers.

The main focus of many private seed companies has been pearl millet and sorghum hybrid seed production. With a few exceptions, they thrive on hybrids and parental lines developed by public sector institutions, NARS, and international research centers. These institutions are open and bring out the details of the materials every year. The scientists working in the private sector are part of the visiting teams to all experiments and get material from the public sector. It is for them to decide what names or numbers they give to their products, which get a high premium in the market backed by considerable production, marketing, and advertising support.

There is no denying that the private sector, because of its efficient infrastructure, plays an important role in supplying seeds to farmers. It is interesting to note that from 1993-94 to 1995-96, 62-70% of

pearl millet seeds were produced by the private sector (Table 14).

Pearl Millet Hybrids for Africa

The lessons learned from the hybrid program in India are important for breeding successful hybrids in Africa (Andrews and Bramel-Cox, 1994). Existing Indian hybrids are not adapted to most pearl millet production areas in Africa due to diseases, pests, and differences in length of the growing season. Diseases and pests (principally downy mildew, ergot, and stem borer) in West Africa are much more aggressive than in India, and hybrids with high levels of durable resistance are needed. Most hybrids and A-lines bred in India are completely destroyed in the seedling stage by downy mildew; if not, they may be attacked by ergot at flowering.

Progress in Identification of Hybrids

The earliest reported information on hybrids in Africa came from two years of tests of intervarietal hybrids, conducted in 1971-72 by IRAT in Senegal (Lambert, 1983). Of 35 hybrids made from 35 open-pollinated varieties on Souna 2, the cross with Iniadi (a landrace from the Togo/Ghana region) gave 59% more grain yield than Souna 2 (Andrews and Kumar, 1996). Two varieties from Mali also produced hybrids that had 27-31% more grain yield than Souna 2 (Table 15). Similar research by Ouendeba et al. (1993, 1995) showed that intervarietal hybrids outyielded the higher-yielding parental populations by 25-80%. ICRISAT, in collaboration with national programs, has recently conducted extensive hybrid tests in both southern and western Africa. Intervarietal hybrids yielded 18-87% more than the best parent in Zimbabwe and 15-99% more than the best parent in Tanzania (Monyo et al., 1996).

Following several years of testing in West Africa, topcross hybrids (inbred × variety hybrids [IVHs]) were in on-farm tests in 1996. In 1995, an advanced IVH trial was grown in Niger, Mali, Chad, and Togo (ICRISAT, 1996). Although hybrids matured earlier at individual locations, they gave up to 8% higher yields than the best variety in the test (1995 was an unusual year of adequate rainfall when late-maturing OPVs were able to give their best yields). Six of the nine hybrids in the test averaged 4-36% more grain yield than their corresponding pollinator OPVs. Three hybrids made with variety GB 8735 showed the highest yield advantages (30-36%), indicating its superior combining ability. It may be noted that GB 8735 is derived from an Iniadi ×

Table 14. Contribution of private company hybrids towards total seed production in pearl millet (1993-94 to 1995-96).

Research sector	(000 tons) 1993-94	1994-95	1995-96
Public hybrids/varieties	5.62	6.51	4.56
Private hybrids	9.38	11.30	11.18
Total	15.00	17.81	15.75
% contribution of Private hybrids	62.5	63.5	71.0

Source: Seed Production & Market Survey.

Table 15. Average grain yields of three highest-yielding West African intervarietal pearl millet hybrids (mean of 1971 and 1972 at Bambay, Senegal).

Intervarietal hybrid	Grain yield (kg ha^{-1})	Percent of control
Iniadi x Souna 2	3660	159
Dori x Souna 2	3020	131
M2D2 x Souna 2	2920	127
Souna 2 (control)	2300	100

Source: Lambert, 1982.

Souna cross; and Iniadi was found to be the best combiner in IRAT's 1971-72 intervarietal hybrid tests.

Multilocational analysis and agronomic evaluation under various levels of soil fertility, drought stress, and plant density have shown that topcross hybrids give a more stable performance than the pollinator OPVs, and their superiority over OPVs increases as stress increases. For example, under low fertility conditions, topcross hybrids averaged 39% more grain yield than OPVs (ICRISAT, 1996). In Namibia, a topcross hybrid (SDMH 92012) made with Okashana 1 averaged 27% more yield than Okashana 1 itself over five locations (ICRISAT, 1995). Okashana 1 (Witcombe et al., 1995) is an early maturing and large-seeded variety—developed from a population based largely on Iniadi germplasm—that is already widely grown in Namibia.

Thus, it is possible to find high levels of heterosis between varieties within the same region and between different varieties and inbreds. Manifestation of this level of heterosis is encouraging for launching a commercial hybrid development program for pearl millet in Africa.

Strategies for Development of Hybrids in Africa

As mentioned earlier, A-lines and hybrids bred in India do not perform well under African conditions. There are, however, practical solutions to these problems that positively indicate the type of hybrids needed in these regions. There are alternatives to single cross hybrids based on A-lines in pearl millet, and the use of a locally adapted OPV as a hybrid parent can confer durable disease resistance as well as local adaptation to topcross hybrids (Talukdar et al., 1996).

Pearl millet hybrids can be made without CMS by utilizing protogyny, a biological characteristic of flowering in pearl millet. These hybrids can be made by using fertile dwarf inbred seed parents with less than 5% selfing in the female. When the pollinator is the dominant tall phenotype, even 20% selfing in the dwarf female does not affect hybrid performance.

Research has shown that greater ergot susceptibility of single cross hybrids based on the A_1 system is due to incomplete restoration of male fertility (i.e., all pollen is not fertile) and to the uniformity of the single cross hybrid, which causes the first panicles on all plants in a field to flower at the same time and thus become female fertile (due to protogynous flowering) before any pollen is produced, providing an ideal opportunity for ergot (Thakur et al., 1989, 1991; Rai and Thakur, 1995).

Landrace varieties and improved OPVs have a built-in capacity to escape ergot, because they are, in fact, genetically variable populations. This results in a narrow spread in flowering, and the first few earliest panicles to flower are quite adequate to provide sufficient pollen to protect the larger number flowering later (indeed this may be a valuable attribute of the weedy "shibras" that always flower earlier than most West African pearl millet cultivars.

It is prudent to conclude that pearl millet hybrids in Africa must be made with an OPV (landrace or improved) as one or both parents and should avoid male sterility (i.e., use of fertile inbred line × variety hybrids [IVH], where a seed parent line or narrow based population is pollinated by an adapted OPV using protogyny). This type of hybrid capitalizes on OPV breeding, and the development time for the hybrid is short, requiring only that a suitable seed parent be identified. There also is no need for the male parent OPV to carry genes for fertility restoration of any CMS system. In theory, the maximum expression of heterosis is achieved between inbred lines, but in practice in less than ideal production situations, there is little difference between inbred × inbred and inbred × variety hybrid yields. Intervarietal hybrids are also likely to have better environmental buffering and give more stable yields across unpredictable environments — a much needed cultivar quality in African pearl millet growing regions.

A new cytoplasmic male sterility system, A_4 (Hanna, 1989), now offers complete restoration of male fertility (Andrews and Rajewski, 1994). This CMS system may be useful in breeding hybrid seed parents for Africa provided it can be demonstrated that its use is not associated with increased susceptibility to ergot.

Seed Production

Sufficient evidence shows that topcross hybrids and intervarietal hybrids are visibly superior to locals in grain yield. Nigeria may provide a better platform for their popularization in Africa, because pearl millet farmers there are relatively more market-oriented and private seed companies in Nigeria provide the necessary infrastructure for hybrid seed production and distribution. Private companies at present do not have a concept of interpopulation hybrids. Therefore, a continuous interaction with them on all aspects (hybrid yield advantage, variability in the parental population and hybrids, and maintenance of parental populations) will be desirable from the very beginning. Namibia provides an example of successful pearl millet seed multiplication based on supervised farmer production as seed is brought and sold at economically attractive prices.

Conclusion

The Indian seed industry has reached a stage of maturity and is in a position to shape itself to compete at national and international levels. Recent economic reforms are opening up opportunities and challenges offered by the globalization of agriculture. In its current state of development, the Indian seed industry, working closely with Indian farmers, can produce high quality seeds to meet international standards at globally competitive prices. The policy environment in India is conducive to seed exports. There is a possibility that once a suitable hybrid is developed for African conditions, its seed can be produced easily and economically in India. The private sector in India can play an important role in this direction.

In African countries, NARS have to be strengthened for development of improved hybrids. Some areas that need attention include training of scientists, exchange of genetic material, joint research with ICRISAT, an improved testing sys-

tem, and seed production. The Indian experience can be considerably useful to Africa and other developing countries in hybrid research and enhancement of pearl millet productivity and stability.

Acknowledgment

The senior author is grateful to R. Madhusudhana and S.R. Venkatachalam for providing valuable assistance in the preparation of this manuscript.

References

Andrews, D.J., and K.A. Kumar. 1996. Use of the West African pearl millet cultivar Iniadi in cultivar development. Plant Genetic Newsletter 105:15-22.

Andrews, D.J., and P.J. Bramel-Cox. 1994. Breeding cultivars for sustainable crop production in low input dryland agriculture in tropics. p. 211-222. *In* Buxton, D.A. (ed.) Intern. Crop Sci. I CSSA, Madison, W.I.

Andrews, D.J., and J.F. Rajewski. 1994. Male fertility restoration and attributes of the A_1 cytoplasmic nuclear male sterile system for grain production in pearl millet. Intl. Sorghum and Millets Newsletter 35:64.

Athwal, D.S. 1965. Hybrid bajra makes a new era. Indian Fmg. 15:6-7.

Athwal, D.S. 1966. Current plant breeding research with special reference to *Pennisetum*. Indian Journal of Genetics and Plant Breeding 26A:73-85.

Athwal, D.S., and V.P. Gupta. 1966. Genetic evaluation of grain fodder quality of *Pennisetum*. Annual Research Report 1965-66, Punjab Agricultural University, Ludhiana, Punjab, India.

Burton, G.W. 1958. Cytoplasmic male sterility in pearl millet [Pennisetum glaucum (L.) R. Br.]. Agronomy Journal 50:230.

Burton, G.W. 1965. Pearl millet Tift $23A_1$ released. Crops and Soils 17:19.

Burton, G.W. 1974. Factors affecting pollen movement and natural crossing in pearl millet. Crop Sci. 14:802-805.

Chavan, V.M., J.A. Patil, and B.B. Chowdhury. 1955. Hybrid bajri in Bombay state. Poona Agric. College Mag. 46:148-150.

Dave, H.R. 1987. Pearl millet hybrids. p. 139-142. *In* Proc. of the International Pearl Millet Workshop, 7-11 April 1986. ICRISAT, Patancheru, AP 502 324, India.

Govila, O.P. 1988. Breeding procedures for cross pollinated crops: Pearl millet. p. 213-223. *In* Chopra, V.L. (ed.) Plant Breeding, Oxford & IBH Publishing Co., New Delhi, India.

Gupta, V.P. 1975. Fodder improvement in *Pennisetums*. Forage Res. 1:54-60.

Hanna, W.W. 1989. Characteristics and stability of a new cytoplasmic-nuclear male sterile source in pearl millet. Crop Sci. 29:1457-1459.

ICRISAT, 1995. Southern and East African Region Annual Report, 1994.

ICRISAT. 1996. Genetic Enhancement Division, Pearl Millet Breeding (West Africa) Annual Report, 1995.

Lambert, C. 1983. L'IRAT et l'amelioration du mil. Agronomy Trop. 38:78-88.

Madhusudhana, R. 1996. Genetic diversification of CMS lines in pearl millet. (Ph.D. Thesis), IARI, New Delhi, India.

Monyo, E.S., S.A. Ipinge, S. Mndolwa, and E. Chintu. 1996. The potential of local landrace varieties in pearl millet improvement. p. 153-162. *In* Leuschner, K., and C.S. Manthe (eds.) Drought tolerant crops for southern Africa, ICRISAT, India.

Nirwal, B.G., and V.C. Upadhyaya. 1979. Growth and yield of hybrid pearl millet 'HB-1' as influenced by inter and intra row spacings and varying levels of nitrogen. Indian J. Agronomy 24(1):17-20.

Ouendeba, B., G. Ejeta, W.E. Nyquist, W.W. Hanna, and A. Kumar. 1993. Heterosis and combining ability among African pearl millet landraces. Crop Sci. 33:735-739.

Ouendeba, B., G. Ejeta, W.W. Hanna, and Anand K. Kumar (*sic*). 1995. Diversity among pearl millet landrace populations. Crop Sci. 35:919-924.

Pokhriyal, S.C., K.V. Unnikrishnan, Balzor Singh, Ramdass, and R.R. Patil. 1976. Combining ability of downy mildew resistant lines in pearl millet. Indian J. Genet. Pl. Breed. 36:403-409.

Rai, K.N., and R.P. Thakur. 1995. Ergot reaction of pearl millet hybrids affected by fertility restoration and genetic resistance of parental lines. Euphytica 83:225-231.

Rai, M. 1992. Nucleus and breeder seed production. p. 141-149. *In* Proc. of the Group Discussion on Management of Change in All India Coordinated Crop Improvement Projects, 24-26 Feb, Hyderabad, India.

Rao, P.K., A.K. Nambiar, and P. Madhav Menon. 1951. Maximization of production by the cultivation of hybrids strains with special reference to cumbu (pearl millet). Madras Agric. J. 38:95-100.

Singh, G., R.A. Maurya. 1969. Response of hybrid bajra to varying plant populations and levels of Nitrogen. Indian J. Agron. 14(2):157-158.

Talukdar, B.S., S.D. Singh, and P.P. Prakash Babu. 1996. Prospects of topcross hybrids in increasing and stabilizing grain yield in pearl millet (in press).

Thakur, R.P., V.P. Rao, and S.B. King. 1989. Ergot susceptibility in relation to cytoplasmic male sterility in pearl millet. Plant Dis. 73:676-678.

Thakur, R.P., V.P. Rao, and S.B. King. 1991. Influence of flowering event in cytoplasmic male sterile lines and F_1 hybrids on infection by *Claviceps fusiformis* in pearl millet. Plant Dis. 75:1217-1222.

Venkatachalam, S.R. 1996. Genetic analysis of male sterile lines and restorers in pearl millet. (Ph.D. Thesis), IARI, New Delhi, India.

Witcombe, J.R. , M.N.V.R. Rao, and W.R. Lechner. 1995. Registration of 'ICMV 88908' pearl millet. Crop Sci. 35:1216-1217.

Impact of Genetic Improvement in Sorghum and Pearl Millet: Developing Country Experiences

A.B. Obilana*, E.S. Monyo and S.C. Gupta

Abstract

Achievements have been made in genetic improvement technology in sorghum and pearl millet in many countries of southern Africa, particularly Botswana, Namibia, Zambia, and Zimbabwe. In the ten-year period 1984-85 to 1994-95, ICRISAT's germplasm and associated breeding efforts of the SADC (Southern Africa Development Community)/ICRISAT Sorghum and Millet Improvement Program (SMIP), in collaboration with the National Agricultural Research Systems (NARS) scientists, have resulted in the release of 32 improved varieties and hybrids of sorghum and pearl millet in eight countries of southern Africa. These releases are more than double (250%) those released in the ten years from 1973-74 to 1983-84. Eighty-seven percent of the releases contain ICRISAT materials. Cultivars released in the four countries used as case study experiences in this paper (Botswana, Namibia, Zambia, and Zimbabwe) account for 20 (63%) of the total 32 sorghum and pearl millet cultivars in the region. Of the 20 released cultivars, eight (40%) have been adopted and are presently being grown by farmers. Adoption studies carried out through surveys by SADC/ICRISAT SMIP, based on seed sales and distribution, and estimates by breeders in the region, based on quantities of seed produced, indicate a variable diffusion pattern in the four countries, with rates of diffusion ranging from one year (for Phofu sorghum variety in Botswana, Okashana 1 pearl millet variety in Namibia, and PMV 2 pearl millet variety in Zimbabwe), through two years (for Kuyuma sorghum variety in Zambia) to five years (for SV2 sorghum variety in Zimbabwe). The areas of current coverage follow a similar dramatic pattern. In Botswana, variety Phofu covered 25% of the total sorghum area (22, 000 ha) within the one year of diffusion, while variety Okashana 1 covered 14% of the total pearl millet area (47, 000 ha) in Namibia. A 36% farm coverage was recorded for variety SV 2 after three years of significant diffusion in Zimbabwe following emergency seed production.

In monitoring the release, on-going adoption, and impact of improved varieties in SADC countries, survey data (1994-95 to 1995-96) from SADC/ICRISAT SMIP indicate an internal rate of return of 27-34% and a stream of net benefits ranging from $ 7.8-28.9 million in Zimbabwe for SV 2 and PMV 2. In Namibia, a rate of return of 13% with net benefit of $ 0.04 million was calculated (Anandajayasekeram et al., 1995). Impact assessments of the other released improved varieties in Botswana and Zambia are still

A. B. Obilana, SADC (Southern Africa Development Community)/ICRISAT Sorghum and Millet Improvement Program (SMIP), Box 776, Bulawayo, Zimbabwe; E. S. Monyo, SADC (Southern Africa Development Community)/ICRISAT Sorghum and Millet Improvement Program (SMIP); and S.C. Gupta, ICRISAT-WCA, Nigeria. *Corresponding author.

going on. The presently moderate impacts generated at farm level by these new improved varieties as a result of genetic improvement (involving research and development activities) has been enhanced and promoted by several important factors: 1) the introduction and development of improved germplasm with farmer-preferred traits of early maturity, drought resistance, and acceptable good quality in grain; 2) seed production; 3) effective on-farm testing for farmer verification; and 4) breeder participation and commitment in technology transfer and exchange.

Conventional breeding programs always have resulted in the development of improved genetic stock, breeding lines, and populations, as well as the release of improved varieties. While these constitute achievements of the programs, they alone do not generate impact. Previous trends in genetic enhancement have been the generation of improved germplasm and the testing of this technology. These breeders' activities are usually followed by release of improved germplasm in the form of varieties or hybrid parents as end products after on-station evaluation. The consequence of this approach ending at variety release, with no planned push of the products into farmers' fields, has been the limited adoption of the series of variety releases by end-users, the farmers. This shortfall has been a major constraint to increased production and productivity of improved sorghum and pearl millet varieties especially in developing countries.

Present trends in genetic enhancement research have shown that targeted and more appropriate variety releases, which can result in increased production of the improved varieties, can be achieved by increased adoption of the technologies by farmers, through on-farm testing and farmer verification (Chintu et al., 1996a and 1996b; Ipinge et al., 1996; Matanyaire and Gupta, 1996; Mangombe and Mushonga, 1996; SADC/ICRISAT SMIP, 1995 and 1996).

The transfer of improved variety technologies into farmers' fields has addressed the need to incorporate preferences of farmers who will accept, adopt, and produce the new improved varieties. It has been shown (Anandajayasekeram et al., 1995; Jenkins et al., 1996) that the incorporation of technology transfer activities into genetic improvement of sorghum and pearl millet, following technology development and testing, has greatly enhanced the release of more farmer-preferred varieties in southern Africa. This innovative strategy has led to the increased adoption for production of the new improved sorghum and pearl millet varieties and hybrids released in national programs.

It therefore should be the breeder's responsibility to participate in and champion the move of outputs from genetic improvement into farmers' fields for increased adoption and production. This is the demand of contemporary genetic enhancement in the improvement of sorghum and pearl millet — that is, breeding for impact!

The purpose of this paper is to show the type, quality, and quantity of impact generated from genetic improvement of sorghum and pearl millet and share our experiences of developing countries from southern Africa sub-region. The strategy we used will be described, and our

achievements highlighted. We will present case studies from four countries of the southern Africa sub-region. The four southern African countries include Botswana (for sorghum), Namibia (for pearl millet), Zambia (for sorghum), and Zimbabwe (for sorghum and pearl millet).

Method

Breeding for impact involves a sequence of significant events in a time-phased and overlapping series of progressive activities. The strategy used in southern Africa by the SADC (Southern Africa Development Community)/ ICRISAT (International Crops Research Institute for the Semi-Arid Tropics) Sorghum and Millet Improvement Program (SMIP), has involved, first, the rationalization of the genetic improvement objectives, followed by a systematic and logical breeding, selection, and testing program.

Rationalization of Breeding Objectives

Based on the initial progress made by the SADC/ICRISAT SMIP in southern Africa during the first two phases (1983-84 to 1993-94) in the development of improved varieties, populations, and breeding lines, the objectives of the genetic improvement program for sorghum and pearl millet for the third phase (1994-95 to 1998) were rationalized. The purpose of the rationalization exercise was to improve on the conventional successes of the genetic improvement program by moving forward from the approach of developing and releasing cultivars and breeding lines to the present strategy of ensuring not only that the cultivars developed are adopted, released, and produced by farmers, but also that the breeding lines are effectively utilized by breeders in collaborative partnership.

The rationalized objectives of the SADC/ICRISAT SMIP breeding program since1994, after improved varieties became available, are:

1) To continue to breed improved varieties and to collect and exchange germplasm with particular reference to drought.

2) To facilitate the transfer of technologies to small-scale farmers through the National Agricultural Research Systems (NARS) and linkages with Non-Governmental Organizations (NGOs), seed companies, and other partner institutions.

3) To evaluate grain quality for various end-uses.

4) To improve the productivity of NARS and NGO research and development in crop improvement through in-country and regional training, collaborative activities, and joint work planning in genetic improvement of sorghum and pearl millet.

One additional aspect of the rationalized objectives is that they have a production system focus targeted at two main production systems: 1) the lowland drought, short season (<100 days) sorghum/millet/rangeland system; and 2) the semi-arid, often-droughted, intermediate season (100-125 and 125-150 days) sorghum/maize/rangeland/millet/legumes system.

Events and Process

The sequence of time-phased events and overlapping series of activities for

generation of impact in genetic improvement include: technology development, technology testing, and technology transfer and exchange. Table 1 shows the events and overlapping sets of activities involved. (Note: All tables appear at the end of this article.) The sets of activities within each event determine the type of outputs from the genetic improvement process. Germplasm movement and utilization generate the breeding lines, populations, and cultivars, including pure line varieties, hybrid parents and hybrids, for testing. Technology testing both on-station in experiment stations and on-farm in farmers' fields, evaluates the performance and adaptation for productivity of the genetic products. Technology transfer and exchange events are based on the good and tested genetic products resulting from technology generation and testing. Farmer verification and preference tests usually enhance the progress and success of technology transfer activities. In the southern Africa region, the systematic progression for breeding, testing, and selection process as a strategy for technology testing is shown in Figures 1 and 2. As shown in Table 1 and Figures 1 and 2, the approach for genetic improvement to generate impact has been multidisciplinary and depends on collaborative partnership with the national programs and their NGOs in developing countries of southern Africa. The national program in Zambia has been more aggressive in this process.

Results and Discussion

Progress in Genetic Improvement in Southern Africa

Significant achievements have been made in the breeding and release for production of improved sorghum and pearl millet cultivars in the SADC region. The successes achieved have been due to the collaborative efforts of the regional SADC/ICRISAT SMIP and some (NARS) in the region. Specifically, successes achieved in some of the NARS have generated impact at both scientific and farmer levels in their respective countries.

Tables 2, 3, 4, 4a, and 5 show the sorghum and pearl millet varieties released in the four target countries for case study (Botswana, Namibia, Zambia and Zimbabwe, respectively) during the ten-year period 1984-85 to 1994-95. Table 6 shows the trend of achievements from prior to 1983 to the period 1984-85 to 1994-95. Table 8 shows the successes achieved in germplasm movement to and from the four target countries. Tables 9, 10, 11, and 12 show the summary yield (t ha^{-1}) and maturity (days to 50% heading) of the released varieties in Botswana, Namibia, Zambia, and Zimbabwe, respectively.

Botswana

In 1994, four new sorghum cultivars were released by the National Variety Release Committee. These cultivars include three pure line varieties (Phofu, Mahube and Mmabaitse) and one single cross hybrid (BSH1) (Table 2). This hybrid is the first ever released in the country. Breeder seeds are being maintained in the country and the backup activity of SADC/ICRISAT SMIP. In 1995 commercial farmers started large-scale production of the foundation seed of variety Phofu in the Pandamatenga area of the country on 400 ha, with backup technical support from the national breeder, the sorghum and pearl millet improvement team in the country,

	Germplasm Acquisition	
	↓	
	Breeding and Observation Nurseries -Farmer Participation	Initial screening Germplasm evaluation
	↓	
SMIP nurseries Country crossing blocks	**Crossing Program** **Backcrossing Program**	Line development Hybrid parent development
	↓	
Breeding lines SMIP nurseries and semi-finished products selected by advanced NARS into their nurseries	**F4/F5 Lines** **Modified Pedigree Breeding** ↓	Early generation testing in one location
SMIP nurseries	**F6/F7 Lines**	Advanced generation testing in 1-2 locations. Head bagging of 2-3 plants/line for seed increase
SMIP test locations	**New Line Trials/Testcross Evaluation** ↓	Replicated trial in 2-3 locations Selection based on visual observation and analyzed data. 1 year duration
NARS specific selections of breeding lines from SMIP test locations	**Preliminary Cultivar Testing** -new varieties, new hybrids -new hybrid parental lines and restorers	1-2 years 2 locations
	↓	
NARS selections and promotion of advanced materials into their national variety trials	**Regional Advanced Cultivar Testing** ↓	1st Stage Regional Collaborative Trials of SMIP and NARS Beginning of multilocational trials-SMIP in 4 locations NARS in 6-10 country locations Joint NARS/SMIP evaluation
	Bilateral Cooperative Trials -specific to requesting NARS **Regional Collaborative Trials** -across all countries	2-3 years for variety replacement 6-10 locations in cooperating countries and SMIP.
	↓	
Breeder seed increase. Seed production training by SMIP regional and in-country	**National Program Testing** ↓	NARS activity in national experiment stations, multilocations, advanced testing, compilation of data. 2 years
Large-scale seed production (NARS and Industry)	**(On-farm Testing)** ↓	Major farmer involvement to identify farmer preferences and release of varieties by NARS. 2 years, multifarm locations
More breeder seed increase (NARS and SMIP)	**On-farm Verification** ↓	NARS/SMIP activity.
Variety description and production of leaflets	**Cultivar Release, Seed Multiplication** **Farmer Adoption and Production**	NARS activity facilitated by SMIP

Figure 1. Progression for breeding, testing and selection process in southern Africa (SADC region) for sorghum by SADC/ICRISAT SMIP.

	Germplasm Acquisition	
	↓	
	Breeding and Germplasm Nurseries -Farmer Participation	Initial screening
	↓	
Crossing block	**Line Selection** **Crossing Program** **Backcrossing Program**	Genetic diversification
	↓	
SMIP nurseries	**Pedigree Program** **Genepool Formation** **Population Development**	Genetic diversification and characterization. Generation advance Shuttle breeding
	↓	
SMIP nurseries	**Recurrent Selection** -inbred line selection **Progeny/Line trials** -S_1 progeny trials **Testcross Trials** **Top Cross Trials**	Population improvement Early generation testing Hybrid parent development and testing
	↓	
Breeding lines and semi-finished products selected by advanced NARS into their nurseries	**Progenies/Line Recombination** -composite variety development -synthetics development -hybrid development	
	↓	
NARS specific selections	**Preliminary Cultivar Testing** -new varieties, new hybrids -new seed parent lines	1-2 years 2 locations
	↓	
NARS selections into their national variety trials	**Advanced Cultivar Testing**	1st stage regional collaborative trials of SMIP and NARS selected entries. Beginning of multilocational trials: 6-10 locations
	↓	
	Bilateral Cooperative Trials -specific to requesting NARS **Regional Collaborative Trials** -across all countries	2-3 years for variety replacement 6-10 locations in SMIP and cooperating countries
	↓	
Breeder seed production and training in seed production	**National Program Testing**	NARS activity in national testing sites for pre-release
	↓	
Variety description Breeder seed production	**On-Farm Verification** **(On-Farm Testing)**	NARS activity facilitated by SMIP with a major component of farmer involvement to identify varieties for release (2 years)
	↓	
Large-scale seed production (NARS and Industry)	**Cultivar Release, Seed Multiplication** **Farmer Adoption and Production**	NARS activity facilitated by SMIP

Figure 2. Progression for breeding, testing and selection process in southern Africa (SADC region)

and SMIP in Matopos. Seeds of varieties Phofu (400 ha), Mmabaitse (120 ha), Mahumbe (24 ha) and the hybrid BSH1 (58 ha) with its parents (52 ha) were produced.

Available data collected on seed production and sales throughout the southern Africa region show that 3,000 mt of seed for these four cultivars were produced in Botswana during 1995 by the private and public sectors (SADC/ICRISAT, 1996). This significant seed production had been widely stimulated by government and donor investments in drought-relief programs. A two-year technical backstopping and in-country hybrid seed production training program by the SMIP breeder led to strengthened capacity of the Botswana NARS to be able to initially produce 35 tons of the BSH1 hybrid and its three parents in 1994.

Among the three releases, variety Phofu with white seeds and stay green trait (a combination of traits that make it useful for dual purpose of food and crop residue) is most popular among Botswana farmers. About two-thirds of the sorghum seed produced in 1995 (2000mt) is of this variety. The hybrid BSH1 (Botswana Sorghum Hybrid 1) has very good white bold seeds with excellent milling quality. The white flour from the milled grain is very sought after by the milling and food industry in Botswana, especially Foods (Botswana) Pvt. Ltd.

The summary yield (t ha^{-1}) and maturity (days to 50% heading) data for the four sorghum varieties and hybrid are shown in Table 9. In the on-station trials that spanned four years and two-four locations, variety Phofu (with an average 3.25 t ha^{-1}) and hybrid BSH1 (with an average 3.83 t ha^{-1}) significantly ($P > 0.01$) outyield the control and farmer varieties including the popular Segaolane (with an average 2.34 t ha^{-1}), by a range of 17 to 75%. In on-farm trials, averaged across two years in nine villages and 108 farmers within three agricultural regions, variety Phofu (with an average 0.73 t ha^{-1}) outyielded farmer varieties, including Segaolane (with average of 0.51 t ha^{-1}), by -2 to 84%. The hybrid BSH1 was not tested on-farm as it was targeted for industrial processing in milling for flour and sorghum meal. It was therefore released based on its higher yield potential, very hard (4.5 out of 5.0 on grain hardness score) and excellent white grain quality for flour yield,and acceptable white flour color.

The variety Phofu was therefore released based on its early maturity, good yield potential, large-sized heads, good field grain quality (better white grain than the popular variety Segaolane, whose white grains turn black with extreme mold infection when exposed to late season moisture) and 99.9% farmer acceptance. These farmer-preferred traits are in addition to its stay green trait with broad leaves, which makes the variety useful for good quality crop residue. The other two varieties, though lower-yielding than the controls, have a niche in the production environment in the country. Variety Mahube is the earliest in the region, heading in only 58 days (taking only 95-100 days to physiological maturity), white variety Mmabaitse is earlier than the controls by over 10 days.

Namibia

The major success of genetic enhancement in Namibia was release of pearl millet variety Okashana 1 in 1990 (Table 3). Present survey data (SADC/ICRISAT,

1996) show that 125 mt of pearl millet seed were produced in 1995. As a result of consistent backstopping from SMIP in Matopos over the past four or five years, coupled with FAO-supported seed production activities in-country, Namibia is now self-sufficient in its seed production capabilities. Up to 313.5 mt of seed have been produced during this period.

Okashana-1 was selected by farmers because of its early maturity and drought tolerance (Table 10). It matures up to 10 days earlier than most of the local landraces thereby making it able to avoid terminal drought which characterizes much of northern Namibia. It has a big advantage over the local landraces in yield only in seasons characterized by severe drought and especially in the north western and north central regions where the rainfall season is short (less than 90 days). Much of the high yields reported in the table are a result of averaging out performance across the country where the northeastern part (Kavango and Caprivi) receives higher rainfall (500-700 mm) compared to the north central and northwestern parts (Owamboland) where Okashana-1 is more popular and rainfall averages only 350-400 mm. In these regions, which cultivate more than 75% of the total hectarage of pearl millet in Namibia, the yield superiority of Okashana-1 is sometimes double that of the local landraces in seasons of extreme drought because its early maturity can be as much as 2-3 weeks earlier than some landraces in the Owamboland region.

Zambia

Success in genetic enhancement of sorghum and pearl millet has been made in Zambia. Between 1987 and 1995 the country released seven cultivars, out of which three (WSH 287, MMSH 375 and MMSH 413) are single cross hybrids (Table 4). Of these hybrids, the earliest released one (WSH 287) is out of production. The two pure line varieties among the releases, Sima and Kuyuma with white seeds, are very popular with farmers in the dry parts of the country. The hybrid MMSH 413 with brown seeds is being selected by the brewing industry for its good malting quality. In 1994-95, more than 544 mt of seeds of the four cultivars were produced and sold to both domestic and export markets.

All five sorghum cultivars released in Zambia, though high-yielding on-station, are not better than the controls (Table 11). However, they have been released based on the target clients. The two hybrids MMSH 375 and MMSH 413 have good malting qualities (40.2 and 38.2 diastatic units per gram) for use in the brewing sector. The two varieties Sima and Kuyuma have very good white grains acceptable for food. Sima has very bold, translucent grains, though it is very late maturing (the days to 50% heading) relative to controls (average 77 days to 50% heading).

The two released pearl millet varieties, Lubasi and Kaufela, are both significantly ($P>0.01$) higher yielding (2.38 t ha^{-1} and 2.04 t ha^{-1}, respectively) and earlier maturing (62 and 60 days to 50% heading, respectively) than the controls (averaging 1.48 t ha^{-1} and 70 days to 50% heading) (Table 4a). On-farm data are not available. These varieties were released mainly for their potentially high yields and early maturity.

Zimbabwe

In Zimbabwe, genetic enhancement achievements have been made in both sorghum and pearl millet. Between 1987 and 1992, three sorghum cultivars (SV1, SV2 and ZWSH1) and two pearl millet cultivars were released (Table 5). However, the only hybrid, ZWSH1, was never produced. Both sorghum variety SV2 and pearl millet variety PMV2 are very popular with farmers in the dry agro-ecologic regions IV and V of the country, for their early maturity (115-120 days and 85-95 days, respectively) relative to the local varieties (160 days for sorghum and 110-120 days for pearl millet). Table 12 shows the summary yield (t ha^{-1}) and maturity (days to 50% heading) data for the three sorghum and two pearl millet cultivars released in Zimbabwe plus controls and farmer varieties. It is obvious that, on-station, the two varieties SV1 (yielding 4.06 t ha^{-1}) and SV2 (yielding on average 3.38 t ha^{-1}) outyield, significantly ($P>0.01$), the controls and farmer varieties (yielding on average 2.73 t ha^{-1}) by a yield range of 5% to 67%.

On-farm variety SV2 (averaging 2.15 t ha^{-1}) was better in yield than the controls and farmer varieties (averaging 1.56 t ha^{-1}) by about 37%. Variety SV1 was not included in on-farm trials. However, SV2 (heading in 63 days) is significantly ($P>0.01$) earlier maturing than the controls and farmer varieties (heading in 76 days). Early maturity is a most preferred trait of farmers in Southern Africa because of frequent droughts; the reason for which SV2 was released for assurance of food and insurance against drought. It is sure to provide food for the farming population, including women and children, early in the season.

Similar observations can be made for the two released pearl millet varieties, PMV-1 and PMV-2. When averaged across 25 on-station testing sites, PMV-1 provided about 13% more grain yield compared to the local (2.27 vs 2.01 t ha^{-1}), whereas PMV-2 was overall 40% superior (2.81 vs 2.01 t ha^{-1}). Under farmer's conditions however, PMV-2 more than doubled the yields of the local landraces, where as PMV-1 provided 37% more grain yields (2.28 vs 1.70 t ha^{-1} for PMV-1 and 1.07 t ha-1 for the local check).

Initial seed production in these popular releases was slow from 1987-1992, due to the erroneous belief of commercial seed producers in Zimbabwe that there was no demand for sorghum and pearl millet seed. However, with the popularization and present increased demand by farmers for their preferred varieties, more concerted efforts are being devoted to seed production in the country. According to available data from seed distribution and sales surveys (SADC/ICRISAT SMIP, 1996), about 1400 mt of SV2 seeds were commercially produced in Zimbabwe in 1995. These seeds were destined for distribution in Zimbabwe, Angola, and Mozambique for agricultural and drought recovery programs.

Adoption of Released Cultivars and Impact

Tables 2 through 5 show the 20 new cultivars of sorghum and pearl millet released by the national programs of Botswana, Namibia, Zambia, and Zimbabwe from 1984 through 1995. These cultivars have been differentially adopted by farmers in each country, resulting in variable impacts. The patterns of adoption leading

to impact are evident in the same tables. Additionally, Table 6 shows a trend in relative achievements in the four countries for cultivar releases and the impact in cultivar releases due to collaboration with the regional SMIP during the 11-year period.

Prior to 1983 and before the inception of the SADC/ICRISAT SMIP, a total of 12 improved varieties of sorghum and pearl millet were released by three of the four target countries: Botswana (8 varieties), Zambia (2 varieties), and Zimbabwe (2 varieties) (Table 6; Anandajayasekeram et al., 1996). Of these, only nine varieties were produced; three of the Botswana releases were never produced. Namibia had no improved varieties during this period. However, during the next 11 years when SMIP was operating, the four countries improved in their capabilities for genetic enhancement and increased their releases of sorghum and pearl millet to 32 cultivars (varieties and hybrids), of which 27 are being produced (Table 6). The national programs have gained strength in breeding that leads to variety releases due in part (for Botswana, Namibia and Zimbabwe) to the technical assistance and facilitation of processes by the regional SADC/ICRISAT SMIP. During the 11-year period, ICRISAT's efforts in germplasm movement and associated breeding in collaboration with these SADC countries have contributed to the release of the cultivars.

The increase of variety releases from seven (six sorghum and one millet) prior to 1983 to 20 (14 sorghum and six millet) during the SMIP era — a more than 100% improvement made by the four countries — is a significant achievement and has a strong impact on genetic enhancement in the southern Africa region.

Noteworthy is the trend in these achievements for each of the countries studied (Table 6). While Namibia started producing its only improved pearl millet during the SMIP era (specifically in 1991 as shown in Table 3), Zambia moved mostly on its own from producing no sorghum and pearl millet varieties prior to 1983, to producing ten improved cultivars (seven sorghum and three pearl millet) between 1984 and 1995. Similar trends are shown in Zimbabwe and Botswana (which is still producing its only old pearl millet variety and eight sorghum varieties, with two old and three new sorghum varieties, and two new pearl millets).

Adoption and Impact Case Studies

Areas of expected coverage and estimates of current coverages for each of the released varieties in Botswana, Namibia, Zambia, and Zimbabwe, are shown in Tables 2 through 5. These estimates of adoption and impact should be considered preliminary, although some have been verified (SADC/ICRISAT SMIP, 1996). The SADC/ICRISAT SMIP is monitoring the adoption of the released improved cultivars and continues to collect data on seed production and distribution. The initial results of a regional survey on the release and adoption of new sorghum and pearl millet varieties indicate evidence of favorable adoption of some of these cultivars (Agrinews, 1996).

Botswana

The adoption pattern and rate of the four newly released sorghum cultivars in

Botswana are shown in Table 2. The year of first significant diffusion for three of the four cultivars was 1995, only one year after their release. The areas of expected coverage were estimated as 40,000-50,000 ha for Phofu, 20,000 ha for Mahube and 10,000-15,000 ha for the hybrid BSH1. These estimates were based on the seed multiplication activities before and after the releases, the areas that can be covered by the quantities of food quality seeds produced, and the strengthened capabilities of the national scientists and breeders to produce hybrid seeds. The mode of distribution of the seeds and its timing also play a role. A regional survey on adoption of the Phofu variety show an estimated 10,000 ha planted by farmers in 1995-96 (SADC/ICRISAT SMIP, 1996).

Based on available quantity of seeds, this 11.24% adoption survey estimate for Phofu is lower than the area of current estimated coverage (25%) (Table 2). The discrepancy is due to delayed and confused distribution of seeds to farmers. Variety Mahube and hybrid BSH1 were appropriately produced as expected, although the adoption surveys on them still have to be carried out. Variety Mmabaitse has no significant diffusion and has since not been produced, because of lack of farmer preference for the variety.

Evidence has thus been provided for a significant impact in Botswana for three of her four new sorghum releases. The main factors responsible for this impact have been intense and systematic in-country seed production, SMIP backstopping for breeder seed, and training in seed production, coupled with a rapid diffusion rate (one year only) due to farmer and industrial preferences for the cultivars. The farmers cited early maturity and stay reen trait for crop residue use; while industries prefer the new varieties for excellent white flour for food and good milling quantities.

Further adoption surveys and plans for an impact assessment are continuing with focus on farmers who planted the new varieties in the north, central, and southern parts of the country in the 1994-95 and 1995-96 seasons.

Namibia

Pearl millet variety Okashana 1 was released in 1990 in the far north of the country, which is the principal crop zone in Namibia (Table 3). The diffusion of this variety was very rapid, with the first significant diffusion recorded one year after its release. In 1992-93, the estimated rate of diffusion reached 9.5% based on seed sales, and 17.0% based on survey data (Table 7; Anandajayasekeran et al., 1995). This rapid rate reached 45% in 1994-95 in the two main production zones of Kavango and Owambo provinces (ICRISAT CCER Report, 1996).

The current area of coverage of Okashana 1 has been estimated at 47,000 ha, 14% of the total millet area (Table 3; SADC/ICRISAT, 1996). This scenario results in an internal rate of return of 13.3%, a calculated benefit of $350,000 (Table 7; Anandajayasekeran et al 1995). Further impact analysis of Okashana 1 in Namibia will be formally completed jointly by SMIP and Namibian scientists in 1996-97.

The exemplary rapid diffusion rate and internal rate of return in less than five

years for the pearl millet variety Okashana 1 has been mainly due to farmer preference for its early maturity. This alleviates food problems under constant drought situations.

Zambia

The impact story of sorghum variety releases and production in Zambia takes a different form and shape. The first significant diffusion of the two most popular of the five releases, varieties Kuyuma and Sima, occurred two to three years after release in 1990, although farmers only started being aware of the varieties in 1996. Presently, initial results of a regional adoption survey show that the varieties Kuyuma and Sima each covers 5,000 ha (13% of current total sorghum area) (Table 4; SADC/ICRISAT SMIP, 1996). However, higher coverages of 50% were estimated for 1993-94 for all improved cultivars in the Siavonga district, the pilot area of the promotional campaign (Verma, 1996, personal correspondence).

Estimates of adoption for the three released hybrids are not available. One of them, WSH 287, is out of production, while the more popular of the remaining two, MMSH 413, is an export commodity and is used for opaque beer production. A rough estimate of current coverage for MMSH 413 is put at 700-800 ha (Verma, 1996, personal correspondence). According to the Zambia national statistics, 47,000 ha were planted to improved sorghum varieties and hybrids in 1995-96 (Verma, 1996, personal correspondence). The impact of these diffusion patterns in Zambia needs to be assessed. Presently, the Zambia NARS, SACCAR and SADC/ICRISAT SMIP are conducting a collaborative adoption impact study of new sorghum cultivars in Zambia.

It is worthwhile to note that impact is being generated from the new cultivar releases in Zambia due to combined efforts of the breeders, who champion the distribution and diffusion of seed, and the national seed company, Zamseed, whose commercial and export production focus is providing spillover effects to neighboring countries. Such spillover effects from the Zimbabwe commercial seed production activities in 1995-96 also are starting to show impact on neighboring countries, especially for drought relief.

Zimbabwe

The impacts of improved cultivar releases in Zimbabwe are recorded for both sorghum and pearl millet. Of the three sorghum cultivars released in 1987 and 1992 (Table 5), only SV 2 variety became popular with farmers. Of the two pearl millet releases, PMV 2 is the only variety that became popular. The pattern of diffusion and trends of impact are different in both situations, as shown in Table 5.

The sorghum variety SV 2, released in 1987, did not record any significant diffusion until 1992. However, this delayed diffusion (caused mainly by lack of seed) has not hindered its rapid and high adoption rate since 1992. Within three years, the area of expected coverage of 60,000 ha (54% of the total sorghum area) has almost been reached, with a current coverage of 40,000 ha (36% of the total sorghum area) (SADC/ICRISAT SMIP, 1996).

This phenomenal rate of adoption has been stimulated by the drought relief emergency seed production of 1992, which resulted in initial production of 493 mt of SV 2 and 161 mt of PMV 2. The project provided a large quantity of good quality seed to small farmers and contributed to improvement of their household food security, following the severe 1991-92 drought (ICRISAT, 1993).

Similar but lower adoption rates were obtained from pearl millet variety PMV 2; current estimated coverage is 35,000 ha (14% of the total pearl millet area), relative to the expected area of coverage of 100,000 ha (41% of total). Lower adoption rates have occurred despite the significant diffusion rate of only one year after PMV 2's release in 1992. The response to pearl millet has not been as phenomenal as the response to sorghum due to complete lack of interest in pearl millet seed production after the 1992 emergency seed production exercise. In order to keep the adoption momentum going, the breeders in SMIP must produce large quantities of breeder seed to support the national program needs in Zimbabwe. An average of two to three tons of pure breeder seed, produced in isolated fields, were supplied to Zimbabwe NARS between 1992 and 1995 for both SV 2 and PMV 2 sorghum and pearl millet varieties.

The impact of these reported adoption trends of sorghum and pearl millet in Zimbabwe has been assessed. An analysis of the rate of return derived from sorghum and pearl millet genetic improvement in Zimbabwe indicated an internal rate of return of 27-34% and a stream of net benefits ranging from $7.8-28.9 million (SADC/ICRISAT SMIP, 1995). According to Anandajayasekeram et al. (1995), the diffusion estimates for SV 2, based on seed sales and survey data, are 29% and 30%, respectively (Table 7). They recorded internal rates of return of 25.8%, with benefits of $0.22-1.29 million.

It is interesting to note that farmers cited early maturity of SV 2 and PMV 2, not productivity gains, as the main reasons for their significant adoption.

Intermediate Outputs Contributing to Impact

Much of ICRISAT's genetic improvement effort in the regional SMIP program has been to offer intermediate genetic outputs that contribute to development of a wider range of finished products by the NARS. These include breeding stock and germplasm with various specialized traits and sources of resistance to alleviate constraints, both abiotic and biotic in nature. Table 8 shows the movement of such germplasm materials into the four case study countries in southern Africa. The materials from SMIP consist of direct reintroductions from ICRISAT into the region, and introductions from west and east Africa, Latin America, and the U.S. (INTSORMIL), totaling approximately 13,000 sorghum samples and 10,000 pearl millet samples. The remainder of the SMIP samples are generated and derived from all these sources, together with the indigenous farmers' collections in the region.

Since the inception of the regional SADC/ICRISAT SMIP in 1983-84, and during the 10-year research period 1984-85 to 1994-95, a total of 85,734 genetic materials of sorghum and pearl millet

have moved into Botswana (8,654 samples), Namibia (3,212), Zambia (11,705), and Zimbabwe (62,168) (Table 8). The availability of diverse and variable germplasm of sorghum and pearl millet for genetic enhancement purposes increased by the following percentages: 25% for Botswana, 112% for Zambia, and 1,196% for Zimbabwe.

This provides evidence for an intermediate "scientific impact" that preceeded the impact on farmers' fields, due to germplasm movement and utilization. The increase in accessibility and availability of diverse and variable germplasm and breeding lines to the NARS in the southern Africa region has led to greater access to international technology. The SMIP project also has contributed to the awareness of the NARS breeders in these countries and their training in genetic enhancement; it also has strengthened their capacities and capabilities for the genetic improvement of sorghum and pearl millet.

Factors Enhancing Generation of Impact of Genetic Improvement of Sorghum and Pearl Millet

Several factors contribute, at different times and in different forms, to achieving impact through breeding at two main levels: the scientist (intermediate) level and the farm level. The several contributing factors to impact generation in the southern Africa region in general and the four countries (Botswana, Namibia, Zambia, and Zimbabwe) specifically, fall within the three main events of technology generation, technology testing, and technology transfer and exchange, as a series of overlapping and time-phased genetic improvement activities (Table 1). The main enhancing factors include:

1. Germplasm introduction, distribution, and utilization.

2. Availability of improved varieties and hybrids.

3. On-farm testing and farmer preference evaluation.

4. Emergency seed production of 1992, following the most severe drought of 1991.

5. Effective collaboration among all partners.

6. Long-term and committed donor support.

7. Commitment of breeders to champion their cause and their confidence in the improved technologies.

Germplasm Introduction, Distribution, and Utilization

The need for alternative crop technology in any crop environment and production system accounts for a great deal in its success. The past failures of maize, the main staple food, in the southern African region, due to consistent drought periods culminating in the 1981-82 drought coupled with the desire of the respective governments in the region to solve the drought problem that resulted in food deficits and loss of some farmers' indigenous germplasm, created the need for crop diversification and use of alternate crop varieties that could withstand the drought. Within an 11-year period (1983-84 to

1994-95) the SADC/ICRISAT Sorghum and Millet Improvement Program (SMIP), which is responsible for genetic enhancement of sorghum and pearl millet in the southern Africa region, together with NARS in Botswana, Namibia, Zambia, and Zimbabwe, collected local germplasm (a total of 3,000 sorghum and 2,500 pearl millet accessions) from the region, and introduced 23,000 exotic sorghum and pearl millet germplasms. The exotic accessions consisted of both indigenous and enhanced germplasm. These were distributed and tested across the whole southern Africa region, and utilized in several ways by each NARS for its genetic enhancement research.

This massive germplasm movement created a favorable base for generation of impact at both intermediate (scientist) and farmer levels.

Availability of Improved Varieties and Hybrids

Through a series of national and regional breeding nurseries, crossing blocks, off-season winter nurseries, and preliminary screening, a total of 96,391 enhanced germplasm, breeding lines, and populations of both sorghum and pearl millet were developed by the NARS (which are strong in breeding research) in collaboration with SADC/ICRISAT SMIP during 1984-85 to 1994-95 (Table 8). Compared to the period 1975-76 to 1982-83 before the inception of SMIP, this is a 460% combined achievement in germplasm enhancement in Botswana, Namibia, Zambia, and Zimbabwe.

From these enhanced genetic stocks, collaborative research efforts in multilocational, multi-year, and multi-disciplinary testing have resulted in the release of 32 improved sorghum and pearl millet varieties and hybrids in eight southern Africa countries in the era of SMIP. Of these, 20 are in Botswana (4), Namibia (1), Zambia (10), and Zimbabwe (5). Only eight (40%) of these cultivars (two sorghum in Botswana, one pearl millet in Namibia, three sorghums in Zambia, and one sorghum and one pearl millet in Zimbabwe) have resulted in impact on farmers' fields.

On-farm Testing and Farmer Preference Evaluation

In collaboration with our National Agricultural Research and Extension System (NARES) partners, the regional SMIP initiated the transfer of technologies to farmers' fields in 1992. The initial countries involved in on-farm testing in 1992-93 were Zimbabwe, Namibia, and Malawi. During the 1993-94 season, on-farm trials on sorghum and pearl millet were conducted in seven of the 12 SADC countries. In Zambia, this activity was done by the NARS on its own since 1989. New improved genotypes and production technologies (IPM on *Striga* and armoured cricket only) were demonstrated on farmers' fields.

The research outcomes of on-farm tests and farmer preference evaluations led to release of new varieties and hybrids in the SADC countries. "Farmer pressure" was especially influential in leading to cultivar releases in Botswana (for sorghum), Namibia (for millet), and most recently Tanzania in November 1995 (for sorghum). It is worthwhile to note that early maturity and grain quality were the two main traits

that influenced choice of cultivars and preference for release.

Emergency Seed Production of 1992

The 1991-92 drought in southern Africa was widely described as "the worst in living memory"; total rainfall in the region of 12 countries ranged from 0.0-350mm, coupled with early cessation and poor distribution of the total rainfall (less than 200mm in most countries). In early 1992, when the magnitude of the drought became apparent, planners quickly assessed the requirements for drought recovery and sustainable intervention during the following 1992-93 cropping season. This unique situation fostered the popularity of sorghum and pearl millet among farmers and in government circles. In response, production of sorghum and pearl millet seeds of the available improved cultivars was carried out under irrigation in the dry winter off-season of 1992.

This project, funded by United States for International Development (USAID) and the Canadian International Development Agency (CIDA), resulted in production of 493 mt of SV 2, 250 mt of kuyuma, both white sorghum varieties, 161 mt of pearl millet (PMV 2 and Okashana 1), and 40 mt of kaufela millet variety. Almost all the seed produced for distribution in Zimbabwe, Zambia, and Namibia reached small farmers.

This project provided the first opportunity for a large number of small farmers in semi-arid regions of Zimbabwe, Namibia, and Mozambique to plant improved sorghum and pearl millet cultivars. (Much had already been done in Zambia by the NARS before this project.) Seeds offered through the project contributed about 35% of the sorghum and pearl millet harvested by small farmers in Zimbabwe and at least 15% of the pearl millet grain harvested in Namibia (ICRISAT 1993). More important, the emergency seed project stimulated and promoted the adoption of new improved cultivars, thus enhancing their impacts at the farmer level, and offered a continuing stream of benefits to some of the poorest farmers in each of the target countries.

Collaboration Among All Partners

SMIP has collaborated effectively with all relevant partners, especially with the weaker NARS in the National Agricultural Research and Extension Systems (NARES), including NGOs in each country, at each stage of technology development, technology testing, and technology transfer, for the generation and assessment of impact due to genetic enhancement. Success has been due to:

- collaborative work planning for research activities including identification of responsibilities, expected outputs, and associated budgets.
- joint travel to research test locations for evaluation of cultivar trials.
- joint data analyses, reporting and publications.
- backup supply of breeder seed and facilitation of seed production in-country.
- national and regional training in seed production and on-farm research.
- experiment station and on-farm field visits by farmers, farmer

groups, seed producers, and non-governmental organizations (NGOs) interested in technology transfer and exchange of improved varieties of sorghum and pearl millet.

Long-Term and Committed Donor Support

The funding support by committed donors to long-term (15 years) research on genetic improvement of sorghum and pearl millet, coupled with the maintenance of a critical mass of research and development scientists provided from such donor funds, has significantly enhanced the development of improved cultivars. Specific support has been given by USAID, BMZ (Bundersministerium fur Wirtschaftliche Zusammenarbeit und Entwicklung)/GTZ (Dentsche Gesellschaft fur Technische Zusammenarbeit), CIDA (Canadian International Development Agency), to SADC/ICRISAT SMIP, and by SIDA (Swedish International Development Agency) to Zambia.

Commitment of Breeders to Champion Their Own Course and Their Confidence in the Improved Technologies

The success of transfer of any technology depends on how good the technology is. A good technology sells itself, and confidence in the technology by the developers and adopters enhances its impact. However, any technology needs a promoter who will champion the push.

The scientists, officers, and agents of the NARS in Botswana, Namibia, Zambia, and Zimbabwe, in collaboration with breeders in SMIP, have developed very good improved varieties and hybrids of sorghum and pearl millet. The improved cultivars have been jointly evaluated for several years on-station (4-8 years) and on-farm (2-4 years) in several locations (2-8 locations) of the target four countries. They have been exposed to farmers through effective demonstrations. Farmers have liked them and preferred them to indigenous cultivars, especially for early maturity and good grain quality for food and malting. At any or all of these stages, the breeders have been in the forefront encouraging the push into farmers fields and working with other scientists, agents, extension officers, NGOs, and seed industry. This commitment and belief in the improved cultivars' performance has been the basis for impact.

Acknowledgments

The authors wish to recognize the significant input of Dr. Leland R. House for the initial large sorghum and pearl millet germplasm seed consignments introduced from all over the world to begin the SADC/ICRISAT SMIP in 1983-84. His activity in acquiring such initial diverse germplasm into the program is highly commendable. His initiative in producing and providing large quantities of improved sorghum and pearl millet following the most severe drought of 1991-92 prompted more awareness by farmers and government policy makers and led to increased adoption of new improved cultivars in the southern Africa region. We thank Dr. Bhola Nath Verma for his useful comments and review of the first draft of this paper.

We also are most grateful to the farmers of southern Africa and to national scien-

tists, especially in Botswana, Namibia, Zambia, and Zimbabwe, for their close collaboration with the regional SADC/ICRISAT SMIP and for making impact on farmers' fields possible in the region.

References

Ministry of Agriculture, Botswana. 1996. Agrinews. 27(3): 11-12.

Anandajayasekeram, P., D.R. Martella, J. Sanders, and B. Kupfuma. 1995. Report on the impact assessment of the SADC (Southern Africa Development Community)/ICRISAT Sorghum and Millet Improvement Program (SMIP), Volume 1. SACCAR (Southern Africa Center for Cooperation in Agricultural Research and Training), Botswana.

Chintu, E.M., C.F.B. Chigwe, A.B. Obilana, R.W. Chirwa, and F.S. Msiska. 1996a. Sorghum variety release in Malawi: The case of Pirira 1 and Pirira 2. p. 19-25. *In* K. Leuschner and C.S. Manthe (eds.) Drought-tolerant crops of southern Africa. Proceedings of the SADC/ICRISAT Regional Sorghum and Pearl Millet Workshop, 25-29 July 1994, Gaborone, Botswana. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Chintu, E.M., E.S. Monyo, and S.C. Gupta. 1996b. On-farm evaluation of pearl millet varieties in Malawi for farmer preferences, grain yield and good quality traits. p. 27-33. *In* K. Leuschner and C.S. Manthe (eds.) Drought-tolerant crops of southern Africa. Proceedings of the SADC/ICRISAT Regional Sorghum and Pearl Millet Workshop, 25-29 July 1994, Gaborone, Botswana. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

ICRISAT. 1993. 1992 drought relief emergency production of sorghum and pearl millet seed: Impact assessment. ICRISAT Southern and Eastern Africa Region Working Paper 93/01. SADC/ICRISAT Sorghum and Millet Improvement Program, Bulawayo, Zimbabwe (semi-formal publication)

Ipinge, S.A., W.R. Lechner, and E.S. Monyo. 1996. Farmer participation in on-station evaluation of plant and grain traits: The case of pearl millet in Namibia. p. 35-42. *In* K. Leuschner and C.S. Manthe (eds.) Drought-tolerant crops of southern Africa. Proceedings of the SADC/ICRISAT Regional Sorghum and Pearl Millet Workshop, 25-29 July 1994, Gaborone, Botswana. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Jenkins, G., F. Miller, F. Muchena, and J.H. Sanders. 1996. Report of Center Commissioned External Review of ICRISAT Southern and Eastern Africa. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Mangombe, N., and J.N. Mushonga. 1996. Sorghum and pearl millet on-farm research work in Zimbabwe. p. 81-90 *In* K. Leuschner and C.S. Manthe (eds.) Drought-tolerant crops of southern Africa. Proceedings of the SADC/ICRISAT Regional Sorghum and Pearl Millet Workshop, 25-29 July 1994, Gaborone, Botswana. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Matanyaire, C.M., and S.C. Gupta. 1996. On-farm evaluation of improved pearl millet varieties in Namibia. p. 59-63.*In* K. Leuschner and C.S. Manthe (eds.) Drought-tolerant crops of southern Africa. Proceedings of the SADC/ICRISAT Regional Sorghum and Pearl Millet Workshop, 25-29 July 1994, Gaborone, Botswana. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

SADC/ICRISAT Sorghum and Millet Improvement Program (SMIP) 1995. Quarterly technical report, October-December, 1995. SADC/ICRISAT SMIP, Bulawayo, Zimbabwe.

SADC/ICRISAT Sorghum and Millet Improvement Program (SMIP) 1996. Quarterly technical report, January-March 1996. SADC/ICRISAT SMIP, Bulawayo, Zimbabwe.

Table 1. Events and overlapping sets of activities that would generate impact in genetic improvement.

Event	Activities	Collaborators
Technology generation	Germplasm movement *exotic introductions *indigenous collections *distribution Germplasm utilization *crossing block *trait management *initial selections *variety development *population and lines development	Breeder Genetic resources scientist Farmers Breeder Entomologist Pathologist
Technology testing	On-station trials *multi-locational effects *year effects On-farm evaluation and verification Farmer preference tests Laboratory grain and food quality screening	Breeder Technology exchange specialist/agronomist Extension specialist Food technologist/scientist Farmers
Technology transfer and exchange	Cultivar releases *line and population releases *breeder seed multiplication and production *training in genetic improvement and breeder seed production Linkages Monitoring adoption Assessing impact	Breeder Seed Producers Technology exchange specialist Extension specialist Economist Farmers

Table 2. Sorghum varieties released in Botswana as a result of collaborative technology development and testing between NARS and ICRISAT, 1984-1995.

Variety name (ICRISAT/NARS acronym)	ICRISAT germplasm used (Yes/No)	Year of release	Year of first significant diffusion	Area of expected coverage (% of total)	Area of current coverage (% of total)	Remarks
1.Phofu (SDS 3220)	Yes	1994	1995	40 000-50 000 ha (45-56%)	22 000 ha (25%)	White-seeded. Has staygreen trait. Dual purpose for food grain and stover.
2.Mahube (SDS 2583)	Yes	1994	1995	20 000 ha (22%)	900 ha (1%)	Red-seeded for malting and animal feed. Tannin-free.
3.BSH1 (SDSH 48)	Yes	1994	1995	10 000-15 000 ha (11-17%)	130 ha (0.2%)	White-seeded with excellent flour quality. Mainly for food.
4.Mmabaitse (BOT 79)	No	1994	-	-	-	White-seeded with brown specks.

Table 3. Pearl millet varieties released in Namibia as a result of collaborative technology development and testing between NARS and ICRISAT, 1984-1995.

Variety name (ICRISAT acronym)	ICRISAT germplasm used (Yes/No)	Year of release	Year of first significant diffusion	Area of expected coverage (% of total)	Area of current coverage (% of total)	Remarks
Okahana 1 (ICMV 88908)	Yes	1990	1991	93 000 ha (56%)	47 000 ha - 1994 (14%) 74 000 ha - 1995 (45%)	Recommended for the north central region of Namibia

Table 4. Sorghum varieties released in Zambia as a result of NARS efforts in technology development and testing with some collaboration with ICRISAT, 1984-1995.

Variety name (ICRISAT/NARS acronym)	ICRISAT germplasm used (Yes/No)	Year of release	Year of first significant diffusion	Area of expected coverage (% of total)	Area of current coverage (% of total)	Remarks
WSH 287	Yes	1987	-	-	-	Dropped
Sima (IS 23520 derivative)	No	1989	1990	7 000 ha (18%)	5 000 ha (13%)	White-seeded for food
Kuyuma (MR4/4606T11; WSV 387)	No	1989	1990	10 000 ha (25%)	5 000 ha (13%)	White- seeded for food
MMSH 375	No	1992	1991	5 000 ha (13%)	n.a.*	Brown-seeded for malting
MMSH 413	Yes	1992	1991	10 000 ha (25%)	n.a.*	Brown-seeded for malting
ZSV 12	No	1995	n.a.*	n.a.*	n.a.*	Pigmented white grain
FSH 22	No	1995	n.a.*	n.a.*	n.a.*	Forage sorghum hybrid

*n.a. = not available

Table 4a. Pearl millet varieties released in Zambia as a result of NARS efforts in technology development and testing with some collaboration from ICRISAT.

Variety name (ICRISAT/NARS acronym)	ICRISAT germplasm used (Yes/No)	Year of release	Year of first significant diffusion	Area of expected coverage (% of total)	Area of current coverage (% of total)	Remarks
Kaufela (ICMV 82132)	Yes	1989	1990	20 000 ha (38%)	10 000 ha (19%)	Recommended for the southern province
Lubasi (LBC)	Yes	1991	1992	324,00 (62%)	20000 ha (62%)	Recommended for the western province

Table 5. Sorghum and pearl millet varieties released in Zimbabwe as a result of collaborative technology development and testing between NARS and ICRISAT, 1984-1995.

Variety name (ICRISAT/NARS acronym	ICRISAT germplasm used (Yes/No)	Year of release	Year of first significant diffusion	Area of expected coverage (% of total)	Area of current coverage (% of total)	Remarks
Sorghum						
1. SV1 (ICSV 112)	Yes	1987	-	500 ha (4%)	500 ha (4%)	White -seeded for food Out of production
2. SV2 (A6460)	Yes	1987	1992	60 000 ha (54%)	40 000 ha (36%)	White -seeded for food
3. ZWSH 1	No	1992	-	-	-	White-seeded with brown specks. Never produced.
Pearl Millet						
1. PMV 1 (RMP 1)	Yes	1987	n.a.*	500 ha (2%)	n.a.*	Recommended for zones 4 and 5
2. PMV 2 (SDMV 89004)	Yes	1992	1993	100 000 ha (41%)	35 000 ha (14%)	Recommended for zones 4 and 5

*n.a. = not available

Table 6. Cultivars released in the four case study countries of Southern Africa showing the trend of achievements of the national and regional breeding programs in genetic improvement and impact generated in the respective countries.

Country	Number of cultivars released prior to 1983			Number of cultivars released in the period 1984-1995			Grand Total
	Sorghum	Pearl Millet	Total	Sorghum	Pearl Millet	Total	
Botswana	7(4)*	1	8(5)*	4	-	4	12(9)*
Namibia	-	-	-	-	1	1	1
Zambia	2(0)	-	2(0)	7	3**	10	12(10)
Zimbabwe	2	-	2	3	2	5	7
Total	11(6)	1	12(7)	14	6	20	32(27)

* number of the cultivars produced are shown in parentheses for sorghum.
** not included in the impact for Zambia.

Table 7. Economic indices of impact generated by and assessed for genetic enhancement of sorghum (SV2) and pearl millet (Okashana 1) in Zimbabwe and Namibia, respectively, 1992-93*.

Economic index	Zimbabwe for SV2	Namibia for Okashana 1
Diffusion estimates (%)	29.0[a] 30.0[b]	9.5[a] 17.0[b]
Average area planted (Ha) per household	0.73 (0.58)[c]	-
Calculated benefits accruing to improved cultivars (U.S. dollars)	1.29M	0.35M
Net benefits (U.S. dollars)**	0.22 M	0.04M
Internal rate of return (%) without fertilizer	25.8	13.3

* Modified from Anandajayasekeram et al (1995).
[a] Based on seed sales.
[b] Based on survey data.
[c] Average area planted for local farmer variety relative to SV2.
** Net benefits after research and transfer of germplasm costs have been deducted.

Table 8. Movement and sources of sorghum and pearl millet germplasm* and breeding lines from genetic enhancement programs into Botswana, Namibia, Zambia and Zimbabwe, 1975-76 to 1982-83 and 1984-85 to 1994-95.

	1975-76 - 1982-83			1984-85 - 1994-95					
	from ICRISAT			ICRISAT		SMIP			
Country	Sorghum	Pearl Millet	Total	Sorghum	Pearl Millet	Sorghum	Pearl Millet	Total	Grand total
Botswana	6594	310	6904	890	13	5067	2684	8654	15558
Namibia	-	-	-	-	28	41	3143	3212	3212
Zambia	4695	822	5517	6811	3362	11467	717	22357	27874
Zimbabwe	4505	292	4797	22504	8092	6752	24820	62168	66965
Total	15794	1424	17218	30205	11495	23327	31364	96391	113609

*The germplasm include re-introductions of indigenous germplasm collected in the SADC region and exotic accessions introduced from the rest of the world.

Table 9. Summary yield (t ha^{-1}) and maturity (days to 50% heading) data of four sorghum cultivars and controls released in Botswana.

	Grain yield t ha^{-1}				
	On-experiment station		On-farm		
Cultivar	Average	Range	Average	Range	Maturity
Phofu	3.25	1.18-4.69	0.73	0.45-1.01	69
Mahube	1.22	0.69-2.01	0.59	0.43-0.75	58
BSH1	3.83	1.21-7.00	-	*	72
Mmabaitse	1.93	0.50-2.84	-	*	70
Control/Farmer variety	2.34	0.72-4.00	0.51	0.46-0.55	86
S.E.±	0.547	0.38-0.88		n.a.	
C.V.%	29.74	18.0-50.0		n.a.	

*Not tested on-farm. BSH1 is an F_1 hybrid. Mmabaitse was not included in on-farm trials.
n.a. = Not available

Table 10. Summary yield (t ha^{-1}) and maturity (days to 50% bloom) data for Okashana-1, the cultivar released in Namibia.

	Grain yield t ha^{-1}				
	On-experiment station		On-farm*		
Cultivar	Average	Range	Average	Range	Maturity
Okashana-1	2.45	0.69-5.25	1.65	1.28-1.73	55
Controls (farmers local)	2.37	0.83-5.46	1.14	1.06-1.24	65
S.E.±	0.269	0.147-0.428	0.076		
C.V.%	30.50	16.0-42.7	38.4		

*Yield data averaged over 5 on-station sites and 21 on-farm environments during 1992-93 season.

Table 11. Summary yield (t ha^{-1}) and maturity (days to 50% heading) data of five sorghum and two pearl millet cultivars with controls released in Zambia.

	Grain yield t ha^{-1}				
	On-experiment station		On-farm*		
Cultivar	Average	Range	Average	Range	Maturity
Sorghum					
WSH 287	3.31	1.03-4.43	n.a.	n.a.	78
Sima	3.29	2.87-3.50	n.a.	n.a.	86
Kuyuma	3.36	3.05-3.77	n.a.	n.a.	78
MMSH375	3.81	2.52-5.67	n.a.	n.a.	79
MMSH 413	4.37	3.20-6.11	n.a.	n.a.	74
Controls/farmer variety	3.33	2.33-5.50	n.a.	n.a.	77
L.S.D.	1.38	0.39-2.79			
C.V.%	32	10-63			
Pearl Millet**					
Lubasi	2.38	0.94-3.82	n.a.	n.a.	62
Kaufela	2.04	0.89-3.33	n.a.	n.a.	60
Controls/farmer variety	1.48	0.32-2.70	n.a.	n.a.	70
L.S.D.	0.76	0.44-1.30	-	-	-
C.V.%	27	12-61	-	-	-

* On-farm data are not available (n.a.)
** Pearl millet data averaged over 10 sites for two seasons.

Table 12. Summary yield (t ha^{-1}) and maturity (days to 50% heading) data of three sorghum and two pearl millet cultivars and controls released in Zimbabwe.

	Grain yield t ha^{-1}				
	On-experiment station*		On-farm**		
Cultivar	Average	Range	Average	Range	Maturity
Sorghum[1]					
SV1	4.06	2.58-6.33	-	-	75
SV2	3.38	2.41-3.79	2.15	1.22-3.15	63
ZWSH1	4.91	3.36-6.45	2.37	0.94-4.05	72
Controls/farmer variety)	2.73	2.29-3.78	1.56	0.45-3.44	76
S.E.±	0.380	0.10-0.74	0.292	0.25-0.68	-
C.V.%	29.71	17.0-48.3	32.88	16.1-67.3	-
Pearl Millet[2]					
PMV-1	2.27	1.64-2.69	1.70	0.67-3.07	60
PMV-2	2.81	2.22-3.23	2.28	1.22-3.17	54
Controls (farmers)	2.10	0.52-2.44	1.07	0.24-1.86	70
S.E.±	0.288	0.11-0.41	0.256	0.10-0.63	-
C.V.%	22.57	13.17-29.34	20.35	8.39-38.33	-

*,1 No. of sites in sorghum experiment station trials are 30 for four years, for SV1 and SV2, and 14 sites for two years for ZWSH1.
**,1 No. of sites in sorghum on farm trials are 15 for two years for all three released cultivars.
**,*2 Pearl millet maturity averaged over 25 on-station sites over 4 years, and 10 on-farm environments over 2 years.

Impact of Genetic Improvement on Sorghum Productivity in India

B.S. Rana*, Swarnlata Kaul, and M.H. Rao

Abstract

Almost one third of total world sorghum is grown as rainfed crop in India. The grain is primarily consumed as human food and green forage and stover for animals. The genetic improvement in plant type, productivity, and resistance to various biotic stresses in a systematically planned manner has resulted in the development and release of 15 white pearly grained hybrids (3.0-3.9 t ha^{-1}) and 15 varieties (2.8-3.6 t ha^{-1}) gradually over a period of three decades. Improved cultivars, particularly the rainy season hybrids, rapidly became the primary components of production systems (Mono- and Inter-sequence croppings) due to assured higher productivity, wider adaptability, short duration and stature, response to applied nutrients, effective components in IPM, acceptability to farmers, and effective seed production support from public and private sectors.

The area under high-yielding varietal (HYV) programs increased from 0.18 million ha in 1966-67, to 1.31 million ha in 1974-75, to 3.5 million ha in 1980-81, and reached 7.1 million ha of the total 11.9 million ha area under sorghum cultivation (TE 1995-96). The accelerations in adoption rate are associated with the time to time development and spread of hybrids of higher potential. This rapid rate of adoption of HYVs has a perceptible impact on productivity, which, over the 25 years between 1968-70 to 1992-94, has increased 201% in rainy season (kharif) and 146% in post rainy season (rabi), resulting in an overall 177% increase. This has been achieved in spite of constant decline in sorghum area from 18 million ha in TE 1967 to 11.89 million ha in TE 1995-96. The sharp decline in sorghum area of 2.3% per annum between 1980 and 1994 is due to falling per capita consumption and a market-driven economy in favor of pulses and oil seed crops replacing rainy season sorghum. In spite of that, yield per ha under rainfed situations increased by 3.22% per annum between 1967-1980 and 1.90% per annum between 1980-1994.

Rainy season sorghum's ability to compete efficiently with other crops in the future would depend on productivity growth, i.e., evolution of hybrids with higher yield potential, closing the yield gaps, reduction per unit cost of cultivation, and creating demand for domestic and export markets. Genetic enhancement in grain mold resistance and value addition through genetic means and post harvest processing would augment food, feed, and industrial uses and ultimately increase the economy. Heterosis breeding and stabilizing yield through incorporation of resistance genes conventionally and through biotechnological techniques are currently high research priorities to break the yield plateau in post rainy season.

B.S. Rana, Swarnlata Kaul, and M.H. Rao, National Research Centre for Sorghum, Rajendranagar Hyderabad-500030 (India). *Corresponding author.

Indian Sorghum in the World Scenario

India is the largest sorghum growing country in the world; in 1994, it represented 29.8% of the world sorghum growing area (11.95 million hectares out of a total 43.52 million hectares worldwide). The U.S., Nigeria, and Sudan are other important sorghum growing countries, representing 11 to 12% of the total area planted to sorghum. India contributes 20% of the total sorghum production, and is the second largest producer of sorghum in the world after the United States, which contributes about 36% of the world's total sorghum production (Fig. 1). While productivity in the U.S., Mexico, and China amounts to over 3.1-3.8 t ha^{-1}, the rainfed productivity in India is 959 kg ha^{-1} under low input management, close to productivity levels in Ethiopia and Nigeria.

India, unlike other countries, has two sorghum producing seasons — kharif (rainy season June/July-September/October) and rabi (post rainy season October-December/January). Different cultivars are generally required for each season, as production conditions are quite different.

From 1979-81 to 1992-94, the total world sorghum growing area area showed a minor change (-3.05%); however, there

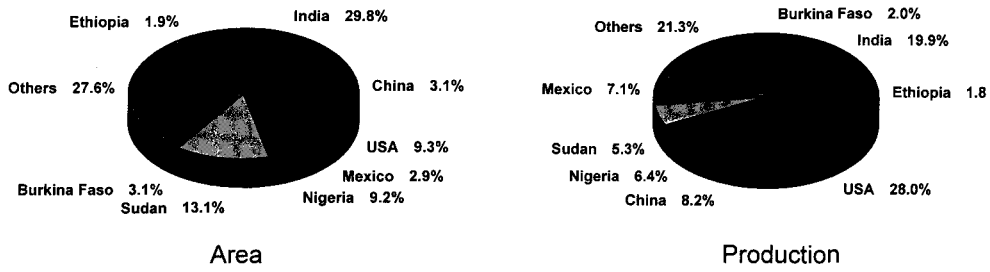


Figure 1. Area and production in major sorghum growing countries, 1992 and 1994.

was a significant decrease in area in Asia (-25.4%), North America (-20.17%), and South America (-45.21%). On the other hand, the growing area in Africa significantly increased by 45.21%, from 13.6 million ha to 20.15 million ha (Table 1). Among Asian countries, production in India during this period improved slightly from 11.4 million tons to 12.42 million tons, despite a 3.41 million ha reduction in the sorghum growing area. The change in total production on the Asian continent (-5.25%) was primarily due to reduction of production in China and Yemen, rather than India.

In Africa, the increase in total production has been primarily due to an increase in the sorghum growing area rather than in productivity. Most Asian countries showed a positive increase in productivity from 1979-81 to 1992-94. Productivity in Africa declined to 16.63% in the same period. Productivity in India increased from 695 kg ha^{-1} to 959 kg ha^{-1}, a 38% increase, while productivity in China increased by 50.46%.

March from Subsistence to Productive System

Before the advent of hybrid technology, the Semiarid Tropics (SAT) system remained at a subsistence level, with an average productivity range from 467 kg ha^{-1} in 1955 to 545 kg ha^{-1} in 1965, and covering a large area from 17.59 million hectares in 1955 to 16.14 million hectares in 1965. Crop diversification in the form of mixed cropping or intercropping with cereals, legumes, and oilseeds had been an important feature of traditional agriculture in the past, providing both insurance against crop failure and food security at the household level.

The essential components of sorghum farming before the era of high-yielding varieties were tall late cultivars with traits important for survival. There is a striking parallelism in tropical sorghum in India and sorghum across the continent in Africa. Rao and Rana (1978) have characterized such sorghums as excessively tall, longer in duration than the length of the growing period, generally photosensitive, low in harvest index, locally preferred, and adaptable. These types are individually superior in low populations (due to better individual plant expression) and inferior in high populations.

Although low productivity involves lower risks, technological changes in a high productivity background can provide

Table 1. Indian sorghum in world scenario.

	Area (M ha)			Production (M t)			Yield (t ha^{-1})		
Particulars	1979-81	1992-94	Change (%)	1979-81	1992-94	Change (%)	1979-81	1992-94	Change (%)
India	16.36	12.95	-20.86	11.38	12.42	9.14	.696	.959	37.91
China	2.83	1.36	-51.94	7.03	5.10	-27.41	2.484	3.752	51.06
U.S/	5.27	4.04	-23.34	19.16	17.48	-8.77	3.636	4.327	19.01
Mexico	1.49	1.28	-14.09	4.99	4.44	-11.09	3.349	3.466	3.50
Nigeria	2.68	4.00	49.25	3.28	4.03	22.97	1.224	1.008	-17.61
Sudan	3.05	5.70	86.99	2.27	3.31	45.81	.744	.580	-22.02
Ethiopia	1.04	0.84	-19.23	1.41	1.10	-22.22	1.356	1.306	-3.70
Burkina Faso	1.05	1.35	28.89	0.62	1.24	100.00	.590	.916	55.17
Others	11.12	12.00	7.88	15.38	13.42	-12.74	1.383	1.119	-19.12
World	44.89	43.52	-3.05	65.52	62.54	-4.55	1.460	1.437	-1.54

productivity assurance and ensure food security at household and national levels. Because low productivity of tropical cultivars is associated with a low harvest index, high biomass productivity, late maturity, and terminal drought vulnerability due to rainfall fluctuations, it was necessary to reoptimize the plant growth phases to appropriately match the crop growth period with the length of the growing season under rainfed agriculture. The 140 day duration of traditional kharif sorghum exceeds the duration of rainfall from July to mid or late September. The production of dry matter exceeds moisture availability in the soil and the longer duration limits the water use efficiency.

Genetic improvement of sorghum in India in the early seventies thus adopted the physiological approach of restructuring the plant in terms of dry matter distribution, increasing harvest index, optimizing height and maturity, and incorporating photo-insensitive genes and multiple resistances to various insects and diseases in an improved genetic background. Parental line improvement has been the torch bearer of hybrid breeding. Modifications of excessive height and maturity period were possible through the introgression of early maturity and dwarfing genes from temperate germplasm of U.S. origin (although dwarf [brachytic] and earlier versions of sorghum were encountered in farmers' fields in Sudan). Selection in such temperate × tropical crosses of sorghum has been described by Rao and Rana (1982).

The relationship of height and maturity to grain yield is curvilinear in a wide range of germplasm (120), including representative temperate and tropical germplasms and their derivatives (Rana et al., 1984). A computer exercise involving linear, quadratic, and product terms determined the optimum plant type to maximize yield. The optimum genotype was characterized by a height of 175-180 cm and flowering at 68-70 days with reduced leaf numbers. Such genotypes combined performance in community (ideal genotype concept) and wider adaptability. These intermediate types between temperate and tropical parents, as a bridge population, offered further opportunities for rapid recombination. These types with optimal dry matter production per unit time and distribution and growth rhythms used water efficiently and formed the basis of improving rainy season sorghum for yield and stability (Rao et al., 1979; Rana and Rao, 1986). As a result, ten varieties (CSV 2 to CSV 11) were developed and released for all India cultivation between 1968 and 1985.

Reduction in duration of maturity coinciding with occasional late rains resulted in grain deterioration, sometimes rendering grain less preferred for human consumption and marketing. Thus, acceptable grain quality has been a major thrust in the program. Rana et al. (1978) utilized hard grain, low water absorption, and tan plant background as selection criteria to breed for grain mold resistance. Tan plant pigment, a simple inherited character, has been useful in furnishing resistance to the most prevalent leaf diseases (Rana et al., 1976). Greater emphasis on these traits in the rainy season in genetic enhancement programs has resulted in more diverse forms with better consumer acceptability

(e.g., hybrids CSH 5, CSH 6, CSH 9, and CSH 11). The increased need for fodder has led to crosses among temperate and tropical derivatives that attain a new optimum relationship between height and yield and accumulation of favorable genes. This idea stemmed from multiple regression of grain yield with harvest index and biomass productivity.

Fifteen hybrids and 15 varieties have been released at the national level, and five hybrids and 25 varieties have been released at state levels since the inception of the All India Coordinated Project in 1969. Some recent genotypes, such as CSV 10, SPV 462, SPV 475 (CSV 13), and CSV 15, with high productivity, multiple resistance, and wider adaptability, are becoming more popular among farmers where hybrid seed supply is limited. The yield potential of currently grown varieties in rainy and post-rainy seasons are given in Tables 2 and 3.

The first change in the history of sorghum transformation was the development and release of the early-maturing dwarf hybrid CSH 1 (CK 60A × IS 84) in 1964. Although the hybrid had a phenomenonal adaptability range, higher productivity than local varieties, and a ratoon crop as an additional bonus, it had problems of susceptibility to grain mold and leaf diseases and reduced fodder quantity. Subsequent improvement in hybrids involved genetic enhancement of these traits in parental lines. Fifteen hybrids (CSH 1 to CSH 15) have evolved so far; the most popular among them, based on the CMS and restorer lines bred in the project, have been CSH 1, CSH 5, CSH 6, CSH 9, CSH 14 in the rainy season, and CSH 8R and CSH 12R in the post-rainy season. CSH 10, a tall hybrid, and CSH 11 (ICSH 153) were not favored by farmers, despite enhanced fodder in the former and grain yield in latter, because of low seed production in CSH 10, small seed, and occasional lodging due to charcoal rot in CSH 11.

Under rainfed conditions, yield potential for various rainy season hybrids is 3.0-3.9 t ha^{-1}, and 2.8-3.6 t ha^{-1} for varieties. Further genetic diversification in rainy season hybrids has been due to the introduction of earliness in CSH 14 and high fodder yield in CSH 13 (kharif and rabi), with grain yield level matching that of the most popular hybrid, CSH 9.

Table 2. Sorghum hybrids and varieties for All India cultivation in kharif (rainy season).

Hybrid/Variety	Grain yield (t ha^{-1})	Fodder yield (t ha^{-1})	Plant height (cm)	Duration (days)
		Hybrids		
Early Duration				
CSH 1	3.0	7.5	150	100
CSH 6	3.4	8.1	161	98
CSH 14	3.8	8.8	181	103
Medium Duration				
CSH 5	3.4	9.3	174	119
CSH 9	3.9	9.8	182	110
CSH 13(K&R)	3.9	14.4	261	110
		Varieties		
CSV 10	2.8	10.1	194	112
CSV 11	3.2	9.6	174	109
SPV 462	3.3	9.7	208	111
CSV 13	3.5	9.7	181	112
CSV 15	3.6	12.1	232	110

Table 3. Sorghum hybrids and varieties for All India Cultivation in rabi (post rainy season).

Hybrid/Variety	Grain yield (t ha^{-1})	Fodder yield (t ha^{-1})	Plant height (cm)	Duration (days)
		Hybrids		
CSH 8R	2.2	3.7	102	115
CSH 12R	2.6	4.7	201	115
CSH 13(K & R)	3.3	5.4	184	113
CSH 15R	3.2	5.6	196	110
		Varieties		
CSV 8R	2.2	4.8	157	120
Swati	2.2	5.3	168	117
CSV 14R	2.3	5.5	165	117
M 35-1	2.1	6.1	151	119

Traits farmers look for in post-rainy season (rabi) cultivars are high yield with matching grain quality and boldness, resistance to shootfly, and fodder quantity equal to that of the popular local variety M 35-1 under receding moisture conditions. Current research strategy targets these traits in rabi adaptation. Breeding for shootfly resistance (Rana et al., 1975; Balakotaiah et al., 1975), charcoal rot resistance (Rana et al., 1982), and increased water use efficiency in limited moisture availability has led to development of hybrids such as CSH 15R, released in 1995, some experimental hybrids, e.g., SPH 634 and SPH 695, and variety CSV 14R. These hybrids for the first time are based on bold seeded rabi type CMS (104A, 116A) and restorer lines (RS 585, RS 615, SPV 492) with adequate levels of multiple resistance to biotic and abiotic stresses. These breeding concepts have been useful to various national and international programs particularly in East, West, and South Africa.

Improved Cultivars as a Primary Component in Production Systems

It was earlier believed that varieties would spread faster due to their self-propagating nature, and small farmers would prefer to retain their seeds rather than buy expensive hybrid seed every year. However, hybrids have emerged as carriers of technology primarily due to higher productivity potential, better stability of performance, low risk, and assured supply of quality seed. Genetic improvement in hybrids also has progressed faster than in varieties (Table 4). Over the last three years, the average hybrid yield progressed 108, 119, and 129% over varieties. The yield potential of hybrids is always higher than varieties, but the best hybrid is 10-32% higher yielding than the best variety at a given time. Hybrids exhibit better homeostatic properties than homozygotes, as the regression coefficient of hybrids is less ($b = 0.73$-0.96) than that of varieties ($b = 0.95$-1.13) in multilocation tests (Table 5).

The varietal program has recently been directed toward dual-purpose breeding. The varieties are selected for enhanced height and thus exhibit 18.6% superiority in fodder yield over popular hybrids. The recently released variety CSV 15 is superior to popular hybrids such as CSH 5 and CSH 6. It took about 18 years to breed such a variety with yield potential matching some popular hybrids. However, the best dual purpose hybrid CSH 13 (kharif

Table 4. Heterotic advantage of hybrids over varieties (rainy season).

Year	No. of locations	Grain yield (t ha^{-1})		Hybrid/ Variety (%)	Range		Best hybrid/ Best variety (%)
		Variety	Hybrid		Variety	Hybrid	
1993	29	3.142(9)	3.404(9)	108	2842-3245	2994-3580	110
1994	33	3.003(10)	3.561(10)	119	2564-3249	2807-3841	118
1995	30	3.036(12)	3.913(17)	129	2599-3285	3174-4334	132
Mean (Wt.)		3.056	3.688				

Table 5. Adaptability of hybrids and varieties (rainy season).

Hybrid	x	b	Variety	x	b
CSH 6	2.807	0.73	SPV 462	2.972	1.11**
CSH 9	3.647	0.96**	CSV 13	3.047	1.13
CSH 14	3.572	0.83**	CSV 15	3.178	0.95**

x = Mean Grain Yield (t ha^{-1}).
b = Regression coefficient of varietal mean over Env. Index, Location = 29
** Significant at 1% against its own deviation.

and rabi) was superior in both grain (10%) and fodder (14.8%) yields over the best dual purpose variety in the trial.

The use of risk aversion in sorghum breeding (Barah et al., 1981) pointed out that yield and risk preference rankings are closely related. In pursuit of low risk and high yield, breeding efforts toward genotype alteration and multi-location testing to identify widely adapted cultivars have been fruitful. The genotypes with high mean and low CV (%) are considered to be highly adapted over a wide range of environments. When eight released genotypes, along with seven additional experimental genotypes, were analyzed against the weighted mean of all the genotypes (3372 kg ha^{-1}) and their mean CV over a period of three years (1993-95) at 27 locations, the hybrid CSH 6, released in 1976, was found lowest yielding and most variable over locations compared to recently bred genotypes (Fig. 2). In the context of the latest genetically improved varieties and hybrids, CSH 5, CSV 13, and SPV 462 were moderate in performance and variation over locations. The recently bred high-yielding varieties, such as SPV 1025, CSV 15, and SPV 881, and hybrids CSH 9 and CSH 14 with the lowest CV (18-21%) exhibited wider adaptability (Table 6).

The low variability and relative yield advantage of hybrids over varieties make them preferred by farmers (Fig. 3). Hybrids had the highest frequencies, in the 3500-4000 kg ha^{-1} range, in contrast with varieties, falling in the 3000-3500 kg ha^{-1} range.

Impact of Improved Cultivars on Crop Management Practices

Response of Improved Cultivars to Applied Nutrients

It was earlier believed that the low value nature of sorghum was the primary reason fertilizer was not applied to traditional cultivars. Studies of Jha and Sarin

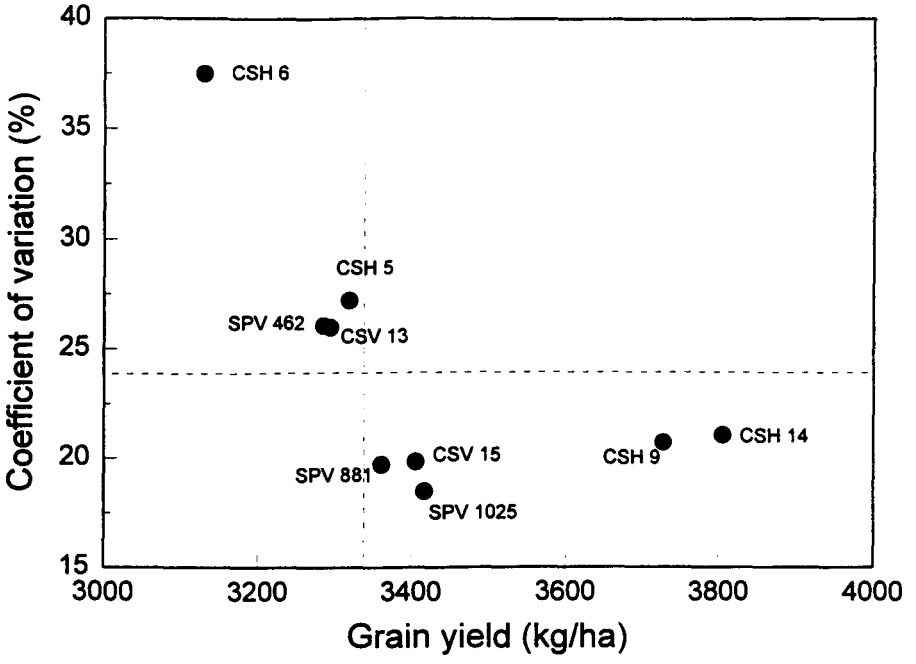


Figure 2. Stability of sorghum varieties and hybrids (1993-95).

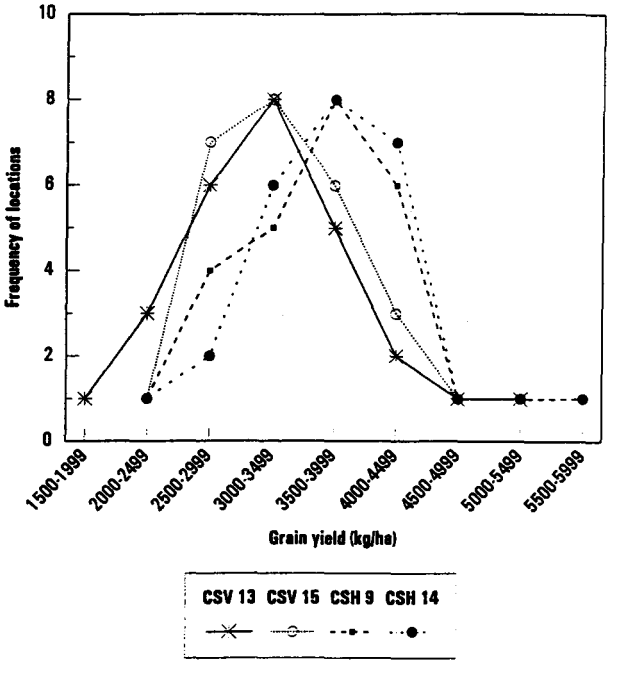


Figure 3. Range of productivity in sorghum hybrids and varieties

Table 6. Varietal productivity and increment (Inc) over preceding dose under different fertility managements in rainy season.

Fertilizer N : P	1993-94 (Loc. 7)		1994-95 (Loc. 6)		Adj
	CSH 9	CSV 13	CSH 9	CSV 15	
			Grain yield (t ha^{-1})		
20 : 10	3.032	2.806	2.603	2.385	2.778
40 : 20	3.776	3.075	3.316	2.749	3.130
60 : 30	4.157	3.429	3.724	3.160	3.516
80 : 40	4.890	4.057	4.400	3.747	4.164
100 : 50	5.039	4.358	4.511	4.287	4.788
Lowest : Highest	1 : 1.66	1 : 1.55	1 : 1.73	1 : 1.80	1 : 1.72
Mean	4.179	3.545	3.711	3.267	3.675

Adj. = Adjusted yield of CSV 15 for year effect equal to the increase in CSH 9 yield in 1993-94 over 1994-95.

(1981), however, indicated that lack of fertilizer was the main reason. They made the plea for development of regionally adapted fertilizer-responsive sorghum cultivars in India.

Because response to applied N occurred in the order of hybrid improved varieties local cultivar, genetic improvement and particularly exploitation of heterosis had an impact on nutrient use. Hybrids have better resource utilization capacity and return per kg N applied. Resource allocation is therefore preferred more toward hybrids in low risk environments where higher yields are more assured.

Because sorghum is a low value crop, farmers have not been inclined to apply fertilizer. However, it also is possible to demonstrate that hybrids, even at native fertility, yield higher than the local cultivars. There is a genotypic-dependent response to applied N under both rainfed and irrigated conditions. Even in the mid-sixties with the introduction of the first sorghum hybrid (CSH 1) and the variety Swarna (later named as CSV 1), it was possible to demonstrate that high-yielding hybrids and varieties responded 2.5 to 3 times more favorably than local cultivars to low doses of N application. The response (kg grain/kg N applied/ha) of CSH 1 vs. local at 0-50 kg/N was 21.2 kg vs. 7.1 kg grain/kg N. At higher doses of fertilizer (50-100 kg N/ha) the response of CSH 1 was 13.76 kg compared to the local cultivar's response of 5.42 kg. Under such situations, farmers found it more economical to apply fertilizer to the hybrids than to traditional cultivars.

Subsequent hybrids and varieties continue to respond to higher doses of balanced fertilizer. Even at the low fertilizer dose of 20 kg N + 10 kg P2O5 in the rainy season, the popular hybrid CSH 9 could yield 2.6-3.0 t ha^{-1}. The optimum recommended dose under rainfed conditions — 80 kg N + 40 Kg P2O5 /ha — can give a yield of 4.4-4.9 t ha^{-1}, about a 65% yield gain over the lowest dose. Improved varieties CSV 13 and CSV 15, with a yield potential of 2.4-4.3 t ha^{-1} under various levels of fertilizer application, achieve an increase of 10-18% for each additional dose of 20 kg N + 10 kg P2O5/ha up to the optimum level. However, the latest dual-purpose variety CSV 15 responded an additional 14% beyond the recommended optimum due to genetically enhanced physiological attributes. Hence, it could be possible to further enhance fodder

yield of this variety by 8-10% by increasing plant density 180,000-200,000 with a marginal increase in grain yield. Such responses can increase profitability in those areas where stover demand is high to sustain large cattle populations.

The rate of response to applied fertilizer under the receding moisture conditions of the post-rainy season was never encouraging. However, with the introduction of improved hybrids like CSH 13R and CSH 15R, it is now possible to demonstrate, at low as well as higher doses of N, a response more than three times greater compared to the popular local variety M 35-1, which could lead to adoption of high management with improved hybrids (Table 7). Under irrigated conditions, the varietal response is still higher than under rainfed conditions. CSH 13R yields 4-4.5 t ha^{-1} under irrigated management, compared to 3.3 t ha^{-1} under rainfed conditions.

Impact of Genetic Improvement on Transformation of Intercropping Practices

Intercropping has been an age-old practice in India with traditional cultivars, but the most scientific approach was adopted after the introduction of short duration and stature high-yielding hybrids. It now is possible to design intercropping systems and identify suitable genotypes to minimize the level of competition between companion crops. Although crop geometry is one management method, the genetic enhancement and modification of sorghum maturity and growth rhythm has had more significant impact on the design and adoption of improved and transgressive systems. A hybrid like CSH 6, which matures in 100 days, is an appropriate choice to be grown with a medium-maturing pigeon pea variety (Table 8). Such a hybrid responds to the closer inter-row spacing in the system and makes the system more remunerative than others, primarily due to the high yield of pigeon pea. As CSH 9 became popular due to higher productivity in about 110-115 days, a new design of intercropping system with a 3:3 row pattern of principal crop and intercrop was evolved to suit this hybrid. The change in row pattern is primarily due to relatively longer duration and vigorous growth of this hybrid.

Improved Cultivars as a Component of IPM

Subsistence systems based on local cultivars were able to resist pests like shootfly but often were damaged by midge and earhead bug in certain areas. Genetic enhancement of yield and plant type could take care of productivity but could not provide adequate levels of resistance to shootfly. However, due to reduced maturity duration, it is possible to

Table 7. Varietal response to applied N in post rainy sorghum.

	Rainfed (N kg ha^{-1})			Irrigated (N kg ha^{-1})		
Hybrid	0-30 N	30-60 N	0-60 N	0-40 N	40-80 N	0-80 N
	Response: Kg grain / Kg N applied / ha					
CSH 13 R	10.9	6.8	8.90	11.8	8.2	10.00
CSH 15 R	9.5	4.8	7.23	19.4	5.4	11.75
M 35-1 (Local)	3.2	1.8	2.17	-	-	-

Table 8. Varietal response to intercrop.

Genotype	Sole sorghum	Intercrop sorghum	Yield loss in sorghum	Pigeonpea as intercrop Yield (t ha^{-1})
		Grain yield t ha^{-1}		
Hybrids				
CSH 6	2.231	2.025	.206	.555
CSH 9	3.044	2.936	.108	.307
Varieties				
Swarna	2.187	1.904	.283	.189
Local	2.199	2.081	.118	.386

plant these genotypes early with the onset of the monsoon to avoid losses due to shootfly and realize their full potential. It also is possible to plant single maturity genotypes in a large area to minimize damage due to midge and ear head bug. Management of major pests like shootfly, midge, and ear head bug, therefore, could be possible by introducing short duration high-yielding cultivars.

Though early maturity has played a crucial role in Integrated Pest Management and has led to better utilization of natural resources (rainfall and nutrients), it causes vulnerability to grain molds due to rains at the time of maturity. Presently this is a major constraint on the impact of high-yielding cultivars in the rainy season. In the post-rainy season, resistance to seedling pests like shootfly is absolutely necessary. Genetic enhancement for shootfly resistance and charcoal rot resistance is important to demonstrate genetic potential in farmers' field.

Rate of Adoption of Improved Cultivars (High-Yielding Varieties)

Impact of Genotypes on Adoption Rate

The advent of hybrid technology and the effective involvement of seed production organizations assured quality seed production and its timely supply to the farmers. The area under high-yielding varietal (HYV) programs has gradually increased from 0.18 million ha in 1966-67, to 1.31 million ha in 1974-75, and to 3.5 million ha in 1980-81 (Fig. 4). Since 1975-76, there has been a constant increase in the total area planted under HYV, particularly hybrids, which covered 7.1 million ha (49.4% adoption) of the total area of 14.36 million ha planted in 1990-91. Despite a significant decline in total sorghum area from 15.8 million ha in 1980-81 to 11.7 million ha in 1994-95, the area under improved cultivars remained the same. Thus, most of the area planted under HYV continued with sorghum, which presently represents 60.5% adoption rate.

Coverage had been low until 1974, in spite of release of the sorghum hybrids CSH 1 and CSH 2 and the variety Swarna between 1964 and 1968. The adoption rate increased between 1975-1982 from 12.2% to 26.7%, primarily due to the introduction of two major hybrids, CSH 5 and CSH 6, which were genetically enhanced in productivity as well as in multiple resistance to leaf diseases and grain mold resistance. It took a few years for seed to increase and make an impact on coverage under these two hybrids.

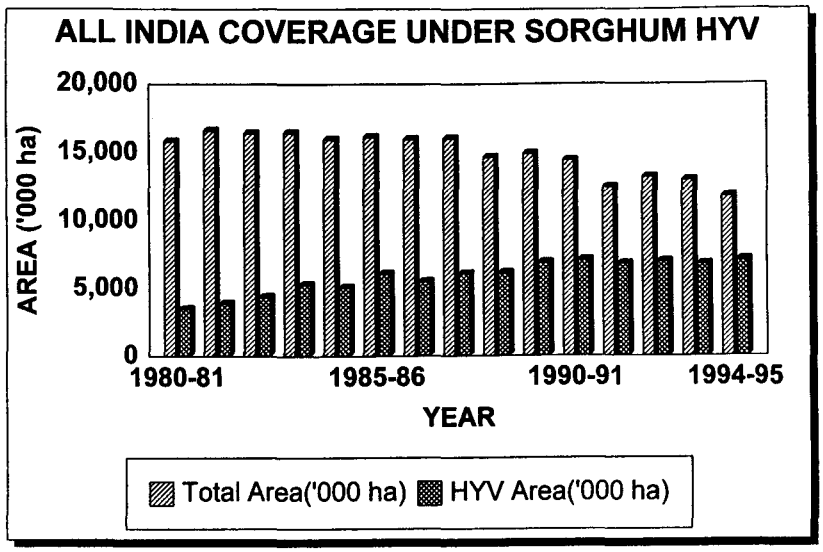


Figure 4. All India coverage under sorghum HYV.

Another significant change took place since the introduction of the presently most popular hybrid CSH 9 in 1982, which accelerated the rate of adoption to the present level of 7.1 million ha. This program has been supported by the release of a number of high-yielding varieties and, in the last few years, by the introduction of number of hybrids bred by private companies.

Skewed Adoption Rates in Various States

Despite the large area of coverage and availability of widely adapted hybrids and varieties, rates of adoption of high-yielding varieties in India vary from state to state (Fig. 5). A statewide analysis revealed that coverage had been fairly fast in those states where sorghum is relatively more important and moisture stress is high, such as Maharashtra, Karnataka, and Tamil Nadu. Currently the highest adoption is in Tamil Nadu (89.7%), followed by Maharashtra (71.9%), Madhya Pradesh (65.2%), Andhra Pradesh (46.2%), and Gujarat (41.2%). Coverage in Karnataka has not grown beyond 30% due to a sharp reduction in rainy season area. The overall coverage in Maharashtra was 4.3 million ha in 1992-93. Almost 100% of the 2.8 million ha rainy season area was under hybrids, and about 1.44 million ha (46.5%) of the 3.1 million ha post-rainy season area was under improved varieties and the improved local cultivar, M 35-1.

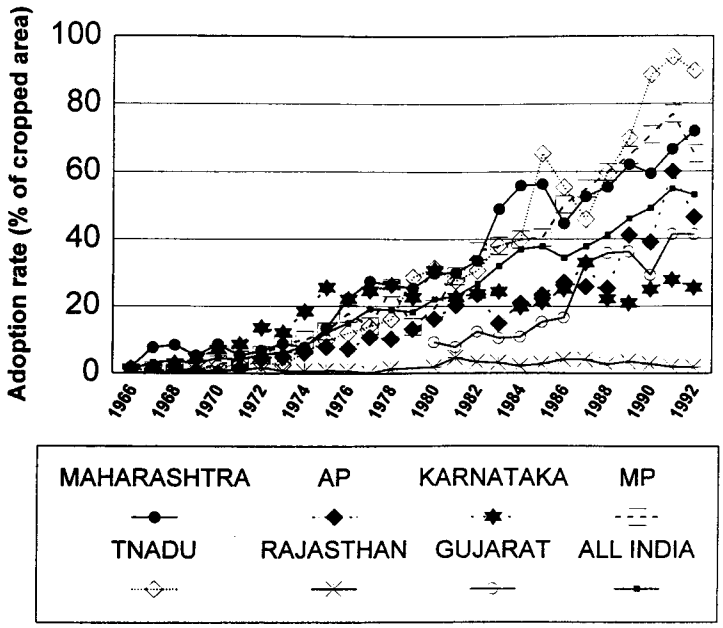


Figure 5. Adoption of HYV (% of cropped area) in different states of India.

Quality Seed Production Scenario

Public hybrids have wide support from both the public and private sectors (Table 9). Of 18,243 tons of certified rainy season hybrid seed, 76% is produced by the public sector and the remainder by the private sector. CSH 9 has emerged as the best-selling hybrid in the country, with a 75.5% share. CSH 5 is another important hybrid, with high levels of production (2071 mt). Among early maturing hybrids, CSH 14 (1117 mt) and CSH 6 (621 mt) are important. Commercial production of the first hybrid CSH 1 has declined due to its replacement by CSH 14. Production of the dual-purpose hybrid CSH 13 has recently begun. Among post-rainy season seed production, the emphasis so far has been on varieties such as CSV 8R (SPV 86), Swati, CSV 14R, and M 35-1, rather than hybrids.

Demand for seed of these hybrids depends on the genetic potential of the hybrid, consumer acceptability, and economy of seed production. Apparent grain quality, seed size, cooking quality (chapati-making quality), storability, degree of grain mold resistance, and lodging resistance have been some of the major determinants for varietal choice of rainy season cultivars. In fact, CSH 9 has most of these favorable traits and a well-established seed grower chain to patronize it over a long period of time.

Almost a dozen private seed companies are presently operating in the country with

Table 9. Certified seed production of public hybrids in 1995-96. (Quantity in tons).

Hybrid	By State Seed Corporations	By Private Sector	Total	%
CSH 1	164.5	30.0	194.5	1.1
CSH 5	1502.1	569.7	2071.8	11.3
CSH 6	621.3	183.6	804.9	4.4
CSH 9	10550.7	3227.6	13778.3	75.5
CSH 14	837.1	280.2	1117.3	6.1
SPH 388	150.6	70.0	220.6	1.2
CSH 13 (K & R)	2.8	3.0	5.8	-
Total	13829.1	4364.1	18243.2	99.6

strong R & D, seed production, and marketing networks. Because none of the hybrids either bred in India or imported under the National New Seed Policy by these companies can be released at the national level, uncertified seed of a number of hybrids is marketed in sizeable quantities (approximately 5100 t) each year under the truthful label and grown randomly. Some might become established in specific areas, too.

Seed production of rainy season hybrids occurs in the post-rainy season, particularly in Andhra Pradesh where minimum winter season temperatures are moderate (> 16° C). Seed production in the rainy season is not feasible because grain mold infection lowers germination rates. The dependence of the northern states on Andhra Pradesh for seed production makes it difficult for them to bring more area under high-yielding varieties and achieve the desired level of impact on sorghum productivity.

Impact of Genetic Improvement on Productivity Enhancement

Rainy Season Productivity

The adoption rate of improved hybrids and varieties has a direct impact on productivity enhancement (Fig.6). Due to fast adoption of hybrids in Maharashtra, the impact on sorghum productivity is evident, as indicated by an average yield of 1778 kg ha^{-1} achieved during 1992-93 and 1542 kg ha^{-1} in 1994-95 from an area of 2.5 million ha, compared to about 548 kg ha^{-1} in 1967-68 (in the era before high-yielding varieties). Productivity increased by an average of 281% (with a maximum increase of about 324% in 1992-93) after the introduction of hybrids (Table 10). In other dual-season states, the increase in productivity per unit area was 233% in Karnataka and 180% in Andhra Pradesh between 1967-68 and 1994-95.

Other states primarily growing rainy season sorghum alone, such as Madhya Pradesh, Gujarat, and Rajasthan with 63.2%, 41.3%, and 1.8% of the total sorghum area under improved cultivars, achieved an average productivity of 1093, 708, and 531 kg ha^{-1}, respectively. The rate of increase during this time was 134% in Madhya Pradesh, 308% in Gujarat, and 171% in Rajasthan. The average yield in Uttar Pradesh increased by 176%, from 525 kg ha^{-1} in 1967 to 925 kg ha^{-1} in 1994-95. There was a significant increase in yield in these states, too, but the relatively low yield is due to the large component of forage sorghum in these states.

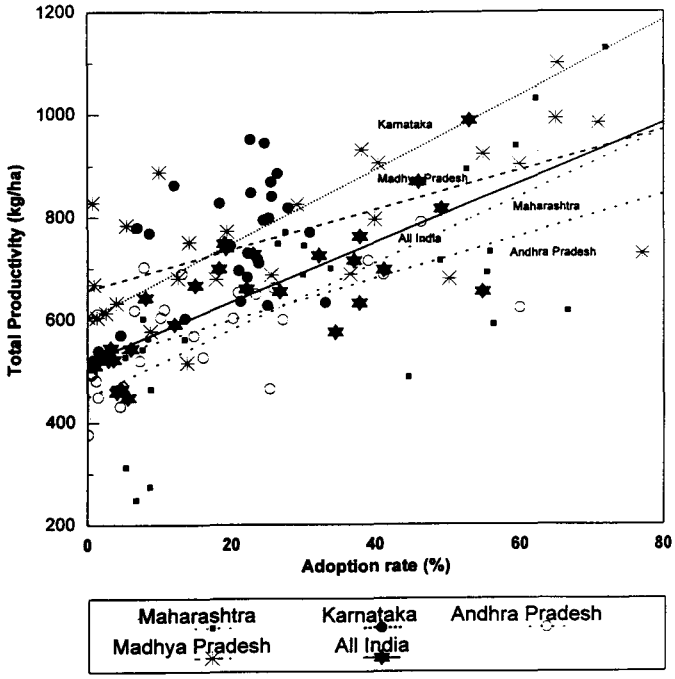


Figure 6. Influence of adoption rate on total productivity in different states.

Table 10. Change in productivity scenario in post HYV era and in best year 1992-93.

Sorghum growing states	Average grain yield (t ha^{-1}) TE* 1967 (A)	TE 1994-95 (B)	% change (B/A)	Best year 1993-94 (C)	% change (C/A)	Area (M ha) TE 1994-95
Rainy season sorghum (Kharif) (K)						
Maharashtra	.548	1.542	281.4	1.778	324.4	2.53
Karnataka	.531	1.236	232.8	1.188	223.7	0.56
Andhra Pradesh	.460	.830	180.43	.820	178.3	0.45
Madhya Pradesh	.693	.929	134.05	1.093	157.7	1.3
Uttar Pradesh	.525	.920	175.23	.929	176.2	0.48
Tamil Nadu	.747	.970	129.85	1.004	134.4	0.44
Gujarat	.215	.635	295.34	.662	307.9	0.29
Rajasthan	.310	.400	129.03	.531	171.3	0.7
Total	.498	1.097	220.3	1.230	246.9	6.86
Post rainy sorghum (Rabi) (R)						
Maharashtra	.480	.564	117.5	.541	112.7	3.29
Karnataka	.583	.679	116.5	.679	116.5	1.61
Andhra Pradesh	.588	.821	139.62	.905	153.9	0.54
Total	.483	.637	131.9	.632	130.8	5.67
All India (K + R)	.492	.891	181	.982	199.5	12.58

*TE = Triennium Ending

Post-Rainy Season Productivity

The post-rainy season crop is primarily grown in a contiguous belt in Maharashtra, Karnataka, and Andhra Pradesh over an area of 5.6 million ha under receding moisture conditions. The adoption rate in this season is limited to improved varieties and improved locals, which have relatively low yield potential but high survival value under biotic and abiotic stresses. Productivity enhancement is limited to 117.5%, 116.5%, and 139.6%, respectively, in these three states in the post-HYV era. Lack of appropriate hybrids for difficult agro-ecological situations, such as severe drought, variable depth of soil, and biotic stresses, are primarily responsible for low impact in this season.

The progress in sorghum productivity in the last 25 years is presented in Fig. 7. There has been a 201% increase in kharif productivity, a 146% increase in rabi productivity, and a 177% increase overall from 1968-70 to 1992-94.

Constraints on Impact

Low Competitiveness of Rainy Season Sorghum

Sorghum is predominantly consumed as a food in India. The most convincing impact on productivity has been seen with rainy season sorghum, but its preference as a food in both rural and urban areas is declining (Radha Krishna and Ravi, 1990), primarily due to a rise in income, a comfortable supply of preferred cereals

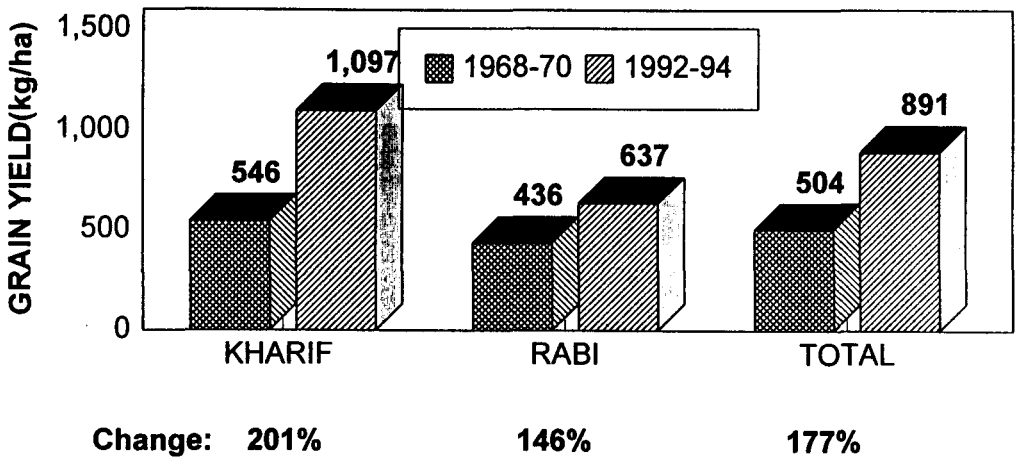


Figure 7. Progress in sorghum productivity in 25 years.

(rice and wheat) in the open market, and their assured supply at subsidized prices through a public distribution system to traditional sorghum eaters. Per capita consumption of sorghum in rural areas fell from 1.64 kg/month in 1972-77 to 0.93 kg in 1990-91 (NSSO - National Sample Survey Organization 1972-73 to 1990-91). (Fig. 8). The consumption of sorghum in urban areas was almost half (46 %) that in rural areas and this also has proportionately declined to 0.40 kg/month/person in recent years. The total cereal consumption fell to 57.7% in rural areas and 51.9% in urban areas between 1972-74 and 1990-91. This decline has been reflected in food sorghum demand in India (although, to a certain extent, increase in population has buffered total consumption).

A micro level investigation of sorghum competitiveness in India revealed low net returns from sorghum (Dayakar et al., 1996). Returns from the post-rainy season are highest for improved rainy season cultivars, followed by local cultivars (Table 11). Relative to sorghum, the net returns from competing crops grown in the same sorghum agro-ecology (rather than in the arid areas of pearl millet ecology) are several times higher. Thus sorghum is being replaced by soybean, sunflower, groundnut, cotton, and other high value crops. In high productivity zones such as Akola (Maharashtra), per hectare profitability (in INR) recorded at research stations for pigeonpea (7653), cotton (4225), or sunflower (3311) is much higher than for improved sorghum cultivars (2271). Soybean is more profitable to farmers and

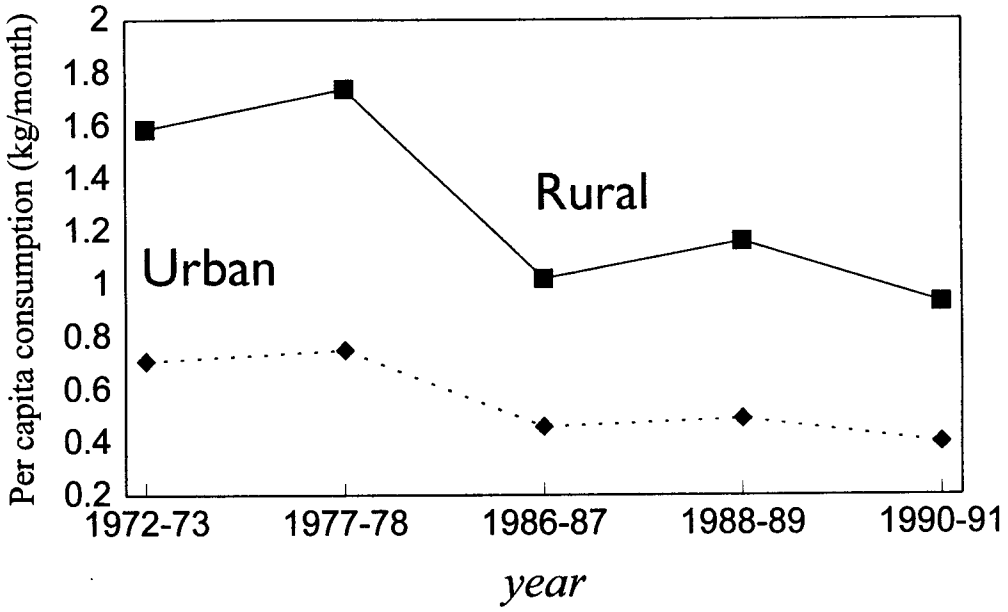


Figure 8. Per capita consumption of sorghum.

is replacing sorghum in this zone and Madhya Pradesh, limiting sorghum cultivation to marginal areas, with negative impact on productivity. High value rainy season crops such as sunflower and cotton compete with post-rainy sorghum in the Bijapur area of Karnataka, as deep vertisols kept fallow for sorghum are diverted to these crops.

The weakening competitiveness of sorghum is due also to unfavorable government policies, such as minimum support prices (MSP) and nonprocurement of sorghum grain when the market price falls below the MSP (Table 12). The productivity of rainy season sorghum, even under low input management, is decidedly higher than productivity of competing dryland crops grown under better management. However, higher market prices, 2.27-3.17 times higher MSPs for competing food crops (Ministry of Agriculture, 1993) such as soybean, sunflower, groundnut and greengram, and a 4.5 times higher MSP for cotton, leave sorghum growers to opt for the cultivation of these high return crops. As real market prices of rainy season sorghum fall below the MSP at Rs.240 per 100 kg (Ministry of Agriculture, 1993) and prices of competing crops are higher than their MSPs, the real return from competing crops has been much higher than from sorghum.

Table 11. Average net returns from sorghum and competing crops.

Crop	Districts		
	Anantapur	Akola	Bijapur
	Net returns (Rs/ha)		
Sorghum (Local)	598	-	3556
Sorghum (HYV)	988	2271	-
Groundnut	3427	-	-
Sunflower	5602	3311	5676
Pigeonpea	3954	7653	-
Cotton	-	4225	10603
Chillies	2965	-	-

Source: NRCS-ICRISAT Sorghum Utilization Survey 1994-95.

Kelly et al. (1994) reported weakening competitiveness of sorghum in the states of Madhya Pradesh, Andhra Pradesh, Karnataka, and Gujarat due to expansion of irrigation favoring irrigated crops such as sugarcane and cotton. Low producer prices for sorghum relative to oilseeds and legumes result in price movements working in favor of those competitive crops and lagging productive growth. Sorghum's ability to compete efficiently with other crops in the future will depend on productivity growth. It may be feasible to improve the competitiveness of sorghum by closing yield gaps, raising yield potential, and reducing the per unit cost of sorghum production. It is possible that production increases in rainy season crops whose food demand is declining may result in price falls, encouraging sorghum substitution for maize in various indus-

Table 12. Competing crops in rainy season.

Crops	Average yield (t ha^{-1})	Cost of production (Rs/100 kg)	Minimum support price (Rs/100kg)	Expected return (Rs/ha)
Sorghum	1.097	341	300	3741
Soybean	.918	592	680	6242
Sunflower	.611	693	950	5804
Groundnut	1.042	759	900	9378
Cotton	.262	832	1350	3510
Greengram	.855	676	800	6840
Sugarcane	71.099	26	43	30215

tries such as for starch, poultry and dairy feed, and breweries.

Yield Gap Analysis

Yield at Research Stations (RS) Vs. District Level

There are significant differences between potential yield and yield that can be realized in farmers' fields (Table 13). Presently the yield gap ranges from 51 to 79% in different states. In Maharashtra, the average grain yield was 1680-5142 kg ha^{-1} at research stations and 1103-2053 kg ha^{-1} in the districts, resulting in a yield gap that varied from 34.3 to 64.6%. This difference can be attributed to low fertilizer and less than optimum plant protection and plant population management. In Karnataka, grain yield of CSH 5 was 3002 kg ha^{-1} at research stations and 1340 kg ha^{-1} at the district level, leaving a gap of 55.4%. In Andhra Pradesh, locals are predominantly grown in the Mahaboobnagar district and both improved and locals are grown in Adilabad. The yield gap was 83% and 75.8%, respectively, in these districts, due to both varietal components as well as management factors.

Yield at Research Stations (RS) Vs. On-Farm Front Line Demonstrations (FLD)

The gap between the varietal yield achieved at research stations and in front line demonstrations on farmers' fields in well-planned experiments with recommended doses of fertilizer and plant protection was 31-44% (Table 14). In Maharashtra, the average grain yield of the dual-purpose variety CSV 15 was 3.36-4.06 t ha^{-1} at 14 Research Stations, compared to yields of 2.1-2.9 t ha^{-1} in 47 FLD resulting in a gap of 16.7-37.5%, which was less than that observed for hybrid CSH 9. The centrally released variety CSV 15 also exhibited better grain and fodder yield potential on farmers' fields in Karnataka, compared to the state release DSV 2. The gaps were 30.9-42.3% for grain yield and much higher (44.4-64.8%) for fodder yield.

Table 13. Yield gap analysis (CSH 9 at research station vs. average yield of district).

Research Station/District	Research Station (RS) (Yield t ha^{-1})			District yield (t ha^{-1})			Gap (%) (A-B) /A x 100
	1992	1993	Mean (A)	1992	1993	Mean (B)	
Maharashtra (Hybrid - CSH 9)							
Parbhani	5.593	3.716	4.654	1.884	1.404	1.644	64.6
Akola	4.356	3.753	4.054	2.104	1.707	1.905	42.5
Buldana	5.185	3.333	4.259	2.598	1.509	2.053	51.7
Nagpur	1.760	1.600	1.680	1.101	1.105	1.103	34.3
Rahuri	3.580	3.802	3.691	1.947	1.492	1.719	53.4
Jalgaon	5.333	4.851	5.142	2.190	1.886	2.038	60.3
Mean	4.301	3.509	3.913	1.971	1.517	1.744	55.4
Karnataka (CSH 5 in RS vs - CSH 5 and other hybrids in district)							
Dharwad (4)	-	3.002	3.002	-	1.340	1.340	55.4
Andhra Pradesh (CSH 9 in RS Vs Locals in district)							
Palem (Mahaboobnagar)	3.895	3.093	3.494	.627	.590	.608	82.6
Adilabad	6.025	4.412	5.218	1.207	1.317	1.262	75.8
Mean	4.950	3.752	4.356	.917	.953	.935	79.2
Grand Mean	4.466	3.507	3.910	1.707	1.322	1.519	61.2

In comparisons of CSV 15 and local cultivars in front line demonstrations at Palem (AP), the yield of improved varieties was 200% greater than that of local cultivars. Thus, genetic improvements made in recent years can help double the yield if the locals are completely replaced in this state. In the post-rainy season, sorghum is grown in receding moisture, and expression of genotypes happens to be sub-normal. The experimental yield of the hybrid CSH 13R is about 3 t ha^{-1}, compared to 2 t ha^{-1} yield of the local cultivar, M 35-1. Although both experienced a significant decline in yield in 29 on-farm trials, the yield of the hybrid (1451 kg ha^{-1}) was still 25.3% higher than that of the local. In another set of on-farm trials, the yields of the recently released variety CSV 14R and M 35-1 were 1.2 t ha^{-1} and 1.0 t ha^{-1}, respectively, against the national average of 639 kg ha^{-1}.

Influence of Low Competitiveness on the Area and Production

After the green revolution in major cereals in the early 1960s, the sorghum growing area has continuously decreased. Even sorghum's own green revolution due to a quantum jump in the productivity of the rainy season crop could not help sustain a large growing area. In the 1960s sorghum was grown on over 18.26 million ha (11.35 million ha in the rainy season and 6.91 million ha in the post-rainy season), with a total production of 9.343 million tons at an average productivity of .51 t ha^{-1}. During that period the total production during the rainy season and post-rainy season was 6.0 and 3.4 million tons, respectively, with an average productivity of .529 t ha^{-1} and .48 t ha^{-1}. Sorghum was grown on a total of about six million ha in Maharashtra alone. This state has shown a rapid rate of adoption of high-yielding varieties since 1975-76, achieving 72% adoption in recent years. Despite the perceptible changes in productivity of the monsoon season crop, there has been a gradual decrease in the sorghum growing area due to low competitiveness of sorghum compared to oilseed and legumes.

An area of 16.14 million ha in 1974-75 was reduced by 22% in two decades in India (Table 15). Most of the reduction (3.39 million ha) occurred in the rainy

Table 14. Yield gap analysis in dual purpose variety CSV 15 in Front Line Demonstrations (FLD) in rainy season.

Zone (RS-FLD No.)	Cultivar	Grain yield (t ha^{-1})			Fodder yield (t ha^{-1})		
		RS	FLD	Gap %	RS	FLD	Gap %
Rahuri (5-20)	CSV 15	4.06	2.6	35.9	11.36	6.0	47.2
	CSH 9 (C)	4.16	2.3	56.2	9.37	5.7	39.2
Akola (5-30)	CSV 15	3.36	2.1	37.5	15.30	6.5	57.5
	CSH 9 (C)	3.57	2.0	44.0	12.70	5.8	54.3
Parbhani (4-20)	CSV 15	3.48	2.9	16.7	11.14	7.5	32.7
Dharwad (2-18)	CSV 15	4.63	3.2	30.9	14.40	8.0	44.4
	SPV 462	4.51	2.6	42.3	12.80	4.5	64.8
Indore (3-24)	CSV 15	2.80	2.7	3.4	14.60	10.0	31.5
	Local	-	2.3	-	-	8.5	-
Palem (1-24)	CSV 15	3.06	2.0	34.6	13.5	-	-
	Local	-	1.0	-	-	-	-

( ) No. Of Research Station (RS) and Front Line Demonstrations (FLD) respectively in parenthesis.

Table 15. Changes over two decades in sorghum area, production and yield.

Season	Area (M ha)		Production (M t)		Yield (t ha^{-1})		% changes of TE 1994-95 over TE 1974-75		
	TE 1974-75	TE 1994-95	TE 1974-75	TE 1994-95	TE 1974-75	TE 1994-95	Area	Production	Yield
Kharif	10.25	6.86	6.11	7.51	.598	1.093	-33.07	22.90	82.82
Rabi	5.89	5.72	2.72	3.63	.454	.639	-3.50	33.77	40.68
Total	16.14	12.58	8.83	11.14	.545	.889	-22.06	20.79	62.96

TE = Triennium Ending

season crop, indicating a -33% change. The post-rainy season crop area has remained at around 5.89 million ha, with a minor fluctuation of -3.5%. In spite of these reductions, the total production of 8.83 million tons increased by 20.79% in the same time period. The production in 1994-95 of 11.14 million tons can be attributed to an 82.82% increase in productivity in the rainy season crop and a 40.68% increase in the post-rainy season crop.

The reduction of area is negligible in Maharashtra, a core sorghum growing state. However, in other states there has been a sharp decline in rainy season area from -14.31% to -66.5%. A serious decline occurred in those states where sorghum is also grown for forage. In the case of Karnataka, a -43.0% reduction in area of the rainy season crop corresponded with an increase of 53.53% in the post-rainy season crop area. In the case of Maharashtra, where moisture stress is more prevalent in the rainy season, and in both Maharashtra and Karnataka, sorghum continues to be better adapted in the post-rainy season than other high value crops.

Compound Growth Rates (CGR) per annum (%) are given in Table 16. In the pre-HYV era ending 1964-65, both area and yield increased at rates of 1.0 and 1.49% per annum, respectively. As some more promising hybrids like CSH 5 and CSH 6 were introduced on a large scale after the mid-seventies, there was a quantitative jump in productivity at 3.22% CGR per annum. This commendable rate was achieved in dryland areas due to genetic improvement. In spite of the sharp decline (2.3% CGR) between 1980-81 to 1994-95, the overall productivity gain has been 1.90% per annum. The extra gain in productivity was realized after the introduction of CSH 9 in 1982-83. Most of the coverage at present has been under this hybrid. On a long-term basis, over 45 years there has been a continuous increase in productivity at the rate of 1.56% per annum, initially due to genetic enhancement within tropical material and in recent years due to the large scale introduction of high-yielding hybrids.

Table 16. All India compound growth rate of sorghum % per annum (1981-82 = 100).

Period	Area	Production	Yield
1949-50 - 1964-65	0.99	2.51	1.49
1967-68 - 1980-81	-1.15	2.04	3.22
1980-81 - 1994-95	-2.30	-0.44	1.90
1967-68 - 1994-95	-1.17	0.79	1.98
1949-50 - 1994-95	-0.54	1.01	1.56

Source: Agricultural statistics at a glance.

Future Needs to Improve and Enhance the Impact on Crop Productivity

SWOT analysis (study of Strength, Weakness, Opportunity and Threat) has

ascertained the future course of action to increase sorghum productivity and profitability under dryland cultivation. The strength (S) of sorghum cultivation in India (besides its utility as a forage crop) has been illustrated above in terms of genetic enhancement of productivity, increased adoption rates, and change in the attitude of the farmers to adopt commercial hybrids and better input management. In the post rainy season, greater utility of sorghum grain and fodder, low cost of cultivation of local cultivars due to their higher survival value under drought and biotic stresses, and high market rate are keeping sorghum more competitive than other crops. Because sorghum is a more assured crop under receding moisture conditions (without rain or supplementary irrigation), other crops could not replace it.

The major weaknesses (W) of sorghum cultivation in India are low productivity of post-rainy season sorghum due to lack of appropriate hybrids; low competitiveness and profitability of rainy season sorghum due to grain mold susceptibility and slackening market demand; low stover quality to sustain animal health; lack of absolute resistance in germplasm to major biotic and abiotic stresses; inability to make major investments in basic research, including the application of biotechnology; and a market scenario unfavorable to the cultivation of kharif sorghum.

Though sorghum is becoming less competitive and less remunerative to the farmer, particularly in assured rainfall and deep soil areas, the answer lies in achieving another quantum jump in moisture-scarce areas. Opportunities (O) to enhance the productivity in selected areas include:

1. Improving post-rainy season sorghum production in dry and irrigated areas utilizing currently available technology.

2. Breaking the yield plateaus through heterosis breeding and stabilizing yields in the post-rainy season through genetic enhancement to incorporate cross resistance to shootfly, charcoal rot, drought and cold.

3. Improving the profitability of rainy season sorghum through: evolving high-yielding hybrids resistant to grain molds; value addition (through genetic means and post-harvest processing) to promote alternate uses; development of dwarf short-duration hybrids to intercrop with low-canopy crops which have replaced sorghum in the past, with particular emphasis on export and alternate domestic uses.

4. Widening the exploitation of genetic diversity in hybrid breeding by converting resistant genotypes into CMS lines using alternate cytoplasms, incorporation of restorer genes in improved combiners, and creation of heterotic gene pools.

5. Applying biotechnology to incorporate resistance to biotic and abiotic stresses where conventional methods could not make much impact and germplasm lacks absolute resistance.

6. Employing Integrated Pest Management strategies with an increased HPR component and environmental protection.

7. Crop modeling and optimizing components of production to sustain higher

yields in inter- and sequence-cropping systems.

8. Genetically improving chapati-making quality and grain storage to bring kharif sorghum under a public distribution system for improving food demand.

The major threats (T) to sorghum cultivation have been its susceptibility to grain molds in the rainy season, which reduces its preference for food and results in a non-remunerative market price; rapid decline in the rainy season sorghum area; increase in crop losses due to biotic stresses in both seasons; and aggressive R&D of multi-national companies in the area of genetic engineering, restricting the opportunities of the national program in future IPR regimes.

Molecular marker-aided selection, besides conventional approaches, can help improve biomass productivity and harvest index under moisture stress, resistance to biotic and abiotic stresses, restoration of fertility in cold weather, and grain quality traits promoting alternate uses (malting quality, carotene content, protein quantity, quality and digestibility, starch quality) and sugar content in stalk juice. Creation and exploitation of heterotic gene pools on the pattern of corn will be useful for evolving hybrids with higher potential in the future. Increased water and nutrient use efficiencies may promote response to applied fertilizer under moisture stress situations and increase productivity and stability in the post-rainy season.

Breeding post-rainy season sorghum with cross resistance to biotic and abiotic stresses will remain a challenging job and will require more resources and more innovative and concerted scientific efforts.

References

Balakotaiah, K., B.S. Rana, D.P. Tripathi, and N.G.P. Rao. 1975. Genetic analysis of some exotic ɔ Indian crosses in Sorghum X. Inheritance of resistance to sorghum shootfly. Indian J. Genet. 35:344-349.

Barah, B.C., H.P. Binswanger, B.S. Rana, N.G.P. Rao. 1981. The use of risk aversion and plant breeding. Concept and Application. Euphytica 30:451-458.

Dayakar, B., T.G. Kelly, and P. Parthasarthy Rao. 1996. Sorghum competitiveness in India. A micro level investigation. IV International Symposium on Sustainable Farming Systems, Nov. 11-16, 1996, Perendeniya, Sri Lanka.

Jha, D., and R. Sarin. 1981. An analysis of levels, patterns and determinants of fertilizer use on farms in selected regions of semi and tropical India. 25. Economics Program Progress Report, ICRISAT.

Kelly, T.G., K. Asokan, and P. Parthasarathy Rao. 1994. Sorghum competitiveness in India. Paper presented at the Rockefeller Foundation Social Science Research Fellows Meeting, 14-18 November, 1994. ILCA, Addis Ababa, Ethiopia.

Ministry of Agriculture. 1993. Analysis of price situation of Agriculture commodities. Tenth Report. Committee on Agriculture, Lok Sabha Secretariat, New Delhi.

NSSO (National Sample Survey Organization) Various rounds 1972-73 to 1990-91: National sample survey per capita consumption and expenditures, Department of Statistics, Ministry of Planning and Programme Implementation, Government of India, New Delhi.

Radha Krishna, R., and C. Ravi. 1990. Food demand projections for India. Centre for Economic and Social Studies (CESS), Nizamia Observatory Campus, Begumpet, Hyderabad, A.P., India.

Rao, N.G.P., and B.S. Rana. 1978. Characterization of tropical land temperate Sorghums and their utilisation. Proc. National Symp. on Genetic Resources, IARI, New Delhi.

Rao, N.G.P., M.J.V. Rao, B.S. Rana, and V.J.M. Rao. 1979. Responses to water availability and modifications of water use efficiency in tropical dryland Sorghums. Proc. National Symp. on Genetic Resources, IARI, New Delhi.

Rao, N.G.P., and B.S. Rana. 1982. Selection in Temperate × Tropical crosses of Sorghum. p. 403-419. Sorghum in the Eighties International Symp. ICRISAT, Hyderabad, Nov. 2-9, 1982.

Rana, B.S., V.J.M. Rao, B.B. Reddy, and N.G.P. Rao. 1983. Overcoming present hybrids yield plateau in sorghum. p.48-57. XV International Genetic Congress Pre-satellite symposium in genetic improvement of heterotic systems. Coimbatore (TNAU) Dec. 7-9, 1983.

Rana, B.S., B.C. Barah, H.P. Binswanger and N.G.P. Rao. 1984. Breeding optimum plant types in sorghum. Indian J. Genet. 44:385-398.

Rana, B.S., D.P. Tripathi, K. Balakotaiah, R. Damodar and N.G.P. Rao. 1975. Genetic analysis of some exotic ɜ Indian crosses in Sorghum XI. Selection for shootfly resistance. Indian J. Genet 35:350-355.

Rana, B.S., D.P. Tripathi, and N.G.P. Rao. 1976. Genetic analysis of some exotic × Indian crosses in sorghum XV inheritance of resistance to sorghum rust. Indian J. Genet. 36(2): 244-249.

Rana, B.S.,V.J.M. Rao and N.G.P. Rao. 1978. Genetic analysis of some exotic × Indian crosses in sorghum XVIII. Breeding for resistance to grain deterioration. Indian J. Genet. 38:322-332.

Rana, BS., V.J.M. Rao, D.P. Tripathi, and N.G.P. Rao. 1977. Genetic analysis of some exotic × Indian crosses in sorghum XVII. Selection criterion for resistance to grain deterioration. Indian J. Genet. 37(2): 430-487.

Rana, B.S., K.H. Anahosur, V.J.M. Rao, R. Parameshwarappa, and N.G.P. Rao. 1982. Inheritance of field resistance to sorghum charcoal rot and selection for multiple disease resistance. Indian J. Genet. 42: 302-310.

Rana, B.S. and N.G.P. Rao. 1986. Genetic improvement of grain sorghums in India. p. 105-114. *In* P.K. Gupta and J.R. Bahl (eds.) Genetics and Crop Improvement. Rastogi & Co., Meerut, India.

Ergot Awareness

Coordinators - G.N. Odvody and R.A. Frederiksen
Texas A&M University

An Ergot Awareness Session was held in association with the International Confeence on Genetic Improvement of Sorghum and Pearl Millet to provide sorghum workers with the most recent information about the biology, disease management, and geographical distribution of sorghum ergot (Bandyopadhyay et al., 1996). The epidemic of sorghum ergot (sugary disease) caused by *Claviceps africana* (Frederickson et al., 1991) in Brazil in 1995 (Ferreira and Casela, 1995 and Reis et al., 1996) was the first report of any ergot species on sorghum in the Western hemisphere. The rapid spread of ergot to other countries in South America and its observation in the Queensland region of Australia in 1996 demonstrated that *C. africana* had rapidly become a global threat to sorghum production. The high incidence of ergot in susceptible male-sterile sorghums in hybrid seed production fields in Brazil and probably Bolivia in 1995 and 1996 raised industry concern about seed movement from ergot-affected countries. Rapid spread to neighboring countries further compounded concerns for the potential introduction of ergot into other regions including the United States. Ergot could cause devastating losses to the commercial hybrid seed production industry in the U.S. if spread or introduction occurs prior to development of adequate disease management practices.

Global authorities N. McLaren (GCRI, South Africa) and R. Bandyopadhyay (ICRISAT,India) provided a summary of the biology, epidemiology, and economic impact of sorghum ergots. The current status of the global threat of ergot was addressed in regional reports from several scientists representing Brazil (R. Schaffert, EMBRAPA/CNPMS), Australia (R. Henzel, DPI) and Argentina (L. Giorda,INTA. A summary was presented of the successful use of triazole fungicides to control ergot on male-steriles in EMBRAPA/CNPMS field experiments (Ferreira et al., 1996) and in commercial hybrid sorghum production fields in Brazil in 1995-96.

Quarantine and other ergot containment issues were addressed by USDA-APHIS (J. Stibick) and the ergot concerns of the seed industry were presented by Pioneer Hybrid Seed Company (K. Porter).

The meeting concluded with an open discussion of ergot issues and needs for future research initiatives and activities.

References

Bandyopadhyay, R., Frederickson, D.E., McLaren, N.W., and Odvody, G.N. 1996. Ergot - a global threat to sorghumInternational Sorghum and Millets Newsletter, v. 37, pp. 1-32

Ferreira, A.S., and Casela, C.R. 1995. Ocorrencia de Claviceps sorghi, agente causal da doenca ergot no BrasilFitopathologia Brasilerira, v. 20, p. 302, Suplemento.

Ferreira, A.S., Pinto,N.F.J.A., and Casela, C.R.. 1996Avaliacao de Fungicidas para o Controle de Ergot ou Doenca Acucarada (*Claviceps africana*) em Sorgho. Pesquisa Em Andamento 14, April 96, 4p

Frederickson, D.E., Mantle, P.G., and de Milliano, W.A.J1991Claviceps africana sp. nov., the distinctive ergot pathogen of sorghum in AfricaMycological Research 95:1101-1107.

Reis, E.M., Mantle, P.G., and Hassan, H.A.G. 1996First report in the Americas of sorghum ergot disease, caused by a pathogen diagnosed as Claviceps africanaPlant Disease 80:463.

Discussion

Session III - Yield and Adaptation Breeding
Session Chair: Wayne Hanna
Rapporteurs - Ouendeba Botorou and James Osborne

J.N. Mushonga - Its noted that pearl millet production in India and southern Africa is declining and yet you talk of more improved populations being developed: What is the cause for this production reduction? What strategy do you propose to stop this?

K.N. Rai - First of all, I did not say that production is going down in India; it is area that is going down. In fact, with increase in productivity, the production in India is going up. In India, the decline in pearl millet area is due to favorable land, previously under pearl millet cultivation, being diverted to other more profitable crops. There is no way this can be stopped, nor is there a need for it so long as this strategy gives overall benefit to the farmers. Breeding more productive cultivars of pearl millet, however, may reduce the rate of decline in the pearl millet area. The same thing may apply to pearl millet areas in southern Africa as well. I do not think that the production in southern Africa is declining.

S.C. Gupta - Area under pearl millet is declining in India because of the availability and increase of resources such as irrigation and fertilizer. With improved resources, farmers have other crops to grow which are more profitable than pearl millet.

S.K. Bhatnagar - Drought plays an important role for unstable pearl millet grain yield in stress environments in the northwestern region of India. Whereas drought has been assigned priority "low" priority in future breeding programs, what is the futuristic look in breeding for drought tolerance?

K.N. Rai - As I mentioned in my presentation, terminal drought is being addressed by breeding for higher yield potential and earliness. However, there is another type of drought which occurs intermittently during plant growth and development. There is no effective screening technique developed and no resistance/tolerance identified to address this type of drought. Thus, the only course left is to conduct and evaluate breeding nurseries and trials in the drought-prone environments and select for what performs best.

Lee House - Concern was expressed that the experience in India of establishing a seed industry may be difficult to repeat in Africa. It is my feeling that the problems thus far experienced in Africa do not so much relate to capability as to organization; i.e., sufficiently high yielding cultivars compared to locals have not been available. It is important to begin with hybrids which also have generally not been available. Development activities related to seed production and marketing have not been part of research programs to develop high yielding management responsive cultivars, and the roll of public

and private sector activity has not been clearly defined, much less implemented. The effort to provide quality seed to farmers in adequate quantity on a timely basis needs much more consideration than it has received.

Osman O. El Nagouly - Hybrids had better response to environments than lines. On the other hand you mentioned that hybrids out yielded lines under stress environments. Would you please give me an explanation for that?

Lee House - Observation that the percentage difference between the yield of a hybrid versus a variety is higher under stress than in the absence of stress is a frequent observation but there are exceptions. I am not aware that the reason for this is known, it may relate to heterosis, to a greater genetic plasticity because of increased heterozygosity and studies at Texas A&M indicate that hybrids better withstand pre-flowering stress than varieties but are not superior in response to post-flowering stress. Hybrids extract soil nutrients at a faster rate than varieties which support growth but may place the hybrid in greater problem if there is stress at the end of the season.

Brhane Gebrekidan - It has been emphasized in the presentations that the success in sorghum and millet production advances in India have been mainly due to research on breeding and the effectiveness of the seed industry. What are the other factors that have contributed to the success in India? What are the lessons for Africa?

Babatunde Obilana - We can give answer to the question on why it seems it is only research and seed companies that achieved the impact being talked about? There are a lot of behind the scenes activities and other technology exchange activities that go to impact achievement. It involves on-farm testing and verification of farmer acceptance involving all collaborators and partners I listed in my paper. It is multidisciplinary, multisectorial and involves farmer pressure to change difficult policies. enabling environment is important too

B.S. Rana - Hybrid confers advantage over varieties in terms of productivity and stability. In India it was earlier conceived that varietal adoption will be faster due to its self propagating nature and poor farmers may save their own seed. But once farmers were convinced about hybrids, they adapted it in spite of higher cost. No one can afford such a time lag by sticking to varietal program. Thus, hybrid program is a must for all developing countries for their prosperity and government policies can be amended accordingly.

Don Vietor - Please describe the climatic conditions in Central America, i.e., rainfall distribution, photoperiod, and temperature, that motivate producers and breeders to select for and maintain photoperiod sensitivity in sorghum, rather than photoperiod insensitivity.

Francisco Gomez - Climatic conditions where photosensitive sorghums are grown in Central America are very distinctive. First, rainfall pattern is bi-modal , May - November. The first (May-July) part of the rainy season is used for sorghums to grow vegetatively, while in the second (August-November) they grow reproductively. This allows the grain to ma-

ture at the end of the season when moisture is very low, avoiding grain molds, bird damage and midge.

Abdelmoneim B. El Ahmadi - I would like to add, one environment where photoperiod sensitive sorghums are grown is along the river bank in the northern parts of Sudan after flood recession. Planting is usually in October and harvest in early February.

A. Blum - During the period of scientific agriculture, only very few major genes brought about a revolution in yield of cereals. These are height and photoperiod sensitivity genes. Both affected harvest index. Reduced height and reduced photoperiod sensitivity increased harvest index and grain yield of the cereals, to a limit. Photoperiod sensitivity is usually used to fit crop growth duration to a climatic situation with a climatic or abiotic limitation so photoperiod sensitivity may be the best option for maximizing yield in these conditions. This, however, involves a certain reduction in harvest index and potential yield.

Francisco Gomez - Yes, but photoperiod sensitivity add significant advantage to certain sorghums in specific environments. Photosensitivity is an adaptive strategy to overcome grain mold, bird damage and midge problems.

R.G. Henzell - Is there any reason why all sorghums should not be tan plant colored?

F.R. Miller - I do not know of reasons to not expect rapid change to tan plant color. Reluctance to change is the only thing holding back a very positive adaptive change. Tan plant color supports superior yield because of better heat-balance/photosynthesis. Tan plant color appears to convey foliar disease resistance improvement. Tan plant color is our only hope to significant international food resource markets via exports. Tan plant color improves the cosmetic appearance of leaves, glumes, bran, and grain. Tan plant color with white grain maximizes light or temperature load from a pure physiolo-chemical point of view. In ten years or less, I expect 90+% of American sorghum hybrids to be tan plant color. There are two genes — P_Q_ which condition color. ppQQ is good but ppqq is best!

Belum V.S. Reddy - Limited studies on tan and nontan plant color isogenic lines showed that nontan plant isogenic lines yielded higher than tan plant color isogenic under post rainy season while the advantage of nontan plant color was not observed in the rainy season when temperature regimes are higher during grain development than in the post-rainy season.

Secondly, in post-rainy season, many segregates from the varietal improvement program with nontan plant color had higher productivity than the tan-plant color varieties in post rainy season. Of course, the hybrid improvement with tan plant color for post rainy season is a different case because the productivity on hybrids is based on gene action difference from varieties. Therefore, we need to study in more detail the advantage/disadvantage of the plant color in relation to different adaptations.

B.S. Rana - The tan plant pigment, an innovation of the All India Sorghum Improvement Programme, confers advantage for resistance to grain molds and leaf diseases in rainy season. This is the reason why one gets cleaner grain than those harvested from non-tan types in rainy season which are otherwise susceptible to above diseases. Since post rainy season crop is grown under receding moisture (without irrigation and no-rain situation) grain molds and leaf diseases are not a problem, and tan plant has no advantage. There is an example where hybrid CSH13R, a tan plant-type, yields 1.5 times more than popular non-tan variety in post rainy season.

Darrell Rosenow - Can you speculate on the heritability of adaptation in photoperiod insensitive sorghums such as in the great difference among photo-insensitive sorghums in their adaptation under shorter day-more tropical environments?

Fred Miller - Perhaps the basic reasons for the major differences among "tropically" and "temperately" adapted sorghums are not fully known. It is known that there are basic differences in base metabolic temperatures — this impacts respiration and finally growth and development. Temperately adapted types grown in tropical environments are physiologically pushed by temperature conditioned reactions toward reproduction. Senescence begins early and loss of plant health causes lodging, etc. Heritability of superior performance in more tropical environments by photoperiod insensitive types is sufficiently high to facilitate easy breeding success.

Edgar Haro - In wheat, there is a black box between 12-14 hours of day length in determining day length sensitive from insensitive types. Sometimes a plant classified as photoperiod sensitive when grown at 12-14 hours of day length behaves as insensitive, the same response may be observed with insensitive types. Is there a good definition of the range in day length for sensitive and insensitive types?

Fred Miller - Please - BTx3197 is very photoperiod insensitive and serves as a base line for further evaluations (12-15 hours day length is the regime of concern.) Experience has shown that few sorghums are absolutely insensitive. Once $\underline{Ma_1}$ is changed to $\underline{ma_1}$, the bulk of the photoperiod response is removed, then temperature responses become evident. I suggest a literature citation — 1968, Crop Science, Miller, Barnes, and Cruzado — which shows how we screened and classified photoperiod response.

Session IV

Breeding Techniques

Session Chair: Ken Kofoid

Rapporteurs: Gary Toenniessen and Aboubacar Toure

Speakers:

D.J. Andrews
H.F.W. Rattunde
K.F. Schertz
P.J. Bramel-Cox
R.H. Smith

Breeding Hybrid Parents

D.J. Andrews*, G. Ejeta, M. Gilbert, P. Goswami,
K. Anand Kumar, A.B. Maunder, K. Porter, K.N . Rai,
J.F. Rajewski, V.S. Belum Reddy, W. Stegmeier, and B.S. Talukdar

Abstract

In both grain sorghum and pearl millet, single cross hybrids are made with cytoplasmic-genic male sterile (CMS) seed parents and pollen parents that restore male fertility. In pearl millet, hybrids also can be made with an inbred (or F_1) seed parent pollinated by a variety. These hybrids probably are the best type for African conditions for reasons of disease resistance, adaptation, and ease of production. Such hybrids can be made with or without CMS.

Improved levels of combining ability for yield, together with desired grain qualities, phenotype, and wide adaptation, are the keys to breeding hybrid parents. Early generation testing to select for combining ability is necessary, but a certain level of per se eliteness together with a good B or R reaction in the CMS system must first be obtained before testing can begin. The concept of heterotic groups is useful in breeding hybrid parents, even if the classification is mostly by sterile (indicating B or maintainer) or fertile (R or restorer) reactions on a CMS sterile system. According to its reaction, new germplasm is added to either the B or R pool. (Germplasm giving an incomplete reaction is normally avoided.) However, new germplasm chosen for its per se values does not necessarily add to the heterotic value of a B or R pool. Ideally a system that screens new germplasm for new alleles, like that proposed by Dudley (1984, 1987), should be used to add genetic diversity to each group.

Balanced breeding programs have both short-term and long-term aims. Better parents are most frequently obtained from elite × elite crosses; however, for sustained improvement, new variability must be found and moved into elite backgrounds. Conventionally such introgression programs have backcrossed to elite lines, which may be satisfactory for pearl millet (because unadapted germplasm is usually a population) and for partly adapted sorghum. However, research on sorghum at Kansas State University has shown distinct advantages of using adapted random mating populations (with genetic male sterility) over lines as recurrent parents to facilitate the discovery and introgression of useful traits from unadapted species, cultivated or wild.

D.J. Andrews and J.F. Rajewski, Department of Agronomy, University of Nebraska, Lincoln, NE 68583-0915; G. Ejeta, Department of Agronomy, Purdue University; M. Gilbert, Cargill Hybrid Seeds, Minneapolis, MN; P. Goswami, Pioneer Overseas Corp., Maharashtra, India; K. Anand Kumar, ICRISAT Sahelian Center, Niamey, Niger; A.B. Maunder, DeKalb Genetics, Lubbock, TX; K. Porter, Pioneer Hi-Bred Intl, Inc., Plainview, TX; K.N. Rai, V.S. Belum Reddy, and B.S. Talukdar, ICRISAT Asia Centre, Hyderabad, India; W. Stegmeier, Ft. Hays Branch Exp. Sta., Kansas State University. *Corresponding author.

Hybrid testing programs first test in ideal conditions and against the known major specific constraints before engaging in extensive multilocation testing in 20 to 100 locations, which will adequately expose new hybrids to the range of environmental variations expected in the target domain. In the U.S. these are known as strip tests, and almost all are placed in farmers' fields and managed by farmers, permitting a good estimation of the G × E interaction of the new hybrids. Performance data (including grain qualities), extensive visual evaluations, farmers' opinions, and seed production are all considered in the decision to release.

Existing breeding methodology should continue to raise yields by around one percent per year. There is adequate untapped genetic variability in cultivated germplasm of both crops (for example, in sorghum less than 10% of this been used in breeding commercial U.S. hybrids). Breeding for quality and defensive traits, even perhaps drought tolerance, may be accelerated by better methods of gene identification and transfer, which may involve marker-assisted selection and/or other biotechnological methods. But the ability of biotechnology to help improve complex traits such as yield potential still is uncertain for both economic and technical reasons (molecular research is specifically needed on methods which will complement combining ability testing). In any case, improvements are needed in existing breeding methods and germplasm characterization to identify, extract, and transfer new genetic variability that will contribute to combining ability.

General Concepts

Breeding hybrid parents in both sorghum and pearl millet follows the same general principles (House, 1985; Andrews, 1987), although there are some differences in technique. In addition — unlike sorghum — several types of hybrids are possible in pearl millet.

In grain sorghum, only single-cross hybrids based on cytoplasmic-nuclear male sterility (CMS) are used. Farmers in many countries have become accustomed to and require totally uniform sorghum hybrids. This preference does not pose severe problems because inbreeding depression is not important in this virtually inbreeding species, and inbred lines (especially seed parents) are relatively high-yielding. Three-way hybrids (using F_1 seed parents to increase seed yields) have been tried, but the heterogeneity in hybrids has not appealed to farmers. Additionally, because biotic resistances may have evolved to operate well in a homozygous state in this species, it has been possible (with some exceptions, e.g., shoot fly resistance) to find and incorporate effective resistances to major pests and diseases into sorghum inbred parental lines.

In pearl millet, only single-cross hybrids have been grown for grain production on a large scale in India (since the mid 1960s). Downy mildew became a major problem on the initial hybrids, and, because of adherence to the single-cross dictum, progress in breeding resistant hybrids was slow (Andrews and Bramel-Cox, 1994). Durable resistance to downy mildew in pearl millet, a naturally cross-pollinating species where traditional cultivars are heterogeneous, heterozygous populations proved difficult to incorporate into inbreds. It was finally done after

20 years, but the reliable supply of hybrids to Indian farmers still partly depends on the diversity created between parental lines and hybrids developed by both the public and private sectors. CMS-based hybrids in pearl millet are still vulnerable to ergot, sporadically serious in India, but a major threat in Africa. Because of inbreeding depression common with a cross-breeding crop like pearl millet, considerable effort has to be made to breed for yield per se in inbred seed parents.

Top cross (TC) hybrids — an inbred seed parent (an F_1 also can be used) pollinated by an open pollinated variety — are practical in pearl millet and have real advantages for Africa in terms of durability of disease resistance and stability of adaptation, which are difficult to obtain in single-cross hybrids. TC hybrids can be made using either a CMS seed parent (an inbred line or F_1) or a normal male fertile line as the seed parent. This second way of making the hybrid, termed a protogyny top cross (PTC), is feasible because of the protogynous nature of flowering in pearl millet. When flowering, each head first becomes completely female fertile for a period of one to several days before anthesis occurs, during which period it is functionally male sterile. Experiments have shown that over 90% hybrid seed can be obtained when such a protogyny "seed parent" is saturated with pollen from an appropriate male "pollinator" variety in a seed production plot (Lambert, 1982). Further experiments have shown that because of morphological and vigor differences between plants of the PTC hybrid and the seed parent (which is normally of dwarf stature), 10 to 20% seed parent selfing has a negligible effect on the performance of the PTC (Andrews et al., 1993). Both the TC and PTC hybrids confer advantages of durability of resistance and stability of performance. In ordinary production situations, their yields are not substantially less than those of single-cross hybrids. PTC hybrids, however, have additional advantages. Since CMS is not involved, there is no additional ergot susceptibility, and it is not necessary for the male parent to carry CMS restorer genes. Since these hybrid varieties are expected to exhibit phenotypic variability, F_1s can be used for seed parents to increase seed yields. PTC hybrids have distinct advantages for Africa, including reduced development time.

Breeding hybrid parents in both species is essentially a balance of selection for per se performance and for combining ability. Some of the requirements of seed parents per se are different from those of male (or pollen) parents. Values of lines per se are easier to select for than combining ability, which can be evaluated only through hybrid performance. Some traits of parental lines per se are well expressed in hybrids. Unfortunately, in the case of yield, the correlation between parents and their hybrids is unreliable.

The physiological basis for heterosis (hybrid vigor) has not yet been explained. More is known about the types of gene action involved in heterosis than how the genes work. General combining ability (GCA) is primarily a function of additive gene action (which can be fixed through selection and inbreeding), while specific combining ability (SCA) depends on non-additive gene action that can only exist in heterozygotes. For grain yield in both crops, estimates of the ratio of contribution of GCA and SCA to hybrid perform-

ance are wide-ranging. The general conclusion is that GCA is more important, but SCA should not be neglected. Hybrid parents need to be genetically complementary for vigor and yield-associated traits, but not for other often recessive traits that would adversely affect height, maturity, grain qualities, or resistance.

Heterotic Groups

The notion of heterotic groups is widely developed in maize (Pollack et al., 1991). Interbreeding between them will result in loss of genetic complementarity. Incorporating new sources of genetic variability will increase the variability in group A but should also complement (and hence show good levels of heterosis with) group B. The opposite applies when seeking new variability for group B. Heterotic groupings could potentially be multi-dimensional, but a bi-dimensional grouping is easier to manage.

Such heterotic groupings originally existed in sorghum, but not in pearl millet. Historically in sorghum, members of the Kafir and Milo races provided contrasting hybrid parents, the female parents being of the Kafir group. When CMS was first discovered in sorghum, Kafirs were found to carry nuclear genes that caused male sterility when put into Milo cytoplasm. The Milo race carried nuclear genes for restoration of male fertility as well as contrasting genetic diversity, which produced good hybrid vigor. The situation now, however, has become complicated with the inclusion of other sources of diversity into both the B Kafir pool and the R Milo pool, although heterotic contrasts obviously exist (Gilbert, 1994). In pearl millet if any heterotic grouping exists with respect to the A_1 CMS system, it is determined by B and R reactions to CMS Tift $23A_1$. More recently in pearl millet the Iniadi (Togo) germplasm apparently forms a third heterotic group, combining well with both the A_1 CMS maintainers derived from Tift 23B and the non-Togo restorers of the A_1 CMS system. The A_4 CMS system in pearl millet produces a different configuration because, while most A_1 B and R lines are maintainers on A_4, Iniadi germplasm does contain R_4 alleles. In general, however, both in pearl millet and sorghum, breeders avoid B × R crosses for the generation of new parental variability except when genes from a specific source have to be incorporated into both parents.

Cytoplasmic-Genic Male Sterility Systems

Several cytoplasmic-genic male sterility systems have been found in both species (Schertz, 1973; Kumar and Andrews, 1984; Worstell et al., 1984; Hanna, 1989). The most widely used system in both crops was the first to be found, designated A_1 for each crop. The other systems have various advantages and disadvantages both for breeding and seed production. Because of the susceptibility in maize to southern leaf blight associated with male sterile Texas cytoplasm, many sorghum breeding programs are trying to develop hybrids in the A_2 CMS system. The use of alternate cytoplasms also opens up the possibilities of different heterotic groupings with potentially new alleles (Gilbert, 1994). In sorghum, most high-yielding restorers on A_1 are maintainers in A_2, and thus can be used as seed parents; however, there are very few complete restorers for the A_2 system. A_3 male steriles, though

they shed no pollen, have plump yellow anthers which cannot easily be distinguished from fertiles. A_4 and 9E have other disadvantages. However, it is easier to develop seed parents with A_2, A_3, and A_4 than it is with A_1.

Early in the development of hybrids in pearl millet, four CMS systems were found; all have disadvantages (Kumar and Andrews, 1984). The first to be found, PT732A, (Madhava Menon, 1959) was not publicized and was not numbered. Appadurai (1982) subsequently showed PT32A CMS was different from A_1, A_2 and A_3, but still it did not give complete sterility. Complete and stable male sterility could not be obtained with A_2 and A_3. Although A_1 has been extensively used commercially, it too has problems. There are modifiers to the full expression of both sterility and complete restoration of fertility, each being environmentally unstable. There is considerable uncertainty about producing a completely sterile A line from a B line in which the first test cross was perfectly sterile; the loss of putative B lines to this cause may exceed 90%. Consequently, reliable steriles and restorers are hard to breed, and some R_1 lines that restore male fertility on some A_1 females act as partial restorers on others. Male sterile A_1 lines can revert to pollen shedders at a low rate (because of both nuclear and cytoplasmic mutations), but sufficient to necessitate careful roguing of both A line and hybrid seed production fields.

By contrast, the new A_4 system in pearl millet (Hanna, 1989) shows up the deficiencies of the earlier systems (Andrews and Rajewski, 1994) and suggests that a similar system needs to be found in sorghum. The A_4 CMS system in pearl millet offers a high success rate because apparently there are no modifiers to the sterility genes and fewer environmental effects on the expression of male sterility and fertility. Observations over the last five years at the University of Nebraska at Lincoln indicate that if the first test cross shows a plant is an A_4 maintainer, then all selections from that plant can be sterilized, and there will be no erosion in the quality of sterility during progressive backcrosses in A line development. A_4 restorer lines do vary in the quantity of pollen their hybrids produce, but this is an attribute of the line and does not seem to change with time or location. Although reasons are still being sought, it has been noted that seed set on selfed $A_4 \times R_4$ hybrids, $A_4 \times B$ crosses, and R_4 selfs in sterile cytoplasm is frequently better than counterparts in the A_1 CMS system. The reason may be simply more fertile vigorous pollen, but the better $A_4 \times B$ seed set may indicate an improvement in stigma receptivity or duration. The lack of modifiers and the better environmental stability of male sterility or fertility means that A_4 greatly simplifies both breeding and seed production. The sterile anthers can look different from A_1 steriles, but are still readily distinguishable from male fertile plants. Initially there was a lack of genetic diversity in R_4 restorers, but this is now improving through crossing and as more germplasm is screened.

Genetic Variability and Selection

New genes are needed for long-term progress in breeding. For convenience we will differentiate between variability that contributes purely to yield potential through better and more efficient growth, and defensive traits that provide protec-

tion from pests, diseases, and physical stresses like drought, thereby allowing the plant to better realize its potential. Yield potential is important at all levels of production, perhaps relatively more so in stress conditions where limited resources must be utilized more efficiently. Large collections of the total cultivated variability of both crops exist, but often only with some basic morphological description. What is lacking, with some exceptions for drought (Rosenow and Clark, 1995), are any systematic evaluations for important attributes such as pest, disease, and stress resistances (Maunder, 1992), or worth in breeding for yield potential.

In long-established breeding programs, the most advanced lines are very different from raw (landrace) germplasm, and simple crosses between the two rarely yield segregates comparable to the advanced parent. In sorghum, the exotic (unadapted) germplasm content usually must be reduced to 12% or less by backcrossing to adapted parents before useful segregants occur (Maunder, 1992). However, because it is often necessary to use unadapted germplasm to obtain specific new traits, many programs have introgression projects. These are easiest when some clearly identifiable trait is needed, and it is here that marker-assisted selection will be able to help further. Breeding for combining ability, however, is more difficult, since initial crosses with raw germplasm do not show whether they can provide new yield genes, and thus introgression programs are often somewhat speculative. In response to the need to access a wider range of germplasm, USDA funded the Sorghum Conversion Program at Texas A&M, starting in 1964. This program has converted many important representatives of the major sorghum races (by removing photoperiod sensitivity and all major dominant height genes except DW_2), providing breeders a useful new diversity, particularly from the Zerazera race. The conversion program was not, however, designed to identify combining ability nor to use anything but grain sorghum; in addition, backcrossing was toward the germplasm source, to otherwise preserve its originality.

Several major seed companies conduct their own sorghum introgression programs. ICRISAT has conducted an extensive germplasm utilization program of its own, but much of its advanced material (which has been used by breeding programs worldwide) has significant Zerazera content. ICRISAT now has a wider program of germplasm utilization, including wild relatives. Populations have contributed to R line production, but pedigree selection is still the principal method for disease- and pest-resistant seed parent development. Recent research at Kansas State University has investigated how best to access useful yield and other genes from adapted, unadapted, and wild sorghum. Using adapted random mating populations instead of elite lines as recurrent parents proved to be superior in extracting useful variability from unadapted or wild relatives, using one or two backcrosses (Menkir et al., 1994). Apart from their use in introgression, random mating populations in sorghum have not demonstrated any superiority over more conventional breeding methods in producing elite hybrid parents.

The situation is different for pearl millet. Good pollen parents, but not seed parents, have been extracted from popula-

tions. Some crosses between raw germplasm and adapted lines or populations also have been productive. These crosses are similar to introgression of unadapted germplasm via adapted populations in sorghum, because, in both cases, populations provide more opportunities for favorable recombinations. In pearl millet, as in sorghum, photoperiod sensitivity has obstructed access to much tropical genetic variability. The most useful source of germplasm for pearl millet breeding worldwide has been the Iniadi landrace (from the Togo/ Ghana/ Burkina Faso region), which has large seed, good combining ability and parental worth, and is unusually photoperiod insensitive (Andrews and Anand Kumar, 1996).

In both crops, breeding new hybrid parental lines has become increasingly dependent on crossing elite by elite lines, B × B lines and R × R lines. This practice progressively narrows the genetic base of breeding programs and requires new traits, especially resistances, to be brought in by pre-breeding, often backcrossing. The success of a backcrossing program greatly depends on the precision with which the desired trait can be identified and thus preserved in the backcrossing/ introgression process. The tendency is to select for genes having major effects or tightly linked gene complexes. Thus, particularly in sorghum, elite × raw germplasm crosses are not used in the expectation of immediate discovery of a new elite line; the most common short-term approach in breeding inbred parents in both crops has been elite × elite line crosses followed by pedigree selection. However, introgression seeking new genes must be a feature of any long-term balanced breeding program.

Selection Procedures

Determination of Heterotic Affinities

In many breeding programs, heterotic affinities are determined solely on the basis of whether the new accession is a restorer or maintainer in regard to the CMS system being used. However, more information is needed. A new accession should contribute new useful genes, either for yield or defensive traits, to its heterotic group and increased heterosis to hybrids with the counterpart group. For disease and pest resistance, resistance levels to various biotypes and segregation patterns among progeny from crosses with known sources of resistance can both provide the helpful information. For yield, however, only crosses with representatives of both heterotic groups can classify the usefulness of a new accession (Dudley, 1984 and 1987; Gilbert, 1994). Gene mapping will eventually help. Most breeding programs do not employ these complicated tests (except for resistance to well known pest biotypes) and rely on the assumption that a new line with obvious per se differences is likely to contain genetic diversity which may prove useful for yield.

Selecting for Combining Ability

Because crosses between elite lines produce a high proportion of progeny with desirable per se values (see parental line criteria below), selection for combining ability can begin at an early stage within F_3 families or even among F_2 plants in R line development. There is general acceptance that early generation testing assists in the selection of good combiners. There is disagreement, however, whether it is worth expending test crossing resources

at a stage when a high proportion of the plants/families tested subsequently will be discarded on per se criteria. Many programs delay testing until the F_4 when more per se selection has been done and then start with two widely adapted tester lines. F_4 also is a common level of inbreeding in pearl millet when the first test crosses will be made.

Selecting for combining ability has sometimes lacked objectivity. Ideally one would like to select for combining ability that would work with any new parent. This is unrealistic because in sorghum, and especially in pearl millet, a few tester lines do not well represent any heterotic group. At the opposite end of the scale, however, it is easy to visualize improving an existing hybrid — the progeny selected from crosses with one parent are best evaluated by using the other parent as the tester. However, this approach will build only on the specificity of one tester and does not broadly expand the potential of the breeding program.

In practice, most breeding programs adopt a compromise. Through experience, or testing, a few of the best A lines and R lines with good general combining ability and wide adaptation have been identified. One or two of these may be used for the initial screening of new early generation lines, then as numbers to be tested are reduced, more testers are used to both substantiate GCA and increase the discovery of added SCA expression. Early generation combining ability tests are not intended to definitively identify the best combiners (this cannot be done without extensive testing), but to increase the probability of retaining them for detection in later tests. The first set of test cross may be screened only visually in one or two environments with possibly a 30 to 40 percent selection pressure. Although one or a few testers may exert strong directional effects in the lines they select, this focus has to be accepted to make progress in selecting for combining ability. The choice of the testers for the initial screening is therefore very important. They should be of contrasting parentage but known to combine well with a broad range of material.

Opinion is divided about when early testing for combining ability in seed parent development should begin: before, during or after male sterile development. As in R line development, theory indicates it is better to begin selection for combining ability early in the inbreeding process, at F_3 or F_4. However, given the uncertainty of developing a completely sterile line in the A_1 CMS system from progeny of a B × B cross, it would seem prudent to at least test cross the plants in question to determine the quality of their sterility reactions before beginning to determine combining abilities. If A_1 CMS is being used, these first test crosses should be on a line known to carry excellent sterile cytoplasm (a related phenotypically similar line, if possible, because homogeneity will be more quickly achieved during backcrossing), since that test cross will constitute the first step in A line development and provide the cytoplasm that will remain thereafter. In sorghum, if A_1 lines have not been developed, it is necessary to sterilize R_1 lines in A_2 or A_3 cytoplasm, to provide appropriate testers (from the "opposite" heterotic group) to directly evaluate the combining ability of the possible B-lines. When breeding seed parents in pearl millet, it is not necessary

to resort to R line sterilization, because potential B line plants can be used directly as females in crosses with appropriate restorer testers, using protogyny to make the test cross.

Thus, apart from combining ability, selection for many of the per se selection criteria for hybrid parents can be rapidly applied in the first two or three segregating generations. Indeed, in many elite × elite crosses, selection can be said to begin with the choice of parents. It is therefore possible to begin testing for combining ability in early generations, while variability for it still exists, and before loss begins through genetic drift, which will occur when no selection pressure is applied during inbreeding.

Quality Criteria

Grain quality criteria are determined by end uses. In sorghum there are three principal end uses for grain: feed, food, and brewing (Bramel-Cox et al., 1995). Pearl millet is almost always grown for food, only occasionally being used for brewing. It is being developed as a potential feed grain in the U.S.

Although genetic variability for feeding quality (nutritional value), including sources of high lysine in protein and higher digestibility from waxy endosperm, has been demonstrated in sorghum, selection is not practiced for feeding quality except for avoiding tannin in the grain. In general food quality grain is assumed to have acceptable feed quality.

Because food quality varies by region and use, quality criteria have been difficult to define, and therefore use. However, flour yield (% recovered after milling) and starch properties, especially water absorption and retention, are usable criteria. Appearance of grain, flour, food product and taste are matters of opinion and are best measured by consumer panels. In general, "food quality" sorghum grain is assumed to be white or cream in color, resistant during ripening to discoloration from surface fungi/bacteria, easy to decorticate and grind into flour, and high in flour yield. Though soft endosperms are desirable for some food products, hard endosperm grains are usually preferred because they tend to be more resistant to damage from pests and are easier to decorticate. These (plus tan plant color, since any discoloration on the grain is less obvious) are the per se criteria plant breeders use when selecting for food quality sorghum. In some areas where moisture conditions are high during maturation, red pericarp sorghum is necessary, and bird depredation may require that food grain sorghum contain tannins. Usually food preparation practices in those areas involve techniques to neutralize the anti-nutritional effects of tannin. Where sorghum is used for brewing, diastatic levels are usable criteria, but opinions on taste of the product are still needed.

Grain quality criteria in pearl millet are less well defined (Andrews and Kumar, 1992). Usually gray plump grain is widely accepted, though in parts of West Africa light brown or cream/white grains are preferred. There is a wide range of protein and lysine in protein levels (which do not affect the starchy endosperm). Intrinsically pearl millet has higher nutritional values than sorghum, being equivalent or slightly better than maize for non-ruminants, particularly poultry.

In neither crop (apart from avoidance of subcoat tannin in sorghum) is there currently any incentive in either food or feed markets to demand higher nutritional quality. Thus there is no motivation for applied breeders to put much emphasis on selecting for nutritional quality.

Parental Line Criteria

Seed (female) parents have a number of particular per se requirements besides stable and perfect male sterility (Andrews, 1987). The lines must be as high-yielding as possible, low tillering (especially in sorghum), or at least have tillers which ripen as quickly as the main head, good head exsertion, good seed set, seed size and seedling vigor; they also must possess a number of per se traits that have a good correlation with hybrid performance, such as height, maturity, disease, and pest and lodging resistance.

Pollen (male) parents should completely restore male fertility, even under low temperatures, but also should have profuse, early and prolonged pollen shed. Pollen parents often are high tillering, which contributes to continued pollen supply and head number in hybrids. In both sorghum and pearl millet, there is genetic variation for anther formation on pedicelled flowers, which mature later than anthers on the sessile flowers. Pollen parents with this useful feature have, in effect, two successive phases of pollen shed from the same head. Pollen parents also should possess many of the same per se traits of seed parents that are heritable in hybrids. In sorghum, the recessive height genes should be as stable as possible. Pollen parents also have been shown to contribute to hybrid seed germination and vigor (Maunder et al., 1988). With the A_1 CMS system in sorghum, high temperature environments put more stress on the expression of male sterility and are thus useful in detecting A-lines which might break down and shed some pollen. The expression of sterility also is weaker at the bottom of the head and on tillers, if any. Conversely, cooler temperatures are useful in both crops in evaluating the capacity of a pollen parent to restore male sterility in hybrids. Experiments showed that R_4 hybrids in pearl millet can shed fertile pollen at temperatures as low as a constant 12° C.

For viable commercial hybrid seed production, the male parent should consistently 'nick' with the seed parent; that is, the male parent should be early enough to start shedding pollen before the stigmas of the seed parent become receptive, and continue to shed pollen throughout the flowering duration of the seed parent. Should the male not meet these requirements, there is the added difficulty of either split planting the male or delayed planting of the seed parent (the latter to be avoided if at all possible). Since anthesis begins in pearl millet only after female flowering, male parents should be about five to seven days earlier than seed parents. Tillering in pearl millet, which can be accentuated by reducing plant density, usually provides a sufficiently long duration of pollen shed. Top cross hybrids in which the male parent is a variety rarely have a problem of pollen supply because of the natural spread in flowering that is normal within any pearl millet variety.

Hybrid Testing

G × E Interaction

The recognition and characterization of a genotype's reaction to environmental variation is paramount in determining its usefulness. While newer hybrids are expected to have higher mean yields or show a superior level of some other useful trait, they also are expected to show stability of performance that is equal or better than existing widely grown hybrids. The first step in determining genotype × environment (G × E) interaction is to recognize adaptation domains; the second step is to recognize that all tests do not contribute equally to the estimation of G × E interaction (Bramel-Cox, 1996). Some tests or locations may provide a poor separation between genotypes either due to poor precision, or because the actual differences between genotypes, though statistically significant, are relatively small. Conversely, some test locations frequently give a good separation between genotype performances and are much more valuable in determining G × E interactions. Since year × location interactions are unpredictable and are not the same as location-within-year variation, an adaptation domain must be sufficiently sampled; there is no substitute for conducting a large number of tests over more than one year. Also, farmers manage crops in a number of ways, often quite differently from the way they are managed at experiment stations; thus numerous on-farm trials, or strip tests, are necessary to properly sample the environmental variability to which the new hybrid will be subjected.

Multilocational Testing

A hybrid testing program must permit a large number of new combinations to be tested each year, but progressively reduce their numbers each season so as to retain and ultimately identify the few unique combinations that are truly superior to currently cultivated hybrids. As numbers are reduced, testing becomes more precise (more replications, bordered plots) and more extensive (better sampling of the adaptation domain, more test locations). After the test cross nursery, the surviving hybrids will first be tested in a few selected environments to determine yield potential (well-managed, often-irrigated) and critical adaptation factors such as resistance to important diseases and insects and drought. Often plant population will be varied. The final stages of hybrid testing will include tests at 20 or more locations, the majority in farmers' fields, and a larger number of strip tests, six to eight rows wide, also in farmers' fields. Besides routine data collection, comprehensive visual comparisons to check hybrids will be made, and farmers' opinions sought at field days. The seed production unit will assess parental characteristics for seed production. All this information will be reviewed before the decision is made to release a hybrid.

Examples of Notable Hybrids

India

Pearl Millet. HB-3 (Hybrid Bajra No. 3, Tift $23A_1$ × J104) was the first widely grown hybrid in India. Released in 1966, it was grown on over one million hectares annually by 1972, before becoming susceptible to downy mildew. Tift $23A_1$ came from Tifton, Georgia, U.S., and J104 was an early inbred from Jamnager, Gujarat, derived from a Rajasthan landrace. This hybrid had a tremendous impact. It was shorter, higher yielding, and

much earlier maturing than local varieties, and it performed well in poor conditions where drought was frequent. It had exceptionally wide adaptation from Tamil Nadu to the Punjab, 9-30° N. It stimulated research interest and involved private enterprise in seed production. As a result, today there are several large seed company pearl millet breeding programs, and over 100 companies producing hybrid seed for 3 of the 10 million hectares of pearl millet grown in the country.

Sorghum. CSH-1 (Coordinated Sorghum Hybrid No. 1, $CK60A_1 \times IS.84$ — both introductions from the U.S.), like HB-3, was the first hybrid released in India in 1964. It rapidly became widely popular for rainfed conditions, as it was early maturing and widely adapted. It too stimulated further research interest and private investment, leading to the production of CSH-9 ($296A_1 \times CS3541$), which has been the most popular hybrid since 1977. Over 100 seed companies now produce 10,000 to 15,000 metric tons of sorghum hybrid seed per year for four million hectares.

HB-3 and CSH-1 were successful for several reasons, but principally because they were widely adapted, earlier and much higher yielding than existing cultivars. However they are both properly termed "first generation hybrids," since it soon became apparent they had deficiencies. Subsequent hybrids have had better adapted parents bred in India and have tended to have better grain quality and be slightly longer maturing. Nevertheless, success of the initial hybrids provided the impetus for an increase in investment in breeding, and they were the direct cause of the phenomenal growth of the hybrid seed industry in India.

Africa

Sorghum. Hageen Dura-1 (HD-1) was released in Sudan in 1983, marking the first time a commercial sorghum hybrid was developed and released in tropical Africa. The female parent ($Tx623A_1$) is a converted Zerazera from Ethiopia. The male parent (K1597) is a yellow endosperm line converted from a Nigerian Kaura. HD-1 was selected for its drought resistance, yield stability, and grain quality and had become very popular in Sudan for these same characteristics. In the last 12 years, the area under HD-1 in Sudan has ranged from 12,000 to over 120,000 hectares. Demand has always exceeded supply, however. Nevertheless, the development, release and diffusion of HD-1 in Sudan has stimulated a significant private seed industry where none existed before. It has also stimulated sorghum research in Sudan leading to the development of second generation hybrids and varieties, some with enhanced resistance to biotic stress including *Striga.*

U.S.

Examples of some exceptionally successful hybrids marketed in the U.S. are given below. Unlike maize, for which about 60% of the hybrids grown in the corn belt are closely related, there is some diversity of parentage among leading sorghum hybrids, and hence reduced nuclear genetic vulnerability. Even so, although introgression of exotic germplasm has been a continuous effort in major sorghum breeding programs, only a small propor-

tion of the total diversity available is represented in marketed products.

Cargill 607E. The female of this hybrid is a Wheatland × Redbine selection crossed with a selection from a Doggett stiff stalk population. The male is a Kafir × Feterita × Caprock selection with a contribution of SA 7536-1 for biotype C greenbug resistance. This hybrid is unique in that it has shown resistance to several biotypes of greenbugs including C, D, E, I, and K. This multigenic resistance to the greenbug has allowed the hybrid to be durable for many years; in addition, when this type of resistance is planted over a wide area, the greenbug mutations may be less frequent.

Dekalb E-57. The female of this hybrid is a Texas Blackhill Kafir × Milo derivative selected for open head and early maturity. The male, which can be traced to a Nigerian Kaura introgressed with Hegari, contributed stiff stalk and drought and anthracnose resistance. Subsequent improvement was made by adding biotype C greenbug resistance to the U.S. form, and smut race 1 resistance to the female for Australian use. Because of stress stability, this hybrid lasted for 27 years.

Dekalb DA-48. The female came from a cross between a high tannin forage of temperate origin (Waconia Orange) and Westland for improved stalk. The male is a Sudanese PI of Snowden's group 47 crossed with the E-57 male, the elite line. Although of low yield and seed quality, the PI contributed excellent anthracnose and mildew resistance (Pathotype 1). This hybrid is now greenbug biotype E-resistant and over one million units have been sold.

Pioneer 8333. The female of this hybrid was derived from a cross between java Kafir and a Kafir by a partially converted line from Ethiopia. The male was derived from a cross between Kaura yellow endosperm material by a line with Feterita background. The hybrid had the unique combination of high yield, greenbug resistance, and downy mildew and head smut resistance. It was adapted over a wide area of the U.S. sorghum belt. It was replaced when the greenbug biotype changed from C to E.

Pioneer 8500. The female of this hybrid is a Kafir line. The male is a derivative of crosses between a partially converted Zerazera and a yellow endosperm Kaura and a different Zerazera line crossed with early "Norghum" germplasm. The hybrid is unique for its combination of exceptional yield, drought tolerance, and extremely fast drydown. It competes successfully with both earlier and later hybrids in the market place.

Future

Sorghum hybrid grain yields have been increasing at about 1% per year, and although there have been irregularities, there is no indication of any plateau. Probably less than 10% of the total genetic variability in cultivated sorghum in the World Collection has contributed to cultivars grown in the U.S. In other countries, this percentage is certainly less. Thus, untapped variability is easily accessible, especially if crossable wild species are included. Further yield increases are constrained, not through insufficient genetic variability, but by lack of more efficient methods to find and select the needed genes.

For defensive and quality traits, where good selection pressure can be applied, progress is likely to be good. For the improvement of combining ability for yield, a very complexly controlled characteristic, it is difficult to envision viable economic alternatives to the current method of making test crosses and measuring their performance. The inevitable question is how can biotechnology help? It can certainly help through marker-assisted selection (MAS) and probably transformation. However MAS is more applicable to defensive traits and works best on simply inherited traits, or possibly on Quantitative Trait Loci (which tend to be combination specific and subject to G × E effects). The great challenge for biotechnologists is to move forward from the stage of characterizing diversity, to identifying genetic patterns that contribute to combining ability for grain yield. Even then the question of cost of operating selection with biotechnological assistance arises, and an economic benefit has to be secure. As competition for research funds increases and operational costs go up, both in public and private sectors, the results of biotechnology-assisted genetic improvement may be available only via patents, and ultimately cultivators will have to pay for those. In any case, for further gain in yield potential we need to improve and effectively use conventional methods of selection, which should continue to give gains on the order of one percent per year.

For pearl millet, the situation may be better, because in comparison to sorghum and maize, yield improvement in the species is still at a relatively early stage, even in India where most advances have been made. In African countries, the 20-25% gain in yield through the change from varieties to hybrids has yet be utilized at the farmers' level. That this yield increase is available has been well demonstrated by tests of adapted hybrids in several countries in Africa, but problems of infrastructure, assured food grain markets, and diversification of end uses are among many that must be overcome to allow hybrids or even improved varieties to be profitably used by smaller farmers there.

References

Andrews, D.J. 1987. Breeding pearl millet grain hybrids. p. 83-109. *In* W.P. Feistritzer and A.F. Kelly (eds.) FAO/DANIDA, regional seminar on breeding and producing hybrid varieties. Nov. 11-13, 1986. Surabaya, Indonesia. FAO, Rome.

Andrews, D.J., and P.J. Bramel-Cox. 1994. Breeding cultivars for sustainable crop production in low-input dryland agriculture in the tropics. p. 211-222. *In* D.A. Buxton (ed.) Intern. Crop Science I. CSSA, Madison, WI.

Andrews, D.J., B. Kiula, and J.F. Rajewski. 1993. The use of protogyny to make hybrids in pearl millet. p. 208-210. *In* J. Janick and J. Simon (eds.) New crops. John Wiley & Sons, New York.

Andrews, D.J., and K.A. Kumar. 1992. Pearl millet for food, feed and forage. Advances in Agronomy 48:89-139.

Andrews, D.J., and K.A. Kumar. 1996. Use of the West African pearl millet landrace Iniadi in cultivar development. Plant Genetic Res. Newsltr, 105:15-22.

Andrews, D.J., and J.F. Rajewski. 1994. Male fertility restoration and attributes of the A_4 cytoplasmic-nuclear male sterile system for grain production in pearl millet. Intl. Sorghum and Millets Newsltr. 35:64

Appadurai, R., T.S. Raveendran, and C. Nagarajan. 1982. A new male-sterility system in pearl millet. Indian J. Agric. Sci. 52:832-834.

Bramel-Cox, P.J. 1996. Breeding for reliability of performance across unpredictable environments. p. 309-339. *In* M.S. Kang and H.G. Gauch (eds.) Genotype by environment interaction. CRC Press, New York, N.Y.

Bramel-Cox, P.J., K.A. Kumar, J.D. Hancock, and D.J. Andrews. 1995. Sorghum and millets for forage and feed. p. 325-364. *In* D.A.V. Dendy (ed.) Sorghum and the millets: Chemistry and

technology. American Assoc. of Cereal Chem., St. Paul, MN.
Dudley, J.W. 1984. A method of identifying lines for use in improving parents of a single cross. Crop Sci. 24:355-357.
Dudley, J.W. 1987. Modification of methods for identifying inbred lines useful for improving parents of elite single crosses. Crop Sci. 27:940-947.
Gilbert, M.L. 1994. Identification and search for heterotic patterns in sorghum. p. 117-126. *In* Proc. 49th annual corn and sorghum res. conf., Dec. 7-8, 1994.
Hanna, W.W. 1989. Characteristics and stability of a new nuclear-cytoplasmic male-sterile source in pearl millet. Crop Sci. 29:1457-1459.
House, L.R. 1985. A guide to sorghum breeding. 2nd Edition. ICRISAT, Patancheru P.O. 502 324, Andhra Pradesh, India.
Kumar, A., and D.J. Andrews. 1984. Cytoplasmic male sterility in pearl millet [*Pennisetum americanum* (L.) Leeke]: A review. Adv. App. Biol. 10:113-143.
Lambert, C. 1982. IRAT et l'amelioration de mil. Agronomie. Trop. 38:78-88.
Madhava Menon, P.M., 1959. Occurrence of cytoplasmic male-sterility in pearl millet *Pennisetum typhoides* Stapf. & Hubb. Curr. Sci. 28:165-167.
Maunder, A.B., D. Sedlak, L. Lambright, and L. Matekaitis.1990. Influence of the pollinator on germination and seedling vigor in sorghum. Sorghum Newsltr. 31:14-14.
Maunder, A.B. 1992. Identification of useful germplasm for practical plant breeding programs. p. 147-169. *In* H.T. Stalker and J.P. Murphy (eds.) Plant breeding in the 1990s. C.A.B. Intl, Wallingford, UK.
Menkir, A., P.J. Bramel-Cox, and M.S. Witt. 1994. Comparisons of methods for introgressing exotic germplasm into adapted sorghum. Theor. Appl. Genet. 89:233-239.
Pollack, L.M., S. Torres-Cardona, and A. Sotomayor-Rios. 1991. Evaluation of heterotic patterns among Caribbean and tropical x temperate maize populations. Crop Sci. 31:1480-1483.
Rosenow, D.T., and L.E. Clark. 1995. Drought and lodging resistance for a quality sorghum crop. p. 82-97. *In* Proc. 50th annual corn and sorghum res. conf., Dec. 6-7, 1995.
Schertz, K.F. 1973. Possible new cytoplasmic-genic sterility systems in sorghum. p. 7-14. *In* 28th annual corn and sorghum res. conf., ASTA.
Worstell, J.V., H.J. Kidd, and K.F. Schertz. 1984. Relationships among male-sterility inducing cytoplasms of sorghum. Crop. Sci. 24:186-189.

Population Improvement of Pearl Millet and Sorghum: Current Research, Impact and Issues for Implementation

H.F.W. Rattunde*, E. Weltzien R., P.J. Bramel-Cox, K. Kofoid, C.T. Hash, W. Schipprack, J.W. Stenhouse, and T. Presterl

Abstract

Populations of pearl millet and sorghum are being developed and improved for a variety of purposes. In this paper, we present a global review of current populations, their composition, and methods for improvement. The potential impact of these programs is indicated by recent results regarding responses to recurrent selection and the linkages of population improvement with development of lines and varieties in these two crops. Recent research on generating interpool populations and modeling responses to alternative recurrent selection methods are presented for population improvement of pearl millet.

Population improvement involves the generation of broad-based gene pools and their improvement through recurrent selection. Favorable genes should be concentrated through recurrent selection, resulting in increased mean of the population and superior performance of the best families (Hallauer, 1981). Population improvement provides ample opportunities for recombination after each cycle of selection.

The tandem cycling of selection and recombination is particularly important for improvement of polygenic traits and for simultaneous improvement of several traits (Doggett, 1982). This method could increase the effective use of non-elite source materials, where the greater opportunities for recombination could break linkages between genes for the desired trait and unfavorable agronomic characteristics.

A wide range of methods have been developed for population improvement. Several reviews of these methods (Hallauer, 1981; Hallauer and Miranda, 1988; Simmonds, 1979; Witcombe, in press) are available in the literature. In this paper we will focus specifically on current activities and research pertaining to population improvement in pearl millet and sorghum. This review covers the period from 1986 to 1996.

Pearl Millet and Sorghum Populations and Their Improvement

The diversity of pearl millet and sorghum random-mating populations and the approaches taken for their improvement

H.F.W. Rattunde, Genetic Enhancement Division, ICRISAT Asia Center, Patancheru, AP 502 324, India; E. Weltzien R., Genetic Enhancement Division, ICRISAT Asia Center; P.J. Bramel-Cox, Genetic Resources Division, ICRISAT Asia Center; K. Kofoid, Kansas State University, Hays, Kansas, USA; C.T. Hash, Genetic Enhancement Division, ICRISAT Asia Center; W. Schipprack, Nordsaat, Maize Breeding Station-South, Mannheim, Germany; J.W. Stenhouse, Genetic Enhancement Division, ICRISAT Asia Center; T. Presterl, Institute of Plant Breeding, Seed Science and Population Genetics, University of Hohenheim, Stuttgart, Germany. *Corresponding author.

and utilization correspond to the range of economic and adaptive requirements being addressed. A recent review provides a list of pearl millet populations developed by ICRISAT and cooperating National Agricultural Research Systems (NARS) in India and Africa (Rai and Kumar, 1994). We document here the genetic composition and selection history of pearl millet (Appendix 1) and sorghum (Appendix 2) populations currently receiving the greatest efforts world wide or representing the most important populations for a particular region.

Pearl Millet Populations

Population Groups

Pearl millet population development in both the Sahelian and Sudanian Zones of Western Africa has focused on intervarietal crosses, primarily between local landraces and elite varieties. Populations for the Sahelian Zone are earlier maturing (less than 100 days), whereas those for the Sudanian Zone mature in 100-150 days (Appendix 1). Populations for both zones are subjected to selection for grain yield, downy mildew resistance, and resistance to insect pests.

Populations being improved in the Asian region can be classified into three groups (Appendix 1). For the drier areas with less than 400 mm rainfall, early-maturing populations (60-75 days in non-stressed environments) are developed from stress-tolerant local germplasm and inter-population crosses between local germplasm and early-maturing elite germplasm. Selection is for adaptation to northern Indian growing conditions and increased productivity of grain and stover, improved seed set, higher tillering (as a determinant of stover quality and yield stability), and downy mildew resistance. A high proportion of germplasm in these populations originates from India and Pakistan, particularly from the driest millet-growing regions.

Populations for the higher rainfall (greater than 400mm) millet-growing regions in Asia contain larger proportions of African germplasm, ranging from half to primarily African-based, and are later-maturing (75-90 days). Selection pressure is predominantly for increased grain yield, panicle size, and downy mildew resistance. These populations vary in the prevalence of Togo germplasm (Andrews and Kumar, 1996) and in expression of stem, grain, and panicle characteristics of the Bold Seeded Early Composite.

A third group of populations in the Asian region includes those that have broader geographic domains or target environments outside of Asia (Appendix 1). These populations should serve new or emerging demands for early-maturing grain hybrids, population hybrids, and industrial uses.

Populations developed in Nebraska likewise provide source material for developing parents for pearl millet grain-hybrids (Appendix 1).

Selection Methods

The recurrent selection methods used most often to improve the populations in the first two Asian groups are full sib progeny (FSP), S_1 progeny, and S_2 progeny methods (Table 1). The full-sib method offers two advantages: 1) FSPs, being non-inbreds, are less affected by environmental stresses and commonly have lower error variances than inbred progenies (Schipprack, 1993); and 2)

FSPs are generated in the random mating phase in the off-season, enabling completion of one cycle of selection per year in the target environment. This method is particularly useful for populations being improved for adaptation to the heat, moisture deficits, and long photoperiods of northwestern India. However, skilled hand crossing is required to produce adequate numbers of full-sib progenies with sufficient seed quantities for multilocation testing, especially for populations with small panicle size. Multiple pollinations of the same two plants and bulking seed from reciprocal crosses between them has proven useful in producing new full sibs.

The three-stage S_2 progeny-testcross procedure is relatively new, but its advantages may lead to increased use in the future. This method begins with full-sib progeny (FSP_{S2}) selection with intensity of 30% (Table 1). Three hundred to four hundred S_1 progenies (S_1P) generated from selected FSP_{S2}s are initially tested for resistance to downy mildew (20-40% selection intensity) in the greenhouse, and the more resistant progenies are then tested for productivity. Single plants from selected S_1P are selfed and test crossed to one elite male-sterile tester; the resulting S_2 test crosses are evaluated primarily for selfed seed set and pollen fertility restoration in the target environment. This procedure, through greater inbreeding, aims to improve seed set, possibly via elimination of translocations that have poor chromosomal pairing with elite material, and to increase the frequency of restorer alleles in the population for use in development of pollen parents for topcross and single-cross hybrids.

The S_1P selection procedure is occasionally used, primarily where increased resistance to downy mildew is required. A large number (500-800) of S_1P are tested for downy mildew resistance using a modified greenhouse testing procedure (Weltzien and King, 1995). The most resistant progenies are then tested in mul-

Table 1. Most commonly used recurrent selection procedures for pearl millet improvement at ICRISAT Asia Center in collaboration with Indian NARS.

Season	Full-sib procedure	S_1 procedure	S_2 testcross procedure
Rainy season 1	Full-sib progenies (FSP_{S0}) tested in the target environment (TE)	Selfing within half-sib or full-sib progenies in the TE	Full-sib progenies (FSP_{S2}) tested in TE
Off season 1	Random mate selected full-sibs by plant to plant crossing to create new full-sib progenies (FSP_{S0})	S_1 progenies tested in a) downy mildew, and b) off-season drought evaluations	Selfing in selected full-sib progenies, S_1 progenies tested for downy mildew resistance
Rainy season 2		Selected S_1 progenies evaluated for yield in TE	More resistant S_1 progenies evaluated for yield in TE
Off season 2		Random mate selected S_1 progenies by forming half-sib or full-sib progenies	Testcross and self within selected S_1 progenies
Rainy season 3			S_2 progeny testcrosses evaluated in TE
Off season 3			Random mate selected S_2 progenies by forming full-sib progenies (FSP_{S2})

tilocation yield trials in collaboration with breeders from the target environments. This procedure is widely used in populations targeting environments with higher, more reliable rainfall, where S_1P testing is more feasible due to less abiotic stress. More populations can be handled with the two-stage S_1P procedure, as yield evaluations occur only every other year.

Selected populations at ICRISAT (IAC) also are improved by backcrossing to enhance specific traits such as bristles (long awns), yellow or white grain color, photoperiod insensitivity, or male sterility. The advantages of this procedure are outlined in a later section on sorghum.

Sorghum Populations

Diverse breeding objectives and studies on selection methodology are being pursued at several universities in the U.S., focused primarily on grain sorghum populations with temperate adaptation.

Purdue University

An array of populations have been developed at Purdue University (Appendix 2). Also, populations containing 0%, 50%, 75%, or 100% of an elite base population based on 20 elite R-lines were developed to study the relationship between the level of eliteness of the initial populations and the performance of their derivatives (G. Ejeta, 1996, personal communication).

University of Nebraska-Lincoln

At the University of Nebraska-Lincoln (UNL), populations based on earlier B- and R-lines and newly utilized germplasm accessions are being generated for various feed grain quality parameters (high and low rate of *in vitro* starch digestibility, total starch content, and pepsin insoluble nitrogen) (J. Pedersen, 1996, personal communication). Two B populations (D.J. Andrews, 1996, personal communication) and a restorer population (J.D. Eastin, 1996, personal communication) have been recently developed (Appendix 2).

Fort Hays Experiment Station

A series of methodology studies is underway at the Fort Hays Experiment Station of Kansas State University (K. Kofoid, 1996, personal communication). A study of alternative family-based selection procedures is being conducted, continuing selection started in Nebraska in the early 1970s in NP3R and NP5R populations. No differences were found among procedures in NP3R based on predicted gains (Table 2). A study testing the feasibility of gametophytic selection for stress tolerance is underway, with selection pressure induced by holding pollen in pollinating bags for either 45 or 90 minutes prior to pollination. No significant response to selection was observed after two years of evaluation. The feasibility of mass selection for drought tolerance is being tested using plants grown in 5 cm diameter cones in the greenhouse. Water is withheld from 30 days after sowing until a visual assessment of plant death reaches 75-80%. Surviving plants are intermated, and recombined seed is sown in the field at high density (530,000 plants ha^{-1}). Also, the effectiveness of single location, single replicate evaluations of S_1 progeny with augmented designs is being compared with a replicated procedure.

Kansas State University

The major research thrusts in population improvement of sorghum at Kansas State University (KSU) include improvement of grain yield and adaptation to drought stress, animal feed value of grain, and *Fusarium* and charcoal rot resistance (Bramel-Cox, 1996, personal communication). Each of these are summarized below.

Divergent S_1 family selection in the population KP9B is being conducted collaboratively between KSU and UNL with selection under optimal [KP9B(MD)] or drought-stress conditions (KP9B(GC)). The fourth cycle of each selection scheme is underway. Predicted gains (Zavala-Garcia et al., 1992) and realized gains (Maciel, 1995) are reported. Also, the same base population, $KP9BC_0$, was improved for three cycles using a modified full-sib method with multi-location evaluation; selection was based on a rank summation index across locations. Predicted gains from this method have been reported by Chisi et al. (1996).

The improvement of feed value of the grain was pursued in the $KP7BC_0$ population with two separate S_1 selection schemes. One scheme uses protein digestibility via the pepsin digestion technique as the sole criterion [KP7B(DG)], whereas the rank summation for grain yield and protein digestibility was used in the other [KP7B(RS)]. Bramel-Cox et al. (1990) describe these criteria and predicted gains from selection.

Selection for resistance to *Fusarium* and charcoal rot (*Macrophomina phaseolina*) in the $KP8BC_0$ population was conducted for two cycles, using toothpick inoculation, on half-sib families at two locations in Kansas (Bramel-Cox and Claflin, 1989).

ICRISAT Asia Center

An array of populations for long-term improvement of key agronomic traits or trait combinations and resistances to major insect pests are being developed and improved at the ICRISAT Asia Center (IAC), India (Appendix 2).

The Shoot Pest population, for shootfly (*Atherigona soccata*) and stem borer (*Chilo partellus*) resistance, and the Head Pest population, for midge (*Contarinia sorghicola*) and earhead bug (*Calocoris angustatus*) resistance, trace their origins to populations begun in the early 1970s at ICRISAT, India. The earlier shoot pest population was mass selected for shootfly and stem borer resistance for approximately one decade, followed by progeny-based selection in the late 1980s (Agrawal and Taneja, 1989; ICRISAT, 1988). By the beginning of this decade, the Head Pest and Shoot Pest populations had relatively high means but low variances. Thus in 1991 introgression of large numbers of diverse sources of resistance was con-

Table 2. Predicted gains from one cycle of alternative family selection methods, using direct selection with 20% selection intensity in two sorghum populations in Kansas, U.S.

Population	Family	Days to anthesis days	Plant height cm	Grain yield kg ha^{-1}	Test weight kg m^3
NP5R	S1	4.8	11.9	270	19.8
NP3R	S1	3.3	11.6	404	23.5
NP3R	HS	2.0	9.0	150	26.0
NP3R	FS	3.6	10.0	361	24.8

Kofoid, unpublished data

ducted into both populations (Wehmann et al., 1992; Appendix 2). These new populations are heavily based on landrace material of tall stature (greater than 2m), with considerable photoperiod sensitivity and segregation for grain characteristics.

Mass selection has been used extensively at IAC for improvement of the Large Grain, High Tillering (Reddy and Prasada Rao, 1993), Early Dual Purpose, and Guinea Grain Mold populations. The Large Grain and High-Tillering populations are being managed as open populations (Reddy, 1994). These populations have predominantly white grain color, except for the Early Dual-Purpose population which is segregating for grain color and testa.

Progeny-based selection methods have been used to improve the US/R and RS/R populations. Two cycles of S_1 progeny selection for increased grain and stover yield within restricted growth duration were recently completed in the US/R(DP) population (Rattunde, 1994). A modified base index with standardized values for grain, stover yield, early maturity and lodging resistance, weighted by the relative economic weights and estimated heritabilities of each trait, was used for selection. The genetic variation for seedling vigor observed in the US/R(C1) and RS/R(C1) populations (Rattunde, 1992) has been exploited through three cycles of full-sib selection for seedling vigor in each population (Rattunde, 1993).

ICRISAT Southern and Western African Programs

The populations developed by ICRISAT and NARS collaborators in the Southern African region (Appendix 2) target contrasting agro-ecological zones (A.B. Obilana, 1996, personal communication; ICRISAT, 1989). Guinea and Caudatum (J. Chantereau, 1996, personal communication) and Guinea × Caudatum (D.S. Murty, 1996, personal communication) populations are currently being developed in Mali (Appendix 2).

Genetic Gains from Population Improvement

Pearl Millet Response to Selection

Substantial increases for grain yield per se have been obtained through progeny-based recurrent selection in an array of populations in India. Gains of 1.9 to 5.0% per cycle in six populations (Super Serere, New Elite, Inter Varietal, Medium, Early and D2 Composites) selected for two to five cycles were exhibited in 1982 in a multi-location evaluation in India (Pheru Singh et al., 1988). A similar range of gains (0.9 to 4.9%) was exhibited by four composites, selected for three to six cycles, when their cycle bulks were evaluated in India from 11°N to 29°N over three years (Rattunde and Witcombe, 1993). The highly significant gains in grain yield were most closely related to increases in the number of seeds per panicle (Table 3). Ten cycles of *per se* selection in the Medium Composite resulted in increases in combining ability of 1.2 to 1.8% per cycle, depending on the tester used, as well as a 4.3% per cycle gain in grain yield in the population per se (Witcombe, in press).

Mass selection is expected to be more effective for plant traits that have relatively high heritabilities on a single plant basis such as plant height (h^2=0.58), panicle length (h^2=0.64) and seed mass (h^2=0.52), and less effective for less heritable traits like grain yield (h^2=0.29) (Rattunde et al., 1989). Mass selection for

grain yield, when conducted in a single location, can also result in location-specific responses (Rattunde, 1988; Table 4).

Recurrent selection for resistance to downy mildew has proven very effective. Two cycles of progeny selection with a modified glasshouse screening procedure in a highly susceptible population, WRajPop88, significantly reduced downy mildew incidence from 13.4% in Cycle 0 to 1.8% in Cycle 2 bulk (Weltzien R. and King, 1995).

Sorghum Response to Selection

Responses to two cycles of S_1 selection for early-maturing, dual-purpose sorghum in the US/R(DP) population were recently evaluated in India, the country of selection, and under rainfed conditions in the Sudan, an important target environment for short-duration sorghums. Large responses of both grain (13.2%) and stover (16.4%) yields were observed in India while maturity was held constant (Table 5, Rattunde, unpublished data). The yield gains were primarily achieved in the first cycle of selection and were associated with a 1.4 day increase in time to flower in that cycle. Time to flower was reduced to near that of the original population in the second cycle. Estimates of genetic variability remained unchanged over the two cycles of selection for grain yield, but were reduced for stover yield and time to flower (Table 6). The pattern of response observed in Sudan was similar to that observed in India (Table 5, Rattunde and Ibrahim, unpublished data). The results from India and Sudan are noteworthy as both grain and stover yields were increased; total biomass was increased within a constant growth duration; and these gains were expressed over a wide range of soil fertility and climatic conditions.

Responses to two cycles of S_1 family selection in KP9B under drought-stress

Table 3. Means of base (C_0) and most advanced selected population (C_t) from five pearl millet composites evaluated at three locations in India in the 1987 rainy season for six agronomic traits.

Composite and cycle	Grain (kg ha^{-1})	Bloom (days)	Height (cm)	Individual seed mass (mg)	Seeds panicle^{-1}	Panicles m^{-2}
MC C_0	2300	50.3	226	8.86	2160	12.5
MC C_8	3160**	50.9	222	9.41	2590*	12.3
IVC C_0	2550	53.0	242	9.61	2730	9.9
IVC C_6	2660	53.5	225*	8.52*	2540	11.1*
NELC C_0	2140	54.2	210	8.33	2440	11.4
NELC C_5	2880**	54.5	224	8.95	3030**	11.0
SRC C_0	1860	55.3	219	8.50	2190	9.3
SRC C_3	2880**	52.3*	235*	8.79	2640**	11.8**
D2C C_0	2110	51.0	153	8.37	2170	12.2
D2C C_5	2490	50.4	160	8.63	2500	11.3
LSD 0.05	390	2.4	16	0.91	394	1.1

*, ** Significant difference between base and advanced cycle population at P<0.05 and P<0.01, respectively.
(Rattunde and Witcombe, 1993).

Table 4. Grain yield responses (kg ha^{-1} deviations from unselected bulk) to one cycle of mass selection for grain yield per se and for an index of physiological determinants of grain yield[a] in the pearl millet Early Composite at the location of selection (PAT) in central India (17°N), Northern India (HSR, 29°N), and Southern India (BSR, 11°N).

Selection criteria	Locations		
	PAT	HSR	BSR
Grain yield per se	351*	133	252
Physiol-index	649**	72	-264

[a]Index based on growth rate, growth duration and harvest index.
*, ** denotes significant differences between base and selected population at P<0.05 and P<0.01, respectively.
(Rattunde, 1988)

Table 5. Progress from S_1 progeny index selection for early dual-purpose sorghum in the US/R (DP) population.

Cycle	Grain (t ha^{-1})		Stover (t ha^{-1})		Flowering (d)	
	India[a]	Sudan[b]	India	Sudan	India	Sudan
Cycle 0	2.77	1.12	4.16	2.04	56.7	65.6
Cycle 1	3.04 (10.0)[c]	1.30 (16.1)	4.96 (19.3)	2.22 (8.8)	58.1 (2.5)	65.2 (-0.6)
Cycle 2	3.13 (13.2)	1.26 (13.0)	4.84 (16.4)	2.06 (1.0)	57.0 (0.6)	63.7 (-2.8)
LSD (P=0.05)	0.05	0.11	0.09	0.18	0.02	0.70

[a]60 FS per cycle, three fertility environments at Patancheru, India 1994.
[b]20 FS per cycle in rainfed environment, Wad Medani, Sudan, 1995.
[c]% change from C0.
(Rattunde, Ibrahim, unpublished)

Table 6. Genetic components of variance and their standard errors of US/R (DP) Sorghum Population Cycle 0 and Cycle 2 full-sibs in India.

Cycle	Grain	Stover	Flowering
Cycle 0	9.2±2.36	78.2±15.58	1.2±1.14
Cycle 2	8.8±2.28	48.6±10.82	0.7±1.37

(Rattunde, unpublished data)

[KP9B(GC)] and optimal conditions [KP9B(MD)] in the midwest U.S. have been evaluated in both low- and high-productivity environments. Grain yield gains of 20% from selection under stress were exhibited at both the high- and low-productivity test sites (Table 7, Maciel, 1995). These gains were larger than those obtained by two cycles of selection under more optimal conditions. Also, the grain yields of the ten best families from both selection schemes were distinctly superior to those from the original KP9BC_0 (Table 8). The best families from selection under optimal conditions were slightly later flowering and distinctly taller than those selected under stress. Estimates of genetic variance were smaller among the stress-selected KP9B(GC)C_2 families as compared to non-stress-selected KP9B(MD)C_2 families (Table 7).

Gridded mass selection for individual panicle grain weight in IAP4R in Iowa

was shown to have effectively increased grain yield by 2.06% cycle^{-1} over three cycles in this broad-based population (Secrist, 1989; Secrist and Atkins, 1991). Mass selection included initial culling of late flowering plants and resulted in decreased time to flower in the Cycle 3 population, relative to Cycle 0. Four cycles of mass selection for cold tolerance in Purdue Population 9, through natural selection with early spring sowings, increased cold emergence by 2.8% cycle^{-1} (Bacon et al., 1986). Four cycles of gridded mass selection for threshed panicle weight significantly increased grain yield 250 kg ha^{-1} (1.2% of C_0 mean), but resulted in highly significant indirect responses for days to flower (1.6 days) and plant height (9 cm) (Maves and Atkins, 1991). Four cycles of mass selection for increased seed size in IAP3BR(M) significantly increased seed size but decreased grain yield (Kwolek et al., 1986). Six cycles of mass selection for shootfly resistance in the original Shoot Pest population had reduced shootfly deadheart frequency from 71.2% to 58.5% (ICRISAT, 1988). Mass selection was not effective for resistance to stem borer (*Chilo partellus*) (ICRISAT, 1988). Seven cycles of mass selection for white grain color and guinea glume and grain type, initially with mild selection intensity, achieved high frequencies of both in the Guinea × Caudatum Grain Mold population.

Table 7. Grain yield (kg ha^{-1}) and genetic variance (σ^2_g) of the sorghum base-population KP9BC$_0$ and the stress-selected KP9B (GC) C$_2$ and non-stress-selected KP9B (MD) C$_2$ at three high- and three low-productivity test sites in the midwest U.S. in 1993 and 1994.

Test sites	KP9BC$_0$	KP9B (GC) C$_2$	KP9B (MD) C$_2$
Mean grain yield			
High	4763	5699 (20%)	**5446 (14%)**
Low	2742	**3284 (20%)**	3155 (15%)
σ^2_g grain yield			
High	360767	109889	**222218**
Low	305681	**306388**	446478

Bold = "direct" selection
(Maciel, 1995)

Table 8. Means of the top 10 families from the base sorghum population KP9BC$_0$ and the stress-selected KP9B (GC) C$_2$ and non-stress selected KP9B (MD) C$_2$ at three high- and three low-productivity test sites in the midwest U.S. in 1993 and 1994.

	Grain kg ha^{-1}	Flower d	Height cm	Seed number/m^2
High-sites				
KP9BC0	6277	68	110	28607
KP9B (GC) C$_2$	7102	69	109	31729
KP9B (MD) C$_2$	6765	71	117	31398
Low-sites				
KP9BC0	3843	65	113	15699
KP9B (GC) C$_2$	4433	67	112	17684
KP9B (MD) C$_2$	4393	68	120	18407

Bold = "direct" selection
(Maciel, 1995)

Issues in Implementation of Population Improvement

Linking Population Improvement with End-Product Development

The economic benefits of population improvement are ultimately realized when genetic material from these populations is used to develop lines and varieties for cultivation by farmers. The interface between population improvement and end product development has rarely received attention in the literature. In this section we review the methods used in sorghum and pearl millet for exploiting improved populations for end-product development. Also, the conflict between maximizing long-term genetic gains through population improvement and developing agronomically elite finished products will be addressed.

Sorghum

Superior families developed and identified through recurrent selection provide a starting point for line development in sorghum. Traditional pedigree selection methods used during the inbreeding process produce pure lines for direct use as varieties or hybrid parental lines or, more frequently, as improved parental material for advancing pedigree breeding activities. Selection against the male-sterile gene would also be required, but is easily handled by identifying sterile plants at flowering. This approach has been used in the development of lines from S_1 families originating in several populations at Purdue (Ejeta, 1996, personal communication), and in the ongoing derivation of restorer lines and dual-purpose varieties out of the US/R(DP) population at ICRISAT (IAC).

In broad-based populations, genetic variation and potential long-term genetic gains are maximized. However, because these populations tend to have low means for critical agronomic traits, frequencies of elite segregates are low. Thus, lines derived from these populations rarely, if ever, possess the full complement of required agronomic characteristics. These lines would represent improved source material useful in crossing with elite lines.

Elite populations, in contrast, would restrict introduction of undesirable alleles for such traits as height, maturity, fertility reaction, and grain and panicle characteristics during population development. These restrictions would be imposed through limiting introduction into the population as well as culling undesirable agronomic types during random mating. A much higher frequency of elite lines would be derived from such populations. However, the narrow genetic base would limit genetic variation and potential long-term genetic gains if it is used as a closed population.

Additive genetic variation σ^2_A is a function of the number of loci segregating (n), the frequency of favorable (p) and unfavorable alleles (q), and the breeding value α (Falconer, 1981); it can be expressed with the following formula:

$$\sigma^2_A = \sum^n 2pq\alpha^2$$

σ^2_A can be increased by increasing either n for the trait of interest or the frequency of p if it is less than 0.5 for the desirable allele. The introduction of new

alleles or increasing the frequency of desirable alleles can be achieved by introgression of exotic source materials.

Researchers at KSU are pursuing introgression into elite populations, using population backcrossing, to accommodate the contradictory goals of deriving elite lines and making long-term gains in the source population (Bramel-Cox and Cox, 1989; Menkir et al., 1994a,b). Introgression of the exotic sources at less than 50% of the nuclear genome by backcrossing to the elite population would maintain the eliteness of the population.

Effective introgression using a population backcross approach would require sampling enough plants during backcrossing to retain a maximum diversity of alleles from the exotic source. Also, when new source material is introgressed into a population already improved for that trait, screening at each level of backcrossing would insure retention of more genes for that trait when handling small population sizes. For example, when introducing new greenbug resistance alleles into an existing greenbug-resistant population, the resulting BC_2F_2 can be put directly into a pedigree program. Alternatively, additional random mating can be done to break undesirable linkages prior to line derivation, as is being done for chinchbug resistance at KSU.

This open-population approach with population backcrossing has been applied in the KP9B and KP7B populations at KSU for such diverse objectives as greenbug resistance, grain-nutritional quality, drought tolerance, chinchbug resistance, heterosis, and cold tolerance. Ten R lines from population introgression of a stress tolerant line (IS22253 from Zimbabwe), a Chinese line (258), and a biotype e greenbug-resistant source (IS2388) are expected to be released from Kansas State University this year.

Pearl Millet

Because pearl millet is a cross-pollinated crop, an array of economically viable variety types can be derived from populations. Descriptions of the different end-products and the methods used to derive them from populations are outlined below:

- Use a population directly as an open-pollinated variety (OPV)

Mass selection within a population for more restricted plant type and phenology is a common method of developing OPVs in pearl millet. This approach is exemplified by the development of ICMV155 through a single cycle of mass selection for grain yield and similar plant height, panicle type, and maturity in the NELC population after four cycles of progeny-based selection (Pheru Sing et al., 1994). A modified mass selection method is quite important in India. In this method, Indian program scientists do single plant selection of selfed plants for agronomic type and adaptation in the target environment, and the resulting S_1 progenies are tested at ICRISAT for resistance to downy mildew. The more resistant progenies are recombined to form the experimental variety (Weltzien R. and Hash, 1995).

- Form an OPV from families selected from a population

Varieties can be produced by recombining families selected on performance information obtained during the testing phase of a progeny-based population improvement program. Generally a small number (10 to 15) of full-sib or S_1 families are selected to produce a variety. A series of experimental varieties can be produced by imposing different selection criteria or different weightings for individual selection criteria. The use of selection indices based on standardized trait values has proved useful for this method of variety development. Because these varieties are narrow-based populations, further selection can be done for enhancing critical traits, such as resistance to downy mildew, or for increasing uniformity for a specific plant type. The variety ICTP 8203, developed from five S2 progenies from the Iniadi landrace population is currently being grown on more than 600,000 hectares in the Indian state of Maharashtra (ICRISAT, 1996).

- Develop topcross hybrids

Populations can be used as the pollen parent to produce topcross hybrids. The first topcross hybrid JBH1 was released in India in 1996. Its pollinator was developed from the Bold Seeded Early Composite via test crossing to select for fertility restoration; progeny testing for agronomic type and resistance to downy mildew; and mass selection for uniform maturity. Initial seed production of this hybrid by a public agency in India is already under way. Diverse topcross pollinators (TCPs) are being developed at ICRISAT (IAC) from an elite, medium-maturity population (MC C_{10}) and from earlier-maturing, Indian landrace-based populations (WRajPop, ERajPop, EHiTiP, CZ-IC 416, and LRE 118). The labor and resources required to produce effective TCPs are relatively modest for populations like MC C_{10}, having high frequency of restorer alleles. However, much greater effort is required to develop TCPs from the more landrace-based populations for use in stress-prone environments, due to their low restoration frequency with current male-sterile lines and more frequent fertility restoration problems under heat and drought conditions in the areas of cultivation. TCPs also are narrow-based populations and would be amenable to continued selection for traits such as resistance to ever-evolving downy mildew pathogen populations and time to flower to nick with male-sterile lines.

- Derive inbreds for use as hybrid parents

Pedigree breeding methods can be used to develop inbred pollen and seed parents from population-derived progenies. Several pearl millet populations have been developed specifically as source material for deriving either pollen or seed parental lines (Appendix 1). The Extra Early R and Extra Early B Composites were constituted by selecting for the non-Togo phenotype in the former and the Togo phenotype in the latter, to develop genetically distinct and heterotic gene pools. The S_2 test cross procedure (Table 1) is well-suited for identification of potential restorer lines.

Open-pollinated varieties (OPVs) play a very important role in Indian farming systems. The cultivation of hybrids is increasing in some areas (ICRISAT, 1996), yet OPVs will continue to play an important role because their broader genetic base contributes to more durable downy mildew resistance; their longer period of pollen shedding reduces risks of ergot and smut; and the grain yields of the best

released OPVs usually are on par with the best released single-cross hybrids [the All-India Coordinated Pearl Millet Improvement Project (AICPMIP) advanced variety and hybrid trial results, 1993-1996].

Collaboration between national program scientists operating in the target environment and scientists with more regional or international focus, such as those at ICRISAT, can be very effective for developing finished products from populations (Weltzien R. and Hash, 1995). Opportunities for collaboration include such activities as identification of population bulks for use as source material; formation of test units; evaluation / selection of test units; and recombination and production of seed (Weltzien R. and Hash, 1995). The effectiveness and growing importance of these efforts is indicated by the predominance of collaboratively bred varieties submitted for testing in the All India Coordinated Pearl Millet Improvement Program since 1994.

Reciprocal Recurrent Selection of Sorghum and Pearl Millet

Comstock et al. (1949) first suggested the use of population improvement to enhance heterosis between two populations. Reciprocal recurrent selection (RRS) maximizes the genetic divergence between the populations for loci with dominance effects, by basing selection on crosses generated with one parent from each population. This method would be useful for crop species where hybrids are commercially viable and large inter-population heterosis is expected or observed. These conditions are met for both pearl millet and sorghum, but especially for pearl millet. Furthermore, this approach allows integration of long-term and short-term breeding objectives (Eyherabide and Hallauer, 1991).

The use of RRS in sorghum, especially full-sib reciprocal recurrent selection, is hampered by the sterility system used to enable random mating. All crosses (test and selection units) would be generated using a male-sterile as the female for which no selfed seed can be produced. Thus from the selected full-sibs, only the male parents from each cross can be used as recombination units, effectively reducing selection intensity and failing to capture genes from those female parents producing superior crosses.

Reciprocal full-sib selection has been used to improve the sorghum populations KP9BC_0 and GTPP7R, a derivative of TP24. 100 to 200 reciprocal full sibs from each population (with that population as male parent) were tested collaboratively by KSU at Garden City and the University of Nuevo Leon in Monterrey, Mexico. The top 15% full sibs were selected from the best stress site, and remnant S_1 seed of the male parents was used for recombination. Estimates of genetic variances, heritabilities, and intra-population predicted gains were reported by Chisi (1993). Estimates for the genetic variability and mean were found to be consistently higher in the TP24 × KP9B (TP24 as female) than the KP9B × TP24 reciprocal crosses, suggesting that significant cytoplasmic effects may exist (P. Bramel-Cox, 1996, personal communication).

Generating Inter-Pool Populations of Pearl Millet

Population Diallel Analyses

Crossing populations representing contrasting genetic sources may exploit het-

erosis, increasing the mean productivity and the genetic variation of the resulting interpool populations. Such population crosses are frequently used in pearl millet population improvement to combine groups of traits and thus increase variability for productivity and adaptation. The choice of parents often is based on knowledge of the performance and specific characteristics of potential parental populations. Knowledge about heterotic patterns among populations could be helpful in choosing parents for making population crosses. Population diallel analyses are designed to allow description of the nature and amount of heterosis generated by population crosses, and should help to identify specific crosses or types of crosses to exploit.

A series of pearl millet population diallels with primary focus on grain yield have been recently conducted in Asia [11 longer duration (Ali, 1996) and ten early-maturing populations (Presterl and Weltzien R., unpublished)], and in Africa [five widely grown improved landraces (Ouendeba et al., 1993) and 11 improved varieties and landraces (ICRISAT, 1992)]. A diallel of five diverse populations also was conducted to study inheritance patterns and methods for improvement of vegetative growth index (Lynch et al., 1995). The early population diallel (Presterl and Weltzien R., unpublished) will be described as an example of this approach using the analysis of Gardner and Eberhart (1966).

Ten early-maturing populations were identified; they varied for yield potential under favorable conditions, adaptation to moisture and heat stress, and yield components such as panicle and grain size and tillering. These populations represented a continuum from local landrace, basically unimproved populations, to highly bred exotic materials, with each having certain merits for the targeted hot, dry millet growing region of northwestern India.

The population cross F_1s and parents were evaluated for three years in multilocation trials in the target region. The results indicated that the F_1 grain yield was determined by both the per se performance of the parental populations and the level of heterosis (Table 9). Heterosis was attributable primarily to specific heterosis of the individual F1 combinations, indicating that the pattern of heterosis was complex. Of the four F1s having the highest grain yields and mid-parent heterosis greater than 20%, two were elite × elite crosses, one an elite × high-tillering landrace cross, and one an elite × high-tillering exotic.

This analysis was useful for describing the level and pattern of heterosis obtainable through formation of interpool populations and for identifying superior populations for further use or improvement. The complex pattern of heterotic expression and the way it was dramatically influenced by the sample of test environments make it difficult, however, to predict more generally which type of populations would combine best.

Farmers' Involvement in Generating Interpool Populations

It is generally assumed that breeders have the full responsibility and comparative advantages over farmers in the choice of germplasm and the breeding activities associated with development of interpool populations (Sperling and Scheidegger, 1996; Ceccarelli et al., 1996). However, experiences in Namibia (Ipinge and Bidinger, 1996, personal communication)

and on-farm varietal evaluations in western Rajasthan from 1992 to 1995 (Weltzien R. et al., 1996a) suggest that for a cross-pollinated crop like pearl millet, some farmers are involved in these activities.

Farmers involved in on-farm pearl millet varietal evaluations saved seed of the experimental varieties that possessed specific traits of interest. This seed was most often sown in mixture with their own variety to reduce risk of failure in the event of severe stress. The mixed sowing and cross pollination between the newly selected genetic material and the local material resulted in interpool populations, which farmers have continued to sow in subsequent seasons.

The potential benefits of farmers' involvement in interpool population formation include:

- ample recombination over several seasons
- larger population sizes than are feasible on experiment stations, with greater possible intensity of selection

Table 9. Percent sums of squares among entries and significance of mean squares from a diallel of early-maturing pearl millet populations for grain yield and stover yield in three Rajasthan environments.

Source of variance	Grain yield	Stover yield
Varieties	44 **	45 **
Heterosis	56 **	55
Average	5 **	4 *
Variety	9	6
Specific	42 **	45

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
(Presterl and Weltzien R., unpublished data)

- reduction in frequency of unadapted genotypes, because both natural selection and farmers' selection operate under the target, albeit variable, environmental conditions (Weltzien R. et al., 1996b)
- breeders' ability to focus more on improvement of traits difficult to select for on a single plant basis (Weltzien R. et al., 1996b; Weltzien R. et al., 1996c).

There is ongoing experimentation at ICRISAT (IAC) to quantify the feasibility of involving farmers in developing population crosses and of managing genetic diversity through evaluation of farmer-generated seed stocks.

Modeling Selection Gains from Alternative Recurrent Selection Methods

Completely and rigorously comparing the effectiveness of the many alternative recurrent selection methods and variants for each through field experimentation is extremely difficult, if not impossible. Computer modeling enables comparisons of alternative methods, without the risk of confounding different genetic materials, selection and test sites, selection intensity, and resources used, as would be the case across independently conducted recurrent selection programs. Furthermore, progress with a given method depends on the effectiveness with which resources are allocated.

A rigorous modeling effort was conducted to compare the effectiveness of a series of selection methods that have been or could be expected to be used for population improvement of pearl millet (Schipprack, 1993). The methods include

mass selection, half-sib, full-sib, S_1 and S_2 family evaluations, as well as two combined methods, S_1 followed by S_2 family, and full-sib followed by S_1 family selection. All methods were compared at common levels of total labor capacity and rates of inbreeding in the population. The ratios of genotypic, genotypic × environmental and error variances used in modeling were based on estimates of these parameters from population progeny trial data from ICRISAT (IAC). The expected response to selection was estimated as gain in General Combining Ability per year (G(y)) by applying the formula

$$G(y) = i_{(\alpha)}\, p_{xy}\, \sigma_y / Y$$

where $i_{(\alpha)}$ is the intensity of selection, p_{xy} the coefficient of the correlation between the selection and the response criterion (GCA), σ_y the standard deviation of the response criterion, and Y the number of years per cycle.

Modeling was first used to optimize resource allocation within each method for the numbers of progenies, locations, and replications tested, to maximize expected gains from that method under the limitations of resources and maintenance of genetic diversity. The optimal configurations of each method were then compared over a range of available labor capacity.

Major differences were found among the alternative methods for estimated selection gains for head yield per year (Table 10). Compared to the estimated gains from the highest ranked full-sib method, the second to fifth ranked methods achieved only 90%, 75%, 71%, and 50% as much progress. The assumed levels of correlation between per se performance and GCA did influence the relative gains. Under a tighter correlation (0.8), the gains from the selfed progeny methods increased, but these were still only 84% of the gains achieved by the full-sib method. The highest ranking method, when assuming a correlation of 0.8, was the combined full-sib/S_1 family method, whose estimated gains were 6% higher than the full-sib method.

The ranking of methods showed no change over a broad range of labor availability (Figure 1). Only at the lowest labor levels and highest correlation between per se performance and GCA were predicted gains from S_1 line selection greater than for full-sib selection (Figure 2). Also the

Table 10. Selection response per year for pearl millet head yield from alternative recurrent selection procedures optimized for allocation of labor modeled under high (P=0.8) and intermediate (P=0.5) correlations of per se performance with GCA.

	Selection response	
Recurrent selection procedure	P=0.5	P=0.8
Mass selection*	0.22	0.22
Half-sib family*	0.34	0.34
Full-sib family	0.51	0.51
S1 line (one stage)	0.27	0.43
S2 line (one stage)	0.23	0.43
S1 line (two stage)	0.26	0.42
S1 line/S2 line	0.26	0.46
Full-sib/S1 line	0.46	0.55

*S1 lines from S_0 single plants used for recombination.
(W. Schipprack, 1993)

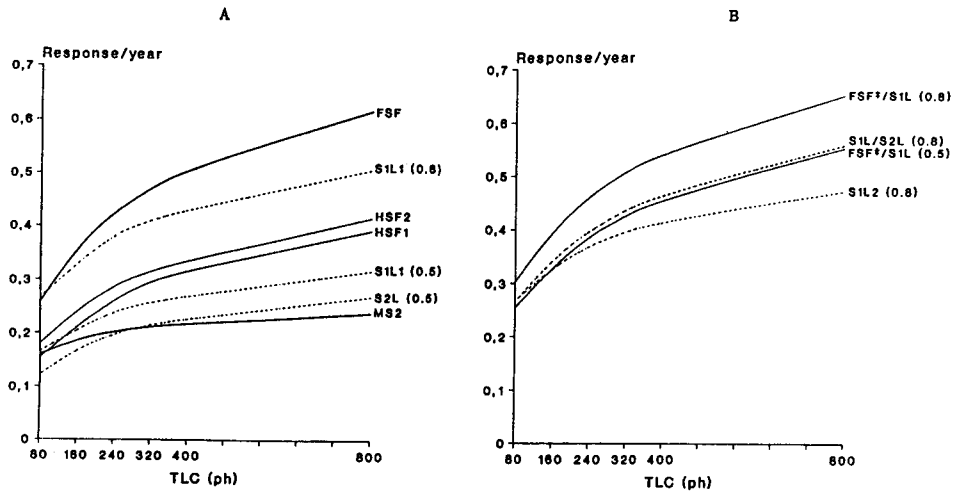


Figure 1. **Standardized selection response per year for head yield (HY) expected from alternative RS procedures without preselection as a function of the total labor capacity (TLC) using the standard optimization conditions. Figures in parentheses indicate the coefficient assumed for the correlation between performance per se and GCA of S_1L.**
A: one-stage RS procedures. B: two-stage RS procedures. (Schipprack, 1993)

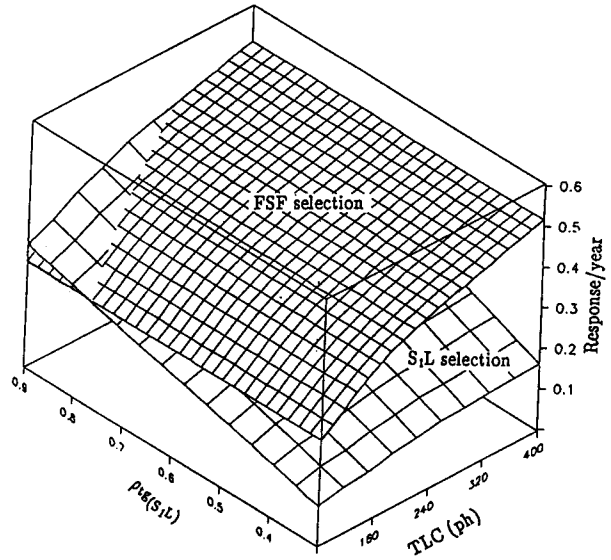


Figure 2. **Standardized selection response per year for head yield (HY) expected from FSF and S_1L selection as a function of the total labor capacity per year (TLC) and the correlation between performance per se and GCA of S_1L [$ptg_{(S1L)}$]. (Schipprack, 1993)**

ranking of methods was similar across a range of assumed levels of dominance (σ^2_D/σ^2_A ratios of 0.25 to 0.75).

In the past, full-sib selection methods were rarely used at IAC for pearl millet (Pheru Singh et al., 1988; Rattunde and Witcombe, 1993). Schipprack's (1993) results have led to extensive use of full-sib evaluation for yield and agronomic traits in India. His results are based on restricting the rate of inbreeding to 1% per year, which would be appropriate when pursuing long-term population improvement. However, when shorter term goals are pursued, a higher rate of inbreeding would be acceptable and the ranking of the recurrent selection methods may change.

Conclusions

Population improvement of pearl millet and sorghum is currently being conducted with diverse materials and objectives. In the future, population improvement will be an essential breeding tool.

Effective utilization of the tremendous genetic diversity available in these species will be vital for genetic enhancement of productivity and stability of these crops. Population improvement allows more recombination and a larger number of favorable alleles than is possible with the same number of plants handled via pedigree methods. The documented gains in population means and superior families achieved through recurrent selection show the effectiveness of this general approach. In pearl millet, the increased use of populations for development of pollinators, especially top cross pollinators, would contribute greatly to the diversification of hybrids available for cultivation.

The choice of specific methods for population improvement will have important consequences for the gains achieved. Modeling the efficiency of alternative evaluation methods for improvement of pearl millet populations showed more than two-fold differences. The open-population approach with introgression via population backcrossing should improve the source populations within the context of an applied program, especially for sorghum. This method would provide both source material for immediate development of finished products as well as longer-term genetic enhancement required for future gains.

The open-pollinated pearl millet varieties and pure-line sorghum varieties derived from populations can be readily propagated by local seed systems. The impact of population improvement could be greatly enhanced if new ways for interfacing research institutions with local seed systems could be explored and developed. This is especially true for regions and conditions where seed enterprises are currently not providing improved products to farmers.

References

Agrawal, B.L., and S.L. Taneja. 1989. Breeding for resistance to stem borer (*Chilo partellus* Swinhoe) in sorghum. International workshop on sorghum stem borers, 17-20 Nov. 1987. International Crops Research Institute for the Semi-Arid Tropics, A.P. 502 324, India.

Ali, A.M. 1996. Development of population diallel cross of pearl millet elite composites. Masters thesis, University of Gezira, Wad Medani, Sudan.

Andrews, D.J., and K. Anand Kumar. 1996. Use of the West African pearl millet landrace Iniadi in cultivar development. Plant Genetic Resources Newsletter 105:15-22.

Andrews, D.J., and J.F. Rajewski. 1995. Registration of NPM-3 grain pearl millet. Crop Sci. 35:1229.

Andrews, D.J., J.F. Rajewski, and L.A. Pallish. 1995. Registration of NPM-1 and NPM-2 grain pearl millet germplasm. Crop Sci. 35:598-599.

Bacon, R.K., R.P. Cantrell, and J.D. Axtell. 1986. Selection for seedling cold tolerance in grain sorghum. Crop Sci. 26:900-903.

Bramel-Cox, P.J., M.A. Lauver, and M.E. Witt. 1990. Potential gain from selection for higher protein digestibility in grain sorghum. Crop Sci. 30:521-524.

Bramel-Cox, P.J., and T.S. Cox. 1989. Use of wild germplasm in sorghum improvement. p. 13-26. *In* D. Wilkinson (ed.) Proc. 43rd annual corn and sorghum industry res. conf. Chicago, IL. 7-10 Dec. 1989. Am. Seed Trade Assoc., Washington, DC.

Bramel-Cox, P.J., and L.E. Claflin. 1989. Selection for resistance to *Macrophomina phaseolina* and *Fusarium moniliforme* in sorghum. Crop Sci. 29:1468-172.

Ceccarelli, S., S. Grando, and R. Booth. 1996. International breeding programs and resource-poor farmers: Crop improvement in difficult environments. *In* P. Eyzaquirre and M. Iwanaga (eds.) Participatory plant breeding: Proceedings of a workshop on participatory breeding, 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Chisi, M., P.J. Bramel-Cox, M.D. Witt, M.M. Claassen, and D.J. Andrews. 1996. Breeding for grain yield stability using full-sib family recurrent selection in sorghum. Crop Sci. 36: (in press).

Chisi, M. 1993. Evaluation of selection procedures in multiple environments to identify parent lines for grain sorghum (*Sorghum bicolor* L. Moench). Ph.D diss. Kansas State University, Manhattan, KS. Diss. Abstracts 9413074.

Comstock, R.E., H.F. Robinson, and P.H. Harvey. 1949. A breeding procedure designed to make maximum use of both general and specific combining ability. J. Am. Soc. Agron. 41:360-367.

Doggett, H. 1982. A look back at the 70s. *In* L.R. House, L.K. Mughogho, and J.M. Peacock (eds.) Sorghum in the eighties: Proceedings of the international symposium on sorghum, 2-7 Nov. 1981. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P., India.

Eyherabide, G.H., and A.R. Hallauer. 1991. Reciprocal full-sib recurrent selection in maize: I. Direct and indirect responses. Crop Sci. 31:952-959.

Falconer, D.S. 1981. Introduction to quantitative genetics. Longman, London and New York.

Gardner, C.O., and S. A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics 22:439-452.

Hallauer, A.R., 1981. Selection and breeding methods. *In* K.J. Frey (ed.) Plant breeding II. The Iowa State University Press, Ames, Iowa.

Hallauer, A.R., and J.B. Miranda, Fo. 1988. Quantitative genetics in maize breeding. The Iowa State University Press, Ames, Iowa.

ICRISAT. 1988. Annual report 1987. International Crops Research Institute for the Semi-Arid Tropics, A.P. 502 324, India.

ICRISAT. 1989. Annual report 1988. International Crops Research Institute for the Semi-Arid Tropics, A.P. 502 324, India.

ICRISAT. 1992. ICRISAT West African programs annual report 1991. B.P. 12404, Niamey, Niger, ICRISAT Sahelian Center, Niamey, Niger.

ICRISAT. 1996. Improving the unimprovable - Succeeding with pearl millet. Number 3 in the "Food From Thought" series. International Crops Research Institute for the Semi-Arid Tropics, A.P. 502 324, India.

Kwolek, T.F., R.E. Atkins, and O.S. Smith. 1986. Comparisons of agronomic characteristics in C0 and C4 of IAP3BR(M) random-mating grain sorghum population. Crop Sci. 26:1127-1131.

Lynch, P.J., E. Weltzien-Rattunde, and K.J. Frey. 1995. Inheritance of vegetative growth index and related traits in pearl millet. Crop Sci. 35:394-396.

Maciel, G. 1995. Impact of the antagonistic versus synergistic selection and per se performance on adaptation in grain sorghum population. Ph.D. Diss. Kansas State University, Manhattan, KS. Diss. Abstracts 9620865.

Maves, A.J., and R.E. Atkins. 1991. Estimates of quantitative genetic parameters in IAP2B(M) random-mating sorghum population. Jour. Iowa Acad. Sci. 98(3):139-144.

Menkir, A., P.J. Bramel-Cox, and M.D. Witt. 1994. Selection for agronomically acceptable inbred lines in adapted x exotic sorghum backcross populations. Crop Sci. 34:1084-1089.

Menkir, A., P.J. Bramel-Cox, and M.D. Witt. 1994. Comparisons of methods for introgressing exotic germ plasm into adapted sorghum. Theor. Appl. Genet. 89:233-239.

Ouendeba, B., G. Ejeta, W.E. Nyquist, W.W. Hanna, and A. Kumar. 1993. Heterosis and combining ability among African pearl millet landraces. Crop Sci. 33:735-739.

Pheru Singh, A., G.B. Raj, M.N.V. Rao, and J.R. Witcombe. 1994. Registration of "ICMV 155" pearl millet. Crop Sci. 34:1409.

Pheru Singh, A., K.N. Rai, J.R. Witcombe, and D.J. Andrews. 1988. Population breeding methods in pearl millet improvement (*Pennisetum americanum*). L'Agronomie Tropicale 43(3): 185-193.

Rai, K.N., and K.A. Kumar. 1994. Pearl millet improvement at ICRISAT: An update. International Sorghum and Millets Newsletter 35:1-29.

Rattunde, H.F. 1988. Mass selection strategies for pearl millet improvement. Ph.D. dissertation, Iowa State Univ., Ames, IA, USA.

Rattunde, H.F., Pheru Singh, A., and J.R. Witcombe. 1989. Feasibility of mass selection in pearl millet. Crop Sci. 29:1423-1427.

Rattunde, H.F.W., and J.R. Witcombe. 1993. Recurrent selection for increased grain yield and resistance to downy mildew in pearl millet. Plant Breeding 110:63-72.

Rattunde, H.F.W. 1992. Seedling vigor and vegetative growth rate in early-maturing sorghum. p. 59-60. *In* Cereals program, annual report 1993. Interational Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Rattunde, H.F.W. 1993. Seedling growth in early-maturing sorghum. p. 51-52. *In* Cereals program, annual report 1993. Interational Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Rattunde, H.F.W. 1994. Population improvement of dual-purpose sorghum. p. 53-55. *In* Cereals program, annual report 1993. Interational Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Reddy, B.V.S. 1994. Genetic diversification. p. 51-53. *In* Cereals program, annual report 1993. Interational Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Reddy, B.V.S., and K.E. Prasada Rao. 1993. Genetic diversification. p. 48-51. *In* Cereals program, annual report 1992. Interational Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Schipprack, W. 1993. Estimation of population parameters and optimization of alternative procedures of recurrent selection in pearl millet [*Pennisetum glaucum* (L.) R. Br.], Disseration, University of Hohenheim, Stuttgart, Germany.

Secrist, R.E. 1989. Comparison of mass selection and S1-testing recurrent selection methods in sorghum. Ph.D. dissertation, Iowa State Univeristy, Ames, IA, USA.

Secrist, R.E., and R.E. Atkins. 1991. Comparison of mass selection and S_1 testing recurrent selection methods in sorghum. 1991. Jour. Iowa Acad. Sci. 98(3):134-138.

Simmonds, N.W. 1979. Principles of Crop Improvement. Longman, New York.

Sperling, L., and U. Scheidegger. 1996. Results, methods and institutional issues in participatory selection: The case of beans in Rwanda. *In* P. Eyzaquirre and M. Iwanaga (eds.) Participatory plant breeding: Proceedings of a workshop on participatory breeding, 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Wehmann, F., S.L. Taneja, H.C. Sharma, and J.W. Stenhouse. 1992. Selection methodology for shoot fly, stem borer, and midge resistance. p. 55-56. *In* Cereals program, annual report 1991. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Weltzien R., E., and C.T. Hash. 1995. Cooperative breeding of open-pollinated varieties. p. 73-76. *In* S.Z. Mukuru and S.B. King (eds.) Eighth EARSAM regional workshop on sorghum and millets, 30 Oct.- 5 Nov. 1992, Wad Medani, Sudan. ICRISAT, Patancheru, AP, India.

Weltzien R., E., and S.B. King. 1995. Recurrent selection for downy-mildew resistance in pearl millet. Plant Breeding 114:308-312.

Weltzien R., E., M.L. Whitaker, and M.M. Anders. 1996a. Farmer participation in pearl lmillet breeding for marginal areas. p. 128-150. *In* P. Eyzaquirre and M. Iwanaga (eds.) Participatory plant breeding: Proceedings of a workshop on participatory breeding, 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Weltzien R., E., M.L. Whitaker, H.F.W. Rattunde, M. Dhamotharam, and M.M. Anders. 1996b. Participatory approaches in pearl millet breeding. *In* J.R. Witcombe and J. Farrington (eds.) Regulatory frameworks in India. ODA, U.K. (in press).

Weltzien R., E., M.L. Whitaker, and M. Dhamotharan. 1996c. Methods for breeding pearl millet with farmers in Rajasthan. p. 127-139. *In* L. Sperling and M. Loevinsohn (eds.) Using diversity and maintaining genetic diversity on-farm. Proceedings of a workshop, 19-21 June 1995, New Delhi, India. IDRC, New Delhi, India.

Witcombe, J.R. 1996. Population improvement. *In* I.S. Khairwal, K.N. Rai, and G. Harinarayana (eds.) Pearl millet breeding. Oxford & IBH, New Delhi, India (in press).

Zavala-Garcia, F., P.J. Bramel-Cox, J.D. Eastin, M.D. Witt, and D.J. Andrews. 1992. Increasing the efficiency of crop selection for unpredictable environments. Crop Sci. 32:51-57.

Appendix 1. Pearl Millet populations currently being developed, improved or representing the most important populations in a region.

Population	Genetic composition/origin	Selection history/use
Institutions: ICRISAT Sahelian Center, Niger, West African NARS. Target Environments: Sahelian Zone, 300-600 mm rain, 60-100 d maturity.		
Gueriniari Intervarietal Composite (GRGB)	Population cross between Guerguera (Niger) and Iniadi (GB 8735 large seeded Togo type), cross combination identified in population diallel (1989-90), five F_1s, selected from original 36 F_1s between 14 selected full-sibs random mated [1994][a]	2 stage S_1, multilocation
ISC Intervarietal Composite (ISC-851)	Approximately 180 F_1s from intervarietal crosses involving 40 West African improved varieties and prominent landraces [1985]	Random mated (3), 2 stage S_1, multilocation
Long Head Gene Pool (LGHP)	Accessions from Western Niger [1989-90]	Random mated (3), 2 stage S_1, multilocation
Medium Maturing Composite (MMC)	Accessions from Northern Nigeria [1989-90]	Random mated (3), 2 stage S_1, multilocation
Institutions: West African NARS, ICRISAT-Mali Target Environments: Sudanian Zone, 600-900 mm rain, 100-150 d maturity		
ICMC-IS 101	Intervarietal cross between Kapelga, photoperiod-sensitive late cultivar from central Burkina Faso, and GT 79, nearly day-neutral cultivar Iniadi from Togo [1992]	One cycle of recurrent selection completed and derivation of elite lines; currently no active breeding
RP 1004	Intervarietal cross between Kapelga, photoperiod-sensitive late cultivar from central Burkina Faso, and GT 85, nearly day-neutral cultivar Iniadi from Togo [1992]	One cycle of recurrent selection completed and derivation of elite lines; currently no active breeding
Institutions: ICRISAT Asia Center, India, Asian NARS Target Environments: Asia, primarily northwestern India, <400 mm rainfall, very early maturity (60 to 70d under favorable conditions).		
Western Rajasthan population (WRajPop 88)	14 landrace accessions from NW India selected from 155 accessions tested in Rajasthan and Patancheru. [1989]	Random mated (3), selection on differing progeny types (C4)
Early Rajasthan population (ERajPop 91)	30 S_1 lines from 4 selected Western Rajasthan landraces IP 3188 (n=3), IP 3228 (12), IP 3464 (10), IP 3246 (5) [1991]	Random mated (3), full-sib selection (C3), multilocation
Early High Tillering Population (EHiTiP 92)	600 full-sibs, 30 from each of 20 population crosses among 9 populations, ERajPop 91, Early Pakistan Pop, LRE 49 x EC C6, HiTiP 88, HiTiP 89, PakLR74 x EC 89, PakLR74, HiTiP TCP, EC C6 [1992]	Random mated (3), full-sib selection (C2), multilocation
CZP-IC 416	Two interpopulation crosses from the early population diallel; EPDT-5 (EC C6 x LRE 128) (58S), EPDT-41 (Pak LR 74 x EC 89) (41 FS) and EPDT-5 x EPDT-41 (82 FS) [1994]	Random mating (3), C1 of testcross (S_2 lines on 841A for seed setting and fertility restoration
RCB-IC 956 (EC 89)	Population cross of EC C6 with BSEC. [1989]	Random mated (2), two cycles, modified mass selection; mild mass selection for earliness, panicle type in Rajasthan, S_1 selection for DM resistance at IRC
RCB-IC 948	Interpopulation cross of EC II with WRajPop 89, selected from an early-population diallel [1990]	Random mated (3), first cycle of S_1 progeny selection initiated,multilocation
Barmer population	5 Western Rajasthan landrace accessions, collected by NBPGR and ICRISAT in 1992, selected on-station by farmers in a drought year at Jodhpur [1994]	Third random mating being completed
Jakharana	Tall, long panicled, late maturing landrace accession from Sikar district, Rajasthan crossed with ICMV 155, a variety derived from the NELC population [1996]	Third random mating being completed
Target Environments: Asia > 400 mm rainfall, particularly more productive pearl millet growing environments throughout the Indian sub-continent and Pakistan		
New Elite Composite II (NELC II)	Crosses of NELC with progenies from a late-population diallel, predominantly African, non-Togo [1994]	Random mated (3), initiate progeny selection, multilocation, augmented design in 1996

Population	Genetic Composition/Origin	Selection History/Use
Smut Resistant Composite III (SRC III)	Crosses of SRC II with progenies from a late-population diallel, predominantly African, non Togo [1994]	Random mated (3), initiate progeny selection, multilocation, augmented design in 1996
Smut Resistant Composite II (SRC II)	Interpool crossing of Smut Resistant Composite and Intervarietal Composites [1987]	Random mated (3), progeny selection, multilocation, augmented design (C3), propose one more cycle of selection and then terminate
Early Smut Resistant Composite II (ESRC II)	One cycle of MSL in SRC II for earliness, largely African, non-Togo (1988)	Progeny selection, multilocation, augmented design (C3)
Medium Composite 94 (MC 94)	Crosses of elite materials from Medium Composite (C10) with elite Bold Seeded Early Composite materials (ICMV 88908 = Okashana 1), 3/4 African, 1/4 Indian, 50% Togo [1990]	Random mated (3), progeny selection, multilocation, augmented design (C1) emphasize reduced height, large grain size
High Head Volume B Composite (HHVBC)	West African Landraces crossed with elite lines (1990)	Progeny selection at IAC (C4), agronomic type, seed setting under selfing
Target Environments: Broad range of existing or potential production systems		
Extra Early R Composite (EERC)	Early progenies under extended day-length from broadest range of composite bulks & lines, non-Togo phenotype [1995]	Random mated (4), initiate mass selection in target environment, progeny downy mildew screening, testcross to determine fertility restoration at IAC
Extra Early B Composite (EEBC)	Early progenies under extended day-length from broadest range of composite bulks & lines, Togo phenotype [1992]	Random mated (4), use as source material to derive B lines
SADC White Grain Composite (SADC WGC)	Developed in Zimbabwe from white grained germplasm accessions [1994]	Propose progeny selection, multilocation, augmented design, for grain yield, potential for industrial & food uses
Early Composite II (EC II)	Early Gene Pool, predominantly Indian [1984]	Progeny selection, multilocation, augmented design [C6] for grain yield, medium duration
Dwarf Nigerian Composite (NCD_2)	Nigerian Composite	Test cross selection (C3) for sterility maintenance on A_4 cytoplasm; backcrossing (BC_2) to convert to A_4 cytoplasm; potential female parent for population hybrids, especially for Western Africa
Institution: University of Nebraska-Lincoln, U.S.		
Target Environments: Dwarf grain pearl millet growing areas		
NPM-1 (PI 574382)	14 selfed plants from Nebraska Dwarf Pearl Millet Population progenies selected for large heads, good self fertility, medium maturity (55-65 d to flower) and height (<80 cm) [1985]. Andrews, et al. 1995. Crop Sci. 35:598.	Random mating (1) with mild selection, unreplicated S_1 (1 cycle), gridded mass selection (2 cycles), use as pollinator or source of restorer lines on A_1 cytoplasm.
NPM-2 (PI 574383)	7 selfed plants from Nebraska Dwarf Pearl Millet Population selected for early maturity (<55 d to flower) dwarf (<60 cm) high-tillering plant type with 4 or more erect tillers and good self fertility [1985]. Andrews et al. 1995. Crop Sci. 35:598.	Random mated (1) with mild selection, unreplicated S_1 (1 cycle), gridded mass selection (2 cycles), use as pollinator or source of restorer lines on A_1 cytoplasm
NPM-3 (PI 574544)	9 dwarf inbred lines of diverse origin (from A_1 maintainer breeding program) identified as restorers on A_4 cytoplasm [1992]. D.J. Andrews and J.F. Rajewski. 1995. Crop Sci. 35:1229.	Random mated (2), use as source of pollinators for A_4 cytoplasm

[a]Year of origin

Appendix 2. Sorghum populations currently being developed, improved or representing the most important populations in a region.

Population	Genetic Composition/Origin	Selection methods/ Recombination
	Institution: Purdue University, Indiana, U.S. **Target Environments: Temperate grain sorghum areas and areas requiring *Striga* or grain mold resistance.**	
Purdue Population 34		
Purdue Population 35	Early B population developed from 30 B lines	Used for line derivation
Purdue Population 37	*Striga* Resistant population from 20 internationally tested *Striga* resistant lines	Used for line derivation
Purdue Population 40	Mold resistant population from elite mold resistant lines	Used for line derivation
	Institution: University of Nebraska - Lincoln, U.S. **Target Environments: Temperate grain sorghum growing areas**	
Nebraska Stress Tolerant Food Quality Population (NP37)	Derived from 2 cycles of S1 progeny selection for drought tolerance in Nebraska/Kansas from Texas Population TP24 [1966][2]	Source of drought tolerant food quality tan plant B lines
Nebraska Early Duration B-Line Population	13 diverse very early maturing B lines from US x tropical food quality introgression program crossed onto sterile F_2 plants from cross CK60Bms_7 x N122B, and backcrossing B-lines to resulting sterile F_2s [1996]	Source for derivation of very early B-lines
Nebraska Medium Duration B-Line Population	26 diverse medium maturing B lines from US x tropical food quality introgression program crossed onto sterile F_2 plants from cross CK60Bms_7 x N122B, and backcrossing B-lines to resulting sterile F_2s [1996]	Source for derivation of medium duration B-lines
Nebraska Population 39 (NP39)	S_2 families (n=100) from TP24R selected out of 900 for grain yield and maturity under severe preanthesis drought stress at Garden City, KS [1988]	Random mated (3), use as tan-plant population for US Great Plains
	Institution: Kansas State University, Manhattan, Kansas **Target Environments: Temperate dry land grain sorghum areas with unpredictable drought and requirement for early maturity**	
Population	Genetic Composition/Origin	Selection History/Use
KP7B	First stage: IAP2Bms_3 sterile plants crossed with BOK 11, BKS 9, BKS 45, BKS 46, BKS 52, BKS 56, BTx 623 and BTx 625, resulting F_2 sample random mated in isolation. Second stage: One sub-population generated by random mating the F_2 sample under extreme drought and heat and selecting agronomically desirable male steriles. A second subpopulation generated by crossing unselected F_2 and Yellow Endosperm Kafir ms_3 steriles as females with BKS 9, BKS 45, BKS 56, BKS 67, BOK 11, BSC 599, B1778, B1887, B4R, BTx 625, BSC 35-6 and BTx 2803, and advancing these F_1s to F_2. The two subpopulations were bulked in equal quantities and random mated in isolation under moderate drought and heat stress. [1984]	Random mated (>3), 2 cycles S_1 selection for protein digestibility or protein digestibility and grain yield. A elite B population
KP8B	Steriles of Yellow Endosperm Kafir ms_3 and the first stage F_2 population of KP7B were crossed with drought tolerant B lines including BKS 9, BKS 18 BKS 67, BSC 35-6, B1887, BSC 599, BTx 2803, B4R and BTx 625. The F_1s were selected for agronomic desirability under drought and heat stress. [1985]	Random mated, 2 cycles half-sib selection for resistance to charcoal rot and *Fusarium*
KP9B	IAP2Bms_3 steriles crossed with all B lines used in first stage of developing KP7B as well as BKS 66, BTx 2749, BTx 2752, D. Redlan, 81H2-138, 81H2-242, 81H5-62, 81H5-112, 81H5-218, 81H6-63, 81H6-69, BKS 67, BKS 68 and B7904. The F_2 was bulked as the major component, with YE Kafir F_2ms_3, and random mated under severe drought and heat in 1983, with selection of agronomically desirable sterile and fertile plants. All selections were grown head-to-row under moderate heat and drought and agronomically desirable sterile plants selected in 1984.	Selection using S_1, full-sib, reciprocal recurrent selection emphasizing adaptation to dryland conditions. An elite B population that is broader based than KP7B

Institution: ICRISAT Asia Center, Patancheru, India

Target Environments: Dual-purpose sorghums for Asian Post-Rainy Season under declining temperature, stored soil moisture and short day conditions

Population	Genetic Composition/Origin	Selection Methods and Criteria/Use
Large Grain Population (ICSP LGP)	9 large grained landraces were crossed to US/B (C6) and resulting F_1s were crossed to alternative accessions from the same set [1990]	Multiple cycles of single-location mass selection for grain size
Shoot Pest Population	F_2s from crosses among 98 landraces and 17 breeding lines representing diverse sources for shoot fly and/or stem borer resistance were introgressed into the original shoot pest population [1992]	Random mating (3), mass selection for shootfly resistance and adaptation to the post-rainy season (C4)

Target Environments: Grain or dual-purpose sorghum areas in Asian Rainy-Season with 90-120 d growth durations

Population	Genetic Composition/Origin	Selection History/Use
B Population (ICSP B)	10 bold-grain lines, 47 progenies of QL3 x 296B with downy mildew resistance, 5 midge resistant lines, approximately 18 high-yielding B-lines, crossed to male steriles (ms3) of US/B-C6 [1989]	Additional introgression of PS 19349, 296B, M 35-1 with continued mass selection for large, round, lustrous grain, grain number and shootfly resistance
US/R Dual Purpose Population (ICSP US/R (DP))	US/R population composed of converted African materials selected from Purdue Populations PP1, PP3 and PP5 and Nebraska Populations NP4BR, NP5R and NP8, contains ms3 [1975]	Random mation (0), S_1 progeny selection for grain and stover yield, early maturity and lodging resistance. Selection initiated in 1991 with S_1 progenies from the US/R C1 and C2 bulks. Two cycles completed.
Early Dual-Purpose Population (ICSP EDP)	Steriles of 22 S_1 progenies selected in the first cycle of improvement of ICSP US/R (DP) were crossed with landraces (IS 869, IS 8101, IS 19159, IS 20545, IS 22500, IS 23897, IS 24335, IS 24436), breeding lines (IS 18758c-591T, IS 18758c-618), and forage variety HC 260. All materials were chosen based on multi-environment data with selection indices containing grain-, stover-yield and early flowering. [1992]	Random mating (3), mass selection for grain and head characteristics
Head Pest Population (ICSP HP)	F_2s from crosses among 27 landraces and 6 breeding lines representing diverse sources of resistance to head bug and midge were introgressed into a bulk of approximately 100 steriles of the previous Head Pest Population [1992]	Random Mating (3), initiated multi-location (India and Kenya) two-stage (S_1/S_2) progeny testing for midge resistance
High Tillering Population (ICSP HT)	21 early-maturing fast-growth lines and 4 uniculm lines tillering under stress from diverse countries, 2 grain grass lines, 3 sudan grass lines, 2 high-tillering forage lines from SADC/ICRISAT, 7 sweet stalk lines, 3 brown midrib lines, 1 anthracnose and 1 downy mildew resistant line were crossed to male steriles of US/B C6 [1990]	Random mating (3), mass selection for tillering (2 to 3 plant^{-1}) at 35 DAE, large leaves with brown midrib and mild pressure for anthracnose resistance (C3)

Target Environment: Higher rainfall areas (>800mm) in Western and Central Africa

Population	Genetic Composition/Origin	Selection History/Use
(Guinea) Grain Mold Population	A Guinea-Caudatum population was formed by crosses of 35 mold-resistant and 4 susceptible lines to 5 US/R and 12 US/B population derivatives in 1984, and resulting progenies of these crossed with 23 mold resistant, 27 high-yielding and 14 dwarf & early lines in 1987. Introgression of 12 conspicuum types initiated 1996 in parallel to mass selection	Random mating (4), mass selection for white-grain and guinea glume (1990-1993) as well as reduced plant height (1993-1996) and against nodal tillers (1996)

Institutions: SADC/ICRISAT SMIP

Target Environments: Contrasting agro-ecological zones prevalent in Southern Africa

SDSP-Hot/Dry	Based on 4 populations (TP24R04/TP15R05, TP21RB03, 84PP-19M, PP-19) with highest grain yields at Sebele, Botswana and Makaholi, Zimbabwe [1992?]	Random mating (4) with selection; populations made available to regional NARS
SDSP-Cool/Dry	Based on 4 populations (TP24R04/TP15R05, TP8, WAEC3PC82R, KP8B) with highest grain yields at Matopos and Lucydale, Zimbabwe [1992?]	Random mating (4) with selection; populations made available to regional NARS

Population	Genetic Composition/Origin	Selection History/Use
SDSP-Drought Conditions	Based on 4 populations (TP24R04/TP15R05, TP15, TP21RB03, KP9BSO) with highest grain yields at Muzarabani, Zimbabwe and Golden Valley, Zambia [1992?]	Random mating (4) with selection; populations made available to regional NARS
SDSP-Broad Adaptation	Based on 4 populations (TP24R04/TP15R05, TP1RB03, ?, ?) with highest grain yields across all zones	Random mating (4) with selection; populations made available to regional NARS
Institutions: CIRAD/ICRISAT **Target Environments: Sudanian Zone of Western Africa**		
Guinea Population	13 Guinea accessions from West Africa (54-14, 54-36, 64-17, 87-86, Nazongala, Oueni, CSM 282, CSM 335, CSM 382, CSM 485, 87-45, 87-46, 50-8) crossed to ms3 source. One (10 accessions) or two-backcrosses (3 accessions) made to the accessions, with accessions as female in last backcross. BC_1F_2 (n=10) and BC_2F_2 (n=3) were bulked. [1994]	Random mating (2) completed in 1996
Caudatum Population	12 Caudatum accessions (IS 2333, IS 2867, IS 3413, IS 3547, IS 8219, IS 8848, IS 23516, CSM 309, CSM 315, Gadiabani, S 8136 from Mali, mostly colored grain and chosen for grain mold resistance) crossed to ms3 source and backcrossed once, using the caudatum accessions as female parents. BC_1F_2 entries bulked. [1994]	Random mating (2) to be completed in 1996. Intended selection for grain mold resistance
Guinea-Caudatum Population	Selected landraces, improved and adapted high yielding lines and a few resistant sources. [1996]	Random mating with selection to be initiated in 1997

[1] Selection cycles completed.
[2] Year the population was generated.

Alternate Cytoplasms and Apomixis of Sorghum and Pearl Millet

K.F. Schertz*, S. Sivaramakrishnan, W.W. Hanna, J. Mullet, Yi Sun, U.R. Murty, D. R. Pring, K.N. Rai, and B.V.S. Reddy

Abstract

Cytoplasmic-nuclear male sterility (CMS) has been an important factor in the improvement of sorghum and pearl millet by increasing yield, expanding production, and stimulating research and breeding. The identification of alternate sterility-inducing cytoplasms and their emerging deployment hold promise for further advances. Current research to determine the cause and control of CMS in these species could lead to greater efficiency and effectiveness in using CMS to select parents and produce hybrids.

Apomixis, although not now used with either sorghum or pearl millet, has the potential to be as important as male sterility in these species. Potential sources have been identified and research is in progress on characterization, introgression, and enhancement. The ability to perpetuate hybrid vigor by self-pollination could be very important in some of the major sorghum and millet growing areas.

Success in identifying and using cytoplasmic-nuclear male sterility to produce hybrid onions (Jones and Emsweller, 1937; Jones and Davis, 1944) had a major impact on crop breeding. Since then, hybrids of many crops, including sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R. Br.], have been mass-produced using cytoplasmic-nuclear male-sterile (CMS) female parents. Apomixis has the potential to become as important in sorghum and millet hybrid production as is CMS, allowing breeders to more rapidly and efficiently use available germplasm to produce hybrids.

K.F. Schertz, Texas A&M University, Department of Soil and Crop Sciences, College Station, TX 77843; S. Sivaramakrishnan, K.N. Rai, and B.V.S. Reddy, ICRISAT; W.W. Hanna and D.R. Pring, USDA-ARS; J. Mullet, Texas A&M University; Yi Sun, Shanxi Academy of Agricultural Science, P.R. China; U.R. Murty, National Research Centre for Sorghum, India. *Corresponding author.

Cytoplasmic Male Sterility

CMS sorghum and millet plants are male-sterile because their pollen is not viable. Female fertility, however, is usually normal. CMS results from specific interaction of the cytoplasm and the nucleus. Plants are male-fertile when the cytoplasm and/or nucleus are compatible. Plants are male-sterile when the cytoplasm and the nucleus are incompatible. Male-sterile combinations are detected in segregating F_2 progeny. Non-adequate combinations in the male-sterile lines are detected by crossing male-steriles by pollen parents and observing F_1 plants for male sterility or fertility. Those male parents that produce male-sterile F_1 plants have the potential to be made into male-steriles by backcrossing. Those male parents that produce fertile F_1 plants are potential male parents. Hybrid seed is pro-

duced by planting male-sterile female parents adjacent to male-fertile parents that have a gene that will restore fertility to the F_1 plants. The hybrid seed produced on the female parent is what the farmer plants.

Although the main cytoplasms used to make male-sterile parents of sorghum and pearl millet hybrids are effective, additional usable cytoplasms have been sought for two reasons: 1) to have additional cytoplasms available if some adversity becomes associated with those usually deployed; and 2) to provide diversity in cytoplasms so that different cytoplasmic-nuclear combinations could be used, thus allowing breeders to more fully exploit the germplasm diversity available.

CMS in Sorghum

Cytoplasmic-male sterility in sorghum was first reported by Stephens and Holland (1954) and its deployment soon followed their efforts and those of their colleagues Quinby, Kramer, Webster, and others. Sorghum yields increased dramatically with the use of hybrids. The milo cytoplasm used in the first hybrids is still the main male sterility-inducing cytoplasm used today. Breeders have learned which lines can be made male-sterile in milo cytoplasm and which will restore fertility and can therefore be used as male parents. There is, however, an awareness of the benefits of using alternative sources of male sterility-inducing cytoplasms.

Scientists in India (Tripathi, 1979; Appathurai, 1964; Rao, 1962), Africa (Webster and Singh, 1964), and the U.S. (Stephens and Holland, 1954; Ross and Hackerott, 1972; Schertz and Ritchey, 1977; Schertz and Pring, 1982) have identified many sources of sterility-inducing cytoplasms of sorghum. Cytoplasms from different sources, however, might not differ in the manner in which they induce male sterility. The main approach to determine sterility-inducing differences among the cytoplasms has been to cross each male-sterile by the same male parent and to determine which F_1s differ in fertility restoration.

From such studies it has been determined that there are four distinct sterility-inducing cytoplasms (A_1 to A_4) and three others that are less distinct. One must keep in mind that the results of such studies are influenced by the male parents used, the nuclear background of the male-steriles, and the environmental conditions in which the F_1s are observed. Reddy and Rao (Reddy, 1996, personal communication) have identified a set of tester lines to distinguish A_1, A_2, A_3, and A_4. Similar studies have been reported by others (Worstell et al., 1984; Schertz and Pring, 1982). The Indian scientists have compared the cytoplasms isolated in the U.S. with the cytoplasms isolated in India, and the following relationships were revealed (U.R. Murty, 1996, personal communication). G_1 (G_2-s, msG_1, G-1-G, G_1A, G_1A-A_3) are analogous to A_3 (Nilwa, IS1112). VZM-1 and VZM-2 are the same. M35-1 and M31-2 are similar. Hagpur A has milo cytoplasm. Restorers are difficult to find for the sterility-inducing cytoplasms identified in India.

The other approach to determine diversity among cytoplasms is molecular. RFLPs have been used to distinguish cytoplasms (Conde et al., 1982; Pring et al.,

1982), most prominently between plants with small anthers, e.g., A_1 and A_2, and those with large anthers, e.g., A_3, A_4, and 9E (Chen et al., 1993), although other distinctions have been made. The A_1/A_2 groups have not been distinguished from each other by mtDNA or ctDNA analyses, to date. The two cytoplasms are readily distinguished from A_3, A_4, 9_E, and several normal cytoplasms by numerous RFLPs.

A potentially important abnormality of the A_1 and A_2 cytoplasms and the A_5/A_6 groups is a deletion in the *rpoC2* chloroplast gene, which encodes the B" subunit of RNA polymerase. This deletion was not detected in the $A_3/A_4/9_E$ cytoplasms or in a number of normal cytoplasm lines. The observation that male-sterile versions of these cytoplasms share the "small anther" phenotype might be consistent with a sporophytic mode of restoration, assuming that microsporogenesis is interrupted early, leading to early collapse of the microspore, analogous to T cytoplasm maize.

Two unusual mtDNA open reading frames, identified as specific to the IS1112C cytoplasm (A_3), might be related to CMS (Tang et al., 1996a). Both configurations resulted from duplication/ recombination events, common in CMS-related genes in many other species. One candidate open reading frame, *orf30*, was generated by recombination events involving the obligate gene *atp6* and sequences of unknown origin. Fertility restoration has no effect on transcription.

A more interesting candidate is *orf107*, which resulted from duplication/recombination with the obligate gene *atp9*. The amino terminus of *orf107* is highly similar to that of *atp9*. The carboxy terminus is highly similar to that of an open reading frame, *orf79*, suspected to cause CMS in the Chinsurah Boro II cytoplasm of rice. Most interestingly, fertile or partially fertile lines are characterized by a transcript processing event that cleaves *orf107* transcripts within the gene, which may dramatically reduce gene product abundance. Such an effect might parallel the behavior of maize mitochondrial *T-urf13* in plants restored to fertility. Leaver and colleagues (Bailey-Serres et al., 1986a,b) showed that the IS1112C ($_A3$) cytoplasm in a maintainer line synthesizes a 12 kD protein, which is the approximate predicted size of the *orf107* gene product, and that this protein is greatly reduced in the male-fertile IS1112C line.

Pring and colleagues have proposed that restoration of the A_3 cytoplasm is gametophytic. All plants of F_2 or BC_1 (A3Tx398 (A3Tx398 × IS 1112C)) lines, which are partially or fully restored, carry the *orf107* transcript processing activity, leading to the possibility that the nuclear gene conferring this activity functions as an *Rf* gene, or is tightly linked to an *Rf* gene. They have examined over 150 individual plants in which segregation could have occurred, and all are partially/fully restored and have the processing activity. A second, independent gene has been identified in segregants from the cross (A3Tx398 × IS 1112C) Tx398, and segregation for pollen stainability suggests a third gene.

Consistent with a gametophytic mode are observations of iodine stainability of pollen in sterile or partially restored lines. Segregation patterns for stainability within the population of an anther are

consistent with Mendelian segregation and a possible three-gene model. It is clear that pollen abortion occurs very late in development.

The environment has an effect on the expression of sterility/fertility, more with some cytoplasms than with others. The same precautions and tests practiced with the cytoplasm initially used also are necessary with the alternate cytoplasms. Plants with A_3 cytoplasm grown in the greenhouse during the winter, without supplemental light, are more sterile than identical plants in the field. A lower percent stainability of pollen was obtained in F_1s or segregating F_2s in the greenhouse. All these plants have the *orf107* processing activity in somatic cells, pointing toward the remaining two/three genes, or altered expression of the processing activity in anthers (D.R. Pring, 1996, personal communication). Murty (1993) has proposed a system of hybrid production relying on the environment to make the female line fertile in selected plantings for seed production.

Leaver and colleagues (Bailey-Serres et al., 1986a,b) and other reports reviewed by Pring et al. (1995) established that the A_4 and 9_E cytoplasms include an abnormal form of the mitochondrial gene *cox1*. In these cytoplasms, an insertional event generates a longer gene than for milo cytoplasm, and identification of the gene product verifies that $A_4/9_E$ *cox1* is indeed larger than *cox1* in milo cytoplasm. The altered *cox1* represents an important consideration as potentially related to CMS in these two cytoplasms. Examinations of the expression of the *cox1* protein in anthers should be done.

A_4 and 9_E have been distinguished by RFLP analysis (Xu et al., 1995). These cytoplasms also share several mtDNA RFLPs that distinguish them from all other cytoplasms examined to date, including polymorphism for the gene *atp9* (Yan and Pring, 1996, personal communication). A report by Sivaramakrishnan et al. (1996) is in press on the characterization of the A_4 cytoplasm.

Nuclear Genes

The nuclear/cytoplasm genetic interaction is varied. In some instances, apparently a single dominant nuclear gene restores fertility, and in others, as many as two or more major genes and several modifiers are involved in restoration of fertility and, conversely, in stability of sterility. Because of this complexity and diversity, the development of females with stable sterility and males with dependable restoration of fertility is difficult. We have a project in progress to map the nuclear genes that control the interaction with the cytoplasm to control male sterility/fertility. Our intent is to develop probes that can be used in marker-assisted selection breeding of parents.

Use of Cytoplasms

Diverse cytoplasms are being researched by ICRISAT, country scientists, and private breeders. The milo A1 cytoplasm is the main cytoplasm used to develop male-sterile female parents, but other cytoplasms are used in a more limited way by some breeders. Many breeders have put their elite female parents into A_2 cytoplasm as insurance against the possibility of a hazard associated with A_1. Others see alternate cytoplasms as a way

to make female parents of local cultivars. A few breeders are actually developing hybrids with A_2 cytoplasm. For example, in China two high-yielding hybrids of females with A_2 cytoplasm crossed by Chinese male parents are in production on 100,000 ha (Niu, et al., 1996, personal communication). Some breeders have said they are using other cytoplasms as well, although identities were not disclosed.

When choosing to use a cytoplasm other than milo, one should consider the advantage to be greater than the extra care needed to work with more than one cytoplasm. It is important to have good molecular markers to distinguish cytoplasms used in breeding and hybrid seed production.

CMS in Pearl Millet

Cytoplasmic-nuclear male sterility was first documented in pearl millet by Burton (1958). A_1, released by Burton (1965), has been the most widely used cytoplasm for producing commercial hybrids. Tift 23A was developed as a female parent with A_1 cytoplasm and became the seed parent in India for the first two millet hybrids released. Even today, A_1 cytoplasm is used most often to make male-sterile female parents of hybrids. Pearl millet yields in India were rather stagnant until 1962. With the advent of hybrids, production more than doubled. Additional sterility-inducing cytoplasms have been identified in pearl millet.

The five distinct cytoplasms (A_1 to A_5) reported in pearl millet have been distinguished mainly by restoration and maintainer relationships when crossed by known sterility maintainer and fertility restorer-lines (Kumar and Andrews, 1984; Hanna, 1989; Rai, 1995). In addition, other cytoplasms presumed to be different from A_1 to A_5, but not thoroughly documented or assigned a number, have been reported (Appadurai, et al., 1982; Aken'Ova, 1985; and Marchais and Pernes, 1985).

The A_1 cytoplasm was released in Tift 23, an inbred with good general combining ability. Since its release in 1965, the A_1 cytoplasm has been transferred to and studied in numerous genetic backgrounds (summarized by Kumar and Andrews, 1984). The A_1 cytoplasm has been the basis of commercial forage hybrids in the U.S., Australia, and South America and of the increasing grain hybrid production in India. The main weakness of the A_1 cytoplasm is that it produces fertile revertants at a frequency as high as 1.64 per 1000 inflorescences. Since an inflorescence can produce 1000 or more seeds, one can readily see how these fertile revertants can rapidly contaminate a CMS population. Rogueing is necessary to eliminate pollen-shedding plants from the CMS population.

The A_2 and A_3 cytoplasms (Burton and Athwal, 1967) have not been used commercially. Male sterility is very unstable in the A_2 cytoplasm, and various levels of pollen shedding have been observed (W.W. Hanna, 1996, personal communication). The A_2 and A_3 cytoplasms were extensively used in breeding lines at Punjab University, Ludhiana, but nearly all the A-lines were unstable for male sterility (K.N. Rai, 1996, personal communication).

The A_4 cytoplasm was transferred from a wild grassy subspecies, *P. glaucum* subspecies *monodii* (Maire) Brunken. The main advantage of this cytoplasm is that no male-fertile revertants have been observed (Hanna, 1989, 1996). Data also indicate that it will be more difficult to find restorers of fertility for the A_4 cytoplasm than for A_1. The stability of the male sterility induced by the A_4 cytoplasm will probably make it a popular cytoplasmic source to produce commercial hybrids in the future. At ICRISAT, the A_4 system is being used to develop male-sterile lines and a male-sterile population.

Rai (1995) assigned A_5 to a cytoplasm shown to be different from A_4. By implication, he assumed it was different from A_1, A_2, and A_3. Data indicate that it may be more difficult to restore A_5 than A_4.

Mitochondrial DNA restriction endonuclease fragment and maize mitochondrial gene probe hybridization patterns have been used to distinguish the cytoplasms in pearl millet (Smith and Chowdhury, 1989). Rajeshwari et al. (1994) characterized diverse cytoplasms of pearl millet by Southern blot hybridization and maize mitochondrial DNA probes. Smith and Chowdhury (1991) found that 4.7-kb, 10.9-kb, and 13.6-kb mitochondrial DNA fragments were associated with CMS. The cloned maize mitochondrial genes *rrn18*, *rrn5*, and *cox1* were located in the repeat regions of these fragments. Smith et al. (1987) compared mtDNAs of male-sterile lines, their male-fertile revertants, and the normal cytoplasm of the fertile maintainer lines. Their results revealed the presence of a unique 4.7-kb Pst1 fragment in the male-sterile line that was not detected in the revertant lines. A 9.7-kb fragment in the revertant line appeared to have replaced the 13.6-kb fragment.

The chimeric mitochondrial gene can be transcriptionally active and is expressed as a novel or variant mitochondrial protein that appears to be related to failure in mitochondrial function in the anther tapetum and microspores, and leads to pollen failure.

Nuclear Genes

Appa Rao et al. (1989) reported that out of 428 diverse accessions from 12 countries, 20.3% were maintainers, 7.5% were restorers, and 65.9% segregated for male fertility restoration when crossed onto a line with an A_1 cytoplasm. Raveendran and Appadurai (1984) observed that restorer genes and modifiers had an additive effect for better male fertility restoration. Rai and Hash (1990) observed fertility restoration to be complex and affected by the environment.

Use of Cytoplasms

The A_1 cytoplasm has been the only cytoplasm used for producing commercial forage and grain hybrids for pearl millet since 1965, when the first grain hybrid, HB-1, was released in India (Kumar and Andrews, 1984). Although the A_1 cytoplasm produces a low frequency of pollen shedders, these fertile revertants are rogued to keep pollen-shedding plants to a minimum in the A-line.

It appears that the A_4 cytoplasm will make an important contribution to hybrid production in the future, mainly because it does not produce fertile revertants. Male

fertility restorers are more difficult to find for this cytoplasm, but they are available. Male fertility restoration is not important for forage production. The first commercial hybrid using the A_4 cytoplasm was Tifleaf 3, a 3-way forage hybrid released in 1995 (W.W. Hanna, 1996, personal communication). Andrews and Rajewski (1995) released an A_4 restorer population for producing grain hybrids. The A_4 cytoplasm was made available to Indian scientists in 1986.

It is expected that the use of diverse cytoplasms of millet will increase. It will be important to make decisions based on expected advantages and to have molecular markers to distinguish cytoplasms.

Apomixis

Apomixis has the potential to become as important in production of sorghum and millet hybrids as is CMS. It was first reported in 1841 and has been studied in a number of species, including many tropical grasses (Asker and Jerling, 1992). Apomixis is a reproductive mechanism by which seed is produced from somatic cells that develop into embryos without fertilization. These cells and the resulting embryos have the same chromosomal and genetic constitution as the plant on which the seed is produced. Of the three basic types of apomixis (Bashaw, 1980), apospory is the only type confirmed in sorghum and millet. As a result of this type of apomixis, all progeny of a plant are derived from somatic cells and are therefore identical to the plant on which the seed is formed. This is true even if the plant on which the seed is formed is a hybrid and heterozygous.

Interest in apomixis for crop improvement increased in the 1950s with the discovery of a sexual plant in apomictic *Cenchrus*. This allowed initiation of a breeding program to produce apomictic cultivars (Bashaw and Hussey, 1992) by crossing the sexual plants by the apomictic plants, as males, and selecting apomictic progeny. The discovery of facultative apomixis in sorghum in the late 1960s (Rao and Narayana, 1968; Hanna et al., 1970) raised the potential for using apomixis in grain crops.

Interest in apomixis of millet and sorghum stems from the need for efficiency of breeding and seed production. With apomixis, one could explore all the available germplasm to make hybrids. Germplasm accessions could be crossed by apomictic male parents and superior apomictic lines could be selected in early generations. The efficiency of seed production would be especially important in some countries. Hybrid seed could be increased by self pollination without the need for making hybrid seed by crossing a female with a male parent. Presently, apomixis research is being pursued in both pearl millet and sorghum.

Apomixis in Pearl Millet

Apomixis is not known to occur naturally in pearl millet but it has been induced in mutation studies (Hanna et al., 1992). One mutant, a facultative apomict, produced various levels (average 26%) of maternal progeny. Another mutant, a female-sterile, produced aposporous embryo sacs but no seed.

Apomixis does occur in other species of *Pennisetum*, and a project was initiated

in the late 1970s to transfer apomixis from a wild apomictic *Pennisetum* species into pearl millet. A number of wild apomictic species were investigated, but the most success was obtained with hexaploid (2n=6x=54) *P. squamulatum* crossed with tetraploid (2n=4x=28) pearl millet (Hanna et al., 1992). This project has progressed to the BC6 with the production of a pearl millet-like plant with 29 chromosomes that produces 95% maternal progeny (W.W. Hanna, 1996, personal communication). One problem encountered since the BC3 is loss of seed set, from good initial seed development to about 5 to 15% at 8 to 10 days post-pollination. Research is now directed toward reducing the seed-set loss.

Apomixis in Sorghum

Apomixis also has been reported in sorghum. In the lines in which it is described, it appears to be of the apospory type, which would make it useful, if it could be perfected. The mechanism and frequency of apomixis were researched in detail in line R473, which resulted from a cross of IS 2942 × Aispuri in India (Rao and Narayana, 1968). R473 has been studied extensively by Murty (Murty and Rao, 1972; Murty et al., 1984). The facultative apomixis in this line is complicated by cross-sterility. The frequency of apomixis was studied by using the segregation of three monogenic traits (bloomless, shriveled endosperm, and plant color) in near isogenic lines. The highly variable frequency of apomixis in R473 does not make it a promising line in its present form. Apomixis in a grain crop such as pearl millet or sorghum would have to be nearly 100%. Recently it has been reported (Niu, et al., 1996, personal communication) that facultative apomixis has been recovered without cross-sterility in a progeny from crossing R473. A low frequency of apomixis has been reported in other lines, but no progress has been reported in improving them. Apomixis has been reported from tissue culture research in Russia (Elkonin et al., 1995).

Transfering apomixis from *Cenchrus ciliaris* to sorghum has been proposed. Efficient and reproducible tissue culture techniques for sorghum and *Cenchrus* have been standardized. Induction of suspension cultures and somatic hybridization have not yet been accomplished.

Use of Apomixis

Apomixis would have the greatest impact for producing pearl millet or sorghum hybrids in countries where hybrids are not now used. It would rapidly make available the increased yield and vigor of hybrids, regardless of the heterozygosity of the parental lines. Large numbers of different true-breeding hybrids from a cross between an apomictic line and a local landrace could be produced. Those selected could be rapidly increased and perpetuated without further crossing. The advantage of hybrid vigor and maintenance of local genetic diversity would be realized.

Apomixis also could have an impact for producing hybrids in countries where hybrids made on CMS females are used. Apomixis would lessen the time to produce hybrids for testing. It would not require CMS and the development and crossing of inbred lines to produce hybrid seed. Instead, hybrid seed could be produced on open-pollinated apomictic hybrids.

Summary

There are now available several distinct male sterility-inducing cytoplasms in both millet and sorghum. They provide a degree of potential protection against associated hazards. More importantly, they provide the diversity needed to exploit more fully the germplasm diversity in hybrid development and production.

In both millet and sorghum, there is a trend toward using the diversity in cytoplasms. In each program the costs will need to be compared to the potential benefits. Not all will want to, nor should, use diverse cytoplasms, but as some do, the diversity of hybrids should increase. As more than a single CMS system is used in a breeding program, it is important to have a method to definitively distinguish the cytoplasms.

Apomictic reproduction has been documented in both pearl millet and sorghum. Aposporous apomixis has been transferred to tetraploid pearl millet, resulting in the production of a high frequency of maternal types. Some seed retention problems, however, need to be solved. The facultative nature of apospory in sorghum requires either that the frequency is increased to a usable level or that a gene(s) from another genus is transferred to sorghum. Efforts are underway at a number of locations to clone the gene(s) controlling apomixis.

Apomixis could have a major impact on hybrid production in both pearl millet and sorghum. It would allow breeders to more rapidly and efficiently use the germplasm available in these species to produce hybrids.

References

Aken'Ova, M.E. 1985. Confirmation of a new source of cytoplasmic-genic male sterility in bulrush millet [*Pennisetum americanum* (L.) Leeke]. Euphytica 34:669-672.

Andrews, D.J., and J.F. Rajewski. 1995. Registration of NPM-3 grain pearl millet. Crop Sci. 35:1229.

Appa Rao, S., M.H. Mengesha, and C. Rajagopal Reddy. 1989. Identification, characterization and geographic distribution of male-sterility restorer and maintainer lines from diverse pearl millet germplasm. Euphytica 40:155-159.

Appadurai, R., T.S. Raveendran, and C. Nagarajan. 1982. A new male sterility system in pearl millet. Indian J. Agric. Sci. 52:832-834.

Appathurai, R. 1964. Diverse plasmons in male sterile sorghum. Madras Agricultural Journal 51:276-278.

Asker, S.E., and L. Jerling. 1992. Apomixis in plants. CRC Press, Boca Raton.

Bailey-Serres, J., L.K. Dixon, A.D. Liddell, and C.J. Leaver. 1986a. Nuclear-mitochondrial interactions in cytoplasmic male-sterile sorghum. Theor. Appl. Genet. 73:252-260.

Bailey-Serres, J., D.K. Hanson, T.D. Fox, and C.J. Leaver. 1986b. Mitochondrial genome rearrangement leads to extension and relocation of the cytochrome c oxidase subunit I gene in sorghum. Cell 47:567-576.

Bashaw, E.C. 1980. Apomixis and its application in crop improvement. *In* W.R. Fehr and H.H. Hadley (eds.) Hybridization of crop plants. American Society of Agronomy and Crop Science Society of America, Madison, WI.

Bashaw, E.C., and M.A. Hussey. 1992. Apomixis in *Cenchrus*. p. 1-4. *In* J.H. Elgin and J.P. Miksche (eds.) Proceedings of the apomixis workshop, February 11-12, 1992, Atlanta, GA. USDA-ARS, ARS-104.

Burton, G.W. 1958. Cytoplasmic male-sterility in pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Agron. J. 50:230.

Burton G.W. 1965. Pearl millet Tift 23A released. Crops Soils 17(5):19.

Burton, G.W., and D.S. Athwal. 1967. Two additional sources of cytoplasmic male-sterility in pearl millet and their relationship to Tift 23A. Crop Sci. 7:209-211.

Chen, Z, S. Muthukrishman, G.H. Liang, K.F. Schertz, and G.E. Hart. 1993. A chloroplast DNA deletion location in RNA polymerase gene *rpoC2* in CMS lines of sorghum. Mol. Gen. Genet. 236:251-259.

Conde, M.F., D.R. Pring, K.F. Schertz, and W.M. Ross. 1982. Correlation of mitochondrial DNA restriction endonuclease patterns with sterility

expression in six male-sterile sorghum cytoplasms. Crop Sci. 22:536-539.

Elkonin, L.A., H.K. Enaleeva, M.I. Tsvetova, E.V. Belyalva, and A.G. Ishin. 1995. Partially fertile line with apospory obtained from tissue culture of male sterile plant of sorghum [*Sorghum bicolor*)L.) Moench]. Annals of Botany 76:359-364.

Hanna, W.W. 1989. Characteristics and stability of a new cytoplasmic-nuclear male-sterile source in pearl millet. Crop Sci. 29:1457-1459.

Hanna, W.W. 1996. Registration of cytoplasmic male-sterile inbred Tift $85D_2A_4$ pearl millet. Crop Sci. 36:824.

Hanna, W.W., M. Dujardin, P. Ozias-Akins, and L. Arthur. 1992. Transfer of apomixis in *Pennisetum*. p. 30-33. *In* J.H. Elgin and J.P. Miksche (eds.) Proceedings of the apomixis workshop, February 11-12, 1992, Atlanta, GA. USDA-ARS, ARS-104.

Hanna, W.W., K.F. Schertz, and E.C. Bashaw. 1970. Apospory in *Sorghum bicolor* (L.) Moench. Science 170:338-339.

Jones, H.A., and G.N. Davis. 1944. Inbreeding and heterosis and their relation to the development of new varieties of onions. U.S. Dept. Agric. Tech. Bull. 874:1-28.

Jones, H.A., and S.L. Emsweller. 1937. A male sterile onion. Proc. Am. Soc. Hortic. Sci. 34:582-585.

Kumar, K.A., and D.J. Andrews. 1984. Cytoplasmic male sterility in pearl millet [*Pennisetum americanum (L.) Leeke): A review. Adv. Applied Biology 10:113-143.*

Marchais, L., and J. Pernes. 1985. Genetic divergence between wild and cultivated pearl millets (*Pennisetum typhoides*). I. Male sterility. Z. Pflanzenzeucht 95:103-112.

Murty, U.R. 1993. Milo and non-milo cytoplasms in *Sorghum bicolor* (L.) Moench. IV. Commercial production and utilization of uniline CMS systems. Crop Improv. 20:190-196.

Murty, U.R., P.B. Kirti, M. Bharathi, and N.G.P. Rao. 1984. The nature of apomixis and its utilization in the production of hybrids ("Vybrids") in *Sorghum bicolor* (L.) Moench. Z. Pflanzenzuech 92:30-39.

Murty, U.R., and N.G.P. Rao. 1972. Apomixis in breeding grain sorghums. p. 517-523 *In* N.G.P. Rao and L.R. House (eds.) Sorghum in the seventies. Oxford and IBH Publ. Co., New Delhi.

Pring, D.R., M.F. Conde, and K.F. Schertz. 1982. Organelle genome diversity among male sterile sorghum cytoplasms. Crop Sci. 22:414-421.

Pring, D.R., H.V. Tang, and K.F. Schertz. 1995. Cytoplasmic male sterility and organelle DNAs of sorghum. p. 461-495. *In* C.S. Levings III and I.K. Vasil (eds.) The molecular biology of plant mitochondria. Kluwer Academic Publishers, Dordrecht.

Rai, K.N. 1995. A new cytoplasmic-nuclear male sterility system in pearl millet. Plant Breeding 114: 445-447.

Rai, K.N., and C.T. Hash. 1990. Fertility restoration in male sterile x maintainer hybrids of pearl millet. Crop Sci. 30:889-892.

Rajeshwari, R., S. Sivaramakrishnan, R.L. Smith, and N.C. Subramanyam. 1994. RFLP analysis of mitochondrial DNA from cytoplasmic male-sterile lines of pearl millet. Theor. Appl. Genet. 88:441-448.

Rao, N.G.P. 1962. Occurrence of cytoplasmic-genetic male sterility in some Indian sorghums. Indian Journal of Genetics and Plant Breeding. 22:257-259.

Rao, N.G.P., and L.L. Narayana. 1968. Apomixis in grain sorghum. Indian J. Plant Breed. 28:121-127.

Raveendran, T.S., and R. Appadurai. 1984. Genetic complementation in fertility-restorer genes in pearl millet. Indian J. Agric. Sci. 54:884-887.

Ross, W.M., and H.L. Hackerott. 1972. Registration of seven iso-cytoplasmic sorghum germplasm lines. Crop Sci. 12:720.

Schertz, K.F., and D.R. Pring. 1982. Cytoplasmic sterility systems in sorghum. p. 373-383. *In* L.R. House, L.K. Mughogho, and J.M. Peacock (eds.) Sorghum in the eighties. Proc. of the international symposium on sorghum. ICRISAT, Pantancheru, A.P. India.

Schertz, K.F., and J.R. Ritchey. 1977. Cytoplasmic-genic male sterility systems in sorghum. Crop Sci. 18:890-893.

Sivaramakrishnan, S., S. Konnon, and B.V.S. Reddy. 1996. Characterization of the A_4 cytoplasmic male sterile lines of sorghum using RFLP of mt DNA. Euphytica: in press.

Smith, R.L., and M.K.U. Chowdhury. 1989. Mitochondrial DNA polymorphism in male-sterile and fertile cytoplasms of pearl millet. Crop. Sci. 29(3):809-814.

Smith, R.L., and M.K.U. Chowdhury. 1991. Characterization of pearl millet mitochondrial DNA fragments rearranged by reversion from cytoplasmic male sterility to fertility. Theor. Appl. Genet. 81:793-799.

Smith, R.L., M.K.U. Chowdhury, D.R. Pring. 1987. Mitochondrial rearrangements in *Pennisetum* associated with reversion from cytoplasmic male sterility to fertility. Plant Mol. Biol. 9:277-286.

Stephens, J.C., and R.F. Holland. 1954. Cytoplasmic male-sterility for hybrid sorghum seed production. Agron. J. 46:20-23.

Tang, H.V., D.R. Pring, F.R. Muzza, and B. Yan. 1996a. Sorghum mitochondrial *orf25* and a re-

lated chimeric configuration of a male-sterile cytoplasm. Curr. Genetics 29:265-274.

Tang, H.V., D.R. Pring, L.C. Shaw, R.A. Salagar, F.R. Muzza, B.Yan, and K.F. Schertz. 1996b. Sorghum and rice share elements of an open reading frame associated with cytoplasmic male sterility. The Plant Journal 10: in press.

Tripathi, D.P. 1979. Characterization of diverse cytoplasmic genetic male steriles in sorghum [*Sorghum bicolor* (L.) Moench]. Ph.D. Thesis. Indian Agricultural Research Institute, New Delhi, India.

Webster, O.J., and S.P. Singh. 1964. Breeding behavior and histological structure of a nondehiscent anther character in *Sorghum vulgare* Pres. Crop Sci. 4:656-658.

Worstell, J.V., H.J. Kidd, and K.F. Schertz. 1984. Relationships among male-sterility inducing cytoplasms of sorghum. Crop Sci. 24, 186-189.

Xu, G.-W., Y.-X. Cui, K.F. Schertz, and G.E. Hart. 1995. Isolation of mitochondrial DNA sequences that distinguish male-sterility-inducing cytoplasms in *Sorghum bicolor* (L.) Moench. Theor. Appl. Genet. 90:1180-1187.

Breeding For Diverse Target Environments

P.J. Bramel-Cox*, G.A. Maciel, F. Zavala-Garcia,
M. Chisi, E.A. Weltzein, and E.O. Monyo

Introduction

The world population is increasing at a rapid rate while the rate of growth in food production has slowed, due, in part, to a shift to more marginal production environments because of the effects of urbanization, desertification, salinization, etc. This shift to marginal land requires that we carefully evaluate the effectiveness of our breeding programs to target increasingly diverse regions. Evans (1993) described two objectives for breeding programs that create a dilemma for future development: 1) globally-oriented public and commercial research programs must develop new cultivars with broad adaptation to a wide range of diverse environments, and 2) local farmers need new cultivars with reliable performance from year to year in a specific locality. This dilemma stems from the fact that breeding for broad adaptation could limit the potential for genetic gain in specific environments (Ceccarelli, 1989; Evans, 1993; Bramel-Cox, 1996).

Crop plants evolve in three distinct stages (Evans, 1993): initial domestication, adaptation to new environments, and increased selection for improved productivity of specific organs. Most of the selection during the first two stages focuses on improved adaptation to specific environments (Bramel-Cox et al., 1991). The focus of the third stage has been on broader adaptation to environments larger than the individual farmer's field. This focus may result in reduced emphasis on the specific use of the crop and a greater homogeneity in the improved crop.

The effectiveness of selection and associated changes brought about by domestication, broad adaptation, and increased yield potential has been well documented (Evans, 1993). Most studies show that improvements in both stress and non-stress conditions have been due to increase in yield potential, usually associated with increase in harvestable yield as a percentage of total biomass. Cecarrelli et al. (1996) discussed the theoretical basis of preferential adaptation that occurs when improved varieties are selected in the more favorable range of target environments. As a result of cross-over in adaptation, new varieties better adapt to the favorable target environments in a region and actually lose adaptation to the poorer target environments. This preferential adaptation has led to greater adoption of improved high-yielding cultivars in favorable conditions where access to the inputs that enhance genetics increase their benefits. Resource-poor farmers living in less favorable environments still

P.J. Bramel-Cox, Genetic Resources Division, ICRISAT, Patancheru P.O. 502 324, A.P. India; G.A. Maciel, UEP De Serra Telhada, IPA-56.900, Serra Talhada, PE, Brazil; F. Zavala-Garcia, Universidad Autonoma de Nuevo Leon, 2928 Playa Monalo Col. Primavera, Monterrey, N.L. Mexico; M. Chisi, Mt. Makulu Research Station, Private Bag 7, Chilanga, Zambia; E.A. Weltzein, Genetic Enhancement Division, ICRISAT, Patancheru P.O. 502 324, A.P. India; E.O. Monyo, SADC/ICRISAT/SMIP, Matopos Research Station, P.O. Box 776, Bulawayo, Zimbabwe. *Corresponding author.

depend on traditional varieties with their greater specific adaptation (Ezaguirre and Iwanaga, 1996).

Bramel-Cox (1996) and Evans (1993) emphasized the need to balance high yield, wide adaptability, and reliable performance in specific conditions in breeding program goals. Breeding programs need to better characterize the target region, develop a better strategy to allocate resources to test environments, develop the optimal population type to buffer against diverse environmental constraints, define the optimal selection criteria to enhance mean performance and reduce environmental sensitivity, improve trait identification for selection, and increase the use of genetic diversity within a crop species for specific adaptation to various stresses. In most cases, the source of improved specific adaptation is found within landrace populations of a crop species which have been farmer-selected over time (Eyzaguirre and Iwanaga, 1996). This paper investigates the potential benefits of each of these options in relation to breeding for broad adaptation across a variable target range, and looks at a new alternative, which would emphasize reliability using farmer participatory breeding or variety selection.

Characterization of Target Regions

The first goal of any analysis of G × E interaction for the target region of a breeding program is to delineate the regional grouping based on predictable attributes (Allard and Bradshaw, 1964). If these attributes are large-scale conditions such as irrigation potential, growing-season duration, or photoperiod response, they can be classified as separate target regions or macro environments (Yau et al., 1991; Ceccarelli, 1989). Various statistical procedures used to delineate or describe target regions of breeding programs include both cluster analysis, using various distance estimates and the product moment correlation coefficient, and pattern analysis, utilizing both classification techniques (such as cluster analysis) and ordination techniques (such as principal coordinate analysis) (Bramel-Cox, 1996).

Cluster analysis is useful for defining environments that differ for the genotype response and for minimizing the interaction component. Westcott (1986) criticized the use of cluster analysis to classify environments or genotypes because it puts a specific structure on a data set without a full understanding of its actual basis or even whether it exists. In addition, there are many possible dissimilarity measures and clustering strategies, and the use of any may result in a different grouping. Instead, Westcott (1986) suggested the use of principal coordinate analysis to quantify the relationship between groups and to superimpose the results on a minimum spanning tree for identifying dissimilar genotypic or environmental groups.

Pattern analysis can be used to delineate further those environments that identify genotype responses fitting the specific objectives of a breeding program, by determining an environment's contribution to the classification and ordination of the lines' performance (Shorter et al., 1977). Several methods to enhance the use of the pattern analysis with various data transformation techniques have been proposed. The best of these is a stand-

ardization technique to determine the relationship of any single environment to the long-term average using a set of representative cultivars (Fox and Rosielle, 1982a,b). The number of genotypes needed to describe a consistent environmental classification depends on the strength of the pooled genetic correlation between environments (Bull et al., 1994). Alternatively, Ivory et al. (1991) used the G × E deviation matrix to allow separation of environments based on ability to discriminate among genotypes.

Another alternative to cluster analysis is to group environments or genotypes using the shifted multiplicative model (SHMM), which is a step-down method based on separability of genotype effects (Cornelius et al., 1992; Crossa et al., 1995). This exploratory method differs from cluster analysis since it uses the entire data set and then subdivides based upon the presence of crossover interactions in the resulting subdivision. The final grouping identifies a set of environments with few or no crossover interactions; thus, the genotype effects are homogeneous within each group.

Strategies for Allocating Resources to Test Environments

Once the target range has been delineated, a commonly used criterion for identifying the best test sites is the heritability estimate. Allen et al. (1978) found the heritability estimate at the selection environment and the genetic correlation between the mean genotypic value at the selection and target environments would be better. Falconer (1989) described gain from selection in the target environment as a correlated response from indirect selection at the test environment. Thus, the value of a test site could be judged by the indirect response to selection for all the specific environments within a target region. The use of the relative efficiency of genetic gain from indirect selection in relation to direct selection at a specific environment has been demonstrated (Zavala-Garcia et al., 1992b).

Generally, all procedures that use various estimates of heritability and genetic correlation to determine the best set of test environments require a large set of multiple location-year trials, with at least a small set of consistent genotypes for the target region (Bramel-Cox, 1996). These analyses are retrospective, but can be useful in defining breeding strategies (Brennen et al., 1981). An early generation test is conducted at a limited number of sites selected to represent the range of all possible genotype interactions in the target region. In the advanced stages of testing, locations that better characterize specific adaptation are used to determine the optimal range for the improved cultivars. This strategy is practical for a target range with very large predictable differences in genotype responses, but not for the target areas described by Fox et al. (1985), Yau et al. (1991), and Zavala-Garcia et al. (1992b), given the unpredictable nature of G × E and our poor understanding of the physiological basis for differential genotypic responses (Blum, 1988). For these target environments, the best strategy is to better use variable selection environments to breed for stable or reliable responses and/or to use alternative population types. Excellent reviews of criteria used to select the best test environments and to optimize gain in widely defined target regions can be found in Blum (1988), Bramel-Cox (1996), and Evans (1993).

The use of stability parameters as direct estimates of sensitivity requires extensive testing in early generations, when the number of entries is high and seed supplies are low. The best allocation of resources in the critical earlier generations would be to identify a limited number of test sites that consistently represented the range of target conditions for the entire region. These multiple locations could be used to select for mean performance or sensitivity, using a criterion such as rank summation. In more advanced generations, these selections would be tested more widely to determine their adaptability for later recommendation or release (Fox et al., 1985; Yau et al., 1991; Brennan et al., 1981).

Optimal Population Development to Buffer Against Diverse Environments

If a set of target environments is characterized largely by seasonal fluctuation, it may be difficult to identify a set of test locations that will predictably select a single genotypic response, or the range of adaptations may be beyond the limits of any single genotype. Breeding programs that attempt to incorporate both specific adaptation to predictable environmental differences and adaptation to the more unpredictable transient fluctuations of the environment require careful evaluation of the optimal genetic systems to develop a "well-buffered" variety (Allard and Bradshaw, 1964). This buffering can be due either to developmental homeostasis of individual genotypes (individual buffering) or to genetic homeostasis between individuals in a variable population (population buffering) (Allard and Bradshaw, 1964). Varieties made up of pure lines or single-cross hybrids are genetically homogeneous populations that rely solely on individual buffering, whereas heterogeneous populations, such as mixtures of pure lines or double and three-way hybrids, rely on population buffering. In some variety types, such as open-pollinated synthetic varieties of cross-pollinated species like maize or pearl millet, both mechanisms are important.

Marshall and Brown (1973) predicted that mixtures would be of no advantage where the environments represented a fairly uniform target area and the components were highly adapted varieties. The stability and yield of mixtures of homozygous pure lines and heterogeneous bulks are influenced by both individual and population buffering. The benefits of population buffering and individual buffering also can be influenced by the degree of heterozygosity. The impact of heterozygosity has been documented for cross-pollinated species, such as maize or pearl millet, but is less important for self-pollinated crops, such as wheat or sorghum. Comparison of G × E interaction mean squares of homozygous versus heterozygous cultivars of various crop species reveals a general advantage for hybrids (Becker and Leon, 1988). On the other hand, the advantage of hybrids in sorghum results more from their higher yield potential than from wider adaptation (Blum et al., 1992).

Schnell and Becker (1986) described a design to separate the relative importance of heterozygosity and heterogeneity to yield and stability. They compared maize and sorghum. In both crops, only heterozygosity was important for yield, while heterozygosity and heterogeneity

were of nearly equal importance for stability. In general, the impact of both types of buffering was of greater importance in maize than in sorghum; thus, the relative importance of individual and population buffering could depend on the mating system of the crop and its previous evolution. For example, in pearl millet, a highly cross-pollinated crop, topcross hybrids between variable landraces and open-pollinated inbred male steriles allow optimal yield and stability from both heterogeneity and an increased level of heterozygosity (Mahalakshmi et al., 1992; Bidinger et al., 1994).

Selection Criteria to Enhance Mean Performance and Reduce Environmental Sensitivity

Gain from selection, realized by improved overall performance and adaptation, results from the efficiency of indirect selection at the specific selection environments for all environments that define the target area, as opposed to the gain that would be realized from direct selection for all the variable conditions that make up the target area (Falconer, 1989). Selection for broad adaptation can be equal to selection for specific adaptation, but is never greater (Wright, 1976). If the interaction of genotypes and environments is large, selection for broad adaptation would be disadvantageous, even with a large number of selection environments. The impact productivity levels of the selection environment on potential gain in the same and different environments has been evaluated in a number of studies with contradictory results (Atlin and Frey, 1990; Bramel-Cox, 1996).

Two types of selection occur with regard to contrasting environments: "synergistic" selection for high performance in high-productivity environments and for low performance in low-productivity environments, and "antagonistic" selection for high performance in low-productivity environments and for low performance in high-productivity environments (Falconer, 1990). For yield across environments, we are interested only in synergistic selection in high-productivity environments or antagonistic selection in low-productivity environments. Falconer (1990) defines the difference in performance under high- and low-productivity conditions as environmental sensitivity, and the effect of antagonistic and synergistic selection on changes in the mean and sensitivity as the "Jinks and Connally rule." Theoretically, this rule predicts that the overall expected response of antagonistic or synergistic selection will be asymmetrical; that is, $R_l + CR_h$ 1 $R_h + CR_l$, where R_l is the direct response from selection at low-productivity conditions, CR_h is the correlated response from selection at low-productivity environments for high-productivity environments, R_h is the direct response from selection at high-productivity environments, and CR_h is the correlated response from selection at high-productivity environments for low-productivity environments. If more than one environment is involved, it also would include the correlated response at all other test sites from selection at one site. This asymmetrical response would be expected for both mean and sensitivity; thus, only one type of selection would be the most effective over all conditions.

Realized gains from direct and indirect selection in low-, medium-, and high-yield environments for drosophila (Paleolog and Maciejowski, 1991), barley

(Ceccarelli and Grando, 1991a, b), oats (Atlin and Frey, 1990), maize (Johnson and Gaedelman, 1989), and sorghum (Marinesco, 1992; Chisi, 1993) were tabulated, and the average mean responses to antagonistic and synergistic selection were compared for each of these selection trials (Bramel-Cox, 1996). The average response of the mean to selection is the sum of the direct response to selection in a specific environment and the gain from indirect selection at all other types of environments, divided by the total number of environments (Falconer, 1990). As Falconer predicted, the responses from antagonistic selection and synergistic selection are not equal. The relative advantage of one type of selection over the other depends on the organism and the range of selection environments for all studies (Falconer, 1990; Bramel-Cox, 1996).

The sorghum production area of Kansas and Nebraska is characterized by large G × E interactions because of large seasonal fluctuations. Categorizing environments as low-, medium- or high-yielding (Ceccarelli and Grando, 1991a), the average relative efficiency of predicted gain from indirect selection was compared to that from direct selection for KP9B C_0, and after one cycle of S_1 family selection under good (KP9B C_1 [M]) and poor (KP9B C_1 [GC]) conditions (Zavala-Garcia et al., 1992b; Marinesco, 1992). In the base population, KP9B C_0, the indirect predicted response to selection was low compared to the direct predicted response, even within groupings of similar environments. Yet in both the low- and high-yielding environments, the average relative efficiency was higher within than between all groups. This was not as evident in the medium group, where the relative efficiency was similar across all groups.

This impact of selection in one type of environment on the breadth of adaptation to different types of conditions also can be seen in a comparison of the number of S_1 families that were high-yielding across all test sites in cycles 1 and 2 (Marinesco, 1992; Maciel, 1996). In the base population, KP9B C_0, 18% of the top 20 families were highest in all six environments, whereas in the two selected cycles, KP9B C_1 (M) and KP9B C_1 (GC), 22% and 15% of the top families were highest overall. The slightly greater increase in gain per cycle from antagonistic selection demonstrates the increased frequency of broadly adapted lines obtained from this type of selection. Scott et al. (1994) found 25-50% of the top ten percent of the best soybean lines over all were identified from high-yielding test sites while 50-75% were identified from low-yielding tests.

Paleolog and Lorkiewicz (1991) evaluated *ebony* drosophila flies selected for improved fecundity in either optimal conditions or alcohol-stress conditions under heat stress. Based upon heterosis between the two divergent selected populations, they found that these two populations were different after 28 generations of selection under optimal and stress conditions, due to different genetic architectures for the same quantitative trait. Antagonistic selection under stress conditions resulted in wider adaptation of the population. Realized gain from selection is a product of the genetic properties of the base population, the kind of selection environment, and the cumulative history of previous selection, either artificial

or natural (Paleolog and Maciejowski, 1991; Paleolog and Lorkiewicz, 1991). These similar results are reported for the two cycles of selection evaluated by Maciel (1996) but to a lesser degree, given the shorter number of cycles.

Falconer (1990) concluded that the total response to selection results from changes in both mean and sensitivity. He described this total response as $R_T = R_m \pm \frac{1}{2}DR_s$, where R_m is the response of the mean, D is the difference in performance between environments in the original population, and R_s is the response of the sensitivity. The impact of changes in sensitivity can be either positive or negative and the magnitude depends on the relative differences between environments (D). If differences are wide, D will be large and R_s will be more important than if D is small. Thus, the impact of changes in sensitivity increases as the diversity of the target region increases. The response of sensitivity is defined as the difference between correlated response and direct response relative to overall differences in the environments, i.e., $(CR_H\text{-}R_L)/D$ for antagonistic selection, and $(R_H\text{-}CR_L)/D$ for synergistic selection. Antagonistic selection will decrease sensitivity, and synergistic selection will increase it if the sum of the direct response, $R_H + R_L$, is greater than the sum of the correlated response, $CR_H + CR_L$. In all the examples given in Bramel-Cox (1996), antagonistic selection resulted in reduced sensitivity, regardless of the impact on response of the mean. Using Falconer's formula, the total response (R_T) to antagonistic selection is equal to the correlated response in high-productivity environments from selection in low-productivity environments (CR_H). The R_T for synergistic selection is equal to the direct response to selection at the high-productivity environment (R_H); thus, the difference between total responses from synergistic selection and antagonistic selection is equal to the difference between the correlated response and direct response in high-productivity environments. For the total response to be greater from antagonistic selection, the response for sensitivity also would have to be positive.

Maciel (1996) evaluated the response of the mean, response of environmental sensitivity, and the total response of sorghum S1 lines derived from a population after two cycles under stress (GC) and nonstress (M) conditions. The results of this analysis are given in Table 1. In this study, antagonistic selection resulted in a greater response to the mean in both the population and the top ten families. Selection under stress conditions (antagonistic) also resulted in increased sensitivity in the population and an increase in the total response to selection when compared to the original population and the cycles selected under non-stress conditions (synergistic). The AMMI analysis was used to describe the complexity of the interaction of the selected cycles in comparison to the C_0. The original population had one significant principal component in the interaction matrix, as did the cycle selected at the stress site, whereas those selected under non-stress conditions had three significant components. Selection under stress had a more simplified pattern of interaction between the lines and environments. Thus in this study, unlike all the studies reported in Bramel-Cox (1996) and Falconer (1990), antagonistic selection resulted in increased sensitivity or no change from the original population as

Table 1. The response of the mean, response of environmental sensitivity, and the total response to selection among S1 families after two cycles under stress (GC and nonstress (M) conditions and in the top 10 families tested in 1993 and 1994 (Maciel, 1996).

Source	C2GC	C2MD	C0
	Response of the mean		
1993 S1	4132	3764	3732
1994 S1	4611	4578	3691
1993 Top Families	5493	5278	3851
1994 Top Families	6014	5775	5041
	Response of sensitivity		
1993 S1	0.91	0.80	1.00
1994 S1	1.21	1.07	1.00
1993 Top Families	1.00	0.80	1.00
1994 Top Families	0.99	0.95	1.00
	Total response		
1993 S1	4960	4492	4642
1994 S1	5956	5767	4802
1993 Top Families	6735	6272	5093
1994 Top Families	7217	6930	6256

compared with synergistic selection. If the main interest of a breeding program is to maximize selection response under optimal conditions and to reduce sensitivity, these goals may be very difficult to achieve (Falconer, 1990). The key to progress toward both goals will be to determine the relationship between the mean and sensitivity and select for both simultaneously, or to use a plan that selects indirectly for one or the other criterion.

Falconer (1990) described the correlation between the mean and sensitivity, r_{ms}, and its impact on the total response to antagonistic or synergistic selection. He concluded that antagonistic selection theoretically results in reduced sensitivity, but its impact on the mean is not predictable (see also Bramel-Cox, 1996). Falconer illustrated four possible configurations of four genotypes with different sensitivities and means. If the genetic correlation between environments is positive, then either type of selection will improve the mean in both environments, because the same genotype is best in both, and sensitivity will remain the same, regardless of the magnitude and direction of r_{ms} or the magnitude of genetic variance in each environment. If the genetic correlation between environments is negative and r_{ms} is positive, then antagonistic selection will reduce or not change performance in the high-productivity environment, whereas sensitivity will be reduced. Alternatively, if r_{ms} is negative, and the genetic variance under the low-productivity environment is greater than under the high-productivity environment, antagonistic selection would lead to $R_L \cong CR_H$ and reduced sensitivity. The most common configurations for a typical range of a crop will be either those in which no crossovers occur in a narrow range, as in the first example, or those in which crossovers occur in the lower range. Thus, antagonistic selection would either not change or reduce performance in the high-productivity environments.

Rosielle and Hamblin (1981) evaluated two alternative procedures to select for performance in stress and non-stress en-

vironments simultaneously. Their focus was on two selection criteria: mean productivity and tolerance. Zavala-Garcia et al. (1992a) defined tolerance in the sorghum population KP9B using the squared Euclidean distances among the eight test environments for each genotype. The relative efficiency of indirect selection with this estimate of tolerance (DT) was very poor in relation to direct selection. Mean productivity was defined using only the two extreme environments (MBW) or two extreme and one intermediate environment (MBIW). A Smith (1936)-Hazel (1943) index was developed, in which environments were selected and weighed to optimize gain across the range of the target area (Zavala-Garcia et al., 1992a). Comparison of the relative efficiency of indirect vs. direct selection for these various criteria in S1 families in KP9B (Zavala-Garcia et al., 1992a) and in full-sib families in KP9B (Chisi et al., 1996) showed that in both population types, the use of mean productivity or selection indices was superior to the use of any single environment or the mean over all the various selection environments.

After reviewing relationships between various estimates of stability, Becker and Leon (1988), Lin et al. (1986), and Leon and Becker (1988) concluded that the best estimate of stability or responsiveness was the linear regression coefficient. This was true despite its many faults, described by these authors as well as Westcott (1986). To overcome these deficiencies, a number of other alternatives have been suggested, including the use of nonparametric measures (Nassar and Hühn, 1987) and pattern analysis (Byth et al.,1976), which involves both classification and ordination techniques. Zobel et al. (1988) described the application of an additive and multiplicative interaction model to the analysis of the main effects and G × E interaction of an analysis of variance. Crossa et al. (1988) compared stability using modified linear regression analysis (Verma et al., 1978) and a spatial method using principal coordinate analysis (Westcott, 1987). The analysis of crossover G × E interactions was described by Gregorius and Namkoong (1986), Baker (1988), and Seyedsadr and Cornelius (1992). Cornelius et al. (1993) demonstrated the application of the shifted multiplicative model (SHMM) described in Seyedsadr and Cornelius (1992). In all the multivariate procedures described, comparison of the genotypes is not as directly quantifiable as the stability parameters described by Becker and Leon (1988) or Lin et al. (1986), nor is the optimal response pattern as simply described. The use of these techniques requires a much better understanding of the basis for differences in the environments and the genotypes' sensitivity to these differences — or the differences between dealing with the G × E interaction using a biometrical approach versus a stress physiological approach (Blum, 1988). Our application of statistical tools to breed for broader adaptation clearly is limited, and progress ultimately will require a better understanding of the physiological basis of the interaction.

The application of multivariate procedures, such as AMMI (Zobel et al., 1988), SHMM (Cornelius et al., 1993), or principal coordinate analysis (Crossa et al., 1988), could be useful to delineate genotypes with desirable responses for selection and cultivar recommendations. Chisi et al. (1996) defined stability as a geno-

type with above average grain yield at all test sites. One hundred full-sib families of KP9B were tested at six environments, and the G × E matrix was partitioned using the AMMI procedure. The three principal component scores, which accounted for about 70% of the G × E variance, were clustered into five groups of genotypes. These five groups were characterized for yield, flowering date, and plant height at the six environments. One group was found to be fairly consistent in its performance across the environments, and genotypes selected from this group would be expected to be better adapted across the target region. This procedure would allow the analysis of the significant portion of the G × E without the noise in the data set. The clusters represent types of responses to the different selection environments. If broad adaptation is defined as the product of a combination of specific adaptations (Ceccarelli, 1989), then selection among these clusters would allow a specific type of response to be targeted. Selection within the desirable cluster for the best performance would optimize the mean for that target range. Selection for specific types of responses was not equivalent to selection using mean productivity, rank summation, or a selection index (Chisi et al., 1996).

Zavala-Garcia et al. (1992b) calculated a Smith-Hazel index using yield and the regression coefficient (b) or yield and the first principal component score (PC). They also selected for both yield and stability using independent culling at a 25% intensity. Both selection indices were more efficient than indirect selection for the stability parameters alone, except in the poorest environment. When the numbers of families in common with those selected directly were compared in the eight environments, the indices were superior to those from independent culling and equal to the two measures of mean productivity and rank summation, except in the poorest environment. Although indirect selection for a wide range of unpredictable environments improved most with the use of an index containing both yield and a stability parameter, the gain over mean productivity or a rank summation using only a subset of environments did not justify the extra resources needed to estimate stability (Zavila-Garcia et al., 1992b).

Barah et al. (1981) reported on the application of risk aversion to breeding for genotypes that perform well overall and have reliable yield for farmers at specific locations — in other words, a balance of mean yield, adaptability, and reliability (Evans, 1993). Witcombe (1988) compared the use of various criteria to select for mean yield and adaptability. Eskridge (1990) suggested the use of the safety-first decision-making procedure to develop an index that weights stability and mean yield. Ceccarelli and Grando (1991b) demonstrated the use of safety-first models and concluded the indices derived could select genotypes with low probability of failure and an acceptable economic threshold in the poorest conditions. In none of these examples would the genotype selected for both mean yield and stability have the best yield under the best conditions.

An alternative for improving the efficiency of selection for tolerance to the various types of stresses that characterize a target region, as well as for yield potential under the more favorable environ-

ments, is to use molecular markers to select indirectly for stress tolerance, yield potential, or both. Paterson et al. (1991) discussed the use of "quantitative trait loci," or QTL mapping, to select indirectly for specific attributes. Paterson et al. (1991) and Hayes et al. (1993) demonstrated that QTLs could show the same range of sensitivities to environments as yield itself. Two classes of genetic markers were identified. The first included constant QTLs, having no environmental interactions; the second class included environment-specific QTLs. Use of genetic markers would give enhanced opportunities to combine both broad adaptation and site-specific adaptation without the need to test in all specific conditions. The key to progress for this strategy is carefully identifying the environment-specific QTLs and determining their impact on both adaptation and yield potential. Identification requires testing under specific conditions to link markers consistently with a trait related to specific adaptation or performance.

Trait Identification for Use in Selection

Wallace et al. (1993), Blum (1988), and Evans (1993) described yield as the result of three physiological components: 1) net accumulated biomass, 2) harvest index, and 3) time needed to develop to harvest maturity. Each of these components is the result of numerous biochemical and physiological processes. The components of yield, environmental potential, and duration of the growing season ultimately determine the pathway to yield by modifying or terminating the other processes (Wallace et al., 1993). In environments in which duration of season varies because of environmental constraints, the G × E interaction is due to the impact of these constraints on the timing of the physiological processes and their total duration. Blum (1988) and Ceccarelli et al. (1991) described this as the impact of location or year on the correlation between multiple traits and yield. This interaction makes it very difficult to identify single traits or even multiple complexes of traits that can be used as alternatives to select for yield under stress conditions or optimal conditions. Ceccarelli et al. (1991) gave an excellent example of the impact of trait associations and seasonal differences in defining the optimal genotype under variable conditions. Because of the complex nature of trait associations and the influence of environment and genetic background, most studies conducted to date on indirect selection criteria have little application in breeding programs (Ceccarelli et al., 1991; Blum, 1988).

In peanuts, the relationship between drought resistance and yield potential under optimal conditions depends on the drought pattern (Nagaswara Rao et al., 1989). These results could be interpreted as evidence that the breadth of adaptation required to combine resistance with some types of stresses and performance in optimal conditions is not genetically feasible. Ceccarelli et al. (1991) stated that it is "the variation in adverse conditions that is the real challenge and not the adverse conditions per se." Thus, although a single trait or genotype may be superior at one year or stress condition, those that are consistently superior across all the stress conditions are desirable. Nagaswara Rao et al. (1989) demonstrated this in peanuts with 12 known patterns of drought and 60 genotypes. In pearl millet, van Oosterom

et al. (1996a, b) described a procedure to initially characterize the pattern of water stress in a test site and use this information to identify the optimal genotypic response for selection. This process is consistent with the conclusion of Chisi et al. (1996).

An alternative procedure for identifying traits for indirect selection is to use a retrospective historical analysis of changes that have occurred through natural selection and artificial selection in a crop species. Blum (1988) and Evans (1993) both described the physiological changes that have resulted from selection for yield. Evans (1993) included an extensive review of this topic for the main physiological processes and their components. He found that the predominant improvements in yield potential have resulted from changes in regulatory processes that control patterns of partitioning and the timing of development. These components are related to harvest index and maturity (Wallace et al., 1993). No changes have been made in the efficiency of the major metabolic and assimilatory processes that result from changes in photosynthesis, respiration, translocation, or growth rate. Continued selection for yield potential under optimal conditions will only continue to alter these regulatory processes (Evans, 1993: Wallace et al., 1993). Continued selection for modifications in regulatory processes without increased efficiency in metabolic or assimilatory processes will result in improvement only if innovations in agronomy allow greater agronomic support of the crop to ameliorate environmental stresses (Evans, 1993). Changes in crop plants since domestication have resulted from empirical selection for yield, but the future may depend more on selection by design (Evans, 1993). Unfortunately, most of the research reviewed by Blum (1988), Evans (1993), Ceccarelli et al. (1991), and Wallace et al. (1993) has little application in designing the optimal genotype for stress and nonstress conditions. Evans (1993) stated "Empirical selection is an extremely powerful agent of change but selection by design may yet prove to be even more powerful when our understanding of the physiology of crop yield is more comprehensive than it is at present." Not only do we need to broaden our understanding of the physiology of yield, but we need to apply it to increase efficiency of selection for adaptation to a wide range of environmental conditions.

Use of Genetic Diversity and Participatory Variety Selection

Bramel-Cox (1996) concluded "Ultimately, genetic gain for broad adaptation will depend upon the more efficient identification and utilization of high levels of adaptation to specific constraints found in exotic germplasm. The transfer of specific traits or adaptations without a concurrent loss in yield potential will depend upon both the physiological trade-offs required for adaptation to those stresses and the efficient introgression of desired genes independent of any undesirable traits. This is one area in which the use of marker-assisted selection may allow better design and selection of optimal genotypes. The definition of an optimal genotype will require a much better understanding of the physiological basis of adaptation and its application to breeding. Although we have been very successful at developing new statistical procedures to quantify G × E interactions and identify those that are most relevant, there is a

limit to the progress to be made from these statistical approaches." This conclusion will be enhanced with a better understanding of the preferences given by farmers to grain yield and other traits used to design an optimal genotype. This is the objective of participatory variety selection and participatory plant breeding (Witcombe and Joshi, 1996).

The integration of all aspects of the plant, environment, and its interactions may develop broadly adapted genotypes that are still unacceptable. The identification and testing of a new variety does not always result in improved productivity, due either to its poor adoption because of certain quality, nutritional, and preference traits or to its preferential adaptation to the higher yielding range of the target region. An alternative approach, particularly for target environments in very marginal areas with resource-poor farmers, is to select or test more directly for these environments using participatory approaches (Ceccarelli et al., 1996; Sperling, 1996; Witcombe and Joshi, 1996)

Francis (1986) concluded that resource-poor farmers, who practice approximately 60% of the global agriculture and produce 15-20% of the world food in the most environmentally sensitive areas, have not benefited from the gains of the green revolution. Kelly et al. (1996) evaluated the basis for the lack of adoption of newly released pearl millet varieties in Rajasthan, an important but more marginal portion of the target environments for the pearl millet breeding programs at ICRISAT and in India. They found that traditional varieties were still of significant importance in the drier regions. A similar result has been reported by Friis-Hansen (1996), Rohrbach et al. (1995), and Franzen et al. (1996). In all these studies, a primary basis for non-adoption was the relatively heavy weight given by farmers to grain and straw yield in the more stressful years.

Future Research Options

If a target region had the configuration described by Falconer (1990), where the cross-over between antagonistic and synergistic selection occurred toward the lower-yielding environments, it would be difficult to breed for both (Ceccarelli et al., 1996). In general, there is a need to allocate more resources to breed specifically for these conditions. Optimizing yields under given environmental conditions is a radical departure from the conventional aim of plant breeding to optimize yields (Friis-Hansen, 1996). Three options for future research programs are: 1) to develop participatory plant breeding programs to better understand the constraints and their implications to the farmers in those specific regions, 2) to optimize the performance of varieties under low or no-input conditions, and 3) to increase the number of varieties developed.

Sperling (1996) described the need for a new conceptual model for a division of labor for future plant breeding programs. Plant breeders would generate new genetic variability, insure access to diverse germplasm, and screen for the minimum required criteria and resistance to abiotic and biotic stresses prevalent in the region. The farmers would take the breeder-developed material as a base to select varieties which would target the agronomic conditions and socioeconomic circumstances in the specific community or re-

gion. Various procedures could be used in a breeding program to link with selection by farmers for specific adaptation or traits (Witcombe and Joshi, 1996). The better of these procedures for self-pollinated crops involve cooperative selection from the early generations to the final release, or farmer selection in the early generations and breeder input in the final testing and release. For cross-pollinated crops, the improved composites could be given by the breeders to the farmer for mass selection to develop improved locally adapted varieties. A 1995 workshop was held on the general use of a participatory plant breeding program approach in comman bean (Kornegay et al., 1996) and rice (Sthapit et al., 1996). This group concluded there was a need in the future to link formal sector breeding with farmers for the breeding, variety selection, and conservation of plant genetic resources. There was an need to combine the best of scientist and farmer knowledge in research and development to maximize both agro-biodiversity and productivity for the future, especially for breeding for reliable varieties in the more marginal or unique target environments.

References

Allard, R.W., and A.D. Bradshaw. 1964. Implications of genotype-environment interactions in applied plant breeding. Crop Sci. 4:503-508.

Allen, F.L., R.E. Comstock, and D.C. Rasmusson. 1978. Optimal environments for yield testing. Crop Sci. 18:747-751.

Atlin, G.N., and K.J. Frey. 1989. Predicting the relative effectiveness of direct versus indirect selection for oat yield in three types of stress environments. Euphytica 44:137-142.

Baker, R.J. 1988. Tests for crossover genotype-environmental interactions. Can. J. Plant Sci. 68:405-410.

Barah, B.C., H.P. Binswanger, B.S. Rana, and N.G.P. Rao. 1981. The use of risk aversion in plant breeding: Concept and application. Euphytica 30:451-458.

Becker, H.C., and J. Léon. 1988. Stability analysis in plant breeding. Plant Breeding 101:1-23.

Bidinger, F.R., E. Weltzein, R.V. Mahalakshmi, S.D. Singh, and K.P. Rao. 1994. Evaluation of landrace topcross hybrids of pearl millet for arid zone environments. Euphytica 76:215-226.

Blum, A. 1988. Plant breeding for stress environments. CRC Press, Inc. Boca Raton, FL.

Blum, A., G. Golan, J. Mayer, B. Sinmena, and T. Obilana. 1992. Comparative productivity and drought response of semi-tropical hybrids and open-pollinated varieties of sorghum. J. Agric. Sci. (Camb.) 118:29-36.

Bramel-Cox, P.J., T. Barker, F. Zavala-Garcia, and J.D. Eastin. 1991. Selection and testing environments for improved performance under reduced-input conditions. p. 29-56. *In* D. Sleper, P.J. Bramel-Cox, and T. Barker (eds.) Plant breeding and sustainable agriculture: Considerations for objectives and methods. CSSA Special Publ. 18. ASA, CSSA, SSSA, Madison, WI.

Bramel-Cox, P.J. 1996. Breeding for reliability of performance across unpredictable environments. p. 309-339. *In* M.S. Kang and H.G. Gauch, Jr. (eds.) Genotype -by- environment interaction. CRC Press, Inc., Boca Raton, FL.

Brennan, P.S., D.E. Byth, D.W. Drake, I.H. DeLacy, and D.G. Butler. 1981. Determination of the location and number of test environments for a wheat cultivar evaluation program. Aust. J. Agric. Res. 32:189-201.

Bull, J.K., M. Cooper, and K.E. Basford. 1994. A procedure for investigating the number of genotypes required to provide a stable classification of environments. Field Crops Res. 38:47-56.

Byth, D.E., R.L. Eisemann, and I.H. DeLacy. 1976. Two-way pattern analysis of a large data set to evaluate genotypic adaptation. Heredity 37:215-230.

Ceccarelli, S. 1989. Wide adaptation: How wide? Euphytica 40:197-205.

Ceccarelli, S., E. Acevedo, and S. Grando. 1991. Breeding for yield stability in unpredictable environments: Single traits, interaction between traits, and architecture of genotypes. Euphytica 56:169-185.

Ceccarelli, S., and S. Grando. 1991a. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica 57:207-219.

Ceccarelli, S., and S. Grando. 1991b. Selection environment and environmental sensitivity in barley. Euphytica 57:157-167.

Ceccarelli, S., S. Grando, and R.H. Booth. 1996. Farmers and crop breeders as partners. International breeding programmes and resource-poor farmers: Crop improvement in difficult environ-

ments. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Chisi, M. 1993. Evaluation of selection procedures in multiple environments to identify parent lines for grain sorghum hybrids [*Sorghum bicolor* (L.) Moench]. Ph.D. diss. Kansas State Univ., Manhattan.

Chisi, M., P.J. Bramel-Cox, M.D. Witt, M.M. Claassen, and D.J. Andrews. 1996. Breeding for grain yield stability using full-sib family recurrent selection in sorghum. Crop Sci. 36: (In Press).

Cornelius, P.L., M. Seyedsadr, and J. Crossa. 1992. Using the shifted multiplicative model to search for "separability" in crop cultivar trials. Theor. Appl. Genet. 84:161-172.

Cornelius, P.L., D.A. Van Sanford, and M.S. Seyedsadr. 1993. Clustering cultivars into groups without rank-change interactions. Crop Sci. 33:1193-1200.

Crossa, J., P.L. Cornelius, K. Sayre, and J.I. Ortiz-Monasterio. 1995. A shifted multiplicative model fusion method for grouping environments without cultivar rank changes. Crop Sci. 35:54-62.

Crossa, J., B. Westcott, and C. Gonzalez. 1988. Analyzing yield stability of maize genotypes using a spatial model. Theor. Appl. Genet. 75:863-868.

Eskridge, K.M. 1990. Selection of stable cultivars using a safety-first rule. Crop Sci. 30:369-374.

Evans, L.T. 1993. Crop evolution, adaptation, and yield. Cambridge University Press, Cambridge, Great Britian.

Eyzaguirre, P., and M. Iwanaga. 1996. Farmer's contribution to maintaining genetic diversity in crops, and its role within the total genetic resources system. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Falconer, D.S. 1989. Introduction to quantitative genetics. p. 322-325. Third edition. Longman Scientific and Technical. Essex, England.

Falconer, D.S. 1990. Selection in different environments: effects on environmental sensitivity (reaction norm) and on mean performance. Genet. Res. Camb. 56:57-70.

Fox, P.N., and A.A. Rosielle. 1982a. Reducing the influence of environmental main-effects on pattern analysis of plant breeding environments. Euphytica 31:645-656.

Fox, P.N., and A.A. Rosielle. 1982b. Reference sets of genotypes and selection for yield in unpredictable environments. Crop Sci. 22:1171-1175.

Fox, P.N., A.A. Rosielle, and W.J.R. Boyd. 1985. The nature of genotype x environment interactions for wheat yield in Western Australia. Field Crops Res. 11:387-398.

Francis, C.A. 1986. Multiple cropping systems. Macmillian, New York.

Franzen, H., P. Ay, F. Begemann, J.A. Wadsack, and H. Rudat. 1996. Variety improvement in the informal sector: aspects of a new strategy. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Friis-Hansen, E. 1996. The role of local plant genetic resource management in participatory breeding. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Gregorius, H.R., and G. Namkoong. 1986. Joint analysis of genotype and environment effects. Theor. Appl. Genet. 72:413-422.

Hayes, P.M., B.H. Liu, S.J. Knapp, F. Chen, B. Jones, T. Blake, J. Franckowiak, D. Rasmusson, M. Sorrells, S.E. Ullrich, D. Wesenberg, and A. Kleinhofs. 1993. Quantitative trait locus effects and environmental intraction in a sample of North American barley germplasm. Theor. Appl. Genet. 87:392-401.

Hazel, L.N. 1943. The genetic basis for constructing selection indices. Genetics 28:476-490.

Ivory, D.A., S. Kaewmeechai, I.H. DeLacy, and K.E. Basford. 1991. Analysis of the environmental component of genotype x environment interaction in crop adaptation evaluation. Field Crops Res. 28:71-84.

Johnson, S.S., and J.L. Gaedelmann. 1989. Influence of water stress on grain yield response to recurrent selection in maize. Crop Sci. 29:558-564.

Kelley, T.G., P. Parthasarathy Rao, E. Weltzein R., and M.L. Purohit. 1996. Adoption of improved cultivars of pearl millet in an arid environment: Straw yield and quality considerations in western Rajasthan. Experimental Agric. 32:161-171.

Kornegay, J., J.A. Beltran, and J. Ashby. 1996. Farmer selections within segregating populations of comman bean in Colombia. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Léon, J., and H.C. Becker. 1988. Repeatability of some statistical measures of phenotypic stability- correlations between single year results and multi years results. Plant Breeding 100:137-142.

Lin, C.S., M.R. Binns, and L.P. Lefkovitch. 1986. Stability analysis: Where do we stand? Crop Sci. 26:894-900.

Maciel, G. 1996. Comparison of the effects of antagonistic versus synergistic selection for improved broad adaptation in a grain sorghum random-mating population Ph.D. Diss. Kansas State Univ., Manhattan.

Mahalakshmi, V., F.R. Bidinger, K.P. Rao, and D.S. Raju. 1992. Performance and stability of pearl millet topcross hybrids and their variety pollinators. Crop Sci. 32:928-932.

Marinesco, O.A. 1992. Effectiveness of selection under stress or low-stress environments for grain yield in a sorghum population [*Sorghum bicolor* (L.) Moench]. Ph.D. Diss. Kansas State Univ., Manhattan. (Diss. Abst. B. 53-1118).

Marshall, D.R., and A.H.D. Brown. 1973. Stability of performance of mixtures and multilines. Euphytica 22:405-412.

Nageswara Rao, R.C., J.H. Williams, and M. Singh. 1989. Genotypic sensitivity to drought and yield potential of peanuts. Agron. J. 81:887-893.

Nassar, R., and M. Hühn. 1987. Studies on estimation of phenotypic stability: Test of significance for nonparametric measures of phenotypic stability. Biometrics 43:45-53.

Paleolog, J., and M. Lorkiewicz. 1991. Selection for female fecundity in *Drosophila* test crosses and lines selected in different environments. II. Response to heat stress and top-crossing. J. Anim. Breed. Genet. 108:363-368.

Paleolog, J., and J. Maciejowski. 1991. Selection for female fecundity in *Drosophila* test crosses and lines selected in different environments. I. Response to selection. J. Anim. Breed. Genet. 108:355-362.

Paterson, A.H., S. Damon, J.D. Hewitt, D. Zamir, H.D. Rabinowitch, S.E. Lincoln, E.S. Lander, and S.D. Tanksley. 1991. Mendelian factors underlying quantitative traits in tomato: Comparison across species, generations, and environments. Genetics 127:181-197.

Rohrbach, D.D., E.S. Monyo, and A.B. Obilana. 1995. Variety release, seed production, and research impact in Southern Africa. International Sorghum Millet Newsletter. 36:35-41.

Rosielle, A.A., and J. Hamblin. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21:943-946.

Schnell, F.W., and H.C. Becker. 1986. Yield and yield stability in a balanced system of widely differing population structures in *Zea mays* L. Plant Breeding 97:30-38.

Scott, R.A., M. Champoux, and W.T. Schapaugh, Jr. 1994. Influence of environmental productivity levels and yield stability on selection strategies in soybean. Euphytica 78:115-122.

Seyedsadr, M., and P.L. Cornelius. 1992. Shifted multiplicative models for nonadditive two-way tables. Comm. Statist. B. Simul. Comput. 21:807-832.

Shorter, R., D.E. Byth, and V.E. Mungomery. 1977. Genotype x environment interactions and environmental adaptation. II. Assessment of environmental contributions. Aust. J. Agric. Sci. 28:223-235.

Smith, H.F. 1936. A discriminant function for plant selection. Ann. Eugenics 7:240-250.

Sperling, L.A. 1996. Results, methods and institutional issues in participatory selection: The case of beans in Rwanda. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Sthapit, B.R., K.D. Joshi, and J.R. Witcombe. 1996. Farmer participatory crop improvement. III: Participatory plant breeding, A case study for rice in Nepal. Experimental Agric. 32: (In Press)

van Oosterom, F.R. Bidinger, V. Mahalakshmi, and K.P. Rao. 1996a. Effect of water availability pattern on yield of pearl millet in semi-arid tropical environments. Euphytica 89:165-173.

van Oosterom, E.J., V. Mahalakshmi, F.R. Bidinger, and K.P. Rao. 1996b. Effect of water availability and temperature on the genotype-by-environment interaction of pearl millet in the semi-arid tropical environments. Euphytica 89:175-183.

Verma, M.M., G.S. Chahal, and B.R. Murty. 1978. Limitations of conventional regression analysis: A proposed modification. Theor. Appl. Genet. 53:89-91.

Wallace, D.H., J.P. Baudion, J. Beaver, D.P. Coyne, D.E. Halseth, P.N. Masaya, J.R. Myers, M.Silbernagel, K.S. Yourstone, and R.W. Zobel. 1993. Improving efficiency of breeding for higher crop yield. Theor. Appl. Genet. 86:27-40.

Westcott, B. 1986. Some methods of analysing genotype-environment interaction. Heredity 56:243-253.

Westcott, B. 1987. A method of assessing the yield stability of crop genotypes. J. Agric. Sci. 108:267-274.

Witcombe, J.R. 1988. Estimates of stability for comparing varieties. Euphytica 39:11-18.

Witcombe, J.R., and A. Joshi. 1996. Farmer participatory approaches for varietal breeding and se-

lection and linkages to the formal seed sector. *In* P. Eyzaguirre and M. Iwanaga (eds.) Participatory plant breeding. Proceedings of a workshop on participatory plant breeding. 26-29 July 1995, Wageningen, The Netherlands. IPGRI, Rome, Italy.

Wright, A.J. 1976. The significance for breeding of linear regression analysis of genotype-environment interactions. Heredity 37:83-93.

Yau, S.K., G. Ortiz-Ferrara, and J.P. Srivastava. 1991. Classification of diverse bread wheat-growing environments based on differential yield responses. Crop Sci. 31:571-576.

Zavala-García, F., P.J. Bramel-Cox, and J.D. Eastin. 1992a. Potential gain from selection for yield stability in two grain sorghum populations. Theor. Appl. Genet. 85:112-119.

Zavala-García, F., P.J. Bramel-Cox, J.D. Eastin, M.D. Witt, and D.J. Andrews. 1992b. Increasing the efficiency of crop selection for unpredictable environments. Crop Sci. 32:51-57.

Zobel, R.W., M.J. Wright, and H.G. Gauch, Jr. 1988. Statistical analysis of a yield trial. Agron. J. 80:388-393.

Sorghum Improvement Using Plant Tissue Culture

Roberta H. Smith*, S. Bhaskaran, Paul M. Hasegawa,
Ray A. Bressan, Keerti S. Rathore, and Ronny R. Duncan

Abstract

This paper reviews the tools of plant tissue culture and plant genetic engineering that have been used for crop improvement. These plant cell culture tools include cell culture regeneration systems which are a foundation to the other plant tissue culture techniques; anther culture for haploid and homozygous diploid production; embryo rescue for obtaining unique hybrids; somaclonal variation and cell selection to obtain cells tolerant to various stresses; and plant genetic engineering to insert traits such as insect and herbicide resistance. Specific examples of the use of these technologies in sorghum and pearl millet improvement programs are described and discussed. Views in regard to which of these technologies will have the highest potential for impact on sorghum improvement programs are discussed.

Techniques in plant cell culture and plant genetic engineering offer new approaches to the plant breeder to develop a wider range of useful cultivars. Indeed, crops are now in the farmer's field with delayed ripening genes, such as Flavr-Savr® tomatoes, Bollgard® cotton with insect resistance, BXN® cotton with herbicide resistance, cucurbits with virus resistance, and insect-resistant corn. The use of plant biotechnology has moved from the laboratory to commercial practice. Many more crop plants are due to be released in the next few years. The age of plant biotechnology is a reality. Unfortunately, the technology has not impacted improvement programs of all the crop plants; in particular, sorghum and pearl millet breeding programs have not yet benefited the way cotton, tomatoes, corn, and cucurbits have. The development of the technology in these other crops, however, will have an impact on accelerating the applications to sorghum and pearl millet breeding improvement programs.

Roberta H. Smith and S. Bhaskaran, Department of Soil & Crop Science, Texas A&M University, College Station, TX 77843; Paul M. Hasegawa and Ray A. Bressan, Center for Plant Environmental Stress Physiology, Purdue University, West Lafayette, IN 47907; Keerti S. Rathore, Crop Biotechnology Center, Texas A&M University, College Station, TX; and Ronny R. Duncan, Department of Crop & Soil Sciences, Georgia Agricultural Experiment Station, Georgia Station, Griffin, Georgia 30223-1797. *Corresponding author.

Cell Culture Regeneration

Fundamental to most plant cell culture applications to a particular crop species is the methodology to regenerate plants from cell cultures. Although it has become routine to regenerate plants from cultured tissue, the fact remains that only meristematic tissues respond to *in vitro* manipulations. Plant hormones and plant growth regulators have played a key role in the successful regeneration from cultured cells. Sorghum, once considered recalcitrant, is now amenable to manipulation *in vitro*. Immature embryos, young

leaf bases, shoot apex and immature inflorescences have been used in sorghum as explants for successful regeneration of plants (Bhaskaran and Smith, 1990). The choice of plant growth regulators in the culture medium, particularly the ratio of auxins and cytokinins, has played a major role in obtaining plants from cultured tissue. It also has been possible to obtain roots, shoots, or embryogenic callus from the same explant by varying the ratio of auxin to cytokinin in the culture medium. Moreover, the ratio of auxin to cytokinin required to obtain plant regeneration can vary with different cultivars. This suggests that genotypic differences in the regeneration potential of immature explants probably reflect differences in endogenous levels or activities of hormones within the explants. Despite repeated efforts, plant regeneration from single cells or protoplasts has not been realized in sorghum, although protoplasts could have been obtained from immature tissues (unpublished observations).

Pearl millet [*Pennisetum americanum* (L.) K. Schum.] regeneration also has been reported (Vasil and Vasil, 1982). Embryogenic cultures from pearl millet immature inflorescense segments gave rise to plants.

Fundamental Studies Using Tissue Culture

In vitro techniques with sorghum explants have been useful in understanding plant-pathogen interactions. One of the major diseases of sorghum, sorghum head smut, caused by the fungus *Sporisorium reilianum*, results in the formation of the sorus, the fungal fruiting body, in place of the normal inflorescence. In less severe infections, the inflorescence develops into a leafy structure, in a phenomenon known as phyllody. Phyllody could be induced from floral primordia, excised from the plant and cultured on a medium that contained gibberellic acid (Bhaskaran et al., 1990). The ability of the fungus to produce gibberellic acid, or an altered metabolism of gibberellins, in smut-infected plants can be inferred from these results.

In vitro techniques also have helped in eliciting filamentous mycelial growth from sporidia of *S. reilianum*, a dimorphic fungus. The fungus exhibits two distinct phases of growth in its life cycle. One is a unicellular yeast-like growth, which is commonly observed under laboratory conditions. A multicellular filamentous type of growth, which is the parasitic phase, has been believed to occur exclusively within the host plant. The trigger for the conversion remained elusive until recently. When an extract from the sorghum floral primordium (the prime target for the pathogen) was provided as the sole carbon source in the culture medium for fungal sporidial growth, differentiation into multicellular filamentous mycelia resulted (Bhaskaran et al., 1991). This was the first report of filamentous growth occurring outside the sorghum plant. Simple carbohydrates such as glucose, sucrose, or fructose prevented host extract-induced mycelial growth, but lactose did not. The sporidial form of the fungus was capable of hydrolyzing sucrose into its component hexoses, while lactose was neither hydrolyzed nor utilized from the culture medium (Bhaskaran and Smith, 1993). The complex interaction of simple and complex carbohydrates in fungal morphogenesis is evident from these results. The

ability to culture filamentous fungal growth *in vitro* opens up the possibility to isolate and characterize the inducer from the host plant and to study the phenomenon of fungal dimorphism and how it is regulated by carbohydrate substrates available to the fungus. Perhaps through these basic studies a strategy to prevent the pathogenic filamentous fungal growth in the host plant could eliminate head smut.

Anther Culture

Plant breeders have many techniques available to develop new lines; *in vitro* anther culture for haploid plant production can provide a rapid method for cereal crop improvement. The immature pollen within the anther can undergo an abnormal developmental pathway, forming an embryo, or callus, which can then develop into a haploid plant. The resulting plant may spontaneously diploidize (the chromosomes double) upon treatment with colchicine. An immediate advantage of sorghum haploids would be expeditious introduction of new genes into the domestic gene pool for use as homozygous parents for the production of hybrids. Another approach would be to culture the anthers of a cross between two desirable parents and select the homozygous diploid combinations that contain the desirable genes of both parents. As similar approaches with rice have shown, using this approach could cut years from sorghum breeding programs.

Following the many successes in rice anther culture, many laboratories have attempted similar work in sorghum without success. However, two published reports describe successful anther culture in sorghum. Rose et al. (1986) reported culturing anthers from 'Advance' sorghum [*S. bicolor* (L.) Moench], obtaining callus and subsequently four albino plants. More recently, Kumaravadivel and Rangasamy (1994) reported anther-derived plants from six cultivars of sorghum, obtaining 248 doubled haploids and 12 haploid plants. This report opens the possibility of anther culture in sorghum for the rapid production of homozygous lines that can be used as recombinant inbreds. A genetic investigation of the selfed progeny from the regenerated plants was undertaken to confirm the pollen origin of the plants as well as analyze their use in crop breeding programs.

Somaclonal Variation and Cell Selection

The entire *in vitro* process, beginning with genotype and explant selection and extending through callus induction, embryogenesis, and plantlet regeneration, can be extremely productive in creating genetic variation. However, only about 50 agronomically useful cultivars or germplasm sources have been released for utilization in production programs (Duncan, 1996), with horticulture crops leading the way. Since many variants are mostly unstable or misunderstood chromosomal aberrations, breeders often question the effectiveness and efficiency of using *in vitro* methods in their programs when conventional methods are available.

Perhaps those concerns will be alleviated with experience and when the philosophical approach of using *in vitro* technology as a breeding tool to create additional diversity is accepted by conven-

tional breeders. This philosophical change should occur parallel with changes in selection strategies. Successful selection of desirable regenerants with improved traits depends on: 1) expression of a wide diversity for specific traits, 2) trait stability over generations, 3) adequate population size in the field to have a reasonable chance of visually selecting desirable variants, and 4) a proper field environment that fosters trait expression.

In sorghum, high plant populations (20,000 plants per genotype culture) will be needed in field trials for selection of useful regenerants (Duncan, 1996; Duncan et al., 1995; Smith et al., 1993). If *in vitro* selective agents are used to target specific traits, the uncontrolled variation induced by the process will require even higher regenerant populations for proper field selection. Often *in vitro* stressing agents cause negative selection pressure by reducing regeneration frequency or by producing weaker or less vigorous seedlings when regenerated. If biotic or abiotic stresses are used in the field selection program, population numbers should be higher in these trials than they would be if no stress were imposed, because selection will be based on good agronomic traits plus biotic or abiotic stress tolerance. Breeding programs must adjust to multiple *in vitro* process ə genotype ə environmental interactions to successfully select and eventually transfer the useful somaclonal variants to production systems.

Five sorghum somaclonal variants have been released (Duncan, 1996). Two variants were stressed *in vitro* with NaCl, but the releases had improved fall armyworm resistance (Duncan et al., 1991a; Isenhour and Wiseman, 1991; Isenhour et al., 1991; Wiseman et al., 1996). Three variants emerged from no *in vitro* stress and had improved tolerance to acid soil stress when the donor parent was highly sensitive (Duncan et al., 1991b, 1992, 1995; Foy et al., 1993; Miller et al., 1992).

Population size and proper field environments are the same criteria used in conventional or mutation breeding programs to select desirable traits. Induced and introduced variation during the *in vitro* process can be a useful source of variability if breeding programs properly adjust to the technology.

Embryo Rescue

The culture of excised embryos at an early stage of development can be useful to plant improvement programs by making it possible to obtain viable hybrids from normally unsuccessful crosses or to overcome seed dormancy problems (Rangan, 1982). De Wet et al. (1976) reported on *Saccharum officinarum* and *S. bicolor* hybrids to generate sorghum with shoot fly resistance. These crosses were made by conventional crossing methods; however, it is possible to make wide crosses using embryo rescue in cell culture. The method involves making the cross and rescuing the embryo prior to the developmental stage where it aborts on the plant and placing it in sterile culture to develop a viable plant from the embryo. To date, there appear to be no reports in the literature on the application of this technique to sorghum or pearl millet improvement. The methodology, however, is generally straightforward and relatively simple. A drawback to this approach is that one would have to go through a selection process to identify plants with desirable traits

and eliminate unwanted characteristics from such hybrids.

Today a greater emphasis is being placed on plant genetic engineering to introduce one or two specific agronomic traits without changing the genetic background of the cultivar.

Plant Transformation

Currently, three popular methods are used to introduce foreign genes into plants: 1) *Agrobacterium*-mediated transformation, 2) protoplast-mediated transformation, and 3) microprojectile bombardment-mediated transformation. Each of these methods involves the use of cultured protoplasts, cells, tissue, or organ explants.

Agrobacterium-Mediated Transformation

Agrobacterium tumefaciens is a pathogenic bacterium that causes crown gall disease in many dicots. It infects plants by transferring a portion of its Ti-plasmid DNA (T-DNA) into host cells, which then becomes integrated into the plant genome. This ability of *Agrobacterium* to transfer the T-DNA into the host cell genome has been harnessed for plant transformation by deleting genes on the T-DNA (disarming) and replacing these with genes of interest. The transfer system is operational even when the T-DNA containing the foreign genes is present on a separate plasmid (binary vector), as long as the *vir* genes are still present on the Ti-plasmid. With *A. tumefaciens* harboring the disarmed (non-oncogenic) Ti-plasmid and binary vector, genes of interest are now being transferred to many dicot genomes in a controlled, efficient, and reproducible manner. As a result, a number of dicot plants engineered for improved quality, viral resistance, insect resistance, and herbicide tolerance either have been released into the market or will be introduced shortly.

In contrast, the progress in the genetic engineering of monocotyledonous plants has been slow because *A. tumefaciens* apparently does not easily infect most monocots. Alternative methods to transform cereals have been developed, and most cereals transformed to date have been obtained using either the microprojectile bombardment (gene gun) method or direct DNA uptake via protoplasts followed by regeneration. These methods are described below. Both, however, are inefficient and require an enormous amount of time and resources to produce a few transformants. Another drawback is that they often generate transformants with a high number of gene copies that are rearranged. Such transgene integrations result in gene expression problems.

For these reasons, efforts have continued to improve the efficiency of *Agrobacterium*-mediated transformation of monocots. These include the development of *Agrobacterium* strains of high virulence, use of *Agrobacterium* with different combinations of chromosomal backgrounds and various combinations of *vir* genes, use of certain factors in the induction medium to increase infection, etc. In some instances, where *Agrobacterium*-mediated transformation of cereals was reported, the efficiencies were very low, and the evidence provided for stable transformation was equivocal.

Some recent reports, however, have shown very high efficiency transformation of rice and maize using *A. tumefaciens* harboring a modified "super-binary" vector (Hiei et al., 1994; Ishida et al., 1996). A combination of factors contributed to the increased transformation efficiencies in these studies: conditions of co-cultivation, choice of tissue as starting material, and most important, the use of a "super-binary" vector (carrying extra *vir* genes). These reports provide, by far, the strongest evidence for stable transformation of any cereal by *A. tumefaciens*. Stable transformation was demonstrated by Southern analysis on a large number of transformants, sequence analysis of T-DNA junctions, as well as genetic analysis of the progeny. Several other labs now have confirmed this finding (Aldemita and Hodges, in press; Dong et al., in press; Park et al., 1996). These extremely encouraging results with rice and maize raise the possibility that other important cereals, such as sorghum, can be transformed using this system.

Protoplast -Mediated Transformation

Initial attempts to transform cereals with *Agrobacterium* were unsuccessful, leading to attempts to use protoplast transformation as a means of obtaining transformed plants. It is possible to isolate protoplasts from suitable tissues of many species by enzymatically digesting the cell wall. DNA can be introduced into these protoplasts by physical (electroporation) or chemical (PEG treatment) means, which can result in stable gene integration. Following transformation, protoplasts of many species can be regenerated into whole plants. One advantage of this method is that plants regenerated from transformed protoplasts are non-chimeric, i.e., each cell in the plant will contain the foreign gene. Rice and maize were the first and only cereals to be transformed via the protoplast method (Toriyama et al., 1988; Rhodes et al., 1988). Since these initial reports, transformation of certain japonica cultivars of rice using protoplasts has become routine in several laboratories (Shimamoto et al., 1989; Rathore et al., 1993). However, transformation of maize and indica cultivars of rice still remains difficult because plant regeneration from protoplasts is highly genotype-dependent and unreliable.

Microprojectile Bombardment-Mediated Transformation

This is a physical method to deliver DNA directly into cells without the need for a biological vector. The method involves coating small gold or tungsten particles with the foreign DNA; these are then shot into living plant tissue, using an explosive force. The particles penetrate the cell wall and the plasma membrane and DNA is delivered into the plant cell. As in the case of protoplasts, the intent is to transform important monocots that are not amenable to *Agrobacterium*-mediated transformation. This method is not specific to certain tissues or cell types and can deliver DNA to cells deeper than the surface layer.

This method has two major advantages over the protoplast method: 1) the transformed cells can be more readily regenerated, and 2) because of shorter culture periods, the regenerated transformed plants are more likely to be fertile. Indeed, fertile transgenic plants of several important dicots and all of the major cereals

including sorghum have now been obtained using the gene gun — or microprojectile bombardment — method (Gordan-Kamm et al., 1990; Christou et al., 1991; Vasil et al., 1992; Somers et al., 1992; Casas et al., 1993; Wan and Lemaux, 1994; Castillo et al., 1994).

Particle bombardment has been used to obtain transgenic sorghum plants using both immature embryos from explants of P898012 (Casas et al., 1993; Kononowicz et al., 1995) and inflorescence explants of SRN39 (A.M. Casas et al., 1996, personal communication). DNA delivery was mediated with the PDS 1000/He Biolistic Delivery System (Bio-Rad), and parameters were optimized based on transient expression of GUS and R/C1 maize anthocyanin regulatory elements. Transformed cells/tissues were selected utilizing the *bar* gene, encoding for phosphinothricin acetyltransferase (PAT) as the selectable marker and bialophos selection pressure. Over 60 Ignite resistant plants have been regenerated. The presence of transgenes (*bar*, *uidA* or *luc*) has been detected in primary regenerants by Southern blot analyses. Restriction fragment patterns indicate the likelihood that the transgenic plants originated from seven independent transformation events. Functional expression in progeny of herbicide resistance and PAT or luciferase enzyme genes has been determined to be inherited through the five generations analyzed to date. Analyses of genetic data indicate that co-transformation can result in effective segregation of the selectable marker from the other transgenes. These results indicate the potential for application of transformation technology in sorghum improvement.

One of the biggest disadvantages of the particle bombardment method appears to be extremely low efficiency of obtaining stable transformation events. The main reason for this poor efficiency appears to be death of cells following particle penetration (Hunold et al., 1994). A number of improvements have been made to increase the efficiency of stable transformation over the years, but the method still remains extremely labor- and resource-intensive and far from routine for most of the important crop plants.

Summary

A number of plant cell culture tools can be applied to enhance conventional sorghum and pearl millet breeding programs. Somaclonal variation has had some success in providing usable germplasm. From a practical viewpoint, however, many breeders feel there is already significant genetic variation that needs to be evaluated without generating more through cell culture.

There appear to be useful applications of anther culture to enhance sorghum conversion and breeding programs. Certainly transformation technology will be useful, particularly if care is taken in the selection of genes and proper agronomic practices prevent the spread of these genes into weedy species which readily cross with sorghum. Research in rice, maize, and wheat plant biotechnology has received a lot of funding and is a major source of technology that can be applied to sorghum and pearl millet. Realistically, until funding is available for the development of these technologies in sorghum, their application will be delayed.

References

Aldemita, R.R., and T.K. Hodges. 1996. *Agrobacterium tumefaciens*-mediated transformation of japonica and indica rice varieties. Planta: in press.

Bhaskaran, S., and R.H. Smith. 1990. Regeneration in cereal tissue culture: A review. Crop Science 30:1328-1336.

Bhaskaran, S., R.H. Smith, and R.A. Frederiksen. 1990. GA_3 reverts floral primordia to vegetative growth in sorghum. Plant Science 71:113-118.

Bhaskaran, S., R.H. Smith, and R.A. Frederiksen. 1991. A factor that promotes mycelial development in *Sporisorium reilianum* in vitro. Bot. Gaz. 152(4):453-459.

Bhaskaran, S., and R.H. Smith. 1993. Carbohydrates, invertase activity, growth, and dimorphism in *Sporisorium reilianum*. Mycopathologia 122:35-41.

Casas, A.M., A.K. Kononowicz, U.B. Zehr, D.T. Tomes, J.D. Axtell, L.G. Butler, R.A. Bressan, and P.M. Hasegawa. 1993. Transgenic sorghum plants via microprojectile bombardment. Proc. Natl. Acad. Sci., USA 90:11212-11216.

Casas, A.M., A.K. Kononowicz, R.A. Bressan, and P.M. Hasegawa. 1995. Cereal transformation through particle bombardment. Plant Breed. Rev. 13:235-264.

Castillo, A.M., V. Vasil, and I.K. Vasil. 1994. Rapid production of fertile transgenic plants of rye (*Secale cerale* L.). Bio/technology 12:1366-1371.

Christou, P., T.L. Ford, and M. Kofron. 1991. Production of transgenic rice (*Oryza sativa* L.) plants from agronomically important indica and japonica varieties via electric discharge particle acceleration of exogenous DNA into immature zygotic embryos. Bio/technology 9:957-962.

De Wet, J.M., S.C. Gupta, J.R. Harlan, and C.O. Grassl. 1976. Cytogenetics of introgression from saccharum into sorghum. Crop Science 16:568-572.

Dong, J., W. Teng, W.G. Buchholz, and T.C. Hall. 1996. *Agrobacterium*-mediated transformation of Javanica rice. Molecular Breeding: in press.

Duncan, R.R. 1996. Tissue culture-induced variation and crop improvement. Adv. Agaron. 58:210-240.

Duncan, R.R., D.J. Isenhour, R.M. Waskom, D.R. Miller, M.W. Nabors, G.E. Hanning, K.M. Petersen, and B.R. Wiseman. 1991a. Registration of GATCCP100 and GATCCP101: Fall armyworm resistant hegari regenerants. Crop Sci. 31:242-244.

Duncan, R.R., R.M. Waskon, D.R. Miller, R.L. Voigt, G.E. Hanning, D.A. Timm, M.W. Nabors. 1991b. Registration of GAC102 acid soil tolerant hegari regenerant. Crop Sci. 31:1396-1397.

Duncan, R.R., R.M. Waskom, D.R. Miller, G.E. Hanning, D.A. Timm, and M.W. Nabors. 1992. Registration of GC103 and GC104 acid-soil tolerant Tx430 regenerants. Crop Sci. 32:1076-1077.

Duncan, R.R., R.M. Waskom, and M.W. Nabors. 1995. *In vitro* screening and field evaluation of tissue-culture-regenerated sorghum [*Sorghum bicolor* (L.) Moench] for soil stress tolerance. Euphytica 85:373-380.

Foy, C.D., R.R. Duncan, R.M. Waskom, and D.R. Miller. 1993. Tolerance of sorghum genotypes to an acid, aluminum toxic Tatum subsoil. J. Plant Nutri. 16:97-127.

Gordon-Kamm, W.J., T.M. Spencer, M.L. Mangano, et al. 1990. Transformation of maize cells and regeneration of fertile transgenic plants. Plant Cell 2:603-618.

Hiei, Y., S. Ohta, T. Komari, and T. Kumashiro. 1994. Efficient transformation of rice (*Oryza sativa* L.) mediated by *Agrobacterium* and sequence analysis of the boundaries of the T-DNA. Plant J. 6:271-282.

Hunold R., R. Bronner, and G. Hahne. 1994. Early events in microprojectile bombardment: Cell viability and particle location. Plant J. 5:593-604.

Isenhour, D.J., and B.R. Wiseman. 1991. Fall armyworm resistance in progeny of maize plants regenerated via tissue culture. Florida Entomol. 74:221-228.

Isenhour, D.J., R.R. Duncan, D.R. Miller, R.M. Waskom, G.E. Hanning, B.R. Wiseman, and M.W. Nabors. 1991. Resistance to leaf-feeding by the fall armyworm (Lepidoptera: Noctuidae) in tissue culture derived sorghums. J. Econ. Entomol. 84:680-684.

Ishida, Y., H. Saito, S. Ohta, Y. Hiei, and T. Komari. 1996. High efficiency transformation of maize (*Zea mays* L.) mediated by *Agrobacterium tumefaciens*. Nature Biotechnol. 14:745-750.

Kononowicz, A.K., A.M. Casas, D.T. Tomes, R.A. Bressan, and P.M. Hasegawa. 1995. New vistas are opened for sorghum improvement by genetic transformation. African Crop Sci. J. 3:171-180.

Kumaravadivel, N., and S.R. Sree Rangasamy. 1994. Plant regeneration from sorghum anther cultures and field evaluation of progeny. Plant Cell Reports 13:286-290.

Miller, D.R., R.M. Waskom, R.R. Duncan, P.L. Chapman, M.A. Brick, G.E. Hanning, D.A. Timm, and M.W. Nabors. 1992. Acid soil stress tolerance in tissue-culture-derived sorghum lines. Crop Sci. 32:324-327.

Park, S.H., S.R.M. Pinson, and R.H. Smith. 1996. T-DNA integration into genomic DNA of rice following *Agrobacterium* inoculation of isolated shoot apices. Plant Mol. Bio. 32:1135-1148.

Rangan, T.S. 1982. Ovary, ovule and nucellus culture. p. 105-129. *In* B.M. Johri (ed.) Experimental embryology of vascular plants. Springer-Verlag, Berlin.

Rathore, K.S., V.K. Chowdhury, and T.K. Hodges. 1993. Use of *bar* as a selectable marker gene and for the production of herbicide-resistant rice plants from protoplasts. Plant Mol. Bio. 21:871-884.

Rhodes, C.A., D.A. Pierce, I.J. Mettler, D. Mascarenhas, and J.J. Detmer. 1988. Genetically transformed maize plants from protoplasts. Science 240:204-207.

Rose, J.B., J.M. Dunwell, and N. Sunderland. 1986. Anther culture of *Sorghum bicolor* (L.) Moench I. Effect of panicle pretreatment, anther incubation temperature and 2,4-D concentration. Plant Cell Tissue Organ Culture 6:15-22.

Shimamoto, K., R. Terada, T. Izawa, and H. Fujimoto. 1989. Fertile transgenic rice plants regenerated from transformed protoplasts. Nature 338:274-276.

Smith, R.H., R.R. Duncan, and S. Bhaskaran. 1993. *In vitro* selection and somaclonal variation for crop improvement. p. 629-633. *In* D.W. Buxton (ed.) Int'l crop science congress. Crop Sci. Soc. Amer., Madison, WI.

Somers, D.A., H.W. Rines, W. Gu, H.F. Kaeppler, and W.R. Bushnell. 1992. Fertile, transgenic oat plants. Bio/technology 10:1589-1594.

Toriyama K., Y. Arimoto, H. Uchimiya, and K. Hinata. 1988. Transgenic rice plants after direct gene transfer into protoplasts. Bio/technology 6:1072-1074.

Vasil, V., and I.K. Vasil. 1982. Characterization of an embryogenic cell suspension culture derived from cultured inflorescences of *Pennisetum americanum* (pearl millet, Gramineae). Amer. J. Bot. 69(9):1441-1449.

Vasil V., A.M. Castillo, M.E. Fromm, and I.K. Vasil. 1992. Herbicide resistant fertile transgenic wheat plants obtained by microprojectile bombardment of regenerable embryogenic callus. Bio/technology 10:667-674.

Wan, Y., and P.G. Lemaux. 1994. Generation of large numbers of independently transformed fertile barley plants. Plant Phy. 104:37-48.

Wiseman, B.R., D.J. Isenhour, and R.R. Duncan. 1996. *In vitro* production of fall armyworm (*Spodoptera frugiperda*)-resistant maize and sorghum plants. p. 67-80. *In* Y.P.S. Bajaj (ed.) Biotech. in agri. and forestry, Vol. 36 - Somaclonal variation in crop improvement II. Springer-Verlag, Berlin.

Discussion

Session IV - Breeding Techniques
Session Chair: Ken Kofoid
Rapporteurs - Gary Toenniessen and Aboubacar Toure

Bhola Nath Verma - The application of population improvement in self-pollinated crops dates back to over 30 years. The selection gains for complex traits like yield and for multiple traits reported are generally reported for 2-3 cycles for a number of logical reasons. These results in the absence of estimates of genetic variation over cycles, are not very conclusive evidence of the success of the population improvement concept in self pollinated crops. I am wondering if somebody has results over 8-10 selection cycles without infusing added variability from outside into populations to demonstrate the success of the concept?

H.F.W. Rattunde - I am not aware of any recurrent selection of more than eight cycles in sorghum closed populations. However, for both self-pollinated and cross pollinated crops, genetic variance would be a function of the initial number of genes segregating, the selection pressure changing gene frequencies, and the effective population sizes as it affects inbreeding and genetic drift.

Steve A. Eberhart - When the commercial product will be a hybrid, reciprocal recurrent selection has many advantages for population improvement. Heterotic groups are very important, and the establishment of a world-wide female group and a male group is needed. With the availability of genetic steriles (ms_3, ms_7, etc.) and A, and A_2 male-sterile cytoplasm in sorghum, the RRS inbred testers procedure can be very effective (note that pedigree breeding as practiced in corn and sorghum is a special variation of this procedure). For pearl millet, reciprocal full sib selection (FR) is suggested. Multistage selection rather than index selection for multiple traits and multiple testers (early, medium, late maturity) are desirable. Two nursery seasons per year are essential. Reference: S.A. Eberhart, W. Salhuona, R. Sevilla, and S. Taba. 1995. Principles of tropical maize breeding. Maydica 40:339-355.

B.S. Rana - I handled apomictic R473 line as a plant breeder and crossed it with almost 50 lines without any maternal plant appearing in F_1 except a couple of plants in two crosses. These crosses segregated perfectly without any maternal type appearing in F_2 generation. How can inheritance or expression of apomixis be explained? R473 was used as a female parent).

K.F. Schertz - Your experience is similar that we observed. I can't explain the result. Some possibilities are that in R473 apomixis is variable or that apomixis is very complexly inherited and not all necessary alleles were present in progeny.

B.S. Rana - When restorers (of A_1) are sterilized in A_2 cytoplasm the resulting cms lines differ in restoration pattern when crossed with a single restorer. How can this differential behavior be explained?

K.F. Schertz - The differential behavior in this example is probably related to the different nuclear gene combination that result from the crosses.

B.S. Rana - The seasonal interactions are observed more frequently in A_2 based cms lines rather than in A_1 based cms lines. What may be the possible reason?

K.F. Schertz - The seasonal interactions observed with A_2 are like those observed with A_1 in its early years of use. Breeders have learned how to manage this with A_1 and are mostly successful. Learning will be needed with A_2.

B.S. Rana - Certain post-rainy lines when crossed with A_1 cms show perfect sterility in F_1 and BC_1 but in further backcrosses partial seed set increases. How can this mechanism be explained?

K.F. Schertz - The problem described is one of the most difficult in breeding cms male-sterile parents. Apparently with continued back crossing nuclear alleles that increase fertility are being introduced from the recurrent parent. We need molecular markers that can be used to select against these alleles.

Joseph Ochieng - Since heritability estimates are a function of not only genotypes (family differences) but also of environment (site and season), what magnitude of selection response and selection limits would you expect for breeding under stress versus selection under nonstress? What genetic explanation would be advanced for whatever the answer?

Paula Bramel-Cox - The answer to this question depends upon the genetic correlation between the selection or testing environment and the target environments. It also depends upon the heritability in both types of environments. The basis of the response to selection is the impact of indirect selection at the selection or testing site for the target environment. The effectiveness of this indirect selection would need to be judged in relation to that of direct selection in the various environments in the target range. The actual limits to the response for either type of environment would ultimately depend on the genetic variance of the reference (breeding) population for adaptation to the entire range of the target environment. Falconer (1990) described this very well in his paper and in his book on quantitative genetics in 1989. I do not generally favor the use of heritability itself to quantify the value of a specific selection environment. It is an unpredictable estimate that has been shown to have a wide confidence interval when estimated repeatedly. The explanation for this is GE interaction and the large inherent error associated with the estimate of the genetic variance.

John Witcombe - I was pleased to see you mentioned participatory breeding techniques. Would you like to expand on why sorghum is particularly suited to the use of participatory approaches?

Paula Bramel-Cox - You can likely give the reasons better than I.

John Witcombe - Sorghum is particularly suited to these approaches because there was an expressed need — The failure of classical approaches to provide solutions for all farmers as evidenced by the high proportion of farmers still growing landraces. Sorghum was predominantly self-pollinating with a high inherent rate of seed increase that favored the successful use of participatory approaches, and it was grown in the marginal agricultural environments for which the effectiveness

of such approaches had been demonstrated.

David Andrews - We need to put PPB in perspective. It is not a universal solution and should not become a "bandwagon". It has implications that breeders, who did make successful varieties, did not really know what they were doing. Two aspects of PPB are useful for all breeders, especially in developing countries: 1) early generation breeding material does need to be exposed and evaluated in farmers conditions, 2) breeders must be familiar with farmers problems and preferences. However, while farmers may be effective evaluators of germplasm, they are not aware of the full implications of that choice. Only the breeders know the wider possibilities (including those not evident to farmers), and how these may be integrated into the generation of successful cultivars. There are additional adverse consequences of PPB when the introduction of hybrids is considered. This relates to the benefits of mobilizing private enterprise that follow the development of a market for hybrids.

John Witcombe - Perhaps breeders did not know what they were doing when they selected almost exclusively for yield in multilocational trials. Farmers had more diverse needs such as fodder yield as well as grain yield. Breeders had failed to replace very old varieties such as the rabi sorghum "Maldandi" and new approaches needed to be tried. Participating varietal selection could be used to aid hybrid breeding. Finally, the word participatory meant collaboration between breeders and farmers. An example was a recently released variety of rice "Machhapuchre-3" in Nepal, a result of participatory plant breeding. The release proposal had the names of two farmers and three breeders showing that the real meaning of the approach is that it is participative.

Belum Reddy - Sorghum improvement now is a team effort involving breeders, physiologist, entomologist, pathologists and economists. All are involved in constraints assessment through interaction with farmers. To say that breeders do not know what they are doing, despite the team effort, is a self-defeating comment. Secondly, as defined by Allard and Bradshaw (1964), breeders attempt/aim at broad adaptability or specific adaptation or a variation of both. In the case of farmer participatory breeding, what we are attempting to aim at is specific adaptation. Farmers, within a village differ in their perception of what they need and if so, how far can we extend our efforts. Thirdly, regarding improvement for post rainy season in India beating M35-1, I am not sure if we can solve it involving farmers, because we know clearly what farmers need, but we do not get that desirable segregation.

Eduardo Teyssandier - 1) Which culture medium do use for immature embryo rescue? 2) For obtaining somaclonal variants, do you use undifferentiated tissue or cell cultures as a source?

Roberta Smith - 1) This has been published. 2) It is necessary to go through callus.

Henry Nguyen - What is the efficiency of the Agrobacterium - mediated and particle bombardment sorghum transformation approaches?

Roberta Smith - The efficiency for sorghum is low. Agrobacterium looks better for rice.

Session V

Breeding for Resistance to Biotic Stress

Session Chair: John Witcombe

Rapporteurs: Larry Claflin and Neil Muller

Speakers

R.G. Henzell
G.C. Peterson
R.P. Thakur
C.W. Magill
J.W. Stenhouse
C.T. Hash

Breeding for Resistance to Panicle Pests of Sorghum and Pearl Millet

R.G. Henzell*, G.C. Peterson, G.L. Teetes, B.A. Franzmann, H.C. Sharma, O. Youm, A. Ratnadass, A. Toure, J. Raab, and O. Ajayi

Abstract

*Host plant resistance (HPR), as a component of integrated pest management, has been employed for few of the many insects recorded as pests of the panicles of sorghum [*Sorghum bicolor *(L.) Moench] and even fewer for pearl millet [*Pennisetum glaucum *(L.) R.B]. This paper reviews global HPR breeding programs for sorghum midge [*Stenodiplosis sorghicola *(Coquillett)], earhead bug (*Calocoris angustatus *Lethierry), African sorghum head bug [*Eurystylus oldi *(Poppius)], corn earworm [*Helicoverpa armigera *(Hübner) and* Helicoverpa zea *(Boddie)], and millet head miner [*Heliocheilus albipunctella *(de Joannis)]. Major progress has been made in combining enhanced levels of HPR to sorghum midge with local adaptation in the breeding programs at ICRISAT Asia Center and Texas A&M University and in Australia. On-farm adoption of this developed technology has occurred rapidly and at a high level in Australia. Breeding for HPR to other insects has attracted less effort. HPR research for earhead bugs in India and African sorghum head bugs in West Africa has progressed to the point that cultivars with resistance to these pests soon will be available to farmers. The open panicle type is routinely selected in breeding programs in regions where corn earworm is a pest. Breeding programs for HPR to millet head miner need further development.*

While tremendous progress has been made through breeding to improve sorghum and pearl millet for adaptation and utilization, it has been at a cost of increased susceptibility to some biotic and abiotic stresses. Emphasis on yield has narrowed the genetic base and reduced natural plant defense mechanisms. Changes in phenotype and maturity, as well as production in vast monocultures, have exacerbated the problem.

The close association of insects with their host plants provides a unique opportunity to disrupt this relationship by incorporating resistance genes. Even slight changes in the compatibility of the host plant and the insect can significantly reduce damage and increase the complementary effects of other IPM tactics. However, host-plant resistance (HPR), as a component of integrated pest management, has been employed for only a few

R.G. Henzell, Queensland Department of Primary Industries, Hermitage Research Station, Warwick 4370, Australia; G.C. Peterson, Texas Agricultural Experiment Station, Route 3, Box 219, Lubbock, Texas 79401-9757; G.L. Teetes, Department of Entomology, Texas A&M University, College Station, Texas 77843-2475; B.A. Franzmann, Queensland Department of Primary Industries, Box 102, Toowoomba 4350, Australia; H.C. Sharma, ICRISAT Asia Center, Patancheru 502 324, Andhra Pradesh, India; O. Youm, ICRISAT Sahelian Center, BP 12404, Niamey, Niger; A. Ratnadass, Centre de Coopération Internationale en Recherche Agronomique pour le Développement - Department des Cultures Annuelles (CIRAD/CA), ICRISAT West and Central African Regional Program (WCARP), BP 320, Bamako, Mali; A. Toure, Institut d'Economie Rurale (IER), Station de Recherche Agronomique de Sotuba, BP 258, Bamako, Mali; J. Raab, Dekalb Genetics Corporation, Route 2, Box 373, Bishop, TX 78343; O. Ajayi, ICRISAT West African Sorghum Improvement Program (WASIP), Nigeria IITA Office, Sabo Bakin Zuwo Road, PMB 3491, Kano, Nigeria. ICRISAT Publication Number CP 1154. *Corresponding author.

of the many insects recorded as panicle pests of sorghum [*Sorghum bicolor* (L.) Moench] and for even fewer insect pests of pearl millet [*Pennisetum glaucum* (L.) R.B] (Harris, 1995).

These factors have led to increased effort to develop insect-resistant sorghum and pearl millet. Much progress has been made and gains are expected to be durable. New sources of resistance will be found in sorghum and pearl millet; some now relatively insignificant insects may increase in importance; and techniques to introduce alien genes for resistance will be developed. These factors demand that current efforts to develop insect-resistant sorghum and pearl millet continue and even increase in intensity.

This review describes the global HPR breeding programs for sorghum midge [*Stenodiplosis sorghicola* (Coquillett)]; the sorghum panicle feeding bugs; earhead bug (*Calocoris angustatus* Lethierry) and African sorghum head bug [*Eurystylus oldi* (Poppius)]; corn earworm [*Helicoverpa armigera* (Hübner) and *Helicoverpa zea* (Boddie)]; and millet head miner [*Heliocheilus albipunctella* (de Joannis)].

Progress in developing HPR to panicle feeding insects in sorghum and pearl millet was reviewed in the International Consultative Workshop on Panicle Insect Pests of Sorghum and Pearl Millet (Nwanze and Youm, 1995); breeding for resistance to sorghum midge was reviewed by Henzell et al. (1994) in Australia, Peterson et al. (1994) in the U.S., and Sharma et al. (1994a) in Asia and Africa. Literature since then and personal communications have been used to bring this review up to date.

Sorghum Midge

Midge is the most ubiquitous and damaging insect species attacking sorghum. It is found almost everywhere the crop is grown and has been the subject of much research since its first discovery in 1894 in Queensland (Tryon, 1895). Estimates of annual costs to production (in U.S. dollars) are $28 million in Texas (Peterson et al., 1994), $294 million in the semiarid tropics (ICRISAT, 1992), and $7.9 million in Australia. Additional costs are associated with restricted planting window opportunities and the effect of insecticides on the biosystem and cleanliness of the end-product.

A breeding program for resistance to sorghum midge began at Texas A&M University soon after usable resistance was found (Johnson et al., 1973). Similar programs began at the Queensland Department of Primary Industries, Australia, in 1975 (Henzell et al., 1980) and at the ICRISAT Asia Center in India in 1980 (Sharma et al., 1994a). In addition, the private sectors in Australia and the U.S. breed for resistance to sorghum midge. This review is mainly of the public sector programs in Texas, Australia, and ICRISAT.

Sources of Resistance to Sorghum Midge

Sources from S. bicolor

Many sorghum genotypes have been reported to be sources of resistance to sorghum midge. Peterson et al. (1994) listed 31 resistant lines (Table 1). These products of the Sorghum Conversion Program (Stephens et al., 1967) form the basis of the sorghum midge resistance breeding programs in Texas and Austra-

lia. The Sorghum Conversion Program converts tall, late maturing sorghum lines to short, early-maturing lines that can be used in temperate regions. In Texas, each converted line has been evaluated for resistance to midge. Without the Sorghum Conversion Program, the Texas and Australian midge resistance breeding programs would not exist.

At ICRISAT, 15,000 accessions from the world sorghum collection have been evaluated for resistance to midge (Sharma, 1985; Sharma et al., 1992a; Sharma et al., 1993a). Some shown to be resistant have proved to be derived lines, leaving 19 lines which are shown in Table 2. There are now 49 known sources of resistance (Tables 1 and 2). The key lines used in the Australian program are TAM2566 (IS 12666C), SC165-14E, SC173-14E (IS 12664C), SC108-14E (IS 12608C), SC414-14E (IS 2508C), SC574-14E (IS 8337C) and AF28 (Henzell et al., 1994).

TAM2566 (Johnson et al., 1982a) has been the major source of resistance used

Table 1. Sources of midge resistance identified in the Sorghum Conversion Program in Texas.

IS Number[1]	SC Number[2]	Groups[3]	Year identified[4]	Reaction to A1 Cytoplasm[5]
IS 12666C	SC175-9	Zerazera	1973	R
IS 2579C	SC423-14E	Zerazera	1973	R
IS 2508C	SC414-14E	Caudatum-Kafir	1973	R
IS 12608C	SC108-14E	Zerazera	1973	R
IS 2549C	SC228-14E	Zerazera	1976-79	R
IS 2862C	SC655-14E	Caffrorum-Birdproof	1976-79	R
IS 3071C	SC237-14E	Dobbs	1976-79	R
IS 6392C	SC490-14E	Nandyal	1976-79	R
IS 7064C	SC420-14E	Caudatum-Kafir	1976-79	R
IS 7142C	SC564-14E	Caudatum	1976-79	R
IS 8231C	SC645-14E	Caffrorum-Darso	1976-79	R
IS 8233C	SC643-14E	Caffrorum-Darso	1976-79	B
IS 8263C	SC328-14E	Dobbs	1976-79	R
IS 8337C	SC574-14E	Caudatum-Nigricans	1976-79	R
IS 12593C	SC84-14E	Durra-Nigricans	1976-79	partial
IS 8232C	SC642-14E	Caffrorum-Darso	1983-85	R
IS 8237C	SC644-14E	Caffrorum-Darso	1983-85	B
IS 8112C	SC725-14E	Caudatum	1983-85	R
IS 2740C	SC708-14E	Caudatum	1983-85	R
IS 3390C	SC572-14E	Caudatum-Kafir	1983-85	R
IS 7132C	SC693-14E	Dobbs	1983-85	R
IS 2685C	SC692-14E	Dobbs	1983-85	R
IS 957C	SC810-14E	Caudatum-Durra	1983-85	R
IS 7193C	SC694-14E	Dobbs	1983-85	R
IS 2144C	SC741-14E	Caudatum-Kaura	1983-85	R
IS 12572C	SC62-14E	Caudatum-Nigricans	1983-85	R
IS 8179C	SC752-14E	Caudatum-Kafir	1991-92	?
IS 6919C	SC846-14E	Durra	1991-92	B
IS 2655C	SC113-14E	Caudatum-Nigricans	1991-92	R
IS 3693C	SC632-14E	Caffrorum	1991-92	B
IS 17211C	SC1072-14E	Caffrorum	1991-92	R&B

[1]IS Number = International sorghum number. The C following the number indicates the converted line.
[2]SC = Sorghum Conversion number. The underlined number is the stage of conversion. E = line in exotic cytoplasm.
[3]Based on Murty et al., 1967.
[4]Lines were evaluated in at least one of the years indicated.
[5]R=restorer, B=maintainer: Schuering and Miller, 1978.

in the sorghum midge resistance breeding program at Texas A&M University (Peterson et al., 1994). SC62-14E has a diverse plant phenotype with loose panicles and glumes that do not tightly clasp the kernel. SC846-14E is a B line with white kernels and tan plant color. AF28 (Rossetto et al., 1975) has a very high level of resistance (Peterson et al., 1994) and was used to produce Tx2782 (Peterson et al., 1984) and several lines from the USDA Georgia sorghum breeding program (Hanna et al., 1989; Hanna et al., 1993). It is interesting to note that the converted BC_4 version of AF28 (SC1203-14E) is not resistant to sorghum midge (Peterson et al., 1994); therefore AF28 has been re-entered in the conversion program.

At ICRISAT, the major source of resistance used is DJ 6514, an Indian landrace (Sharma et al., 1994a). SC423-14E (IS 2579C), TAM2566, AF28, DJ 6514, IS 10712, IS 7005, and IS 8891 have the highest levels of resistance when tested across seasons, locations, and no-choice (cage tested) conditions. These lines are diverse, at least taxonomically. However, IS 7005 was converted and released in 1986 as SC679-14E which, when tested in Texas, showed a very low level of resistance. Interestingly, DJ 6514 loses some of its resistance in Kenya and Yemen, but AF28 and IS 8891 are as resistant there as at other locations (Sharma et al., 1994a). The possibility of a diversity of biotypes is being investigated (Sharma et al., 1996a).

An initiative at ICRISAT led to development of a population containing the male sterility genes ms_3 and ms_7. The population includes a significant portion of the known resistant sources and will serve as a source of resistance genes. Two

Table 2. Sources of midge resistance identified in the World collection at ICRISAT.

IS Number	SC Number	Designation	Group[1]	Reaction to A1 cytoplasm[2]
IS 3461		Bari	Nigrican/Guineense	R
IS 7005	SC679-14E	Katatilansa	Nigrican/Guineense	R
IS 8671			Caudatum/Nigricans	R
IS 8751		ExGaloa Selusa	Caudatum	R
IS 8884		E 549	Nigricans	R
IS 8887		E 552	Nigricans	R
IS 8891		E 556	Nigricans	R
IS 8918		E 583	Caudatum/Nigricans	R
IS 9807	SC1546-4	Kigo	Caudatum/Conspicuum	R
IS 10712		0317	Caudatum	R
IS 15107		2-2-6-2	Caudatum	R
IS 18563		V-71-1-1-1	Caudatum	R
IS 18695	SC504C		Caudatum	R
IS 18698		AF28	Caudatum	R
IS 19474	SC1549-3	Var-Lope	Caudatum	R
IS 19476	SC1550-3	Var-Godo	Caudatum	R
IS 22806			Caudatum	R
IS 26789			Durra	R

[1]Based on Murty et al. 1967
[2]R = restorer
Source: Sharma, 1985; Sharma et al., 1992a; Sharma et al., 1993a.

random mating populations, TP8 and TP23, were developed at Texas A&M University.

Wild Sorghum as a Source of Resistance

Many varieties of wild sorghum in Africa, India, and Australia are possible resistance sources. Franzmann and Hardy (1996) have shown that 16 of the 17 known indigenous (one not yet tested) Australian sorghum varieties were either non-hosts or had very few eggs laid in them when infested with midge in cage tests. These are from four subgenera other than *Sorghum*, the subgenus containing *S. bicolor*. However, at this time, attempts to cross any of these sorghum varieties with *S. bicolor* have failed (Huelgas et al., 1996). No other wild sorghum has yet been tested.

Alien Genes for Resistance

The introduction of alien genes for resistance to all pests via transformation is closer now that transformation has been achieved in the U.S. (Casas et al., 1993) and Australia (Rathus et al., 1996). The list of possible alien resistance genes is increasing (I. Godwin, 1996, personal communication). For example, two known groups of *Bacillus thuringiensis* (Bt) toxins, Cry II and Cry IV, have insecticidal properties against Dipterans. In addition, a number of protease inhibitors, mostly of plant origin, also may have some efficacy against midge. Plant lectins, amylases, and polyphenoloxidases are other candidates for testing.

Diversity of resistance, particularly of genes for resistance and of mechanisms of resistance, is critical not only for developing derived lines with higher levels of resistance by gene pyramiding, but also for developing lines with increased durability (greater longevity) of resistance. Not enough is known about the diversity of genes for midge resistance and of mechanisms of resistance. This is high priority.

Mechanisms of Resistance to Sorghum Midge

Antixenosis (non-preference)

Antixenosis (non-preference), especially oviposition antixenosis, is the most important mechanism of resistance (Franzmann, 1993; Rosetto et al., 1984; Sharma, 1985; Sharma et al., 1990ab; Waquil et al., 1986a). Fewer eggs are laid in resistant sorghum because fewer attempts at oviposition are successful (Waquil et al., 1986b), and females die before all their eggs are laid (Henzell et al., 1993). The reason for this difficulty in egg-laying is unknown, but the most frequently suggested cause is glume characters, especially short and tough glumes held tightly together (Ball and Hastings, 1912; Geering, 1953; Rosetto et al., 1984; Sharma et al., 1990b).

Resistance to sorghum midge may be caused, in part, by asynchrony between the time of spikelet flowering and the presence or abundance of insects (Jimenez, 1992; Diarisso et al., 1995). Midge-resistant sorghum flowers during the early morning hours, thus avoiding much midge oviposition.

Antixenosis to panicle visiting by females has been recorded in many genotypes (Franzmann, 1988; Sharma and

Vidyasagar, 1994; Teetes and Johnson, 1978; Waquil et al., 1986a).Variations in reflective light spectrum and chemical emissions from panicles apparently influence host selection by females. Yellow and white colors are attractive (Sharma et al., 1990a; Wiseman et al., 1972), as is ethanolic extract of flowering sorghum panicles (H.C. Sharma, 1996, personal communication).

Antibiosis

Resistant genotypes adversely affect the development of midge larvae, reducing their size and survival (Waquil et al., 1986b) and slowing development and reducing fecundity of emerging females (Sharma et al., 1993b). The reason for this antibiosis is not clear, but it may be structural. For example, some resistant sorghum genotypes have larger ovaries than susceptible ones. A disruption of the relationship between newly hatched larvae and the condition of the ovary may affect survival and development.

Tolerance

Increased kernel size has been proposed as a form of resistance that allows some genotypes to compensate for midge damage (Sharma et al., 1994a). However, data showing such genotypic differences are inconclusive. For example, Franzmann and Butler (1993) and Waquil and Teetes (1990) found that susceptible and resistant genotypes responded in the same way to midge damage. Sharma et al. (1994a), however, showed that the resistant genotypes tested compensated more than did the susceptible genotypes. It is doubtful that this form of resistance is important.

SC423-14E exhibits an interesting resistance mechanism. Midge larvae infesting this sorghum line sometimes are pushed from between the glumes and exposed. It is common for pupae to be visible between the glumes of most sorghum just before adult emergence. The process by which larval exposure occurs on SC423-14E is not known.

The Genetics of Resistance to Sorghum Midge

The genetics of resistance to sorghum midge were reviewed by Sharma et al. (1994a), Peterson et al. (1994), and Henzell et al. (1994). Resistance was found to be controlled by recessive to partially dominant genes, the number of which is unknown (Widstrom et al., 1972; Bergquist et al., 1974; Teetes and Johnson, 1978; Rossetto and Igue, 1983; Boozaya-Angoon et al., 1984; Widstrom et al., 1984; Agrawal et al., 1988). Both general and specific combining ability effects are significant (Page, 1979; Patil and Thombre, 1985; Agrawal et al., 1988), but resistance is controlled largely by additive gene action (Sharma et al., 1996b).

In summary, the inheritance of midge resistance seems to be complex. It is a polygenic trait that varies from recessive to partially dominant. It follows that resistant hybrids can be produced only by crossing resistant parents having common resistance genes. Significant measured and observed specific combining ability effects suggest some diversity of resistance genes. Preliminary supporting evidence is coming from the molecular marker work of Y.Z. Tao (1996, personal communication) in Australia. Results suggest that some of the chromosome re-

gions putatively linked with midge resistance differ in QL39 and QL41, the parents of a set of recombinant inbred lines used in Tao's study. Also, by pyramiding the diverse genes, diversity of resistance should result in progeny of crosses having a higher level of resistance than that of their parents. This has been observed. For example, QL29 has a higher level of resistance than either of its parents, QL23 and SC165-14E (Henzell et al., 1986). The evidence is strong for diversity of resistance genes, but more information is needed about the genetics of resistance in the various resistance sources. Molecular marker technology is a vehicle by which this can be achieved.

Breeding Methods For Resistance to Sorghum Midge

The major aims of midge resistance breeding programs vary. In the private sector and at ICRISAT, the aim is development of midge-resistant cultivars. In the public programs in the U.S. and Australia, however, the aim is to identify and develop germplasm for use in other programs. The difference in these aims is not discreet; there is some germplasm development in the private sector, and public breeders in Australia, U.S., and India are developing midge-resistant germplasm in a relatively adapted genetic background so that some of their products have been used directly to produce cultivars.

In each program, a number of multigenic characters are undergoing simultaneous selection. Therefore, the breeding method should involve cycles of crossing parents, selection of superior segregates, and recombination of at least a sample of selections to commence a new cycle, with an infusion of new material when available. Most programs use the pedigree and limited backcross methods rather than a population approach. The ICRISAT and Texas populations are not being selected under midge pressure at this time.

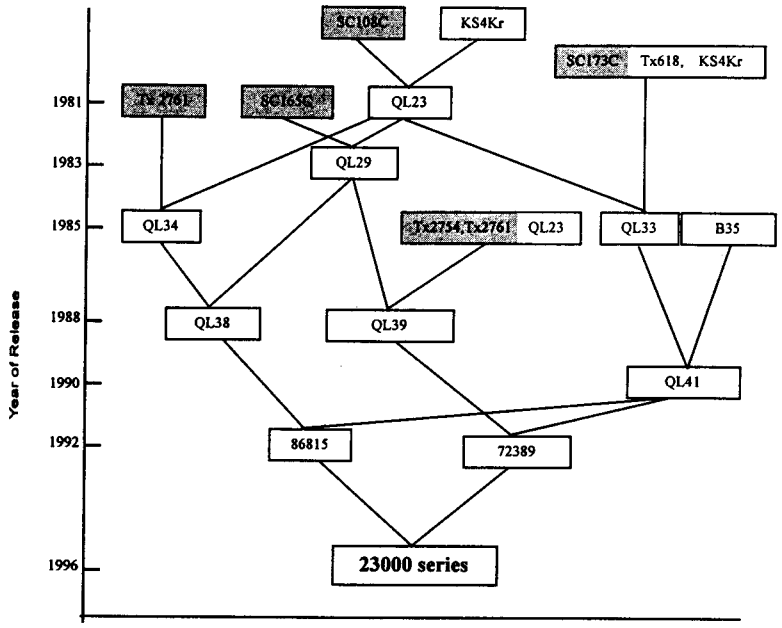
Sharma et al. (1992a) described the breeding method used at ICRISAT. For developing R-lines, DJ 6514 was crossed with locally adapted susceptible germplasm (IS 3443) to produce ICSV 197, a line with the same level of resistance as DJ 6514, but with better agronomic type (except for small grain size). ICSV 197 then was crossed with A 6250 (a Zerazera line) to produce high-yielding, large kernel hybrids with a significant but reduced level of midge resistance. ICSV 745 and ICSV 735 are examples. A similar procedure was used to develop the B lines, a number of which are now undergoing male sterilization in A_1 cytoplasm, these having two doses of locally adapted, susceptible germplasm and one of DJ 6514.

An aim of the Texas program has been the development of germplasm that combines resistance from several different sources. The method used (Peterson et al., 1994) is similar to that of other programs, but relies less than ICRISAT's program on backcrossing to locally adapted but susceptible materials, probably because converted lines (locally adapted at least for height and maturity) are used as sources of resistance.

A method of crossing, evaluation, selection, and subsequent recombination to start a new cycle with an occasional infusion of new material is used in the Australian B-line breeding program (Figure 1)

(Henzell et al., 1994). This method has been used to combine a high level of midge resistance and stay green in the 23000 series lines. Sources of midge resistance were SC108C-14E, SC165C-14E, SC173C-14E, Tx2754, and Tx2761. The stay green source was B35. Intermediate lines or derivatives from these sources combined to form the 23000 series were QL38, QL39 and QL41.

Molecular marker studies show a fragment of chromosome on linkage group B (Y.Z. Tao, 1996, personal communication) from SC165-14E that has been retained through at least four generations of crossing and phenotypic selection (Jordan et al., 1996; D. Jordan, 1996, personal communication). Conservation of this region also has been observed in a number of independent crosses in the B-line program. Data (Y.Z. Tao, 1996, personal communication) suggest this region is linked with resistance to sorghum midge in the QL39 × QL41 recombinant inbred lines. This region is found in the 23000 series lines, as well as 72389, one of their parents. The 72389 line has only a moderate level of resistance, whereas the 23000 series lines have a high level. So there are other unidentified midge resistance genes in the series lines, most likely from QL38 or QL39, which have not yet been linked with markers.



The pedigrees of the key crosses in the QDPI B line breeding. Midge resistant sources shaded.

Figure 1. Pedigree chart of the key crosses used to develop the 23000 series B-lines. Shaded boxes are midge-resistant sources, drawn lines indicate parentage and illustrate conservation of chromosome regions from SC165, B35 and Tx2754 × Tx2761.

Screening and Selection Methodology For Resistance to Sorghum Midge

Conventional

In conventional programs, initial selection is carried out by comparing seed sets in field evaluations (Peterson et al, 1994; Henzell et al,. 1994; and Sharma et al., 1994a). Also, tests are planted in localities and times so flowering occurs when midge are most abundant. At ICRISAT, Australia, and some areas of Texas, infestor rows are used to increase midge abundance. However, there is no need for infestor rows at Corpus Christi, Texas, because of the high (80-100midge/panicle/day) midge population.

At ICRISAT, final selection is based on a head cage test (Sharma et al., 1988), which overcomes any chance that differences in seed set are due to visiting antixenosis. This is not the practice in Australia or Texas because there is a strong correlation (r = 0.89) between field and cage test data (D. Butler and B.A. Franzmann, 1996, personal communication).

In each program, temporal and spatial variation in midge abundance in field tests is accounted for by recording flowering dates and by placing check genotypes at regular intervals in the test site. An alternative no-choice test developed by Franzmann (1996) assumes that oviposition antixenosis is the major mechanism of resistance. Differences in the number of eggs laid in a cage under laboratory conditions by five ovipositing females on 50 flowering spikelets of different sorghum genotypes over the course of six hours at 25°C are highly correlated with damage data collected in the field. This is a rapid test that can be used to evaluate advanced breeding lines.

Marker-Assisted Selection

Resistance to sorghum midge is a good example of a trait for which marker-assisted selection would be useful. The heritability of resistance is variable, largely because of temporal and spatial variation in midge abundance, which can affect the genetic, environmental, and genetic × environment variance components of heritability. Techniques to address the problem of variation in midge abundance can be expensive and time-consuming.

The only project to find molecular markers linked with resistance to sorghum midge is in Australia (Tao et al., 1996). One problem encountered in this project has been the difficulty in collecting good phenotypic data for resistance (the same reason that led to the need for molecular markers). Nevertheless, a number of chromosome regions, including that from SC165-14E mentioned above, have been putatively linked with resistance (Y.Z. Tao, 1996, personal communication). These regions are found mainly on the B and G linkage groups. The putative linkages will be tested before marker-assisted selection is used. Testing will begin in 1996-97.

Data from retrospective analysis of pedigrees in the Australian B-line program (D. Jordan, 1996, personal communication) have provided evidence supporting the linkages determined by Y.Z. Tao. For example, the chromosome region from SC165-14E, shown by Jordan to be retained through a number of cycles

of crossing and selection, is one of the regions shown by Tao to be putatively linked with resistance to sorghum midge.

Results of Breeding for Resistance to Sorghum Midge

Increased resistance to sorghum midge, combined with good agronomic traits, has proven to be an achievable breeding objective in each of the programs, including private sector programs in Australia.

Texas

In Texas, hybrids that combine high levels of resistance to midge and good agronomic type have been produced (Peterson et al., 1994) (Table 3). Recent emphasis has been placed on developing females that, when crossed with males such as Tx2880 and Tx2882, produce hybrids with excellent midge resistance and yield comparable to susceptible hybrids in the absence of midge. Three females (including two selections of MB110) are being increased and tested before release in 1997. Yield, in the absence of midge, of the hybrids AMB110 × RTx2880 and AB110 × RTx2882 is being evaluated in commercial plantings by commercial seed companies and Extension Service personnel.

TAM2566, the first sorghum midge-resistant line released in Texas, was a derivative of SC175-9 (Johnson et al., 1982a). Tx2754 to Tx2781 were released in 1979, with resistance derived primarily from SC175-9 (Johnson et al., 1982b). Resistance in ISR1, released in 1979 (Johnson et al., 1982b), and Tx2782, released in 1981 (Peterson et al., 1983), was derived from the Brazilian line AF28. The first released lines to use resistance sources other than SC175-9 were Tx2801 to Tx2815, released in 1983 (Peterson et al., 1985). Resistance in these lines is derived from SC175-9, SC237-14E, SC423-14E, SC414-14E, or SC644-14E. Resistant lines Tx2869 to Tx2890 were released in 1989 (Peterson et al., 1991), with resistance derived from TAM2566, Tx2782, or SC423-14E. One random mating population, TP8R, has been released. These lines and others from the Sorghum Conversion Program have had a major

Table 3. Grain yield and sorghum midge damage rating of selected hybrids in the 1993 Texas Sorghum Midge Hybrid Test.

Hybrid	Class[2]	Yield (kg ha^{-1})			Midge damage rating[1]		
		Mean	CC[3]	CS[4]	Mean	CC	CS
AMB110 × Tx2880	R × R	4260	2300	6210	3.0	4.7	1.3
AMB110 × Tx2882	R × R	3720	1700	5740	3.7	5.3	2.0
ATx2755 × Tx2767	R × R	2990	540	5440	4.8	7.7	2.0
ATx399 × RTx430	S × S	1240	590	1890	8.3	8.3	8.3
Whole Test Mean		2960	140	4500	4.7	6.2	3.1
$LSD_{.05}$		1150	840	1730	1.4	1.6	1.3

[1]Rated on scale of 1 to 10 where 1 = 0.10% blasted seed, 2 = 11-20% blasted seed, ..., 9 = 81+% blasted seed.
[2]Class = Classification. R = Resistant; S = Susceptible
[3]CC = Corpus Christi
[4]CS = College Station

impact on sorghum midge resistance breeding programs throughout the world.

ICRISAT

At ICRISAT, significant progress has been made in producing agronomically acceptable lines with resistance to sorghum midge. ICSV 197 (DJ 6514 × IS 3443), the most significant development in breeding for resistance to midge at ICRISAT (Sharma et al., 1994a), has DJ 6514's level of resistance combined with improved agronomic type. Subsequent crosses with ICSV 197 have resulted in lines such as ICSV 745, ICSV 735, ICSV 758, ICSV 804, ICSV 88032. ICSV 745 has been released in Karnataka, India, and is being tested on farms in Andhra Pradesh, India, and in Sudan. ICSV 735, ICSV 758, and ICSV 804 are in on-farm trials in Mayanmar. ICSV 735 is being tested in Sudan and India. Significant progress has been made in producing females with moderate levels of resistance and good agronomic type (Reddy and Sharma, 1992). They are undergoing final testing before release.

Australia

In Australia, progress has been made in both private and public programs in developing lines and hybrids that combine resistance with good agronomic type. Farmers now have access to resistant hybrids that yield at least as much as susceptible hybrids in the absence of midge, and have a level of resistance high enough to significantly affect the integrated management of the pest.

QL23 and QL25 through QL41 have been officially released from the QDPI breeding program (Henzell et al., 1994). An additional 76 lines have been sold to the private sector in Australia and the U.S. under a plan whereby companies pay an upfront fee [currently $500 (Australian) per line] and then a royalty on any line or derived line. Germplasm from the QDPI sorghum breeding program is available free to public institutions. Nearly all hybrids developed and sold by the private sector in Australia now have a level of midge resistance. The level of resistance varies from low (with an economic threshold twice that of a susceptible hybrid) to moderate (with an economic threshold seven times that of a susceptible hybrid).

Progress in increasing levels of resistance in the QDPI program is illustrated in Figure 2. QL39's level of resistance probably represents "field immunity" to midge in Australia. QL38 has a similar level of resistance. One season's data indicate some of the 23000 series female lines also have high resistance, combined with the stay green trait. Less progress has been made in developing R-lines, and therefore hybrids, with high levels of stay green and resistance to midge. However, one year's (1995-96) data indicate some hybrids with 23000 series females and some advanced males have resistance levels significantly greater than that of AQL39 × QL36, which has a moderate level of resistance.

On-Farm Adoption of Cultivars with Resistance to Sorghum Midge

In India, progress has been made in transferring midge-resistant sorghum to farmers. ICSV 745 was released as DSV 3 in Kanataka. Also, on-farm tests in Andhra Pradesh and Tamil Nadu are proving that grain yield of ICSV 745 is comparable to that of commercial cultivars. ICSV 735 is planted on a limited scale in Andhra

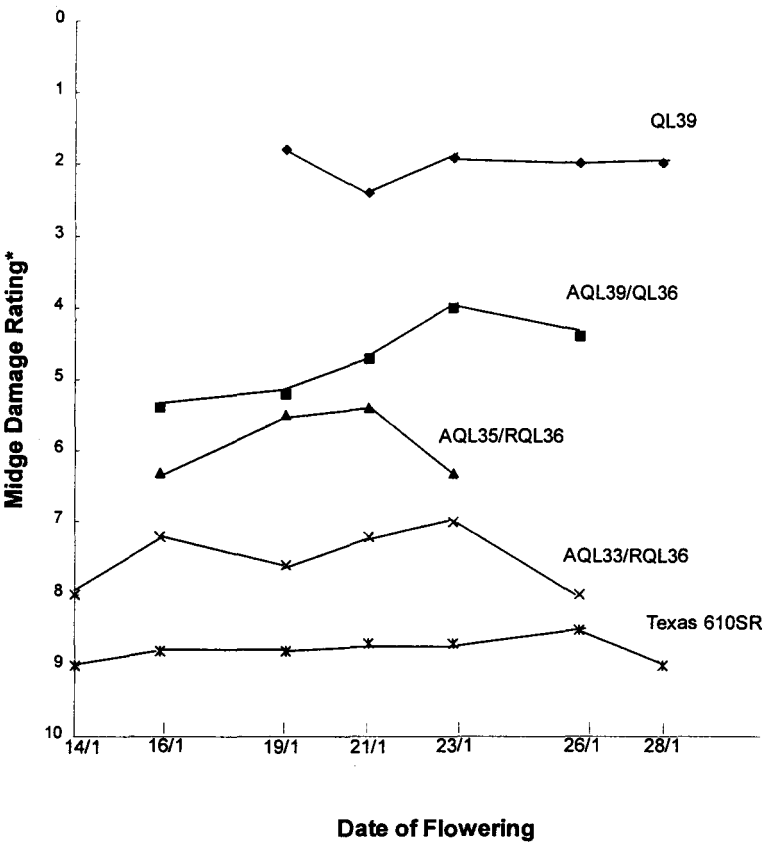


Figure 2. Midge damage ratings of five genotypes following field infestation.

Pradesh. ICSV 804 is cultivated over a large area in Myanmar.

In the U.S., DK60 is the only midge-resistant hybrid marketed. It is a full season hybrid and has gained acceptance in the delta region of Louisiana and Mississippi (J. Raab, 1996, personal communication). The area planted to resistant hybrids in the U.S. is expected to increase if hybrids such as AMB110 × RTx2880 prove equal in yield to susceptible hybrids in the absence of midge.

In Argentina, DA49 was introduced in 1992. It is a medium-maturity hybrid and is gaining widespread acceptance. DA50 was introduced in 1994. It is a medium-full season hybrid and is gaining in popularity in the eastern sorghum growing region (J. Raab, 1996, personal communication).

In Australia, the first midge-resistant hybrid was marketed in 1985 (N. Muller, 1996, personal communication) Since then, Australian farmers have readily accepted hybrids with midge resistance, and in 1994-95 more than 80% of the sorghum production area was planted with hybrids with some level of resistance. Reasons for this immediate adoption vary:

- Damage by midge and the cost of chemical control were major economic constraints, even though midge abundance in fields is relatively lower in Australia than, for example, in the coastal bend of Texas. Therefore, relatively low levels of resistance were needed to greatly reduce the impact of midge.
- Farmers understand that resistance does not imply immunity and there is a threshold for a particular resistance level above which chemical control should be added to their pest management strategies.
- A joint seed industry/QDPI plan to standardize the measurement and description of midge resistance (Franzmann et al.,1996) has been coupled with economic injury level research. Consequently, farmers receive consistent information from the various seed companies on the level of resistance in particular hybrids and on their midge control management strategies.
- Resistance to sorghum midge is a major breeding objective in both private and public sectors, because Australia is currently free of greenbugs, sorghum downy mildew, shoot fly, and panicle feeding bugs, which otherwise would require division of resources.

Durability of Resistance to Sorghum Midge

One question relating to HPR is the inadvertent selection of resistant biotypes in the pest population in response to the host plant resistance. However, it is thought that resistance to sorghum midge will be long-lived for the following reasons:

- Selection pressure on the pest is relatively low because the resistance level of the host plant does not approach immunity and, in many situations, selection will apply to only one or two midge generations per year.
- Abundant forage and wild sorghum serve as alternate hosts for the insect, thus maintaining avirulent genes in the pest population.
- Midge resistance is a multigenic trait, although this does not necessarily confer durability.
- The fitness of the pest is not (Franzmann, 1990) or only slightly affected (Sharma et al., 1993) by HPR.
- The major biological effect of resistance on sorghum midge is that fewer eggs are laid in spikelets of resistant sorghum, most likely due to spikelet structure. This factor can be overcome by modifications to the ovipositors of females, increase in their oviposition rate, earlier activity, or increased longevity. It is unlikely (although not known) that there is significant genetic variation in the midge population for these traits.

Prospects and Research Needs for Breeding for HPR to Sorghum Midge

Globally, prospects are that HPR will play a major role in the integrated pest management of sorghum midge, and breeders will consider midge resistance no more than an additional trait necessary for local adaptation. Prospects vary

among the countries in which sorghum midge is a significant constraint to production.

In Australia, it is likely midge resistance levels will be reached and combined with good agronomic type, so HPR will be the only component farmers will use in the integrated management of sorghum midge. Future work on durability of resistance may necessitate re-evaluation of this prospect.

In the U.S., sorghum hybrids resistant to midge will be accepted when they perform comparably to susceptible hybrids in the absence of midge. Experimental hybrids are close to, if not already at, this yield level. Producers are increasingly concerned about input costs, and innovative producers will adopt the technology when available. Soon afterward, other producers will adopt the technology as they see the economic and ecological benefits. Since at least one seed company is currently marketing a sorghum midge-resistant hybrid, other companies will follow suit. Most likely, seed companies will develop midge-resistant hybrids with at least one resistant parent derived from germplasm developed through a public breeding program. A similar prospect applies to Argentina.

In India, midge infestations are common, particularly in the states of Karnataka, Tamil Nadu, and Maharashtra, while 10-20% midge damage is common in most of the sorghum growing areas. Sorghum midge is a serious pest in Myanmar. Because of a strong private and public sector seed industry in India, resistance to sorghum midge will largely be utilized in hybrids. Production of midge-resistant cultivars will not only stabilize production, but also will minimize the use of insecticides. Dual purpose midge-resistant cultivars will be useful in northern India, where midge cause much damage.

In Africa, midge outbreaks are common in Nigeria, Niger, Burkina Faso, Benin, Ethiopia, Sudan, Kenya, Yemen, and Tanzania. Midge resistance in these countries can be provided by varieties because of a limited or non-existent seed industry.

In order to achieve the prospective outcomes described above, the following research needs must be met:

1. Financial support for breeding and entomology must continue, at least at the current level. Developing sorghum resistant to midge combined with high yield potential is an obtainable breeding objective with predicted lasting benefits. Benefits include greater efficiency of production and a chemically cleaner product and environment.

2. The world collection needs to be continually searched for additional sources of resistance. The Texas/USDA Sorghum Conversion Program has provided invaluable sources of resistance to midge and it is essential that the program continue.

3. Genes and mechanisms of resistance in the various sources need to be identified and combined to produce higher resistance levels and more durable resistance. Identification of a genetically dominant source of resistance would be a major benefit to breeding and deployment by the seed industry.

4. The cause of resistance and how it affects the insect needs to be determined to enable breeders to more efficiently select among progeny and improve the efficiency of their programs.

5. Genetic transformation promises access to a new source of resistance genes. There are a number of possible useful alien genes. Before this technology can be reliably accessed, however, much work needs to done in these areas:

- development of an efficient transformation system
- identification and testing of the efficacy of potential toxins coded by alien genes
- development of suitable constructs
- development of a strategy for deployment of alien genes. For example, should largely single, alien genes be used alone, alternatively pyramided on constructs, or pyramided with existing host resistance genes?

6. The possibility of selecting HPR-breaking biotypes of the pest (as has been indicated for DJ 6514's resistance in Kenya and Yemen) needs to be addressed. The question of biotype development also arises when viewing conflicting data from different countries on levels of resistance, although these differences are more likely due to differences in methodology. The implications of resistance-breaking biotypes of midge are serious enough that this question needs to be resolved. Linking DNA analysis of sorghum midge populations with evidence of midge population × sorghum genotype differential interaction would be useful.

7. Molecular markers for resistance to sorghum midge will play a major role in future breeding programs. Research in this area needs to be strengthened because this technology will greatly enhance breeding efficiency. For example, markers can be used for marker-assisted selection as well as provide information on numbers, locations, and gene action for resistance. This information could be used to direct pyramiding of genes, predict the resistance of inbred lines and hybrids, facilitate backcrossing of resistance genes into different genetic backgrounds, etc.

8. More research is needed on the relationship between sorghum midge abundance and damage to resistant hybrids. This information is essential for managing and adopting sorghum cultivars with midge resistance. Midge resistance will be part of an IPM approach. Producer trust in this technology will depend on economic thresholds that provide protection from risk.

9. The seemingly negative correlation between midge resistance and kernel size needs to be further investigated. Resistance evaluation should include selection for larger seed and glumes that do not adhere to the caryopsis.

Sorghum Panicle Feeding Bugs

Panicle feeding bugs are increasing in importance in West Africa and India. In West Africa, *Eurystylus oldi* causes quantitative and qualitative losses by feeding and laying eggs in maturing sorghum panicles (Ratnadass and Ajayi, 1995). In India, *Calocoris angustatus* causes damage by feeding on developing grain (Hiremath and Thontadarya, 1984). Sharma and

Lopez (1989) recorded yield losses as high as 54-89% in India. For both insects, molds growing on damaged grains can significantly affect grain quality. The importance of the panicle feeding bugs has increased with the introduction of improved cultivars (Ratnadass et al., 1995).Yield losses caused by these pests in the semi-arid tropics have been estimated to cost $198 million (ICRISAT, 1992).

The discovery of host-plant resistance to *C. angustatus* (Sharma and Lopez, 1992) and *E. oldi* (Sharma et al., 1992a, 1994a; Ratnadass et al., 1994a, 1995) has led to breeding programs in India (ICRISAT Asia Center) and West Africa (Mali), the key features of which are described below.

Sources of Resistance to Sorghum Panicle Feeding Bugs

It is important to recognize the slight, but significant, differences in the biology and behavior of *E. oldi* and *C. angustatus* (Ratnadass et al., 1994b). The former causes damage by feeding and laying eggs in the developing caryopsis, while the latter causes damage by feeding on the grain (eggs are laid in the spikelets at anthesis). This difference leads to slight differences in sources and mechanisms of resistance to the two pests (Ratnadass et al., 1994b).

Guinea sorghum, the dominant race in West Africa, is resistant to both head bug species (Sharma et al., 1994b). This is a relatively low-yielding sorghum, with long glumes and vitreous grain. In general, if Guinea sorghum is crossed with other taxonomic groups, the offspring are low-yielding and lose most of the desirable grain charactistics (A. Toure, 1996, personal communication). However, at ICRISAT Asia Center, a number of lines have been developed from crosses with elite Zerazera material that combine the Zerazera plant type with the grain and glume type of Guinea sorghum (J.W. Stenhouse, 1996, personal communication). More advanced material has been developed by backcrossing these derivatives with other guinea sorghum. Hybrids based on this material in A_1 cytoplasm will be tested in West Africa. Evidence suggests this material will be useful in developing head bug and grain mold resistant cultivars for West Africa (J.W. Stenhouse, 1996, personal communication).

Malisor 84-7, a line derived from a random mating population in Mali, is resistant to *E. oldi* and *C. angustatus* under both natural and artificial infestations (Sharma et al., 1994b; Ratnadass et al., 1994a). It has moderate yield potential, medium height, and good grain quality, and has proven to be a useful source of resistance in breeding programs for both insects.

Sharma and Lopez (1992) and Sharma et al. (1992a, b) reported that IS 17610, IS 17645, IS 21443, and IS 17618 have moderate levels of resistance to *C. angustatus,* and that CSM 388, S 29, IS 14322, Malisor 84-7, and 'Sakoika' are good sources of resistance to *E. oldi.* Ratnadass et al. (1995) reported that loose-panicled types IS 17645, IS 20740, and IS 20638 supported fewer head bugs (*E. oldi*) than other *C. angustatus*-resistant genotypes, possibly reflecting the difference in biology of the two insects. With the exception of Malisor 84-7, all the above lines are Guinea sorghum.

Mechanisms of Resistance to Sorghum Panicle Feeding Bugs

Antixenosis

Oviposition antixenosis is an important component of resistance to panicle feeding bugs in sorghum (Sharma and Lopez, 1990). For example, in cage tests, *C. angustatus* laid fewer eggs on lines IS 2761, IS 17610, IS 17618, and IS 17645 (Sharma and Lopez, 1990), and *E. oldi* laid fewer eggs on CSM 388 (Sharma et al., 1994b). Ratnadass et al. (1995) reported that under head-cage conditions, fewer *E. oldi* bugs developed on IS 20740, IS 20638, IS 17645, and IS 23748.

For *C. angustatus,* which lays its eggs between the glumes at anthesis, factors associated with oviposition antixenosis include long, hard, and less hairy glumes. Long glumes that cover the grain for 20 days after anthesis and (possibly) faster hardening of grain are associated with resistance to *E. oldi* (Sharma et al., 1994b). However, Malisor 84-7, which is resistant to both *E. oldi* and *C. angustatus*, does not have these glume traits. Its resistance is associated with faster grain hardening (Fliedel et al., 1993); free phenolic compounds and tannins are not involved.

Visiting antixenosis has been reported to be a mechanism of resistance to these insects (Sharma and Lopez, 1990; Sharma et al., 1994b; Ratnadass et al., 1995) in some lines (e.g., IS 2761 and IS 6984). These lines have proved to be susceptible (or less resistant) under no-choice head-cage conditions, and their usefulness in farmers' fields is not clear.

Antibiosis

There is evidence of antibiosis operating against *C. angustatus*. Post-embryonic development of *C. angustatus* is prolonged by 1-2 days on IS 17610, IS 17618, and IS 17645. Survival and establishment of first instar nymphs is relatively lower on IS 17645 compared with the susceptible checks CSH 1 and CSH 5 (Sharma and Lopez, 1990). Growth rate and efficiency of conversion of ingested food into body mass are lower on IS 6984 and IS 2761, compared with CSH 5.

Tolerance

There is evidence of genotype differences in extent of damage caused by *C. angustatus*. For example, IS 9692, CSH 1, IS 17645, and IS 17610 suffered less damage per insect than did IS 2761, IS 6984, and CSH9 (Sharma and Lopez, 1993). The same response was observed with 87W810 (Ratnadass et al., 1995). The reason for this apparent tolerance is not known. The usefulness of this mechanism of resistance may be limited to low bug density situations.

Genetics of Resistance to Sorghum Panicle Feeding Bugs

Relatively little is known about the inheritance of resistance in sorghum to these panicle feeding bugs. The mechanisms of resistance suggest a multigenic character. Malisor 84-7's resistance to *E. oldi* under artificial infestation is recessive in nature, with no maternal effects (Ratnadass et al., 1995). In a recent study, resistance to *E. oldi* under natural infestation was shown to be controlled by addi-

tive gene action (A. Ratnadass, 1996, personal communica-tion).

Resistance to *C. angustatus* is controlled by additive gene action. General combining ability effects of PM 7061A for susceptibility are negative while the general combining ability effects of 296A are positive for susceptibility (H.C. Sharma, 1996, personal communication).

Breeding Methods for Resistance to Sorghum Panicle Feeding Bugs

Rapid progress has been made using pedigree and limited backcross methods. However, greater long-term progress is more likely using population breeding because of the multigenic nature of resistance and other traits contributing to local adaptation. Information on the genetics of resistance and different mechanisms of resistance will come, not only from conventional studies, but also from molecular marker research.

Screening and Selection Methodology for Resistance to Sorghum Panicle Feeding Bugs

A reliable artificial infestation head-cage technique has been developed in West Africa and India to screen sorghum lines for resistance to *E. oldi* (Sharma et al., 1992b) and *C. angustatus* (Sharma and Lopez, 1992). These tests have been essential in identifying sources of resistance to panicle feeding bugs and selection of resistant segregates.

The cage test is used for final testing of materials that have been selected in field trials (Ratnadass et al., 1994a, 1995; Sharma and Lopez, 1992). The field tests are planted in localities where infestation levels are likely to be high. Infestor rows of susceptible genotypes are planted earlier to increase bug abundance. Number of insects visiting each line is assessed and the damage caused is rated visually.

A simple method to assess damage and screen for *E. oldi* resistance proposed by Doumbia et al. (1995) involves comparing grain damage of unprotected and protected (by bags, cages or chemical treatment) panicles under natural infestation conditions.

Marker-assisted selection is not being used in head bug resistance breeding programs. However, research aimed at identifying RFLP markers linked with Malisor 84-7 resistance genes is underway using F_2 and F_3 progeny from the Malisor 84-7 × S34 cross (A. Ratnadass, 1996, personal communica-tion, and A. Toure, 1996, personal communication).

Results of Breeding for Resistance to Sorghum Panicle Feeding Bugs

Results from ICRISAT's West African and Asia Center breeding programs suggest that combining resistance to sorghum panicle feeding bugs with local adaptation is readily achievable. Promising material with a useful level of resistance and acceptable agronomic characteristics has been selected from crosses of Malisor 84-7 and high-yielding West African lines (Ratnadass et al., 1995).

The Guinea-derived material described earlier (J.W. Stenhouse, 1996, personal communication) represents significant progress toward developing panicle feeding bug-resistant cultivars that also are

adapted to West African conditions. The resistance of some of this material to *C. angustatus* has been confirmed (H.C. Sharma, 1996, personal communication).

Future Prospects and Research Needs for Breeding for Resistance to Sorghum Panicle Feeding Bugs

Prospects are good that deployment of HPR will play a major role in the integrated management of sorghum panicle feeding bugs in West Africa and India, considering the importance of these pests and of the crop.

Research needs to achieve this outcome include:

1. Continued breeding and associated entomology research at the current level in West Africa and at an increased level in India. Results indicate that combining host-plant resistance with local adaptation is achievable and long-standing.

2. Identification of new sources of resistance.

3. Determination of the genes and mechanisms of resistance to pyramid diverse resistance genes and combine diverse resistance mechanisms, leading to higher levels of more durable resistance.

4. Expansion of molecular marker research to increase breeding efficiency through marker-assisted selection, and to increase knowledge of the genetics of resistance.

5. Enhancement of economic threshold information as it is essential for proper management and adoption on farms of cultivars with resistance to panicle feeding bugs.

Sorghum Head Caterpillars

Worldwide, a number of head caterpillars damage developing grain (Sharma and Teetes, 1995). Of these, *H. armigera* in Australia, Africa, and India and *H. zea* in the U.S. are most significant. To complicate matters, *H. armigera* prefers to oviposit on midge-resistant hybrids (Scholz and Webster, 1993).

Despite the importance of head caterpillars, there is no current breeding activity except for some breeders who routinely select for open-panicles because of reported higher larval numbers on compact panicles than on loose panicles. The causes of this observed difference have not been fully studied (Franzmann, 1986; Teetes et al., 1992)

Reports of reliable HPR are inconclusive. An alternate hope is that alien genes introduced via transformation will provide sufficient resistance so HPR can be incorporated into the integrated management of these pests.

Millet Head Miner

Pearl millet is an important food crop in the harsh environment of West Africa, especially in Sahelian countries where soil is sandy and acidic and rainfall is scarce, poorly distributed, and erratic (Nwanze and Harris, 1992). Pearl millet panicles are attacked by a variety of insect pests (Nwanze and Harris, 1992), including millet head miner, *H. albipunctella*, which has become a serious pest in sub-Saharan West and Central Africa regions

since the first outbreaks in the mid 1970s. Damage to pearl millet by *H. albipunctella* is caused by larvae feeding on floral glumes and pedicles. Yield loss caused by this pest is variable but can be as high as 100% (Krall et al., 1995). The development of reliable techniques for managing this pest must receive high priority.

Sources of Resistance to Millet Head Miner

Resistance to insect pests of pearl millet, in general, has been discussed by Jotwani (1978), Gahukar (1984), Nwanze (1985), Sharma (1987), Sharma and Davies (1988), and Nwanze and Harris (1992). A number of reports of genotype differences in HPR to millet head miner are summarized in Table 4 (Youm and Kumar, 1995). Added to this list are DGP1, 410 × DGP1, and MBH-110 (Youm and Kumar, 1995). However, it is not clear that each of these lines is resistant, since some have escaped damage due to their phenology (Youm and Kumar, 1995).

Mechanisms of Resistance to Millet Head Miner

Few studies have been conducted to identify mechanisms of resistance to millet head miner (Youm and Kumar, 1995). Oviposition antixenosis has been suggested as a mechanism. Fewer eggs are laid on pearl millet with short involucral bristles and long floral pedicels, because eggs normally are laid at the base of florets or stuck to rachis and pedicels (Guevremont, 1982, 1983). However, Bal (1992) and Youm and Kumar (1995) showed that this mechanism does not always explain differences. Compactness of panicle, tolerance, and antibiosis have been suggested as mechanisms of resistance (Table 4). Youm and Kumar (1995) concluded that the mechanism of resistance to the millet head miner is not known.

Screening and Selection Methodogy for Resistance to Millet Head Miner

The most significant progress in research into HPR to millet head miner has been made in the area of screening.

Field Evaluation Using Natural Infestations

Resistance evaluation under artificial infestation by millet head miner is more reliable than evaluation under natural infestation (Youm and Kumar, 1995), due to the variation in insect abundance within and between seasons. Variation within a season results in temporal escapes (pseudo-resistance), and variation between seasons results in different levels of damage, which complicate the assessment of genotype variation.

Evaluation Using Artificial Infestations

To overcome such difficulties, a head cage technique was developed in which panicles are enclosed in a cage and artificially infested with millet head miner larvae (Sharma et al., 1992b; Youm and Kumar, 1995). This technique is more reliable than evaluation under natural conditions and is an important step in developing a more reliable breeding program for HPR. The plant growth stage of 1/3 panicle exertion is the most susceptible for artificial infestation by larvae, and one week-old larvae are more virulent

Table 4. Pearl millet reported resistant to millet head miner, and probable mechanism.

Variety	Mechanism	Observations/ comments	Source
ICMS 7703 ICMS 7838 ICH 165 Souna CIVT II	Temporal escape (pseudo-resistance)	Results based on a 3-year study. High variability in percentage of attack. Other factors not investigated.	Gahukar (1987)
IBMV 8001 Souna ICMS 7838 H24 38 ICMS 7819	Oviposition nonpreference	Mechanisms not known, further re-evaluation needed, IBMV 8001 reported susceptible (Bal 1992).	Gahukar (1984) (in Gahukar et al. 1986), N'Doye and Gahukar (1987), Gahukar et al. (1986) (in Bal 1992)
H9-127 ICMS 7819	Tolerance	True mechanism probably unknown	Gahukar et al. (1986), (in Bal 1992), N'Doye And Gahukar (1987)
IBMV 8001 3/4 HK-78	Antibiosis	Tolerance and nonpreference mechanisms attributed to ICMS 7819.	
Nigerian Composite HK B-Tif CIVT HKP	Nonprefeence bristles to lower infestation	HKP susceptible (ICRISAT 1987)	[Gahukar (1981, 1984, 1986), ICRISAT (1984), Guevremont (1982,
Zongo Nieluva Boudouma IBMV 8302 INMG1 INMG 52 SRM-Dori P3 Kolo IBMV 8001 Kassa-blaga Youmee-Nini Tass-Yombo	Compactness, position, and length of bristles	Mechanisms not studied, further evaluation may be necessary	1983), Maïga (1984), CILSS (1985) in N'Doye and Gahukar 1987]

Source: Youm & Kumar, 1995.

than one day-old larvae. However, first instar larvae (1-2 days old) should be used when infesting so resistance to early instars can be identified. Infestation by 25-45 larvae per panicle is sufficient to cause 51-60% damage to susceptible pearl millet plants and is sufficient to screen pearl millet varieties for damage response to the millet head miner.

A laboratory rearing technique has been developed to supply sufficient larvae for artificial screening. An artificial diet (Bioserv Inc #9782, New Jersey, U.S.) can be used to successfully mass rear the insects through seven generations without their going into diapause. Rearing takes place under these environmental conditions: 12:12 day:night photoperiod; 60-70% relative humidity; and 28°C. Further

research is needed to develop a less expensive diet that can be developed locally.

Future Prospects and Research Needs for Resistance to Head Miner

Prospects for HPR to the head miner are not clear due to limited research in this area. Research needs include:

1. High priority given to breeding for HPR to the millet head miner and associated entomology.

2. Search for additional sources of resistance.

3. Determination of the mechanisms of resistance.

4. Determination of the genetics of resistance.

5. Further refinement of screening and selection techniques for resistance, particularly rearing of the insect in the laboratory.

Acknowledgments

The authors gratefully acknowledge the assistance of Dr. I. Godwin in developing the discussion on alien genes and of Dr. Y.Z. Tao and Mr. D. Jordan for the molecular marker information.

References

Agrawal, B.L., C.V. Abraham, and L.R. House. 1988. Inheritance of resistance to midge, *Contarinia sorghicola* Coq., in sorghum, *Sorghum bicolor* (L.) Moench. Insect Sci. Applic. 9:43-45.

Bal, A.B. 1992. Les principaux insectes du mil au Senegal: Improvement du parasitisme et methodes de lutte. p. 13-23. *In* John Libbey and Eurotext (eds.) La lutte integree contre les ennemis des cultures vivrieres dans le Sahel: Actes du deuxieme seminaire sur la lutte integree contre les ennemis des cultures vivriers dans le Sahel, 4-9 Janvier 1990, Bamako, Mali. Institute du Sahel, Bamako, Mali.

Ball, C.R., and S.N. Hastings. 1912. Grain sorghum production in the San Antonio region of Texas. USDA Bur. Plant Ind. Bull. No. 237:12-25.

Bergquist, R.R., P. Rotar, and W.C. Mitchell. 1974. Midge and anthracnose head blight resistance in sorghum. Trop. Agric. 51:431-435.

Boozaya-Angoon, D., K.J. Starks, D.E. Weibel, and G.L. Teetes. 1984. Inheritance of resistance in sorghum, *Sorghum bicolor*, to the sorghum midge, *Contarinia sorghicola* (Diptera: Cecidomyiidae). Environ. Entomol. 13:1541-1543.

Casas, A.M., A.K. Kononowicz, U.B. Zehr, D.T. Tomes, J.D. Axtell, J.D. Butler, R.A. Bressan, and P.M. Hasegawa. 1993. Transgenic sorghum plants via microprojectile bombardment. Proc. Nat. Acad. Sci., USA 90:11212-11216.

Diarisso, N.Y., B.B. Pendleton, and G.L. Teetes. 1995. Sorghum spikelet morphology and flowering time as causes of resistance to sorghum midge. Ann. Pl. Resist. Insects Newsl. 21:19.

Doumbia, Y.O., K. Conare, and G.L. Teetes. 1995. A simple method to assess damage and screen sorghums for resistance to *Eurystylus marginatus*. p.183-189. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Proc. int. consult. work., 4-7 Oct 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Fliedel, G., A. Ratnadass, and M. Yajid. 1993. Study of some physicochemical characteristics of developing sorghum grains in relation to head bug resistance. Presented at the ICC Int. Symp. Cereal Sci. Tech.: Impact on a Changing Africa, 9-13 May 1993, Pretoria, South Africa. (Limited distribution).

Franzmann, B.A. 1986. Effect of grain sorghum panicle type on *Heliothis armigera* (Hübner). Sorghum Newsl. 29:58.

Franzmann, B.A. 1988. Components of resistance to sorghum midge in grain sorghum. p. 277-278. *In* K.S. McWhirter, R.W. Downes, and B.J. Read (eds.) Proc. 9th Australian plant breeding conference, Agriculture Research Institute. Private Mail Bag, Wagga-Wagga, New South Wales, Australia.

Franzmann, B.A. 1990. Midge fecundity after development on resistant sorghum. Sorghum Newsl. 31:61.

Franzmann, B.A. 1993. Ovipositional antixenosis to *Contarinia sorghicola* (Coquillett) (Diptera:

Cecidomyiidae) in grain sorghum. J. Aust. Ent. Soc. 32:59-64.

Franzmann, B.A. 1996. Evaluation of a laboratory bioassay for determining resistance levels to sorghum midge *Contarinia sorghicola* (Coquillett) (Diptera: Cecidomyiidae) in grain sorghum. Aust. J. Ent. 35:119-123.

Franzmann, B.A., and D.G. Butler. 1993. Compensation for reduction in seed set due to sorghum midge in midge-susceptible and resistant sorghum. Aust. J. Exp. Agric. 33:193-196.

Franzmann, B.A., D.G. Butler, R.G. Henzell, D.S. Fletcher, and J.H. Cutler. 1996. A sorghum industry scheme assigning midge resistance levels to commercial hybrids. p. 359-363. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proceedings of the third Australian sorghum conference, 20-22 February 1996, Tamworth. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No. 93.

Franzmann, B.A., and A.T. Hardy. 1996. Testing the host status of Australian indigenous sorghums for the sorghum midge. p. 365-367. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proceedings of the third Australian sorghum conference, 20-22 February 1996, Tamworth. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No. 93.

Gahukar, R.T. 1984. Insect pests of pearl millet in West Africa: A review. Trop. Pest Manag. 30:142-147.

Gahukar, R.T. 1987. Relationship between spike worm (*Raghuva albipunctella*) infestation and flowering of pearl millet, and some sources of resistance. Agronomie 7:595-598.

Gahukar, R.T., H. Guevremont, V.S. Bhatnagar, Y.O. Doumbia, M. Ndoye, and G. Pierrard. 1986. A review of pest status of the millet spike worm, *Raghuva albipunctella* de Joannis (Noctuidae: Lepidoptera) and its management in Sahel. Insect Sci. Applic. 7:457-463.

Geering, Q.A. 1953. The sorghum midge, *Contarinia sorghicola* (Coq.) in east Africa. Bull. Ent. Res. 44:363-366.

Guevremont, H. 1982. Etudes sur la minese de l'epiet autres insectes du mil. Rapport annuel de recherches pour l'annee 1981. Section Protection des Vegetaux, Centre National de Recherches Agronomiques de Tarna, Maradi, Niger.

Guevremont, H. 1983. Recherches sur l'entomofaune du mil. Rapport annuel de recherches pour l'annee 1982. Section Protection des Vegetaux, Centre National de Recherches Agronomiques de Tarna, Maradi, Niger.

Hanna, W.W., B.R. Wiseman, R.R. Duncan, and K.F. Schertz. 1989. Registration of Tift MR 88 midge resistant sorghum germplasm. Crop Sci. 29:245-246.

Hanna, W.W., B.R. Wiseman, and R.R. Duncan. 1993. Registration of Tift MR 9115, and Tift MR 9120 midge resistant sorghum germplasm. Crop Sci. 33:1118.

Harris, K.M. 1995. World review of recent research on panicle insects of sorghum and pearl millet. p. 7-25. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Int. consult. workshop, 4-7 Oct 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324 Andhra Pradesh, India.

Henzell, R.G., R.L. Brengman, and B.A. Franzmann. 1993. Advances in breeding for host plant resistance to the sorghum midge and for stay green in grain sorghum. p. 163-167. *In* Proc. 10th Aust. breed. conf. 18-23 April 1993, Gold Coast, Queensland, Australia.

Henzell, R.G., R.L. Brengman, and F.D. Page. 1980. Transference of sorghum midge resistance into agronomically acceptable lines. *In* Proc. Aust. agron. conf. April 1980. Queensland Agricultural College, Lawes, Queensland, Australia.

Henzell, R.G., R.L. Brengman, F.D. Page, D.S. Fletcher, L.van Slobbe, and G. Foster. 1986. Breeding for midge resistance in grain sorghum in Queensland. p. 7.10-7.18. *In* M.A. Foale and R.G. Henzell (eds..) Proc. first Aust. sorghum conf., 4-6 February 1986. Queensland Agricultural College, Gatton, Queensland, Australia.

Henzell, R.G., B.A. Franzmann, and R.L. Brengman. 1994. Sorghum midge resistance research in Australia. Int. Sorghum Millets Newsl. 35:41-47.

Hiremath, I.G., and T.S. Thontadarya. 1984. Seasonal incidence of the sorghum earhead bug, *Calocoris angustatus* Lethiery (Hemiptera:Miridae). Insect Sci. Applic. 5:469-474.

Huelgas, V.C., P. Lawrence, S.W. Adkins, Muhammad U. Mufti. 1996. Utilisation of the Australian native species for sorghum improvement. p. 369-375. *In* M.A. Foale, R.G. Henzell, and J. Kneipp (eds.) Proc. third Aust. sorghum conf., 20-22 February 1996, Tamworth, New South Wales. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No. 93.

ICRISAT. 1992. The Medium-term Plan. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, 502 324, Andhra Pradesh, India.

Jimenez Mass, N.C. 1992. Mixed planting of sorghum midge (Diptera: Cecidomyiidae) resistant and susceptible sorghums to enhance and assess

non-preference resistance. M.S. thesis, Texas A&M University, College Station, Texas, USA.
Johnson, J.W., D.T. Rosenow, and G.L. Teetes. 1973. Resistance to the sorghum midge in converted exotic sorghum cultivars. Crop Sci. 13:174-175.
Johnson, J.W., D.T. Rosenow, G.L. Teetes, and F.R. Miller. 1982a. Registration of TAM 2566 sorghum germplasm line. Crop Sci. 22: 1271.
Johnson, J.W., R.E. Schaffert, and G.L. Teetes. 1982b. Registration of ISR 1 sorghum germplasm line. Crop Sci. 22:1271-1272.
Jordan, D.R., R.G. Henzell, Y. Tao, I.D. Godwin, M. Cooper, and C.L. McIntyre. 1996. Combining genetic mapping with pedigree analysis to provide insight into genetic changes achieved by sorghum breeding. p. 377-382. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proc. third Aust. sorghum conf., 20- 22 February 1996, Tamworth. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No. 93.
Jotwani, M.G. 1978. Investigations on insect pests of sorghum and millets with special reference to host plant resistance. Final Technical Report (1972-1977). Research Bulletin of the Division of Entomology. Indian Agricultural Research Institute, New Delhi, India.
Krall, S., O. Youm, and S.A. Kogo. 1995. Panicle insect pest damage and yield loss in pearl millet. p. 135-145. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Proc. int. consult. workshop, 4-7 October 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.
Nwanze, K.F. 1985. Some aspects of pest management and host plant resistance in pearl millet in the Sahel. Insect Sci. Applic. 6: 461-465.
Nwanze, K.F., and K.M. Harris. 1992. Insect pests of pearl millet in West Africa. Rev. Agric. Entomol. 80:1133-1155.
Nwanze, K.F. and O. Youm (eds). 1995. Panicle Insect Pests of Sorghum and Pearl Millet: Proc. Int. Consult. Workshop, 4-7 October 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.
Page, F.D. 1979. Resistance to sorghum midge (*Contarinia sorghicola* Coquillet) in grain sorghum. Australian Journal of Experimental Agriculture and Animal Husbandry, 19, 97-101.
Patil, R.C., and M.V. Thombre. 1985. Inheritance of earhead midge resistance in sorghum. Sorghum Newsl. 27:90.
Peterson, G.C., J.W. Johnson, G.L. Teetes, D.T. Rosenow and R.E. Schaffert. 1983. Registration of Tx2782 midge resistant sorghum germplasm line. Crop Sci. 24: 389-390.
Peterson, G.C., J.W. Johnson, G.L. Teetes, D.T. Rosenow, and R.E. Schaffert. 1984. Registration of Tx 2782 midge resistant sorghum germplasm line. Crop Sci. 24:389-390.
Peterson, G.C., J.W. Johnson, G.L. Teetes, B.R. Wiseman, A. Sotomayor-Rios, J.W. Jones, and K. Schaefer. 1991. Registration of 22 midge-resistant sorghum germplasm lines. Crop Sci. 31:498-499.
Peterson, G.C., G.L. Teetes, and B.B. Pendleton. 1994. Resistance to the sorghum midge in the United States. Int. Sorghum Millets Newsl. 35:48-63.
Peterson, G.C., G.L. Teetes, and D.T. Rosenow. 1985. Registration of midge resistant sorghum germplasm. Crop Sci. 25:372.
Rathus, C., A.L. Adkins, R.J. Henry, S.W. Adkins, and I.D. Godwin. 1996. Progress towards Transgenic sorghum. p. 409-412. *In* M.A. Foale, R.G. Henzell, and J. Kneipp (eds.) Proc. third Aust. sorghum conf., 20- 22 Feb 1996, Tamworth. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No. 93.
Ratnadass, A., and O. Ajayi. 1995. Panicle insect pests of sorghum in West Africa. p. 29-38. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Proc. int. consult. workshop, 4-7 October 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.
Ratnadass, A., O. Ajayi, G. Fliedel, and K.V. Ramaiah. 1995. Host-plant resistance in sorghum to *Eurystylus immaculatus* in West Africa. p. 191-199. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Proc. int. consult. workshop, 4-7 October 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.
Ratnadass, A., B. Cisse, and K. Malle. 1994a. Notes on the biology and immature stages of West African sorghum head bugs *Eurystylus immaculatus* and *Creontiades pallidus* (Heteroptera: Miridae). Bull. Ento. Res. 84:383-388.
Ratnadass, A., K.V. Ramaiah, H.C. Sharma, and B. Cisse. 1994b. Reaction de varieties de sorgho aux attaques de la punaise des panicules *Eurystylus immaculatus* Odhiambo (Heteroptera, Miridae) en Afrique de l'Ouest [Reaction of some sorghum cultivars to attack by the head bug *Eurystylus immaculatus* Odhiambo (Heteroptera, Miridae) in West Africa]. p. 333-343. *In* J.M. Menyonga, T. Bezuneh, J.Y. Yayock,

and I. Soumana (eds.) Progress in food grain research and production in semi-arid Africa: Proc. SAFGRAD inter-network conf., 7-14 Mar 1991, Palais des Congres, Niamey, Niger. Semi-Arid Food Grain Research and Development, Ouagadougou, BP 1783, Burkina Faso.

Reddy, B.V.S., and H.C. Sharma. 1992. Breeding midge-resistant seed parents and restorers. p. 38-40. *In* Cereals program annual report 1992. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India. (Limited distribution).

Rossetto, C.J., W. Goncalves, and J.L.M. Diniz. 1975. Resistencia de variedade AF 28 a masc do sorgo, *Contarinia sorghicola*, no arsenic de outers variedness. An. Soc. Ent. Brazil 4:16-20.

Rossetto, C.J., and T. Igue. 1983. Inheritance of resistance to *Contarinia sorghicola* (Coquillett) of sorghum variety AF 28. Brag. 42:211-219.

Rossetto, C.J., G. Nagai, and J. Overman. 1984. Mechanisms of resistance in sorghum variety AF 28 to *Contarinia sorghicola* (Diptera: Cecidomyiidae). J. Econ. Entomol. 77:1439-1440.

Scholz, B.C.G., and D.E. Webster. 1993. Heliothis oviposition on midge resistant and susceptible sorghum hybrids. Sorghum Newsl. 34:27.

Schuering, J.F., and F.R. Miller. 1978. Fertility restorers and sterility maintainers to the milo-kafir genetic cytoplasmic male sterility system in the sorghum world collection. The Texas Agricultural Experiment Station, Texas USA. MP 1367.

Sharma, H.C. 1985. Screening for sorghum midge resistance and resistance mechanisms. p. 275-292. *In* Proc. int. sorghum ent. workshop, 15-21 July 1984, College Station, Texas, USA. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru 502 324, Andhra Pradesh, India.

Sharma, H.C. 1987. Host plant resistance to insects in pearl millet. p. 297. *In* Proc. int. pearl millet workshop, 7-11 April 1986. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, 502 324, Andhra Pradesh, India.

Sharma, H.C., C.V. Abraham, P. Vidyasagar, and J.W. Stenhouse. 1996a. Gene action for resistance to sorghum midge, *Contarinia sorghicola*. Crop Sci. 36:259-265.

Sharma, H.C., B.L. Agrawal, P. Vidyasagar, C.V. Abraham, and K.F. Nwanze. 1993a. Identification and utilisation of resistance to sorghum midge, *Contarinia sorghicola* (Coquillett) in India. Crop Prot. 12:343-351.

Sharma, H.C., and J.C. Davies. 1988. Insects and animal pests of millets. Sorghum and Millets Information Center, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India.

Sharma, H.C., Y.O. Doumbia, and N.Y. Diorisso. 1992a. A head-cage technique to screen sorghum for resistance to mirid head bug, *Eurystylus oldi* Odh. in West Africa. Insect Sci. Applic.13:417-427.

Sharma, H.C., Y.O. Doumbia, M. Haidara, J.F. Scheuring, K.V. Ramaiah, and M.F. Beninati. 1994a. Sources and mechanisms of resistance to sorghum head bug, *Eurystylus immaculatus* Odh. in West Africa. Insect Sci. Applic. 15:39-48.

Sharma, H.C., K. Leuschner, and P. Vidyasagar. 1990a. Factors influencing oviposition behaviour of the sorghum midge, *Contarinia sorghicola*. Ann. Appl. Biol.116:431-439.

Sharma, H.C., and V.F. Lopez. 1989. Assessment of avoidable losses and economic injury levels for the sorghum head bug, *Calocoris angustatus* Leth. (Hemiptera:Miridae) in India. Crop Prot. 8:429-435.

Sharma, H.C., and V.F. Lopez. 1990. Mechanisms of resistance in sorghum to head bug, *Calocoris angustatus*. Ent. Exp. Applic. 57:285-294.

Sharma, H.C., and V.F. Lopez. 1992. Screening for plant resistance to sorghum head bug, *Calocoris angustatus* Leith. Insect Sc. Applic. 13:315-325.

Sharma, H.C., and V.F. Lopez. 1993. Survival of *Calocoris angustatus* (Hemiptera: Miridae) nymphs on diverse sorghum genotypes. J. Econ. Entomol. 86:607-613.

Sharma, H.C., S.Z. Mukuru, and K.F. Nwanze. 1996b. Stability of resistance to the sorghum midge *Contarinia sorghicola*. p. 429-435. *In* M.A. Foale, R.G. Henzell, and J. Kneipp (eds.) Proc. third Aust. sorghum conf. 20-22 February 1996, Tamworth. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No 93.

Sharma, H.C., B.V.S. Reddy, J.W. Stenhouse, and K.F. Nwanze. 1994b. Host plant resistance to sorghum midge. Int. Sorghum Millets Newsl. 35:30-41.

Sharma, H.C., S.L. Taneja, K. Leuschner, and K.F. Nwanze. 1992b. Techniques to screen sorghums for resistance to insect pests. Information Bulletin No. 32. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh, 502 324, India.

Sharma, H.C., and G.L. Teetes. 1995. Yield loss assessment and economic injury levels for panicle-feeding insects of sorghum. p. 125-134. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Proc. int. consult. workshop, 4-7 October 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid

Tropics, Patancheru 502 324, Andhra Pradesh, India.

Sharma, H.C. and P. Vidyasagar. 1994. Antixenosis component of resistance to sorghum midge, *Contarinia sorghicola* (Coq.) in *sorghum bicolor* (L.) Moench. Ann. Appl. Biol. 124:495-507.

Sharma, H.C., P. Vidyasagar, and K. Leuschner. 1988. No-choice cage technique to screen for resistance to sorghum midge (Cecidomyiidae: Diptera). J. Econ. Entomol. 81:415-422.

Sharma, H.C., P. Vidyasagar, and K. Leuschner. 1990b. Components of resistance to the sorghum midge, *Contarinia sorghicola.* Ann. Appl.Biol. 116:327-333.

Sharma, H.C., P. Vidyasagar, and V. Subramanian. 1993b. Antibiosis component of resistance in sorghum to midge. Ann. Appl. Biol. 123:469-483.

Stephens, J.C., F.R. Miller, and D.T. Rosenow. 1967. Conversion of alien sorghums to early combine types. Crop Sci. 7:396.

Tao, Y.Z., C.L. McIntyre, and R.G. Henzell. 1996. Application of molecular markers to Australian sorghum breeding programs. I. Construction of a RFLP map using sorghum recombinant inbred lines. p. 443-450. *In* M.A. Foale, R.G. Henzell, and J. Kneipp (eds.) Proc. third Aust. sorghum conf., 20-22 February 1996, Tamworth. Australian Institute of Agricultural Science, Melbourne, Australia. Occasional Publication No. 93.

Teetes, G.L., and J.W. Johnson. 1978. Insect resistance in sorghum. p.167-189. *In* Proc. of the 33rd Annual corn and sorghum res. conf. Chicago, Illinois, U.S.A.

Teetes, G.L., M.J. Scully, and G.C. Peterson. 1992. Partial life tables for corn earworm (Lepidoptera: Noctuidae) on compact- and loose-panicle sorghum hybrids. J. Econ. Entomol. 85:1393-1401.

Tryon, H. 1895. The insect enemies of cereals belonging to the genus Cecidomyia. Trans. Nat. Hist. Soc. Queensland 1:21-29.

Waquil, J.M., and G.L. Teetes. 1990. Impacto do dano da mosca do sorgo, Contarinia sorghicola (Coquillett, 1898), no peso de cada grao remanescente a infestacao. An. Soc. Ent. Brasil 19:201-209.

Waquil, J.M., G.L. Teetes, and G.C. Peterson. 1986a. Sorghum midge (Diptera: Cecidomyiidae) adult ovipositional behaviour on resistant and susceptible sorghum hybrids. J. Econ. Entomol. 79:530-532.

Waquil, J.M., G.L. Teetes, and G.C. Peterson. 1986b. Comparison of immature sorghum midge (Diptera: Cecidomyiidae) development on resistant and susceptible sorghums. J. Econ. Entomol.79:833-837.

Widstrom, N.W., B.R. Wiseman, and W.W. McMillan. 1972. Some gene effects conditioning resistance to midge and webworm injury in sorghum. Sorghum Newsl. 15:22-23.

Widstrom, N.W., B.R. Wiseman, and W.W. McMillian. 1984. Patterns of resistance in sorghum to the sorghum midge. Crop Sci. 24:791-793.

Wiseman, B.R., N.W. Widstrom, and W.W. McMillian. 1972. Flight movements and color preference of sorghum midge. J. Econ. Entomol. 65:767-770.

Youm, O., and K.A. Kumar. 1995. Screening and breeding for resistance to millet head miner. p. 201-209. *In* K.F. Nwanze and O. Youm (eds.) Panicle insect pests of sorghum and pearl millet: Proc. int. consult. workshop, 4-7 October 1993, ICRISAT Sahelian Center, Niamey, Niger. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Breeding for Resistance to Foliar- and Stem-Feeding Insects of Sorghum and Pearl Millet

G.C. Peterson*, B.V.S. Reddy, O. Youm,
G.L. Teetes, and L. Lambright

Abstract

Grain sorghum and pearl millet yield and yield stability are constrained by a diverse array of insect pests. Primary insect species vary according to the locale, with no foliar or stem pest of either crop classified as a cosmopolitan pest. Foliage pests of grain sorghum in the United States are greenbug (Schizaphis graminum), yellow sugarcane aphid (Sipha flava), chinch bug (Blissus leucopterus), fall armyworm (Spodoptera frugiperda), corn leaf aphid (Rhopalosiphum maidis), and Banks' grass mite (Oligonychus pratensis). Biotype development has been a problem only with greenbug, the key foliage pest of sorghum in the U.S. Foliage pests of grain sorghum outside the U.S. are shoot fly (Atherigona soccata), spotted stem borer (Chilo partellus), and sugarcane aphid (Melanaphis sacchari). Primary pests of pearl millet are locusts/grasshoppers and stem borers. In the U.S., primary emphasis in developing sorghum resistant to insects has involved greenbug. Hybrids resistant to biotypes C and E were available to producers within a few years after the biotypes appeared. One biotype I-resistant hybrid has been available to growers, and additional hybrids are becoming available. The other insect pests of sorghum in the U.S. are occasional or restricted to a small geographic area, and a limited amount of research has been done to develop insect-resistant hybrids. Resistance to shoot fly has been incorporated into resistant varieties. Stem borer resistance also has been incorporated into improved varieties although the resistance is less than desired. Sources of resistance to sugarcane aphid have been identified. Sugarcane aphid resistance is mostly quantitative and can easily be incorporated into adapted varieties. Programs at Texas A&M University and ICRISAT are using molecular genetics to improve understanding of the fundamental nature of the plant/insect interaction, to increase the durability of resistance, and to make genes from other species available to sorghum breeders and entomologists. The natural genetic variability present in the species will become increasingly important as genotypes are developed to address insect pests in the future.

Sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R. Brown] yield and yield stability are constrained by several insect species. The diverse array of foliar- and stem-feeding insects that infest the crops are mostly region-specific; few are cosmopolitan; and only a few are classified as key pests. Most foliar- and stem-boring insects of sorghum and pearl millet are classified as occasional pests. Significant

*G.C. Peterson, Texas A&M University Agricultural Research and Extension Center, Route 3, Box 219, Lubbock, TX 79401-9757, USA; B.V.S. Reddy, ICRISAT Asia Center; O. Youm, ICRISAT Sahelian Center; G.L. Teetes, Department of Entomology, Texas A&M University; L. Lambright, DeKalb Genetics Corporation. *Corresponding author.

research effort has been expended to evaluate thousands of lines from the world collection of sorghum for resistance to foliar- and stem-infesting insects. Much less insect resistance evaluation has been done for pearl millet. The success of evaluation and the subsequent breeding effort to transfer resistance into elite genotypes depends on the biology and ecology of the insect and its mode of infestation, inheritance of the resistance, evaluation technique, and economic importance of the insect.

Types of Foliage-Infesting Insects

Foliage-infesting insects of sorghum in the U.S. are greenbug [*Schizaphis graminum* (Rondani)], yellow sugarcane aphid [*Sipha flava* (Forbes)], chinch bug [*Blissus leucopterus leucopterus* (Say)], fall armyworm [*Spodoptera frugiperda* (J.E. Smith)], corn leaf aphid [*Rhopalsiphum maidis* (Fitch)], and Banks' grass mite [*Oligonychus pratensis* (Banks)]. Biotype development is a problem only with greenbug, the key foliage insect pest of sorghum in the U.S. Primary foliage pests of sorghum outside the U.S. are shoot fly [*Atherigona soccata* (Rondani)], sugarcane aphid [*Melanaphis sacchari]* (Zehntner)], and spotted stem borer [*Chilo partellus* (Swinhoe)]. *C. partellus* is the most important stem borer of sorghum, but other borer species include *Coniesta ignefusalis* (Hampson), *Busseola fusca* (Fuller), *Sesamia cretica* (Lederer), and *Eldana saccharina* (Walker). Common foliage- and stem-infesting insect pests of pearl millet are grasshoppers/locusts and stem borers.

While resistance to several occasional sorghum insect pests in the U.S. has been found, these insects do not consistently cause enough damage to sorghum to justify large research expenditures to develop resistant genotypes. In the U.S., however, significant public and private research expenditures have been made to develop and deploy genetic resistance to manage greenbug in sorghum. These research efforts have been largely successful, but the dynamic nature of greenbug has resulted in new biotypes with which research programs have been forced to deal. Sorghum varieties with genetic resistance to shoot fly and spotted stem borer are grown commercially. Varieties with genetic resistance to sugarcane aphid could be easily developed.

Greenbug

Greenbug is predominately a Western Hemisphere insect pest. The geographic origin of greenbug is unknown, but it is probably Mediterranean. The earliest record of greenbug is from Italy in 1847 (Rondani, 1852). In 1863, Passerini in Italy first recorded sorghum infested by greenbug. By 1907, the greenbug had been reported in Europe, Asia, Africa, and North America (Webster, 1909). The greenbug is present in South America, but not Australia. Greenbug damage and control costs in sorghum in the U.S. are estimated at approximately $21 million per year (G.L. Teetes, 1996, personal communication). While the insect has been a pest of small grains since the late 19th Century (Webster and Phillips, 1912), it has been a key pest of sorghum only since 1968 (Harvey and Hackerott, 1969). However, greenbug was reported to infest johnsongrass [*S. halepense* (L.) Pers.] as early as 1909 (Webster and Phillips, 1912), and serious damage to sorghum in

Kansas was first reported in 1916 (Hayes, 1922).

The greenbug that first caused widespread damage to sorghum throughout the great plains of the U.S. in 1968 was designated biotype C (Harvey and Hackerott, 1969). Currently, ten biotypes of greenbug have been identified, although only four (C, E, I, and K) are virulent on sorghum. Biotype development has consistently challenged plant breeders and entomologists to develop elite resistant hybrids. Public (USDA, Kansas, Oklahoma, and Texas) and private plant breeders initiated breeding programs to incorporate resistance into elite genotypes soon after resistance sources were identified. Much evaluation to identify germplasm resistant to greenbugs (biotypes C, E, and I) was done by Kansas State University scientists at Hays, Kansas (Table 1). That program evaluated approximately 23,000 accessions for resistance to biotypes C (ten resistance sources identified) and E (six resistance sources identified). Approximately 6,000 accessions were evaluated for resistance to biotype I (seven resistance sources identified).

Identified and widely used sources of resistance to biotype C greenbug were SA7536-1, KS30, IS809, and PI264453 (Hackerott and Harvey, 1971; Schuster and Starks, 1973; Teetes et al., 1974a, b). Resistance was reported to be effective in the seedling-stage plants (Hackerott et al., 1969; Johnson, 1971; Starks et al., 1971; Starks, et al., 1972; Teetes and Johnson, 1972; Weibel et al., 1972; Teetes et al., 1974a) and adult-stage plants (Hackerott and Harvey, 1971; Harvey and Hackerott, 1971; Johnson, 1971; Johnson and Teetes, 1972; Teetes et al., 1974b).

Inheritance of resistance to biotype C greenbug was determined to be dominant or incompletely dominant. Resistance derived from *Sorghum virgatum* (Hack.) Stapf was reported to be conferred by dominant genes at more than one locus (Hackerott et al., 1969). Resistance derived from IS809, SA7536-1, PI220248, P302236, and PI264453 was reported as incompletely dominant and simply inherited (Johnson, 1971; Johnson and Teetes, 1972; Weibel et al., 1972). Original resistance sources were not suitable for commercial use, and considerable breeding effort was expended to produce commercially acceptable parental lines for resistant hybrids. Many public breeding lines with resistance to biotype C were developed and released from public breeding

Table 1. Sources of resistance to the greenbug, *Schizaphis graminum*.

Biotype	Number of entries screened		Resistance Sources
C & E	23,000	C -	PI226096, PI297181, PI297213, PI302137, PI302178, PI302231, PI302233, PI302236, PI308442, PI308976, IS809, KS30, SA7536-1, PI229828, PI38108
		E -	PI220248, PI229828, PI264453, PI494893, PI514604, PI524770
		(All are also resistant to C)	
I	6,000	PI266965, PI550607, PI550610, IS25246, IS27002, IS27834, IS27903	

programs, including RTx2737 and ATx2752, which were extensively used to produce commercial sorghum hybrids (Johnson et al., 1982a, 1982b, 1982c; Peterson et al., 1985). Biotype C-resistant hybrids were available by the mid-1970s and widely grown in the U.S.

Biotype E greenbug was first identified in 1979 (Porter et al., 1982). Most biotype C-resistant sources were ineffective against biotype E. Resistance to biotype E derived from Capbam, PI220248, and PI264453. The resistance was reported to be inherited as a dominant character (Johnson et al., 1981). Dixon et al. (1991) used crosses between susceptible and resistant parents and among resistant sources to study the complementarity of resistance among several sources of resistance to biotype E. They concluded that resistance was complexly inherited and partially dependent on the resistant and susceptible parents. Also, they indicated the possibility of major factors for resistance being present in the cytoplasms of Capbam and PI264453. Puterka and Peters (1995), using Pioneer 8493 with resistance derived from PI264453, concluded that resistance to biotypes E and C was controlled by a duplicate dominant gene-modifier gene, and that the modifier gene also was, when dominant, epistatic to one of the duplicate genes. Biotype E resistance was deployed in commercial hybrids. The most commonly used biotype E resistance source in commercial hybrids was Capbam, introduced from Russia in the early 1970s. Capbam is the resistance source expressed in Tx2783, a commonly used parental line (Peterson et al., 1983). Additional released germplasm lines resistant to biotype E also were derived from Capbam (Peterson et al., 1991).

Biotype I greenbug was identified in 1990 (Harvey et al., 1991). All biotype C and E resistance sources were susceptible to biotype I greenbug. Subsequent research resulted in identification of several sources of resistance to biotype I (Andrews et al., 1993). Two of the resistance sources, PI550607 and PI550610, are resistant to biotype E. Preliminary research led to the conclusion that biotype E resistance in PI550607 is controlled by a single gene, while resistance to biotype I is controlled by at least two genes.

Cargill 607E, a commercial hybrid resistant to biotype E greenbug from an unknown source, was used to assess inheritance of resistance. Segregation ratios indicated that for biotype E, two genes conditioned resistance (Kofoid and Harvey, 1992). Data indicated that four genes conditioned resistance to biotype I. Results of these experiments also indicated that the genes for resistance to biotype E were involved with resistance to biotype I. With the exception of Cargill 607E, sorghum hybrids resistant to biotype I are only beginning to be deployed commercially.

Only recently, another greenbug biotype, biotype K, was identified (Harvey et al., in press). Biotype K occurred without any selection pressure from widespread use of resistant hybrids. Biotype K rendered some biotype I resistance sources ineffective, and those that retained resistance had low levels.

Yellow Sugarcane Aphid

The yellow sugarcane aphid, recognized for more than 100 years as a pest of sorghum (Forbes, 1884), is an occasional pest especially devastating to seedling plants. The aphid feeds on the underside of seedling sorghum leaves. Purple discoloration of leaf tissue in the feeding area is the first symptom of injury to small (1-7 cm tall) plants (Breen and Teetes, 1986). As feeding continues, the purple color extends from the aphid-feeding site toward the stem. Affected tissue often becomes yellow or necrotic. If aphids remain, seedling plants may die. Insecticide, applied at planting time, is the common management tactic, although plant resistance could potentially offer effective management at no additional cost to farmers.

Most sorghum is susceptible to yellow sugarcane aphid. Davis et al. (1978) evaluated 209 lines and identified none as resistant. Starks and Mirkes (1979) reported similar results after evaluating 3,600 lines. Webster (1990) evaluated more than 5,000 Ethiopian sorghum lines and identified three lines with apparently useful levels of resistance. The lines — PI453951, PI457715, and PI457709 — are all tall and extremely photoperiod-sensitive under temperate U.S.conditions. The lines have been entered in the Sorghum Conversion Program (Stephens et al., 1967). Webster (1990) concluded that antibiosis and tolerance at low level were the components of resistance. Antixenosis (nonpreference) was not a resistance mechanism. Paliani (1993) obtained similar results in studies using PI457709 and PI453951. Genetic analysis of F_2 populations of susceptible lines crossed to PI457709 indicated that resistance was probably inherited as a single dominant gene. The Texas A&M University breeding/entomology program has been working to transfer resistance into adapted lines suitable for use in hybrid production. The resistance from PI457709 and PI453951 has been transferred into temperately adapted lines. Research is on-going to improve agronomic traits in the resistant lines. Progeny have been developed to combine resistance to yellow sugarcane aphid and biotype E greenbug.

Chinch Bug

Chinch bug is an occasional insect pest of cereal crops including sorghum. Recent infestations have been confined primarily to central Kansas and southern Nebraska. Infestations of chinch bug in south Texas occur mostly in seedling sorghum. Prior to the 1950s, the chinch bug was the most important insect pest of sorghum in the U.S. After this period, its economic importance declined and the chinch bug now causes economic damage only sporadically.

Resistance to chinch bug in sorghum was identified many years ago. Early research led to the conclusion that Milo varieties were very susceptible (Hayes, 1922); Feterita varieties were susceptible or intermediate in resistance; and Kafir varieties were the most resistant (Dahms, 1943). Coincidentally, during the early years of sorghum production in the U.S., Kafir varieties commonly were grown in chinch bug-infested areas of Oklahoma, Kansas, and Texas, while milo varieties were grown in areas where the insect was not as severe (Snelling et al., 1937).

Dahms and Sieglinger (1954) evaluated 37 varieties and identified 15 with resistance. Starks and Weibel (1982) evaluated 60 cultivars and identified 35 with resistance. Mize and Wilde (1986) evaluated six lines and identified three as resistant. About 4,500 sorghum lines have been evaluated for resistance to chinch bug at Kansas State University during the last five to ten years (G. Wilde, personal communication). From these evaluations, chinch bugs on seven sorghum plant introductions, PI308223, PI308388, PI381848, PI510915, PI511023, and PI524746, produced half as many eggs per female as females on susceptible check sorghums. Apparently no chinch bug-resistant hybrids are currently being grown.

Corn Leaf Aphid

Corn leaf aphids commonly and normally infest the whorls of sorghum plants. Classified as an occasional pest, only rarely does this insect cause economic damage. Conversely, corn leaf aphids generally play a beneficial role in maintaining high levels of natural enemies that help suppress the abundance of other sorghum insect pests. On occasion, corn leaf aphids infest the panicles of sorghum and the copious amounts of honey dew produced by the aphids make the panicles sticky. Panicle infestations are rare, occurring most frequently in Australia. Corn leaf aphids transmit maize dwarf mosaic virus, which is usually managed by plant resistance to the virus.

Resistance sources for corn leaf aphid have been identified. McColloch (1921) evaluated 17 varieties and reported resistance in Piper sudan grass. Howitt and Painter (1956) evaluated 595 varieties, confirmed the conclusion of McColloch, and selected a highly resistant plant (428-1) from Piper sudan grass. Sources of resistance also have been found within converted exotic sorghums (Teetes et al., 1976). Several Zerazera sorghums exhibit high levels of resistance, especially TAM428, derived from SC110-9.

No evaluations of sorghum lines or hybrids for resistance to corn leaf aphid have been reported in the last 20 years. The Zerazera sorghums are extremely useful in sorghum improvement and could contribute resistance to hybrids.

Fall Armyworm

Fall armyworm occasionally infests sorghum and is usually more serious if sorghum is planted late. The insect can damage both foliage and kernels in panicles. Foliage- and panicle-stage sorghum has been evaluated extensively for resistance (Table 2). Wiseman and Gourley (1982) found a line from CIMMYT, CM1821, to be resistant in the seedling stage. Wiseman and Lovell (1988) evaluated sorghum lines from Ethiopia (3,364) and Yemen (2,000) and identified 11 lines with resistance in the seedling stage. The lines are being converted to short, early genotypes in the Sorghum Conversion Program. Diawara et al. (1990, 1991, and 1992) evaluated 240 converted sorghum lines in the whorl stage and found additional sources of resistance. Meckenstock et al. (1991) reported that resistance in AF28 was caused by antibiosis. They also found several Honduran maicillo criollo varieties had higher levels of antibiosis than AF28.

Table 2. Mechanisms of resistance in whorl-stage sorghum to the fall armyworm.*

Cultivar	Mechanisms of resistance		
	Tolerance	Nonpreference	Antibiosis
CM1821	X	X	
PI452571		X	
PI452771		X	
PI452962		X	
PI453130		X	
PI453281		X	
PI453299		X	
PI453356		X	
PI454733		X	
PI456111		X	
PI457624		X	
AF28			X
San Bernardo III			X
Hilate-179			X
Lerdo-104			X
IS 1056C			X
IS 2177C			X
IS 2246C			X
IS 4023C			X
IS 7273C		X	
IS 7399C			X
IS 7444C		X	
IS 7794C		X	
IS 7947C		X	
IS 12573C		X	
IS 12679C		X	
IS 12680C			X
GATCCP100			X
GATCCP101			X

*Duncan et al., 1991; Isenhour et al., 1991; Diawara et al., 1991; Diawara et al., 1992; Meckenstock et al., 1991; and Wiseman and Gourley, 1982.
Source: Wiseman, 1992.

The first regenerated sorghum lines reported resistant to fall armyworm were GATCCP100 and GATCCP101 (Duncan et al. 1991). Both lines are tissue culture regenerates of Hegari, a sorghum line originally introduced into the U.S. in 1908. The lines possess a higher level of leaf-feeding resistance to fall armyworm larvae than does the non-regenerated susceptible parent, Hegari.

Spider Mites

Spider mites are usually considered secondary pests of sorghum in the U.S. and occasional pests elsewhere. Several species infest sorghum, including Banks' grass mite, two-spotted spider mite (*Tetranychus urticae* Koch), and sugarcane leaf mite [*O. indicus* (Hirst)]. The most common spider mite infesting sorghum is Banks' grass mite. Spider mites are generally a problem in hot, dry environments when sorghum is drought-stressed. Infestations usually are more damaging in the reproductive stage of plant growth (Ehler, 1974). Natural enemies play a minor role in suppressing spider mite abundance, because mite infestations usually are separated temporally and spatially from natural control.

Because of the occasional incidence of damaging infestations of spider mites in sorghum, only a limited amount of germplasm has been evaluated for resistance. Foster et al. (1977a, b) identified spider mite-resistant germplasm. The most promising source of resistance was SC599-6, a partially converted Rio selection. This line has post-flowering drought resistance and is nonsenescing (maintains green leaves and plant stalks for a longer time than most lines). The nonsenescing trait probably contributes to a higher concentration of total sugars in the leaves that may be associated with the resistance. The resistance is probably a tolerance type, since spider mite abundance is similar on resistant and susceptible lines, although the resistant lines continue to maintain green leaves. Archer et al. (1986) reported that sorghum lines with drought tolerance had less mite damage than other lines. They concluded that the dhurrin levels in SC599-6 were significantly higher than in other varieties. Spider mite numbers also were lower on SC599-6 than on other lines. Peterson et al. (1987) evaluated 202 converted exotic sorghum lines and 251 elite breeding lines. A differential response to spider mites was exhibited among the lines. Lines with post-flowering drought tolerance exhibited a higher level of spider mite resistance than did non-drought-tolerant lines. However, lines that exhibited resistance to spider mites but did not have post-flowering drought tolerance also were identified.

Breeding for spider mite resistance is not being done. Any resistance in hybrids would be simply as an artifact of selection for other plant traits, such as drought resistance. No hybrids are marketed as spider mite-resistant.

Sorghum Shoot Fly

Shoot fly is an important insect pest of seedling sorghum primarily in Asia and Africa. It does not occur in Australia or the Americas. More than 14,000 germplasm lines have been evaluated for resistance to sorghum shoot fly (Taneja and Leuschner, 1984). Data from these evaluations indicated that 42 lines were less susceptible than susceptible checks (Table 3). Five germplasm lines, IS1054, IS1071, IS2394, IS5484, and IS18368, were stable for resistance across locations.

Resistance to shoot fly in sorghum is apparently a complex characteristic. Resistance has been classified into four components: antibiosis, nonpreference for oviposition, recovery resistance, and seedling resistance (Blum, 1972). Resistance is caused primarily by ovipositional non-preference and is governed by additive genes (Rana et al., 1975; Balakotaiah et al., 1975). Vedamurthy (1967), Langham (1968), and Borikar and Chopde (1980) studied progeny from crosses of resistant by susceptible parents. Results varied with insect pest abundance. Susceptibility was dominant, or nearly completely dominant, under high insect abundance, but resistance was partially dominant when insect abundance was low. Agrawal and House (1982) reported resistance to be polygenic and controlled by genes with predominately additive effects. Sharma et al. (1977) concluded that one single recessive gene (*npo*) governed non-preference to oviposition, while two duplicate recessive genes (*dh1dh1*, *dh2dh2*) governed resistance to "dead heart" formation. Rana et al. (1981) concluded that under low to moderate shoot

Table 3. Sorghum germplasm lines identified as less susceptible to shoot fly at ICRISAT Center, Patancheru, India.

Pedigree	Origin	Glossy[1]	Trichomes[2]	Shoot fly incidence (%)	
				Egg laying[3]	Deadhearts[4]
IS 923	Sudan	G	+	48.6	43.9
IS 1034	India	NG	+	35.8	36.4
IS 1057	India	NG	+	42.4	41.1
IS 1071	India	G	+	54.7	47.6
IS 1082	India	G	+	45.3	38.5
IS 1096	India	G	+	42.1	40.3
IS 1104	India	G	+	50.8	43.6
IS 2122	U.S.	G	+	45.5	40.7
IS 2123	U.S.	G	+	40.6	35.0
IS 2146	Nigeria	G	+	39.5	38.0
IS 2195	India	G	+	43.2	34.5
IS 2309	India	G	+	40.0	36.5
IS 2265	Sudan	G	+	32.4	37.5
IS 2269	U.S.	G	+	42.0	40.0
IS 2291	Sudan	G	+	43.5	42.7
IS 2309	Sudan	G	+	37.6	40.4
IS 2312	Sudan	G	+	43.6	43.0
IS 2394	South Africa	G	+	47.4	41.8
IS 3962	India	G	+	39.5	35.7
IS 4224	India	NG	+	42.6	40.6
IS 4646	India	G	+	41.9	39.0
IS 4663	India	G	+	46.6	38.9
IS 4664	India	G	+	38.4	33.8
IS 5072	India	NG	+	42.7	40.2
IS 5210	India	G	+	43.4	42.3
IS 5469	India	G	+	43.9	44.6
IS 5470	India	G	+	41.1	36.9
IS 5480	India	G	+	46.4	35.3
IS 5484	India	G	+	43.4	36.6
IS 5511	India	NG	+	45.4	42.7
IS 5538	India	G	+	41.4	40.8
IS 5566	India	G	+	37.0	36.4
IS 5604	India	G	+	39.0	38.9
IS 5613	India	G	+	42.5	37.6
IS 5622	India	G	+*	44.1	42.1
IS 5636	India	G	+	46.6	44.5
IS 5648	India	G	+	41.9	37.0
IS 18366	India	G	+	44.2	40.9
IS 18368	India	G	+	45.4	41.1
IS 18369	India	G	+	36.3	38.3
IS 18371	India	G	+	42.7	36.8
IS 18551	Ethiopia	G	+	36.8	31.3
CSH 1	India	NG	+	66.4	67.6
IS 1054 (Maldandi)	India	NG	+	59.1	49.9

[1] G=Glossy; NG - Nonglossy; [2]+=trichomes present on leaves; +*=trichomes present only on upper leaf surface
[3] Mean of 4 seasons (replicated) [4]Mean of 5 seasons (replicated).
Source: Taneja and Leuschner, 1984

fly abundance, ovipositional nonpreference was caused by partially dominant genes, but was recessive under high abundance. Morphological traits also influenced resistance to shoot fly. Gibson and Maiti (1983) reported that trichomes on the abaxial leaf surface were controlled by a single recessive gene. Agrawal and Abraham (1985) determined that glossiness was quantitatively governed and controlled by both additive and non-additive genes. Glossiness was highly correlated with shoot fly resistance and could perhaps be linked with unknown antibiotic factors.

Spotted Stem Borer

The spotted stem borer is an economically important pest of sorghum in East Africa, India, and the Far East. Depending on the plant stage during insect attack, feeding may lead to loss of leaf area, dead hearts, or stem and peduncle tunneling. Although each kind of damage may result in serious economic loss, not all are significant in a given locality. Criteria to select for resistance include amount of leaf feeding, percentage of plants with dead hearts, and the extent of stem/peduncle tunneling. Ability of the plant to tolerate or compensate for damage by producing tillers, for example, would be an important factor for reducing yield loss caused by stem boring. Because of the nature of the insect/plant interaction, resistance to spotted stem borer should be based on yields of infested and noninfested plants, as this method will effectively integrate the value of all resistance, tolerance, and recovery factors.

Most evaluation of germplasm from the world collection for resistance to spotted stem borer has been done in India. The All Indian Coordinated Sorghum Improvement Project (AICSIP) evaluated 6,243 germplasm lines between 1965 and 1977. Initial evaluation was done in single row nonreplicated trials with advanced selections made in replicated trials based on leaf injury and stem tunneling. Twenty-four lines were less damaged under natural and artificial infestations (Srivastava, 1985; Rana et al., 1985) (Table 4). ICRISAT subsequently evaluated approximately 16,000 germplasm lines for resistance. Identification under natural and artificial infestations for low percentage of dead heart and low stem tunneling resulted in identification of 72 resistant lines (Table 5).

Sugarcane Aphid

The sugarcane aphid infests sorghum in Africa, Asia, the Far East, and tropical Americas. It is not a pest of sorghum in the U.S. Although it infests sorghum during all growth stages, economic damage most commonly occurs during late growth stages (Van Rensburg, 1973a). Damage is more severe when the crop is drought-stressed, when aphid feeding results in leaf drying and further plant stress.

Table 4. Germplasm lines identified as sources of resistance to stem borer (*Chilo partellus*) through long-term evaluation efforts by the Indian Sorghum Improvement Program (AICSIP).

IS 1044	IS 4764	IS 5031
IS 1056	IS 4776	IS 5470
IS 1115	IS 4782	IS 5837
IS 1151	IS 4827	IS 6041
IS 4424	IS 4841	IS 3096
IS 4552	IS 4875	IS 7273
IS 4651	IS 4934	IS 8314
IS 4689	IS 4994	IS 9136
IS 4747	IS 5030	

Table 5. Sources of resistance to sorghum stem borer identified by ICRISAT, 1979-86.

Origin	IS Number
India	1044, 1082, 1119, 2195, 2205, 2375, 2376, 4273, 4546, 4637, 4756, 4757, 4776, 4881, 4981, 5075, 5253, 5429, 5469, 5470, 5480, 5538, 5566, 5571, 5585, 5604, 5619, 5622, 8320, 13100, 17742, 17745, 17747, 17750, 17948, 17966, 18333, 18366, 18662, 18677, 21969, 22039, 22091, 22145, 23411
Nigeria	7224, 18573, 18577, 18578, 18579, 18580, 18584, 18585
U.S.	2122, 2123, 2146, 2168, 2269, 10711, 20643
Sudan	2263, 2291, 2309, 2312, 22507
Uganda	8811, 13674
E. Germany	24027
Ethiopia	18551
Pakistan	9608
YAR	23962
Zimbabwe	12308

Source: Taneja and Leuschner, 1985.

Cultural practices and natural controls partially suppress sugarcane aphid abundance on sorghum. Generally, natural controls are late occurring and do not suppress sugarcane aphid abundance enough to prevent damage (Van Rensburg, 1973b).

Evaluation of sorghum germplasm has resulted in identification of many sources of resistance. More than 10,000 sorghum lines have been evaluated for resistance, including 454 lines from the Sorghum Conversion Program. Resistance has been reported from China (Chang, 1981; Chang and Fang, 1984), Japan (Setokuchi, 1976), Taiwan (Pi and Hsieh, 1982a), India (Venugopol et al., 1979; Mote and Kadam, 1984; Mote et al., 1985), and Africa (Manthe, 1992). The resistance sources are listed in Table 6.

Genetic inheritance of resistance to sugarcane aphid has been studied using several resistance sources. A study in China using PI257595 (highly resistant), 129-3A (moderately resistant), and RTx430 (susceptible) showed that resistance to sugarcane aphid was monogenic and controlled by a dominant gene (Hsieh & Pi, 1982; Pi & Hsieh, 1982b). Additional research showed that PI257595 and 129-3A have the same resistance gene, although 129-3A has modifier genes (Pi and Hsieh, 1982a). One study indicated that dominant and additive gene action were both present, with additive gene action accounting for most of the resistance (Hsieh and Pi, 1988). An additional study using the cross RTx430 э 129-3A suggested the presence of complementary gene action (Chang and Fang, 1984). Manthe (1992) concluded that crosses of resistant (TAM428 or SC170-*14*) by susceptible lines segregated in a ratio consistent with dominant resistance. The resistance seemed to be monogenic.

Table 6. Sources of resistance to the sugarcane aphid and country where identified.	
Taiwan	PI257595 (IS12608C/SC108), Agr. 452560 Shallu, 129-3A
China	TAM428, PI257595 (IS12608C/SC108), IS12610C (SC110)
Japan	Senkinshiro, Suzuho, PE954 177, IS12612C (SC112), IS8100C (SC424)
India	IS103, IS122, IS530, IS656, IS956, IS1056, IS1063, IS1115, IS1117, IS1132, IS1172, IS1461, IS2033, IS2180, IS2189, IS2217, IS2228, IS2251, IS2414, IS2587, IS2931, IS3572, IS3582, IS3962, IS3923, IS4949, IS4645, IS4619, IS4640, IS5332, IS5668, IS5246, IS6496, IS9396, IS8893, IS6882, IS7456, IS9281, IS8160, IS8345, IS9539, IS8117, IS8348, PJ 4R, Dagdi, Harm Jogri, Lakadi, Kuchkuchi
Botswana	Converted lines IS1133C (SC202), IS1134C (SC203), IS1139C (SC205), IS1144C (SC451), IS1366C (SC210), IS1598C (SC214), IS5188C (SC245), IS5887C (SC248), IS6389C (SC489), IS6426C (SC497), IS12158C (SC984), IS12599C (SC90), IS12609C (SC109), IS12610C (SC110), IS12637C (SC146), IS12645C (SC154), IS12661C (SC170), IS12664C (SC173), IS12677C (SC186), IS5887C (SC248), SC464
Texas lines	TX2737, Tx2783, TAM428
Zimbabwe cultivars	Brown Tswera, Hudende, Red Nyoni, Serena, Nyanize, Chimunda, Red Swazi
SADC/ICRISAT breeding lines	SDS1513, SDS2293-1, SDS2293-6, SDS2298, SV2
South African breeding lines	SA1221, SA1469, SA1470, SA1471

Millet Stem Borer

The millet stem borer is a persistent and often damaging insect pest of pearl millet. The species is restricted to mainland Africa south of the Sahara and has been recorded most frequently in West Africa (Senegal, Mali, Gambia, Guinea Bissau, Benin, Burkina Faso, Chad, Mauritania, Ghana, Niger, and Nigeria). It also has been recorded in Sudan, Ethiopia, and Angola and is probably more widely distributed in tropical Africa than published records indicate. It is not known to be important on other cereal crops (Youm et al., 1996).

Larvae cause two kinds of damage during feeding and development (Youm, 1990; Youm and Gilstrap, 1994): 1) early-sown millet is attacked by first-generation larvae that damage young plants and cause dead-hearts; 2) seedlings of late-sown millet are exposed to higher numbers of second- or third-generation larvae that tunnel extensively in the stems and may kill the plant. Stem tunneling may cause lodging and panicle chaffiness in older plants, because disruption of the vascular system prevents kernel formation (Harris, 1962; Ndoye, 1979; Nwanze, 1989; Ajayi and Labe, 1990).

Early evaluations for resistance to the millet stem borer are not widely documented, and breeding efforts were mostly unsuccessful because of a lack of a multidisciplinary approach. In many programs, breeders worked separately from entomologists, leading to the development of many varieties with unknown status with regard to resistance or suscep-

tibility to the millet stem borer. Most efforts toward a multidisciplinary approach occurred in the early to mid 1980s.

Varietal evaluation for resistance to millet stem borer has been conducted in Niger, Nigeria, Senegal, and other countries in the Sahelian region, and some plant characteristics have been linked to resistance. For example, the millet variety Zongo reportedly produces a sticky secretion in stem tunnels caused by feeding and developing larvae, and thus offers some resistance by antibiosis (Ndoye, 1977). Nwanze (1985) reported that an increased rate of tillering in certain millet varieties is a tolerance mechanism for minimizing losses caused by the millet stem borer. Ajayi (1985) suggested that hairiness of the leaves and leaf sheaths could explain differences in levels of stem borer infestation of the three millet types (gero, dauro, maiwa) in Nigeria. Stem hardness, size, and thickness affected progeny development (Nwanze and Harris, 1992). Fewer eggs were laid on plants with trichomes than on trichomeless plants (ICRISAT, 1994). Oviposition nonpreference and leaf sheath morphology and attachments should be considered in efforts to identify resistance.

Review of research on the millet stem borer shows that documented and tested resistant millet varieties are not available, although a number of varieties are reported tolerant. Mechanisms of resistance to millet stem borer are yet to be fully assessed and documented. Nwanze and Harris (1992) stated that screening for resistance against pearl millet insect pests is hampered by lack of screening techniques for uniform and optimum infestation of millet plants. Results of most studies on varietal resistance were based on natural infestation, resulting in much variability and inconclusive results.

Breeding for resistance to insect pests requires the availability of adequate numbers of insects in the damaging stage, either under natural or artificial conditions. Past difficulties in breeding for resistance to the millet stem borer included unavailability of both an effective screening technique and a rearing technique for mass production of the millet stem borer due to a lack of facilities in National Agricultural Research Programs (NARS).

Early research efforts in pearl millet improvement in West Africa, in collaboration with NARS and funded by UNDP, consisted initially of breeders with little to no multidisciplinary research. With the establishment of the ICRISAT Sahelian Center in the early 1980s, more multidisciplinary research has been undertaken, with development of rearing and evaluation techniques as the main focus.

A technique has been developed for mass rearing millet stem borer in the laboratory. Such insects can be used to assess millet varieties for their reaction to millet stem borer larvae. Current research is, therefore, focused on determining damage thresholds on susceptible varieties so infestation levels can be used to assess varieties for their reactions to millet stem borer.

Research on evaluating for resistance to the millet stem borer focuses on two areas: 1) development of evaluation at early vegetative plant growth, and 2) assessment of varieties at later stages using

exit holes and a moth production index as resistance evaluation criteria.

Lukefahr (1989) has developed artificial infestation techniques using infested millet stems; he also has used stem borer exit holes as a measurable and repeatable technique for evaluating pearl millet varieties for resistance. The technique to evaluate resistance to millet stem borer consists of placing vertical bundles of infested stems at regular intervals in plots where varieties of millet are being evaluated. This technique has been improved and can be used by NARS where adequate mass rearing facilities are not available (Youm unpublished, ICRISAT, 1991). This procedure is similar to the infester row technique, where infested stems are spread between rows of young millet plants and left in the field during the entire period of pearl millet growth. This allows emerging adults to lay eggs directly on preferred plants.

The best technique for infesting millet with the millet stem borer is to use caged millet plants (ICRISAT, 1991). Research has shown that an initial 200 larvae per cage, or 2,000 ha^{-1}, resulted in at least 85% infestation.

A rapid method for evaluating for resistance to spotted stem borer (Nwanze and Reddy, 1991) possibly could be re-assessed for adaptation to the millet stem borer. This method uses field microplots and trays to assess resistance at the seedling stage. Assessment of damage after maturity based on the number of exit holes, as well as the use of a moth production index, can be considered an appropriate method to assess resistance of pearl millet genotypes.

Breeding and Evaluation Methodology

Development of improved varieties, lines, and hybrids with resistance to foliar- or stem-infesting insect pests does not differ from breeding for other stress or quality factors. Thus, any breeding method appropriate for sorghum may be used to develop insect-resistant genotypes. The most common breeding methods would be pedigree, backcross, or random-mating populations. If resistance is evaluated in the greenhouse, as for greenbug, only resistant genotypes are taken to the field for further selection or crossing. If resistance evaluation is done in the field, resistant genotypes should be identified before pollination to expedite development of new plant populations. The methodology of each breeding method and how it may be used is not addressed in this paper. The appropriate method to use will be specific to a particular research program, the genetics of resistance, other research objectives, and needs of other collaborators.

Similarly, methodology to evaluate resistance of sorghum or pearl millet populations depends on the insect and its mode of attack. Plant breeders, in collaboration with entomologists, have developed techniques to evaluate germplasm for resistance to the different sorghum insect pests. The techniques range from seedling stage greenhouse evaluation using artificial infestations (greenbug, sugarcane aphid, yellow sugarcane aphid, fall armyworm), to field evaluations at different plant growth stages, using natural and artificial infestations (greenbug, shoot fly, stem borers, sugarcane aphid, yellow sugarcane aphid, spider mites, fall army-

worm). To evaluate for resistance, test entries are exposed to natural or artificial infestations by the insect and compared with either uninfested plants or standard susceptible or resistant (if known) checks. Resistance evaluation techniques have proven reliable and relatively efficient for evaluating large numbers of test entries. Currently, different resistance genes cannot be accurately distinguished for pyramiding (stacking) into a single genotype; it also is not possible to determine whether a single line or variety contains different kinds of resistance (seedling resistance and adult plant tolerance for greenbugs, or resistance to early stage infestation and recovery resistance for shootfly and stem borers). Additional evaluation techniques and methodology are needed to allow development of elite germplasm with durable resistance as the 21st Century approaches.

Biotechnology

While significant research efforts have been devoted to developing resistance to several foliar- or stem-infesting insect pests of sorghum, success stories are limited. In the U.S., breeding for greenbug reistance has been successful. Sorghum midge-resistant sorghum in India and Australia, and stem borer and shoot fly-tolerant varieties in East Africa and India are good examples of the success of conventional breeding methodology in developing insect-resistant germplasm (Sharma, 1993). Many experimental varieties described as "highly promising," "having good potential," or "superior to susceptible checks" have not been grown beyond experiment station fields. Nwanze et al. (1995) stated that lack of elite insect-resistant varieties and hybrids is due to resistance too low to result in significant protections from insect pests when transferred into agronomically improved sorghum; when resistance is high, progenies are agronomically undesirable. In addition to cultivated sorghum varieties lacking usable resistance to major foliage insects, resistance to some insects is quantitatively inherited and difficult to incorporate into elite, high-yielding varieties or hybrids.

The new tools of molecular biology, collectively known as biotechnology, offer potential contributions in many areas and can help to: 1) identify sorghum genotypes with different resistance genes; 2) assess the genetic relationship between resistant genotypes; 3) stack or pyramid resistance genes into a single genotype or hybrid; 4) reduce the time necessary to transfer a usable level of resistance into an improved genotype; and 5) transfer genes from related species into adapted sorghum genotypes. Additional benefits will accrue as the technology becomes more refined and progress is made in understanding the nature of resistance to foliar- and stem-infesting insect pests of sorghum and millet. Potentially useful kinds of biotechnology include molecular maps developed using RFLPs or PCRs, transformation, interspecific hybridization, and marker-assisted selection. This list does not include other technologies that have been or are being developed that will be of benefit.

At Texas A&M University, sorghum breeders and entomolgists collaborate with molecular geneticists to develop molecular maps for sorghum genotypes resistant to greenbug biotypes. Molecular maps for the different sources of resis-

tance to greenbug are being developed. They offer the potential to determine more accurately than conventional methodology the location of the resistance gene(s) and the inheritance of resistance. When completed, such maps will lead to new insight into greenbug resistance, development of new biotypes, and the evolutionary relationships between the insect and its hosts. Accurate determination of the inheritance of resistance will lead to more accurate and directed breeding/selection programs to incorporate resistance into elite genotypes. Molecular markers for resistance genes from different resistance sources will enable a genetic improvement team to accurately identify different resistance sources or mechanisms and, in doing so, to eventually stack the genes into a single genotype. This could improve the durability of resistance and make it more difficult for the insect to overcome.

Interspecific hybridization will enable movement of resistance genes between related species. At ICRISAT, more than 340 accessions of wild relatives of sorghum belonging to sections *Chaeto*, *Hetero*, *Stipo*, *Para*, and *Sorghum* were evaluated for resistance to shoot fly (ICRISAT, 1988, 1989). Seven accessions showed very high levels of resistance to shoot fly, with one close to immunity. However, considerable difficulty has been encountered in trying to cross the accessions with cultivated sorghum. Attempts to cross other accessions with cultivated sorghum are continuing. If direct hybridization is not successful, techniques such as embryo rescue and protoplast fusion offer additional opportunities to recover the resistance genes.

Genetic transformation, the technology of transferring foreign genes to sorghum, is advancing rapidly (Bennetzen, 1995; Kononowicz et al., 1993). Research is currently being conducted at ICRISAT to transform a range of materials (Nwanze, 1995); collaborative research is underway on at least three techniques: 1) direct gene transfer to protoplasts, 2) use of a particle gun for transformation (Casas et al., 1993), and 3) use of *Agrobacterium* for transformation (Gould et al., 1991).

The genetic relationship of sorghum to other crop plants will become increasingly important in the future. Evidence exists that several important food crops such as sorghum, corn, and rice descended from a common ancestor approximately 65 million years ago (Paterson et al., 1995). Paterson et al. (1995) concluded that "convergent domestication of sorghum, rice, and maize appears to result from mutations at corresponding genetic loci, which would suggest that few genes with large effects determine the genotypes studied." They also concluded that comparative maps of the three species reveal a common order of genes and monogenic phenotypes over large chromosomal tracts. It is possible that genes for specific traits could be identified and moved between species. Possible relationships between wheat and sorghum also are important. Greenbug originally infested small grains and only recently became a pest of sorghum. Yet subsequent biotype changes for greenbug virulence on sorghum do not necessarily correspond to virulence changes on wheat. Through comparative mapping of greenbug resistance genes in sorghum and wheat, the chromosomal location of the effective genes will be determined in each

species. Cloning will enable scientists to assess evolutionary changes in gene structure brought about by mutation. If the changes are consistent between crop species, then the question of why biotype changes do not affect both species may be asked and answered.

As the tools of molecular genetics are used to determine genetic relationships of plant resistance to an insect, companion studies should be conducted on the insect itself. This is especially important for an insect that develops biotypes, as in the case of greenbug. In developing genetic resistance to insect pests, breeders and entomologists are forcing change in the dynamic relationship between two living organisms. Unless this forced evolutionary change can be understood from both sides (host and insect), scientists will have only a partial picture of the genetic nature of resistance. In devising future control strategies, the genetics of the plant and the insect are of equal importance.

Future Research

As the 21st Century approaches, plant scientists need to develop research programs and improved cultivars or hybrids with less dependence on expensive and environmentally disruptive inputs. As public concern about the environment and environmental degradation continues to grow, agriculture will be increasingly challenged to produce a safe, dependable food supply free of chemical residue. While the success stories of insect-resistant varieties may not be as great as desired, success can be achieved when sufficient resources are expended to deal with a problem. In the Western Hemisphere, the primary example of success is sorghum resistance to greenbug. Each time the insect has changed, crop improvement specialists have responded by incorporating genetic resistance into elite high-yielding parental lines for hybrids. While not all sorghum hybrids are greenbug-resistant, they could be.

During the last 50 years, a near green revolution has occurred in sorghum production throughout the world. Research on systems of sterility conducted in Texas at Chillicothe and Lubbock resulted in significant increases in sorghum yields in the developed world. Hybrid sorghum is possible throughout the world's sorghum production regions, provided the proper conditions are present. Even now the use of hybrid sorghums continues to increase. The Sorghum Conversion Program, initiated in Texas and Puerto Rico in 1963, made a portion of the genetic variability in the world collection of sorghum available to breeders worldwide. Many improvements made in sorghum during the last 25 years can be traced directly back to germplasm from the Sorghum Conversion Program. But the genetic improvements and yield increases needed for the future will be more difficult to achieve, especially for defensive traits such as resistance to insects.

To make the necessary genetic improvements in sorghum and pearl millet, breeders and other scientists will need to incorporate molecular biology (biotechnology) into their programs to a greater extent. The exciting tools of biotechnology will give scientists the opportunity to study insect resistance more thoroughly. Relationships between resistance genes can be accurately determined, resistance genes (some with different mechanisms)

can be stacked in different combinations to improve the durability of resistance, and, through cloning, evolutionary relationships of the host-insect pest interaction can be assessed. These developments will allow plant improvement teams to develop genotypes with greater environmental fitness, more resistance to stress, better grain quality, and improved yield potential. These new genotypes will be grown in environments more challenging than current production environments.

Sorghum improvement teams are fortunate to work with a crop that exhibits in nature almost unlimited variability. Molecular biology, and the ability to move genes between species, may make that variability truly unlimited! Breeders and entomologists have together produced genotypes with improved yield and resistance to insects. These genotypes have been widely grown and have contributed to stabilized and increased yields. The future is constrained only by the creativity of scientists and their ability to manipulate genes into the combinations needed for the 21st Century.

Control of the millet stem borer requires good understanding of the insect pest bioecology and development of sound integrated pest management strategies. Pearl millet breeding for resistance and tolerance to the millet stem borer requires a long-term approach and is a vital component of integrated pest management. A combination of cultural practices, resistant cultivars, and pheromone technology would be effective, and the exchange of genetic material and research information would contribute to an interdisciplinary approach to pest management in millet.

Key priority areas include comparative assessment of evaluation techniques for resistance to the millet stem borer and re-evaluation of varieties that possess certain traits that are thought to confer tolerance or resistance, such as stem hardiness, stem thickness, high tillering, and ability to produce a sticky secretion within the stem when attacked. Further research is needed on factors linked to oviposition nonpreference, such as length and density of trichomes. More research is needed to develop economic thresholds levels (ETLs) for millet stem borer. A locally made diet for mass producing millet stem borer should be improved to reduce costs associated with rearing. Studies to search for further sources of resistance and the determination of mechanisms and genetics of resistance are priority research areas.

References

Agrawal, B.L., and C.V. Abraham. 1985. Breeding sorghum for resistance to shoot fly and midge. p. 371-383. *In* Proc. of the international sorghum entomology workshop, 15-21 July 1984. Texas A&M University, College Station, TX.

Agrawal, B.L., and L.R. House. 1982. Breeding for pest resistance in sorghum. p. 435-446. *In* Proc. of the international symposium on sorghum in the eighties, 2-7 Nov. 1981. ICRISAT, Patancheru, Andhra Pradesh, India.

Ajayi, O. 1985. The effects of planting date and varieties on stem borer infestation and damage of pearl millet. Nigerian J. Entomology 6:71-77.

Ajayi, O., and Labe, D.A. 1990. The effects of sowing date and planting method on stem borer damage in dauro millet. Ann. Applied Biology 111:487-494.

Andrews, D.J., P.J. Bramel-Cox, and G.E. Wilde. 1993. New sources of resistance to greenbug, biotype I, in sorghum. Crop Sci. 33:198-199.

Archer, T.L., E.O. Bynum, Jr., and G.C. Peterson. 1986. Importance of plant senescence on grain sorghum resistance to the Banks grass mite (Acari: Tetranychidae). J. Econ. Entomol. 79: 15-17.

Balakotaiah, K., B.S. Rana, D.P. Tripathi, and N.G.P. Rao. 1975. Genetic analysis of some

exotic and Indian crosses in sorghum and inheritance of resistance to sorghum shoot fly. Indian J. Genet. Pl. Breeding 35:344-347.
Bennetzen, J.L. 1995. Biotechnology for sorghum improvement. African Crop Sci. J. 3:161-170.
Blum, A. 1972. Sorghum breeding for shoot fly resistance in Israel. p. 180. *In* M.G. Jotwani and W.R. Young (eds.) Control of sorghum shootfly. Oxford and IBH, New Delhi.
Borikar, S.T., and P.R. Chopde. 1980. Inheritance of shoot fly (*Atherigona soccata*) resistance under three levels of infestation in sorghum. Maydica 25:175-183.
Breen, J.P., and G.L. Teetes. 1986, Relationships of yellow sugracane aphid (homptera: Aphididae) density to sorghum damage. J. Econ. Entomol. 79:1106-1110.
Casas, A.M., A.K. Kononowicz, U.B. Zehr, D.T. Tomes, J.D. Axtell, L.G. Butler, R.A. Bressan, and P.M. Hasegawa. 1993. Transgenic sorghum plants via microprojectile bombardment. Proc. Natl. Acad. Sci. USA. 90:11212-11216.
Chang, P., and M. Fang. 1984. Studies on the resistance of sorghum variety to sorghum aphid, *Melanaphis sacchari* (Zehntner). Chinese J. Entomol. 4:97-105.
Chang, S. 1981. Sources of resistance in sorghum to sugarcane aphid, *Melanaphis sacchari* (Zehntner). Rep. of the Corn Res. Center, Taiwan DAIS 15:10-14.
Dahms, R.G. 1943. Insect resistance in sorghums and cotton. J. Am. Soc. Agron. 35:704-715.
Dahms, R.G., and J.B. Sieglinger. 1954. Reaction of sorghum varieties to the chinch bug. J. Econ. Entomol. 47:536-537.
Davis, F.H., G.L. Teetes, and J.W. Johnson. 1978. Yellow sugarcane aphid in sorghum. Sorghum Newsl. 21:112-113.
Diawara, M.M., B.R. Wiseman, and D.J. Isenhour. 1991. *Spodoptera frugiperda* (Lep.: Noct.) resistance in converted sorghum accessions: A research summary. Sorghum Newsl. 32:46-49.
Diawara, M.M., B.R. Wiseman, and D.J. Isenhour. 1992. Sorghum resistance to whorl feeding by larvae of the fall armyworm (Lep.: Noct.). J. Agric. Entomol. 9:41-53.
Diawara, M.M., B.R. Wiseman, D.J. Isenhour, and G.R. Lovell. 1990. Resistance to fall armyworm in converted sorghums. Fla. Entomol. 73:111-117.
Dixon, A.G., P.J. Bramel-Cox, and T.L. Harvey. 1991. Complementarity of genes for resistance to greenbug [*Schizaphis graminum* (Rondani)], biotype E, in sorghum [*Sorghum bicolor* (L.) Moench]. Theor. Appl. Genet. 81:105-110.
Duncan, R.R., D.J. Isenhour, R.M. Waskom, D.R. Miller, M.W. Nabors, G.E. Hanning, B.R. Wiseman, and K.M. Peterson. 1991. Registration of GATCCP100 and GATCCP101 fall armyworm resistant hegari regenerates. Crop Sci. 31:242-244.
Ehler, L.E. 1974. A review of the spider-mite problem on sorghum and corn in West Texas. Tex. Agric. Exp. Stn. B-1149.
Forbes, S.A. 1884. Thirteenth report of the state entomologist for Illinois for 1883, Springfield, Ill. Donnelley, Chicago.
Foster, D.G., G.L. Teetes, and J.W. Johnson. 1977a. Field evaluation of resistance in sorghums to Banks grass mite. Crop Sci. 16:821-823.
Foster, D.G., G.L. Teetes, J.W. Johnson, and C.R. Ward. 1977b. Resistance in sorghums to the Banks grass mite. J. Econ. Entomol. 70:259-262.
Gibson, P.T., and R.K. Maiti. 1983. Trichomes in segregating generations of sorghum matings. I. Inheritance of presence and density. Crop Sci. 23:73-75.
Gould, J., M. Devey, O. Hasegawa, E.C. Ulian, G. Peterson, and R.H. Smith. 1991. Transformation of *Zea mays* using *Agrobacterium tumefaciens* and shoot apex. Pl. Physio. 95:426-434.
Hackerott, H.L., and T.L. Harvey. 1971. Greenbug injury to resistant and susceptible sorghum in the field. Crop Sci. 11:641-643.
Hackerott, H.L., T.L. Harvey, and W.M. Ross. 1969. Greenbug resistance in sorghum. Crop Sci. 9:656-658.
Harris, K.M. 1962. Lepidopterous stem borers of cereals in Nigeria. Bull. Entomol. Res. 53:139-171.
Harvey, T.L., and H.L. Hackerott. 1969. Recognition of a greenbug biotype injurious to sorghum. J.Econ. Entomol. 62:776-779.
Harvey, T.L., and H.L. Hackerott. 1971. Research on greenbugs and resistance in sorghum. p. 84-86. *In* Proc. of the seventh biennial grain sorghum research and utilization conference. Lubbock, TX.
Harvey, T.L., K.D. Kofoid, T.J. Martin, and P.E. Sloderbeck. 1991. A new greenbug virulent to E-biotype resistant sorghum. Crop Sci. 31:1689-1991.
Harvey, T.L., G.E. Wilde, and K.D. Kofoid. 1996. Designation of a new greenbug, biotype K, injurious to biotype I resistant sorghum. Crop Sci. (in press).
Hayes, W.P. 1922. Observations on insects attacking sorghum. J. Econ. Entomol. 51:349-356.
Howitt, A.J., and R.H. Painter. 1956. Field and greenhouse studies regarding the sources and nature of sorghum (*Sorghum vulgare* Pers.) resistance to the corn leaf aphid, *Rhapalosiphum amidis* (Fitch). Kans. Agric. Exp. Stn. Bull. 82.
Hsieh, J., and C. Pi. 1982. Genetic study on aphid resistance in sorghum. J. Agric. Assoc. China, New Series 117:6-14.

Hsieh, J., and C. Pi. 1988. Diallel analysis of resistance to aphid in sorghum. J. Agric. Assoc. China 142:67-84.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1988. Annual report 1987. ICRISAT, Patancheru, 502 324, A.P. India.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1989. Annual report 1988. ICRISAT, Patancheru, 502 324, A.P. India.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1991. West African programs annual report 1990. Niamey, Niger: ICRISAT Sahelian Center.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1994. West African Programs Annual Report 1993. Niamey, Niger: ICRISAT Sahelian Center.

Johnson, J.W. 1971. Evaluation of sorghum for greenbug resistance. Sorghum Newsl. 14:114-116.

Johnson, J.W., D.T. Rosenow, and G.L. Teetes. 1982a. Registration of four composites of greenbug-resistant sorghum germplasm. Crop Sci. 22:1273.

Johnson, J.W., D.T. Rosenow, G.L. Teetes, and J.M. Phillips. 1982b. Registration of 19 greenbug resistant sorghum germplasm lines. Crop Sci. 22:1272.

Johnson, J.W., and G.L. Teetes. 1972. Evaluation of sorghum hybrids and lines for adult plant greenbug resistance. Sorghum Newsl. 15:137.

Johnson, J.W., G.L. Teetes, J.M. Phillips, and V. Riggs. 1981. Resistance to biotype E greenbug in sorghum. Sorghum Newsl. 24:84.

Johnson, J.W., G.L. Teetes, and D.T. Rosenow. 1982c. Registration of TAM2567 and TAM2568 greenbug resistant sorghum germplasm lines. Crop Sci. 22:1271.

Kofoid, K.D., and T.L. Harvey. 1992. Inheritance of resistance to greenbug biotypes E and I in the sorghum hybrid 'Cargill 607E'. Agronomy Abstracts. 1992 ASA/CSSA/SSSA Annual Meetings. 1-6 Nov. 1992. Minneapolis, MN.

Kononowicz, A.K., A.M. Casas, D.T. Tomes, R.A. Bressan, and P.M. Hasegawa. 1993. New vistas are opened for sorghum improvement by genetic transformation. African Crop Sci. J. 3:171-180.

Langham, R.M. 1968. Inheritance and nature of shoot fly resistance. M.S. thesis, University of Ahmedu Bello, Zaria, Nigeria.

Lukefahr, M.J. 1989. Considerations in the development of a host-plant resistance program against the pearl millet stem borer. p. 145-149. *In* International workshop on sorghum stem borers, 17-20 Nov. 1987. ICRISAT, Patancheru, India.

Manthe, C.S. 1992. Sorghum resistance to the sugarcane aphid (Homoptera: Aphididae). Ph.D. dissertation, Texas A&M University, College Station, Tx.

McColloch, J.W. 1921. The corn leaf aphid (*Aphis maidis* Fitch) in Kansas. J. Econ. Entomol. 14:89-94.

Meckenstock, D.H., M.T. Castro, H.N. Pitre, and F. Gomez. 1991. Antibiosis to fall armyworm in Honduras landrace sorghum. Environ. Entomol. 20:1259-1266.

Mote, U.N., and J.R. Kadam. 1984. Incidence of *Aphis sacchari* (Zent.) in relation to sorghum plant characters. Sorghum Newsl. 27:86.

Mote, U.N., M.D. Shinde, and D.R. Bapat. 1985. Screening of sorghum collections for resistance to aphids and oily malady of winter sorghum. Sorghum Newsl. 28:13.

Mize, T.W., and G. Wilde. 1986. New resistant germplasm to the chinch bug (Heteroptera: Lygaeidae) in grain sorghum: Contribution of tolerance and antixenosis as resistance mechanisms. J. Econ. Entomol. 79:42-45.

Ndoye, M. 1977. Synthèses de quelques résultats sur les insectes foreurs des mils et sorgho au Sénégal. Centre nationale de recherches agrononomiques, Bambey, Senegal

Ndoye, M. 1979. L'entomofaune nuisible au mil à chandelle (*Pennisetum typhoides*) au Sénégal. p. 515-530. *In* Compte rendu des travaux, Congrès sur la Lutte Contre les Insectes en Milieu Tropical, 13-16 Mar 1979, Part 1. Chambre de Commerce et d'Industrie, Marseilles, France

Nwanze, K.F. 1985. Some aspects of pest management and host plant resistance in pearl millet in the Sahel. Insect Sci. Applic. 6:461-465.

Nwanze, K.F. 1989. Insect pests of pearl millet in Sahelian West Africa. I. *Acigona ignefusalis* (Pyralidae, Lepidoptera): Distribution, population dynamics and assessment of crop damage. Trop. Pest Management 35:137-142.

Nwanze, K.F., and K.M. Harris. 1992. Insect pests of pearl millet in West Africa. Rev. Agric. Entomol. 80:1133-1155.

Nwanze, K.F., and Y.V.R. Reddy. 1991. A rapid method for screening sorghum for resistance to *Chilo partellus* (Swinhoe) (Lepidoptera: Pyralidae). J. Agric. Entomol. 8:41-49.

Nwanze, K.F., N. Seetharama, H.C. Sharma, and J.W. Stenhouse. 1995. Biotechnology in pest management: Improving resistance in sorghum to insect pests. African Crop Sci. J. 3:209-215.

Paliani, A.L.P. 1993. Sorghum resistance to yellow sugarcane aphid (Homoptera: Aphididae). M.S. thesis, Texas A&M University, College Station, TX.

Paterson, A.H., Y.R. Lin, Z. Li, K.F. Schertz, J.F. Doebley, S.R.M. Pinson, S.C. Liu, J.W. Stansel, and J.E. Irvine. 1995. Convergent domestica-

tion of cereal crops by independent mutations of corresponding genetic loci. Science 269:1714-1718.

Peterson, G.C., T.L. Archer, and D.T. Rosenow. 1987. Evaluation of grain sorghum genotypes for resistance to the Banks grass mite. Sorghum Newsl. 30:66-67.

Peterson, G.C., T.L. Archer, G.L. Teetes, and J.W. Jones. 1991. Registration of 10 biotype E greenbug-resistant sorghum germplasm lines. Crop Sci. 31:499-500.

Peterson, G.C., J.W. Johnson, G.L. Teetes, and D.T. Rosenow. 1983. Registration of Tx2783 greenbug resistant sorghum germplasm line. Crop Sci. 24:390.

Peterson, G.C., J.W. Johnson, G.L. Teetes, and D.T. Rosenow. 1985. Registration of greenbug biotype C resistant sorghum germplasm. Crop Sci. 25:373.

Pi, C., and J.S. Hsieh. 1982a. Preliminary studies on aphid resistance in sorghum. Natl. Sci. Counc. Monthly, ROC. 10:153-160.

Pi, C., and J.S. Hsieh. 1982b. Studies on grain quality and aphid resistance in sorghum. Proceedings of the Plant Breeders Symposium. R.O.C. Regional Society of SABRAO and Agricultural Association of China.

Porter, K.B., G.L. Peterson, and O. Vise. 1982. A new greenbug biotype. Crop Sci. 22:847-850.

Puterka, G.J., and D.C. Peters. 1995. Genetics of greenbug (Homoptera: Aphididae) virulence to resistance in sorghum. J. Econ. Entomol. 88:421-429.

Rana, B.S., M.G. Jotwani, and N.G.P. Rao. 1981. Inheritance of host plant resistance to the sorghum shoot fly (*Atherigona soccata*, India). Insect Sci. Applic. 2:105-109.

Rana, B.S., B.U. Singh, and N.G.P. Rao. 1985. Breeding for shoot fly and stem borer resistance in sorghum. p. 347-360. *In* Proc. of the international sorghum entomology workshop, 15-21 July 1984. College Station, TX.

Rana, B.S., D.P. Tripathi, K. Balakotaiah, R. Damodar, and N.G.P. Rao. 1975. Genetic analysis of some exotic x Indian crosses in sorghum and selection for shoot fly resistance. Indian J. Genet. 35:350-355.

Rondani, C. 1852. *Aphis graminum* n. sp. Nouv. Ann. Sci. Nat. Bologna 6:9-11.

Schuster, D.J., and K.J. Starks. 1973. Greenbugs: Components of host-plant resistance in sorghum. J. Econ. Entomol. 66:1131-1134.

Setokuchi, O. 1976. Ecology of *Longuinguis sacchari* (Zehntner) (Aphididae) infesting sorghums. IV. Varietal difference of sorghums in the aphid occurrence. Proc. Assoc. Pl. Prot. Kyushu 22:139-142.

Sharma, H.C. 1993. Host plant resistance to insects in sorghum and its role in integrated pest management. Crop Prot. 12:11-34.

Sharma, H.C., M.G. Jotwani, B.S. Rana, and N.G.P. Rao. 1977. Resistance to sorghum shoot fly *Atherigona soccata* Rondani and its genetic analysis. J. Entomol. Res. 1:1-12.

Snelling, R.O., R.H. Painter, J.H. Parker, and W.M. Osborn. 1937. Resistance of sorghums to the chinch bug. USDA Tech. Bull. 585.

Srivastava, K.P. 1985. Screening for sorghum stem borer resistance. p. 189-200. *In* Proc. of the international sorghum entomology workshop, 15-21 July 1984. College Station, TX.

Starks, K.J., and K.A. Mirkes. 1979. Yellow sugarcane aphids: Plant resistance in cereal crops. J. Econ. Entomol. 74:486-488.

Starks, K.J., and D.E. Weibel. 1982. Sorghum cultivars rated resistant to chinch bug *Blissus leucopterus*. Sorghum Newsl. 25:82-83.

Starks, K.J., D.E. Weibel, and J.W. Johnson. 1972. Sorghum resistance to the greenbug. Sorghum Newsl. 15:130.

Starks, K.J., D.E. Weibel, E.A. Wood, J.W. Johnson, and A.J. Casady. 1971. Greenbug resistance in sorghum. Sorghum Newsl. 14:97.

Stephens, J.C., F.R. Miller, and D.T. Rosenow. 1967. Conversion of alien sorghums to early combine genotypes. Crop Sci. 7:396.

Taneja, S.L., and K. Leuschner. 1984. Resistance screening and mechanisms of resistance in sorghum to shoot fly. p. 115-129. *In* Proc. of the international sorghum entomology workshop, 15-21 July 1984. College Station, TX.

Teetes, G.L., and J.W. Johnson. 1972. Mechanisms of greenbug resistance in sorghum. Sorghum Newsl. 15:135-136.

Teetes, G.L., J.W. Johnson, and D.T. Rosenow. 1976. Screening for corn leaf aphid resistant sorghums. Sorghum Newsl. 19:128.

Teetes, G.L., C.A. Schaefer, and J.W. Johnson. 1974a. Resistance in sorghums to the greenbug; laboratory determination of mechanisms of resistance. J. Econ. Entomol. 67:393-396.

Teetes, G.L., C.A. Schaefer, J.W. Johnson, and D.T. Rosenow. 1974b. Resistance in sorghum to the greenbug: Field evaluation. Crop Sci. 14:706-708.

Van Rensburg, N.J. 1973a. Notes on the occurrence and biology of the sorghum aphid in South Africa. J. Entomol. Soc. S. Afr. 36:293-298.

Van Rensburg, N.J. 1973b. Population fluctuations of the sorghum aphid *Melanaphis* (*Longuinguis*) *pyrarius* (Passerini) forma *sacchari* (Zehntner). Phytophylactica 5:127-134.

Vedamurthy, G. 1967. Insect pests of sorghum and their control (including sources of resistance). PANS 13:121-126.

Venugopal, M.S., S. Sadakathulla, and M. Mani. 1979. Differential susceptibility of some sorghum varieties to aphids. Sorghum Newsl. 22:71.

Webster, F.M. 1909. Investigations of *Toxoptera graminum* and its parasites. Ann. Entomol. Soc. Am. 2:67-87.

Webster, F.M., and W.J. Phillips. 1912. The spring grain-aphis or 'green bug'. USDA Bur. Entomol. Bull. 110:1-153.

Webster, J.A. 1990. Yellow sugarcane aphid (Homoptera: Aphididae): detection and mechanisms of resistance among Ethiopian sorghum lines. J. Econ. Entomol. 83:1053-1057.

Weibel, D.E., K.J. Starks, E.A. Wood, Jr., and R.D. Morrison. 1972. Sorghum cultivars and progenies rated for resistance to greenbugs. Crop Sci. 12:334-336.

Wiseman, B.R. 1992. Foliage-feeding lepidopterous insects attacking sorghum in the Americas. Sorghum Newsl. 33:40-45.

Wiseman, B.R., and L. Gourley. 1982. Fall armyworm (Lep.: Noct.) infestation procedures and sorghum resistance evaluations. J. Econ. Entomol. 75:1048-1051.

Wiseman, B.R., and G.R. Lovell. 1988. Resistance to the fall armyworm in sorghum seedlings from Ethiopia and Yemen. J. Agric. Entomol. 5:17-20.

Youm, O. 1990. Evaluation of natural enemies associated with the millet stem borer, *Haimbachia ignefusalis* (Hampson) (Lepidoptera: Pyralidae) in Niger. Ph.D. dissertation, Texas A&M University, College Station, Tx.

Youm, O., and F.E. Gilstrap. 1994. Habitat site selection, crop damage and oviposition preference by *Coniesta* (= *Haimbachia*) *ignefusalis* (Lepidoptera: Pyralidae). Inter. J. Pest Management 40:231-236.

Youm O., K.M. Harris, and K.F. Nwanze. 1996. *Coniesta ignefusalis* (Hampson), the millet stem borer: A handbook of information. (In En. Summaries in En., Fr., Es.) Information Bulletin 46. International Crops Research Institute for the Semi-Arid Tropics, Patancheru 502 324, Andhra Pradesh, India.

Breeding for Disease Resistance in Sorghum

R.P. Thakur*, R.A. Frederiksen, D.S. Murty, B.V.S. Reddy,
R. Bandyopadhyay, L.M. Giorda, G.N. Odvody and L.E. Claflin

Abstract

*Sorghum [*Sorghum bicolor *(L.) Moench], a staple cereal of the semiarid tropics is host to a large number of pathogens, including fungi, bacteria, viruses, and nematodes. These pathogens, individually or in combination, may result in significant economic losses to grain and forage production. Breeding cultivars that tolerate pathogens' attack and still produce adequate yield is the most effective means of managing these diseases. Diseases of major importance are grain mold, charcoal rot, anthracnose, downy mildew, leaf blight, smut, and ergot. Several others are locally important in some years. Since the last global conference on sorghum diseases in 1992, significant advances have occurred in disease resistance research, including improvement and refinement of screening techniques, identification of new sources of resistance, and a better understanding of the genetic basis of resistance. Conventional breeding methods, such as backcrossing, pedigree selection, and recurrent selection, continue to be used to develop disease-resistant cultivars with major resistance genes and several new cultivars resistant to important diseases have been released. Use of molecular techniques for sorghum genome mapping and the identification of markers for disease resistance genes have opened up new opportunities for rapid transfer of resistance, particularly those controlled by several genes, into agronomically elite material. Future efforts should focus on genetic characterization of resistance sources, establishment of effective systems for monitoring host resistance and changes in pathogen virulence, and enhancement of international cooperation in using emerging information and technologies for better management of diseases, leading to improved sorghum productivity.*

Breeding for disease resistance is an integral part of a crop improvement program aimed at sustained productivity. Plant diseases cause an annual estimated loss of 540 million tons of crop production, valued at 50 billion U.S. dollars (James, 1981). Sorghum, the fifth major crop of the world, is grown on about 52 million ha annually in tropical, subtropical, and temperate environments and serves as host to over one hundred pathogens, including fungi, bacteria, viruses, and nematodes. These pathogens, individually or in combination, lead to considerable yield loss (Table 1). In most of Africa and Asia, sorghum is grown mainly for food by resource-poor farmers and is often unprotected by chemicals for both economic and technical reasons.

R.P. Thakur, ICRISAT Asia Center, Patancheru, Andra Pradesh 502 324, India; R.A. Frederiksen, Department of Plant Pathology and Microbiology, Texas A&M University, College Station, TX 77843; D.S. Murty, ICRISAT, BP 320, Bamako, Mali; B.V.S. Reddy, ICRISAT Asia Center, Patancheru, Andra Pradesh, 502 324 India; R. Bandyopadhyay, ICRISAT Asia Center, Patancheru, Andra Pradesh 502 324, India; L.M. Giorda, EEAINTA Manfredi, Cordoba, Argentina; G.N. Odvody, Department of Plant Pathology and Microbiology, Texas A&M University, Corpus Christi, TX 79401 and L.E. Claflin, Department of Plant Pathology, Kansas State University, Manhattan, KS 66506. ICRISAT Conference Paper CP 1149. *Corresponding author.

Table 1. Estimates of yield loss due to various sorghum diseases

Disease	Yield loss (%)	Reference
Downy mildew	10-78	Anahosur & Laxman (1991)
Acremonium wilt	50	Wall et. al., (1989)
Anthracnose	55-67	Thomas et. al., (1996)
Rust	29-50	Hepperly (1990)
Rhizoctonia sheath blight	35-42	Pascual & Raymundo (1988)
Gray leaf spot	20	Wall et. al., (1989)
Sooty stripe	5	Wall et. al., (1989)
Maize dwarf mosaic virus	54	Wall et. al., (1989)
Charcoal rot	15-60	Pande & Karunakar (1992)
Head smut	16	Narro (1986)
Ergot	10-80	Sangitrao (1982)

Disease management through genetic manipulation has been the most effective means of reducing losses in many crop species. However, managing all diseases by genetic means is neither feasible nor possible. Breeding for resistance is one of several methods of protecting the crop; therefore, before a resistance breeding program begins, it must be clearly determined that:

a) the disease is of sufficient economic importance,

b) sufficient information is available on the nature of the host-pathogen system,

c) well-defined sources of resistance are available, and

d) the expected economic output will occur within a given time.

Disease control through host genetic manipulation is difficult and has been slower for charcoal rot and grain mold, in which gene effects are small, compared to downy mildew, anthracnose, and leaf blight, in which gene effects are large.

Breeding for disease resistance in sorghum began about three decades ago (Rosenow, 1992; Rosenow and Frederiksen, 1982; Rao et al., 1980; Mukuru, 1992). During the past few years, several genes conferring disease resistance have been identified and transferred in cultivars, primarily through conventional breeding methods. With the advent of modern molecular techniques however, significant advances have occurred in molecular characterization of resistance genes and identification of markers for tagging. Present day breeding for disease resistance is a collaborative effort of pathologists, molecular biologists, and breeders working across locations and regions. Essential requirements for successful deployment and management of disease resistance genes include:

- access to collection of diverse host germplasm,
- efficient disease screening techniques,
- effective resistance factor(s),
- knowledge of heritability of resistance,
- strategy of resistance deployment, and
- appropriate method for monitoring resistance.

Priority Diseases

The 1992 Second World Review of Sorghum and Pearl Millet Diseases identified 16 important diseases: grain mold, downy mildew, charcoal rot, leaf blight, rust, gray leaf spot, anthracnose, sooty stripe, zonate leaf spot, bacterial stripe, ergot, head smut, long smut, covered smut, loose smut, and nematodes.

Priority diseases for different regions of the world were identified on ratings from 1 (least important) to 7 (most important): a) health hazard; b) farming system; c) method of spread/survival; d) pathogen variability; e) lack of control method; f) prevalence/distribution; and g) effect on yield/quality. The priority diseases for each region, listed here from highest to lowest are:

- *Western Africa*: grain mold, long smut, anthracnose, gray leaf spot, and sooty stripe
- *Eastern Africa*: anthracnose, covered smut, leaf blight, loose smut, and grain mold
- *Southern Africa*: grain mold, leaf blight, anthracnose, covered smut, ergot, and downy mildew
- *Americas and Europe*: anthracnose, grain mold, root and stalk rots, head smut, viruses, and downy mildew
- *Asia and the Far East (India, Thailand, Philippines, Japan)*: grain mold, stalk rots, ergot, downy mildew, and leaf spots
- *Worldwide*: grain mold, anthracnose, leaf blight, and leaf spots

Priority rankings must be continuously updated because diseases, pathogens, host cultivars, and cropping systems change over time and space. For example, before 1995, ergot had not been reported in the Americas, but now the disease has appeared in Brazil, Argentina, and Bolivia (Reis et al., 1996). It is feared that the pathogen may continue to spread throughout the Americas. The importance of ergot in the Americas is now much higher than it was in 1992.

The 1992 workshop also recommended the following priority research areas for various diseases:

- *Grain mold*: standardize the evaluation procedure; study heritability of resistance and gene action; continue to search for new sources of resistance.
- *Anthracnose*: evaluate known sources of resistance through multilocation tests; monitor pathogen variability through host differentials; determine mechanism of resistance; develop more effective screening techniques; identify and utilize sources of resistance by conventional breeding and molecular methods; determine inheritance of resistance and gene action; establish an International Working Group on Anthracnose of the Gramineae.
- *Stalk rot*: improve screening methods; develop a multilocation cooperative program.
- *Ergot*: identify the pathogen in different parts of the world; determine the relationship between flower biology and infection in different lines; improve screening techniques; assess yield loss.
- *Downy mildew*: study variability in virulence; use monogenic and oli-

gogenic R genes in resistance breeding; continue international communication through a working group.

- *Leaf diseases*: determine economic importance; develop effective screening techniques; develop a uniform scoring scale; continue multilocation evaluation; study host-pathogen interaction, pathogen variability, and epidemiology.
- *Head smut*: breed disease resistant cultivars; monitor pathogen variability.
- *Long smut*: develop screening techniques; identify new sources of resistance.

Access to Diverse Germplasm

The ICRISAT gene bank at Asia Center houses the a collection of over 35,000 sorghum accessions, representing all sorghum growing environments and regions in the world. These accessions have been characterized and catalogued for easy and quick access by researchers. A large number of lines have been screened for resistance to various diseases by researchers at ICRISAT, INTSORMIL, and many national programs. The Genetic Resource Division of ICRISAT and Texas A&M Univsersity both maintain lists of disease-resistant accessions and converted sorghum lines for specific and multiple disease resistance. Fortunately sorghum landraces exhibit a wide range of diversity and the world collection of sorghum contains sources of resistance to most diseases. Resistance to several diseases is stable and significant progress has been made in breeding disease-resistant varieties and hybrids (Mukuru, 1992; Rosenow and Frederiksen, 1982). However, progress has been limited in developing resistance to other diseases, such as grain mold and stalk rot.

Disease Screening Techniques

Effective disease screening techniques are crucial for identifying sources of resistance. Development of a screening technique requires an understanding of the biology of the pathogen and disease epidemiology. Effective field screening techniques have been developed for downy mildew (Pande and Singh, 1992), stalk rot (Mahalinga et al., 1989; Pande and Karunkar, 1992), anthracnose (Pande et al., 1994), leaf blight (Sifuentes et al., 1993), sooty stripe (Thomas et al., 1993), ergot (Tegegne et al., 1994; Musabyimara et al., 1995), and grain mold (Bandyopadhyay and Mughogho, 1988).

These techniques have been used by scientists in many developing countries. However, there is always room for further refinement and improvement of screening techniques. One important limitation for success in field screening has been the lack of control over weather. Some weather factors can be partly controlled, mainly RH (through supplemental irrigation) and temperature (by adjustment of the timing of planting). These adjustments, however, vary and environments remain far from optimum at many locations, causing large variations in results in multilocation/ multiyear evaluations. Often in multilocation experiments, differences in disease reactions resulting from variable weather factors is construed as variation in pathogenicity or the existence of different pathotypes or races. This high variability underscores the need to develop a more precise greenhouse

screening technique that controls weather variables to provide optimal conditions for infection and disease development. Creating and maintaining such facilities in developing countries is not easy.

Obtaining isolates of pathogens from different locations and maintaining and evaluating them under controlled conditions is one solution to the problem of variable results in multilocation experiments. Effective greenhouse techniques are available for downy mildew (Narayana et al., 1995), anthracnose (Pande et al., 1994), leaf blight (Sifuentes et al., 1993), and grain mold (Singh et al., 1993).

Sources of Resistance

Lines resistant to several sorghum diseases are available (Table 2); however, sources of stable resistance to individual diseases, particularly in the desirable agronomic backgrounds (especially for grain mold) are limited. Resistance stability depends in part on the nature of the pathogens involved. For example, resistance sources to charcoal rot are more stable than those for anthracnose and downy mildew, because the anthracnose and downy mildew pathogen populations are more variable than that of the charcoal rot pathogen (Fredericksen et al., 1995). For variable pathogens where physiologic races are known to exist, new sources of resistance need to be regularly identified. Sorghum lines resistant to a disease at the regional level are easier to identify than those at the global level. For example, QL 3 is a good source of downy mildew resistance in most parts of the world, but it has shown susceptibility in Zimbabwe (R.A. Frederiksen, 1996, personal communication). International disease nurseries, such as the Uniform Head Smut Nursery and the Anthracnose Virulence Nursery, are designed as much to detect differences in pathogen populations as they are to evalu-

Table 2. Sources of resistance to some major sorghum diseases[1]

Disease	Resistance source	Reference
Grain mold	IS 14384, - 14388 (colored grain)	Mukuru (1992)
	IS 7173, -23773, -23783, -34219 (white grain)	Singh et al. (1993)
Downy mildew	QL-3 India, SC414-12	Sifuentes & Frederiksen (1988)
	Tx 430, IS 20450,-20468,-20478	Craig & Odvody (1992); Karunakar et al. (1994)
Anthracnose	SC 326-6, SC 599-11E	Tenkouano & Miller (1993)
	NP 20BR, NP 26	Pederson et al. (1995)
Leaf blight	87BL2598	Duncan et al. (1988)
Sooty stripe	IS 23818, E 35-1	Thomas et al. (1993)
Ergot	ETS 2454, -3135, 3147 etc.	Bandyopadhyay (1992), Tegegne et al. (1994)
Head smut	Krish 13, QL lines	Dodman et al. (1986)
Charcoal rot	Q 101, -102, -103, -54	Karunakar et al. (1993)
Rust	IS 2300, -3443, C-40, IS 31446, -18758 etc.	Singh et al. (1994)
Multiple disease resistance		
Sooty stripe, Gray LS, anthracnose, zonate LS	MPC 123, 2219Ax 3274-1-2	Bhasker et al. (1993)
Head smut and anthracnose	Jinong 105	Chen et al. (1991)
Leaf blight, rust, Zonate etc.	87BL2598	Duncan et al. (1988)

[1]In addition a large number of converted lines with resistance to single and multiple diseases are available at TAMU (Collins et al., 1996.

ate host resistance (ISAVN Report, 1996). Identification of a few test sites, or "hot spots," where one or more diseases are severe is important to identify the best sources of disease resistance. Through these nurseries, lines have been identified with good levels of resistance in particular countries or regions. Sources of multiple disease resistance also have been identified, but utilization of such sources is often time- and resource-consuming.

Stable resistance can be identified through multilocation tests. Durability of resistance is a function of time and area under coverage. Usually, monogenic resistance for variable pathogens will be less durable than polygenic resistance; however, polygentic resistance usually is more difficult to breed for and requires more time and resources. Resistance may be more stable and durable for a less variable pathogen than for a more variable one.

Currently resistance to several sorghum diseases is based on major genes from a limited group of cultivars. Reports also are available on polygenic/quantitative resistance to grain mold and stalk rots. Horizontal or dialatory resistance also has been reported for anthracnose. Polygenic sources of resistance should also be exploited by breeders if and when they are available. Use of modern molecular techniques for gene identification and transfer should be used where feasible.

Inheritance and Genetics of Resistance

Rosenow (1992) summarized information on the inheritance of resistance to some sorghum diseases. Although detailed information on the genetics of resistance to several diseases is still needed, it is generally recognized that, except for complex diseases such as stalk rot, grain mold, etc., resistance to most diseases is controlled by major genes (Table 3). Although significant progress has been made in the past few years, and today we have much more information about the inheritance of disease resistance, however, much more information is still needed.

Grain mold. Panicle and grain characters influence grain mold resistance. Resistance has been reported to be monogenic (Rao and Rana, 1989); additive gene action has been reported for *Fusarium* (Kataria et al., 1990); both additive and nonadditive gene action have been reported, with recessive genes in some cases and dominant genes in others (Dabholkar and Baghel, 1983; Murty and House, 1984) and with greater influence of the environment (Indira et al., 1991).

Anthracnose. Resistance to anthracnose has been reported to be governed by major genes with partial dominance or additive effects in A 2267-2 and IS 8283 (Sifuentes and Mughogho, 1992), by a single dominant gene with no cytoplasmic influence (Reddy and Singh, 1993), and by a single locus with multiple alleles (Murty and Thomas, 1989; Tenkouano and Miller, 1993).

Stalk rot. Significant General Combing Ability (GCA) effects were noted for *Macrophomina phaseolina* and *Fusarium moniliforme* (Bramel Cox et al., 1988). Resistance has been reported to be governed by recessive complementary genes (Venkatrao et al., 1983), partial domi-

Table 3. Inheritance of resistance of some sorghum disease.

Disease	Inheritance pattern	Reference
Grain mold	Intermediate/dominant/ additive/duplicate	Kataria et al (1990)
Anthracnose	Dominant	Tenkouano & Miller (1993)
Downy mildew	Dominant/partially dominant	Craig & Schertz (1985) Sifuentes & Frederiksen (1988) Reddy et al. (1993)
Charcoal rot	Recessive/intermediate/recessive	Tenkouano et al. (1993)
Fusarium stalk rot	Dominant/intermediate	
Fusarium head blight	Dominant/intermediate	
Acremonium wilt	Recessive/intermediate	
Head smut	Dominant/intermediate/additive	Cao et al. (1988)
Covered kernel smut	Dominant	
Loose kernel smut	Dominant	
Rust	Dominant	Patil et al. (1972)
Gray leaf spot	Recessive	Bangarwa et al. (1987)
Leaf blight	Dominant	Sifuentes et al. (1993)
Sooty stripe	Recessive/intermediate	Galiba (1983)
Zonate leaf spot	Recessive/intermediate/ additive/dominant	Grewal (1988)
Oval leaf spot	Recessive	Grewal et al. (1987)
Target leaf spot	Recessive	Tsukiboshi et al. (1990)
Ladder spot	Recessive	Rosenow and Frederiksen (1982)
Bacterial stripe	Recessive	Rosenow and Frederiksen (1982)
Bacterial streak	Recessive/intermediate	Rosenow and Frederiksen (1982)
Maize dwarf mosaic virus	Dominant/recessive	Rosenow and Frederiksen (1982)

nance (Indira and Rana, 1983), non-additive genetic variance with a high degree of dominance (Indira et al., 1983), and dominant and recessive epistatic interactions between two loci with a third modifying locus; nonsenescence alone does not provide resistance (Tenkouano et al., 1993).

Downy mildew. Resistance has been reported to be governed by a set of six dominant genes (Bhat et al., 1982), three gene pairs (Rana et al., 1982), two genes in QL 3 and one gene in SC 414-12 (Sifuentes and Frederiksen, 1988. Depending on the sorghum lines and pathotypes involved, the number of genes and gene actions were variable. Reddy et al. (1992) proposed a two-locus model with independent segregation and a combination of complementary and inhibitory inter-allelic interactions. Gimenes-Fernandes and Pena (1986) reported no influence of cytoplasm on resistance, and de Milliano and In't Veld (1988) reported the influence of environment on resistance expression in QL 3.

Leaf blight. Resistance to leaf blight is reported to be governed by a single dominant gene with no cytoplasmic influence in two sorghum lines: A 2267-2 and ICSB 26 (Sifuentes et al., 1993).

Head smut. Both qualitative and quantitative inheritance have been reported (Cao et al., 1988; Cao and Wang, 1988; Yang et al., 1992). A_2 cytoplasm was reported to be more susceptible than A_1 (Rodriguez-Herrera et al., 1992, 1993).

Maize dwarf mosaic potyvirus. Resistance is reported to be governed by three dominant-recessive factors and four epis-

tatic effects; Krish type resistance is determined by one dominant factor (Nk allele; Mijavec, 1991).

Progress on Resistance Incorporation and Resistance Deployment

Conventional Breeding Methods

In the tropics, sorghum landraces are generally tall and late-maturing. Foliar diseases usually are limited to the lower leaves until flowering and rarely affect grain yields. However, introductions can suffer badly from these diseases, leading to poor yields. Crop improvement programs employ diverse exotic germplasms to improve both grain yield and the agronomic characters of local cultivars. Unless caution is exercised in the selection of exotic parents, based on their resistance to local diseases, the resulting improved cultivars could bring in "second generation" problems.

Choice of parents is the first crucial step in any hybridization and selection program. Usually an agronomically good high-yielding cultivar is crossed to other parents with disease resistance, pest resistance, good grain quality, local adaptation, etc. Appropriate weight should be given to the maturity period, height, grain quality, and status of resistance to various stress factors of the parents involved in the cross. The genetic basis of resistance should suggest the selection procedure.

At ICRISAT, pedigree breeding with selection for resistance based on families and agronomic desirability within the selected families of single crosses, and frequently in three-way crosses, has resulted in disease-resistant, high-yielding cultivars. It has been found that a third parent in the cross can supplement useful traits/recessive genes and increase their frequency in the segregating populations without seriously affecting agronomic eliteness. Specific improvement for resistance to a simple disease (e.g., rust) can be obtained by straightforward backcross breeding. Recurrent selection procedures to accumulate favorable alleles for multiple disease resistance factors also can be used in long-term selection programs. Development of random mating gene pools to preserve, recombine, and improve disease and pest resistance of sorghum has been found to be useful at ICRISAT.

Considerable progress has been made at ICRISAT in transferring resistance to individual diseases into several B and R lines. Some of the promising resistant B lines are: anthracnose-resistant SPAN 94037B, 94008B and 94033B; downy mildew-resistant SPDM 94006B, -94008B, and 94051B; rust-resistant SPRV 94003B and 94010B; leaf blight-ressitant SPLB 94001B, 94007B, and 94017B; and grain mold-resistant SPGM 94009B, 94033B (white grains), SPGM 94066B, 94052B, 94017B (colored grains). Some disease-resistant R lines and varieties have also been developed: grain mold-resistant ICSV 95011, ICSV 95017 (white grains), ICSV 95029, ICSV 95039 (colored grains); rust- and anthracnose-resistant ICSV 745, -93073, and -93080.

Molecular Techniques

A recent review by Bennetzen (1995) provides background on the roles and uses of modern molecular techniques for genetic improvement of sorghum. Several

DNA marker technologies have been used to generate the first detailed genetic maps of sorghum. Weerasuriya (1995) has mapped various traits in a recombinant inbred population of sorghum, including resistances to anthracnose and rust.

Neutral markers would assist in the introgressing of resistance genes into agronomically elite lines. A number of useful DNA markers for disease resistance genes have been identified [for both single genes and multiple loci (QTL)] for head smut, anthracnose, downy mildew, Acromonium wilt, and virus disease (Oh et al., 1993). Using marker-assisted selection (MAS) breeding, it should be possible to precisely and effectively transfer these resistance genes into agronomically acceptable cultivars. This technique has major advantages if resistance is governed polygenically, the pathogen is highly variable, and multiple resistance genes need to be transferred. For example, there are three known pathotypes of sorghum downy mildew present in Texas. Sorghum cultivars must be resistant to all three in areas where the disease is present. To effectively reduce the shift from one pathotype to another, it is important to introduce more than one gene at a time to control the disease. Genetic markers are required for tagging the different genes for resistance. This represents a practical method of pyramiding resistance genes.

Transformation

Transformation of sorghum has been demonstrated using both mechanical and biological methods (for details refer to R. Smith et al., elsewhere in these Proceedings). However, very little has been done with sorghum transformation at this time.

Integrated Disease Management

The principle of integrated crop management is to conserve, protect, and enhance good sorghum germplasm as well as that of other crops. In many respects, disease management has stressed integration, but it was based on management of host resistance genes rather than pesticides. With the advent of the microchip and advances in satellite technologies, development of precise crop management systems is even more feasible than before. The rational reasons for crop management must be tempered to ensure both a reasonable quantity of production and stewardship of resources.

Sorghum is rarely grown in isolation. In developing countries it is frequently grown as a mixture of landrace cultivars intercropped with other commodities. In western agriculture, large uniform fields of hybrids may be remarkably productive, but even under these conditions other agricultural commodities may be grown. Management of diseases and other pests of sorghum requires an intimate knowledge of the agro-ecosytem in which the host is grown. Consequently, agricultural programs and policies must be directed toward the most responsible practices that support or protect the environment and biodiversity. Currently, programs to develop integrated crop management protocols are being developed in many agricultural settings (Teng and Penning de Fries, 1992).

The general principles of sanitation, residue management, soil fertility management, crop rotation, mixed-cropping, etc. should be followed to reduce the initial inoculum threshold, spread of secon-

dary inoculum in a crop, and dissemination of inoculum either as seed borne or seed contaminants. These applications are, however, location and production system-specific and need to be developed and followed accordingly. It would be best to include disease management methods as part of an integrated crop management system, thus requiring a holistic approach to longer term sustainable agriculture.

Focus for the Future

Genetic Characterization of Resistance

Large numbers of sorghum lines are reported to be resistant to one or more diseases, but very little information is available on the specific genes that contribute the resistance. Efforts should shift from identifying more sources of resistance to characterizing the available sources for proper utilization. Molecular techniques should be used to more reliably identify markers and transfer them to useful backgrounds.

Effective Monitoring System

Every year a number of cultivars are released, but very few become popular with farmers and growers. A method to monitor cultivar performance at the farm level for disease reaction must be developed. The resulting information would provide guidance for the development and deployment of new cultivars. Often, conditions for evaluation and monitoring at research stations are quite different from the real world conditions in farmers' fields. Currently there is no known effective method for managing such a monitoring network at the global level. Such a monitoring system, however, would provide information on both cultivar performance and development of new virulent pathogen populations.

Controlled Environment Facilities

To enhance gains from the resistance breeding process, effective and rapid screening methods are essential. Mass screening of segregating breeding materials can be effectively done on pot-grown seedlings in a greenhouse. This method often is not employed in developing countries due to the lack of financial resources. Field screenings augmented with artificial inoculation and irrigation also often suffer from inadequate funding. Results from natural field screens are often inconsistent due to variable inoculum pressure and unfavorable environmental conditions for infection and disease development. It is essential, therefore, that controlled environment facilities be created in each country for use in resistance breeding.

International Cooperation

Collaborative international nurseries and trials have been very useful, in that these have provided opportunities to scientists to examine the performance of materials at their respective locations and select the most desirable ones for the region. ICRISAT and INTSORMIL have promoted international cooperation well, but further improvement is always possible. Special working groups should be created to tackle regionally or globally important disease problems.

References

Anahosur, K.H., and M. Laxman. 1991. Estimation of loss in grain yield in sorghum genotypes due to downy mildew. Indian Phytopathol. 44:520-522.

Bandyopadhyay, R. 1992. Sorghum ergot. p. 235-244. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds). Sorghum and millets diseases: A second world review. ICRISAT, Patancheru, AP 502 324, India.

Bandyopadhyay, R., and L.K. Mughogho. 1988. Evaluation of field screening techniques for resistance to sorghum grain molds. Plant Dis. 72:500-503.

Bangarwa, K.S., G.P. Lodhi, and R.P.S. Grewal. 1987. Inheritance of resistance to red leaf spot disease in sorghum. Indian J. Genet. Pl. Breed. 47:351-352.

Bennetzen, J.L. 1995. Biotechnology for sorghum improvement. African Crop Science 3:161-170.

Bhasker, R.B., S.T. Ahmed, and S.D. Katiyar. 1993. Evaluation of advanced forage sorghum genotypes for multiple resistance against major foliar diseases. Sorghum Newsletter 34:23.

Bhat, M.G., B.T.S. Gowda, K.H. Anahosur, and J.V. Goud. 1982. Inheritance of plant pigmentation and downy mildew resistance in sorghum. SABRAO Journal 14:53-59.

Bramel-Cox, P.J., I.S. Stein, D.M. Rodgers, and L.E. Claflin. 1988. Inheritance of resistance to *Macrophomina phaseolina* (Tassi) Goid. and *Fusarium moniliforme* Sheldon in sorghum. Crop Science 28:37-40

Cao, Y.H., X.L. Wang, J.H. Ren, and C.H. Nan. 1988. Study of resistance to head smut in sorghum and its inheritance. Acta Genetica Sinica 15:170-173 (English abstract).

Chen, X.Q., H.P. Xu, C.C. Qiao, F.T. Huai, H. Song, Z.Y. Lei, G.F. Luo, B.R. Yi, and K.Z. Xu. 1991. Study of cytoplasmic male sterility in Chinese sorghum. Crop Genetic Resources 3:4-6.

Collins, S.D., R.A. Frederiksen, G.N. Odvody, D.T. Rosenow, and F.R. Miller. 1996. Disease resistant converted sorghum lines. Mimeograph.

Craig, J. and G.N. Odvody. 1992. Current status of sorghum downy mildew control. p. 213-217. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds). Sorghum and millets diseases: A second world review. ICRISAT, Patancheru, AP 502 324, India.

Craig, J., and K.F. Schertz. 1985. Inheritance of resistance in sorghum to three pathotypes of *Peronosclerospora sorghi.* Phytopathology 77:1530-1532.

Dabholkar, A.R., and S.S. Baghel. 1983. Diallel analysis of grain mould resistance in sorghum. Genetica Agraria 37:327-334.

de Milliano, W.A.J., and N. In't Veld. 1988. Incomplete resistance of the sorghum variety QL3 (India) against sorghum downy mildew in Zimbabwe. Sorghum Newsletter 31:103.

Dodman, R.L., R.G. Henzell, and N.R. Obst. 1986. Sorghum head smut in Queensland. p. 3.50-3.54. *In* Proceedings of the first Australian Sorghum Conference, Gatten, Queensland, Australia 4-6 Feb 1996.

Duncan, R.R., D.T. Rosenow, and R.A. Frederiksen. 1988. Registration of sorghum disease-resistant fertility restorer germplasm line 87BL2598. Crop Sci. 28:1037.

Frederiksen, R.A., M.O. Thomas, R. Bandyopadhyay, and L.K. Mughogho. 1995. Variable pathogens of sorghum. p. 11-23. *In* J.F. Leslie and R.A. Frederiksen (eds.). Disease analysis through genetics and biotechnology. Iowa State University, Ames, Iowa.

Galiba, M. 1983. Inheritance of resistance to sooty stripe disease. Sorghum Newsletter 26:120.

Gimenes-Fernandes, N., and A.M. Pena. 1986. Inheritance of resistance to *Peronosclerospora sorghi* (Weston & Uppal) C.G. Shaw on sorghum [*Sorghum bicolor* (L.) Moench]. Summa Phytopathologica 12(3-4):137-151.

Grewal, R.P.S. 1988. Genetic basis of resistance to zonate leaf spot disease in forage sorghum. Theoretical and Applied Genetics 76(4):550-554.

Grewal, R.P.S., G.P. Lodhi, and R.S. Paroda. 1987. Inheritance of field resistance to sorghum oval leaf spot.Ind. of Genet. Pl. Breed. 47:41-45.

Hepperly, P.R. 1990. Sorghum: II. Control and losses. J. Agric. Univ. Puerto Rico 74:37-44.

Indira, S., and B.S. Rana. 1983. Host plant resistance to *Macrophomina phaseolin* in F1 varietal crosses of sorghum. International Journal of Tropical Plant Diseases 1(2):187-192.

Indira, S., Jitendra Mohan, and B.S. Rana. 1991. Genotype X environmental interaction for grain mould resistance and seed weight in sorghum. Indian Phytopathology 44(4): 523-525.

Indira, S., B.S. Rana, and N.G.P. Rao. 1983. Genetics of host plant resistance to charcoal rot in sorghum. Indian Journal of Genetics and Plant Breeding 43(3):472-477.

ISAVN (International Sorghum Anthracnose Virulence Nursery) Report. 1996. ISAVN -A draft summary report 1992-95. Mimeograph 14 pp.

James, C. 1981. The cost of disease to world agriculture. Seed Sci. & Technol. 9:679-685.

Karunakar, R.I., S. Pande, K. Satyaprasad, and P. Ramarao. 1993. Varietal reaction of non-senescent sorghums to pathogens causing root and stalk rot of sorghum in India. Int. J. Pest Management 39:343-346.

Karunakar, R.I., Y.D. Narayana, S. Pande, L.K. Mughogho, and S.D. Singh. 1994. Evaluation of early-flowering sorghum germplasm accessions for downy mildew resistance in the greenhouse. Intl. Sorghum and Millets Newslet. 35:102-103.

Kataria, S.K., R. Singh, and P.K. Shrotria. 1990. Inheritance of resistance to grain mould fungi in three sorghum *Sorghum bicolor* crosses. Environment and Ecology 8(4):1111-1113.

Mahalinga, D.M., K.H. Anahosur, and R.K. Hegde. 1989. Screening sorghum genotypes against stalk rot and grain mold caused by species of Fusarium. Current Res. Univ. Agril. Sciences, Bangalore 18:5-6.

Mijavec, A. 1991. Study of resistance of *Sorghum bicolor* (L.) Moench genotypes to maize dwarf mosaic virus. Zbornik Radova Poljoprivrednog Fakulteta, Universitet u Beogradu 36(596):9-37.

Mukuru, S.Z. 1992. Breeding for grain mold resistance. p. 273-285.*In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds). Sorghum and millets diseases: A second world review. ICRISAT, Patancheru, AP 502 324, India.

Murty, D.S. and L. R. House. 1984. Components of generation means for resistance to grain mold causing fungi *Curvularia* and *Fusarium* in sorghum. Cereal Research Comm. 12:237-244.

Murty, D.S. and M.D. Thomas. 1989. Preliminary studies on the inheritance of resistance to leaf anthracnose and gray leaf spot diseases of sorghum [*Sorghum bicolor* (L.) Moench]. Sorghum Newslett. 31:83.

Musabyimana, T., C. Sehene, and R. Bandyopadhyay. 1995. Ergot resistance in sorghum in relation to flowering, inoculation technique and disease development. Plant Pathol. 44:109-115.

Narayana, Y.D., L.K. Mughogho, and R. Bandyopadhyay. 1995. Evaluation of greenhouse inoculation techniques to screen sorghum for resistance to downy mildw. Euphytica 86:49-53.

Narro, S.J. 1986. Head smut of sorghum (*Sphacelotheca reiliana*). p. 9. *In* Proceedings of the fifth Biennial Smut Workers Workshop, Ciudad Obregon, Sonora, Mexico, 28-30 April 1986, Mexico.

Oh, B.J., P.S.B. Gowda, G.W. Xu, R.A. Frederiksen, C.W. Magill. 1993. Tagging Acremonium wilt, downy mildew and head smut resistance genes in sorghum using RFLP and RAPD markers. Sorghum Newsletter 34:34

Pande, S., and R.I. Karunakar. 1992. Stalk rots. p. 219-234.*In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds). Sorghum and millets diseases: A second world review. ICRISAT, Patancheru, AP 502 324, India.

Pande, S., and S.D. Singh. 1992. Successful transfer of ICRISAT downy mildew resistance screening technology: an example of transfer of technology. p. 331-334. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds). Sorghum and millets diseases: A second world review. ICRISAT, Patancheru, AP 502 324, India.

Pande, S., R.P. Thakur, R.I. Karunakar, R. Bandyopadhyay, and B.V.S. Reddy. 1994. Development of screening methods and identification of stable resistance to anthracnose in sorghum. Field Crops Research 38:157-166.

Pascual, C.B., and A.D. Raymundo. 1988. Evaluation of resistance and yield loss in sorghum due to Rhizoctonia sheath blight. Philippine Phytopathology 24:67.

Patil Kulkarni, B.G., A. Puttarudrappa, N.B. Kajjari, and J.V. Goud. 1972. Breeding for rust resistance in sorghum. Indian Phytopathol. 25:166-168.

Pederson, J.F, R.R. Duncan, and B.E. Johnson. 1995. Registration of NP26 sorghum population. Crop Sci. 35:946.

Rana, B.S., K.H. Anahosur, M.J.V. Rao, V.J.M. Rao, R. Parameshwarappa, and N.G.P. Rao. 1982. Inheritance of field resistance to sorghum downy mildew. Indian Journal of Genetics and Plant Breeding. 42(1):70-74.

Rao, N.G.P., R.V. Vidyabhushanam, B.S. Rana, V. Jay Mohan Rao, and M.J. Vasudeva Rao. 1980. Breeding sorghums for disease resistance in India. p. 430-443. *In* Sorghum diseases: A world review, Proceedings of the First International Workshop on Sorghum Diseases, 11-15 Dec 1978, ICRISAT, Hyderabad, India.

Rao, C.H., and B.S. Rana. 1989. The genetics of characters related to grain deterioration in Sorghum. Journal of Maharashtra Agricultural Universities 14(3):356-357.

Reddy, Belum V.S., L.K. Mughogho, Y.D. Narayana, K.D. Nicodemus, and J.W. Stenhouse. 1992. Inheritance pattern of downy mildew resistance in advanced generation of sorghum. Ann. Appl. Biol. 121:249-255.

Reddy, Belum V.S., and S.D. Singh 1993. Breeding for resistance -sorghum anthracnose. p. 17. *In* Cereals Program Annual Report 1992. ICRISAT, Patancheru, A.P. 502 324, India.

Reis, E.M., P.G. Mantle, and H.A. Hassan. 1996. First report in the Americas of sorghum ergot disease, caused by a pathogen diagnosed as Claviceps africana. Plant Dis. 80:463.

Rodriguez-Herrera, R., H. Williams-Alanis, and J. Aguirre-Rodriguez. 1992. Incidence of head smut in isogenic sorghums for cytoplasm type. Sorghum Newsletter 33:35.

Rodriguez-Herrera, R., H. Williams-Alanis, and J. Aguirre-Rodriguez. 1993. Comparative performance of isogenic sorghums in A_1 and A_2 cytoplasms. III. Head Smut. Sorghum Newsletter 34:22.

Rosenow, D.T. 1992. Using germplasm from the world collection in breeding for disease resistance. p. 319-324.*In* W.A.J. de Milliano, R.A.

Frederiksen, and G.D. Bengston (eds). Sorghum and millets diseases: A second world review. ICRISAT, Patancheru, AP 502 324, India.

Rosenow, D.T., and R.A. Frederiksen. 1982. Breeding for disease resistance in sorghum. p. 447-455. *In* Sorghum in the eighties: Proceedings of the Internatinal Symposium on Sorghum, 2-7 Nov. 1981, ICRISAT Center, India. Vol. 1.

Sangitrao, C.S. 1982. Studies on ergot disease of sorghum in Vidarbha. Ph.D. thesis submitted to PKV Akola, MS, India. 212 pp.

Sifuentes, J., and R.A. Frederiksen. 1988. Inheritance of resistance to pathotypes 1, 2, and 3 of *Peronosclerospora sorghi* in sorghum. Plant Disease 72(4):332-333.

Sifuentes, J.A., and L.K. Mughogho. 1992. Inheritance of resistance - sorghum anthracnose. p. 23-25. *In* Cereals Program, ICRISAT, 1992. Annual Report 1991. Patancheru, A.P. 502 324, India, Cereals Program, International Crops Research Institute for the Semi-Arid Tropics (Semi-formal publication).

Sifuentes, J.A., L.K. Mughogho, and R.P. Thakur. 1993. Inheritance of resistance to sorghum leafblight. p. 16-17. *In* Cereals Program, ICRISAT, 1993. Annual Report 1992. Patancheru, A.P. 502 324, India, Cereals Program, International Crops Research Institute for the Semi-Arid Tropics (Semi-formal publication).

Singh, S.D., K.E.P. Rao, S.S. Navi, and M.V. Satyanarayana. 1993. Identification of resistance to grain mold in white grain sorghum. Sorghum Newsletter 34:24.

Singh, S.D., P. Sathiah, and K.E.P. Rao. 1994. Sources of rust resistance in purple-colored sorghum. Intl. Sorghum and Millets Newslet. 35:100-101.

Tegegne, G., R. Bandyopadhyay, T. Mulatu, and Y. Kebede. 1994. Screening for ergot resistance in sorghum. Plant Dis. 78:873-876.

Teng, P.S., and F.W.T. Penning de Fries.1992. Systems Approaches for Agricultural Development. Elsevier Applied Science, New York.

Tenkouano, A., and F.R. Miller 1993. A single locus with multiple alleles as the genetic basis of anthracnose resistance in sorghum. Sorghum Newsletter 34:45

Tenkouano, A., F.R. Miller, R.A. Frederiksen, and D.T. Rosenow. 1993. Genetics of nonsenescence and charcoal rot resistance in sorghum. Theor. Appl. Genet. 85:644-648.

Thomas, M.D., F. Bocoum, and A. Thera. 1993. Field inoculation of sorghum with sclerotia and conidia of *Ramulispora sorghi* formed *in vivo.* Mycologia 85:807-810.

Thomas, M.D., I. Sissoko, and M. Sacko. 1996. Development of leaf anthracnose and its effect on yield and grain weight of sorghum in West Africa. Plant Dis. 80:151-153.

Tsukiboshi, T., S. Kasuga, and T. Kimigafukuro. 1990. Inheritance of resistance to target leaf spot caused by *Bipolaris cookei* (Saccardo) Shoemaker in sorghum *[Sorghum bicolor* (L.) Moench]. J. Japanese Society Grassland Science 35:302-308.

Venkatarao, D.N., V.K. Shinde, and C.D. Mayee. 1983. Inheritance of charcoal rot and other qualitative characters in sorghum. Journal of Maharashtra Agricultural Universities 8(2):177-178.

Wall, G.C., J.M. Jeger, and R.A. Frederiksen. 1989. The relationship of yield loss to foliar diseases on sorghum grown by subsistance farmers in southern Honduras. Tropical Pest Management 35:57-61.

Weerasuriya, Y.M. 1995. The construction of a molecular linkage map, mapping of quantitative trait loci, characterization of polyphenols, and screening of genotypes for Striga resistancein sorghum. Ph.D. Dissertation, Purdue University, West Lafayette, IN, USA.

Yang, X., Z. Yang, and Y. Shi. 1992. Genetic effect of the resistance to head smut in sorghum. Liaoning Agric. Sci. 3:15-19.

Tagging Sorghum Genes for Disease Resistance: Expectations and Reality

C.W. Magill*, K. Boora, R. Sunitha Kumari, Jairo Osorio, B.J. Oh, B. Gowda, Yunxing Cui, and Richard Frederiksen

Abstract

RAPD analysis has proven to be effective in identifying DNA polymorphisms linked to specific genes that affect resistance to fungal pathogens. Bulked segregant analysis of resistant and susceptible F_2 progeny of crosses between selected parents has readily identified markers linked to genes that control resistance to six different fungi. However, placing the RAPD markers that segregate in crosses between resistant and susceptible parents onto a high density RFLP map that is already available, thus identifying potentially closer markers or markers that flank the resistance gene, has turned out to be more difficult than expected. The main problem has been that these same markers do not segregate in the cross that was used for making the RFLP map (BTx623 × IS 3620C). Failure to detect differences in the mapping parents was anticipated when the original RAPD primer was used for PCR, but not when pairs of longer primers (SCARS) based on the sequence of the cloned RAPD fragments were used, or when the RAPD fragment itself was used as an RFLP probe. Of various methods for circumventing this problem, the ability to identify BAC clones that include the tagged sequence seems most promising.

In addition, heterologous probes for a number of genes that function in host defense against pathogen attack have been mapped, and studies of their role in sorghum have begun. As more genes become tagged, we anticipate that breeders will be able to take advantage of commercially available automated services to identify progeny with desirable combinations of resistance alleles, and thus to create varieties with relatively stable resistance to multiple diseases (gene stacking). Tagging and the availability of the BAC library and saturated RFLP map will hasten the isolation and functional analysis of resistance genes, not only making them available for direct use in genetic engineering, but also leading to novel approaches for inducing resistance.

Tagging Resistance Genes Via RFLPs

Some years ago, soon after we initiated collaborative efforts to establish a sorghum RFLP map, we began to search for tags to identify genes that were known to confer resistance to specific pathogens of sorghum. Initially, we chose clones from linkage groups as they were being established, and used them to test for RFLPs that co-segregated with disease resistance. Crosses between selected susceptible and resistant parents were made so that

C.W. Magill, K. Boora, R. Sunitha Kumari, Jairo Osorio, B.J. Oh, B. Gowda, Yunxing Cui, and Richard Frederiksen, Department of Plant Pathology and Microbiology, Texas Agricultural Experiment Station, Texas A&M University, College Station, TX 77843. *Corresponding author.

linkage between RFLP markers and disease response could be established in the F_2 progeny. This entails a great deal of work since a complete set of RFLP probes and many restriction enzymes may be required in order to detect linkage for each cross. A more serious problem is that mapping by DNA hybridization requires large amounts of DNA for each of the F_2 plants for restriction and blotting with a variety of endonucleases.

While these problems can be managed, an unexpected problem also arose as soon as we tried to use RFLP markers identified from the mapping cross with other crosses. The problem, which has been described by Oh et al. (1996), was this: F_2 progeny of a R × S cross between SC325 (resistant to sorghum downy mildew pathotypes 1 and 3) and RTx7078 (susceptible) segregated very nicely into ratios showing that a dominant allele of a single gene controlled disease resistance (disease reactions of the F_2 were scored on F_3 progeny). RFLP markers, detected by random genomic clones pSbTx552 and pSbTx361, showed linkage at 5 and 7.9 units, respectively.

Unfortunately, the former marker was not included on the RI (recombinant inbred) map, since it did not produce readily scored polymorphisms with the standard enzymes used. The latter probe hybridized to three different *Eco*RI fragments, all of which are polymorphic and have been mapped to locations on three different chromosomes. In the R × S cross, 3 sets of polymorphisms also were detected, but with *Eco*RV digests, and it was not possible to decipher which of the bands corresponded to those used in mapping.

Attempts to use markers linked to each of the polymorphic sites in the mapping cross also were futile; markers that mapped close to the pSbTx361 markers on the RFLP map were monomorphic in the R × S cross. Only a marker that was almost 30 map units from the nearest pSbTx361 allele in the mapping cross could be used, and it did not show linkage to resistance. The strong hybridization of probe pSbTx361 to sites on three different chromosomes and the apparent change in linkage relationships relative to other RFLP probes when tested on different cultivars suggest the possibility that the DNA fragment in pSbTx361 may be cloned from a mobile element. From this experience, we learned to prefer for mapping clones that detect unique sequences.

Tagging Resistance Genes Via RAPDs

The next approach we used has proven to be quite successful in locating tags that segregate with genes for resistance, but has not greatly improved our ability to find nearby flanking markers. This approach, the use of RAPD markers for bulked segregant analysis, has been used for single genes segregating for resistance to downy mildew, sorghum head smut, anthracnose, and leaf blight; it also has been used to tag a gene for grain mold resistance. Brief accounts of some of the more interesting observations follow.

Downy Mildew Resistance in SC414 (Gowda et al., 1995)

Previous crosses between SC414 and RTx7078, showing that a single dominant gene controls resistance to *Peronosclerospora sorghi*, were confirmed when 18 of 74 F_2 progeny were susceptible. DNA from the parents and bulks of five to seven of the susceptible F_2s were amplified using 674 different RAPD primers, 237 of which revealed differences in the parents. Of these, only two, $PAL1_{360}$

and $OPQ8_{510}$, showed bands that were unique to the resistant parent but absent in the susceptible bulks. However, when individuals in the bulks were tested singly, recombinants could be detected. Our results using standard RAPD protocols showed that if DNA from one heterozygous plant is included in a five-plant bulk (this corresponds to ten map units), no visible bands or very faint bands may result.

Since our purpose was merely to identify RAPD loci linked to the target gene to use for mapping — and thus to identify other markers that may be more closely linked — identification of markers within ten map units was considered acceptable. Unfortunately, although both of the linked RAPD bands were cloned and used as hybridization probes, no polymorphisms were seen with any of the five enzymes for which blots were available for the mapping cross. Furthermore, when longer primers extending into the sequence of the cloned fragments (Sequence Characterized Amplified Regions, or SCARS) were made (Maisonneuve et al., 1994), no PCR polymorphisms were detected between the mapping parents, and even the distinct polymorphism seen with the RAPD primers disappeared. In hindsight, this should have been expected, since the most critical region of the primer for binding and extension during amplification is the 3' end, and the mismatch giving rise to the RAPD fragment was now in the 5' half of the extended primer, which is less critical.

Anthracnose Resistance in SC326-6

One hundred fifteen F_2 progeny of a cross between BTx623 (susceptible) and SC326-6 (resistant) were grown in the field and inoculated with approximately 10^6 conidia of *Colletotrichum graminicola*. Only 34 were scored as resistant on the basis of failure to produce sporulating lesions. Twenty progeny from each of the F_2s were then tested in the greenhouse; 20 resistants produced only resistant progeny, while the 81 susceptibles produced either all susceptible (30 plants) or a few resistant progeny. These data show that resistance in SC326-6 is inherited as a single gene recessive condition, and thus differs from any previously described genes for anthracnose resistance.

Altogether, 1,271 distinct bands were amplified from 300 RAPD primers (Operon®). At least one band from 166 of the primers was missing or different in size in comparisons between BTx623 and SC326-6. Three of the primers that showed differences in the parents gave the same polymorphisms in bulks of DNA from homozygous resistant (ss) or susceptible (SS) F_2 progeny. Primers OPF7 and OPL4 resulted in a band present in SC326-6 and the resistant bulks, but absent in susceptibles. OPK16 amplifies a band that segregates with the susceptibles, but which also was found in four of the 20 resistants when individuals were tested. The OPL4 fragment has been used as an RFLP probe and identifies a *Bam*HI fragment that seems to be closely linked to the recessive allele for resistance, which therefore could be of great value in the identification of heterozygotes. A survey blot of the parents digested with the five standard (low cost) restriction enzymes did not reveal useful polymorphisms for mapping on the available recombinant inbred mapping population

Leaf Blight Resistance in SC326-6

The same cultivar that is resistant to anthracnose is also resistant to leaf blight

caused by *Exerohilum turcicum*. As before, the 115 F_2 plants were grown in the field and scored at three ten-day intervals following inoculation. Plants which developed sporulating lesions were scored as susceptible, and again the evaluations were verified by greenhouse inoculations on 20 F_3 seedlings from each F_2. In this case, 29 F_2s were susceptible, and 86 were resistant; only 26 of the latter seemed to be homozygous as determined from progeny tests. These data show that a single dominant gene accounts for the leaf blight resistance in SC326-6 versus BTx623.

For leaf blight, only one of the 166 primers that gave different amplification products in the parents also showed the same difference in the bulks (2 μg of DNA from each of the 29 susceptibles or from the 26 homozygous resistants were combined to make the bulks). However, this primer, OPD12, amplified a 329 bp band in the resistant parent and bulk, and a 270 bp product in the susceptibles, so it effectively tagged both alleles.

Both unique amplimers have been cloned and sequenced. Other than sequences identical to the RAPD primer OPD12 at each end, they share no sequence homology, which is somewhat of a surprise since it was assumed they may represent length polymorphisms of the same locus. Attempts to use the cloned fragment of OPD12R, which is linked in coupling phase to the resistance locus, to locate the fragments on the RFLP map have been frustrating. The OPD12R clone hybridizes to multiple fragments when used as a probe. It detects at least nine bands in *Eco*RI digested DNA from each parent, none of which are polymorphic. It hybridizes to at least nine *Hin*dIII fragments, one of which gives a very dark band with DNA from SC326-6 and the resistant bulk, but a light band from BTx623 and the susceptible bulk. The same apparent "band-density" *Hin*dIII polymorphism also is seen when BTx623 is compared to IS3620C, the other parent in the mapping cross. However, it was impossible to confidently or reliably score the 137 recombinant inbreds used for mapping based on light versus dark autoradiographic spots.

An attempt also was made to develop SCAR primers based on the base sequence of OPD12R. A forward 19-mer primer and a reverse 18-mer primer matching the internal bases of the cloned fragment were made. PCR using these primers amplified the expected band in the resistant parent and bulk; it did not amplify a band in the susceptible parent BTx623, but did produce a lightly visible band in the susceptible bulk. When DNA from each plant used to make the bulk was amplified with the SCAR primers, five of the 29 produced a band. Assuming that these five plants are heterozygous, evidence for five recombinants in 58 gametes suggests a map distance of eight to nine cM, and demonstrates why locating closer markers is important.

Since the SCAR primers do not amplify DNA from BTx623, which is one of the mapping parents, they also were tested with the other parent, IS3620C, and the same sized band was amplified. Surprisingly, when DNA from the 137 RI progeny was the target for PCR amplification, all but one, which appears to be a "drop-out," gave the band. Since IS3620C was the maternal parent of the original mapping cross, the most logical explanation is that the band is derived from organelle DNA and is maternally inherited. This explanation raises just as large a question, however: in that case, the DNA fragment

would be located in the nucleus of one cultivar but in the cytoplasm of another! Even though the ends and the sizes of the fragments amplified from SC326-6 and IS3620C are the same, it will still be critical to verify that the sequences are truly the same.

A third approach for locating the gene tagged by the OPD12 fragments seems more promising. Since the smaller OPD12S fragment is amplified only in BTx623, it was used as a hybridization probe on filters containing a bacterial artificial chromosome (BAC) library, also constructed from BTx623 and made available by Dr. Rod Wing, then in our Center for Crop Biotechnology (Woo et al., 1994). These BAC clones contain an average of 157 kB, appear to be quite stable, and are easy to manipulate.

Robot-prepared filters containing DNA from over 1300 clones were hybridized to OPD12S. As expected from the multiple banded pattern seen on restriction digests, several positives were identified (15 clear twin-spots on the autoradiographs). The corresponding BAC cultures were grown and the extracted BAC-DNA was subjected to RAPD-PCR using primer OPD12. Only BAC #C26H18 gave the 270 bp RAPD band expected for the locus linked to leaf blight resistance. Preliminary tests using the BAC as a hybridization probe show several polymorphisms that differentiate the resistant and susceptible parents and bulks, which should allow accurate mapping. In this case OPD12S has been mapped to linkage group H in the order *umc*18-1.5-D12S-3.0-*txs*645.1. In addition, our colleagues Jim Price and Dave Stelly have developed a method for *in situ* hybridization using the BACs, which is being used to integrate the physical and genetic maps of sorghum. Once a BAC has been mapped, nearby BACs can be identified by hybridization to previously mapped RFLP markers, greatly simplifying the processes of walking to and cloning specific genes for resistance.

Head Smut Resistance in BTx635

Molecular tags to track resistance genes for head smut, caused by *Sporisorium reilianum*, would be especially useful. Because symptoms do not usually appear until the time of heading, extra time, work, and field or greenhouse space must be dedicated to the breeding program. In addition, it is not at all unusual to have a 30% or greater rate of escape, so that susceptible lines may be inadvertently carried forward. BTx635 has been determined to have two different forms of resistance. One form, referred to as meristematic resistance, is effective even if spores are injected into seedlings, while the non-meristematic form seems to prevent initial penetration by the fungus, but is bypassed by injection. Based on F_3 progeny tests of 190 F_2s of a cross between BTx635 and B3, a completely susceptible variety, meristematic resistance is inherited as a single gene recessive trait. (At least 12 F_3s were scored per F_2; if none developed head smut, the F_2 was considered to be homozygous resistant. On this basis, 50 of the 190 progeny were resistant and 140 were susceptible.)

RAPD analysis using a bulk of ten resistant individuals revealed a band with one primer that was linked at approximately ten map units. In a follow up experiment, a new bulk was made from those plants that included both the RAPD and resistant phenotypes. AFLP analysis (Prabhu and Gresshoff, 1994) based on these plants has subsequently revealed

two bands which seem to be closely linked to resistance (no recombinants in 60 progeny). In addition, after eliminating the plants that show meristematic resistance, it has been possible to identify a RAPD marker linked to the non-meristematic form of resistance, which also segregates as a single gene, but in this case resistance is dominant. This form of resistance presents an even greater problem of escapes. No attempts have been made as yet to place any of the RAPD or AFLP tags on the RFLP map.

Grain Mold Resistance in Sureño

Grain mold is probably a more serious problem in sorghum than in other crops because the grain is exposed to the environment during maturation and drying. Losses are generally the result of deterioration in food quality rather than accumulation of mycotoxins. Although the presence of many different fungi can make grain mold difficult to control, the primary problems seen in our studies arise from *Fusarium moniliforme* and *Curvularia lunata.*

Many different host factors that can affect losses have been identified, including: the types and levels of tannins and polyphenols in the seed; enzymes, such as chitinases and β-glucanases; ribosome-inhibiting proteins; and proteins such as sormatin that alter the permeability of fungal membranes. In addition, Dr. Kumari has identified three other fungal inhibiting proteins and demonstrated that grain hardness, which is directly proportional to prolamine content, is a major factor in mold resistance (Kumari and Chandrashekar, 1994a, b).

There are also great varietal differences in relative resistance. For example, less than 15% of surface-sterilized grains of the cultivar Sureño typically become infected with *F. moniliforme*, while with the same treatment, 68% of SC-120 seeds become infected. Taken together, these observations suggested that resistance to grain mold was likely to be inherited as a quantitative trait, so a QTL approach to identify and tag useful genes was followed. Seed from 143 selfed F_2 plants from a cross between Sureño and SC-120 were collected; 200 were used for *in vitro* tests of resistance to *Fusarium*, 30 were used for hardness tests, and 30 more were grown for DNA extraction. One bulk included the 21 F_2s identified as being most susceptible, and the other included 16 F_2s with low susceptibility to grain mold.

From more than 700 Operon and UBC RAPD primers screened, 264 revealed one or more polymorphisms between the parents; five of these also showed clear differences in the bulks. Two of the primers identified bands that clearly segregated in the two categories when tested with each of the individuals in the bulks. Three bands amplified by OPN-5 were found in all but one of the resistant progeny and in none of the susceptibles; OPA-12 amplified a band in all of the resistants but in none of the 14 susceptibles for which common bands were amplified.

Other differences seen in the bulks seemed to show linkage with factors affecting resistance, but more recombinants were obvious when individuals were tested. The three RAPD fragments from OPN-5 and the one amplified by OPA-12 have been cloned and used as RFLP hybridization probes. Though three of the four did not reveal polymorphisms with DNA from the mapping parents, clone OPN-5-1R did, and it was mapped between *isu* 94 and *umc*88.2 on linkage group B. A summary of the gene tagging results is presented in Table 1.

Mapping Defense Response Genes

We are part of a team of sorghum researchers headed by Gary Hart and John Mullet that has created an RFLP map for sorghum. The current map is based on a population of 140 recombinant inbreds, which means that seed can be dispensed and others can use the same mapping population. The map now has over 280 markers on the ten linkage groups. Clones of defense response genes from other hosts have been generously provided by other researchers for use in mapping. A summary of the mapping information is shown in Table 2.

Zeamatin is a protein that permeabilizes fungal membranes (Darnetty et al., 1993; Vigers et al., 1991). The maize protein is related to osmotins, which are expressed in high levels in seeds of several species. It was not surprising that the maize zeamatin clone hybridized well to sorghum, especially since sorghum stores a similar protein (sormatin) in the seed. It was a little surprising that pathogenesis-related protein P-23 from tomato also hybridized quite well and detected polymorphisms with almost every enzyme tested on the mapping parents. P-23 also is a thaumatin-like protein, or an "osmotin," and thus is in the same class of proteins as zeamatin. A BLAST (Altshul et al., 1990) search shows a small stretch of 27 similar amino acids (of 233), but these are clearly different genes that are detected. PR1b, a barley cDNA clone from a gene activated after inoculation with downy mildew, also hybridized well.

Although there are known PR proteins in many other plant species with sequence homology, no specific function for these

Table 1. Summary of resistance genes for which linked markers have been identified

Disease	Source of resistance	Tag	Reference
Downy mildew	SC414	RAPD:$PAL1_{360}$; 13.5cM*	Gowda et al., 1995
		RAPD:$OPQ8_{510}$; 9.5cM*	
Downy mildew	BTx623[1]	RFLP:*txs*1053; 12 cM	Gowda et al., 1995
		RFLP *txs*1092(2); 14 cM (LGC)	
Downy mildew	SC325	RFLP:*txs*552; 5 cM	Oh et al., 1996
		RFLP:*txs*361 (1-3?);8 cM	
Head smut	SC325	RFLP:*txs*1294; 20 cM	Oh et al., 1994
		RFLP:*txs*560; 9 cM (LGH)	
		RAPD: OPG5-2; 6 cM	
Head smut	BTx635	RAPD:<2cM	Osorio Diss (In Prep)
	(2 genes)	AFLP:<20 cM	
Leaf blight	SC326-6	RAPD: OPD12S[2]; 5-8 cM	Boora et al. (In Prep)
		RAPD: OPD12R*; 5-8 cM	
Anthracnose	SC326-6	RAPD: OPF7(R)* <3 cM	Boora et al. (In Prep)
		RAPD: OPL4 (R)[3] <3 cM	
		RAPD: OPK16 (S)* ~6 cM	
Grain mold	Sureño	RAPD: OPA12* <3 cM	Sunitha Kumari et al.
		RAPD: OPN5 (R)[4] <3 cM	(In Prep)
		RAPD: OPN5 (S)* <3 cM	
Acremonium wilt	IS 3620C	RFLP: *txs*1225; 20cM (LGA)	Oh et al., 1993

[1] Resistant to pathotype 1 only
* No segregation detected using clone as an RFLP probe on mapping parents
[2] Mapped to LG H between *umc*18 and *txs*645.1
[3] Clone also serves as RFLP marker for recessive resistance allele
[4] Maps between *isu*94 and *umc*88.2 on LG B

proteins has been defined (Muradov et al., 1993). A clone for a protein that inhibits translation on eukaryotic ribosomes (ribosome inhibiting protein, or RIP) (Walsh et al, 1991)., representing one of at least two known types of RIPs in maize, was mapped, as was a maize chitinase (Huynh et al., 1992). Both of these map between the same two genes on the same chromosome, although the RFLPs detected differ and there is no sequence homology between them.

Some work has been done to identify genes and pathways that are activated in sorghum in response to fungal pathogens. For example, Dr. Cui has examined the pathogen-induced induction of mRNA synthesis for chalcone synthase and phenylalanine-ammonia lyase, two genes in the pathway that leads to flavonoids with antifungal properties in sorghum (Nicholson et al., 1987; Snyder and Nicholson, 1990). He has shown that both messages are induced by exposure to a maize pathogen (*Bipolaris maydis*), and, in the case of downy mildew, exposure to *P. sorghi* leads to a significantly greater increase in resistant varieties than in susceptibles. While such responses may provide a basis for resistance, they are considered to be downstream events from the recognition of the pathogen by the host, so are not considered to be direct candidates for resistance genes. Differences in the speed, level, or duration of the responses, however, may be important in "field resistance" or tolerance to disease, which may provide a more durable or stable form of disease management than is often seen in a single gene resistance system.

In an unexpected observation, one of the RAPDs that shows linkage to grain mold resistance also seemed to show mRNA induction in *Fusarium*-treated leaves. The clone does have a 300 base sequence at the 5' end that is an open reading frame followed by two stops, so it could be the end of a defense response protein. Sequence comparisons using the open reading frame did not reveal any homology to deposited DNA or protein sequences. We should be able to take advantage of the BAC library to determine if the RAPD is actually part of a defense response protein as the data seem to suggest.

Where Is This Research Leading?

The most obvious use, and indeed the whole reason for attempting to tag genes for disease resistance, is the possibility of marker-assisted selection to combine or "stack" resistance genes. Just as important as the ability to create new cultivars that combine genes for resistance to multiple pathogens is the ability to combine different genes for resistance to the same pathogen. If independent loci, each of which conditions resistance to the same pathogen, can be identified (this is one of the

Table 2. Map locations of known defense response genes

Cloned Gene	LG	Between Markers	Source of clone (donor)
Pro-RIP	A	*umc*124.3 & *umc*83	maize (T. Hey, DowElanco)
chitinase	A	*umc*124.3 & *umc*83	maize (Q.K. Huynh, Monsanto)
PR-1b	B	*umc*149.2 & *umc*122	barley (K.J. Scott)
zeamatin	B	*txs*1164 & *txs*1075.2	maize (C.P. Silitrennikoff)
Pal-1	H	*txs*2068 & *txs*1379	sorghum (Y. Cui)
P-23	H	*txs*164 & d3	tomato (I. Rodrigo)

side advantages of mapping each locus; those that map to different positions can't be alleles), crosses can be made, and F_2 progeny that include at least one resistance allele for both genes can be identified from the DNA in a small, non-destructive tissue segment. Either allele-specific primers for multiplex PCR or allele-specific oligonucleotide probes can be designed for use in semi- or fully-automated equipment and readers. Equipment and designs such as SSCP (single strand conformational polymorphism) and allele-specific PCR primers already in use to detect point mutations in human genetic defects (such as cystic fibrosis and muscular dystrophy) should be readily adaptable. DuPont already has a robotic workstation for extracting DNA from multiple leaf samples.

It is difficult to predict the price per sample that will evolve, assuming that market competition develops. However, when compared to the complexity and time required in trying to combine just two genes for resistance to the same pathogen by classical breeding methods, which may require a backcross to two different recessive testers after each generation of backcrossing or selfing, marker-assisted selection will be economically feasible.

The availability of the BAC library, the RFLP map, and the associated probes that identify loci throughout all 10 sorghum chromosomes will have a dramatic impact on identifying and cloning genes of agronomic importance. As indicated previously, Price and Stelly and their students have already shown that BACs can be identified by hybridization to a clone used in RFLP mapping; this means it will be possible to bracket resistance genes based both on mapping information and physical location. Once a disease resistance marker is associated with a BAC, the problems we have experienced in finding the linkage group and nearby markers should be eliminated. Further, since the neighboring RFLP markers can then be used to identify other nearby BACs, a tremendous head start toward positional cloning will be realized. Such a system is already proving its worth in *Arabidopsis*, where complete sets of overlapping BAC clones are now available for some chromosomes.

Recent observations indicate that gene orders on monocot chromosomes tend to be conserved and that there is often sufficient base sequence conservation among the 14 or so resistance genes that have already been cloned to permit cross-species PCR primers or hybridization probes to be used to identify equivalent genes in different species. These observations suggest that success in developing highly specific tags for disease resistance genes should improve at an exponential rate.

As the genes are isolated, we can anticipate that sequence information will provide clues as to function, and that this knowledge will lead to new concepts in disease control. For example, knowledge of the molecular interactions that permit pathogen recognition and of the signal transduction pathway component that triggers the defense response may make it possible to artificially induce resistance in genetically susceptible hosts. However, we anticipate that the most valuable product will be durable resistance made possible by combinations of resistance genes in high-yielding, stress-resistant cultivars. The resistance genes themselves will provide the tags — allele-specific PCR primers — that will permit identification of recombinant progeny from seedling leaf

samples produced by classical breeding methods.

Acknowledgements

Support for this research from the Rockefeller Foundation, Pioneer Hi Bred International, Inc., the USDA Sorghum Crop Germplasm Committee, and the Texas Agricultural Experiment Station is gratefully acknowledged.

References

Altshul, S.F., W. Gish, W. Miller, E.W. Meyers, and D.J. Lipman. 1990. Basic local alignment search tool. J. Mol. Biol. 215:403-410.

Darnetty, J.F.L., S. Muthukrishnan, M. Swegle, and A.J. Vigers. 1993. Variability in antifungal proteins in the grains of maize, sorghum and wheat. Physiologia Plantarum 88:339-349.

Gowda, P., G-W. Xu, R. Frederiksen, and C. Magill. 1995. DNA based markers for downy mildew resistance genes in sorghum. Genome 38:823-826.

Huynh, Q.K., C.M. Hironaka, E.B. Levine, C.E. Smith, J.R. Borgmeyer, and D.M. Shah. 1992. Antifungal proteins from plants: Purification, molecular cloning, and antifungal properties of chitinases from maize seed. J. Biol. Chem. 267: 6635-6640.

Kumari, S.R., and A. Chandrashekar. 1994a. Isolation and purification of three antifungal proteins from sorghum endosperm. J. Sci. Food Agric. 64:357-364.

Kumari, S.R., and A. Chandrashekar. 1994b. Relationships between grain hardness and the contents of prolamin and three anti-fungal proteins in sorghum. J. of Cereal Sci. 20:93-99.

Maisonneuve, B., Y. Bellec, P. Anderson, and R.W. Michelmore. 1994. Rapid mapping of two genes for resistance to downy mildew from *Lactuca serriola* to existing clusters of resistance genes. Theor. Appl. Genet. 89:96-104.

Muradov, A., L. Petrasovits, A. Davidson, and K.J. Scott. 1993. A cDNA clone for a pathogenesis-related protein. Plant Mol. Biol. 23:439-442.

Nicholson, R.L., S.S. Kollipara, J.R. Vincent, P.C. Lyons, and G. Cadena-Gomez. 1987. Phytoalexin synthesis by the sorghum mesocotyl in response to infection by pathogenic and non-pathogenic fungi. Proc. Natl. Acad. Sci. USA. 84:5520-5524.

Oh, B.J., P.S.B. Gowda, C.W. Magill, and R.A. Frederiksen. 1993. Tagging acremonium wilt, downy mildew, and head smut resistance genes in sorghum using RFLP and RAPD markers. Sorghum News Ltr. 35:35.

Oh, B.J., R.A. Frederiksen, and C.W. Magill. 1994. Identification of molecular markers linked to head smut resistance gene (SHS) in sorghum by RFLP and RAPD analysis. Phytopathology 84: 830-833.

Oh, B., R. Frederiksen, and C. Magill. 1996. Identification of RFLP markers linked to a gene for downy mildew resistance (*Sdm*) in sorghum. Can. J. Bot. 74:315-317.

Prabhu, R.R., and P.M. Gresshoff. 1994. Inheritance of polymorphic markers generated by DNA amplification fingerprinting and their use as genetic markers in soybean. Plant Mol. Biol. 26:105-116.

Snyder, B.A., and R.L. Nicholson. 1990. Synthesis of phytoalexins in sorghum as a site-specific response to fungal ingress. Science 248:1637-1640.

Vigers, A.J., W.K. Roberts, and C.P. Selitrennikoff. 1991. A new family of plant antifungal proteins. Molec. Plant-Microbe Interactions 4: 315-323.

Walsh, T.A., A.E. Morgan, and T.D. Hey. 1991. Characterization and molecular cloning of a proenzme form of a ribosome-inactivating protein from maize. J. Biol. Chem. 266:23422-23427.

Woo, S.-S., J. Jiang, B.S. Gill, A.H. Paterson, and R.A. Wing. 1994. Construction and characterization of a bacterial artificial chromosome library for *Sorghum bicolor*. Nucleic Acids Res. 22:4922-4931.

Breeding for Grain Mold Resistance in Sorghum

J.W. Stenhouse*, R. Bandyopadhyay,
S.D. Singh and V. Subramanian

Abstract

This paper reviews research on grain molds and describes the incidence and extent of grain mold problems in sorghum. Techniques for breeding for grain mold resistance include development of screening methodologies, identification of resistant germplasm and resistance mechanisms, and resistance breeding. Limited improvements in selection for grain mold resistance can be made through conventional breeding methods; biotechnological methods offer considerable promise for the future and should receive research priority.

Grain molds have been defined as "fungi that grow in or on seeds" (Williams and McDonald, 1983). They affect sorghum and pearl millet grown in warm and wet conditions between flowering and harvest (Williams and Rao, 1981; Williams and McDonald, 1983). They are much more widespread in sorghum than in millet because of the nature of the growing environments of the two crops.

Grain molds in sorghum have been extensively reviewed (Forbes et al., 1992; Williams and Rao, 1981). They are caused by non-specialized fungi of several genera that are widely distributed in nature. These include: *Fusarium*, *Curvularia*, *Phoma*, *Alternaria*, and *Cladosporium* species (Castor and Frederiksen, 1980; Denis and Girard, 1980; Rao and Williams, 1980; Williams and Rao, 1981; Williams and McDonald, 1983). In pearl millet, there are few reports of major damage due to grain molds, but many fungi have been isolated from pearl millet grain. The most frequently reported genera are *Helminthosporium* and *Curvularia* (Williams and McDonald, 1983).

The problem of grain molds is encountered throughout the humid tropical and subtropical regions. It is particularly severe in areas where improved, short- and medium-duration cultivars that mature before the end of the rains have been adopted (Bandyopadhyay et al., 1988; Williams and McDonald, 1983). Under these conditions, harvested grain yields are often reduced, but more significantly, grain quality is adversely affected (Rao et al., 1980; Williams and Rao, 1980). The physical effects of molds on the grain may include discolored pericarp, softened and chalky endosperm, decreased grain size and density, sprouting, presence of mycotoxins, and altered composition of phenolic compounds (Waniska et al., 1992). Grain molds are most common and severe on white-grained sorghum and have re-

J.W. Stenhouse, R. Bandyopadhyay and S.D. Singh, ICRISAT, Patancheru, Andhra Pradesh 502 324, India; V. Subramanian, House No. 6-1-285/8/1, Padmaraonagar, Secunderabad, Andhra Pradesh 500 025, India. *Corresponding Author.

portedly restricted adoption of improved sorghum cultivars in Africa (Mukuru, 1992).

Major efforts to breed for mold resistance in sorghum have resulted in significant progress, but grain molds remain a major constraint to sorghum production in much of India, Africa, Latin America, and the U.S. Annual global losses to grain molds have been estimated at $130 million (ICRISAT, 1992). Much less work has been carried out on grain molds of pearl millet and no reliable estimates of damage are available.

This paper summarizes the current situation in breeding for resistance to grain molds and attempts to evaluate future prospects of such breeding efforts. It concentrates on resistance in white-grained sorghum, because effective mechanisms for resistance are already available in brown- and red-grained sorghum.

Screening Methodologies

Several screening techniques for grain mold resistance have been developed and tested (Williams and Rao, 1981; Bandyopadhyay and Mughogho, 1988; Singh and Prasada Rao, 1993). The simplest and most common approach is to evaluate test materials under natural incidence of grain mold in field conditions. This approach remains widely used today, but is unsatisfactory unless rains are frequent and prolonged throughout the flowering and grain-filling period (Williams and Rao, 1981).

More stringent techniques using sprinkler irrigation to maintain high humidity during the grain-filling period, with and without inoculation with conidial-mycelial suspensions, were developed at Texas A&M (Castor, 1977) and ICRISAT (Bandyopadhyay and Mughogho, 1988). These techniques were shown to be reliable in discriminating between susceptible and resistant genotypes over several rainy seasons (Bandyopadhyay et al., 1988). However, they were not successful when ambient humidity and temperature were low (Bandyopadhyay and Mughogho, 1988). It was, therefore, impossible to test photoperiod-sensitive germplasm that flowered later than the first week of September at ICRISAT Asia Center (IAC) using the Bandyopadhyay and Mughogho (1988) technique. The techniques also have been criticized as too severe, imposing a level of disease pressure far higher than levels normally observed in farmers' fields. Recent work at ICRISAT has developed a methodology based on misting technology that has been effective in promoting grain mold during the dry season (Butler and Bandyopadhyay, 1991). This technique, however, has not been systematically applied by ICRISAT in germplasm screening or in breeding programs for mold resistance because of the high costs of setting up the required misting systems. A similar system has been established and is being used by Pioneer Hi-Bred Inc. in the U.S. (M. Hood, 1995, personal communication).

A basic requirement of any grain mold resistance screening technique is that test entries should be evaluated at the same growth stage, and selection practiced within groups of material with similar maturity. Bandyopadhyay and Mughogho (1988) proposed that evaluation for resistance be carried out a constant 14 days after physiological maturity. Major envi-

ronmental effects are clearly discernible in the mold ratings of lines with different maturity within the same screening nursery. But within the same maturity group, reliable comparisons of mold reactions can be made. Failure to consider maturity classification while screening leads to selection of late-maturing, mold-escaping material.

A laboratory-based screening method has been developed recently and used to screen photoperiod-sensitive germplasm that could not be reliably screened using field screening techniques (Singh and Prasada Rao, 1993). Surface-sterilized seed are dip-inoculated with spore suspension of a single or mixed culture of pathogens, and incubated in petriplates for approximately five days before visual rating for mold. An advantage of this method is that resistance to individual pathogens can be identified separately. The same technique has been used to test Zerazera conversion lines and has identified 43 new sources of resistance, among which four were highly resistant (Singh et al., 1995). Lines identified as resistant by this method have been field-tested (following short-day treatments to induce early flowering in the photosensitive group) to confirm their resistance.

Work on several aspects of the epidemiology of sorghum grain molds continues at ICRISAT. Field and laboratory studies by pathologists and agroclimatologists are attempting to define the precise moisture and humidity requirements for development of the different grain mold fungi and the effects of infection at different stages of the grain development process. It is hoped that this information will lead to refinement of the field screening methodologies to allow better discrimination between lines with moderate levels of resistance than is currently possible, and also to select more reliably between individual plants in segregating progenies.

Sources of Resistance

The problem of grain molds and the search for resistance are relatively recent phenomena, becoming important only from about 1970 (Williams and Rao, 1981). The first sources of resistance identified were lines showing reduced mold symptoms under natural field conditions (Gray et al., 1971; Koteswara Rao and Poornachandrudu, 1971). Subsequently, many reports have identified sources of resistance from different situations and using different screening techniques (Zummo, 1976; Glueck and Rooney, 1976; Rao and Williams, 1977; Rana et al., 1978; Castor and Frederiksen, 1980; Denis and Girard, 1980; Glueck and Rooney, 1980; Bandyopadhyay and Mughogho, 1988; Prasada Rao et al., 1995; Singh et al., 1995).

Later, systematic screening of germplasm identified a large number of accessions with high levels of resistance to grain molds (Bandyopadhyay et al., 1988). In the same screening exercise, lines that had been identified as resistant under natural infection were found susceptible to grain molds. The majority of the resistant germplasm lines had a testa and high tannin levels. A number of Guinea lines, however, lacked testa and tannins, but remained highly resistant. These lines subsequently were used to demonstrate that white-grained sorghum with high levels of resistance to grain

molds could be developed (Mukuru, 1992). The same lines have been used in improvement of Guinea sorghum at ICRISAT.

Recently, new white-grained sources of resistance have been identified among photoperiod-sensitive Guinea sorghum germplasm in a limited screening exercise (Prasada Rao et al., 1995). Further, Zerazera lines with resistance also have been identified among conversion lines from ICRISAT (Singh et al., 1995). Both these sets of new resistance sources have been identified using *in vitro* screening techniques. Their resistance has, however, subsequently been confirmed in the field.

Resistance Mechanisms

After resistant germplasm was identified, work on mechanisms of resistance rapidly followed. The link between high tannin content and grain mold resistance was quickly identified (Harris and Burns, 1973). Work at the Texas Agricultural Experiment Station identified endosperm texture as contributing to resistance to molding; corneous endosperm types were more resistant than those with floury endosperm (Glueck et al., 1977; Glueck and Rooney, 1980). Grain hardness was identified as a mechanism of resistance to grain molds (Rana et al., 1978; Jambunathan et al., 1992). Mold-resistant cultivars have significantly harder grain than mold-susceptible cultivars. Other structural characteristics of sorghum grain contributing to grain mold resistance include thin pericarp, thick and continuous surface wax layer, and grain integrity (Glueck and Rooney, 1980).

The level of flavan-4-ols was found to be much higher in mature grain of mold-resistant cultivars than in mold-susceptible cultivars (Jambunathan et al., 1986) and was shown to be at least twice as high throughout the grain development period (Jambunathan et al., 1990). Total phenolic content in grain also has been shown to be consistently higher in resistant cultivars than susceptible ones (Hahn and Rooney, 1986; Mansuetus et al., 1988). A search for polyphenols in grain that showed major differences in concentrations in resistant and susceptible white-grained cultivars has failed to identify any that could form the basis for selection for resistance.

In studies of multiple grain traits that contribute to grain mold resistance, the presence of a testa has been shown to be the single most important trait conferring grain mold resistance (Esele et al., 1993). Red pigmentation of the pericarp also confers resistance, but to a lesser extent. Both these mechanisms of resistance are found only in pigmented sorghum, however, and are unsuitable for use in breeding food quality sorghum for grain mold resistance.

Panicle and glume traits have been shown to affect grain mold. These include open panicle and long glumes, both of which are reported to reduce grain mold incidence (Glueck et al., 1977). Grain mold also has been shown to be negatively correlated with glume cover, length, and area (Mansuetus et al., 1990). Phenolic compounds in the glumes have been shown to afford some protection from grain molds (Mansuetus et al., 1988). Resistant cultivars also respond more quickly than susceptible ones to fungal invasion when levels of phenolic com-

pounds in their glumes are increased (Waniska et al., 1992).

Recently, anti-fungal proteins have been identified in sorghum grains and appear to play a role in protecting the grain from fungal attack. Rapid grain filling also seems to result in resistance to grain molds (Singh et al., 1995).

Resistance Breeding

The first white-grained sorghums identified with resistance to grain molds under natural field infection included a number of derivatives of Zerazera germplasm from Sudan and Ethiopia. These were used extensively in breeding for grain mold resistance in India and at ICRISAT and have produced many agronomically desirable high-yielding progenies. The fact that derivatives of this material are clearly superior in resisting grain molds to earlier white-grained varieties and hybrids (e.g., CSH 1 in India) testifies to their inherent tolerance. However, varieties and hybrids based on this material also are the ones that continue to be affected by grain molds, indicating that their levels of resistance can be overcome by severe mold pressure.

The Zerazera germplasm accessions and their conversion lines have been used from the mid-1970s onward. In particular, E 35-1, CS 3541, SC 108-3, SC 108-4-8, and SC 120 were widely used in the ICRISAT program (Murty et al., 1980) and the Indian program. Similarly, SC 170 and SC 110 have been extensively used in the U.S. (Duncan et al., 1991). This Zerazera material combined several other desirable traits in addition to tolerance to grain molds. It has been so successful and so widely used in the breeding programs of the U.S., India, and ICRISAT that it has come to dominate the elite improved germplasm. Serious concerns have been expressed about the extent to which this is true and the narrowness of the genetic base (Duncan et al., 1991).

The Zerazera material was largely used, and continues to be used, in conjunction with field screening under natural infection. More severe screening methods fail to discriminate effectively between the intermediate levels of resistance found among this material. Multilocational testing under natural infestation, backed up by screening under sprinkler irrigation at a few selected locations, as is practiced by the All India Coordinated Sorghum Improvement Project (AICSIP), make it possible to evaluate finished cultivars quite effectively. However, the deficiencies of screening under natural infection make it difficult to select systematically in segregating generations for grain mold resistance and render the breeding process rather hit-or-miss.

ICRISAT began using other resistant sources in the mid 1980s in conjunction with field screening with sprinkler irrigation. In particular, resistant Guinea germplasm lines were used, and by the late 1980s a number of white-grained derivatives of this material with high levels of grain mold resistance had been produced (Mukuru, 1992). The sprinkler irrigation technique has thus been helpful in screening segregating materials and selecting mold-resistant lines. However, it has been able to do this only with colored grain sorghum and Guinea derivatives with high levels of resistance. White-grained sorghum of races other than

Guinea have shown only moderate levels of resistance, and it has been difficult to differentiate between individual plants in early generation segregating progenies.

Improvement of Guinea Sorghum

The availability of grain mold-resistant Guinea sorghum has triggered an effort at ICRISAT to improve materials of this type. Both pedigree and population breeding approaches have been used to develop derivatives that combine white grain color with the plant type and yield levels of improved sorghum, yet retain the Guinea grain and glume traits. Some success is now being achieved and a number of dwarf early lines with semi-compact heads and Guinea grain and glumes have been produced through pedigree breeding. These lines appear competitive for yield, even with elite varieties from different genetic backgrounds. Population breeding methods have produced similar lines, but these have poorer yield potential. Neither pedigree nor population breeding products have been screened or selected for grain mold resistance.

Similar breeding efforts with Guinea sorghum are underway in several programs in West Africa, notably those in Mali and Burkina Faso. The focus of these programs is not primarily grain mold resistance, but production of high-yielding varieties with acceptable grain quality for local food preparations. However, the hard corneous grain of many traditional Guinea cultivars that is of interest to local consumers is also a contributing factor for grain mold resistance. In this respect, the quality requirements for food and for grain mold resistance coincide. Therefore, achieving one is likely, at least in part, to contribute to achieving the second.

Future Prospects

Currently, grain molds are a problem only in areas where improved white-grained cultivars have been adopted. This includes most of India and parts of China, the U.S. and Latin America. For most of Africa, traditional cultivars continue to predominate and grain molds are not a problem.

In those parts of West Africa where Guinea sorghum is preferred, the answer to the grain mold problem would appear to be to remain with that type of cultivar. Guinea sorghum has natural resistance to grain molds because of its combination of very hard corneous grain, open panicles, and extensive glume coverage (both in terms of the extent of grain coverage and its duration during grain development). Traditional cultivars also escape grain mold pressure by maturing after the end of the rainy season. Introduction of shorter duration cultivars of other races will probably result in grain mold becoming a severe constraint to production, as in India. It remains to be seen whether the productivity of Guinea sorghum in West Africa can be increased through shorter duration to avoid terminal drought stress, as happened in India, without creating a grain mold problem, as also happened in India.

For other areas of Africa, where sorghum with a pigmented pericarp or testa is extensively grown, the situation is likely to be the same: introduction of early white-grained cultivars could lead to a

dramatic increase in the grain mold problem. The switch to improved white cultivars without colored pericarp or testa will only be worthwhile if the yield advantage they offer over traditional cultivars is substantial. This is only likely to be the case with hybrid cultivars. While varieties remain predominant, it seems advisable to retain the traditional grain qualities. In developing white-grained hybrids for these areas, as should certainly be done, great care should be taken to learn from the Indian experience. The breeding programs should include only material known to have reasonable levels of grain mold tolerance, and grain mold should be constantly monitored.

Conventional Breeding Approaches

Substantial improvements in grain mold resistance already have been achieved. The situation in India, where the grain mold problem is most acute, illustrates the point. The first released hybrid, CSH 1, is highly susceptible to grain molds. Subsequently released hybrids have demonstrated progressively better mold resistance. CSH 9, currently the most widely grown hybrid, shows good field tolerance to grain molds, although it also succumbs when conditions are severe. The most recently released hybrid, CSH 16, has shown improved grain mold resistance over CSH 9 in several years of trials, although its performance in farmers' fields remains to be seen.

These improvements in Indian commercial hybrids have largely come from the use of Zerazera germplasm. In particular, breeding restorer lines with the hard corneous grain characteristic of Zerazera germplasm, rather than the softer grain characteristic of early Durra-based restorer lines used for early hybrids, has improved grain mold resistance. The contribution of CS 3541 has been noteworthy in this regard. Further improvements in grain mold resistance can probably be achieved through the same approaches. In particular, breeding male-sterile lines with harder, more corneous grain is likely to be a fruitful line of work for developing grain mold-resistant hybrids. However, the extent to which grain hardness can be manipulated to achieve this is limited, since grain quality is likely to be compromised. This is especially true in India where the accepted quality standard is the relatively soft Maldandi grain and, because of the strong preference of farmers and plant breeders alike for large grain size, a trait usually negatively related to grain hardness and mold resistance.

In the U.S., the use of Zerazera germplasm has increased as both private and public sector breeding programs place greater emphasis on white grain and tan plant characteristics. White-grained sorghum is, and is likely to remain, a minor sector of U.S. sorghum production. But increased interest in use of sorghum in food preparations in the home market and opportunities for export to sorghum-consuming countries is driving a renewed interest in this germplasm. Tie ups between U.S. seed companies and seed companies in other countries also are leading many U.S. companies to retain in their programs white-grained sorghum lines they might earlier have discarded; the best lines are likely to find a place in the sorghum programs of their overseas partners. A likely spillover from this will be grain mold-resistant white-grained sorghum hybrids that can compete in the U.S. market.

As for India, the effects of this work are likely to be felt first among restorer lines, and only later in male-sterile lines, because of the generally longer time period involved in breeding the latter. The extent to which grain hardness can be used to achieve grain mold resistance in sorghum for the U.S. market is also limited by quality considerations. The major end use of sorghum there is animal feed and the quality parameters for feed are probably more flexible than for human food. However, harder, more corneous grain is likely to result in reduced digestibility or increased costs for processing to achieve the same digestibility, either of which might adversely affect the position of sorghum relative to maize, its main competitor in the feed market.

Expanded systematic screening and selection of breeding materials for grain mold resistance under sprinkling and misting conditions is likely to help identify superior materials. The first products of such screening and selection are now becoming available in the public sector breeding programs in India and in the private sector in the U.S. These are likely to lead to improved levels of grain mold resistance in commercial hybrids. The balance of work on restorer lines and male-sterile lines, however, remains in favor of the former, while improvement of male-sterile lines may well prove more critical.

Manipulation of specific traits also can be used to increase grain mold resistance. For example, glume pigmentation might protect against mold attack. There is ample evidence that grain molds are inhibited by polyphenols in the grain and glumes, although there is limited understanding of which particular compounds are active (Waniska et al., 1989). Caution must be used, however, because efforts to improve mold resistance through glume pigmentation may lead to greater levels of grain discoloration. We must attempt to identify forms of glume pigmentation that afford grain mold protection but do not leach into the grain. Similarly, manipulation of the extent of glume cover also may prove beneficial for grain mold resistance. Generally, the greater the extent of glume cover and the longer the grain remains covered during grain development, the greater the protection from grain molds. As for glume pigmentation, however, there is a down side to this trait: increased glume cover can lead to threshing problems, limiting the usefulness of the trait. Another potential new trait for manipulation is rate of grain filling.

Biotechnological Approaches

Because grain mold resistance is expressed late in the life cycle of the crop, difficult to measure, and complex in its inheritance and subject to large environmental effects, it is a textbook example of the type of trait suitable for marker-assisted selection. Attempts to identify molecular markers for genes involved in grain mold resistance are already under way at Texas A&M University and Purdue University, and progress is reported elsewhere in these proceedings. These efforts represent a good beginning, but study of more populations will be required to clarify our understanding of the processes at play in determining grain mold resistance and to identify resistance genes that will be useful, particularly for white-grained cultivars. This work should be accorded high priority as the most

promising avenue for significant advances in our understanding of and ability to manipulate grain mold resistance.

Antifungal proteins have emerged in recent years as potentially potent weapons in fighting disease. This is true for grain molds, as for other fungal pathogens. However, realizing their full potential probably requires rather revolutionary approaches. Antifungal proteins have evolved along with the fungal pathogens against which they act and must have established a balance with them. It is therefore unlikely that the antifungal proteins of a particular plant species will give complete protection against that species' fungal pathogens. The true potential of antifungal proteins is likely to be achieved only when they are deployed against fungal pathogens with which they have not evolved. This implies transfer of antifungal proteins between species and all the difficulties this involves.

Antifungal proteins first must be identified in one species and shown to act effectively against pathogens of another species. The gene for that protein then must be identified or constructed and introduced into the target species, complete with the regulatory genes to turn it on. None of these steps is easy. Much basic information on how and where antifungal proteins act and how to introduce them into new species in functional forms remains to be gathered.

Conclusions

Further gains in grain mold resistance can be achieved through conventional breeding. However, the gains possible through the known resistance mechanisms in white sorghum are mostly self-limiting. Hard grain can be used only to the point where it affects grain quality. Glume pigmentation and cover can be used only to the extent that they do not lead to grain discoloration or threshing problems. Therefore, our expectations of what can be achieved should remain realistic. Even with improved and expanded screening and selection, we can at best anticipate only marginal increases in the levels of resistance available in improved white-grained cultivars.

Biotechnological approaches hold promise, but are far from realization. Marker-assisted selection should begin to help in the short-term future, but it is likely to take many years before all the potentially useful genes that could be pyramided are marked. Antifungal proteins as agents to enhance grain mold resistance lie even further in the future because we still lack much of the knowledge required to deploy them. The potential for either of these approaches to take us beyond currently available resistance levels also remains unclear. These areas of work, however, are the most likely to yield significant results and deserve greater attention in the future.

The grain mold problem in sorghum might be assuaged but will not be solved in the foreseeable future by resistance breeding. Therefore, we must look for such complementary methods as grain processing for managing the problem. We must anticipate an increase in grain mold problems in pearl millet as white grain cultivars become more important. Grain molds will continue to occupy us for many years to come.

References

Bandyopadhyay, R., and L.K. Mughogho. 1988. Evaluation of field screening techniques for resistance to sorghum grain molds. Plant Disease 72:500-503.

Bandyopadhyay, R., L.K. Mughogho, and K.E. Prasada Rao. 1988. Sources of resistance to sorghum grain molds. Plant Disease 72:504-508.

Butler, D.R., and R. Bandyopadhyay. 1991. Evaluation of sprinkler irrigation and misting to promote grain mold. p. 22-23. *In* ICRISAT cereals program report 1990. Cereals Program, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502 324, India. (Limited distribution.)

Castor, L.L. 1977. Seed molding of grain sorghum. Development of high yielding disease and insect resistant sorghum cultivars. Third annual progress report, TAES-US/AID Contract ta-c-1092. Texas Agricultural Experiment Station, College Station, Texas, USA.

Castor, L.L., and R.A. Frederiksen. 1980. *Fusarium* and *Curvularia* grain molds in Texas. p. 93-102. *In* Sorghum diseases, a world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Denis, J.C., and J.C. Girard. 1980. Factors affecting the development of sorghum grain molds in Senegal. p. 144-153. *In* Sorghum diseases, a world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Duncan, R.R., P.J. Bramel-Cox, and F.R. Miller. 1991. Contributions of introduced sorghum germplasm to hybrid development in the USA. p. 69-102. *In* Use of plant introductions in cultivar development, Part I. CSSA Special Publication no. 17. Crop Science Society of America, Madisón, WI, USA.

Esele, J.P., R.A. Frederiksen, and F.R. Miller. 1993. The association of genes controlling caryopsis traits with grain mold resistance in sorghum. Phytopathology 83(5):490-495.

Forbes, G.A., R. Bandyopadhyay, and G. Garcia. 1992. A review of sorghum grain mold. p. 265-272. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds.) Sorghum and millets diseases: A second world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Glueck, J.A., and L.W. Rooney. 1976. Physical and chemical characterization of sorghum lines with resistance to grain deterioration. Cereals Foods World 21:436-437.

Glueck, J.A., and L.W. Rooney. 1980. Chemistry and structure of grain in relation to mould resistance. p. 119-140. *In* Sorghum diseases, a world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Glueck, J.A., L.W. Rooney, D.T. Rosenow, and F.R. Miller. 1977. Physical and structural properties of filed deteriorated (weathered) sorghum grain. p. 102-112. *In* Third annual progress report, TAES-US/AID Contract ta-c-1092. Texas Agricultural Experiment Station, College Station, Texas, USA.

Gray, E., G.D. Lacefield, and G.D. Lowe. 1971. Head mold on grain sorghum. Plant Disease Reporter 55:337-339.

Hahn, D.H., and L.W. Rooney. 1986. Effect of genotype on tannins and phenols of sorghum. Cereal Chemistry 63:4-8.

Harris, H.B., and R.E. Burns. 1973. Relationship between tannin content of sorghum grain and preharvest seed molding. Agronomy Journal 65:957-959.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1992. Medium Term Plan 1994-98. Volume 3. Research theme datasets. Patancheru, Andhra Pradesh 502 324, India: ICRISAT. 229 pp. (Limited distribution.)

Jambunathan, R., L.G. Butler, R. Bandyopadhyay, and L.K. Mughogho. 1986. Polyphenol concentration in grain, leaf and callus tissues of mold-susceptible and mold-resistant sorghum cultivars. Journal of Agricultural and Food Chemistry 34:425-429.

Jambunathan, R., M.S. Kherdekar, and R. Bandyopadhyay. 1990. Flavan-4-ols concentration in mold-susceptible and mold-resistant sorghum at different stages of grain development. Journal of Agricultural and Food Chemistry 38:545-548.

Jambunathan, R., M.S. Kherdekar, and J.W. Stenhouse. 1992. Sorghum grain hardness and its relationship to mold susceptibility and mold resistance. Journal of Agricultural and Food Chemistry 40:1403-1408.

Koteswara Rao, B., and P. Poornachandrudu. 1971. Isolation of head molds and assessment of moldy grain in certain sorghum varieties. Andhra Agriculture Journal 18:153-156.

Mansuetus, S.B.A., R.A. Frederiksen, R.D. Waniska, G.N. Odvody, J. Craig, and D.T. Rosenow. 1988. The effects of glume and caryopses characteristics of sorghum on infection by Fusarium moniliforme Sheldon. Sorghum Newsletter 31:100.

Mansuetus, S.B., R.A. Frederiksen, R.D. Waniska, G.N. Odvody, and J. Craig. 1990. The role of glumes of sorghum in resistance to grain mold. Phytopathology 80(10):1069. (Abstract.)

Mukuru, S.Z. 1992. Breeding for grain mold resistance. p. 273-285. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds.) Sor-

ghum and millets diseases: A second world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Murty, D.S., K.N. Rao, and L.R. House. 1980. Breeding for grain mold resistant sorghums at ICRISAT. p. 154-163. *In* Sorghum diseases, a world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Prasada Rao, K.E., S.D. Singh, and J.W. Stenhouse. 1995. Grain mold resistance in guinea sorghum germplasm. International Sorghum and Millets Newsletter 36:94-95.

Rana, B.S., R. Parameswarappa, K.H. Anahosur, V.J.M. Rao, M.J. Vasudeva Rao, and N.G.P. Rao. 1978. Breeding for multiple insect/disease resistance. All India Coordinated Sorghum Improvement Project Workshop, 17-19 April 1978, Dharwad, India.

Rao, N.G.P., R. Vidyabhushanam, B.S. Rana, V.J.M. Rao, and M.J.V. Rao. 1980. Breeding sorghums for disease resistance in India. p. 430-433. *In* Sorghum diseases, a world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Rao, K.N., and R.J. Williams. 1977. The ICRISAT sorghum pathology program. International Sorghum Workshop, 6-13 March 1977, ICRISAT, Hyderabad, India.

Rao, K.N., and R.J. Williams. 1980. Screening for sorghum grain mold resistance at ICRISAT. p. 107-108. *In* Sorghum diseases, a world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Singh, S.D., and K.E. Prasada Rao. 1993. Sorghum grain molds — identification of resistance. p. 20. *In* ICRISAT cereals annual report 1992. Cereals Program, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, Andhra Pradesh 502 324, India. (Limited distribution.)

Singh, S.D., S.S. Navi, J.W. Stenhouse, and K.E. Prasada Rao. 1995. Grain mold resistance in white grain sorghum. International Sorghum and Millets Newsletter 36:95-96.

Waniska, R.D., G.A. Forbes, R. Bandyopadhyay, R.A. Frederiksen, and L.W. Rooney. 1992. Cereal chemistry and grain mold resistance. p. 265-272. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds.) Sorghum and millets diseases: A second world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, India.

Waniska, R.D., J.H. Poe, and R. Bandyopadhyay. 1989. Effects of growth conditions on grain molding and phenols in sorghum caryopsis. Journal of Cereal Science 10:127-225.

Williams, R.J., and D. McDonald. 1983. Grain molds in the tropics: problems and importance. Annual Review of Phytopathology 21:153-178.

Williams. R.J., and K.N. Rao. 1981. A review of sorghum grain moulds. Tropical Pest Management 27:200-211.

Zummo, N. 1976. Notes on the cereals improvement program. p. 5-15. *In* Cropping system meeting. Institute for Agricultural Research, Samaru, Ahmadu Bello University, Zaria, Nigeria.

Breeding for Pearl Millet Disease Resistance

C.T. Hash*, J.R. Witcombe, R.P. Thakur,
S.K. Bhatnagar, S.D. Singh, and J.P. Wilson

Abstract

*Breeding for disease resistance contributes to the maintenance and stability of grain, stover, and forage yields of pearl millet [*Pennisetum glaucum *(L.) R. Br.]. In breeding improved pearl millet, moderate levels of resistance to many pathogens of minor importance must be maintained so they do not lead to major production constraints. Although 111 diseases caused by different biotic factors have been reported in pearl millet in India and Africa, just five are sufficiently important to warrant international crop improvement efforts. These five and their causal organisms are: downy mildew [*Sclerospora graminicola *(Sacc.) J. Schröt.], smut [*Moesziomyces penicillariae *(Bref.) K. Vánky], ergot (*Claviceps fusiformis *Loveless), rust (*Puccinia substriata *Ellis & Barth. var. indica Ramachar & Cummin* = P. penniseti *Zimm.), and Pyricularia leaf spot [*Pyricularia grisea *(Cooke) Sacc.]. Screening techniques, sources of resistance, inheritance of resistance, and conventional breeding methods are reviewed for each.*

Of the two major pearl millet panicle diseases, smut is the most widespread. Genetic solutions are easier to obtain for smut than for ergot, and resistant open-pollinated cultivars and hybrid parental lines are available. Because smut resistance often is at least additive or partially dominant, breeding of smut-resistant hybrids is relatively simple. Breeding for ergot resistance is more complex, because resistance appears to be governed by multiple recessive loci. While ergot-resistant inbred seed parents are now available, breeding ergot-resistant hybrids will require considerable resources. A more cost-effective solution is to breed ergot-resistant open-pollinated pearl millet for ergot-endemic areas where alternative cereal crops cannot be grown.

The causal organisms of downy mildew, rust, and Pyricularia leaf spot can rapidly evolve new virulent host-directed pathotypes, while those of smut and ergot are not yet able to do so. In the case of the diseases caused by pathogens capable of rapid host-directed evolution, resistance of genetically heterogeneous cultivars appears to be more durable than that of genetically uniform single-cross hybrid cultivars.

Lack of a reliable system for regenerating large numbers of plants from tissue culture is a serious constraint to the development and application of several emerging technolo-

C.T. Hash, R.P. Thakur, and S.D. Singh, ICRISAT Asia Center, Patancheru, Andhra Pradesh 502 324, India; J.R. Witcombe, Centre for Arid Zone Studies, University of Wales, Bangor, UK; S.K. Bhatnagar, All India Coordinated Pearl Millet Improvement Project, Mandor, Rajasthan, India; J.P. Wilson, USDA-ARS, Coastal Plain Experiment Station, Tifton, GA, U.S. ICRISAT Conference Paper CP 1151. *Corresponding author.

gies for enhancing pearl millet disease resistance. A molecular-marker-based genetic map of pearl millet has permitted identification of at least 16 quantitative trait loci (QTLs) for downy mildew resistance. Detection of QTLs for resistance to rust and Pyricularia is expected in the near future. Each of the QTLs thus far detected for downy mildew resistance appears to be effective against only a few of the pathogen populations against which they have been tested. Marker-assisted selection will permit breeding of modified three-way hybrid cultivars that are uniform for agronomic characters but heterogeneous for their resistances. Such hybrids are expected to be less vulnerable to epidemics of new pathogen strains that have evolved when genetically uniform single-cross hybrids resistant to downy mildew (in India) or rust (in the U.S.) have been widely or repeatedly cultivated.

Breeding for disease resistance contributes to the maintenance and stability of grain, stover, and forage yields of pearl millet [*Pennisetum glaucum* (L.) R. Br.]. Disease resistance is a major concern in pearl millet improvement programs globally, and breeding for disease resistance has been the subject of several reviews (Louvel, 1982; Williams and Andrews, 1983; Williams, 1984a; Andrews et al., 1985a; Wilson et al., 1993a; Talukdar et al., 1994; Rai and Anand Kumar, 1994).

In breeding improved pearl millet, it is necessary to maintain moderate levels of resistance to many pathogens of minor importance (Madan Mohan et al., 1978; Singh et al., 1993b) to keep potentially serious production constraints from becoming major problems. For diseases of major importance in most parts of Africa and southern Asia (such as downy mildew, caused by *Sclerospora graminicola* [Sacc.] J. Schröt.), genetically heterogeneous open-pollinated cultivars must have moderately high levels of durable resistance because of the slow rate of replacement of open-pollinated cultivars once they are adopted by farmers. Because of their genetic uniformity, single-cross hybrids require still higher levels of resistance against major diseases. Resistance durability is not as critical in hybrids because of their higher replacement rates. However, genetically uniform single-cross hybrids have the potential for spectacular epidemics.

Hybrids with durable resistance are still desirable since considerable learning costs — to producers and consumers of seed, grain and fodder — often are associated with cultivar changes. Resistance of hybrid parents to *Sclerospora graminicola* in seed production areas is essential, although this can be backstopped by treating their foundation seed with metalaxyl. Reliance on metalaxyl alone to protect hybrid parents is a less satisfactory alternative. Further, hybrid seed parents resistant to smut (caused by *Moesziomyces penicillariae* [Bref.] Vánky), rust (caused by *Puccinia substriata* Ellis & Barth. var. *indica* Ramachar & Cummin = *P. penniseti* Zimm.) and ergot (caused by *Claviceps fusiformis* Loveless), should increase options in sites and seasons suitable for seed multiplication and thus help reduce seed costs. Topcross hybrids and three-way hybrids are heterogeneous cultivar types, and thus have some of the disease resistance requirements and attributes of both single-cross hybrids and open-pollinated cultivars. In future, these

heterogeneous hybrids should provide interesting alternatives to the major cultivar types (open-pollinated varieties and single-cross hybrids) currently available to breeders, seed production agencies, and pearl millet farmers.

This paper briefly discusses screening methods, sources of resistance, modes of inheritance, and breeding procedures for improving host-plant resistance to major pearl millet diseases in Asia, Africa, and the Americas. Both well-known conventional procedures and emerging biotechnology-assisted breeding strategies are described. Opportunities for more effective resistance gene deployment strategies, which become possible once marker-assisted selection schemes can be implemented, are discussed in some depth. The very limited literature on resistance to minor pathogens of pearl millet is not reviewed. To begin, major diseases of pearl millet and regions where they are currently of greatest importance are briefly highlighted.

Major Diseases: Importance and Distribution

Although 111 diseases caused by different biotic factors have been reported on pearl millet in India and Africa, four — downy mildew, smut, ergot, and rust — are most important (Williams, 1976; Singh et al., 1993b). These diseases directly reduce grain yield by affecting grain formation. In addition, ergot can reduce grain quality (Thakur and Williams, 1980; Mantle, 1992). Downy mildew and smut are present in all major pearl millet production areas of Asia and Africa, while ergot is less widespread. Of these four, only smut and rust have found their way to the Americas. Although *Sclerospora graminicola* infects wild and weedy *Setaria* spp in the Americas, populations of this fungus causing downy mildew on pearl millet in the western hemisphere have not yet been described.

In the southeastern United States, rust and a leaf spot complex are important reducers of pearl millet forage quality. In years of high rust severity, losses in dry matter yield and quality are substantial (Monson et al., 1986), and reductions in digestible dry matter yields can reach 50% (Wilson et al., 1991b). These and other foliar diseases (Singh et al., 1990d) also occur in Asia and Africa, but losses there are usually considered negligible because symptoms typically appear late in the season and primarily on older leaves.

Grain yield losses to downy mildew probably do not exceed 20% per year worldwide. However, this disease can reach alarmingly high levels when a single genetically uniform pearl millet cultivar is repeatedly and extensively grown in a region where downy mildew is present (Andrews, 1987; Singh et al., 1987b). As the pathogen population adapts to this uniform host, inoculum levels build up and it is only a matter of time before the third component of the disease triangle — favorable environmental conditions — coincides with the available inoculum and now-susceptible host. An epidemic then occurs. Losses within the region can reach 30-40%, and the susceptible host genotype must be withdrawn from cultivation. Such yield losses have been reported in India from regions where one single-cross hybrid (e.g., HB 3, BJ 104, MBH 110, or MLBH 104) was widely cultivated for several years. This repeated, widespread

use of a single cultivar with genetically uniform host-plant resistance exerts high selection pressure on pathogen populations.

However, high grain yield losses due to this disease seldom occur where heterogeneous landraces and improved open-pollinated cultivars are grown. Thus, heterogeneous cultivars can be retained in cultivation longer before they must be replaced. The first official release of a heterogeneous topcross hybrid pearl millet cultivar, Jawahar Bajra Hybrid-1 (JBH-1), recently occurred in Madhya Pradesh in India (G.S. Chauhan, 1996, personal communication). JBH-1 is produced by crossing a pollinator population onto a conventional cytoplasmic male-sterile inbred seed parent. It will be interesting to see if this heterogeneous hybrid becomes popular, and then whether its downy mildew resistance proves as durable as that of popular open-pollinated cultivars.

Both smut and ergot are potentially important pearl millet diseases (Thakur and King, 1988a, 1988b). However, susceptible stages of host development seldom coincide with weather conditions favoring these diseases in most pearl millet growing areas. This is especially true for ergot in areas that depend on pearl millet as the staple food crop (King, 1976). Thus losses are often not economically significant. Indeed, current information suggests that ergot and smut may not be of much practical importance, because the damage they cause is largely cosmetic. However, these diseases are important in breeding nurseries, forage production plots (ergot only), more humid grain production regions where maize or sorghum are often viable alternative crops, and rainy season hybrid seed production plots where they adversely affect yield and quality of seed produced on male-sterile lines.

Downy Mildew *(Sclerospora graminicola)*

Since shortly after the onset of the hybrid era for pearl millet in India, downy mildew has been a major research focus by both ICRISAT and the Indian national program (Singh et al., 1993a). Considerable progress appears to have been made over the past 30 years, since early 1966 when P.R. Mehta stated during his introductory remarks at a symposium held in Chandigarh, India, on diseases of millet and their control: "Our knowledge of 'downy mildew' of jowar and bajra, in so far as related to the control of the diseases, is no more advanced today than what it was 40 years back. It is well known that all attempts ... have shown that the enormous number of 'sporangia' produced are apparently functionless .... Today we do not know of any technique to produce high degree of infection of these diseases with certainty ...." This could not truthfully be said today (Singh and Williams, 1980). Research to improve screening systems and to identify and use host-plant resistance has been successful, allowing this serious threat to pearl millet cultivation in India to be largely controlled — at least for the moment.

Screening Techniques

Over the past two decades, ICRISAT has developed highly effective field and greenhouse screening techniques for pearl millet downy mildew.

Field Screening Technique

A large-scale field screening technique, using sporangia as the main inoculum source, was developed at ICRISAT Asia Center (Williams et al., 1981). However, the same field should be used each year to encourage a buildup of oosporic inoculum in the soil because oospores also play a significant role in producing primary infection. Genes conferring host resistance to sporangial inoculum cannot be assumed to be the same as those conferring resistance to oosporic inoculum. The field screening technique has five major components:

- Infector rows: mixtures of two or more susceptible host genotypes, sown before the test material on every fifth or ninth row (or any other arrangement that permits easy sowing and cultivation of the rows of test material) through the entire length of the field. From emergence to the 1-2 leaf stage, these infector rows are spray-inoculated with a sporangial suspension in the early evening (1800-1900 h). Furrow irrigation is provided eight to ten hours before inoculation to ensure high humidity necessary for successful infection.
- Test rows: the materials being screened, sown in the intervening rows after the infector rows have developed 50-60% downy mildew incidence, generally three to four weeks after the infector rows are sown.
- Indicators and controls: materials of known disease reaction (susceptible and resistant) sown with the test materials at regular intervals, generally after every 10 to 15 rows. Highly susceptible indicators are sown alternately with the controls. It is advisable to use a number of different indicator and control genotypes known to differ in degree of susceptibility. A set of such materials for pearl millet downy mildew in India currently might include HB 3 or Tift 23DB (extremely susceptible) and 7042(S) (highly susceptible) as indicators, and 843B (moderately susceptible), 81B (moderately resistant), ICMP 423 and/or ICMB 89111 (resistant), and ICMB 88004 and/or IPC 715 (highly resistant) as controls. Such a range of indicators and controls enables useful interpretation of screening data when disease pressure is unusually high or low.
- Scoring system: Because downy mildew is a systemic disease, a plant is normally scored as susceptible even if disease symptoms appear on only one tiller or panicle, or even a single nodal tiller. Therefore, disease incidence (%) is the most appropriate measurement. Data should be collected twice during the growing season. The first count of diseased plants (DP1) and total plants (TP) should be taken 20-25 days after sowing the test material. All diseased plants should be uprooted to account for infected plants that die or disappear prior to the second count due to cultural practices or heavy rainfall, particularly during the rainy season. A second count of additional diseased plants (DP2) should be taken at soft-dough stage when downy mildew may appear also as green ears on plants that previously appeared disease-free (latent infection), on nodal tillers, or quite frequently on

basal shoots. Disease incidence for each entry is then calculated as 100% × [(DP1 + DP2)/TP]. Disease incidence on indicators Tift 23 and HB 3 should exceed 80% if field screening of test materials is to be reliable.

- Water management: High humidity is necessary for spore production and the infection process. For field screening this can be provided by sprinklers, spray from perforated pipes, or furrow irrigation, but misters are ideal. At ICRISAT Asia Center, we use frequent furrow irrigation during the first two weeks after sowing test materials, followed by routine weekly or biweekly irrigation as required for crop growth. High humidity for the first two weeks after sowing is sufficient for development of an effective downy mildew nursery, as pearl millet is highly susceptible to infection during this period. Thereafter, regular irrigation maintains humidity required for later development and/or expression of latent infection without adversely affecting crop growth.

This field screening technique is now used at most sites where effective field research on pearl millet downy mildew is conducted (Singh et al., 1993a).

Greenhouse Screening Technique

Several greenhouse and laboratory screening techniques have been developed (Singh and Gopinath, 1985) and refined (Singh et al., 1993a; Jones, 1994; Weltzien and King, 1995) that use inoculum of uniform concentration to inoculate seedlings of uniform age, in controlled environments, in order to improve disease incidence heritability. Potted seedlings at the coleoptile-to-one-leaf-stage of development are inoculated by placing a drop of sporangial suspension (1×10^6 sporangia mL^{-1}) at the tip of each seedling or by spray inoculation with a hand sprayer. Inoculation at about 20°C with freshly prepared, chilled (0-4°C) inoculum is followed by overnight incubation in a chamber maintained at about 20°C and >95% relative humidity. Pots are kept on greenhouse benches at 25-30°C. Seedlings are evaluated two weeks after inoculation when infected plants show clear symptoms of chlorosis with downy growth. This permits easy screening of large numbers of plants of many different test materials in a small space and a short time. Of course, use of appropriate indicator and control entries randomized within the test material facilitates data interpretation. Spray inoculation of potted seedlings is now used extensively at ICRISAT Asia Center (Singh and Gopinath, 1985; Singh et al., 1993a; Weltzien R. and King, 1995), considerably reducing the size of field disease nurseries since many susceptible plants/entries are discarded in this initial stage of screening. However, resistance of advanced breeding products must still be confirmed in the field.

Sources of Resistance

Over the past two decades, ICRISAT has evaluated about 3500 germplasm accessions, from almost all pearl millet growing countries, for their reaction to downy mildew. Many highly resistant sources have been identified (Singh, 1990). To date, preliminary identification of resistance is done in the downy mildew nursery at ICRISAT Asia Center, but could be made more reliable by screening a small number (15-25) of S_1 or full-sib progenies from each accession in the

greenhouse. Identified accessions and breeding material are tested at known downy mildew hot-spots worldwide in the International Pearl Millet Downy Mildew Nursery (IPMDMN), which has operated annually since 1976. Many sources of resistance have been identified that can be grouped into four broad categories.

Stable Sources of Conventional Resistance

More than two years of testing in IPMDMN have been completed for sources of stable resistance (including both gene bank accessions and elite breeding products), with disease incidence markedly lower than in susceptible controls at all site × year combinations. Disease incidence is typically >0% under field screening conditions, and markedly higher under severe laboratory screening conditions.

- Gene bank accessions: These downy mildew resistance sources have shown a very high degree of stability across sites and years. However, their resistance can be overcome under greenhouse conditions by using very high inoculum levels and/or very early (e.g., coleoptile stage) inoculation. They include P7 (ICML 12), SDN 503 (ICML 13), 700251 (ICML 14), 700516 (ICML 15), and 700651 (ICML 16) registered by Singh et al. (1990a). In addition, several other sources, including IP 16438, IP 16762, P310-17, and P1449-3, have been identified. Many are breeding lines from western Africa. Several, including P7, 700651, 700516 and P310-17, have been utilized in breeding programs. Mapping populations are available, or under development, to tag resistance genes of P310-17 and P1449-2.
- Breeding lines: Several elite inbred lines and composites developed by breeders at ICRISAT Asia Center express downy mildew resistance that holds across sites and years in IPMDMN.
- Dwarf inbred pollinator ICMP 85410 (Hash and Witcombe, 1994; Talukdar et al., 1997), which likely derives its resistance from SC14(M)-1, was resistant across sites in one year of testing, but this resistance was overcome at some sites in western Africa in later years (S.D. Singh, unpublished). Molecular markers for quantitative trait loci controlling resistance of ICMP 85410 against downy mildew isolates from India and western Africa have been identified (Jones, 1994; Jones et al., 1994; Jones et al., 1995). Pedigree selection for resistance in progenies derived from crosses with ICMP 85410 is effective (B.S. Talukdar, unpublished).
- Tall inbred pollinator ICMP 423 (Rai et al., 1994) is the male parent of an unsuccessful hybrid released in India. It also has been converted into a male-sterile line (ICMA 90111) based on the EGP 261 cytoplasm (Rai and Hash, 1993). Resistance in ICMP 423, ICMB 90111 and ICMA 90111 has proven effective across years and sites in IPMDMN (S.D. Singh, unpublished). However, this resistance has been difficult to manipulate with pedigree selection, suggesting its inheritance is complex.
- ICMR 312 (Witcombe et al., 1996) is a topcross pollinator based on the

Bold Seeded Early Composite. It is genetically heterogeneous for genes controlling downy mildew resistance (Talukdar and Singh, 1993) and has shown exceptionally stable resistance across years and sites in IPMDMN (S.D. Singh, unpublished). Hybrids based on this topcross pollinator are marketed in India (B.S. Talukdar, unpublished).

Reselected Sources of Resistance

These sources have been developed through pure line selection of variability within susceptible parents at ICRISAT Asia Center. The classic example is ICML 22 (7042 DMR), a downy mildew-resistant version of 7042 (IP 2696), a landrace from Chad (Singh et al., 1992). Other important features of this line are its earliness, photoperiod insensitivity, and fertility restoration ability (Singh et al., 1994). Because of these important traits, ICML 22 is being used in breeding pollinators at ICRISAT Asia Center. While highly resistant across India, this line is susceptible in western Africa (S.D. Singh, unpublished). Segregation patterns in backcross progenies suggest ICML 22 carries at least three independently inherited resistance genes (C.T. Hash, unpublished). Downy mildew resistance also has been selected for successfully from within seed lots of the susceptible parental lines of elite hybrid BJ 104 (Singh et al., 1992). Resistance of these sources is typically not effective in western Africa.

Sources of Recovery Resistance

Recovery resistance is a phenomenon in which systemically infected plants outgrow the disease to produce healthy panicles (Singh and King, 1988). Host genotypes with this trait do not prevent spore germination and penetration, disease symptom development, or sporulation, thus allowing the pathogen to complete its life cycle. The pathogen and host coexist, apparently without adversely affecting yield. This trait is heritable, but plants must first be infected — susceptible to some degree — before phenotypic scoring for this type of resistance is possible. Plants with this type of resistance quickly recover from the disease, if infected, and subsequently behave like conventional resistant genotypes. Marker-assisted selection would allow this type of resistance to be pyramided with more conventional resistances.

Recovery resistance has been discovered in many pearl millet accessions and breeding lines, but only a few have a high level. Through pedigree breeding, the level of recovery resistance was increased to more than 95% in a selection from ICMB 1 — maintainer of ICMA 1 (81A), widely used in commercial hybrid seed production in India (Singh and Talukdar, 1996). Other sources of this type of resistance include SDN 503, P1449, and ICMB 841.

Sources of "Complete Resistance"

These are highly inbred genetic stocks developed from gene bank accessions at ICRISAT Asia Center without selection for agronomic eliteness (S. Appa Rao, 1996, personal communication). Five accessions (IP 18292, IP 18293, IP 18294, IP 18295, and IP 18298) initially showed zero disease incidence, regardless of inoculum level or seedling age at the time of inoculation, when tested across sites in India and at Bengou (Niger) and Cinzana (Mali) (Singh, 1992). However, in subsequent years, none continued to be dis-

ease-free at all test sites and under all screening conditions. Hence these sources appear to provide nothing more than qualitative resistance that is otherwise similar to more conventional quantitative resistance from sources described above. They do not provide a magic bullet that can be used to protect otherwise susceptible hybrid parents." Mapping populations are available, or under development, to tag resistance genes of IP 18292 and IP 18293.

Inheritance of Resistance

There are several published reports on the inheritance of downy mildew resistance. However, all such studies have been hampered because both the pathogen and host are allogamous and highly variable (Thakur et al., 1992b), and segregation for host plant resistance generally shows continuous variation (Singh et al., 1980; Basavaraju et al., 1981a; Dass et al., 1984; Shinde et al., 1984). In addition, regional variability in the pathogen populations used and difficulties maintaining high and uniform disease pressure have led to conflicting conclusions from earlier studies (Jones et al., 1995). However, a meaningful summary is still possible.

First, there is clear evidence that the A_1 cytoplasm is not associated with susceptibility or resistance to downy mildew (Anand Kumar et al., 1983; Yadav et al., 1993; Yadav, 1994; Yadav, 1996). However, there is ample evidence that genes in the nucleus control host plant reaction to this disease. Except in one case where resistance was reported to be recessive (Singh et al., 1978), resistance is generally dominant and variation in segregating populations is continuous (Singh et al., 1993a). In the few cases where clear Mendelian segregations have been observed, one, two (Deswal and Govila, 1994), or even three (C.T. Hash, unpublished) dominant genes have governed resistance. However, all published studies on the inheritance of resistance to this disease also suggest the presence of minor genes.

Overall the picture of the mode of inheritance remains unclear and incomplete, due in part to the variable pathogen populations used in all these studies. Evaluation of segregating host populations with single-spore cultures of the pathogen could help, but would be less useful in applied breeding for resistance against variable field populations of the pathogen.

Quantitative inheritance studies of downy mildew resistance in pearl millet have been more successful, identifying parental materials with the ability to transmit high levels of resistance. Many authors (e.g., Tyagi and Iqbal Singh, 1989; Deswal and Govila, 1994; Kataria et al., 1994) have generally concluded that nonadditive gene action is responsible for much of the heritable variability, agreeing with simpler studies that show resistance to be dominant or partially dominant. Such nonadditive gene action can contribute substantially to general combining ability (GCA), since parents having dominant resistance can be expected to have high GCA for this trait when compared with more susceptible parents. However, high GCA for disease resistance (e.g., ICMP 423 = IPC 0094 in Talukdar et al., 1994) does not mean that such resistance will be easy to manipulate in a pedigree or backcrossing program.

Recent inheritance studies based on molecular marker genetic linkage maps are yielding interesting results (Jones et al., 1994, 1995; Hash et al., 1995) that will facilitate genetic manipulation of disease resistance. These are described in greater detail in the section on marker-assisted selection and emerging technologies.

Conventional Breeding Methods

Conventional breeding procedures use greenhouse or field screening methods to incorporate adequate levels of downy mildew resistance into breeding populations, parental lines, and experimental open-pollinated varieties that have superior agronomic performance and product quality. Pure line selection (selection within partially inbred lines), pedigree selection, backcrossing, induced mutation, and recurrent selection procedures have all been used in breeding for resistance to downy mildew, with varying degrees of success. Marker-assisted selection (MAS), a new tool for pearl millet breeders, will permit more effective pedigree and backcross improvement of downy mildew resistance in future.

Pedigree and recurrent selection (Andrews et al., 1985a; Rattunde and Witcombe, 1993; Singh et al.,1988a; Weltzien R. and King, 1995) are the most widely and successfully used methods for improving pearl millet downy mildew resistance. Procedures used are similar to those described elsewhere for this and many other crops so they are not covered in detail here. Inbred seed parents bred at ICRISAT Asia Center since the mid-1980s and most inbred restorer lines in the ICRISAT Pollinator Collection have been developed using pedigree or pedigree-bulk selection for downy mildew resistance. Pedigree-bulk methods use selfed seed bulked from selected plants of individual selected progenies in order to reduce row requirements and retain intra-progeny variability. However, if greenhouse screening facilities are sufficient for effective panicle-to-row screening of all single-plant selections, the number of nursery rows required by a pedigree selection procedure will not be unduly large.

Backcrossing

Conventional backcrossing procedures have seldom been used in breeding for resistance to pearl millet downy mildew. However, initial difficulties with unreliable screening procedures have largely been overcome, and this method is expected to be used more often in the future. The only reported success using backcrossing thus far has been breeding of downy mildew-resistant seed parents MS 5054 and MS 5141 in the elite genetic background of Tift 23 by the Indian Agricultural Research Institute (Pokhriyal et al., 1976; Murty et al., 1983). In this case the number of backcrosses was not sufficient to fully recover plant type of the elite recurrent parent, although morphological and molecular marker genotypes of Tift $23DB_1$ and MS 5141 are similar (Liu et al., 1992). Backcrossing is a simple procedure for transferring a single resistance gene. Sedcole (1977) indicates plant numbers to be crossed for 95% probability of transferring the gene each generation. While a single resistance gene seems unlikely to remain effective very long in cultivation, parallel backcrossing programs for several individual resistance genes with a common recurrent parent, followed by pyramiding (or other deploy-

ment strategies) at a later stage, will require fewer plants and resources per generation than would simultaneous transfer of the same resistances in a single series of backcrosses.

In each generation, segregation for resistance should be confined to the female parent to reduce chances of losing the resistance gene due to segregation distortion among male gametes (Busso et al., 1995) and to permit use of stored pollen of the elite recurrent parent (Hanna, 1995).

As in the pedigree method, plant pairs of the susceptible and resistant parents are selfed and crossed. Selfs of each parental plant and the individual F_1 progenies are screened (preferably in the greenhouse) to confirm their expected disease reactions. A resistant F_1 progeny, with parents having selfed progenies of expected disease reactions, is advanced. This assumes the donor's resistance is not recessive. A single typical plant of this F_1 progeny is crossed, as female, with pollen collected from typical plants of the susceptible recurrent parent. Seedlings of the BC_1F_1 generation are screened in the greenhouse under high inoculum pressure, with the original susceptible and resistant parental lines serving as controls. Disease-free BC_1F_1 seedlings are transplanted to the field. Five disease-free BC_1F_1 plants are crossed as females with pollen of the recurrent parent. Seedlings of each of the resulting BC_2F_1 progenies are screened against downy mildew, and disease-free seedlings of one progeny having the expected 1:1 segregation of diseased:disease-free seedlings are transplanted to the field. This procedure is repeated each generation until BC_6F_1 seed is produced.

Seedlings of the BC_6F_1 progenies also are screened against downy mildew, and disease-free seedlings from one BC_6F_1 progeny are transplanted to the field. Five disease-free plants are selfed to produce the BC_6F_2. After screening, disease-free seedlings are transplanted to the field from one BC_6F_2 progeny that yields the expected 1:3 segregation of diseased:disease-free plants. Twelve BC_6F_2 plants are selfed and harvested. Twelve BC_6F_3 progenies are screened, using large numbers of seedlings. Remnant seeds of uniformly resistant BC_6F_3 progenies are bulked as the new resistant version of the recurrent parent.

This description assumes the recurrent parent genotype is largely recovered by the backcrossing procedure alone, without any explicit selection for parental characteristics. By the BC_6F_1 generation, 99% recovery of the recurrent parent genome is expected, so except in cases of tight linkage between alleles conferring susceptibility and those controlling other agronomically important traits, this assumption is reasonable. Increasing the number of plants in any earlier generation will increase the opportunity for selecting recurrent parent traits, potentially reducing the number of backcrosses required to recover the recurrent parent phenotype for traits other than downy mildew resistance. Failure to recover resistance in the recurrent parent plant type in the BC_6F_1 suggests either that there is tight linkage between the donor's resistance gene and genes controlling important recurrent parent traits, or that some backcrosses were in fact selfs. In pearl millet, the latter possibility should be strongly considered, and several additional backcrossing generations attempted, before claiming unfa-

vorable linkage. Of course, once broken, such an unfavorable linkage becomes a favorable one, so it is well worthwhile to try further backcrosses to break any undesirable linkages detected.

Because a complete population backcrossing program requires at least 20 parallel backcrossing programs in order to avoid inbreeding depression in the resulting BC_6 resistant population, such a program cannot generally be justified given its large resource requirement.

Induced Mutation

Three groups of reports have indicated success using mutagens to induce downy mildew resistance in agronomically superior but susceptible pearl millet hybrid parental lines: 1) Raut et al., 1973; Murty, 1973, 1974, 1977; Murty et al., 1983; Pokhriyal and Jain, 1974; 2) Gill et al., 1979, 1981; and 3) Andrews and Anand Kumar, 1982; Anand Kumar et al., 1984. However, there is evidence for doubt in two of these cases, and in no case is there evidence that if resistance resulted from mutation, the original parental line and derived resistant mutant line differ for only a few loci.

The first group of reports describe how MS 5071B was derived by mutation from Tift 23B and then backcrossed to Tift 23A to produce MS 5071A. However, even before NHB 3 (MS 5071A × J 104) was released as a replacement for susceptible HB 3 (Tift 23A × J 104), whatever induced resistance it had was overcome by the pathogen. Gill et al. (1979, 1981) describe Pb 204, which was bred by means similar to those used for MS 5071. However, no hybrids were ever released on this seed parent. In the final case, during the breeding of 81A and 81B, the parental lines Tift 23DA and Tift 23DB were so susceptible to downy mildew, it was not possible to select for the Tift 23D plant type. Selection was initially for downy mildew resistance, vigorous dwarf plants, and stable maintenance of cytoplasmic male-sterility. Seed set and results from preliminary combining ability testing were later used to identify the A/B pair that is widely used in India as 81A and 81B (Anand Kumar et al., 1984). There is no doubt that this breeding program was successful in producing a seed parent that made a substantial positive contribution to Indian agriculture over the past decade. However, both morphological data and molecular marker data suggest that 81B is the product of an outcross involving Tift 23DB, and not simply an induced mutant of Tift 23DB (Rai and Hanna, 1990; Liu et al., 1992).

Since most induced mutations are expected to be recessively inherited, it seems unlikely they will produce parental lines with improved resistance expressed in their hybrids. Dominant resistance in products of mutation breeding programs is more likely the result of outcrossing with an unknown resistance donor than the product of mutation per se. Therefore, it seems preferable to use planned crosses with well-characterized resistance donors in an appropriate pedigree, backcross, or recurrent selection breeding scheme, instead of relying on uncharacterized resistances that random pollen might bring into a mutation breeding program.

Selection for Within-Line Variability

In this variation of pure line breeding, selection for downy mildew resistance is

done within a susceptible line using pedigree procedures. A large population of a susceptible line is grown in the disease nursery or inoculated in the greenhouse. Disease-free plants are selfed and the selfed progenies of these are screened panicle-to-row against the disease. The process of selection and selfing is repeated for several generations until several progenies with desired levels of resistance and the morphological characters of their susceptible progenitor have been identified. A notable success with this method was the development of ICMA 841 and ICMB 841 from the susceptible 5141A and 5141B (Singh et al., 1990c). Molecular fingerprinting suggests that the source seedlot of MS 5141B used in breeding ICMB 841 included derivatives of outcrosses to an unidentified source of downy mildew resistance, and that in fact these outcross derivatives were selected (Liu et al., 1992). ICMA 841, the male-sterile counterpart of maintainer line ICMB 841, has been exploited commercially in India as a female parent of several F_1 hybrids, including ICMH 423, Pusa 23, and Pusa 322. Pusa 23 is presently the most widely grown public-bred hybrid in India.

This method provides an opportunity to revive once-popular cultivars that have become susceptible to downy mildew; it has been recommended as a routine operation to maintain purity and disease resistance of parents of good hybrid cultivars (Singh et al., 1992). However, if purity is maintained for an inbred parental line, within-line genetic variability for resistance may be limited and selection to maintain resistance to an evolving pathogen population will not likely be effective. This procedure is expected to be more effective with heterogeneous genotypes such as open-pollinated cultivars and top-cross pollinators.

Recurrent Selection

This procedure has proven effective for breeding downy mildew resistance that is durable for a long period following release and widespread adoption of improved open-pollinated cultivars. Many different recurrent selection schemes are possible in pearl millet, ranging from simple mass selection (unlikely to be very effective for downy mildew resistance) to complex progeny-based selection. For any recurrent selection scheme based on S_1 or full-sib progenies, selection for resistance between progenies will be much more effective than selection within them.

Singh et al. (1988a) describe recurrent selection for downy mildew resistance based on S_1 progeny screening in the downy mildew nursery at ICRISAT Asia Center. Refined screening procedures now allow screening of about 600 S_1 progenies per population in the greenhouse each selection cycle, using two 50-seedling pots for each S_1 progeny, arranged in a completely randomized design with appropriate indicators and controls. Approximately 50% of these progenies having higher downy mildew incidence are rejected. The remaining 50% are evaluated for agronomic traits in single-replication augmented design trials, at several locations. In the field, any progeny with even one downy mildew-infected plant is rejected. About 50 agronomically superior downy mildew-free S_1 progenies selected from these field trials are then recombined the following season — either by manual full-sib crossing or by random mating in isolation — to produce the cycle bulk population for the next round of recurrent selection. If full-sibs

are made, these are screened in the greenhouse, and remnant seed of the most resistant ones sown in the target environment to identify agronomically superior progenies. These procedures have been effective in maintaining or improving levels of downy mildew resistance in ICRISAT's pearl millet composite populations (Rattunde and Witcombe, 1993).

Marker-Assisted Selection

Marker-assisted selection (MAS) uses as selection criteria highly heritable 'tags' that are genetically linked to portions of the genome controlling characters of interest. These markers can be morphological traits; proteins, including isozymes; or DNA markers such as restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs), and others. MAS is an excellent alternative to time-consuming test crosses otherwise required to pyramid genes (such as downy mildew resistance genes) exhibiting epistasis (Gale and Witcombe, 1992; Miklas et al., 1992; Paterson et al., 1991). MAS and graphical maps based on markers (Fähr et al., 1993) can help breeders more rapidly recover recurrent parent genotypes in backcrossing programs (Lande and Thompson, 1990; Hospital et al., 1992) and more efficiently identify desired recombinants in pedigree programs.

In order to use MAS in improvement of pearl millet downy mildew resistance, it is necessary to have:

- a donor parent with identified linked markers for some of its resistance genes;
- an elite parent with inadequate resistance, which has different marker alleles than the donor parent and lacks these resistance genes (at least the specific alleles linked to markers in the donor genome); and
- a system for efficiently determining genotype (or at least phenotype) at the marker loci in individual segregating plants derived from crosses between the resistance source and elite parent.

To date, markers have been identified for at least 16 different putative downy mildew resistance quantitative trait loci (QTLs) in pearl millet.The effectiveness of MAS is now being evaluated at ICRISAT Asia Center in collaboration with the Centre for Arid Zone Studies, and it appears promising indeed. MAS has advanced as far as the BC_2F_4 and BC_4F_1, and interesting recombinants have been identified (Figure 1). The first products of this MAS program are expected to reach pearl millet breeders and pathologists in late 1997 as versions of elite maintainer line 843B having different combinations of resistances from ICMP 85410.

Since MAS for downy mildew resistance is currently being tested, one can now contemplate deploying downy mildew resistance genes in ways that were not previously practical (Hash and Witcombe, 1996). Possibilities include 1) pyramided resistance genes in hybrids based on a single seed parent, 2) hybrids based on male-sterile synthetics (whose parents are near-isogenic derivatives of a single seed parent, into which different resistance genes have been backcrossed using MAS), and 3) three-way hybrids based on a male-sterile F_1 (whose parents

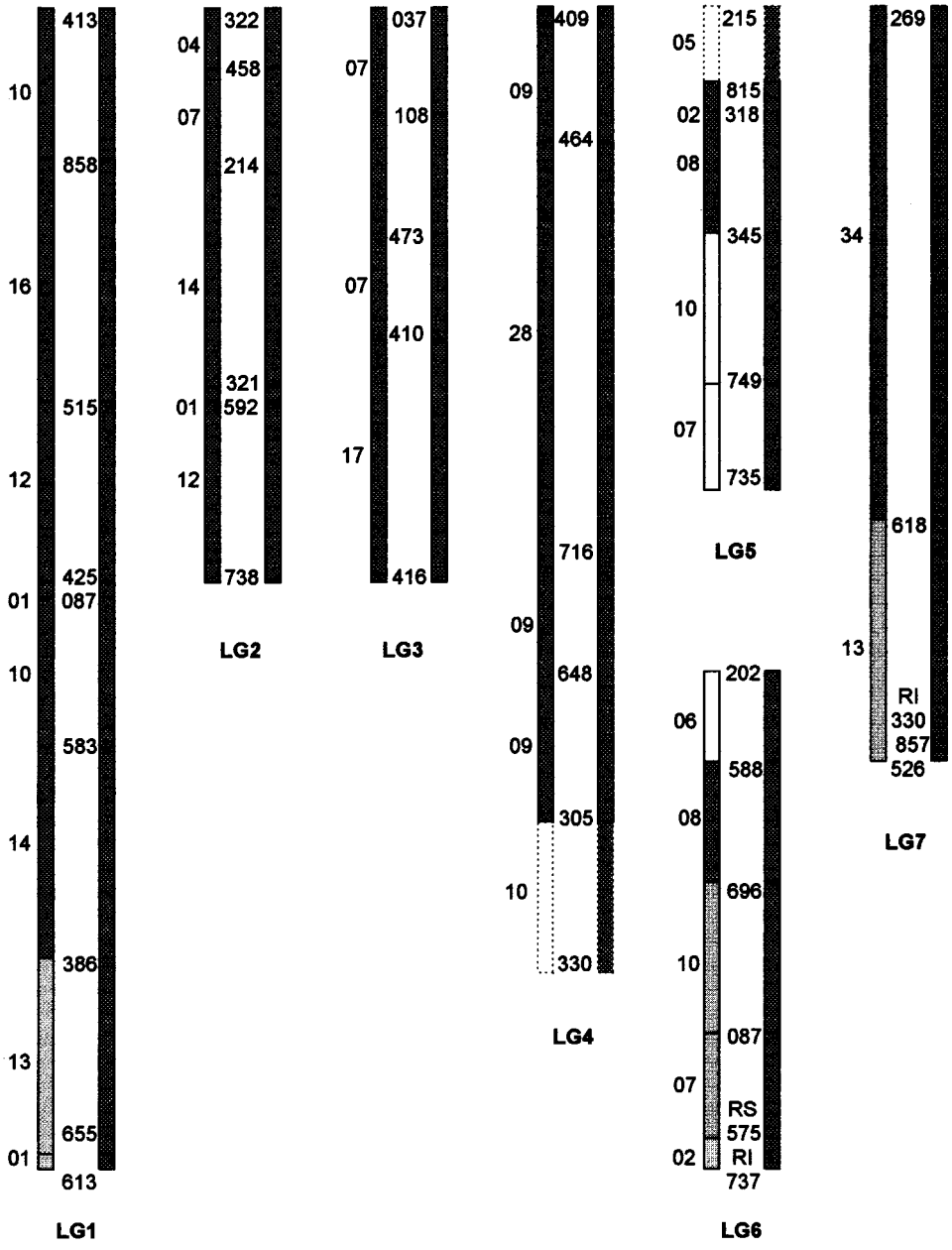


Figure 1. Distribution of downy mildew resistance donor ▭ and elite recurrent parent ▬ genome segments across all seven pearl millet linkage groups (LG) in BC1F1 selection[{ICMP 85410-P7-2-P1 x 843B-P3)-P1 x 843B)-P1 x 843B-P3-P1]-P7 x 843B-P5}-P46. Abbreviated marker loci names are given between homolgous chromosome pairs, map distances between pairs are given (cM) to the left of each chromosome pair. Solid empty regions ▭ represent genome segments where parental marker polymorphism exists, but data are missing. Dashed regions, ▬ and ⊏⊐, represent genome segments for which no parental marker polymorphism exists. Solid shaded regions ▭ represent genome segments in which a recombination event has occurred. This plant is expected to be heterozygous for quantitative trait loci located in LG 6 and LG7 that confer resistance against downy mildew isolates from India (RI) and Senegal (RS). Marker data courtesy of M.A. Kolesnikova (1996).

are a maintainer line, into which one set of resistance genes have been backcrossed, and a male-sterile line that is near-isogenic to the maintainer except it has the male-sterile cytoplasm and a second set of resistance genes). Of these three new types of hybrids, the last appears to offer several advantages:

- all the resistances in the seed parent of the three-way hybrid are pyramided, and this pyramid can be protected using systemic fungicides (e.g., metalaxyl) in hybrid seed multiplication plots to reduce selection pressure in the pathogen for virulence effective against the full pyramid;
- there are fewer resistances to be pyramided in any line to achieve a given total number of resistance genes in the hybrid seed parent (e.g., two pyramids of three genes each in parents of the F_1 seed parent with a six-gene pyramid);
- frequency of pyramided resistances in the hybrid is reasonably high;
- breeder seed of the maintainer line and its near-isogenic male-sterile line (which are similar except for pollen production ability and resistance gene complement) can be supplied to producers of foundation seed of the F_1 seed parent without complicating the seed multiplication chain (Figure 2); and
- the hybrid cultivated over potentially large areas is genetically heterogeneous for downy mildew resistance — mimicking to a certain degree the variability (and hopefully durability) of open-pollinated cultivars for this character — but phenotypically uniform for other agronomic characters.

Marker-assisted selection offers pearl millet breeders a key for reconciling conflicting desires for uniformity for agronomic characters and variability for resistance factors. If it can contribute to stable, higher yields of pearl millet grain and fodder, then MAS is a tool breeders should become familiar with so as to exploit it more fully when costs of using it come down.

Smut

Moesziomyces penicillariae (Bref.) Vánky (syn. *Tolyposporium penicillariae* Bref.) causes smut in pearl millet. Descriptions of the pathogen (Ramakrishnan, 1963; Subba Rao and Thakur, 1983; Chahal et al., 1986) and screening techniques (Thakur et al., 1983a; Thakur and King, 1988b) are available, and a summary of work at ICRISAT Asia Center on identification and utilization of host plant resistance to this disease has recently been published (Thakur et al., 1992a). Smut is normally most severe on the upwind borders of isolated fields, especially on the earliest flowering panicles of uniform single-cross hybrids, where pollen availability is limited. It also can be serious on hybrid cultivars with long protogyny and/or poor fertility restoration, especially when rainfall during flowering results in poor anther dehiscence.

Screening Techniques

An effective screening technique for smut resistance in pearl millet (Thakur et al., 1983a) involves:

- inoculation of panicles by injecting aqueous suspension of sporidia of

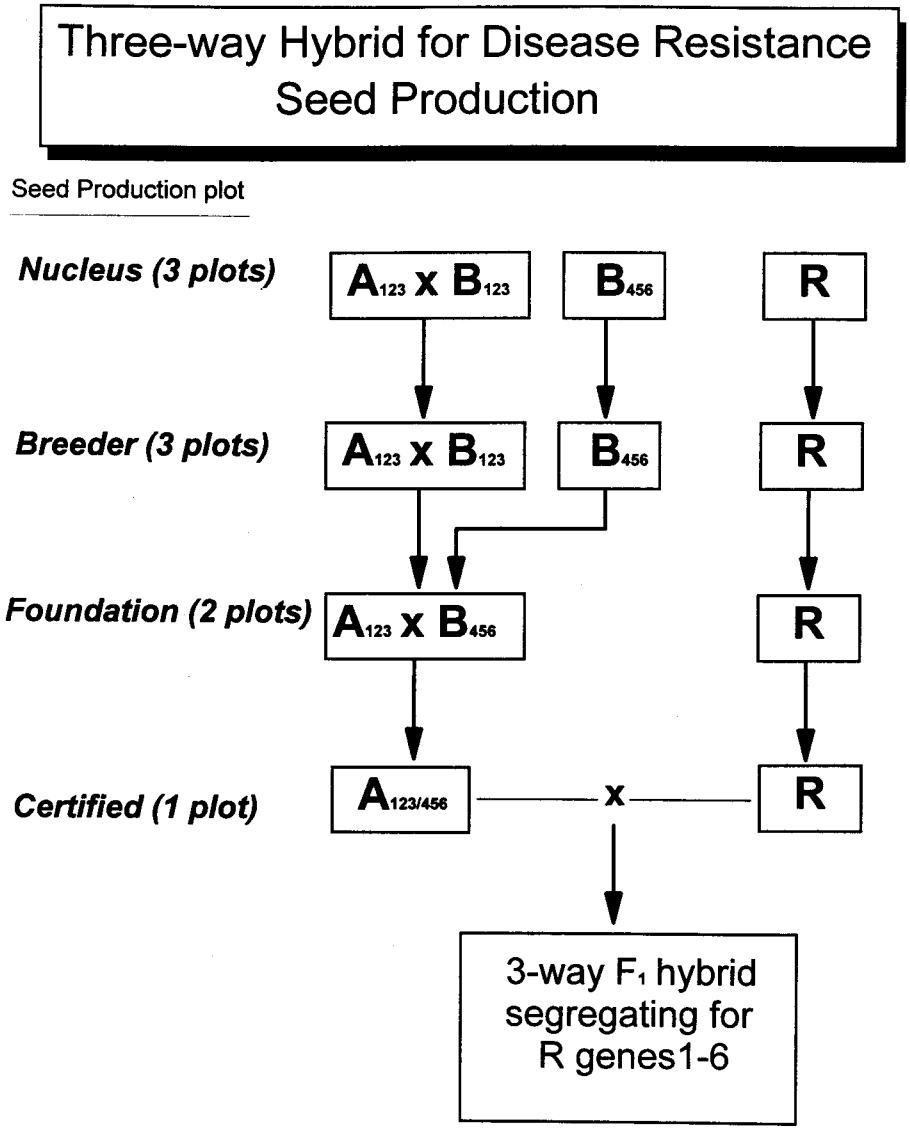


Figure 2. **Seed multiplication scheme for modified three-way hybrid cultivars that are heterogeneous for their disease resistance gene complement, but uniform for other agronomic characters.**

M. penicillariae (1×10^6 mL^{-1}) into the 'boot';

- covering the inoculated panicles with parchment paper selfing bags (polythene bags [Wells et al., 1987] can inhibit seed set by causing high moisture and high temperature conditions);
- providing high humidity (80% RH) by using an overhead sprinkler twice a day for 30 minutes each at 10 am and 5 pm on rain free days; and
- removing bags 15-20 days after inoculations and scoring panicles for smut severity using a standard smut severity assessment key (Thakur and King, 1988b).

Sources of Resistance

Sources of smut resistance have been identified in gene bank accessions from Cameroon, India, Lebanon, Mali, Niger, Nigeria, and Togo, representing diverse agroecological zones (Thakur et al., 1986, 1992a; Thakur and King, 1988b). Following pedigree breeding and artificial screening of progenies of crosses involving smut-resistant lines, a large number of agronomically diverse smut-resistant lines were identified. Recently nearly 400 smut-resistant lines (assigned ICMSR numbers) have been characterized for their agronomic attributes and reactions to smut and downy mildew (Thakur et al., 1992a). These lines have subsequently been deposited with the Genetic Resources Division at ICRISAT Asia Center and have been assigned accession numbers (IP 19685 - IP 20081). Many of these lines were evaluated at key hot spots in Africa and India, and several with stable resistance to smut were identified (Thakur et al., 1986; Thakur and King, 1988b, 1988d). Many of these lines have improved agronomic traits and combined resistance to smut and downy mildew (Thakur et al., 1992a).

Inheritance of Resistance

Reports conflict as to whether host reaction to smut is affected by cytoplasm (Khairwal et al., 1986; Yadav et al., 1992; Thakur et al., 1992a). These are discussed thoroughly by Yadav (1994).

Observations at ICRISAT Asia Center (Thakur and Chahal, 1987) and earlier evidence (Yadav, 1974) indicate that resistance to smut is dominant and simply inherited. Phookan (1987) and Chavan et al. (1988) have reported both dominant and additive gene actions for smut resistance, but additive genetic effects are much larger than dominance effects.

Breeding Methods

Breeding for smut-resistant open-pollinated varieties through recurrent selection has shown promise. Two population varieties derived from the Smut Resistant Composite (SRC) population (constituted in 1979 at ICRISAT Asia Center) — ICMV 82131 and ICMV 82132 — and two synthetics — ICMS 8282 and ICMS 8283 — have shown a high level of resistance to smut and downy mildew and have yielded on par with the control variety WC-C75 (Andrews et al., 1985a; Thakur and Chahal, 1987). ICMV 82132 performed well in several tests in Africa and has been released as 'Kaufela' in Zambia. Dwarf versions of ICMV 82132 have been produced (e.g., ICMV 89074 and ICMV 93074) and are available for testing in regions where the height of

ICMV 82132 (often ≥ 2.5 m) would be considered excessive. A number of partially inbred lines derived from the SRC have been introgressed in other composites at ICRISAT Asia Center to increase levels of smut resistance, and SRC was merged with the Intervarietal Composite (IVC) to form the Smut Resistant Composite II (SRC II). A subset of SRC II flowering one week earlier than the original was produced by a single cycle of mass selection for early flowering, and named the Early Smut Resistant Composite II (ESRC II). Open-pollinated varieties selected from ESRC II, including ICMV 91773 and ICMV 93771, have performed well in trials in India and Kenya. This composite is an excellent source of medium-early breeding material with compact cylindrical panicles, high grain yield potential, and excellent downy mildew resistance, at least for Asia, in addition to its smut resistance.

Significant progress has been made in incorporating smut resistance from unadapted source materials into commercially useful male-sterile lines using pedigree-bulk procedures in crosses between the source material and adapted elite maintainer lines. ICMA 88006 is the first smut-resistant male-sterile line developed using these methods. It also is resistant to downy mildew, has high seed yield and superior agronomic attributes, compared to currently available male-sterile lines (Thakur et al., 1992a). Several additional smut resistant male-sterile lines have been bred at ICRISAT Asia Center in recent years. Breeding and evaluation of smut-resistant hybrids that can be produced on these new male-sterile lines are in progress at public and private research centers in India.

Phenotypic MAS for smut resistance is also possible. The *tr* allele confers trichomeless plant structures, and is easily identifiable in homozygous plants. Smut resistance is a pleiotropic effect of the *tr* allele, or *tr* is closely linked to resistance gene(s) (Wilson, 1995).

Ergot

Claviceps fusiformis Loveless [syn. *C. microcephala* (Wallr.) Tul.], the causal fungus of ergot of pearl millet, was first described by Loveless (1967) and later by Siddiqui and Khan (1973), Kumar and Arya (1983), Thakur et al. (1984) and Chahal et al. (1985). Screening techniques (Thakur et al., 1982; Thakur and King, 1988a) are available, and a summary of work at ICRISAT Asia Center on identification and utilization of host plant resistance to ergot has recently been published (Thakur et al., 1993). Longer protogyny periods usually result in higher disease incidence. Infection of an individual floret may take place through stigma, style, or ovary wall (Willingale and Mantle, 1985). Infection most commonly occurs through fresh stigmas; 36 hours after infection a constriction develops in the fused stylodia concurrently with hyphal invasion of the upper ovary wall (Willingale and Mantle, 1987). Similarly, a constriction develops as a result of pollination (Thakur and Williams, 1980; Willingale et al., 1986) and stigma withering occurs within three hours following pollination (Thakur and Williams, 1980). Stigmatic constriction and withering is much faster after pollination than after inoculation with conidia of the pathogen. Abundance of pollen reduces ergot infection (Thakur and Williams, 1980).

Screening Technique

Screening for ergot resistance was initiated in India under the All-India Coordinated Pearl Millet Improvement Project (AICPMIP) during the late sixties, but success was limited due to lack of a reliable technique. Systematic research at ICRISAT Center since 1976 has resulted in the development of an effective field screening technique (Thakur and Williams, 1980) that involves:

- bagging panicles at the boot-leaf stage with parchment selfing bags to allow stigma emergence in a pollen-protected environment;
- inoculating panicles 3-4 days later by briefly opening the bags and spraying panicles at the full protogyny stage (>75% fresh stigmas) with an aqueous conidial suspension (1×10^6 conidia mL^{-1}) produced from honey dew of infected panicles;
- providing high humidity (>80% RH) with overhead sprinklers twice a day for 30 minutes each at 10 am and 5 pm on rain-free days;
- removing bags two weeks later and scoring ergot severity using a standard ergot severity key.

Reliance on natural screening conditions can give misleading results, especially when early-flowering or late-flowering test entries escape infection (Jain et al., 1988).

Sources of Resistance

Screening of a large number of pearl millet inbred lines in AICPMIP trials in India, at different locations in Africa, and at ICRISAT Asia Center failed to reveal lines with a satisfactory level of ergot resistance. Resistant lines were developed by intermating less susceptible plants and selecting resistant progenies under high disease pressure for several generations following pedigree and recurrent selection procedures (Gill et al., 1980; Chahal et al., 1981; Thakur et al., 1982). A number of lines have shown high levels of resistance across different locations in India and western Africa over several years (Thakur et al., 1985; Thakur and King, 1988a). Lines with high levels of resistance combined with good agronomic traits also have been identified that can be used as donors for developing ergot-resistant varieties (Thakur and King, 1988c). About 300 ergot-resistant inbred lines and populations (ICMER numbers) have been evaluated for their agronomic attributes and reactions to diseases (Thakur et al., 1993). Many of these lines and populations possess improved agronomic traits and combined resistance to ergot, smut, downy mildew, and rust (Thakur et al., 1988).

Attempts were made to select ergot-resistant lines using tissue culture techniques, with sclerotial extract and culture filtrate of *C. fusiformis* as the selective agents (Bajaj et al., 1980; Sharma and Chahal, 1990). Regenerants have been isolated from the surviving callus masses of susceptible lines repeatedly exposed to the culture filtrate. Regenerated plants reportedly showed improved resistance levels of 15-92% higher than the original susceptible lines (Chahal and Sharma, 1988).

Inheritance of Resistance

Inheritance of ergot resistance is relatively complex, and can involve cytoplas-

mic × nuclear interactions (Thakur et al., 1993; Yadav, 1994). Resistance is recessive and polygenically controlled (Thakur et al., 1983b). Ergot-resistant hybrids, therefore, cannot be bred unless both parents possess the same resistant genes (Virk et al., 1987; Rai and Thakur, 1995). Of course, this can be expected to reduce heterosis for grain and stover yield. More detailed genetic studies are needed to better understand the nature and inheritance of ergot resistance.

Breeding Methods

Attempts were made to incorporate resistance in both the seed parent and pollinator, using backcross breeding procedures (Andrews et al., 1985a). Besides ergot-resistant composites, efforts are being made to develop ergot-resistant male-sterile lines to permit hybrid seed production in ergot-prone environments and for possible development of ergot-resistant hybrids. Using pedigree breeding methods, ergot resistance has been incorporated into an agronomically elite inbred background, and ergot-resistant male-sterile lines have been bred at ICRISAT Asia Center. Three of the promising male-sterile lines (ICMA 91113, ICMA 91114, and ICMA 91115) were evaluated for their hybrid production potential using ergot-resistant pollinator parents. In a preliminary yield trial comparing several hybrids based on ergot-resistant male-sterile lines to the commercial hybrid ICMH 423, the hybrids yielded 11-17% more grain and time to 50% flowering was similar or earlier (Thakur et al., 1993). Unfortunately, most of these hybrids were both susceptible to ergot and male-sterile (the resistance donor used in both parents was a maintainer of the A_1 cytoplasmic-genic male-sterility system).

Three synthetic varieties (ICMS 8031, ICMS 8032 and ICMS 8034), constituted using ergot-resistant inbred lines, compared well for grain yield with a popular open-pollinated commercial variety WC-C75 and hybrid BJ 104 at ICRISAT Asia Center, but were much later to flower. The synthetic varieties showed 12-15% ergot severity compared with 24% in WC-C75 and 54% in BJ 104 (Thakur et al., 1993). The ICRISAT Ergot Resistant Composite (ERC), constituted in 1985 using 52 ergot-resistant populations, is one of the most productive composites in its maturity class and is being used at ICRISAT Asia Center as a source population in crosses to form a new late composite.

Rust

Rust, caused by *Puccinia substriata* var. *indica* or *P. penniseti* (some nomenclatue controversy exists), is among the important pearl millet diseases. It occurs in almost all areas where pearl millet is cultivated. Where pearl millet is traditionally grown for grain, rust has usually been considered a minor problem because its late appearance — generally after the grain-filling stage — causes little or no loss in grain yield. However, the disease has been observed as early as the seedling stage and, in such cases, substantial reduction in grain and fodder yield and quality can occur (Ramakrishnan, 1963; Monson et al., 1986; Wilson et al., 1991b; Wilson et al., 1995; S.D. Singh, unpublished). In India this disease has become increasingly important for several reasons, including large-scale cultivation of high-yielding but rust-susceptible cultivars, large-scale seed production during the

summer season, and overlapping crops — particularly in Tamil Nadu and Gujarat. Worldwide this disease is probably of greatest importance on multicut forage hybrids where even low rust severities can result in substantial losses of digestible dry matter yield (Wilson et al., 1991b). Recent virulence changes in rust populations in the southeastern United States (Wilson, 1993; Tapsoba and Wilson, 1996) are complicating the introduction of pearl millet grain hybrids in that region, and have clearly demonstrated the potential importance of this disease on genetically uniform susceptible cultivars. Recent reviews provide more information (Pathak and Choudhary, 1991; Singh and King, 1991; Wilson et al., 1993a).

Screening Techniques

Because rust has not been considered of great economic significance in most pearl millet production areas, little research has been done to develop screening techniques in India or Africa. In India, screening against rust has been based largely on testing materials at locations where rust occurs in severe form every year if sowing is done at the appropriate time. However, these known field inoculation procedures have been compared at ICRISAT:

- urediniospores from earlier-sown infector rows;
- spraying urediniospores on 25-40 day old crops; and
- spreading of uredinia-bearing leaves among 25-30 day old test plants.

Spraying urediniospores twice, at 25 and 35 days after sowing, gave the best results (S.D. Singh, unpublished; Singh and King, 1991). Both field and greenhouse screening procedures are used at the Coastal Plain Experiment Station in Tifton, Georgia (Wilson, 1994).

Resistance Sources

In recent years, several efforts have been made to identify resistance sources for pearl millet rust. Suresh (1969) was the first to report high levels of rust resistance in open-pollinated cultivars. He identified PT 826/4 and PT 829/4 as highly resistant and PT 829/3, PT 833/2, PT 833/4, PT 835/6, and PT 829/8 as tolerant.

At ICRISAT Asia Center, a large number of gene bank accessions have been evaluated for their reaction to downy mildew and rust, and many with resistance to these two diseases have been identified (Singh, 1990). Most of these promising materials have been tested at four to seven locations for six to seven years in India. Five lines, 700481-21-B (ICML 17), IP 537 B (ICML 18), IP 11776 (ICML 19), IP 2084 (ICML 20), and P 24 (ICML 21), have shown a high degree of rust resistance across all hot spot locations and over years (Singh et al., 1990b). ICML 11, a selection from 7042 (IP 2696), a landrace from Chad, has been identified as highly rust-resistant (Singh et al., 1987a). Dominant resistance is also available in ICRISAT-bred seed parents 852A and 852B, based on a Maiwa cross, as well as ICMA 96222 and ICMB 96222 that are derived from a cross involving 852B (K.N. Rai, 1996, personal communication).

Slow-rusting genotypes have been reported in pearl millet (Hanna et al., 1981;

Singh and Sokhi, 1983; Hanna and Wells, 1993). Slow rusting has been transferred into the genetic background of Tift 23DB from a tall, short-day sensitive introduction from Senegal, and the product released as Tift $89D_2$ (Hanna and Wells, 1993). ICMP 451 (Anand Kumar et al., 1995) appears to be another elite inbred source of this character and QTL mapping of it is underway (C.T. Hash, unpublished). Additional sources of partial resistance recently evaluated by Wilson (1994) include a number of elite inbred pollinators from India, suggesting that perhaps rust is important for grain and stover yield even there.

A wild relative of pearl millet, *P. americanum* (L.) Leeke subsp *monodii*, was reported immune to rust (Hanna et al., 1982), and this resistance also has been transferred into an agronomically elite seed parent background by backcrossing (Hanna et al., 1987). Once commercially deployed, a single dominant gene that controlled much of this resistance was rapidly overcome (Wilson, 1993). Several other groups also have reported resistance to pearl millet rust (Rao and Rao, 1983; Govindarajan et al., 1984). A number of potentially new sources of resistance to this disease have been identified in landraces collected from Burkina Faso (Wilson et al., 1989a, 1990, 1991a). Plants from selected landraces were selfed six times and S_6 seed from rust-resistant plants bulked to form Tift #3 and Tift #4 germplasm (Wilson and Burton, 1991), which were released as sources of rust resistance genes.

In summary, many more sources of various types of rust resistance are available now than even a decade ago. Deployment of sources in resistant cultivars has begun, and the pathogen has demonstrated its ability to rapidly evolve in response to host plant resistance. Characterization of genes controlling these resistances is now needed to permit their effective and sustainable utilization.

Inheritance of Resistance

In nearly all cases so far reported, pearl millet rust resistance was demonstrated to be controlled by a single dominant gene, except in one entry, 700481-23-2, in which complementary gene action was reported (Sokhi et al., 1987). The gene identified by Andrews et al. (1985b) was designated as Rpp_1, while that identified by Hanna et al. (1985) was designated Rr_1. Resistance conferred by Rr_1 was rapidly overcome following its deployment in single-cross grain and forage hybrids in the southeastern United States (Wilson, 1993).

Breeding Methods

Conventional pedigree (Hanna, 1993), pedigree-bulk, and backcross breeding are being used in segregating materials produced from crosses of agronomically elite, rust-susceptible hybrid parents and donors with stable resistance. However, this does not appear to be sufficient to achieve durable resistance in single-cross forage hybrids. For pedigree and pedigree-bulk breeding, three-way crosses [(susceptible parent × resistant donor) × susceptible parent] appear to offer the most efficient way to quickly recover desirable recombinants. Researchers at Tifton, Georgia, are developing molecular markers for genes contributing to rust resistance to provide breeders greater op-

tions in resistance gene deployment (Ozias-Akins, 1996, personal communication). Once available, such markers should facilitate breeding of pearl millet hybrids heterogeneous for rust resistance (Wilson et al., 1993b). Such hybrids, similar in concept to multiline varieties of self-pollinated crops, might provide a more effective strategy for rust resistance gene deployment than deploying individual resistances serially or pyramiding resistance genes in genetically uniform hybrids (Wilson et al., 1993a). This is conceptually identical to options discussed above for using markers in breeding for resistance to downy mildew.

Pyricularia Leaf Spot

Magnaporthe grisea is the teleomorph of the complex group of Ascomycete fungi composed of interfertile anamorphs [*Pyricularia grisea* (Cooke) Sacc. = *Pyricularia oryzae*] that cause *Pyricularia* leaf spot or blast of rice and/or other gramineae, including pearl millet. Because of the importance of rice blast, this fungus and the diseases it causes are among the best studied in the world (Zeigler et al., 1994, Skinner et al., 1993). Pearl millet forage yield losses due to leaf spots or blight in the U.S. are caused primarily by this pathogen (Wilson and Gates, 1993). The pathogen is highly variable, with many strains specialized in their host range to varying degrees (e.g., Urashima, 1993). Some, but not all, isolates from pearl millet can infect rice, and vice versa. However, unlike rust and downy mildew causal organisms, this pathogen does not obligately pass through a sexual stage in order to survive from season to season. Therefore genetic recombination of virulences occurs less frequently. This suggests breeding for durable resistance to *Pyricularia* leaf spot in pearl millet might be easier than breeding for durable resistance to rust or downy mildew, but rice breeders have not found durable blast resistance easy to achieve.

Screening Techniques and Sources of Resistance

Field and greenhouse screening techniques (Wilson and Hanna, 1992a) are used, similar to those outlined above for rust. Both landraces and wild relatives of pearl millet have served as sources of resistance to this disease (Hanna et al., 1987; Wilson et al., 1989a; Wilson et al., 1991a; Wilson and Hanna, 1992b). Tift 186 (Burton, 1977) and its d_2 dwarf backcross derivative Tift 383 (Burton, 1980) were described as resistant to *Pyricularia* at the time they were registered.

Inheritance of Resistance

Host reaction to leaf spot caused by *Pyricularia grisea* in pearl millet is not affected by cytoplasm (Wilson and Hanna, 1992a). The wild accession of *P. americanum* subsp *monodii* that served as the resistance donor in breeding Tift $85D_2B_1$ carried three independent dominant resistance genes (Hanna and Wells, 1989), but backcrossing and selection for resistance successfully transferred only one. Four landrace accessions from Burkina Faso have been shown to each have a single dominant gene for leaf spot resistance that is inherited independently of that in Tift $85D_2B_1$ (Wilson et al., 1989b).

Breeding Methods

Hanna et al. (1987) bred *Pyricularia*-resistant Tift $85D_2B_1$ by backcrossing one

of three independent dominant resistance genes (Hanna and Wells, 1989) from a wild grassy accession of *P. americanum* subsp *monodii* from Senegal into the genetic background of Tift $23D_2B_1$. Tift $85D_2A_1$ was then bred by backcrossing Tift $85D_2B_1$ to Tift $23D_2A_1$. Tift $85D_2A_1$ is the female parent of the leaf spot and rust resistant dwarf forage hybrid 'Tifleaf 2' (Hanna et al., 1988). *Pyricularia* resistance of Tift $90D_2E_1$ was then bred by pedigree selection in progeny from a cross involving Tift $85D_2B_1$ as donor (Hanna, 1993). Hybrids heterogeneous for their *Pyricularia* resistance genes may be required for durable resistance.

Potential of Emerging Technologies

Several emerging technologies may contribute significantly to improvement of host plant resistance to pearl millet diseases. These include somaclonal variants arising from tissue culture, *in vitro* selection, genetic transformation, dihaploid production from cultured anthers, and use of saturated genetic linkage maps for marker-assisted selection (MAS). The first two of these areas will require reliable systems for plantlet regeneration from cultures of protoplasts, cells, or callus.

While many published reports claim successful tissue culture of pearl millet — including regeneration of plants from protoplasts (Vasil and Vasil, 1980), downy mildew resistant plants from *in vitro* culture of infected tissues (Prasad et al., 1984), and ergot-resistant plants following *in vitro* culture and selection (Sharma and Chahal, 1990) — these techniques are not yet being applied to any great extent in public-sector breeding programs. Tissue culture has been used to generate highly resistant somaclones of Tift 23B, 81B, and 843B at the Downy Mildew Research Laboratory of the All India Coordinated Pearl Millet Improvement Project in Mysore. Resistance of these somaclones has remained stable under epiphytotic conditions through the fifth seed generation (AICPMIP, 1995). Perhaps breeders are slow to adopt this technology because of the genotype specificity of regeneration systems, or the cost and complexity of these procedures may simply be too great.

Genetic transformation may rely upon tissue culture systems, but other approaches also are available. Once again there have been no applications of this technology to pearl millet improvement, although here the difficulties associated with these procedures in cereals (Smith and Hood, 1995) are certainly an explanation. Further, a few reports describe methods for producing plantlets from cultured pearl millet anthers or microspores (Bui-Dang-Ha and Pernès, 1982), but there are no reports of practical or strategic application of this technique to problems in pearl millet improvement. In each of these emerging areas it appears "it has been much more difficult and expensive than anticipated to extrapolate the results of these efforts [research on 'model systems'] to other studies, particularly those of an applied nature" and "this predicament is ... a failure of science in general to recognize that the eventual relevance of any research should receive attention in order for society to benefit" (Helentjaris, 1992). For pearl millet to take advantage of future transgenic applications, further work in these areas is essential, with the expressed objective of obtaining an ap-

plied result useful to farmers; otherwise, the research resources should be applied elsewhere.

In contrast, the considerable potential of MAS (Tanksley et al., 1989; Lande and Thompson, 1990; Paterson et al., 1991; Gale and Witcombe, 1992; Lande, 1992; Miklas et al., 1992) as a tool for pearl millet improvement has been recognized. A saturated genetic linkage map (Figure 3), based upon molecular markers, has been developed (Liu et al., 1994a, 1994b; Devos et al., 1995) as was done previously (Smith et al., 1989) for its close relative napiergrass (*P. purpureum*). Markers are being identified to assist breeders in selecting individual plants carrying specific resistance alleles of interest (Jones, 1994; Jones et al., 1994, 1995). This map was initially based on restriction fragment length polymorphism (RFLP) markers, since these can reveal an almost unlimited number of polymorphisms (Botstein et al., 1980) and can be used directly to tag loci controlling traits of interest for MAS. Additional markers (including isozymes, other proteins, other types of DNA markers, and field-scorable morphological traits) are being added to the map's basic framework. Further, a skeleton map based on sequence tagged sites (STS — markers based on the polymerase chain reaction with less stringent requirements for large quantities of good quality DNA) has been developed (Money et al., 1994) that should reduce the cost of transferring this map to other breeding populations. While more recent estimates (Hospital et al., 1992) of the gains from MAS compared to conventional methods suggest that only two generations can be gained during backcross transfer of a single dominant gene that can be effectively selected using conventional procedures, the advantages of this breeding tool will be considerably greater when working with quantitative traits or characters whose expression is affected by factors in the genetic, biotic, or physical environment.

Due to the high costs of current RFLP-based mapping technologies, MAS can now be used in applied breeding programs only to follow segregation of important genes contributing to expression of characters of high economic value and that are difficult or expensive to reliably measure. For more extensive future use, MAS systems will have to be less expensive and more efficient than alternative methods of selecting for the character of interest; PCR-based markers (RAPDs, STS, SCARS and SSRs) offer this possibility. Otherwise MAS will not be very useful to breeders and should not be used except in constructing novel genetic tools such as contig lines (i.e., contiguous chromosome segment substitution lines) and chromosome substitution lines. When considered better than all other alternatives, markers can be used effectively in identifying desirable segregants. Individual segregants are characterized for their marker genotypes at loci previously identified as tightly linked to genes of interest in the parent(s). Selection is then made among these segregants for the best combination of marker genotypes. Ideally, selection might be for individuals having marker alleles of a resistance donor parent in portions of the genome tightly linked to resistance gene(s) of interest, and marker alleles of an agronomically elite parent in the remainder of their genomes.

In the case of pearl millet, greenhouse or laboratory screening for downy mildew

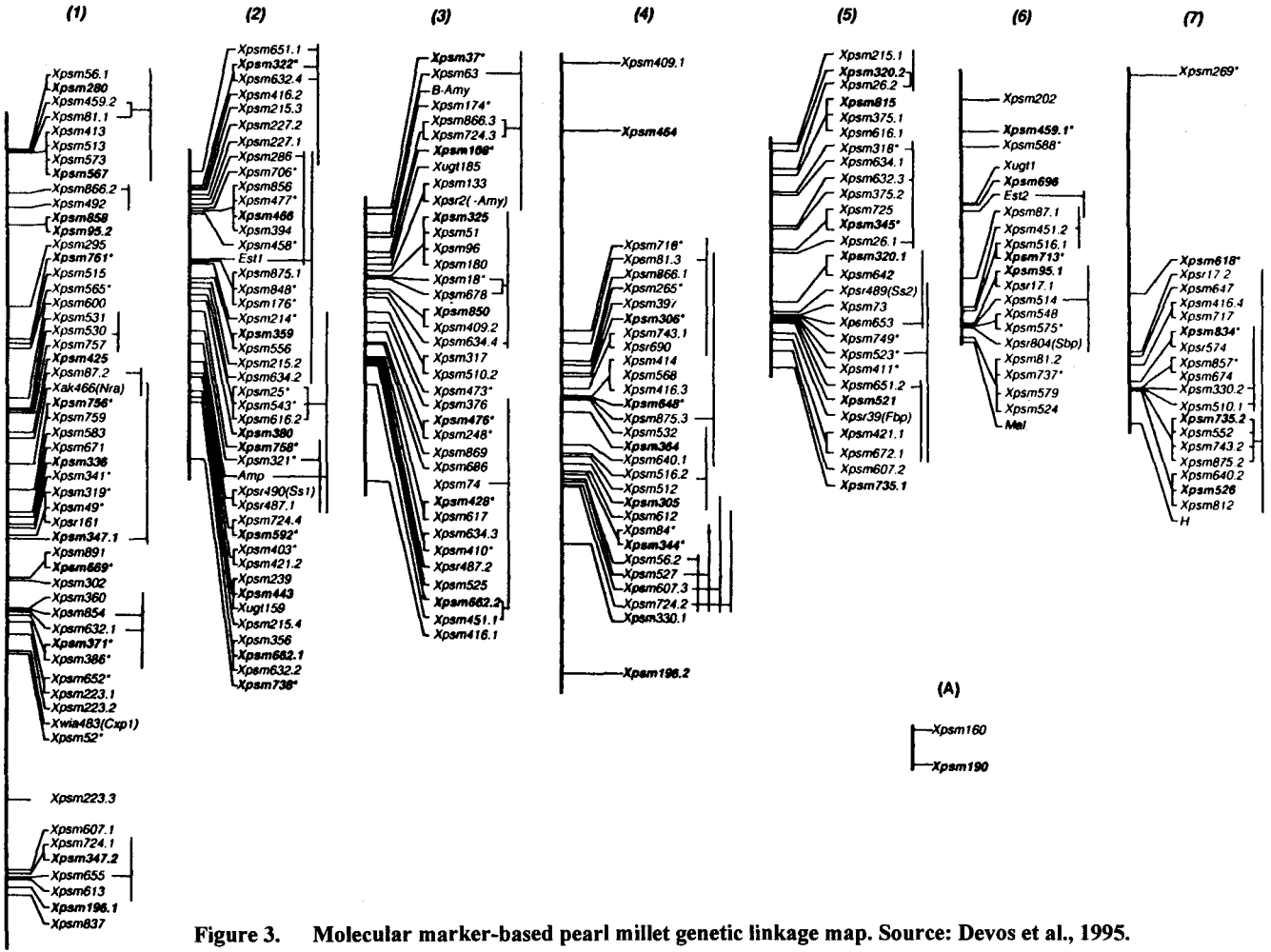


Figure 3. Molecular marker-based pearl millet genetic linkage map. Source: Devos et al., 1995.

resistance is relatively inexpensive and efficient against a single pathogen isolate or a few isolates from a single country. However, to pyramid resistances from different sources or select for resistance effective in other geographical areas, available alternatives are either costly or inefficient and slow. Conventional screening in such cases requires either multilocational evaluation of progenies against a range of *S. graminicola* populations, or evaluation against a multinational range of pathogen isolates in a region where *S. graminicola* and any potential hosts are of no economic importance. Considerable time is required to produce the progenies to be tested, send them to appropriate testing locations, evaluate them there, and summarize the evaluation results before actually selecting among them. However, once this is done, MAS methods should be much faster and less expensive, and should offer higher heritabilities for resistance (nearly 1.0) than routine multilocational screening against pathogen populations.

The first molecular marker to be used extensively in breeding for disease resistance in plants was the allozyme variant *Apse*, which was found closely linked to a gene for nematode resistance in tomato (Rick and Fobes, 1974). More recent examples of application of this tool to crop improvement include detection of RAPD markers linked to a gene for nematode resistance in sugar beet (Uphoff and Wricke, 1992) and use of RFLP markers to localize genes contributing to resistance to blast in rice (Yu et al., 1991; McCouch et al., 1994), phytophthora in soybean (Diers et al., 1992), and downy mildew in lettuce (Michelmore et al., 1991). The latter two diseases are caused by fungi similar to that inciting pearl millet downy mildew, where RFLP markers for resistance also have been identified (Jones et al., 1994, 1995; Hash et al., 1995). Techniques using the polymerase chain reaction (PCR) have been used to confirm transfer of DNA and stable disease resistance from wild to cultivated barley (Xu and Kasha, 1992). RFLP markers have been used to show:

- less than expected recovery of recurrent parent genome following backcross transfer of disease resistance genes in maize (Ma, 1991),
- that the downy mildew-resistant pearl millet inbreds 81B (Anand Kumar et al., 1984) and ICMB 841 (Singh et al., 1990c) are probably derived from outcrosses rather than their published pedigrees (Liu et al., 1992), and
- that recombination rates are similar in male and female gametes of pearl millet (Busso et al., 1995), but that segregation distortion is much higher among male gametes than among female gametes.

Development of bulk segregant analysis (Michelmore et al., 1991), similar in many ways to the concept of near-isogenic populations (Burton and Wells, 1981), has dramatically reduced the time and expense required to identify molecular markers for new resistance genes of large effect. However, it can miss genes of smaller effect (E.S. Jones, 1996, personal communication). Molecular markers also are being used to characterize populations of pearl millet pathogens (Sastry et al., 1995). Overall, it looks like molecular markers, and MAS, will become important tools for pearl millet breeders in the decade ahead.

Conclusions

This review has presented many details of breeding for disease resistance in pearl millet. The conclusions are similar to those of previous reviews in this area: success requires an effective screening method (often with inoculation and always with a satisfactory assessment scale), heritable variation, and knowledge of the genetic structure of the host and pathogen populations. Without all these factors, a disease resistance breeding program is not likely to be able to provide durable resistance. Initiating a breeding program to improve pearl millet disease resistance before these necessary components are in place would simply be a waste of resources.

Many opportunities are now available to pearl millet breeders: many resistance genes, lots of genetic variability, and good screening systems for the most important diseases. Needed now are refinement of procedures and reduction of the time and expense of combining adequate levels of disease resistance with tolerance or resistance to other stress factors in pearl millet production environments and high yield potential. At its simplest, marker-assisted selection offers breeders a new array of disease-screening methods with maximized heritabilities. Although not a universal solution to all breeding problems, MAS offers tremendous opportunities to breed for important characters — and combinations of characters — that are otherwise difficult and expensive to assess. Most important, this new kit of breeding tools offers scope for new strategies (e.g., in resistance gene deployment) that would be impractical using conventional approaches.

References

AICPMIP. 1995. Annual Report. Promotion of research and development efforts: Hybrids of pearl millet. Downy Mildew Research Laboratory, University of Mysore, Mysore, India.

Anand Kumar, K., R.P. Jain, and S.D. Singh. 1983. Downy mildew reactions in pearl millet lines with and without cytoplasmic male sterility. Plant Disease 67:663-665.

Anand Kumar, D.J. Andrews, R.P. Jain, and S.D. Singh. 1984. ICMA-1 *(sic)* and ICMB-1 *(sic)* pearl millet parental lines with A1 cytoplasmic-genic male sterility system. Crop Science 24:832.

Anand Kumar, K., K.N. Rai, D.J. Andrews, B.S. Talukdar, S.D. Singh, A.S. Rao, P.P. Babu, and B.P. Reddy. 1995. Registration of ICMP 451 parental line of pearl millet. Crop Science 35:605.

Andrews, D.J. 1987. Breeding pearl millet grain hybrids. p. 83-109. *In* W.P. Feistritzer and A.F. Kelly (eds.) Hybrid seed production of selected cereal oil and vegetable crops. FAO Plant Production and Protection Paper 82. Food and Agriculture Organization of the United Nations, Rome, Italy.

Andrews, D.J., and K. Anand Kumar. 1982. Induction of downy mildew resistance in pearl millet male-sterile Tift 23D2. Mutation Breeding Newsletter 20:1-3.

Andrews, D.J., S.B. King, J.R. Witcomb *(sic)*, S.D. Singh, K.N. Rai, R.P. Thakur, B.S. Talukdar, S.B. Chavan, and P. Singh. 1985a. Breeding for disease resistance and yield in pearl millet. Field Crops Research 11:241-258.

Andrews, D.J., K.N. Rai, and S.D. Singh. 1985b. A single dominant gene for rust resistance in pearl millet. Crop Science 25:565-566.

Bajaj, Y.P.S., P.S. Phul, and S.K. Sharma. 1980. Differential tolerance of tissue culture of pearl millet to ergot extract. Indian Journal of Experimental Biology 18:429-432.

Basavaraju, R., K.M. Safeeulla, and B.R. Murty. 1981. Genetic variance and heritability for resistance to downy mildew in pearl millet. Indian Journal of Genetics and Plant Breeding 41:137-143.

Botstein, D., R.L. White, M.H. Skolnick, and R.W. Davis. 1980. Construction of a genetic linkage map in man using restriction fragment length polymorphisms. American Journal of Human Genetics 32: 314-331.

Bui-Dang-Ha, D., and J. Pernès. 1982. Androgenesis in pearl millet. I. Analysis of plants obtained from microspore culture. Zeitshrift für Pflanzenzüchtung 108:317-327.

Burton, G.W. 1977. Registration of Gahi 3 pearl millet (Reg. No 40). Crop Science 17:345-346.

Burton, G.W. 1980. Registration of pearl millet inbred Tift 383 and Tifleaf 1 pearl millet (Reg. PL 8 and Reg. No. 60). Crop Science 20:293.

Burton, G.W., and H.D. Wells. 1981. Use of near-isogenic host populations to estimate the effect of three foliage diseases on pearl millet forage yield. Phytopathology 71:311-333.

Busso, C.S., C.J. Liu, C.T. Hash, J.R. Witcombe, K.M. Devos, J.M.J. de Wet, and M.D. Gale. 1995. Analysis of recombination rate in female and male gametogenesis in pearl millet (*Pennisetum glaucum*) using RFLP markers. Theoretical and Applied Genetics 90:242-246.

Chahal, S.S., and S.B. Sharma. 1988. Development of new ergot resistant pearl millet plants through *in vitro* procedure. p. 260. *In* Abstracts of Papers, 5th International Congress of Plant Pathology, Kyoto, Japan, 20-27 Aug 1988. Commemorative Association for the Japan World Exposition, Kyoto, Japan.

Chahal, S.S., K.S. Gill, P.S. Phul, and N.B. Singh. 1981. Effectiveness of recurrent selection for generating ergot resistance in pearl millet. SABRAO Journal 13:184-186.

Chahal, S.S., V.P. Rao, and R.P. Thakur. 1985. Variation in morphology and pathogenicity in *Claviceps fusiformis*, the causal agent of pearl millet ergot. Transactions of the British Mycological Society 84:325-332.

Chahal, S.S., K. Kumar, and G.S. Gill. 1986. Identity and variation in two isolates of *Moesziomyces penicillariae*, the causal organism of pearl millet smut. Plant Disease Research 1:59-64.

Chavan, S.B., R.P. Thakur, and K.P. Rao. 1988. Inheritance of smut resistance in pearl millet. Plant Disease Research 3:192-197.

Dass, S., R.L. Kapoor, R.S. Paroda, and D.S. Jatasra. 1984. Gene effects for downy mildew (*Sclerospora graminicola*) resistance in pearl millet. Indian Journal of Genetics and Plant Breeding 44:280-285.

Deswal, D.P., and O.P. Govila. 1994. Genetics of resistance to downy mildew (*Sclerospora graminicola*) in pearl millet (*Pennisetum glaucum*). Indian Journal of Agricultural Sciences 64:661-663.

Devos, K.M., T.S. Tittaway, C.S. Busso, M.D. Gale, J.R. Witcombe, and C.T. Hash. 1995. Molecular tools for the pearl millet nuclear genome. International Sorghum and Millets Newsletter 36:64-66.

Diers, B.W., L. Mansur, J. Imsande, and R.C. Shoemaker. 1992. Mapping phytophthora resistance loci in soybean with restriction fragment length polymorphism markers. Crop Science 32:377-383.

Fähr, S., M.M. Messmer, A.E. Melchinger, M. Lee, and W.L. Woodman. 1993. Graphical genotype of maize inbred B86 revealed by RFLPs. Plant Breeding 110:29-34.

Gale, M.D., and J.R. Witcombe. 1992. DNA markers and marker-assisted applications in plant breeding, with particular reference to pearl millet breeding. p. 323-332. *In* J.P. Moss (ed.) Biotechnology and crop improvement in Asia. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Gill, K.S., P.S. Phul, and B.L. Bharadwaj. 1979. Induction of resistance to downy mildew by irradiation in male-sterile lines of pearl-millet. p. 43. *In* Programme and abstracts: Symposium on the role of induced mutations in crop improvement, September 10-13, 1979. Department of Genetics, Osmania University, Hyderabad, India.

Gill, K.S., S.S. Chahal, and P.S. Phul. 1980. Strategy to develop ergot resistance in pearl millet. p. 159-161. *In* V.P. Gupta and J.L. Minocha (eds.) Trends in genetical research in *Pennisetums*. Punjab Agricultural University, Ludhiana, India.

Gill, K.S., P.S. Phul, L.N. Jindla, and N.B. Singh. 1981. Pb 204A—a new downy mildew resistant male-sterile line in pearl millet. Seeds & Farms 7:19-20.

Govindarajan, K., C. Nagarajan, T.S. Raveendran, M.M. Prasad, and N. Shanmugam. 1984. A new source of resistance to pearl millet rust disease. Madras Agricultural Journal 71:210.

Hanna, W.W. 1993. Registration of pearl millet parental lines Tift 8677 and A_1/B_1 Tift $90D_2E_1$. Crop Science 33:1119.

Hanna, W.W., and L.E. Towill. 1995. Long-term pollen storage. Plant Breeding Reviews 13:179-207.

Hanna, W.W., and H.D. Wells. 1989. Inheritance of *Pyricularia* leaf spot resistance in pearl millet. Journal of Heredity 80:145-147.

Hanna, W.W., and H.D. Wells. 1993. Registration of parental line Tift $89D_2$, rust resistant pearl millet. Crop Science 33:361-362.

Hanna, W.W., H.D. Wells, and G.W. Burton. 1981. Resistance to rust (*Puccinia substriata* var *indica*) in pearl millet. Phytopathology 71:878-879.

Hanna, W.W., H.D. Wells, and G.W. Burton. 1982. Transfer of disease immunity from a wild subspecies to pearl millet. Agronomy Abstracts 1982:69.

Hanna, W.W., H.D. Wells, and G.W. Burton. 1985. Dominant gene for rust resistance in pearl millet. Journal of Heredity 76:134.

Hanna, W.W., H.D. Wells, and G.W. Burton. 1987. Registration of pearl millet inbred parental

lines, Tift 85D2A1 and Tift 85D2B1. Crop Science 27:1324-1325.

Hanna, W.W., H.D. Wells, G.W. Burton, G.M. Hill, and W.G. Monson. 1988. Registration of 'Tifleaf 2' pearl millet. Crop Science 28:1023.

Hash, C.T., and J.R. Witcombe. 1994. Pearl millet mapping populations at ICRISAT. p. 69-75. *In* J.R. Witcombe and R.R. Duncan (eds.) Use of molecular markers in sorghum and pearl millet breeding for developing countries. Overseas Development Administration, London, U.K.

Hash, C.T., and J.R. Witcombe. 1996. Resistance gene deployment strategies for open-pollinated crops using marker-asssited selection. Downy Mildews Newsletter No. 9: 8.

Hash, C.T., G.P. Cavan, F.R. Bidinger, C.J. Howarth, and S.D. Singh. 1995. Downy mildew resistance QTLs from a seedling heat tolerance mapping population. International Sorghum and Millets Newsletter 36: 66-67.

Helentjaris, T.G. 1992. RFLP analyses for manipulating agronomic traits in plants. p. 356-372. *In* H.T. Stalker and J.P. Murphy (eds.) Plant breeding in the 1990s. C·A·B International, Oxon, U.K.

Hospital, F., C. Chevalet, and P. Mulsant. 1992. Using markers in gene introgression breeding programs. Genetics 132:1199-1210.

Jain, A.K., S.K. Tripathi, and S.N.P. Verma. 1988. Screening of pearl millet varieties for ergot disease resistance under natural condition. (in Hindi) Bharitaya Krishi Anusandhan Patrika 5:58-60.

Jones, E. 1994. Mapping quantitative trait loci for resistance to downy mildew in pearl millet. Ph.D. thesis, School of Biological Sciences, University of Wales, Bangor, U.K. 191 pp.

Jones, E.S., J.R. Witcombe, C.T. Hash, S.D. Singh, M.D. Gale, D.S. Shaw, and C.J. Liu. 1994. Mapping QTLs controlling resistance to downy mildew in pearl millet and their application in plant breeding programmes. p. 76-79. *In* J.R. Witcombe and R.R. Duncan (eds.) Use of molecular markers in sorghum and pearl millet breeding for developing countries. Overseas Development Administration, London, U.K.

Jones, E.S., C.J. Liu, M.D. Gale, C.T. Hash, and J.R. Witcombe. 1995. Mapping quantitative trait loci for downy mildew resistance in pearl millet. Theoretical and Applied Genetics 91:448-456.

Kataria, R.P., H.P. Yadav, C.R. Beniwal, and M.S. Narwal. 1994. Genetics of incidence of downy mildew (*Sclerospora graminicola*) in pearl millet (*Pennisetum glaucum*). Indian Journal of Agricultural Sciences 64:664-666.

Khairwal, I.S., S. Singh, and Om Prakash. 1986. Smut reactions of pearl millet lines and hybrids with and without cytoplasmic male sterility. Indian National Science Academy B52:751-754.

King, S.B. 1976. Downy mildew and ergot of pearl millet. p. 97-101. *In* R.J. Williams (ed.) Proceedings of the consultants' group meetings on downy mildew and ergot of pearl millet, 1-3 October 1975. International Crops Research Institute for the Semi-Arid Tropics, Begumpet, Hyderabad, A.P. 500 016, India.

Kumar, A., and H.C. Arya. 1983. On taxonomy of the fungus causing ergot disease of pearl millet in India. p. 287-279. *In* H.C. Arya, N. Sankhla, M.N. Tewari, N.S. Shekhawat, and S.P. Purohit (eds.) Advancing frontiers in plant sciences, 26-30 Nov 1983, Jodhpur, Rajasthan, India. Scientific Publishers, Jodhpur, India.

Lande, R. 1992. Marker-assisted selection in relation to traditional methods of plant breeding. p. 437-451. *In* H.T. Stalker and J.P. Murphy (eds.) Plant breeding in the 1990s. C·A·B International, Oxon, U.K.

Lande, R., and R. Thompson. 1990. Efficiency of marker-assisted selection in the improvement of quantitative traits. Genetics 124:743-736.

Liu, C., J. Witcombe, T.S. Pittaway, M. Nash, C.T. Hash, and M. Gale. 1992. Restriction fragment length polymorphism in pearl millet, *Pennisetum glaucum*. p. 233-241. *In* Complexes d'Espèces, Flux de Gènes, et Resources Génétiques des Plantes. Colloque International en Hommage à Jean Pernès, Professeur à l'Université d'Orsay, Paris XI. Lavoisier-Technique et Documentation, Cachan Cedex, France.

Liu, C.J., J.R. Witcombe, C.T. Hash, C.S. Busso, T.S. Pittaway, M. Nash, and M.D. Gale. 1994a. Construction and application of RFLP-based genetic maps in pearl millet. p. 57-64. *In* J.R. Witcombe and R.R. Duncan (eds.) Use of molecular markers in sorghum and pearl millet breeding for developing countries. Overseas Development Administration, London, U.K.

Liu, C.J., J.R. Witcombe, T.S. Pittaway, M. Nash, C.T. Hash, C.S. Busso, and M.D. Gale. 1994b. An RFLP-based genetic map of pearl millet (*Pennisetum glaucum*). Theoretical and Applied Genetics 89:481-487.

Louvel, D. 1982. Breeding millet (Pennisetum) for disease resistance. Centre National de Recherches Agronomiques, Bambey, Senegal.

Loveless, A.R. 1967. *Claviceps fusiformis* sp. nov., the causal agent of an aglactia of sows. Transactions of the British Mycological Society 50:15-18.

Ma, Y. 1991. "Near-isogenic line" revisited by DNA markers in maize. Botanical Bulletin of Academia Sinica 32:179-186.

Madan Mohan, K.G. Mukerji, and Kavita Rani. 1978. Diseases of bajra. Seeds & Farms 4:35-38.

Mantle, P.G. 1992. Ergot disease of pearl millet: Toxicological significance and a mechanism for disease escape. p. 129-132. *In* W.A.J. de Milliano, R.A. Frederiksen, and G.D. Bengston (eds.) Sorghum and millets diseases: A second world review. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

McCouch, S.R., R.J. Nelson, J. Tohme, and R.S. Zeigler. 1994. Mapping of blast resistance genes in rice. p. 167-186. *In* S.A. Leong, and P.S. Teng (eds.) Rice blast disease. R.S. Zeigler, CAB International, Oxon, U.K.

Mehta, P.R. 1966. Introductory remarks. p. 37-39. *In* Bulletin of the Indian Phytopathological society No. 3. Proceedings of the symposia on diseases of rice, maize, sorghum and millets, held at Chandigarh on 1st & 2nd January, 1966. The India Phytopathological Society, New Delhi, India.

Michelmore, R.W., I. Paran, and R.V. Kesseli. 1991. Identification of markers linked to disease-resistance genes by bulked segregant analysis: A rapid method to detect markers in specific genomic regions by using segregating populations. Proceedings of the National Academy of Science (US) 88:9828-9832.

Miklas, P.N., S.D. Haley, J.R. Stavely, and J.D. Kelly. 1992. Pyramiding resistance to bean rust using molecular markers. Agronomy Abstracts 107.

Money, T.A., C.J. Liu, and M.D. Gale. 1994. Conversion of RFLP markers for downy mildew resistance in pearl millet to sequence-tagged sites. p. 65-68. *In* J.R. Witcombe and R.R. Duncan (eds.) Use of molecular markers in sorghum and pearl millet breeding for developing countries. Overseas Development Administration, London, U.K.

Monson, W.G., W.W. Hanna, and T.P. Gaines. 1986. Effects of rust on yield and quality of pearl millet forage. Crop Science 26:637-639.

Murty, B.R. 1973. Mutation breeding for resistance to downy mildew in Pennisetum. Mutation Breeding Newsletter No. 2.

Murty, B.R. 1974. Mutation breeding for resistance to downy mildew and ergot in *Pennisetum* and to *Ascochyta* in chickpea. p. 89-100. *In* Induced mutations for disease resistance in crop plants. International Atomic Energy Agency, Vienna, Austria.

Murty, B.R. 1977. Breeding Procedures in Pearl-Millet (*Pennisetum typhoides* S. & H.). Indian Council of Agricultural Research, New Delhi, India.

Murty, B.R., S.R. Thakur, N. Prakash, S.L. Mehta, and S.T. Bhakta. 1983. Mutation breeding for downy mildew resistance in pearl millet: Nucleo-cytoplasmic interactions in disease resistant lines. p. 119-124. *In* Induced mutations for disease resistance in crop plants II. International Atomic Energy Agency, Vienna, Austria.

Paterson, A.H., S.D. Tanksley, and M.E. Sorrells. 1991. DNA markers in plant improvement. Advances in Agronomy 46:39-90.

Pathak, V.N., and S.L. Choudhary. 1991. Pearl millet rust. Indian Journal of Mycology and Plant Pathology 21:138-147.

Phookan, A.K. 1987. Studies on pearl millet smut with special reference to pathogenic variability, inheritance of resistance, and chemical control. Ph.D. thesis, Haryana Agricultural University, Hisar, India.

Pokhriyal, S.C., and H.K Jain. 1974. Breeding for disease resistance in pearl millet. Mutation Breeding Newsletter No. 3:8-9.

Pokhriyal, S.C., K.V. Unnikrishnan, B. Singh, Ramdass, and R.R. Patil. 1976. Combining ability of downy mildew resistant lines in pearl millet. Indian Journal of Genetics and Plant Breeding 36:403-409.

Prasad, B., M.S. Prabhu, and C. Shantamma. 1984. Regeneration of downy mildew resistant plants from infected tissues of pearl millet (*Pennisetum americanum*) cultured *in vitro*. Current Science 53:816-817.

Rai, K.N., and K. Anand Kumar. 1994. Pearl millet improvement at ICRISAT—an update. International Sorghum and Millets Newsletter 35:1-29.

Rai, K.N., and W.W. Hanna. 1990. Morphological changes in an inbred line of pearl millet selected for downy mildew resistance. Journal of Genetics & Breeding 44:199-202.

Rai, K.N., and C.T. Hash. 1993. A new source of cytoplasmic-nuclear male sterility in pearl millet. p. 67-68. *In* Annual report 1992 (Semi-formal publication). Cereals Program, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Rai, K.N., and R.P. Thakur. 1995. Ergot reaction of pearl millet hybrids affected by fertility restoration and genetic resistance of parental lines. Euphytica 83:225-231.

Rai, K.N., B.S. Talukdar, S.D. Singh, A.S. Rao, A.M. Rao, and D.J. Andrews. 1994. Registration of ICMP 423 parental line of pearl millet. Crop Science 34:1430.

Ramakrishnan, T.S. 1963. Diseases of millets. Indian Council of Agricultural Research: New Delhi, India. pp. 156.

Rao, A.P., and M.P.P. Rao. 1983. Resistance to rust in bajra germplasm. Andhra Agricultural Journal 30:57-58.

Rattunde, H.F.W., and J.R. Witcombe. 1993. Recurrent selection for increased grain yield and resistance to downy mildew in pearl millet. Plant Breeding 110:63-72.

Raut, R.N., B. Sharma, S.C. Pokhriyal, M.P. Singh, and H.K. Jain. 1973. Induced mutations: Some basic findings and applied results. Indian Journal of Genetics and Plant Breeding 34A:311-315.

Rick, C.M., and J.F. Fobes. 1974. Association of an allozyme with nematode resistance. Reports of the Tomato Genetics Cooperative 24:25.

Sastry, J.G., W. Ramakrishna, S. Sivaramakrishnan, R.P. Thakur, V.S. Gupta, and P.K. Ranjekar. 1995. DNA fingerprinting detects genetic variability in the pearl millet downy mildew pathogen (*Sclerospora graminicola*). Theoretical and Applied Genetics 91:856-861.

Sedcole, T.R. 1977. Number of plants necessary to recover a trait. Crop Science 17:667-668.

Sharma, S.B., and S.S. Chahal. 1990. Development of regenerants from pearl millet cell lines resistant to culture filtrate of *Claviceps fusiformis*. Plant Disease Research 5:175-181.

Shinde, R.B., F.B. Patil, and R.A. Sangave. 1984. Resistance to downy mildew in pearl millet. Journal of the Maharashtra Agricultural University 9:337-338.

Siddiqui, M.R., and I.D. Khan. 1973. Renaming *Claviceps microcephala*, ergot fungus on *Pennisetum typhoides* in India as *Claviceps fusiformis*. Transactions of the Mycological Society of Japan 14:195-198.

Singh, B.B., and S.S. Sokhi. 1983. Effect of rust of millet on yield components. Indian Phytopathology 36:89-91.

Singh, F., R.K. Singh, R.M. Singh, and R.B. Singh. 1978. Genetic analysis of downy mildew (*Sclerospora graminicola*) resistance in pearl millet [*Pennisetum typhoides* (Burm.) S. & H.). Zeitschrift für Pflanzenzüchtung 81:54-59.

Singh, F., R.M. Singh, R.B. Singh, and R.K. Singh. 1980. Genetic studies of downy mildew resistance in pearl millet. p. 171-172. *In* V.P. Gupta and J.L. Minocha (eds.) Trends in genetical research of *Pennisetums*. Wesley Press, Ludhiana, India.

Singh, P., K.N. Rai, J.R. Witcombe, and D.J. Andrews. 1988. Population breeding methods in pearl millet improvement (*Pennisetum americanum*). L'Agronomie Tropicale 43:185-202.

Singh, S.D. 1990. Sources of resistance to downy mildew and rust in pearl millet. Plant Disease 74:871-874.

Singh, S.D. 1992. New sources of resistance. p. 33. *In* Annual report 1991 (Semi-formal publication). Cereals Program, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Singh, S.D., and R. Gopinath. 1985. A seedling inoculation technique for detecting downy mildew resistance in pearl millet. Plant Disease 69:582-584.

Singh, S.D., and S.B. King. 1988. Recovery resistance to downy mildew in pearl millet. Plant Disease 72:425-428.

Singh, S.D., and S.B. King. 1991. Pearl millet rust: Present status and future research needs. International Journal of Tropical Plant Disease 9:35-52.

Singh, S.D., and B.S. Talukdar. 1996. Recovery resistance to downy mildew in pearl millet parental lines ICMA 1 and ICMB 1. Crop Science 36:201-203.

Singh, S.D., and R.J. Williams. 1980. The role of sporangia in the epidemiology of pearl millet downy mildew. Phytopathology 70:1187-1190.

Singh, S.D., D.J. Andrews, and K.N. Rai. 1987a. Registration of ICML 11 rust resistant pearl millet germplasm. Crop Science 27:367-368.

Singh, S.D., S.L. Ball, and D.P. Thakur. 1987b. Problems and strategies in the control of downy mildew. p. 161-172. *In* J.R. Witcombe and S.R. Beckerman (eds.) Proceedings of the international pearl millet workshop, 7-11 April 1986, ICRISAT Center, India. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Singh, S.D., S.B. King, and P. Malla Reddy. 1990a. Registration of five pearl millet germplasm sources with stable resistance to downy mildew. Crop Science 30:1164.

Singh, S.D., S.B. King, and P. Malla Reddy. 1990b. Registration of five pearl millet germplasm sources with stable resistance to rust. Crop Science 30:1165.

Singh, S.D., P. Singh, K.N. Rai, and D.J. Andrews. 1990c. Registration of ICMA 841 and ICMB 841 pearl millet parental lines with A1 cytoplasmic-genic male sterility system. Crop Science 30:1378.

Singh, S.D., W.A.J. de Milliano, E. Mtisi, and P. Chingombe. 1990d. Brown leaf spot of pearl millet caused by *Bipolaris urochloae* in Zimbabwe. Plant Disease 74:931-932.

Singh, S.D., P. Singh, D.J. Andrews, B.S. Talukdar, and S.B. King. 1992. Reselection of a pearl millet cultivar utilizing residual variability for downy mildew reaction. Plant Breeding 109:54-59.

Singh, S.D., S.B. King, and J. Werder. 1993a. Downy mildew disease of pearl millet. Information Bulletin no. 37. International Crops Research Institute for the Semi-Arid Tropics: Patancheru, A.P. 502 324, India.

Singh, S.D., Sanam Lal, and S. Pande. 1993b. The changing scenario of maize, sorghum, and pearl millet diseases. p. 130-139. *In* H.C. Sharma and M. Veerabhadra (eds.) Pests and pest management in India—The changing scenario. Plant Protection Association of India, (NPRTI), Ra-

jendranagar, Hyderabad, Andhra Pradesh 500 030, India.

Singh, S.D., G. Alagarswamy, B.S. Talukdar, and C.T. Hash. 1994. Registration of ICML 22 photoperiod insensitive, downy mildew resistant pearl millet germplasm. Crop Science 34:1421.

Skinner, D.Z., A.D. Budde, M.L. Farman, J.R. Smith, H. Leung, and S.A. Leong. 1993. Genome organization of *Magnaporthe grisea*: genetic map, electrophoretic karyotype, and occurrence of repeated DNAs. Theoretical and Applied Genetics 87:545-557.

Smith, R.H., and E.E. Hood. 1995. *Agrobacterium tumefaciens* transformation of monocotyledons. Crop Science 35:301-308.

Smith, R.L., M.K.U. Chowdhury, and C.S. Shank. 1989. Use of restriction fragment length polymorphisms (RFLP) markers in genetics and breeding of napiergrass. Proceedings of the Soil and Crop Science Society of Florida 48:13-18.

Sokhi, S.S., H.S. Bariana, and P.P.S. Pannu. 1987. A note on genetics of resistance in pearl millet against rust. Indian Phytopathology 40:423-424.

Subba Rao, K.V., and R.P. Thakur. 1983. *Tolyposporium penicillariae*, the causal agent of pearl millet smut. Transactions of the British Mycological Society 81:597-603.

Suresh, S. 1969. A preliminary study on the reactions of pearl millet, *Pennisetum typhoides* (S & H), inbreds and open pollinated lines to 'green ear' and 'rust' diseases. Madras Agricultural Journal 56:88-90.

Talukdar, B.S., and S.D. Singh. 1993. Stability and heritability for downy mildew resistance in two pearl millet pollinators. p. 70-71. *In* Annual report 1992 (Semi-formal publication). Cereals Program, International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Talukdar, B.S., P.P. Prakash Babu, A.M. Rao, C. Ramakrishna, J.R. Witcombe, S.B. King, and C.T. Hash. 1997. Registration of ICMP 85410 dwarf, downy mildew resistant, restorer germplasm line of pearl millet. Crop Science 37: In press.

Talukdar, B.S., S.D. Singh, and C.T. Hash. 1994. Breeding for resistance to diseases in pearl millet. p. 176-185. *In* H.G. Singh, S.N. Mishra, T.B. Singh, Hari Har Ram and D.P. Singh (eds.) Crop breeding in India. International Book Distributing Company, Lucknow, U.P. 226 004, India.

Tanksley, S.D., N.D. Young, A.H. Paterson, and M.W. Bonierbale. 1989. RFLP mapping in plant breeding: New tools for an old science. Bio/Technology 7:257-264.

Tapsoba, H., and J.P. Wilson. 1996. Pathogenic variation in *Puccinia substriata* var. *indica* in the southeastern United States and screening for resistance in pearl millet germ plasm. Plant Disease 80:395-397.

Thakur, R.P., and S.S. Chahal. 1987. Problems and strategies in the control of ergot and smut in pearl millet. p. 147-160. *In* J.R. Witcombe and S.R. Beckerman (eds.) Proceedings of the international pearl millet workshop, 7-11 April 1986, ICRISAT Center, India. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Thakur, R.P., and S.B. King. 1988a. Ergot disease of pearl millet. Information Bulletin no. 24. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Thakur, R.P., and S.B. King. 1988b. Smut disease of pearl millet. Information Bulletin no. 25. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Thakur, R.P., and S.B. King. 1988c. Registration of four ergot resistant germplasms of pearl millet. Crop Science 28:382. Errata—Crop Science 29:1102.

Thakur, R.P., and S.B. King. 1988d. Registration of six smut resistant germplasms of pearl millet. Crop Science 28:382-383.

Thakur, R.P., and R.J. Williams. 1980. Pollination effects on pearl millet ergot. Phytopathology 70:80-84.

Thakur, R.P., R.J. Williams, and V.P. Rao. 1982. Development of ergot resistance in pearl millet. Phytopathology 72:406-408.

Thakur, R.P., K.V. Subba Rao, and R.J. Williams. 1983a. Evaluation of a new field screening technique for smut resistance in pearl millet. Phytopathology 73:1255-1258.

Thakur, R.P., B.S. Talukdar, and V.P. Rao. 1983b. Genetics of ergot resistance. p. 737. *In* Abstracts of contributed papers of the XV International Congress of Genetics, 12-21 Dec 1983, New Delhi. Part 2. Oxford & IBH, New Delhi, India.

Thakur, R.P., V.P. Rao, and R.J. Williams. 1984. The morphology and disease cycle of ergot caused by *Claviceps fusiformis* in pearl millet. Phytopathology 74:201-205.

Thakur, R.P., V.P. Rao, R.J. Williams, S.S. Chahal, S.B. Mathur, N.B. Pawar, S.D. Nefade, H.S. Shetty, Govind Singh, and S.G. Bangar. 1985. Identification of stable resistance to ergot in pearl millet. Plant Disease 69:982-985.

Thakur, R.P., K.V. Subba Rao, R.J. Williams, S.C. Gupta, D.P. Thakur, S.D. Nafade, N.V. Sundaram, J.A. Frowd, and E.J. Guthrie. 1986. Identification of stable resistance to smut in pearl millet. Plant Disease 70:38-41.

Thakur, R.P., S.D. Singh, and S.B. King. 1988. Registration of four populations of pearl millet germplasm with multiple disease resistance.

Crop Science 28:381-382. Errata—Crop Science 29:1102.

Thakur, R.P., S.B. King, K.N. Rai, and V.P. Rao. 1992a. Identification and utilization of smut resistance in pearl millet. Research Bulletin no. 16. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Thakur, R.P., K.G. Shetty, and S.B. King. 1992b. Selection for host-specific virulence in asexual populations of *Sclerospora graminicola*. Plant Pathology 41:626-632.

Thakur, R.P., K.N. Rai, S.B. King, and V.P. Rao. 1993. Identification and utilization of ergot resistance in pearl millet. Research Bulletin no. 17. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Tyagi, C.S., and Iqbal Singh. 1989. Genetics of downy mildew resistance in pearl millet. Bhartiya Krishi Anusandhan Patrika 4:24-30.

Uphoff, H., and G. Wricke. 1992. Random amplified polymorphic DNA (RAPD) markers in sugar beet (*Beta vulgaris* L.): Mapping the genes for nematode resistance and hypocotyl color. Plant Breeding 109:168-171.

Urashima, A.S. 1993. Host range, mating type, and fertility of *Pyricularia grisea* from wheat in Brazil. Plant Disease 77:1211-1216.

Vasil, V., and K. Vasil. 1980. Isolation and culture of cereal protoplasts. II. Embryogenesis and plantlet formation from protoplasts of *Pennisetum americanum*. Theoretical and Applied Genetics 56:97-100.

Virk, D.S., S.S. Chahal, and B.K. Mangat. 1987. Factorial analysis for ergot resistance in pearl millet. Crop Improvement 14:153-156.

Wells, H.D., W.W. Hanna, and G.W. Burton. 1987. Effects of inoculation and pollination on smut development in near-isogenic lines of pearl millet. Phytopathology 77:293-296.

Weltzien R., E., and S.B. King. 1995. Recurrent selection for downy mildew resistance in pearl millet. Plant Breeding 114:308-312.

Williams, R.J. 1976. Proceedings of the consultants' group meetings on downy mildew and ergot of pearl millet, 1-3 October 1975. International Crops Research Institute for the Semi-Arid Tropics, Begumpet, Hyderabad, A.P. 500 016, India.

Williams, R.J. 1984a. Disease resistance in pearl millet. Review of Tropical Plant Pathology 1:245-296.

Williams, R.J., and D.J. Andrews. 1983. Breeding for disease and pest resistance in pearl millet. FAO Plant Protection Bulletin 31:136-158.

Williams, R.J., S.D. Singh, and M.N. Pawar. 1981. An improved field screening technique for downy mildew resistance in pearl millet. Plant Disease 65:239-241.

Willingale, J., and P.G. Mantle. 1985. Stigma constriction in pearl millet, a factor influencing reproduction and disease. Annals of Botany 56:109-115.

Willingale, J., and P.G. Mantle. 1987. Stigmatic constriction in pearl millet following infection by *Claviceps fusiformis*. Physiological and Molecular Plant Pathology 30:247-257.

Willingale, J., P.G. Mantle, and R.P. Thakur. 1986. Post-pollination stigmatic constriction, the basis of ergot resistance in selected lines of pearl millet. Phytopathology 76:536-539.

Wilson, J.P. 1993. Identification of virulence in *Puccinia substriata* var. *indica* to Rr_1 in pearl millet. Plant Disease 77:100.

Wilson, J.P. 1995. Mechanisms associated with the *tr* allele contributing to reduced smut susceptibility of pearl millet. Phytopathology 85:966-969.

Wilson, J.P. 1994. Field and greenhouse evaluation of pearl millet for partial resistance to *Puccinia substriata* var. *indica*. Plant Disease 78:1202-1205.

Wilson, J.P., and G.W. Burton. 1991. Registration of Tift #3 and Tift #4 rust resistant pearl millet germplasms. Crop Science 31:1713.

Wilson, J.P., and R.N. Gates. 1993. Forage yield losses in hybrid pearl millet due to leaf blight caused primarily by *Pyricularia grisea*. Phytopathology 83:739-743.

Wilson, J.P., and W.W. Hanna. 1992a. Effects of gene and cytoplasm substitutions in pearl millet on leaf blight epidemics and infection by *Pyricularia grisea*. Phytopathology 82:839-842.

Wilson, J.P. and W.W. Hanna. 1992b. Disease resistance in wild *Pennisetum* species. Plant Disease 76:1171-1175.

Wilson, J.P., G.W. Burton, H.D. Wells, J.D. Zongo, and I.O. Dicko. 1989a. Leaf spot, rust and smut resistance in pearl millet landraces from central Burkina Faso. Plant Disease 73:345-349.

Wilson, J.P., H.D. Wells, and G.W. Burton. 1989b. Inheritance of resistance to *Pyricularia grisea* in pearl millet accessions from Burkina Faso and inbred Tift 85DB. Journal of Heredity 80:499-501.

Wilson, J.P., G.W. Burton, J.D. Zongo, and I.O. Dicko. 1990. Diversity among pearl millet landraces collected in central Burkina Faso. Crop Science 30:40-43.

Wilson, J.P., G.W. Burton, J.D. Zongo, and I.O. Dicko. 1991a. Disease resistance and morphologic traits of pearl millet landraces from southern Burkina Faso. Crop Science 31:641-645.

Wilson, J.P., R.N. Gates, and W.W. Hanna. 1991b. Effect of rust on yield and digestibility of pearl millet forage. Phytopathology 81:233-236.

Wilson, J.P. W.W. Hanna, and K. Bondari. 1993a. Directed use of germplasm resources for breeding rust resistant pearl millet. Plant Pathol., (Trends in Agric. Sci.) 1:67-74.

Wilson, J.P., W.W. Hanna, and R.N. Gates. 1993b. Stability of forage yield and quality in pearl millet hybrids heterogeneous for rust resistance. Euphytica 72:163-170.

Wilson, J.P., W.W. Hanna, G. Gascho, and D.M. Wilson. 1995. Pearl millet grain yield loss from rust infection. p. 54-56 *In* I.D. Teare, J. Woodruff, and D.L. Wright (eds.) Proceedings: First national grain pearl millet symposium. Rural Development Center, Coastal Plain Experiment Station: Tifton, Georgia, U.S.A.

Witcombe, J.R., M.N.V.R. Rao, and W.R. Lechner. 1995. Registration of 'ICMV 88908' pearl millet. Crop Science 35:1216-1217.

Witcombe, J.R., M.N.V.R. Rao, B.S. Talukdar, S.D. Singh, and A.M. Rao. 1996. Registration of ICMR 312 pearl millet topcross pollinator germplasm. Crop Science 36:471.

Xu, J., and K.J. Kasha. 1992. Transfer of a dominant gene for powdery mildew resistance and DNA from *Hordeum bulbosum* into cultivated barley (*H. vulgare*). Theoretical and Applied Genetics 84:771-777.

Yadav, R.P. 1974. Inheritance of smut resistance in pearl millet. Agra University Journal of Res. Sci. 23:37-39.

Yadav, O.P. 1994. Influence of A_1 cytoplasm in pearl millet. Plant Breeding Abstracts 64:1375-1379.

Yadav, O.P. 1996. Downy mildew incidence of pearl millet hybrids with different male-sterility inducing cytoplasms. Theoretical and Applied Genetics 92:278-280.

Yadav, O.P., I.S. Khairwal, and S. Singh. 1992. Smut severity of pearl millet hybrids with male sterile and male fertile cytoplasm. Euphytica 64:139-142.

Yadav, O.P., V.K. Manga, and G.K. Gupta. 1993. Influence of A_1 cytoplasmic substitution on downy mildew incidence in pearl millet. Theoretical and Applied Genetics 87:558-560.

Yu, Z.H., D.J. Mackill, J.M. Bonman, and S.D. Tanksley. 1991. Tagging genes for blast resistance in rice via linkage to RFLP markers. Theoretical and Applied Genetics 81:471-476.

Zeigler, R.S., S.A. Leong, and P.S. Teng (eds.). 1994. Rice Blast disease. CAB International, Oxon, UK.

Discussion

Session V - Breeding for Resistance to Biotic Stress
Session Chair: John Witcombe
Rapporteurs - Larry Claflin and Neil Muller

B.S. Rana - There is no adequate resistance to earhead bug in germplasm. The lines reported tolerant are late with lax panicle which adds to escape mechanism. Do you think that biotechnology may help in this direction to evolve resistance for this type of bug?

R.G. Henzell - If, in fact, there is no useful HPR to earhead bug in sorghum, then, yes, there are very likely "alien" genes for resistance that could be transformed into sorghum.

Swarnlata Kaul - You have mentioned antixenosis and antibiosis mechanisms of resistance? How do you select for these individual mechanisms? Are the genes governing these the same or different?

R.G. Henzell - The genetics of the possible different resistance mechanisms are not known. Currently, there is no attempt to select on the basis of different mechanisms, largely because, by far, the major mechanism is oviposition antixenosis.

B.S. Rana - The resistance breeding involves germplasm screening, development of usable sources and recombination of resistance in improved background. The Indian program has achieved encouraging results on these aspects and especially for enhancing resistance in high yielding background. For example — shootfly resistant varieties were earlier introduced and now a resistant and high yielding hybrid (CSH15R) was released last year with a number of desirable traits required for post rainy season. Parental lines of this and other promising hybrids are bred in the Indian program. We have also developed charcoal rot resistant lines with shootfly resistance with round grain better than E36-1, resistance source. Another illustration can be given. Last year, the International Grain Mold Resistance Nursery was evaluated by us along with our breeding material. There was continuous rain for almost 15 days on a matured crop. All of the entries of the International Nursery, even red grain entries, succumbed to molds but a number of our breeding lines stood the mold. One of the red grain selection from our breeding nursery handled by S.L. Kaul was found almost immune. The Program has developed lines with cross resistance based on multilocation multiyear testing. I therefore urgently urge the speakers of this session to make use of this voluminous information available with the Indian program so that both material and information can be shared with the International community.

Stan King - Do you see IAC helping NARS in West Africa with marker-assisted selection (MAS) for downy mildew resistance and if so, how?

Tom Hash - Yes.The ICRISAT-Cambridge Laboratory - University of Wales

team has identified resistance QTLs effective against individual pathogen populations from Western and Central Africa. These are being backcrossed individually into a common genetic background that will be distributed as near-isogenic differential lines to pathologists via the International Pearl Millet Downy Mildew Virulence Nursery. These differentials will allow pathologists in West African NARS to monitor virulence in their local populations of *Sclerospora graminicola*. This will allow identification of resistance genes that will be effective against these pathogen populations. ICRISAT scientists at IAC can then assist in using MAS to incorporate these resistances into appropriate pearl millets identified by NARS scientists.

Yu Li - Genetic mapping (gene tagging) strategies appear to be different for qualitative and quantitative traits. I was wondering which strategies should be used. If different maps for the same pest or disease resistance exist, how do breeding programs use them?

Tom Hash - Gene tagging strategies need not be different for qualitative and quantitative traits—the methods based on skeleton maps and trait evaluation of complete mapping populations are appropriate for both and can tag genes controlling the traits of interest, regardless of their mode of inheritance or type of genetic effects. These methods also provide opportunities for tagging genes for characters other than the primary target trait in a population. Unfortunately, this is not the case for bulk-segregant analysis. Although potentially less expensive in the short term, bulk-segregant analysis does not provide as great of opportunities to build genetic tools for future use. Therefore, I would recommend use of skeleton map transfer to a complete mapping population based on parents that differ for several important target traits. Once genes controlling traits of interest have been tagged, the breeder need not really be concerned with the mode of inheritance of the target trait. Marker-assisted selection using these tags (which will have heritabilities very close to 1.0) can even be conducted in locations or environments where the target trait is not expressed. Breeders can use markers for resistances from different resistance sources to rapidly and efficiently identify segregants with multiple resistances. Different maps provide breeders with a wider range of possible linked polymerphic markers that can be tried when trying to transfer resistances in crosses with parents not previously involved in mapping studies.

Issoufou Kollo Abdourhamane - Downy mildew is a minor problem and has always been. If ICRISAT would like to help West Africa, more emphasis should be placed on other pests or diseases such as *Striga hermonthica* which are more important in this area. Downy mildew is not now important but it can become so in the future. We need to do things that can help African breeders develop resistant material.

Tom Hash - Downy mildew is not yet an important yield constraint on pearl millet in Africa because of the genetically heterogenous cultivars — both landraces and improved OPVs — used there by farmers. However, attempts to increase yield and adaptation to abiotic stress by exploiting heterosis could allow downy mildew to become a major problem in

Africa, as occurred in India when single-cross hybrids were introduced. This is a clear case where genetic uniformity dramatically increases genetic vulnerability of the crop.

When we have identified effective sources of resistance to *Striga* and insect pests such as head miner, then the molecular tools currently being developed with pearl millet downy mildew resistance as a model system can be used to breed genetic components of integrated management systems for these major pearl millet production constraints in West Africa. ICRISAT and other agencies are making substantial research investments to develop the improved screening systems for host plant resistance to *Striga* and head miner that should eventually allow identification of suitable resistance sources.

David Andrews - Though downy mildew is a 'minor' problem in West Africa, it has the potential to become a 'huge' problem if the historic equilibrium between host resistance genes and the pathogen is unwittingly disturbed (by breeders) by the introduction and cultivation of new cultivars with insufficient durable resistance.

David Andrews - Is there any evidence of host plant resistance to ergot in sorghum that would be effective in cms hybrids?

R.P. Thakur - Yes, sorghum lines resistant to ergot have been identified, but their effectiveness in cms hybrids needs to be determined.

Admasu Melake Berhan - The number of mapped RAPD markers are low. Why are only a few markers useful? If this research is repeated, would you use other markers?

C.W. Magill - RAPD s are the easiest and quickest way to identify DNA sequences linked to resistance genes and I would definitely use them again. Relatively close markers were identified for each "R" gene attempted. The inability to place many on the map may be bad luck. With BAC's, inverse PCR, and other methods for identifying flanking sequences we expect to construct maps in a routine fashion. We are willing to change when better techniques become available.

Yu Li - Genes which control head smut resistance to Race 5 have been mapped. The predominant races in China are 2 and 3 and, therefore should new markers be generated and, in this case, would any of the maps that have been generated be of any use in China?

C.W. Magill - The meristematic resistance (recessive) is functional against all races. In general, it appears that there are clusters of resistance genes and mapping may locate several. The problem of pathogenic variability is one reason we try to identify tags from different sources of resistance. It will be much easier to identify recombinant progeny that confer resistance to two or more races or pathogens using DNA tests than testing each generator against both races or pathogens.

Gebisa Ejeta - Your results showed that a simple RAPD marker for resistance to a *Fusarium* sp. is a simple gene for resistance to a simple uniform organism. Is this plausible?

C.W. Magill - Almost any answer is feasible. The petri plate tests were made using a single culture of *Fusarium* isolated from infected seeds, therefore, it could be specific to this strain. Conversely, the frequency of spontaneously developing fungi on test plates were recorded. In general, but not 100%, the *Fusarium* resistant ones were low in incidence of other fungi.

Peter Esele - Only one probe was mapped in Sureño. What is the possible significance of that simple probe in breeding for resistance to grain mold?

C.W. Magill - If "theory" holds up, a probe could identify this region of DNA in any hybrid. If closely related to a gene that contributes to resistance then it may apply "across the board." If cross specific, the probe would be useful only in the Sureño X susceptible cross. We hope and expect the former is true.

Koushik Seetharaman - 1) Is there any evidence that a line with multiple resistance traits have lower yield than lines with fewer traits? 2) Is this factored into the definition of yield potential as we know it now?

R.P. Thakur - 1) Generally yes, but the yield level can be improved while using multiple resistance traits in a resistance breeding program. 2) Question not clear to me, probably the answer is same as for 1).

Oscar Rodriguez - Have you been aware of any new race or shift to a new race of leaf blight on sorghum?

R.P. Thakur - No, there is no such evidence of a new race of the leaf blight pathogen, although there is an indication of existence of different ecotypes.

Terry Wheeler - What is the problem with sprinkler irrigation to induce disease, since it is regulatable?

J.W. Stenhouse - Sprinkler irrigation readily achieves surface wetness but is less effective in maintaining consistently high air humidities, particularly when ambient humidity levels are low. To maintain adequate humidities, we must apply large quantities of irrigation water, leading to very high grain mold pressure. Misting, with frequent application of small amounts of water, is much more effective in controlling air humidity and can be adjusted to manipulate disease pressure to all dissemination between lines with intermediate and low levels of resistance.

David Andrews - You should clarify that some other resistance components are needed to go along with long glumes in obtaining resistance and/or avoidance of grain molds. In the *membranaceum* subgroup, for instance, you would need in addition to the long glumes a moderate level of surface (pericarp/outer endosperm layer) mold resistance, and threshability.

J.W. Stenhouse - Yes, we are thinking of the guinea glume types that normally go with hard grain as well. Personally, I don't think there is any scope for using the membranaceum sorghums because of the threshing problems associated with them.

Session VI

Breeding for Resistance to Moisture Stress/Drought

Session Chair: Abraham Blum

Rapporteurs: Mike Gilbert and Issoufou Kapran

Speakers:

C.J. Howarth
D.T. Rosenow
H.T. Nguyen
R.C. Muchow
V. Mahalakshmi

Seedling Survival of Abiotic Stress:Sorghum and Pearl Millet

Catherine J. Howarth*, Eva Weltzien Rattunde,
Francis R. Bidinger, David Harris

Abstract

This paper reviews the responses of sorghum and pearl millet seedlings to abiotic stress and considers the implications for crop production, particularly with respect to the arid and semi-arid tropics. The growing season in much of this area is characterized by high temperatures, high evaporative demand, unreliable and irregular rainfall, and soils of poor structure, low fertility, and low water-holding capacity. Poor seedbed preparation and inadequate sowing methods can increase the likelihood of abiotic stresses developing. Such conditions result in reduced seedling growth rates, injury, and ultimately mortality during the germination and seedling emergence stages. The wide range of causes of stand failure means there is no single solution. For a given target environment it is necessary to define the reasons for a stand establishment problem and to understand the requirements of the farmer. Genetic variation for seedling stress tolerance, however, has been shown to exist in both sorghum and pearl millet. Screening techniques have been developed and used in population improvement programs and in identification of molecular markers linked to the thermotolerance trait. Potential thus exists for the genetic improvement of these crops for survival of abiotic stresses to complement solutions brought about by changes in agronomic practice.

Failure of seedling establishment is a major factor limiting crop production. This paper discusses the main environmental causes of crop establishment failure in pearl millet [*Pennisetum glaucum* (L.) R.Br.] and sorghum [*Sorghum bicolor* (L.) Moench] in the semi-arid and arid tropics. Rain-fed agriculture predominates in these areas of South Asia and the Sahelian-Sudanian zone of Africa; sorghum characteristically is grown where mean annual rainfall is 600-1000 mm and pearl millet in areas where the mean is from 200-600 mm per year (Sivakumar et al., 1984; Spencer and Sivakumar, 1987). The mean rainfall is not only low (and evaporative demand high), but also very erratic in its distribution through the growing season and variable between years. Pearl millet is one of the most drought- and heat-tolerant grasses to be domesticated. Its progenitors were desert grasses found on the southern fringes of the Sahara; pearl millet landraces have grown in the Sahel since 3000 BC and probably in India for some 2500 years (Brunken et al., 1977; de Wet et al., 1992). It is still primarily grown by subsistence farmers under harsh environmental conditions where no other cereal can be grown; it may be described as a crop of necessity rather than choice (Bidinger and Parthasarathy Rao, 1990).

Catherine J. Howarth, Institute of Grassland and Environmental Research, Plas Gogerddan, Aberystwyth, Dyfed SY23 3EB, UK; Eva Weltzien Rattunde and Francis R. Bidinger, ICRISAT, Patancheru, Andhra Pradesh 502324 India; David Harris, Centre for Arid Zone Studies, University of Wales, Bangor, Gwynedd LL57 2UW UK. *Corresponding author.

If pearl millet and sorghum are already so well-adapted, why is improvement needed? It is not so much a question of improving the adaptive range, but of improving yield and yield stability under conditions of abiotic stress. Improvements in yield and yield potential are well documented (e.g., Harinarayana, 1987), but these are expressed under favorable conditions quite unlike those encountered in many farmers' fields in marginal environments. Adaptation to specific environmental stresses is a larger determinant of crop yield than is yield potential in these environments (Evans, 1993). Both improved hybrids and open pollinated varieties do not necessarily possess the stress tolerance of landraces with low grain yield potential and may have no yield advantage over traditional landraces in these harsh environments (Weltzien and Witcombe, 1989; Bidinger et al., 1994; Yadav, 1994).

Although modern cultivars account for more than 50% of the area sown to pearl millet in India as a whole, adoption has been limited in locations with lower and less reliable rainfall. In these areas pearl millet is the staple cereal crop and mean yields remained unchanged from 1956 to 1988 at 144 kg ha^{-1}, with grain yields of 50 kg/ha not uncommon (Gupta et al., 1992). An increasing unpredictability of yield also was found over this time period. In sub-Saharan Africa, adoption of improved pearl millet cultivars is limited for many reasons (Bidinger and Parthasarathy Rao, 1990; Ouendeba et al., 1995). Plant breeders may be unfamiliar with the specific production conditions and thus may have set inappropriate goals (Haugerud and Collinson, 1990). Farmers in Rajasthan indicated that they have not adopted improved cultivars of pearl millet primarily because of poor grain yield in low rainfall years (Kelley et al., 1996). Poor stand establishment and straw yield were other important characteristics (Weltzien et al., 1996). Genetic advances achieved under favorable conditions and using elite breeding material do not necessarily benefit farmers in marginal areas (Weltzien and Fischbeck, 1990). Research with pearl millet has shown it is possible, however, to produce landrace-based topcross hybrids that combine the stress adaptation of indigenous landraces with the improved yield potential from elite male sterile lines (Bidinger et al., 1994; Yadav and Manga, 1995). Considerable genetic diversity exists for survival of abiotic stresses, no doubt due to selection in response to local environmental conditions. Blum and Sullivan (1986) found that landraces of sorghum and millet that had evolved in dry regions tended to be more drought-resistant than races that evolved in humid regions. Today as human populations increase, traditional management practices and landraces may not be sufficient.

Abiotic Causes of Crop Establishment Failure

Despite the level of environmental adaptation that both pearl millet and sorghum display, failure of seedling establishment due to abiotic stress is a major problem. The environmental sensitivity of a plant varies throughout its development (Levitt, 1980), but the seedling phase is particularly vulnerable. The growing season in much of the arid and semi-arid tropics is characterized by high temperatures, high radiation, high evaporative demand, unreliable and irregular

rainfall, and soils of poor structure, low fertility, and low water-holding capacity. Farmers sow on the first significant rainfall of the monsoon. The timing of the onset of the monsoon is variable both in time and place (Van Oosterom et al., 1996). A hot, dry seedbed environment during crop establishment is very likely, with soil surface temperatures often greater than 55°C (Figure 1; Gupta, 1986; Hoogmoed and Klaij, 1990; Peacock et al., 1993).

For a farmer in such environments, the timing of seed sowing is critical. If the farmer chooses to sow after an early, pre-monsoon rain, seedbed conditions will be extremely hot and there is high risk of low moisture availability without subsequent substantial rainfall. Delay in sowing after rain can result in insufficient moisture in the seed zone of the soil for germination to take place. In the sandy soils of many pearl millet growing environments, moisture depletion to less than 2% often occurs three to four days after rainfall (Peacock et al., 1990). If sowing is delayed until a later rain, chances of drought stress at the end of the season are greater. Van Oosterom et al. (1996) calculated the probability of an 80-day rainy season based on sowing date, and found if planting were

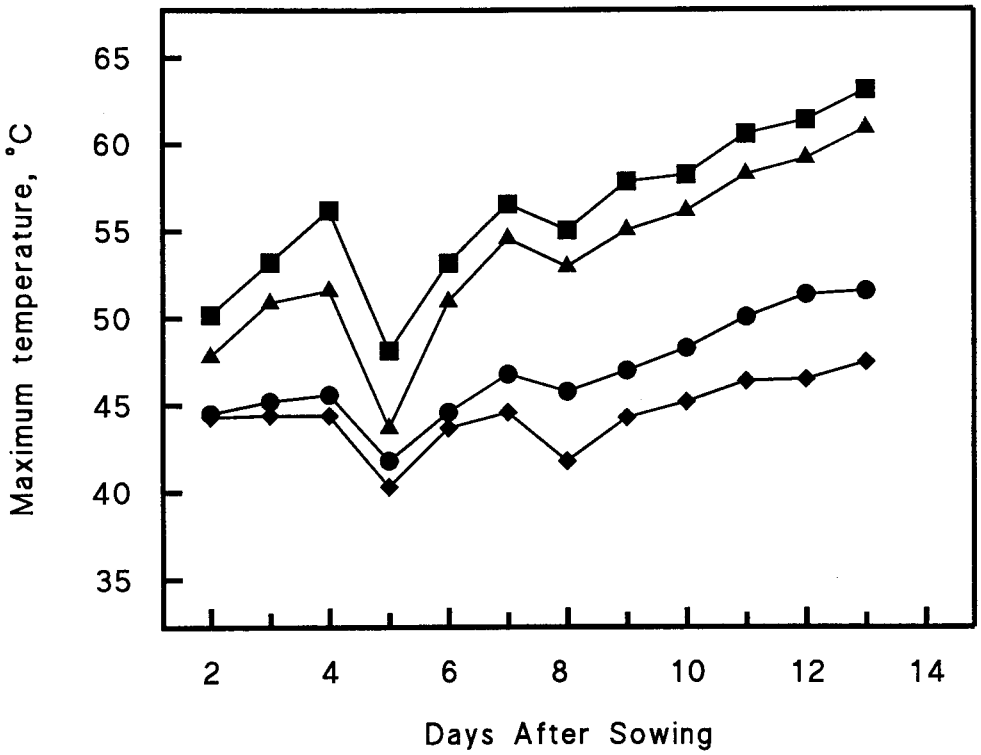


Figure 1. **Maximum daily temperature recorded for each day of the first two weeks after sowing in June 1991, at Fatehpur-Shekhawati Research Station, Rajasthan Agricultural University, India. Measurements were taken of air temperature (●) and soil temperatures at depths of 0.5 cm (■); 1.5 cm (▲); and 5 cm (◆). Each temperature point is the mean of three readings.**

delayed from early June to late June, the probability dropped from over 80% to less than 50% in most sites in Rajasthan. By mid July, the probability was 20% or less in all sites. Thus if resowing has to take place due to poor crop establishment, the risks of crop failure increase because the length of the growing season is reduced. In addition, soil nitrate availability is decreased due to leaching (Greenland, 1958). Late planting results in lower grain yields (Krause et al., 1990; Maiti and Soto, 1990), although Reddy and Visser (1993) found differences between genotypes in the yield reduction of both straw and grain as influenced by sowing date. Re-sowing also places additional demands on labor and seed.

Poor stand establishment results not only in sub-optimal plant populations in farmers' fields but also in an uneven distribution of plants (Soman et al., 1987a). Although the tillering capacity of pearl millet might enable it to compensate better than sorghum for variation in plant population, controlled experiments simulating the range of plant populations and spacing found in farmers' fields indicated that yields were greatly reduced by uneven plant spacing; the same total plant population yielded 47% less in an uneven spacing compared to the control. No amount of favorable weather during the growing season can compensate for the poor plant stands so common in the semi-arid tropics. Farmers often use high seeding rates, which could compensate for seedling survival of only 50%, but often stands of 10% or lower are found in farmers' fields (Soman et al., 1987b).

Seedling death can occur at one of three defined stages in crop establishment: germination, emergence, and post emergence. Table 1 summarizes the major causes. We will consider the sensitivities of these crops to abiotic stresses at each of these stages and describe the screening techniques available. The prevalent climatic variables must be characterized in detail to help explain what actually affects seedling growth and survival. Mean maximum air temperatures in July range from 30 to 35°C for sorghum growing areas, and from 35 to 40°C in millet growing areas (Sivakumar et al., 1984). Summary environmental data can appear to minimize the problem; mean daily air temperature or even mean maximal daily air temperatures do not indicate diurnal variations in temperature, nor the absolute extremes reached. Moreover, the temperatures actually encountered by the germinating and emerging seedling must be

Table 1. Causes of crop establishment failure at different developmental stages.

A. Germination
- ♦ Seed quality
  - ◇ maturation conditions
  - ◇ maturity
  - ◇ threshing damage
  - ◇ storage conditions
  - ◇ seed treatment
  - ◇ dormancy
  - ◇ viability
- ♦ Moisture availability
- ♦ Temperature

B. Emergence
- ♦ Sewing depth
- ♦ Temperature
- ♦ Moisture Availability
- ♦ Soil surface crusting/compaction

C. Seedling Survival
- ♦ Temperature
- ♦ Moisture availability/Flooding
- ♦ Soil nutrient status
- ♦ Wind/ sand blast
- ♦ Radiation
- ♦ Humidity

considered. Figure 2 presents the diurnal temperature cycle in Rajasthan five days after sowing. Although a maximum air temperature of approximately 46°C was measured, soil temperatures at 0.5 cm depth varied from nearly 60°C at mid-day to a pre-dawn minimum of less than 20°C. At 5 cm depth (where seed is sown), the temperature ranged from 28 to 44°C during a 24-hour period. Greater depths (10 cm depth) were more buffered, but even so, a maximum of 40°C was detected. In many reports, detailed temperature measurements are not presented, making it difficult to interpret the reasons for seedling death.

The conditions for seedling establishment are hardly ideal in the semi-arid tropics. After the initial planting rain, and in the absence of subsequent rain, the soil surface rapidly dries out and gets hotter and hotter (Figure 1). The drying surface layers mean roots have to rapidly grow to access soil moisture. The shoot often has to penetrate a soil surface crust, and once emerged, the shoot is exposed to extremes of temperature, low humidity, high radiation, and wind. The sowing methods used by farmers, particularly when mechanized, are not ideal; the sowing implement used does not firm the soil around the seed, and drier soil from the surface re-

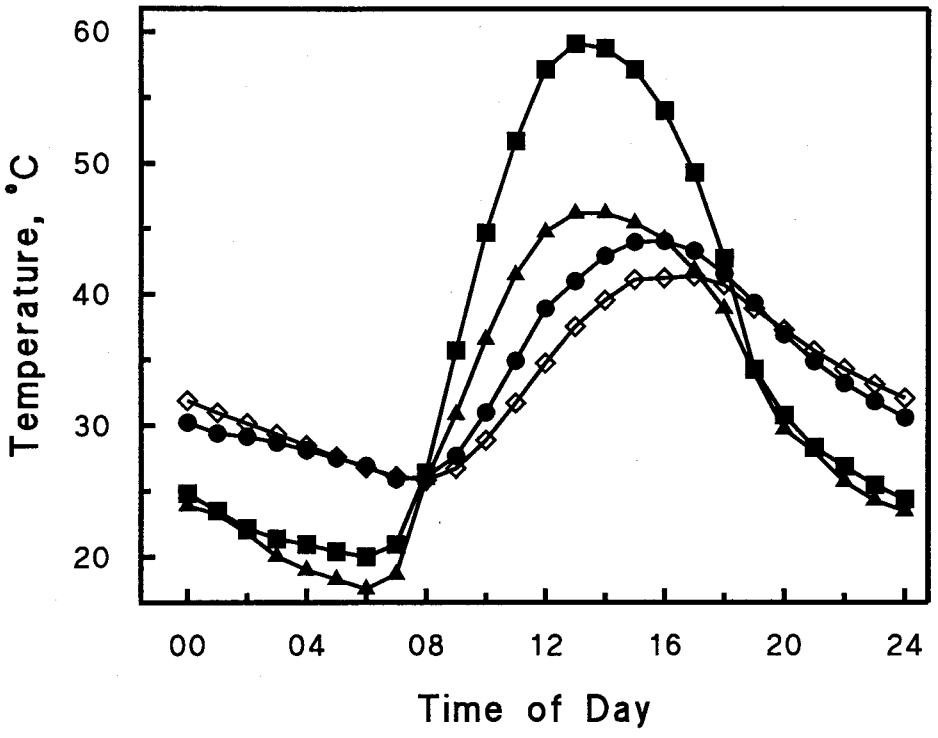


Figure 2. Diurnal temperature data recorded 5 days after sowing in June 1989 at Fatehpur, Rajasthan. Each measurement is the mean value of three thermocouples placed at either 10 cm (◇), 5 cm (●), or 0.5 cm (■) depth of soil; or 150 cm above the soil surface (▲).

duces the average seed zone moisture content. The loose structure of sandy soil compounds this. Compacted soil around the seed would improve moisture migration from the soil to the seed. Even if farmers in the semi-arid tropics used improved soil preparation and planting technologies, genetic improvements that increase adaptation to the physical constraints to stand establishment would improve resultant stands.

Once the abiotic factors limiting stand establishment in farmers' fields have been defined, the genetic variation available for a given trait must be determined to ascertain the possibilities for improvement. Screening techniques are required to characterize this variation, to identify appropriate breeding material, and ultimately to select for improved adaptation. The technique used for routine screening must be applicable for large numbers; economical, rapid, and straightforward to assess; and able to detect heritable genetic differences. Screening also needs to fit into a fixed calendar determined by other aspects of a breeding program. Screening techniques in general can be based in either the field or the laboratory.

Screening in the target environment has the advantage of using relevant stress levels. However, there are many difficulties with respect to field screening, particularly in relation to abiotic stress. The natural climate is not always reliable and is certainly variable both day to day and year to year; screening often is limited to small portions of the year; and the target environment is not always conveniently situated. Laboratory screening is not affected by these problems and can be conducted under controlled conditions without being subject to the variability of the natural environment. Laboratory-based screening often targets one aspect of response to stress, not the integrated effects of the environment on many physiological and developmental processes. Dissecting a complex process such as seedling survival of stress into component parts that are under simpler genetic control should permit rapid and precise improvement. An understanding of the physiology of seedling response to stress is required to enable the development of such screening techniques. It is important, however, that a laboratory-based technique have a significant relationship to field performance. Although the effects of heat and drought are often examined separately, in the field these stresses frequently occur concurrently, along with low fertility, and the interactions between these stresses must be considered as well. For example, reduced water supplies may result in heat injury due to reduced transpirational cooling.

Germination

Without adequate germination, no seedling establishment is possible. Seeds can fail to germinate due to problems with viability as well as abiotic stress. Soman et al. (1987b) found that the germination of seeds that emerged poorly in farmers' fields was excellent under standard laboratory conditions. However, many factors, both management and environmental, affect the germinability of seeds, as indicated in Table 1. Harvest of immature pearl millet seed can limit subsequent germination and seedling vigor, although Appa Rao et al. (1993) found full germinability by 21 days after pollination. By 28 days, maximum dry matter accumula-

tion had occurred and subsequent seedling vigor was maximal. This confirmed the results of Fussell and Pearson (1980) who found that harvest at or after the middle of grain filling did not reduce seed viability. They suggested that this robustness of the grain-filling process and early viability of seeds confer ecological advantage to a crop grown in semi-arid climates where grain development may be terminated by drought or high temperatures. However, longevity of germinability was found to be maximal if seeds were allowed to mature for at least 35 days after pollination (Kameswara Rao et al., 1991). Immature sorghum seeds also reach a high germination capacity by two weeks before physiological maturity (Maiti et al., 1985; Mora-Aguilar et al., 1992). Sorghum seeds developing on plants subjected to drought stress showed a high level of germination earlier in the maturation period as compared to control seeds (Benech-Arnold et al., 1991).

Pre-harvest sprouting also leads to loss of seed viability (Maiti et al., 1985). Germinability has also long been known to be affected by environmental conditions experienced by the mother plant during grain filling (Clark et al., 1967). The influence of environment during the development and maturation of seeds is evidenced by the difference in seedling responses of seed produced in different seasons and/or sites (Peacock et al., 1993). This must be considered when assessing seedling characteristics of different genotypes of both sorghum and pearl millet. In addition, Lawlor et al. (1990) showed that the production environment influenced the minimum temperatures for germination and root elongation of sorghum seedlings. There are few reported studies on the influence of high temperatures during grain filling on subsequent seed germination. Both Fussell and Pearson (1980) and Mohamed et al. (1985) examined the effect of temperatures between 19 and 33°C on pearl millet. Seeds that had developed at 19°C had poor viability, but there was no difference in the viability of seed produced in the other environments tested.

Germinability is affected by seed storage conditions and seed treatment. In India, sun heating of sorghum grain to reduce insect infestation is common (More et al., 1992). Short-term exposure to high temperatures (12 minutes at 70°C) did not affect germinability and was sufficient to effectively reduce insect infestation as well as fungal contamination. Higher temperatures, however, significantly reduced germination. Longer term temperature treatments were not considered. Singh et al. (1988) examined 35 lines of pearl millet for the retention of viability in response to accelerated aging (80% RH, 40°C, 14 days). Variation between genotypes was found with a range of viability loss between 18 and 84 percent.

Moisture levels in farmers' fields generally are sufficient to ensure adequate germination (Soman et al., 1987b; Peacock et al., 1993). Smith et al. (1989), using polyethylene glycol to simulate drought stress, found pearl millet seed germination more resistant to low water potentials than that of sorghum, although differences between genotypes are apparent (Gurmu and Naylor, 1991). In moist soil, temperature is the main environmental factor governing the germination of seeds. However, in both pearl millet and sorghum, the final germination per-

centage is maximal over a wide range of temperatures (from approximately 12 to 40°C) with small variation between genotypes (Carberry and Campbell, 1989; Dunbabin et al., 1994; Garcia-Huidobro et al., 1982a; Harris et al., 1987; Khalifa and Ong, 1990; Mohamed et al., 1988; Brar and Stewart, 1994; Radford and Henzell, 1990; Mortlock and Vanderlip, 1989). The rate of germination, defined as the reciprocal of the time taken for half the population to germinate, usually increases linearly with temperature, at least within a defined range. From controlled temperature experiments, it is possible to calculate base, maximal, and optimal temperatures for germination, the so-called cardinal temperatures (Garcia-Huidobro et al., 1982a). These authors found an optimum temperature of 34°C for germination at constant temperature, with base and maximum temperatures of 12°C and 47°C, respectively.

Greater genotypic variation is found in the effect of temperature on the rate of germination (Dunbabin et al., 1994; Mohamed et al., 1988; Khalifa and Ong, 1990). Within a seed population, Garcia-Huidobro et al. (1982a) detected large variations in germination rates and found seeds that germinated earlier were less sensitive to high temperatures. The rate of germination largely determines how long a seedling will take to emerge in a particular soil environment and, therefore, the duration of its exposure to high temperature. In general, pearl millet germinates more quickly within its optimal range than does sorghum (Mortlock and Vanderlip, 1989). The high optimum temperature for germination and seedling growth indicates the general adaptation of pearl millet and sorghum. Above the optimal temperature, however, both the final percentage of germination and germination rate fall rapidly. This great sensitivity to supra optimal temperatures suggests that small differences in soil temperature at the time of germination may have profound effects on germination and hence establishment of the crop.

The above reports all measure germination at constant temperatures, whereas in the field a diurnal cycle of temperatures is found, even if seed zone temperatures are not as extreme as those at the soil surface (Figures 1 and 2). Garcia-Huidobro et al. (1982b) found that germination rates at alternating temperatures were greater at higher amplitudes of temperature variation, although temperatures above 42°C inhibited germination. In this case, the two temperature regimes were for 12 hours at constant temperatures rather than a normal diurnal cycle. In the field, seeds usually experience high temperatures for a few hours each day rather than 12 hours. The sensitivity of seeds to high temperature is likely to delay or prevent successful germination in the field. Shorter term treatments at high temperature were examined by Garcia-Huidobro et al. (1985). Seeds were most sensitive to short-term treatments at 45°C or 50°C when they were absorbing water. The adverse effects of high temperature were much less severe when seeds were allowed to imbibe water for eight hours at control temps before exposure to high temperature. This implies that germination would be more successful when seeds are sown in the early evening, after which soil temperatures remain relatively low for at least 18 hours. Laboratory germination studies in general overestimate field germination and emergence (Raj and

Khairwal, 1994). Factors that affect successful emergence in the field are discussed in the next section.

Emergence and Seedling Survival

Even if seed germination is successful, diminishing soil water availability after germination greatly affects seedling growth and survival. Line source irrigation systems, which provide a range of moisture regimes, have been used to understand the development and effects of moisture stress. Sorghum cultivars exhibit genotypic differences in their ability to both emerge at low soil moisture conditions (Soman, 1990) and subsequently grow (O'Neill and Diaby, 1987). Locally adapted Malian millet varieties not only did not show genotypic differences but also were capable of up to three times greater seedling growth than the best sorghum entry under water stress (O'Neill and Diaby, 1987).

Polyethylene glycol can be used to simulate drought under controlled temperature conditions. For example, similarities in early seedling growth in two contrasting sorghum cultivars were found under field and simulated drought conditions (Gurmu and Naylor, 1991). Cell elongation is reduced at low water potentials and thus roots may not be able to grow sufficiently fast to permit escape from the rapidly drying surface layers of soil and penetration of deeper moisture containing layers. Significant genotypic variation in seedling root growth exists in pearl millet (M'Ragwa et al., 1995). Longer term survival on drying soil depends on the initiation and growth of nodal roots. In both pearl millet and sorghum, a single primary root develops on germination of the seed, and later, when the seedling has developed two to three leaves, the first adventitious or nodal roots develop at the shoot base. Reduced soil surface moisture levels can inhibit nodal root formation (Blum and Ritchie, 1984; Gregory, 1983; Harris, 1996) although this depends on drying rate (Soman and Seetharama, 1992).

One strategy for maintaining adequate moisture in the seed and root zone for a longer time period is deeper sowing of the seed, but in this case, growth depends longer on seed reserves before emergence occurs. In both sorghum and pearl millet, deeper sowings result in longer mesocotyl length, reducing the effect of sowing depth on shoot meristem depth (Soman and Seetherama, 1992; Harris, 1996; Howarth, Peacock, and Jayachandran, unpublished). Sowing depth also consequently does not affect nodal root number or growth. Genotypic differences in mesocotyl growth rates have been shown in both sorghum and pearl millet (Mohamed et al., 1989; Radford and Henzell, 1990; Soman et al., 1989), indicating that this characteristic is worth considering if deeper plantings are to be used.

Seedling vigor measurements also have been used to assess the importance of vigor differences in seedling survival of drought stress. Early vigor had a positive association with both days to wilting initiation and days to permanent wilting under conditions of moisture stress in pearl millet (Manga and Yadav, 1995). The moisture stress in this experiment did not commence until 20 days after sowing, by which time an extensive root system would have been established. Seed size, as well, accounted for significant differ-

ence in vigor and response to drought stress; larger seeds within a seed lot produced more vigorous seedlings. Harris (1996) also found that vigor expressed as the rate of emergence in sorghum was linked to successful stand establishment; seed that emerged faster produced more complete stands. Fast seedling growth and consequent early seedling establishment is one strategy to escape a stressful environment, particularly as the conditions for seedling establishment become increasingly less optimal with time after sowing. However, rapid development of a greater leaf area might result in a faster depletion of soil water resources. Measurements of leaf growth in the field indicate that the thermotolerant pearl millet landrace IP3201 has a relatively slow rate of leaf growth compared to the thermosensitive cultivar ICMV155 under moderate stress. When the stress level was increased, however, IP3201 continued to grow, whereas ICMV155 showed a greatly reduced growth rate (Howarth, Jayachandran, and Peacock, unpublished). In extreme environments, a conservative growth strategy may ensure survival.

Temperature is the main factor determining the rate of plant growth, but developmental processes (e.g., germination, radicle elongation, leaf growth) differ in their cardinal temperatures (Ong and Montieth, 1985). Again, most studies have been conducted at constant temperatures. The temperatures for maximal mesocotyl and coleoptile rates for both sorghum and pearl millet are below maximal temperatures for germination (Carberry and Campbell, 1989; Ong and Monteith, 1985; Radford and Henzell, 1990). This indicates that the ability to germinate at high temperature, usually defined as successful by radicle protrusion through the seed coat, may not mean that subsequent seedling growth can occur at that temperature. Radford and Henzell (1990) also found significant differences between genotypes in seedling growth rate and response to temperature. As for germination, seedlings stop growing at temperatures less than 10°C higher than the optimum temperature for growth (Ong and Monteith, 1985). Soil temperatures also affect root growth. Long term treatment at 40°C resulted in severe inhibition of primary root growth in sorghum (Pardales et al., 1991). However, after six days at 40°C, followed by treatment at 25°C, seedlings were able to recover by the initiation of nodal roots. Temperature cycling of 40°C day and 25°C night did not have a deleterious effect on root growth.

Specific effects of temperature need to be determined by controlling temperature independently of moisture status. This can be done in the field by changing the radiation absorption of the soil by covering the surface with kaolin or charcoal (Wilson et al., 1982; O'Neill and Diaby, 1987). Maximal diurnal soil temperatures can be altered by up to 20°C, both at the soil surface and at the depth of sowing. These experiments indicate that high soil surface temperatures delay or prevent seedling emergence of sorghum and pearl millet, and that in both species genetic variation exists in the ability to emerge under these conditions.

The charcoal pit screening method has considerable potential (O'Neill and Diaby, 1987). It is easy to run and requires no sophisticated equipment, but is limited to use in the hot season and cannot differentiate lines with relatively small differ-

ences in field emergence. Soman and Peacock (1985) developed a laboratory screening system for seedling emergence under high temperature with no water stress. Seeds are sown in sand-filled clay pots placed in a water bath, and the soil surface is heated with a bank of infrared lamps placed above the pots. Lynch (1994) conducted recurrent selection for emergence in this pot test and also for germination at a constant 45°C. Improved emergence under high temperature conditions was obtained using the former; the germination selection procedure was ineffective. Kasalu et al. (1993) found field emergence correlated more closely with the ability to germinate at control temperatures than with germination ability at high temperature.

A laboratory screening technique based on embryo protein synthesis for the assessment of high temperature susceptibility during germination and seedling growth of sorghum also has been developed (Ougham and Stoddart, 1985). A strong correlation was found between the ability of imbibing embryos to synthesize protein at temperatures above 40°C and germination at high temperatures. Ougham et al. (1988) subsequently compared the embryo protein synthesis method with emergence at high temperature in pots using the technique of Soman and Peacock (1985) and found a high degree of correlation, except for two lines that showed anomalous behavior, suggesting a greater complexity of the overall emergence process compared to germination.

Extensive research has been conducted to examine individual proteins induced by high temperature and their potential for use in screening techniques. Protein synthesis is a very thermosensitive process, and in two-day old sorghum and pearl millet seedlings, temperatures above 45°C result in a very rapid shut-down in *de novo* protein synthesis (Howarth, 1989; Howarth, 1990a; Howarth and Ougham, 1993). However, either an acclimation period of two hours at 45°C or a gradual temperature increase from 35-50°C results in induced tolerance of both growth and protein synthesis at previously lethal temperatures (Howarth, 1990c,1991; Howarth and Skøt, 1994). Synthesis of the heat shock proteins (HSP) occurs concomitantly with this acclimation process. The precise function of HSPs in thermotolerance is not understood (Vierling, 1991; Howarth and Ougham, 1993; Waters et al., 1996); however, the strong correlation between their synthesis and thermotolerance suggests they could be used in screening systems (Vierling and Nguyen, 1992). The kinetics of their synthesis and breakdown is complex (Howarth and Skøt, 1994) and must be considered before they can be used in large scale screening. Induced thermotolerance does not persist from one day to the next, although a subsequent heatshock, during which HSPs are again synthesized, returns the tissue to a thermotolerant state. The ability to survive repeated heat shock is of prime importance in parts of the world with high midday temperatures, and genotypic differences in this ability have been shown (Howarth, 1991).

Sustained seedling growth following emergence depends not only on the physiological processes for germination and emergence, but also on the capacity of the seedling to elongate, produce leaves, and

become autotrophic. Post-emergence seedling death due to abiotic stress under field conditions is primarily caused by the prevalent high soil surface temperatures, at least in the first ten days following sowing, and only after that does water deficit start to take effect (Stomph, 1990; Peacock et al., 1993). Peacock et al. (1990) developed a laboratory technique to control the temperature of a localized region of seedlings in order to simulate the elevated soil surface temperatures that can occur in the field. The rate of leaf growth in *Graminae* is largely determined by the temperature of the shoot apex (Watts, 1971; Peacock, 1975). At 29 hours of treatment of only the shoot meristem at 52°C (the rest of the plant being maintained at 30°C), leaf growth ceased, although plant water relations were unaffected. An accumulation of soluble carbohydrates in the shoots of plants treated at high shoot meristem temperatures and a decline in root carbohydrate concentration suggest that root starvation was occurring due to heat-induced phloem blockage (Peacock et al., 1990). Heat shock proteins may be important in protecting meristematic tissue during the daily increase in temperature and are found to be associated with this region when seedlings are heat girdled (Howarth, 1990b).

In pearl millet growing areas in the Sahel and Rajasthan, farmers' fields often contain many trees. The localized areas under these trees have a higher soil nutrient status as well as a less extreme microclimate, and frequently a better stand establishment of pearl millet. Vandenbelt and Williams (1992) examined the effect of *Faidherbia albida* trees on soil surface temperature and pearl millet seedling growth in Niger, and found that the canopy of the tree reduced the maximum soil temperature at 2 cm depth by up to 10°C, although air temperatures were less affected. In a seedling growth experiment using a shade gradient and adequate soil moisture, it was found that seedling growth rates over six weeks were correlated with the mean daytime soil surface temperature, with no seedlings surviving temperatures higher than 46.6°C. This further suggests that soil surface temperatures are critical for seedling growth and survival.

A field screening procedure for emergence and seedling survival at high soil surface temperatures has been developed and used to identify genetic differences for seedling survival (Peacock et al., 1993). This procedure is used in Rajasthan in the hot and dry pre-monsoon season and has proved effective at identifying genotypes of superior heat tolerance (Weltzien et al., 1994; Howarth et al., 1995b). Selected results are shown in Table 2, which illustrates a range of response of both emergence and seedling survival. The sorghum genotype used was the most thermosensitive entry. Local landrace populations (IP3201 and IP3175) and the hybrid HHB67 were the most thermotolerant. A population cross between IP3201 and ICMV155 has subsequently been made and the 155 fullsibs produced have been screened in the field. Bi-directional selection for seedling thermotolerance was conducted based on the considerable differential between the high and low 20% of entries found (Table 2). This technique, however, can be used only for two months of the year at most in an unpredictable environment where early monsoon rains will prevent its success. The

Table 2. Field data obtained from selected pearl millet genotypes screened at Fatehpur-Shekhavati Agricultural Research Station, Rajasthan Agricultural University.

Entry	Emergence	Thermo-tolerance index
HHB 67	0.77	0.86
IP 3201	0.75	0.85
IP 3175	0.75	0.79
ICMH 451	0.74	0.75
Sadoré Local	0.73	0.73
W Raj. Pop.	0.65	0.70
ICMH 423	0.77	0.61
ICTP 8203	0.65	0.57
ICMV 155	0.44	0.47
BSEC C4	0.79	0.37
Sorghum (SPV386)	0.59	0.30
Cycle 1 selection (high)*	0.65	0.69
Cycle 1 selection (low)*	0.54	0.38

Thermotolerance index calculated as the ratio of seedlings surviving to the total number of seedlings that emerged.

All results the mean of experiments conducted in 1989 and 1990 (from Peacock et al., 1993) except for * which represent the mean values for the selected fraction (high or low 20%) from 155 fullsibs produced from a population cross of IP 3201 and ICMV 155 and screened in 1992 (from Weltzien et al., 1994).

results obtained from field screening depend on the actual environmental conditions experienced that year.

To overcome these limitations, a number of laboratory-based methods for evaluating post emergence seedling death have been devised (Howarth et al., 1995a). These include the use of a sand bed, which can be heated electronically to simulate diurnal soil temperatures in Rajasthan, and the use of an electrolyte leakage test as a measure of membrane thermostability. Initial results screening the 155 fullsibs produced from the IP3201 and ICMV155 cross indicate that both procedures show good correlations with field results, but with higher heritabilities and increased flexibility regarding when and where the screening techniques are conducted (Weltzien et al., 1994; Howarth et al., 1995b).

Although temperature and drought have been considered separately, tolerance to one stress often is combined with tolerance to another (O'Neill and Diaby, 1987; Maiti et al., 1994). These stresses also often occur concurrently. As indicated in Table 1, there are a number of other environmental reasons for stand failure. For example, wind storms carrying sand can cause considerable stand reduction (Klaij and Hoogmoed, 1993). Soil fertility effects on seedlings have been less extensively studied, but low fertility can reduce survival of other stresses by affecting seedling vigor. The soils where pearl millet and sorghum grow are often of very low fertility. Payne et al. (1991), examining the influence of phosphorus and water on growth of pearl millet, found that the efficiency of dry matter production decreased under both control and drought stress conditions when the soil phosphorus supply was inadequate. The possibility of improving early growth by the use of phosphorus-containing seed coatings was examined by Rebafka et al. (1993). Pearl millet is very small-seeded with low phosphorus reserves; thus, an external supplement could improve growth. However, although seed coating did improve early growth, there were considerable deleterious effects on seedling emergence, possibly due to the absence of glumes in pearl millet. Salinity is another abiotic stress encountered during seedling establishment that can affect growth and survival. Azhar and McNeilly (1988) found considerable genetic variation in sorghum for growth under salinity stress and conducted a genetic analysis identifying considerable dominance effects.

Soil surface crusting results from the beating action of rainfall and subsequent drying of the soil at high temperature, causing difficulties for emerging seedlings, which need to break through this barrier. Soman et al. (1984) developed a screening technique for emergence under crusting conditions and found that pearl millet was much more affected than sorghum, as the seedling is smaller and less vigorous. Sorghum lines vary in their ability to emerge under soil crusting conditions. Soman et al. (1992) examined the relationship between sorghum coleoptile morphology and emergence potential and found that mesocotyl growth rate correlated best with emergence. This is effectively an avoidance strategy, as faster growing genotypes were able to emerge before maximal crust formation had occurred. Significant differences between pearl millet genotypes exist for coleoptile and mesocotyl growth rate (Soman et al., 1989). Emergence through crusts was further studied by Mason et al. (1994) using piston displacement as an *in vitro* screening technique. In this study, coleoptile length showed no correlation, but coleoptile diameter showed a high correlation with the ability of sorghum to emerge through the simulated soil crust; avoidance of a soil crust by fast growth was not possible in this test. Seedlings emerge through crusts, either due to high pressure exerted by an individual seedling or to cumulative force exerted by a group of seedlings (Taylor, 1962). Joshi (1987) found that the mixed sowing of pearl millet and greengram resulted in improved emergence because of the joint thrust from legume and pearl millet together. The use of precision planters ensures even spacing of seed, requiring individual seedlings to emerge through a crust. Farmers rarely use precision planting equipment and often sow mixtures of cereals and legumes, thus minimizing the problem.

Improvement of Stand Establishment

This review has shown that considerable genetic variation exists for tolerance to the environmental constraints on germination, emergence, and seedling survival in sorghum and pearl millet. The desirability of a plant trait in an environment depends not only on the risk of stress but on the attitude of farmers toward risk and on the specific requirements of the local farming system (Van Oosterom et al., 1996; Weltzien et al., 1996). Each environment poses a different set of problems, and in marginal environments where the climate is highly variable, it often is difficult to precisely define the causes of crop failure, but they must be at least approximated if successful crop improvement is to occur.

As Boyer (1982) points out, there is often a dramatic difference between maximal and average yields for any given crop species. The actual yield achieved depends on the environmental conditions the crop encounters. Stress can be defined as a condition that limits a plant in realizing its potential for growth, development, and reproduction; extremes of stress result in plant death. Plants rarely grow in optimal environments, so they can be considered to be under some degree of stress at all times. For pearl millet and sorghum growing in marginal environments this is certainly the case. Variation exists in the ability to survive and grow under stress conditions. The task is to exploit this variation and combine improved tolerance to

stress with increased yield potential so that not only is the discrepancy between yield under optimal conditions and actual yield reduced but also yield stability increased.

New technologies, improved screening techniques, and knowledge of appropriate germplasm can now exploit natural variation to a greater effect. It is only possible, however, to improve the degree of tolerance; there always will be a level beyond which it is not possible to improve. For seedlings, where stress often results in death, improvement in stress tolerance targets the ability to survive these stress conditions. To improve adaptation to other stresses (for example, terminal drought), it often is necessary to target an enhancement in relative performance, often measured as yield, rather than survival. The tasks involved in improving relative performance have received much attention from breeders and physiologists (Richards, 1989; Evans, 1993; Ludlow and Muchow, 1990). Seedling survival and the ability to yield well are not expected to be as closely interrelated as are stress tolerances reflecting relative performance. Thus combining seedling stress tolerance and yielding ability would not be expected to need as much multi-location testing as is the case for relative yield improvement. Only yielding ability in the target environment should need to be evaluated for materials with improved seedling stress tolerance.

Understanding of the processes that lead to a failure of stand establishment has advanced sufficiently to permit development of specific screening methods. The screening techniques described above have direct application in the genetic improvement of these traits. However, fewer studies are reported in which both the genetic variation identified and screening systems developed have been exploited in crop improvement. To do this it is necessary to select for improved adaptation and then to evaluate the response to selection for improved establishment ability in the field. Screening methods tend to be developed using control genotypes with extreme differences in performance, often with many genetic differences for other traits. The results obtained often are specific to the actual cultivars and growing conditions used. It is harder to distinguish genotypes showing an intermediate response to a given stress. The capacity for improvement of stress tolerance, however, can be found within a species and is amenable to conventional breeding techniques.

Adaptation to a given constraint is complex. Plant physiology can identify not only critical components of adaptation but also genes or regions of chromosomes linked to a given trait. This is done using molecular markers, such as restriction fragment length polymorphisms (RFLPs), combined with physiological screening, which permits the mapping, identification, manipulation, and combination of specific genes involved in tolerance. The challenge is to identify specific physiological or biochemical processes and to develop rapid, high-throughput screening techniques based on them. Molecular marker maps exist for both sorghum (Hulbert et al., 1990; Chittenden et al., 1994; Pereira et al., 1994; Xu et al., 1994) and pearl millet (Liu et al., 1994) and have been used to identify quantitative trait loci (QTLs) associated with downy mildew resistance (Jones et al.,

1995; Hash et al., 1995). A similar approach is being used to detect QTLs associated with seedling thermotolerance (Howarth et al., 1994). Once identified, marker-assisted selection can be used to precisely improve the required character by following closely the movement of desired and undesirable gene segments in the breeding process.

The potential of these modern, precision breeding methods is considerable. Mapping potential physiological and biochemical components of adaptation also provides information on their involvement in adaptation and is a new way of elucidating the mechanism of plant response to the environment. Genetic mapping not only shows in a much clearer fashion how traits are genetically correlated, but how they are linked on the chromosomes. Active collaboration between geneticists, molecular biologists, physiologists, breeders, germplasm collectors, and other relevant disciplines is required to ensure success. Genetic improvement of stand establishment is thus possible by plant breeding, and potential progress is substantial.

Plant breeding, however, is not the only way forward, and management solutions also must be considered, particularly as the current tillage and sowing methods used in farmers' fields are not very sophisticated. Agronomic factors such as seedbed preparation, sowing methods, timeliness of sowing, and sowing depth can exacerbate environmentally-induced stress and result in poor crop stands. Compaction of the soil after sowing to ensure good soil-seed contact and minimize evaporation, for example, could assist in stand establishment. Traditional sowing methods, however, can be appropriate for the conditions encountered in some cases. For example, stand establishment, survival, and yield were better under the hill planting used in the Sahel than drilling seed (Klaij and Hoogmoed, 1993). Hill planting provides a certain amount of protection from the extremes of temperature and from sand-bearing winds. It is not easily mechanized, however, and the large number of seedlings growing together can result in rapid development of water deficit. Pre-sowing tillage increases initial stands and subsequent seedling survival (Joshi, 1987; Klaij and Hoogmoed, 1993). Surface application of farmyard manure can reduce the likelihood of crusting, maintain moisture in the surface layer of soil (Joshi, 1987), and minimize the prevalence of temperature extremes at the soil surface. This practice resulted in a faster rate of emergence, increased total emergence, and reduced seedling mortality of pearl millet (Joshi, 1987) but had no significant effect on stand establishment in sorghum (Harris, 1996).

If planting technologies are refined to more precision-based methods and mixed cropping no longer practiced, then crusting could perhaps be a bigger problem in crop establishment. Pre-sowing seed priming, either by soaking in water or in osmotic solutions, has been investigated to examine its potential to improve emergence (Bradford, 1986; Joshi, 1987; Maiti and Moreno, 1995; Harris, 1996). Primed seeds germinate more rapidly and uniformly and the rate of emergence is increased (Harris, 1996), although final stand establishment is not necessarily improved (Joshi, 1987). Priming conditions, the temperature and timing of any intervening period before sowing, and soil

conditions at sowing will all influence the results obtained and need to be optimized. Recent data from on-farm trials with upland rice, maize, and chickpea in semi-arid India show that farmers value on-farm seed priming for the benefits they gain from fast, vigorous crop establishment.

Conclusion

Increasing stand establishment through a combination of well-adapted, improved cultivars and management practices remains a challenge. Seedling traits affecting establishment warrant high priority for research. Genetic improvement is most needed in those areas where dependence on the pearl millet and sorghum crop is so great, particularly if increases in population pressure result in the expansion of crop production into more and more marginal areas. Climatic change could exacerbate this need. Locally adapted germplasm often is capable of surviving the environmental conditions and should be widely used in breeding for improved stand establishment. An understanding of both the prevailing conditions and the farmers' requirements is critical. For a farmer to adopt a change in these high risk environments, demonstration of improvements actually on farmers' fields is necessary. Varieties that perform well in national yield trials at research stations are not necessarily appropriate for these severe environments. Targeting of crop improvement research specifically for these environments is thus required.

References

Appa Rao, S., N. Kameswara Rao, and M.H. Mengesha. 1993. Germinability and seedling vigor of pearl millet seeds harvested at different stages of maturity. Field Crops Res. 32:141-145.

Azhar, F.M., and T. McNeilly. 1988. The genetic basis of variation for salt tolerance in *Sorghum bicolor* (L.) Moench seedlings. Plant Breeding 101:114-121.

Benech Arnold, R.L., M. Fenner, and P.J. Edwards. 1991. Changes in germinability, ABA content and ABA embryonic sensitivity in developing seeds of *Sorghum bicolor* (L.) Moench induced by water stress during grain filling. New Phytol. 118:339-347.

Bidinger, F.R., and P. Parthasarathy Rao. 1990. Genetic and cultural improvements in the production of pearl millet: A comparative assessment for India and Sahelian/Sudanian Africa. p. 194-206. *In* S.K. Sinha et al. (eds.) Proceedings of the international congress of plant physiology, 1988, New Delhi, India. Society for Plant Physiology and Biochemistry, New Delhi.

Bidinger, F.R., E. Weltzien R., R.V. Mahalakshmi, S.D. Singh, and K.P. Rao. 1994. Evaluation of landrace topcross hybrids of pearl millet for arid zone environments. Euphytica 76:215-226.

Blum, A., and J.T. Ritchie. 1984. Effect of soil surface water content on sorghum root distribution in the soil. Field Crops Res. 8:169-176.

Blum, A., and C.Y. Sullivan. 1986. The comparative drought resistance of landraces of sorghum and millet from dry and humid regions. Ann. Bot. 57:835-846.

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443-448.

Bradford, K.J. 1986. Manipulation of seed water relations via osmotic priming to improve germination under stress conditions. Hort. Sci. 21 (5):1105-1112.

Brar, G.S., and B.A. Stewart. 1994. Germination under controlled temperature and field emergence of 13 sorghum cultivars. Crop Sci. 34:1336-1340.

Brunken, J., J.M.J. De Wet, and J.R. Harlan. 1977. The morphology and domestication of pearl millet. Economic Bot. 31:163-174.

Carberry, P.S., and L.C. Campbell. 1989. Temperature parameters useful for modeling the germination and emergence of pearl millet. Crop Sci. 29:220-223.

Chittenden, L.M., K.F. Schertz, Y.R. Lin, R.A. Wing, and A.H. Patterson 1994. A detailed RFLP map of *Sorghum bicolor* x *S. propinquum* suitable for high-density mapping suggests ncestral duplication of sorghum chromosomes or chromosmal segments. Theor. Appl. Gen. 87:925-933.

Clark, L.E., J.W. Collier, and E. Langston. 1967. Dormancy in *Sorghum bicolor* (L.) Moench. I. Relationship to seed development. Crop Sci. 7:497-501.

De Wet, J.M.J., F.R. Bidinger, and J.M. Peacock. 1992. Pearl millet (*Pennisetum glaucum*) - A cereal of the Sahel. p. 259-267. *In* G.P. Chapman (ed.) Desertified grasslands: Their biology and management. Linnean Society, London.

Dunbabin, T., J. Learmonth, R.E.L. Naylor, and C. E. Mullins. 1994. Temperature effects on the germination of *Sorghum bicolor* under a constant temperature regime. Asp. Appl. Biol. 39:179-184.

Evans, L.T. 1993. Crop evolution, adaptation and yield. Cambridge University Press, Cambridge, U.K.

Fussell, L.K., and C.J. Pearson. 1980. Effects of grain development and thermal history on grain maturation and seed vigour of *Pennisetum americanum*. J. Exp. Bot. 31:635-643.

Garcia-Huidobro, J., J.L. Monteith, and G.R. Squire. 1982a. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). I. Constant temperature. J. Exp. Bot. 33:288-296.

Garcia-Huidobro, J., J.L. Monteith, and G.R. Squire. 1982b. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). II. Alternating temperature. J. Exp. Bot. 33:297-302.

Garcia-Huidobro, J., J.L. Monteith, and G.R. Squire. 1985. Time, temperature and germination of pearl millet (*Pennisetum typhoides* S. & H.). III. Inhibition of germination by short exposure to high temperature. J. Exp. Bot. 36:338-343.

Greenland, D.J. 1958. Nitrate fluctuations in tropical soils. J. Agric. Sci. 50:82-92.

Gregory, P.J. 1983. Response to temperature in a stand of pearl millet (*Pennisetum typhoides* S. & H.). III. Root development. J. Exp. Bot. 34:744-756.

Gupta, B.S., B.K. Mathur, and M.L. Purohit. 1992. Trend, growth and technological development of pearl millet (*Pennisetum glaucum*) crop in different agro-climatic zones of western Rajasthan. Indian J. Agric. Sci. 62:273-275.

Gupta, J.P. 1986. Moisture and thermal regimes of the desert soils of Rajasthan, India and their management for higher plant production. J. Hydro. Sci. 31:347-359.

Gurmu, M., and R.E.L. Naylor. 1991. Effects of low water availability on germination of two sorghum cultivars. Seed Sci. Technol. 19:373-383.

Harinarayana, G. 1987. Pearl millet in Indian agriculture. p. 5-17. *In* Proceedings of the international pearl millet workshop, 7-11 April 1986, ICRISAT Center, India. ICRISAT, India.

Harris, D. 1996. The effects of manure, genotype, seed priming, depth and date of sowing on the emergence and early growth of *Sorghum bicolor* (L.) Moench in semi-arid Botswana. Soil Tillage Res. (in press).

Harris, D., Q.A. Hamdi, and A.C. Terry. 1987. Germination and emergence of *Sorghum bicolor*: Genotypic and environmentally induced variation in the response to temperature and depth of sowing. Plant Cell Env. 10:501-508.

Hash, C.T., G.P. Cavan, F.R. Bidinger, S.D. Singh, and C.J. Howarth. 1995. Downy mildew resistance QTLs from a seedling heat tolerance mapping population. Internat. Sorghum and Millet Newsl. 36:66-67.

Haugerud, A., and M.P. Collinson. 1990. Plants, genes and people: Improving the relevance of plant breeding in Africa. Exp. Agric. 26:341-362.

Hoogmoed, W.B., and M.C. Klaij. 1990. Soil management per crop production in the West African Sahel. I. Soil and climate parameters. Soil Tillage Res. 16: 85-103.

Howarth, C.J. 1989. Heat shock proteins in *Sorghum bicolor* and *Pennisetum americanum*. I. Genotypic and developmental variation during seed germination. Plant Cell Env. 12:471-477.

Howarth, C.J. 1990a. Heat shock proteins in *Sorghum bicolor* and *Pennisetum americanum*. II. Stored RNA in sorghum seed and its relationship to heat shock protein synthesis during germination. Plant Cell Env. 13:57-64.

Howarth, C.J. 1990b. Gene expression and thermal sensitivity of seedling growth of sorghum and pearl millet: Effects of localised imposition of heat stress. J. Exp. Bot. 41:C3.18.

Howarth, C.J. 1990c. Heat shock proteins in sorghum and pearl millet; ethanol, sodium arsenite, sodium malonate and the development of thermotolerance. J. Ex. Bot. 41:877-883.

Howarth, C. J. 1991. Molecular responses of plants to an increased incidence of heat shock. Plant Cell Env. 14:831-841.

Howarth, C.J., G.P. Cavan, K.P. Skøt, R.W.H. Layton, C.T. Hash, and J.R. Witcombe. 1994. Mapping QTLs for heat tolerance in pearl millet. p. 80-85. *In* J.R. Witcombe (ed.) Proceedings of an ODA plant sciences research programme conference on the use of molecular markers in sorghum and pearl millet breeding for developing countries, 29 March - 1 April 1993, University of East Anglia, Norwich.

Howarth, C.J., and H.J. Ougham. 1993. Gene expression under stress. Tansley Review. New Phytol. 125:1-26.

Howarth, C.J., and K.P. Skøt. 1994. Detailed characterisation of heat shock protein synthesis and induced thermotolerance in seedlings of *Sorghum bicolor* L. J. Exp. Bot. 45: 1353-1363.

Howarth, C.J., K.P. Skøt, E. Weltzien R., J.M. Peacock, and C.J. Pollock. 1995a. Development

of methods for evaluating seedling thermotolerance. J. Exp. Bot. 46:3.24.

Howarth, C.J., K.P. Skøt, E. Weltzien R., R. Jayachandran, and F.R. Bidinger. 1995b. Assessment of screening methods for seedling thermotolerance. J. Exp. Bot. 46:3.25.

Hulbert, S.H., T.E. Richter, J.D. Axtell, and J.L. Bennetzen. 1990. Genetic mapping and characterisation of sorghum and related crops by means of maize DNA probes. Proc. Nat. Acad. Sic. USA, 97: 4251-4255.

Jones, E.S., C.J. Liu, M.D. Gale, C.T. Hash, and J.R. Witcombe. 1995. Mapping quantitative trait loci for downy mildew resistance in pearl millet. Theor. Appl. Gen. 91:448-456.

Joshi, N.L. 1987. Seedling emergence and yield of pearl millet on naturally crusted arid soils in relation to sowing and cultural methods. Soil Till. Res. 10:103-112.

Kameswara Rao, N., S. Appa Rao, M.H. Mengesha, and R.H. Ellis. 1991. Longevity of pearl millet (*Pennisetum glaucum*) seeds harvested at different stages of maturity. Ann. Appl. Biol. 119:97-103.

Kasalu, H., S.C. Mason, and G. Ejeta. 1993. Effect of temperature on germination and seedling emergence of grain sorghum genotypes. Trop. Agric. (Trinidad) 70:368-371.

Kelly, T.G., P. Parthasarathy Rao, E. Weltzien R., and M.L. Purohit. 1996. Adoption of improved cultivars of pearl millet in an arid environment: Straw yield and quality consideration in western Rajasthan. Exp. Agric. 32:161-171.

Khalifa, F.M., and C.K. Ong. 1990. Effect of supra-optimal temperatures on germination of pearl millet [*Pennisetum glaucum* (L.) R. Br.] hybrids. Ann. Arid Zone 29:279-288.

Klaij, M.C., and W.B. Hoogmoed. 1993. Soil management for crop production in the West African Sahel. II. Emergence, establishment and yield of pearl millet. Soil Till. Res. 25:301-315.

Krause, M.A., R.R. Denson, T.G. Baker, P.V. Preckerl, J. Lowenberg-Deboer, K.C. Reddy, and K. Maliki. 1990. Risk sharing versus low-cost credit systems for international development. American J. Agric. Economics 72:911-922.

Lawlor, D.J., E.T. Kanemasu, W.C. Albrecht III, and D.E. Johnson. 1990. Seed production environment influence on the base temperature for growth of sorghum genotypes. Agron. J. 82:643-647.

Levitt, J. 1980. Responses of plants to environmental stress. Vol. 1. Chilling, freezing and high temperature stress. Academic Press, New York.

Liu, C.J., J.R. Witcombe, T.S. Pittaway, H. Nash, C.T. Hash, C.S. Busso, and M.D. Gale. 1994. An RFLP based gene map of pearl millet (*Pennisetum glaucum*). Theor. Appl. Gen. 89:481-487.

Ludlow, M.M., and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Advances in Agronomy 43:107-153.

Lynch, P.J. 1994. Recurrent selection in pearl millet for improving stand establishment at high temperature. Plant Breeding 113:237-241.

Maiti, R.K., and G.L. Soto Gomez. 1990. Effect of four sowing date environments on growth, development and yield potential of 15 pearl millet cultivars [*Pennisetum americanum* (L.) Leeke] during autumn-winter seasons in Marin, N.L., Mexico. J. Exp. Bot. 41 (233):1609-1618.

Maiti, R.K., and L.S. Moreno. 1995. Seed imbibition and drying as a technique in evaluating sorghum lines for adaptation to dry sowing in the semi-arid tropics. Exp. Agric. 31:57-63.

Maiti, R.K., M. de la Rosa-Ibarra, and N.D. Sandoval. 1994. Genotypic variability in glossy sorghum lines for resistance to drought, salinity and temperature stress at the seedling stage. J. Plant Physiol. 143:241-244.

Maiti, R.K., P.S. Raju, and F.R. Bidinger. 1985. Studies on germinability and some aspects of pre-harvest physiology of sorghum grain. Seed Sci. Technol. 13:27-35.

Manga, V.K., and O.P. Yadav. 1995. Effect of seed size on developmental traits and ability to tolerate drought in pearl millet. J. Arid Env. 29:169-172.

Mason, S.C., J. Lasschuit, and J.M. Lasa. 1994. Interrelationship of sorghum coleoptile morphology with emergence potential in crusted soils. Eur. J. Agron. 3:17-21.

Mohamed, A., F.L. Barnett, R.L. Vanderlip, and B. Khaleeq. 1989. Emergence and stand establishment of pearl millet as affected by mesocotyl elongation and other seed and seedling traits. Field Crops Res. 20:41-49.

Mohamed, H.A., J.A. Clark, and C.K. Ong. 1985. The influence of temperature during seed development on the germination characteristics of millet seeds. Plant Cell Env. 8:361-362.

Mohamed, H.A., J.A. Clark, and C.K. Ong. 1988. Genotypic differences in the temperature responses of tropical crops. I. Germination characteristics of groundnut (*Arachis hypogea* L.) and pearl millet (*Pennisetum typhoides* S. & H.). J. Exp. Bot. 39 :1121-1128.

Mora-Aguilar, R., L.E. Mendoza-Onofre, and J.C. Molina-Moreno. 1992. Germination and viability of immature sorghum seeds under laboratory conditions. Sorghum Newsl. 33:63

More, H.G., B.C. Stenning, and N. Magan. 1992. Effect of high temperature treatment on disinfestation and quality characteristics of sorghum. Ann. Appl. Biol. 120:161-171.

Mortlock, M.Y., and R.L. Vanderlip. 1989. Germination and establishment of pearl millet and sorghum of different seed qualities under controlled high-temperature environments. Field Crops Res. 22:195-209.

M'Ragwa, L.R.F., C.E. Watson Jr., and L.M. Gourley. 1995. Selection response for seedling root length and coleoptile length in pearl millet. Crop Sci. 35:1032-1036.

O'Neill, M.K., and M. Diaby. 1987. Effects of high soil temperature and water stresses on Malian pearl millet and sorghum during seedling stage. J. Agron. Crop Sci. 159:192-198.

Ong, C.K., and J.L. Monteith. 1985. Response of pearl millet to light and temperature. Field Crops Res. 11:141-160.

Ouendeba, B., G. Ejeta, W.W. Hanna, and A.K. Kumar. 1995. Diversity among African pearl millet landrace populations. Crop Sci. 35:919-924.

Ougham, H.J., J.M. Peacock, J.L. Stoddart, and P. Soman. 1988. High temperature effects on seedling emergence and embryo protein synthesis of sorghum. Crop Sci. 28:251-253.

Ougham, H.J., and J.L. Stoddart. 1985. Development of a laboratory screening technique, based on embryo protein synthesis, for the assessment of high-temperature susceptibility during germination of *Sorghum bicolor*. Exp. Agric. 21:343-355.

Pardales, J.R. Jr., A. Yamaughi, and Y. Kono. 1991. Growth and development of sorghum roots after exposure to different periods of a hot root-zone temperature. Env. Exp. Bot. 31:397-403.

Payne, W.A., R.J. Lascano, L.R. Hossner, C.W. Wendt, and A.B. Onken. 1991. Pearl millet growth as affected by phosphorus and water. Agron. J. 83:942-948.

Peacock, J.M. 1975. Temperature and leaf growth in *Lolium perenne*. II. The site of temperature perception. J. Appl. Ecol. 12:115-123.

Peacock, J.M., P. Soman, R. Jayachandran, A.U. Rani, C.J. Howarth, and A. Thomas. 1993. Effects of high soil surface temperature on seedling survival in pearl millet. Exp. Agric. 29:215-225.

Peacock, J.M., W.B. Miller, K. Matsuda, and D.L. Robinson. 1990. Role of heat girdling in early seedling death of sorghum. Crop Sci. 30:138-143.

Pereira, M.G., M. Lee, P. Bramel-Cox, W.Woodman, J. Doebley, and R. Whitkus. 1994. Construction of an RFLP map in sorghum and comparative mapping in maize. Genome 37:236-243.

Radford, B.J., and R.G. Henzell. 1990. Temperature affects the mesocotyl and coleoptile length of grain sorghum genotypes. Aust. J. Agric. Res. 41:79-87.

Raj, L., and I.S. Khairwal. 1994. Rate of germination, seedling vigour and field emergence in pearl millet hybrids and their parents. Ann. Arid Zone 33:121-123.

Rebafka, F.-P., A. Bationo, and H. Marschner. 1993. Phosphorus seed coating increases phosphorus uptake, early growth and yield of pearl millet [*Pennisetum glaucum* (L.) R. Br.] grown on an acid sandy soil in Niger, West Africa. Fertilizer Res. 35:151-160.

Reddy, K.C., and P.L. Visser. 1993. Late planting effects on early versus late pearl millet genotypes in Niger. Exp. Agric. 29:121-129.

Richards, R.A. 1989. Breeding for drought resistance: Physiological approaches. p. 65-79. *In* Baker, F.W.G. (ed.) Drought resistance in cereals. CAB International, Wallingford, U.K.

Singh, J., O.P. Govila, and P.K. Agrawal. 1988. Preliminary results from a study of seed germinability of pearl millet (*Pennisetum typhoides* L.) F_1 hybrids and their parent during accelerated aging test. Seed Sci. Technol. 16:685-692.

Sivakumar, M.V.K., A.K.S. Huda, and S.M. Virmani. 1984. Physical environment of sorghum- and millet-growing areas in South Asia. p. 63-83. *In* Agrometeorology of sorghum and millet in the semi-arid tropics: Proceedings of the international symposium, 15-20 Nov 1982, ICRISAT Center, India. ICRISAT, India.

Smith, R.L., C.S. Hoveland, and W.W. Hanna. 1989. Water stress and temperature in relation to seed germination of pearl millet and sorghum. Agron. J. 81:303-305.

Soman, P. 1990. Development of a technique to study seedling emergence in response to moisture deficit in the field: The seed bed environment. Ann. Appl. Biol. 116:357-364.

Soman, P., R. Jayachandran, and F.R. Bidinger. 1987a. Uneven variation in plant-to-plant spacing in pearl millet. Agron. J. 79:891-895.

Soman, P., R. Jayachandran, and J.M. Peacock. 1992. Effect of soil crusting on seedling growth in contrasting sorghum lines. Exp. Agric. 28:49-55.

Soman, P., and J.M. Peacock. 1985. A laboratory technique to screen seedling emergence of sorghum and pearl millet at high soil temperature. Exp. Agric. 21:335-341.

Soman, P., J.M. Peacock, and F.R. Bidinger. 1984. A field technique to screen seedling emergence of pearl millet and sorghum through soil crusts. Exp. Agric. 20:327-334.

Soman, P., K.N. Rai, and F.R. Bidinger. 1989. Dwarfing gene effects on coleoptile length in pearl millet. Crop. Sci. 29:956-958.

Soman, P., and N. Seetharama. 1992. Genotypic and environmental variation in nodal root growth of post-rainy season (*rabi*) sorghum. Exp. Agric. 28:331-341.

Soman, P., T.J. Stomph, F.R. Bidinger, and L.K. Fussell. 1987b. Improvement in stand establishment in pearl millet. p. 159-171 *In* J.M. Menyonga et al. (eds.) Proceedings of an international drought symposium on food grain production in semi-arid Africa, held at the Kenyatta Conference Centre, Nairobi, Kenya, 19-23 May 1986. OAU/STRC-SAFGRAD, Burkina Faso.

Spencer, D.S.C., and M.V.K. Sivakumar. 1987. Pearl millet in African agriculture. p. 19-31. *In* Proceedings of the international pearl millet workshop, 7-11 April 1986, ICRISAT Center, India. ICRISAT, India.

Stomph, T.J. 1990. Seedling establishment in pearl millet [*Pennisetum glaucum* (L.) R.Br.]: The influence of genotype, physiological seed quality, soil temperature and soil water. Doctoral dissertation, University of Reading, 210pp.

Taylor, H.M. 1962. Seedling emergence of wheat, grain sorghum and guar as affected by rigidity and thickness of surface crusts. Soil Sci. Soc. America Proc. 26:431-433.

Vandenbelt, R.J., and J.H. Williams. 1992. The effect of soil surface temperature on the growth of millet in relation to the effect of *Faidherbia albida* trees. Agric. Forest Meteor. 60:93-100.

Van Oosterom, E.J., M.L. Whitaker, and E. Weltzien R. 1996. Integrating genotype by environment interaction analysis, characterization of drought patterns, and farmer preferences to identify adaptive plant traits for pearl millet. p. 383-402. *In* M. Cooper and G.L. Hammer (eds.) Plant adaptation and crop improvement. CAB International.

Vierling, E. 1991. The roles of heat shock proteins in plants. Ann. Rev. Plant Physiol. Plant Mol. Biol. 42:579-620.

Vierling, R.A., and H.T. Nguyen. 1992. Heat-shock protein gene expression in diploid wheat genotypes differing in thermal tolerance. Crop Sci. 32:370-377.

Waters, E.R., G.J. Lee, and E. Vierling. 1996. Evolution, structure and function of the small heat shock proteins in plants. J. Exp. Bot. 47:325-338.

Watts, W.E. 1971. Role of temperature in the regulation of leaf extension in *Zea mays*. Nature 229:46-47.

Weltzien, E., and G. Fischbeck. 1990. Performance and variability of local barley landraces in near-eastern environments. Plant Breeding 104:58-67.

Weltzien R., E., C.J. Howarth, R. Jayachandran, and F.R., Bidinger. 1994. Seedling thermotolerance: A comparison of screening methods. Agron. Abstracts, p. 113.

Weltzien R., E.M.L. Whitaker, and M.M. Anders. 1996. Farmer participation in pearl millet breeding for marginal environments. *In* P. Eyzaguirre and M. Iwanga (eds.) Participatory plant breeding. IPGRI, Rome, Italy.

Weltzien, E., and J.R. Witcombe. 1989. Pearl millet improvement for the Thar desert, Rajasthan, India. Vorträge für Pflanzenzüchtung 15:23-26.

Wilson, G.L., P.S. Raju, and J.M. Peacock. 1982. Effect of soil temperature on seedling emergence in sorghum. Indian J. Agric. Sci. 52:848-851.

Xu, G.W., C.W. Magill, K.F. Schertz, and G.E. Hart. 1994. A RFLP linkage map of *Sorghum bicolor* (L.) Moench. Theor. Appl. Genet. 89:139-145.

Yadav, O.P. 1994. Relative performance of pearl millet hybrids and open-pollinated varieties in arid environments. Internat. Sorghum Millets Newsl. 35:67-68.

Yadav, O.P., and V.K. Manga. 1995. Relative performance of pearl millet hybrids and varieties under rainfed conditions in Haryana, India. International Sorghum and Millets Newsletter 36:45-47.

Breeding for Pre- and Post-Flowering Drought Stress Resistance in Sorghum

D.T. Rosenow*, G. Ejeta, L.E. Clark, M.L. Gilbert,
R.G. Henzell, A.K. Borrell, and R.C. Muchow

Abstract

Drought stress is a major constraint to sorghum production worldwide. The stage of growth at which moisture stress occurs is important in determining the response of sorghum to soil moisture stress. Two distinctly different types of drought stress responses have been identified. One type (pre-flowering) is expressed when plants are under significant moisture stress prior to flowering during the panicle development stage. The other response (post-flowering) occurs when plants are under severe moisture stress during the grain-filling stage. The term "stay green" is used to describe post-flowering drought resistance. Plant symptoms indicating either a desirable or undesirable response to stress at these two stages have been described and can be visually rated in the field. The distinct visual responses are reliable indicators of a genotype's response to drought and are predictable and repeatable across locations and years under similar stress conditions. Large genetic variation exists among sorghum lines for response to pre- and post-flowering drought, and sources of resistance have been identified and utilized in breeding programs. The empirical approach, using conventional breeding techniques with large field screening nurseries in semi-arid environments, has proven successful in screening and breeding for drought resistance. However, variability in rainfall plus large interactions between timing of stress and stage of plant growth often make screening difficult and slow. Molecular markers have been identified for some pre- and post-flowering drought resistance traits and should improve the efficiency and speed of developing drought-resistant cultivars.

Drought stress is the primary factor reducing sorghum production worldwide. Sorghum possesses excellent drought resistance compared to most other crops and is traditionally grown in low rainfall areas of the world. This means the crop often experiences severe moisture stress during its growth. Improving drought resistance in sorghum would increase and stabilize grain and food production in low-rainfall, harsh environmental regions of the world.

Improving drought tolerance in sorghum has recently received increased emphasis both in the U.S. and internationally. Only in recent years have sorghum breeding and screening nurseries been devoted primarily to selecting for improved drought tolerance. This emphasis on field screening under severe drought stress at

D.T. Rosenow, Texas Agricultural Experiment Station, Texas A&M University, Lubbock, TX 79401; G. Ejeta, Department of Agronomy, Purdue University, West Lafayette, IN 47907; L.E. Clark, Texas A&M University Research Center, Vernon, TX 76384; M.L. Gilbert, Cargill Hybrid Seeds, P.O. Box 5645, Minneapolis, MN 55440; R.G. Henzell and A.K. Borrell, Queensland Department of Primary Industries, Hermitage Research Station, MS 508, Warwick, QLD 4370, Australia; R.C. Muchow, CSIRO, 306 Carmody Road, St. Lucia, QLD 4067, Australia. *Corresponding author.

different stages of growth has enhanced our understanding of drought tolerance in sorghum and how to manipulate it in breeding programs.

Drought or *drought stress*, as I will discuss it in this paper, refers primarily to inadequate soil moisture and not to direct effects of heat. High air temperature often is associated with soil moisture stress and certainly compounds the stress of plants. It sometimes is sufficient to kill plants, especially those weakened by soil moisture stress. However, this paper will deal only with drought as a soil moisture deficit or stress. The terms *drought resistance* and *tolerance*, as used in this paper, are essentially synonymous.

Although field screening nurseries under natural rainfall have proven successful, progress is often slow due to variability in timing and quantity of rainfall. New molecular techniques, especially molecular markers, are powerful tools in studying inheritance and increasing efficiency of selecting for complex traits. Molecular markers linked to quantitative trait loci (QTLs) should be useful in breeding programs to evaluate breeding progeny for the presence of genes conditioning drought tolerance in sorghum. The potential and techniques of molecular markers in breeding for drought resistance in sorghum are discussed by Tuinstra et al. (1996) and by Nguyen et al. elsewhere in these proceedings. Even if molecular markers prove successful and economical in sorghum, field evaluation still will be needed for many traits, and some drought evaluation under actual field conditions will be necessary to verify lab results and to determine performance in F_1 hybrids.

Drought Stress Responses in Sorghum

Growth stage of sorghum is important to understand when discussing drought resistance. The three growth stages of sorghum are:

1) Seedling establishment (early vegetative stage): GS1

2) Pre-flowering (panicle differentiation to flowering): GS2

3) Post-flowering (grain/flowering fill to physiological maturity of grain): GS3

Drought resistance at the seedling establishment or early vegetative stage (GS1) is obviously an important trait, especially in the harshest environments. Drought and/or heat at this stage can result in plant death and significant loss of stand. Although some screening techniques have been developed in Mali and at ICRISAT, and differences among genotypes exist, little has been done specifically to breed for this trait in sorghum or relate it to drought tolerance at other growth stages. Significant differences among genotypes for seedling survival have not been noted in the U.S.

Two distinctly different types of drought stress responses have been identified and described in sorghum and are related to the stage of growth at which stress occurs (Rosenow and Clark, 1981; Rosenow et al., 1983; Rosenow, 1993a, 1993b). The pre-flowering response occurs when plants are under significant moisture stress prior to flowering in GS2, specifically from panicle differentiation or shortly thereafter until flowering. The

post-flowering response occurs when plants are under severe moisture stress during the grain-filling stage (GS3), and especially during the latter portion of grain fill. Distinct visual plant symptoms indicate either a desirable or undesirable response to these two types of stress. These traits can be subjectively rated in the field.

Symptoms of pre-flowering drought stress susceptibility include: leaf rolling; uncharacteristic leaf erectness; leaf bleaching; leaf tip and margin burn; delayed flowering; "saddle effect," in which only end plants next to alleyways produce a panicle; poor panicle exsertion; panicle blasting and floret abortion; and reduced panicle size. Tolerance to pre-flowering drought stress is indicated by the alternative condition in each instance. Since the panicle is directly affected, severe pre-flowering stress can result in drastic reductions in grain yield.

Symptoms of post-flowering drought stress susceptibility include premature plant (leaf and stem) death or plant senescence, stalk collapse and lodging, and stalk rot (charcoal rot, *Macrophomina phaseolina*), along with a significant reduction in seed size, particularly at the base of the panicle. Tolerance is indicated when plants remain green and fill grain normally. Such green stalks also have good resistance to stalk lodging and to charcoal rot (Table 1). These cultivars are referred to as having good "stay green." This term is now commonly used by sorghum workers to describe post-flowering drought resistance and is considered an important drought resistance trait. The post-flowering response is most obvious and distinct in plants grown under favorable soil moisture and growth conditions until flowering, with severe water deficit developing during the late stage of grain fill. When water stress develops gradually and occurs over the entire season, these distinct stress responses may not be as obvious. Sometimes there is a blending of the pre-and post-flowering types of stress response. Whereas pre-flowering drought directly affects panicle size, grain number, and grain yield, post-flowering moisture stress losses occur primarily through lodged plants, but sometimes through reduced seed size.

High-yielding genotypes with a large grain sink size relative to the vegetative portion of the plant tend to be more sus-

Table 1. Relationship among stay green (LPD), lodging, and charcoal rot of selected sorghum lines.

	Lubbock-F403		Lubbock-F407		
Designation	LPD rating[1]	Lodging %[2]	LPD rating[1]	Charcoal rot rating[3]	Lodging %[2]
B1	2.3	0	2.9	0.7	0
B2-2	2.1	0	2.8	0.8	0
B35	2.2	0	2.7	0.5	0
BTx623	3.7	26	4.7	2.0	40
BTx625	4.7	80	4.6	3.4	38
BTx378	4.9	53	-	-	-
Tx7000	-	-	4.6	3.4	13

[1]Leaf and plant death rating: 1 = all green, 3 = 50% of leaf area dead, 5 = entire plant dead.
[2]Moisture stress type lodging.
[3]Stalks inoculated with infested toothpick rated on 1-5 scale: < 1 = < one internode infected, 3 = 3 internodes, 4 = > 3 internodes, 5= death, sclerotia.

ceptible to post-flowering drought stress than are low grain-producing genotypes. Susceptibility to charcoal rot is predisposed by severe water stress during the latter stages of grain fill. Because of this strong relationship, charcoal rot is treated primarily as a post-flowering drought stress problem. Genotypes are rated for presence or absence of premature leaf and plant death when they are under water stress at or near maturity — not by inoculation of stalks with charcoal rot infested toothpicks. Tenkouano et al. (1993) studied the genetics of nonsenescence (stay green) and charcoal rot in sorghum and reported that only a few genes were involved, some of which influenced both traits. The relationship between stay green, lodging resistance, and charcoal rot was discussed by Rosenow and Clark (1995) and is shown in Table 1.

Excellent sources of resistance to each type of stress (pre- and post-flowering) have been identified (Table 2). High levels of both types of resistance are generally not found in the same genotype. However, some genotypes possess good levels of resistance to both types. In some cases resistance is dominant while in others it is recessive, and this is important when breeding parental lines for hybrids.

Breeding and Screening Procedures

Several reviews and papers have been published on the use of physiological traits in sorghum to improve drought resistance and potential use in breeding pro-

Table 2. Lines with pre- and post-flowering drought tolerance sorghum.

Pre-flowering tolerant	Post-flowering tolerant
Tx7078	SC23-14 (IS 12543C)*
TAM 422	SC33-14 (IS 12553C)
Tx7000 (Caprock)	SC35-14 (IS 12555C)
Tx430 (Tx2536 x SC70-6)	B35 (SC35-6, IS 12555 der)
BTx623 (BTx3197 x SC170-6)	SC38-14 (IS 12558C)
BTx3197 (C. Kafir-60)	SC56-14 (IS 12568C)
Tx2536 (Y.E. x Feterita)	SC237-14 (IS 3071C)
Tx2737 (Y.E. deriv.)	SC265-14 (IS 6705C)
Tx432 (SC599-6 x SC110-9)	SC328-14 (IS 8263C)
P898012 (Feterita)*	SC599-14 (IS 17459C, Rio)
P954035 (SC33-9der)*	SC599-6 (R9188, Rio deriv.)
SC23-14 (IS 12543C)*	SC701-14 (IS 3462C)*
SC103-14 (IS 2403C)	SC1017-14 (IS 11549C)
SC414-12E (IS 2508 der)	P898012 (Feterita)*
SC701-14 (IS 3462C)*	P954035 (SC33-9 der)*
1790E (SC56 x SC33)*	BKS9
82BDM499 (SC173 x SC414)	KS19 (Y.E. deriv.)
P37-3 (Tx2794 x K22/35)	Tx2908 (R8503; SC 599-6 x Tx430))
P40-1 (Tx2794 x K22/35)	1790E (SC56 x SC33)*
TnGbResW	1778 (SC56 x SC170)
RS610 (Hybrid)	R1922 (SC56 x SC110)
Hageen Durra 1 (Hybrid)	88V1080 (Tx430 x R9188)
Early Hegari	(P407*?)UC(SC33der)
CSM-63* (Mali)	NSA440
Ajabsido (Sudan)	Karper 669
Koro Kollo (Sudan)	CSM-63* (Mali)
Segaolane (Botswana)	QL36 (Australian line)
El Mota (Niger)	BQL41 (Australian line)
(Many Commercial Hybrids)	(Few Commercial Hybrids)

*Both pre- and post-flowering tolerance

grams (Downes, 1972; Jordan and Monk, 1980; Jordan and Sullivan, 1982; Kramer, 1980; Levitt, 1972; Sullivan, 1972; Turner, 1979; Peacock and Sivakumar, 1987; Sullivan and Ross, 1979; Krieg, 1993; and Ludlow, 1993). These include traits such as heat tolerance, desiccation tolerance, osmotic adjustments, rooting depth, and epicuticular wax. Although technologies exist for evaluating these traits, little use has been made of them in breeding programs. Others have reported on the use of various breeding and screening techniques for drought resistance in sorghum (Blum, 1983, 1987; Christiansen and Lewis, 1982; Ejeta, 1987; Garrity et al., 1982; Jordan et al., 1983; and Seethrama et al., 1982). Some of these combine screening for physiological traits along with visual selection for agronomic adaptation. Little if any progress using specific physiological traits has been documented, partly because physiological mechanisms involved in drought tolerance are still poorly understood (Bonhert et al., 1995). It appears that individual physiological traits identified to date are not sufficiently related to overall drought response or field performance to merit selection based on them.

A recent review by Muchow et al. (1996) discusses recent advances and current needs in sorghum physiology. They cover yield accumulation and the physiological basis of the drought-resistant traits, including osmotic adjustment, stay green (leaf area maintenance), transpiration efficiency, and use of stem reserves in grain filling. The stay green trait has been successfully used in Australia to improve lodging resistance under terminal stress (Henzell et al., 1992; Henzell and Hare, 1996), with a positive association of stay green and grain yield under water-limited environments. Although the stay green trait also has been successfully used in Texas and by certain private companies to provide post-flowering drought resistance and lodging resistance (Rosenow and Clark, 1995; also see Johnson et al. elsewhere in these proceedings), the physiological basis for stay green is not well understood.

Previous papers have described certain aspects of evaluation for drought resistance in the Texas program (Clark et al., 1986; Rosenow, 1984, 1987, 1989, 1993a, 1993b; Rosenow and Clark, 1981, 1995; Rosenow et al., 1983; and Rosenow and Ejeta, 1985). The primary approach is to utilize naturally occurring soil moisture stress under the low-rainfall conditions of West Texas. Germplasm is evaluated in nurseries under dryland, low-rainfall conditions, and under limited irrigation where yield potential is expressed but post-flowering moisture stress is allowed to develop. In the dryland nurseries, pre-flowering stress commonly occurs. Large field screening nurseries are utilized at several locations with different stress environments, different planting dates, and different water regimes (amounts and timing). This approach helps to insure stress at different stages of growth. Sandy soil or shallow soil sites are best suited for pre-flowering evaluation, while heavier and deeper soils are best for evaluating post-flowering stress.

In the post-flowering screening nurseries, irrigation is applied during the early growth stages to produce good growth and yield expression. Irrigation is terminated prior to anthesis, allowing moisture stress to develop after flowering and intensify

during grain fill. In these nurseries, plots or entries are subjectively rated for the amount of premature leaf and plant death. Ratings are made on a 1 to 5 scale, where 1 = completely green, 3 = 50% of leaf area dead and 5 = all plants dead. Ratings are normally made at or soon after physiological maturity, but can be made anytime that differences appear among genotypes. Visual ratings on leaf death have been shown by Wanous et al. (1991) and Borrell et al. (1996) to be an excellent method of evaluating actual percentage of green leaf area. High correlations between visual stay green ratings and chlorophyll content (as measured by a chlorophyll meter) also support the use of visual ratings (see Nguyen et al., elsewhere in these proceedings). Percentage of plants lodged due to stress also is recorded. In West Texas, the nursery often is left standing for an extended period following maturity for exposure to strong winter winds and to allow stalk lodging to occur. This facilitates the identification of entries whose stalks are weakened by water stress. Knowledge of maturity is critical because sorghum is most susceptible to post-flowering stress during a period just prior to physiological maturity. Plants a few days earlier or later in maturity may show little premature senescence. Therefore, flowering notes are taken on all plots, and comparisons are made only among entries of similar maturities.

In pre-flowering screening nurseries where severe water deficits occur prior to flowering during the panicle development stage, subjective ratings can be recorded whenever distinct differences in drought response appear. Rating is done on a 1-5 scale, where 1 = excellent and 5 = very poor response. Prior to heading, ratings can be made on leaf stress symptoms that indicate drought susceptibility, such as rolling, excessive erectness, bleaching, and firing. Ratings can be made on each trait separately or combined into a single overall drought susceptibility rating. Leaf rolling is normally the first visible symptom of drought stress. Excessive leaf erectness usually follows. Some cultivars have erect leaves in the absence of stress, so care must be used when evaluating this trait. The leaf angle of the lower leaves generally indicates whether or not a cultivar has genetically controlled erect leaves. Leaf bleaching refers to a loss in green color during the hottest portion of the day, causing a bleached effect. Care also must be used when scoring this trait because there is a range from dark to light green leaf color among different genotypes, even in the absence of stress. Leaf margin and tip burn are usually the last vegetative drought responses to appear. Scoring of the early vegetative response is most efficient when done within related germplasm. Widely diverse material may give different appearing responses, with a poorer relationship of vegetative symptoms to eventual performance.

Some cultivars are susceptible to another kind of leaf necrosis called leaf firing, where large sections of the leaf die rapidly, usually at about flowering time. It is very genotype-specific and is likely due to high temperatures that exceed the temperature tolerance of the tissue in the portion of the leaf blade directly exposed to the sun. This type of leaf firing is different from the leaf margin and tip burn described previously and does not appear to correlate well with final yield. Drought-induced leaf necrosis is characterized by the absence of anthocyanin pigment and

is thus distinctively different from coloration due to other causes, such as disease or insect injury.

Later-appearing symptoms caused by moisture stress prior to flowering include delay in flowering, panicle and floret abortion, poor panicle exsertion, reduced panicle size, and the "saddle" effect. These symptoms can be rated individually or in combination. Delay in flowering is evaluated by comparison with non-stressed plantings. These late-appearing symptoms are the best evaluation of pre-flowering drought tolerance, and ratings may be made at or after maturity. Evaluation of pre-flowering drought tolerance in very early-maturing genotypes is difficult because they often escape water stress.

In field screening nurseries, standard checks are used every five or ten plots. Alternating every fifth plot with a pre-flowering tolerant, post-flowering susceptible line, such as Tx7078 or Tx7000, and a post-flowering tolerant, pre-flowering susceptible line, like B35-6 or R9188, provides a reference for comparison. By comparing ratings with those of the adjacent checks, we can adjust for variability within the field. Whenever possible, furrow-dikes are placed between beds in our dryland nurseries to encourage uniform water penetration and soil moisture. We maintain the furrow-dikes throughout the entire year to maintain a uniform soil moisture profile. We use short (5-6 m), single row plots in most screening nurseries. Multiple row plots are used only for special studies.

Although not identical in all aspects, several public and private sorghum breeding programs utilize the same principles as described for the Texas program. In the public breeding program in Queensland, Australia, breeding progeny are routinely rated in regular field breeding nurseries for premature leaf and plant senescence at or near physiologic maturity. The stay green trait from IS12555(SC35) has been successfully used in Australia to develop post-flowering drought stress resistance and lodging resistance in parental lines and commercial hybrids (Henzell et al., 1992; Henzell and Hare, 1996). At Purdue University, specific nurseries have been used in dry environments, such as Mexico, to screen for pre- and post-flowering drought response. In Sudan, nurseries in the past (Ejeta, 1987) have been designed to specifically evaluate for either pre- or post-flowering stress. Nurseries in the sandy soil, low rainfall areas consistently provided excellent pre-flowering stress. Nurseries in heavy, deep soils worked well for post-flowering evaluation due to the rapid cessation of rainfall at the end of the rainy season, or through irrigation manipulation.

Several private seed companies also now plant nurseries specifically to induce moisture stress at specific stages of growth. Cargill and Crosbyton both have nurseries for post-flowering stress. DeKalb had a charcoal rot screening nursery for many years, where post-flowering moisture stress was imposed. From this nursery several parental lines were developed that have shown excellent stay green, charcoal rot resistance, and lodging resistance (A.B. Maunder, 1996, personal communication). In recent years, DeKalb has used only a single pre-plant irrigation on nurseries in West Texas in an attempt to enhance both pre- and post-flowering stress in the same nursery. Pacific Seeds in Australia uses stay green evaluations similar to those used in the public program in Queensland.

In addition to field screening, sprinkler irrigation gradient systems have been used in dry environments to manipulate timing and quantity of water applied. The advantage is two-fold: researchers can a) evaluate plant response to a wide range of stress under otherwise identical conditions; and b) manipulate onset, cessation, and degree of stress. In these evaluations, it is important to recognize the different drought stress responses before interpreting results from the gradient system. Disadvantages of the system are the influence of wind on water distribution and the inability to control precipitation. The amount and frequency of irrigation may be less than ideal. However, reaction under the system in West Texas correlates well with our field evaluation. The use of gradients would be of little value in areas where rainfall is high during the regular crop season. Use of gradient systems may be of limited value in the off-season due to maturity changes and different yield responses, especially with photosensitive or partially photoperiod-sensitive sorghum affected by different day lengths. Line-source irrigation systems with drop nozzles can be very useful in field nurseries to manipulate the quantity and timing of irrigation.

Rainout shelters also are used to supplement evaluations made in field nurseries. Untimely rains often prevent evaluation or restrict field evaluations during the growing season. Rainout shelters can be used to improve the efficiency of selection by controlling both timing and amount of water applied, while otherwise maintaining a near normal field environment. Pre- and post-flowering stress ratings under shelters in Texas have corresponded well with known field reactions. Single-row plots of 400 breeding selections can be evaluated for the pre-flowering drought stress in one 40 ft x 60 ft (about 12 m x 18 m) area. Disadvantages are the initial cost and labor during the season. The shading effects during periods of damp rainy weather can have a detrimental effect on plant growth and development.

Another modified field technique uses large sheets of black plastic secured over the soil to exclude rainfall. Seed is then sown through small cross-cuts in the plastic, and as the plants grow, a rather watertight seal develops around the base of the stem (Borrell and Douglas, 1996).

Summary and Conclusions

The stay green trait has proven useful, using the empirical approach described, in enhancing post-flowering drought resistance and lodging resistance in parental sorghum lines and hybrids (Henzell et al., 1992; Henzell and Hare, 1996; Rosenow and Clark, 1995), but progress has been slow. Most commercial sorghum hybrids possess good resistance to pre-flowering drought stress, but only a few have good post-flowering resistance. Factors contributing to limited success in drought resistance breeding are: 1) lack of knowledge of inheritance of drought resistance traits; 2) the expense and time (often years) required to effectively screen breeding progeny; 3) variable testing environments giving different drought responses from year to year due to the timing of stress and stage of growth interaction; 4) concerns over negative yield relationships with drought resistance traits; 5) the emphasis on widely adapted hybrids with little effort directed to the lowest rainfall environments; 6) widely variable target environments; 7) lack of agronomically desirable sources of drought resistance, especially stay green;

8) the different pre-vs. post-flowering response of many sorghum lines; 9) the complex nature of drought and resistance and the many environmental and plant factors interacting with both; 10) lack of specific measurable traits associated with drought resistance; and 11) lack of knowledge about most of the genetic and physiological mechanisms involved in resistance.

The heritability of most drought resistance traits is not well understood, but there has been considerable effort the past few years studying the stay green trait. Walulu et al. (1994) determined that the stay green trait from SC35(IS12555), a Durra from Ethiopia, was conditioned by a single (or maybe two) genes primarily dominant in nature. This supports research by Tenkouano et al. (1993) showing that nonsenescence and charcoal rot resistance were controlled by only a few genes. A recent diallel study at ICRISAT by van Oosterom et al., (1996) on inheritance of stay green found that slow senescence rate was dominant over fast rate, and that inheritance of the onset of senescence under post-flowering stress was additive.

Observations in the Texas A&M sorghum breeding program have indicated that resistance in some stay green sources (SC35, SC33, SC56) is dominant in nature, while in others (SC599, Tx435, Tx2908, and B1, a BTx625 × B35 derivative) it is recessive, while in still others (BQL41, QL36, and NSA440) it is partially dominant. A large number of sorghum parental A and R lines were classified for stay green and lodging and for their expression of dominance in the stay green trait in F_1 hybrids (Rosenow and Clark, 1995; Rosenow et al., 1995). The best combination of resistance to pre- and post-flowering stress and good grain yield in an F_1 hybrid often has been a cross between a high stay green female and a high pre-flowering, high-yielding male parent. Pre-flowering stress resistance is primarily a dominant trait, at least in breeding hybrids. Hybrid vigor itself appears to contribute a significant degree of tolerance to pre-flowering stress. Breeding for improved grain yield in varieties and developing early-maturing, short, high-yielding hybrids with improved grain-to-stover ratio requires greater dry matter accumulation during grain fill, tending to make them relatively more susceptible to post-flowering stress.

In the World Sorghum Collection, good pre-flowering stress resistance is more common than post-flowering stress resistance. The Durra types from Ethiopia (e.g., SC35 and SC33), along with SC56, a Caudatum-Nigricans from Sudan, appear to be excellent sources of the dominant stay green. Exotic sorghum has been very useful in the Texas A&M drought breeding program, with the best sources of stay green and lodging resistance coming from converted sorghums from the Texas A&M/USDA-ARS Sorghum Conversion Program. Some introductions of photoperiod-insensitive sorghum, such as Ajabsido and Koro Kollo from Sudan, Segaolane from Botswana, and El Mota from Niger, possess outstanding pre-flowering drought resistance and can be used directly in breeding programs.

Concern has been expressed over the possible negative effect of drought resistance, especially stay green, on yield potential. Recent research in Australia should reduce these concerns. Borrell and Douglas (1996) have shown that sorghum hybrids with the stay green trait have a significant yield advantage when water is

limited during the grain fill period, with rate of leaf senescence negatively correlated (r^2=0.55*) with grain dry mass. In another study they assessed the relationship between rate of leaf senescence and total above-ground dry mass and harvest index. They found that rate of leaf senescence was negatively correlated with total above-ground dry mass under terminal stress (r^2=0.59**) but was not correlated with harvest index. This result is encouraging, suggesting that the association between high grain sink/source ratio and senescence under water stress as suggested by some workers can be broken. They also found that rate of leaf senescence was positively correlated with amount of stem resources mobilized, possibly explaining the association between stay green and lodging resistance. Henzell et al. (1992) reported a significant negative correlation between visual senescence ratings (higher = more senescence) and grain yield in 76 hybrids grown under water-limited conditions. Unpublished data in Texas indicate that some hybrids with excellent stay green will yield as well as non-stay green hybrids under high yield conditions (8000 plus kg ha^{-1}), while often being superior in yield under severe post-flowering stress. A summary of performance of commercial hybrid trials in Kansas by Johnson et al. (described elsewhere in these proceedings) showed that the grain yield of stay green hybrids was superior to that of two standard commercial hybrids. Tuinstra et al. (1996) reported that some pre-flowering resistance QTLs were associated with higher grain yield under fully irrigated conditions and with improved agronomic performance under drought conditions. Our research in Texas (Crasta, 1996, personal communication) determined that some QTLs for stay green in the cross B35 × Tx430 were positively associated with grain yield under stress and with yield under full irrigation.

We believe stay green and most other drought resistance traits can be manipulated in breeding materials quite independently of yield potential. Yield under good moisture, high-yield conditions does not necessarily have to be sacrificed, and grain yields will be superior under stress conditions.

Recent biotechnology research in sorghum at Texas A&M/Texas Tech and Purdue offers some exciting possibilities to enhance breeding for drought resistance. Molecular markers have been identified for some resistance in some pre-flowering drought stress parameters (Tuinstra et al., 1996) and for the post-flowering stress resistance trait stay green (Nguyen and Rosenow, 1993; also see Nguyen et al., elsewhere in these proceedings). Although five QTLs conditioning the stay green trait were identified with RFLP analysis of RILs from the cross B35 ×Tx7000, two linked QTLs appear to be the most important. The five QTLs are being evaluated for effectiveness in identifying stay green progeny in two test populations; they also are being used to screen progeny in a program to backcross stay green into elite parental lines.

Not only will molecular markers increase the efficiency of selection for drought resistance, but they also will be powerful tools for studying inheritance of complex traits and identifying new traits contributing to drought tolerance, yield, and agronomic performance. Fine mapping of QTLs and development of near-isogenic lines for specific DNA sequences that condition drought resistance should provide excellent materials for studying the physiological/biochemical processes involved with specific drought

resistance genes. Molecular biologists, crop physiologists and breeders working collaboratively will greatly increase the ability to develop new cultivars with higher levels of drought resistance.

Acknowledgement

Research partially funded by USAID Grant No. DAN-1254-G-00-0021-00 through INTSORMIL, the International Sorghum and Millet CRSP.

References

Blum, A. 1983. Genetic and physiological relationships in plant breeding for drought resistance. Agri. Water Manage. 7:195-202.

Blum, A. 1987. Genetic and environmental considerations in the improvement of drought stress avoidance in sorghum. p. 91-99. *In* Food grain production in semi-arid Africa. Proc. International Drought Symposium, May 19-23, 1986, Nairobi, Kenya.

Bonhert, H.J., D.E. Nelson, and R.G. Jensen. 1995. Adaptations to environmental stresses. Plant Cell 7:1099-1111.

Borrell, A.K., and A.C.L. Douglas. 1996. Maintaining green leaf area in grain sorghum increases yield in a water-limited environment. p. 315-322. *In* Proc. of the third Australian sorghum conf., 20-22 February 1996, Tamworth, NSW. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Borrell, A.K., R.G. Henzell, and A.C.L. Douglas. 1996. Visual rating of green leaf retention is highly correlated with measured green leaf area in sorghum. p. 323-326. *In* Proc. of the third Australian sorghum conf., 20-22 February, 1996, Tamworth, NSW. Australian Institue of Agricultural Science, Melbourne, Occasional Publication No. 93.

Christiansen, M.N., and C.F. Lewis. 1982. Breeding plants for less favorable environments. John Wiley & Sons, NY.

Clark, L.E., D.T. Rosenow, and C.J. Gerard. 1986. Management and breeding of sorghum to increase and stabilize production under drought and heat stress. p. 26-39. *In* Proc. forty-first annual corn and sorghum res. conf. Dec. 10-11, Chicago, IL.

Downes, R.W. 1972. Discussion: Physiological aspects of sorghum adaptation. p.256-274. *In* N.G.P. Rao and L.R. House (eds). Sorghum in the seventies. Oxford and IBH Publishing Co., New Delhi, India.

Ejeta, G. 1987. Breeding sorghum hybrids for irrigated and rainfed conditions in Sudan. p. 121-130. *In* Food grain production semi-arid Africa. Proc. International Drought Symposium, May 19-23, 1986, Nairobi, Kenya.

Garrity, D.P., C.Y. Sullivan, and W.M. Ross. 1982. Alternative approaches to improving grain sorghum productivity under drought stress. p. 339-356. *In* Drought resistance in crops with emphasis on rice. International Rice Research Institute (IRRI), Manila, Philippines.

Henzell, R.G., R.L. Brengman, D.S. Fletcher, and A.N. McCosker. 1992. Relationship between yield and non-senescence (stay green) in some grain sorghum hybrids grown under terminal drought stress. p. 355-358. *In* Proc. of the second Australian sorghum conf., 4-6 February 1992, Gatton, QLD. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 68.

Henzell, R.G., and B.W. Hare. 1996. Sorghum breeding in Australia: Public and private endeavours. p. 159-171. *In* Proc. of the third Australian conf., 20-22 February 1996, Tamworth, NSW. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Jordan, W.R., and R.L. Monk. 1980. Enhancement of drought resistance of sorghum: Progress and limitations. p.185-204. *In* Proc. 35th annual corn and sorghum res. conf., Am. Seed Trade Assn., Chicago, IL.

Jordan, W.R., and C.Y. Sullivan. 1982. Reaction and resistance of grain sorghum to heat and drought. p.131-142. *In* Sorghum in the eighties. ICRISAT. Proc. International Sorghum Workshop, Nov. 2-7, 1981. Hyderabad, India.

Jordan, W.R., W.A. Dugas, and P.J. Shouse. 1983. Strategies for crop improvement for drought-prone regions. Agric. Water Mag. 7:281-299.

Kramer, P.J. 1980. Drought, stress, and the origin of adaptations. p. 7-20. *In* N.C. Turner and P.J. Kramer (eds). Adaptation of plants to water and high temperature stress. Wiley-Interscience, New York.

Krieg, D.R. 1993. Stress tolerance mechanisms in above ground organs. p. 65-79. *In* Proc. of a workshop on adaptation of plants to soil stresses, August 1-4, 1993, Lincoln, NE. INTSORMIL Publication No. 94-2.

Levitt, J. 1972. Responses of plants to environmental stresses. Academic Press, New York.

Ludlow, M.M. 1993. Physiological mechanisms of drought resistance. p. 11-34. *In* Mabry, Nguyen, and Dixon (eds). Proc. of symposium on applications and prospects of biotechnology. Nov.

5-7, 1992, Lubbock, Texas, USA. IC2 Institute, Univ. of Texas, Austin.

Muchow, R.C., A.K. Borrell, and G.L. Hammer. 1996. Recent advances and current needs in sorghum physiology. p. 141-157. *In* Proc. of the third Australian sorghum conf., 20-22 February, 1996, Tamworth, NSW. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Nguyen, H.T., and D.T. Rosenow. 1993. Identification of molecular genetic markers linked to drought tolerance traits in grain sorghum. *In* Proc. 18th biennial grain sorghum res. and util. conf., Feb. 28 - March 2, 1993, Lubbock, Texas.

Peacock, J.M., and M.V.K. Sivakumar. 1987. An environmental physiologist's approach to screening for drought resistance in sorghum with particular reference to Sub-Saharan Africa. p. 101-120. *In* Food grain production in semi-arid Africa. Proc. International Drought Symposium, May 19-23, 1986, Nairobi, Kenya.

Rosenow, D.T. 1984. Breeding for resistance to root and stalk rots in Texas. p. 209-218. *In* Sorghum root and stalk rots: A critical review. Proc. of the Consultative Group Discussion on Research Needs and Strategies for Control of Sorghum Root and Stalk Rot Diseases, 27 November - 2 December 1983, Bellagio, Italy. ICRISAT, Patancheru, A.P. 502 324, India.

Rosenow, D.T. 1987. Breeding sorghum for drought resistance. p. 83-89. *In* J.M. Menyonga, Taye Bezuneh, and Anthony Youdeowei (eds). Food grain production in semi-arid Africa. Proc. International Drought Symposium, Sponsored by OAU/STRC-SAFGRAD. May 19-23, 1986, Kenyatta Conference Center, Nairobi, Kenya.

Rosenow, D.T. 1989. Breeding for drought tolerance, p.123-126. *In* Proc. International sorghum and millet CRSP conference. January 3-5, 1989, Scottsdale, Arizona. INTSORMIL Publication Number 89-3.

Rosenow, D.T. 1993a. Breeding for drought resistance under field conditions. p. 122-126. *In* Proc. 18th biennial grain sorghum research and utilization conference, Feb. 28 - March 2, 1993, Lubbock, TX.

Rosenow, D.T. 1993b. Screening plants for drought. p. 133-141. *In* Proc. of a workshop on adaptation of plants to soil stresses. August 1-4, 1993, Lincoln, NE. INTSORMIL Publication No. 94-2.

Rosenow, D.T., and L.E. Clark, 1981. Drought tolerance in sorghum. p. 18-30. *In* Proc. 36th annual corn and sorghum res. conf., December 9-11, 1981, Chicago, IL

Rosenow, D.T., and L.E. Clark. 1995. Drought and lodging resistance for a quality sorghum crop. p. 82-97. *In* Proc. Fiftieth annual corn and sorghum industry research conference, December 6-7, 1995, Chicago, IL. American Seed Trade Assn.

Rosenow, D.T., and G. Ejeta. 1985. Techniques and concepts on collaborative drought tolerance research sorghum in West Africa. p. 73-80. *In* Proc. INRAN/INTSORMIL/NCRP sorghum and millet workshop. Oct. 13-17, 1985. Niamey, Niger.

Rosenow, D.T., J. E. Quisenberry, C.W. Wendt, and L.E. Clark. 1983. Drought tolerant sorghum and cotton germplasm. Agricultural Water Manag. 7:207-222.

Rosenow, D.T., C.A. Woodfin, M.S. Beder, G. Gebeyehu, A.N. McCosker, and H.T. Nguyen. 1995. Stay green reaction of sorghum lines in F1 hybrids. p. 49. *In* Proc. 19th biennial grain sorghum research and utilization conference, March 5-7, 1995, Lubbock, TX.

Seethrama, N., B.V. Subba Reddy, J.K. Peacock, and F.R. Bidinger. 1982. Sorghum improvement for drought resistance. p. 317-356. *In* Drought resistance in crop plants with emphasis on rice. IRRI, Philippines.

Sullivan, C.Y. 1972. Mechanisms of heat and drought resistance in grain sorghum and methods of measurement. p. 247-163. *In* N.G.P. Rao and L.R. House (eds). Sorghum in the seventies. Oxford and IBH Publishing Co., New Delhi, India.

Sullivan, C.Y., and W.M. Ross. 1979. Selecting for drought and heat resistance in grain sorghum. p. 263-281. *In* H. Mussell and R.C. Staples (eds). Stress physiology in crop plants. Wiley- Interscience, New York.

Tenkouano, A., F.R. Miller, R.A. Frederiksen, and D.T. Rosenow. 1993. Genetics of nonsenescence and charcoal rot resistance in sorghum. Theor. Appl. Genet. 85:644-648.

Tuinstra, M.R., E.M. Grote, P.B. Goldsbrough, and G. Ejeta. 1996. Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. Crop Sci. 36:1337-1344.

Turner, N.C. 1979. Drought resistance and adaptation to water deficits in crop plants. p. 343-372. *In* H. Mussel and R.C. Staples (eds). Stress physiology in crop plants. Wiley-Interscience. New York.

van Oosterom, E.J., R. Jayachandran, and F.R. Bidinger. 1996. Diallel analysis of the stay-green trait and its components in sorghum. Crop. Sci. 36:549-555.

Walulu, R.S., D.T. Rosenow, D.B. Wester, and H.T. Nguyen. 1994. Inheritance of the stay green trait in sorghum. Crop Sci. 34:970-972.

Wanous, M.K., F.R. Miller, and D.T. Rosenow. 1991. Evaluation of visual rating scales for green leaf retention in sorghum. Crop Sci. 31:1691-1694.

Part A

Use of Biotechnology in Sorghum Drought Resistance Breeding

Henry T. Nguyen*, Wenwei Xu, Darrell T. Rosenow, John E. Mullet, and Lynne McIntyre

Abstract

Drought is the most prevalent abiotic stress limiting plant growth and productivity. Selection for drought resis'tance is difficult due to the timing and intensity of water deficit stress and large interactions between the plant (especially at the growth stage) and other environmental factors. The inability to rapidly and precisely screen large breeding populations for drought resistance traits such as stay green and osmotic adjustment limits selection progress in traditional breeding programs. Molecular marker technology provides a powerful tool to overcome this selection problem and to dissect the genetic basis of drought resistance traits in plants. This paper reviews the current status, challenges, and perspectives in genome mapping, gene tagging, marker-assisted selection, and genetic engineering for the improvement of drought resistance in sorghum.

Drought is the most prevalent abiotic environmental stress factor limiting plant growth, survival, and productivity (Bohnert and Jensen, 1996; Boyer, 1982). In response to water deficit, plants have developed adaptive mechanisms to overcome drought. Drought resistance is the phenotypic expression of a number of morphological characteristics and physiological mechanisms, including drought escape, dehydration avoidance, and dehydration tolerance (Ludlow, 1993). Sorghum originates in the dry areas of Africa and is a major crop in the arid and semi-arid regions in the U.S. and the world due to its adaptation to stressful environments.

Drought resistance in sorghum is a complex trait affected by several interacting plant and environmental factors. Over the past 15 years, Dr. Darrell Rosenow and his co-workers have focused considerable effort on drought resistance as a primary breeding objective. They have found that the growth stage (GS) at which moisture stress occurs is very important in determining the response or reaction of sorghum to water stress. Using field screening nurseries in West Texas, they have identified and described two distinct responses to drought stress in sorghum (Rosenow and Clark, 1995). The pre-flowering response is expressed when plants are stressed during panicle differentiation prior to flowering (GS-2). The other distinct response, post-flowering, is expressed when moisture stress occurs during the grain filling stage (GS-3).

Henry T. Nguyen, Plant Molecular Genetics Laboratory, Department of Plant and Soil Science, Mail Stop 2122, Texas Tech University, Lubbock, TX 79409 and Texas A&M University Agricultural Research and Extension Center, Route 3, Box 219, Lubbock, TX 79401; Wenwei Xu, Plant Molecular Genetics Laboratory, Texas Tech University; Darrell T. Rosenow, Texas A&M University Agricultural Research and Extension Center; John E. Mullet, Department of Biochemistry and Biophysics, Texas A&M University; Lynne McIntyre, CSIRO Division of Tropical Crops and Pastures, Australia. *Corresponding author.

Stay Green Trait and Drought Resistance in Sorghum

Post-flowering resistance is especially critical because the negative impact of drought on yield is important at this stage of development. Yield reduction can result from reduced seed size, premature plant death, stalk rot, and lodging of post-flowering drought-susceptible cultivars. The term stay green has been used to describe the post-flowering drought resistance response (Rosenow and Clark, 1995).

Drought stress during the post-flowering period accelerates senescence by driving many processes in the same direction as normal senescence (Nooden, 1988). Senescence is an orderly loss of normal functions. The processes of senescence are internally programmed. Under abiotic stress conditions, such as post-flowering drought stress, early onset of senescence affects the assimilatory capacity needed to avoid drastic reduction in grain filling. Therefore, any defense mechanism that postpones senescence and keeps the leaves green will benefit the crop.

In sorghum, stay green genes confer resistance to post-flowering drought stress by preventing the premature death of leaves and stems, plant senescence, stalk lodging, and charcoal rot disease when the plants are exposed to moisture stress during the late stages of grain development. In field performance tests of B35 (stay green line) and Tx7000 (non-stay green line) under post-flowering drought stress and fully-irrigated conditions (no drought stress in the entire growth season), B35 retained much more chlorophyll and lost much less in grain yield under drought stress than did Tx7000 (W.W. Xu, 1996, personal communication). Under severe post-flowering drought conditions, the hybrids from non-stay green parents showed about 20-55% lodging compared to less than 10% lodging in the hybrids with one stay green parent (D.T. Rosenow, 1996, personal communication).

Grain yield and lodging are critically important to producers and are often related. The stay green trait directly benefits sorghum producers by reducing moisture stress-type lodging associated with premature leaf and stalk death. The lodged plants cannot be harvested by combine, resulting in a complete loss of grain of lodged plants. There is a high correlation between a good stay green rating and resistance to lodging. Grain yield is an important consideration when attempting to improve drought resistance. The stay green hybrids (those with A35, the male sterile line of B35) yield as well or better than standard leading commercial hybrids under stress levels, while at the same time exhibiting a good stay green rating and lodging resistance. These findings emphasize the stay green trait as an important target for manipulation aimed to stabilize sorghum yield in drought conditions.

The post-flowering drought response has been observed to be heritable and can be transferred to progenies through conventional breeding methods. Genetic studies have indicated dominant action of major genes. Broad-sense and narrow-sense heritability estimates were 0.80 and 0.60, respectively, indicating that the stay green trait is heritable and that progress from selection can be attained (Walulu et al., 1994). A recent diallel study at the International Crops Research Institute for the Semi Arid Tropics (ICRISAT) showed that inheritance of the onset of senescence under post-flowering drought

stress was additive, but a slow senescence rate was dominant over a fast rate (van Oosterom et al., 1996).

Most commercial sorghum hybrids in the United States possess good tolerance to pre-flowering drought stress but little or no post-flowering stress tolerance. A limited number of sorghum lines with the stay green genes have been identified. Most of these have been found in converted exotic lines from the collaborative Texas A & M University/USDA-ARS Sorghum Conversion Program.

Osmotic Adjustment and Drought Resistance in Sorghum

A common response to water deficit in plants is the accumulation of osmoprotectants such as sugars and amino acids. Osmotic adjustment (OA), an important physiological component of drought resistance that affects crop plant performance under drought stress, has received increasing attention in recent years. As defined by Blum et al. (1996), "osmotic adjustment involves the net accumulation of solutes in a cell in response to a fall in the water potential of the cell's environment. As a consequence of this net accumulation, the osmotic potential of the cell is lowered, which in turn attracts water into the cell and tends to maintain turgor pressure." Osmotic adjustment is important in drought resistance because it allows plants to retain higher turgor at a given level of plant water deficit and to subsequently support carbon assimilation and growth under stress.

Sorghum has a relatively high capacity for OA under water deficit, compared to maize; it also shows diversity for OA, especially for materials evolved in different climates. Variation in OA among sorghum genotypes was found to range from null to 1.7 Mpa (Blum and Sullivan, 1986). In a biparental progeny genetic study, Basnayake et al. (1995) reported that two independent major genes (*oa1* and *OA2*), with some minor effects, control OA in sorghum.

Blum and Sullivan (1986) found that landraces of sorghum from dry habitats had relatively greater capacity for OA than landraces from more humid habitats. This capacity was related to better plant growth under drought stress. Recently it has been clearly demonstrated that OA has a direct positive effect on yield under drought stress for different sorghum genotypes (Ludlow et al.,1990; Santamaria et al.,1990). The effect of OA on sorghum productivity under drought stress is largely ascribed to an increase in root size, root length density, and soil moisture extraction (Tangpremsri et al., 1991a, 1991b). Greater soil moisture extraction is expected to reflect better leaf water status and higher rates of photosynthesis. Ludlow (1993) stated that "OA can have up to 30% yield advantage in water limited conditions." In spite of the positive influence of OA as a drought resistance mechanism, breeding programs have been slow to adopt this trait.

Molecular Marker Technology and Progress in Sorghum Genome Mapping

Selection for drought resistance is difficult due to the timing and intensity of water deficit and interactions between the plant and other environmental factors (especially in the growth stage). Many past studies on drought tolerance have monitored the physiological status of stressed plants compared with unstressed controls, but in general have not included molecu-

lar and genetic analysis of stress tolerance principles (Bohnert et al., 1995).

Rapid and precise evaluation of large breeding populations for stay green and OA is the key to incorporation of these traits in breeding objectives. However, accurate field evaluation for stay green depends on the natural precipitation pattern. Drought is unpredictable in its occurrence, severity, timing, and duration. Its effects are often compounded by other abiotic and biotic stresses, such as extremes of temperature and pathogen and insect damage. Screening for OA currently requires complex measurement procedures and is time-consuming and tedious. Consequently, progress in improving sorghum drought resistance with conventional breeding methods has been slow. Current advances in molecular mapping and plant transformation techniques will provide powerful tools to investigate cause-and-effect relationships between physiological mechanisms and drought resistance, and eventually to improve drought resistance.

Since the pioneer work in sorghum genetics by Graham in 1916, over 50 mutant genes have been identified and used in sorghum breeding (Doggett, 1988). Despite the success of the morphological markers and isozymes, new types of genetic markers have been developed to greatly enhance genome analysis and gene mapping. Since the first introduction of RFLP markers in genetic mapping (Botstein et al., 1980), molecular markers have opened a new era for plant genetics and breeding. Today, genetic markers available for plant geneticists and breeders include morphological markers, isozymes, RFLPs, RAPDs, microsatellites, sequence-tagged sites, and AFLPs.

Significant progress has been made toward the molecular mapping of the sorghum genome. Several linkage maps have been published and some of them are already highly saturated (Hulbert et al., 1990; Binelli et al., 1992; Whitkus et al.,1992; Berhan et al., 1993; Pereira et al., 1994; Chittenden et al., 1994; Xu et al., 1994; Ragab et al., 1994; Tao et al, 1996; W.W. Xu et al., 1996, personal communication). Most of the maps have been developed with F_2 populations and have been constructed mainly with sorghum and maize RFLP probes. Recently, three sorghum RFLP linkage maps have been constructed by Texas Tech University (TTU) and CSIRO-DTCP using recombinant inbred lines (RILs). TTU has constructed two maps derived from the crosses of B35 × Tx7000 and B35 × Tx430 while the CSIRO map is derived from a cross between two inbred lines, QL39 and QL41. Another sorghum RFLP map using RILs from the cross IS3260C × Btx623 is being constructed in the laboratory of Dr. Gary Hart at Texas A&M University.

Sorghum is a diploid cereal with a relatively small genome (748-772 Mbp; Arumuganathan and Earle, 1991). Although it has the same number of chromosomes (2n = 20) as maize, its genome is about three times smaller than that of maize. Sorghum is well known for its drought resistance. Success in mapping genes for drought resistance in this species could serve as a cereal crop model. Map-based cloning using chromosomal landing/walking would be easier in a species with a small genome.

Moreover, sorghum could provide a source of genes for other crops such as maize in which improved drought tolerance is of prime importance. Because of many similarities in the genomes of sorghum and other major cereal crops, the molecular markers tightly linked to the drought tolerance in sorghum may directly benefit other cereal crops. The isolation of a gene based only on the phenotype and map position, referred to as map-based gene cloning (Tanksley et al., 1995), has been successfully used for cloning several genes such as the disease resistant gene *Pto* in tomato (Martin et al., 1993). High-resolution mapping of the target gene is the basis of map-based gene cloning. A sorghum bacterial artificial chromosome (BAC) library has been constructed from the inbred BTx623 at Texas A&M University (Woo et al., 1994) for physical mapping. The molecular mapping of genes controlling stay green and OA in sorghum will open the way for future cloning of such genes and their insertion into drought susceptible sorghum lines or other crops such as maize.

Using recombinant inbred line populations from B35 × Tx 7000, B35 × Tx430, and QL39 × QL41, molecular markers associated with stay green quantitative trait loci (QTLs) have been identified. Work on pre-flowering traits is in progress at TTU, since field conditions have not been consistent over the past three years. Molecular markers linked to OA genes could be identified in the TTU populations. Significant genetic variation for OA in the B35 × Tx430 recombinant inbred line population offers a good possibility for identifying suitable molecular markers for this trait and eventually incorporating them as selection criteria in sorghum breeding programs.

Tagging QTLs Associated with Drought Resistance in Sorghum

Excellent reviews of QTL-tagging have been presented by Tanksley (1993) and Dudley (1993). The underlying genetic basis of using molecular markers to tag the quantitative trait loci is the linkage disequilibrium between alleles at the marker locus and alleles at the QTL. Normally, it is hard to determine whether the detected effect linked with a marker locus is due to one or more linked genes affecting the trait; therefore, the term QTL may describe a region of a chromosome that has a significant effect on a quantitative trait.

Experiments have shown a single "major" QTL can account for 10-50% of phenotypic variation in segregating populations (Tanksley, 1993). Several statistical methods have been developed for systematically searching for QTLs (reviewed by Dudley, 1993; Tanksley, 1993; and Zeng, 1994). Two methods are now widely used: point analysis of one-way ANOVA (Stuber et al., 1992) with SAS (SAS, 1990) and interval mapping with a computer program (such as MAPMAKER/QTL; Lander et al., 1987). All these methods have pros and cons. For example, the interval-mapping algorithm of MAPMAKER/QTL analyzes one trait at a time. However, many traits are genetically correlated. New methods have been developed to fulfill the needs of specific experiments. One of them is composite interval mapping, which combines interval mapping with multiple regression and can analyze several traits at a time (Zeng, 1994; Jiang and Zeng, 1995), and its accompanying computer program, Cartographer, recently released by scientists at

North Carolina University (Jiang and Zeng, 1995).

At TTU, using two recombinant inbred line (RIL) populations developed from the crosses B35 × Tx7000 and B35 × Tx430, QTLs associated with the stay green trait in sorghum (post-flowering drought resistance) have been mapped (W.W. Xu, 1996, personal communication). Obviously, accurate phenotype determination and estimates of genotype э environment interactions are crucial for QTL mapping. The RIL populations allow extensive replicated trials and are ideal genetic materials for mapping drought resistance. The RILs were evaluated in three locations of West Texas from 1993 to 1995. Excellent data were obtained on the stay green trait in 1993 and 1994. Major QTLs of the stay green trait have been located on linkage groups C, G, and H, all together accounting for about 48% of the phenotypic variation. QTLs on linkage group C alone explain about 38% of phenotypic variation. The map resolution at the QTL intervals varies from ~5 cM for QTLs on linkage group C to over 10 cM on linkage groups G and H. QTLs for plant height, maturity, and yield traits are being analyzed, and their relationship to the stay green QTLs will be investigated.

Molecular markers for the stay green trait also have been developed in Australia using an F_6 RIL population derived from a cross between two elite sorghum inbred lines, QL39 and QL41. Both lines were developed by the Queensland Department of Primary Industries, and have been used widely in Australian sorghum breeding programs. QL39 is a senescence line and QL41 is a non-senescence (stay-green) line derived from a cross between B35 and QLD. One hundred and sixty RILs were evaluated in two different locations in Australia in 1994/95 and 1995/96 and on location in India in 1995/96. Associations between RFLP markers and stay green were found in several regions of linkage groups B, D, G, and H. A graphical genotype of QL41 showed that at least two of these regions were inherited from B35. In addition, data from pedigree analysis showed strong evidence of selection for one of these regions. An attempt has been made to match these chromosome regions with the regions identified by Xu et al. at TTU; however, it is difficult to match linkage groups at this stage due to insufficient numbers of common markers.

Recently, a project has been initiated at TTU to identify molecular markers linked to genes conferring osmotic adjustment and its solute components in sorghum under drought stress, using an F_8 recombinant inbred line population from B35 × Tx430. Osmotic adjustment differs significantly between B35 and Tx430. The pilot experimental data showed that Tx430 had a significantly higher OA (0.87 MPa) than B35 (0.57 MPa), which agrees with the findings of Ackerson et al. (1980). The F_8 RILs with almost 100% homozygosity at all loci, can be maintained permanently and used in replicated experiments for accurate measurement of OA and other agronomic traits.

Transgenic Strategy

Genetic engineering of a foreign gene into plants is also a new approach to improve drought resistance. Tarczynski et al. (1993) introduced into tobacco plants

a bacterial gene that encodes mannitol 1-phosphate dehydrogenase. The tobacco plant does not normally produce and accumulate mannitol, but the transgenic tobacco plants synthesize and accumulate the sugar alcohol mannitol. They showed an increased ability to tolerate high salinity due to the production of the osmolyte mannitol. Similarly, Holmstrom et al. (1996) spliced the gene encoding the trehalose-6-phosphate synthase subunit (TPS1) of yeast trehalose synthase to the promoter of the Rubisco small subunit gene, *ats1*, from *Arabidopsis*, and the gene construct was transferred to tobacco by *Agrobacterium*-mediated transformation. When three-week old seedlings were subjected to air-drying, the control seedlings showed signs of wilting after two hours of drying, but the transgenic plants were only marginally affected. After rehydration, transgenic plants recovered turgor and regrew, but the controls died. The synthesis of small amounts of the osmoprotectant trehalose in tobacco greatly increased the plants' ability to survive drought.

Foreign DNA can be introduced into plants through transformation with *Agrobacterium*, introduction of DNA into protoplasts via polyethylene glycol or electroporation, microinjection, and microprojectile bombardment (Potrykus, 1990). In sorghum, transformation of protoplasts by electroporation (Battraw and Hall, 1991) or cell suspensions by microprojectile bombardment (Hagio et al., 1991) resulted in stable expression of transferred genes; however, transgenic plants were not obtained. Scientists led by Dr. Paul M. Hasegawa at Purdue University obtained transgenic sorghum plants after microprojectile bombardment of immature zygotic embryos (Casas et al., 1993). More recently, scientists in Australia also have reported successful transformation of sorghum using microprojectile bombardment (Rathus et. al, 1996).

Application of *Agrobacterium*-mediated gene transfer has been limited until recently in dicotyledonous plants. High efficiency transformation has been established in wheat (Mooney et al., 1991), rice (Hiei et al., 1994), and maize (Ishida et al., 1996). Transgenic sorghum plants were produced via the *Agrobacterium*-mediated method by Dr. Roberta Smith's laboratory at Texas A&M University; however, the efficiency was relatively low. Several factors affect the efficiency of transformation, including the types and stages of tissues infected, the concentration of *A. tumefaciens*, composition of media for tissue culture, selection marker genes, kinds of vectors, and the plant genotype (Ishida et al., 1996).

In addition to physical mapping and map-based cloning of genes, large insert DNA clones such as YACs and BACs can be directly introduced into the desired plant. Stable transformations have been obtained after microprojectile particle bombardment of tomato cell cultures with plasmid and YAC DNA (about 50 kb; Van Eck et al., 1995). Hamilton et al. (1996) recently reported a new binary bacterial artificial chromosome (BIBAC) vector capable of transferring at least 150 kb of foreign DNA into a plant nuclear genome in conjunction with an enhanced system for *Agrobacterium*-mediated plant transformation. They have introduced 150 kb human genomic DNA into tobacco and obtained stable transgenic plants. The ability to introduce high molecular weight

DNA into plants may accelerate gene identification and genetic engineering of plants.

Marker-Assisted Selection for Drought Resistance in Sorghum

Comprehensive sorghum genome mapping and QTL analyses have produced significant information and powerful tools for improving the drought resistance and grain yield in sorghum. Essentially they provide two new approaches. One is to conduct early generation selection and/or gene introgression (backcrossing) by using molecular markers tightly linked to drought resistance genes. The other is to perform high-resolution mapping of the QTLs and to clone the QTLs via map-based cloning techniques, followed by subsequent transformation of these clones into sorghum.

Like most cereal mapping projects, sorghum mapping programs around the world have been using RFLP markers extensively. The common RFLP markers used in various mapping populations and species serve as the backbone of the genetic map and as connecting bridges for integration with other mapping information. Comparative genome mapping has shown that the genome of major grass species (including wheat, maize, foxtail millet, sugarcane, and sorghum) can be aligned by dissecting the individual chromosome into segments and rearranging these linkage blocks into highly similar structures (Moore et al., 1995). Thousands of RFLP clones have been developed and mapped for various plant species, and many are available for public use. For example, sorghum genomic DNA clones are now available from the laboratories of Dr. Gary Hart and Dr. Andy Paterson at Texas A&M University; maize genomic and cDNA clones are available from the Maize RFLP Lab at University of Missouri-Columbia. Rice, oat, wheat, and barley genomic and cDNA clones can be obtained from the laboratories of Dr. Steve Tanksley, Dr. Susan McCouch, and Dr. Mark Sorrell at Cornell University; Dr. Bikram Gill at Kansas State University; Dr. A. Kleinfofs at Washington State University; Dr. Mike Gale at John Innes Center of UK; and Dr. Sasaki at the Japanese Rice Genome Program. The wealth of information available for both sorghum and many other grass species (especially maize and rice) serves as a source of potential DNA markers to conduct genetic mapping and molecular breeding in sorghum. Such comprehensive information can be readily accessible from the plant genome databases (Web site http://probe.nalusda.gov:8300) at the USDA-National Agricultural Library.

High-throughput PCR-based DNA markers, particularly AFLP, have been employed to locate the QTLs associated with the traits of interest in high-density molecular linkage maps. AFLP technology is based on the selective PCR amplification of restriction fragments from a total digest of genomic DNA (Vos et al., 1995; Thomas et al., 1995). AFLP analysis provides a rapid and efficient technique for detecting a large number of DNA markers. Compared to RFLPs, the AFLP technique produces more markers in a limited time and can be automated using robotics for high-throughput analysis. Fully automated instruments also have been developed. AFLP markers are currently used in localized and global mapping of the sorghum genome in Dr.

Henry Nguyen's laboratory. Progress in technology and genetic mapping offers great opportunities for biotechnology to be integrated into existing sorghum breeding programs in order to transfer and combine genes rapidly and easily.

Successful detection of QTLs with molecular markers has been reported for economically important traits in numerous crops (Stuber et al., 1992; Tanksley, 1993). Relative to phenotypic recurrent selection, marker-assisted selection (MAS) would produce rapid responses early in the selection process. Linkage distance between markers and QTLs is the factor which most limits the response from MAS. Marker-assisted selection is more effective when fewer QTLs control the trait (Edwards and Page, 1994). In maize, marker-assisted backcrossing was used to transfer target QTLs into elite inbred lines B73 and Mo17 (Stuber, 1995). The hybrids from enhanced lines yielded 15% higher than the checks, demonstrating MAS can be successfully employed to manipulate complex traits.

Marker-assisted selection consists of two steps: 1) identifying the association between marker alleles and the genes or QTLs controlling the traits, and 2) utilizing the association to develop improved lines or populations. Generally the first step involves characterization of the donor parent and determination of the polymorphic molecular markers between the donor parent and target parent. Then one needs to decide which restriction enzyme-probe combinations to use for the RFLP markers, and the appropriate restriction enzymes and selective primers to use for the AFLP markers. These markers should be within the vicinity of the QTLs or closely linked to the specific genes. Once the marker loci and specific marker alleles (i.e. bands) are chosen, they can be traced in the selection process.

Figure 1 outlines a marker-assisted backcrossing program currently used by TTU to introgress the stay green QTLs from B35 to Tx7000. Molecular markers can be used to select drought-resistant plants without testing the backcross progenies in the drought-stressed conditions. In addition, the selfing step in traditional backcross breeding has been eliminated. The backcross progenies from this scheme will carry the cytoplasm from B35. In the last backcross step, it may be desirable to use Tx7000 as the female parent to make all the NILs have the same cytoplasm as Tx7000.

A bagged but un-emasculated B35 plant was pollinated with Tx7000 and the derived seeds were used in the next step. True hybrid plants were identified with a co-dominant RFLP marker. The selected plants were hand-emasculated and backcrossed to Tx7000. In the spring of 1996, about 120 (B35 × Tx7000) BC_1F_1 seeds were planted in the greenhouse. At the six-leaf stage, leaf samples were harvested from each plant. The DNA from each plant was analyzed with RFLP markers from the stay green QTL regions.

The genomic DNAs from (B35 × Tx7000) BC_1F_1 plants grown in the greenhouse were digested with *Hin*dIII and hybridized with clone TxS713 (Figure 2). The plants with both bands A (from B35) and B (from Tx7000) are heterozygous at this locus and are the candidates for continued backcrossing with the recurrent parent Tx7000. Those with band B do not carry stay green genes and are discarded. Those with band A are either from selfed seeds or from recombination, and therefore are not selected for the next step.

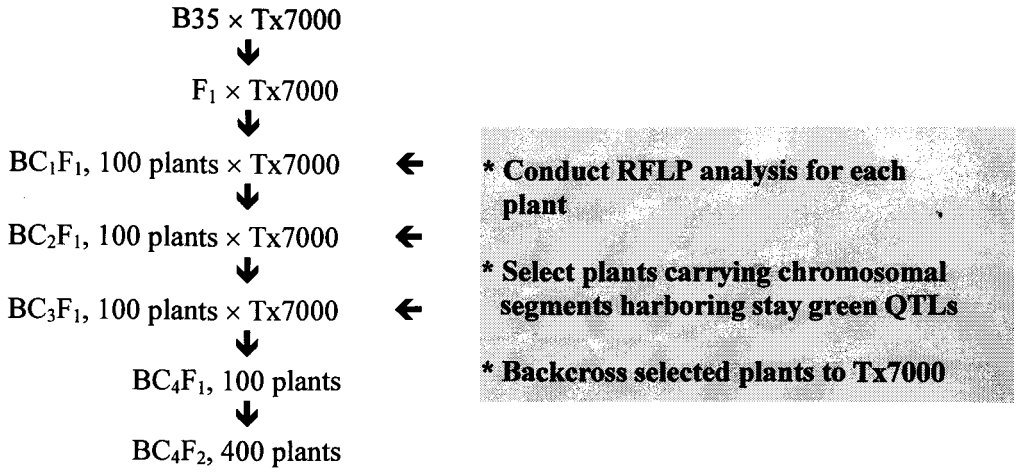


Figure 1. **Molecular marker-assisted introgression of stay green QTLs from B35 to Tx7000. The above figure illustrates how molecular markers can be used to select drought-resistant plants without testing the backcross progenies in the drought-stressed conditions. In addition, the selfing step in traditional backcross breeding has been eliminated. The backcross progenies from this scheme will carry the cytoplasm from B35. In the last backcross step, it may be desirable to use Tx7000 as the female parent to make all the NILs have the same cytoplasm as Tx7000.**

With the results of several marker loci, plants that carry the chromosomal segments harboring the stay green QTLs are selected and backcrossed to Tx7000.

After four generations of backcrossing, the selected plants will be selfed to produce the BC_4F_2 plants (Fig. 1). From the BC_4F_2 plants, a series of near-isogenic lines (NILs) will be identified. These NILs should carry a single defined segment of the donor parent B35 and have a pure genetic background of the recurrent parent Tx7000. Such NILs are ideal for high-resolution mapping of the QTLs with the substitution mapping strategy (Paterson et al., 1990), because they present the whole donor genome divided into a limited number of distinct segments, each present in a different line. Marker-assisted selection will increase the selection efficiency and shorten the breeding

Conclusions and Perspectives

Conventional breeding methods for crop improvement have made a significant contribution to sorghum improvement. However, they have been slow in improving complex traits such as drought resistance, one of the major breeding objectives.

The transfer of desirable traits to increase sorghum productivity requires the use of biotechnology methods, including gene mapping, QTL tagging, MAS technique, map-based gene cloning, and gene transformation. Biotechnology will have a significant impact on the future of sorghum improvement.

Some of the QTLs associated with post-flowering drought resistance have been mapped. Marker-assisted selection offers great opportunity for improving drought resistance and other agronomi-

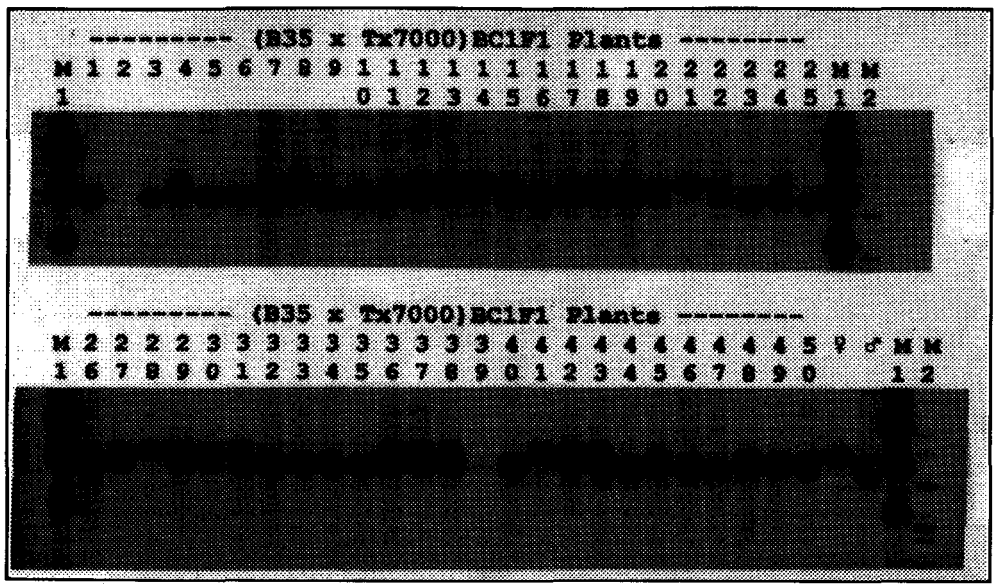


Figure 2. **Molecular marker-assisted backcrossing. The genomic DNAs from (B35 × Tx7000) BC_1F_1 plants grown in greenhouse were digested with *Hind*III and hybridized with close TXS713. The plants with both band A (from B35) and B (from Tx7000) are heterozygous at this locus and are the candidates for continued backcrossing with the recurrent parent Tx7000. Those with band B do not carry stay green genes and are discarded. Those with band A are either from selfed seeds or from recombination, and therefore are not selected for the next step. With the results of several marker loci, plants that carry the chromosomal segments harboring the stay green QTLs are selected and backcrossed to Tx70000.**

cally important traits. Fast DNA extraction, a high resolution genetic map and high-throughput molecular screening techniques are crucial for future large-scale molecular breeding in sorghum. Map-based gene cloning is amenable in sorghum. Gene transformation via microprojectile bombardment and *Agrobacterium* has been established and needs to be refined. In the near future, transformation of selected genes has the potential to enhance drought resistance in sorghum and other crops. However, relevant physiological evaluation and field performance tests will be required to demonstrate the value of target genes. Both conventional and biotechnological breeding are complementary approaches and can be expected to enhance the efficiency of breeding for drought resistance and yield.

References

Ackerson, R.C., D.R. Krieg, and F.J.M. Sung. 1980. Leaf conductance and osmoregulation of field grown sorghum. Crop. Sci. 20:10-14.

Arumuganathan, K., and E.D. Earle. 1991. Nuclear DNA content of some important species. Plant Mol. Biol. Rep. 9: 208-218.

Basnayake, J., M. Cooper, M.M. Ludlow, R.G. Henzell, and P.J. Snell. 1995. Inheritance of osmotic adjustment to water stress in three grain sorghum crosses. Theor. Appl. Genet. 90:675-682.

Battraw, M., and T.C. Hall. 1991. Stable transformation of *Sorghum bicolor* protoplasts with chimeric neomycin phosphotransferase II and beta-glucuronidase genes. Theor. Appl. Genet. 82:161-168.

Berhan, A.M., S.H. Hulbert, L.G. Butler, and J.L. Nennetzen. 1993. Structural and evolution of the genomes of *Sorghum bicolor* and *Zea mays*. Theor. Appl. Genet. 86:598-604.

Binelli, G., L. Gianfranceschi, M.E. Pe, G. Taramino, C. Busso, J. Stenhouse, and E. Ottaviano. 1992. Similarity of maize and sorghum genomes as revealed by maize RFLP probes. Theor. Appl. Genet. 84:10-16.

Blum, A., and C.Y. Sullivan. 1986. The comparative drought resistance of landraces of sorghum and millet from dry and humid regions. Ann. Bot. 57:835-846.

Blum, A., R. Munns, J.B. Passioura, and N.C. Turner. 1996. Genetically engineered plants resistant to soil drying and salt stress: How to interpret osmotic relations? Plant Physiol. 110:1051-1053.

Bohnert, H.J., and R.G. Jensen. 1996. Strategies for engineering water-stress tolerance in plants. TIBTECH 14:89-97.

Bohnert, H.J., D.E. Nelson, and R.G. Jensen. 1995. Adaptations to environmental stresses. Plant Cell 7:1099-1111.

Botstein, D., R.L. White, M. Skolnick, and R.W. Davis. 1980. Construction of a genetic linkage map in man using restriction fragment length polymorphisms. Amer. J. Hum. Genet. 32:314-331.

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443-448.

Casas, A.M., A.K. Konowicz, U.B. Zehr, D.T. Tomes, J.D. Axtell, L.G. Butler, R.A. Bressan, and P.M. Hasegawa. 1993. Transgenic sorghum plants via microprojectile bombardment. PNAS 90:11212-11216.

Chittenden, L.M., K.F. Schertz, Y.R. Lin, R.A. Wing, and A.H. Paterson. 1994. Detailed RFLP map of *Sorghum bicolor* x *S. propinquum*, suitable for high-density mapping, suggests ancestral duplication of Sorghum chromosomes or chromosomal segments. Theor. Appl. Genet. 87:925-933.

Doggett, H. 1988. Sorghum. Longman Scientific and Technical, New York. 512 p.

Dudley, J.W. 1993. Molecular markers in plant improvement: Manipulation of genes affecting quantitative traits. Crop Science 33:660-668.

Edwards, M.D., and N.J. Page. 1994. Evaluation of marker-assisted selection through computer simulation. Theor. Appl. Genet. 88:376-382.

Hagio, T., A.D. Blowers, and E.D. Earle. 1991. Stable transformation of sorghum cell cultures after bombardment with DNA-coated microprojectiles. Plant Cell Reports 10:260-264.

Hamilton, C.M., A. Frary, C. Lewis, and S.D. Tanksley. 1996. Stable transformation of intact high molecular weight DNA into plant chromosomes. Proc. Natl. Acad. Sci. USA. 93:9975-9979.

Hiei, Y., S. Ohta, T. Komari, and T. Kumasho. 1994. Efficient transformation of rice (*Oryza sativa* L.) mediated by Agrobacterium and sequence analysis of the boundaries of the T-DNA. The Plant J. 6:271-282.

Holmstron, K-O, E.M.B Welin, and A.M.E.T. Palva. 1996. Drought tolerance in tobacco. Nature 379:683-684.

Hulbert, S.H., T.E. Richter, J.D. Axtell, and J.L. Bennetzen. 1990. Genetic mapping and characterization of sorghum and related crops by means of maize DNA probes. Proc. Natl. Acad. Sci. USA. 87: 4251-4255.

Ishida Y., H. Saito, S. Ohta, Y. Hiei, T. Komari, and T. Kumashiro. 1996. High efficiency transformation of maize (*Zea mays* L.) mediated by Agrobacterium tumefaciens. Nature Biotechnology 14:745-750.

Jiang, C., and Z-B. Zeng. 1995. Multiple trait analysis of genetic mapping for quantitative trait loci. Genetics 140:1111-1127.

Lander, E.S., P. Green, A. Abrahamson, A. Barlow, W.J. Daly, S.E. Lincoln, and L. Newburg. 1987. Mapmaker: An interactive computer package for constructing primary genetic linkage maps of experimental and natural populations. Genomics 1:174-181.

Ludlow, M.M. 1993. Physiological mechanisms of drought resistance. p.11-34. *In* T.J. Mabry, H.T. Nguyen, R.A. Dixon, and M.S. Bonness (eds.) Biotechnology for aridland plants. IC2 Institute, Univ. of Texas, Austin.

Ludlow, M.M., J.M. Santamaria, and S. Fukai. 1990. Contribution of osmotic adjustment to grain yield in *Sorghum bicolor* (L.) Moench under water-limited conditions. 2. Water stress after anthesis. Aust. J. Agric. Res. 41:67-78.

Martin, G.B., S.H. Brommoncshenkel, J. Chunwongse, A. Frary, M.W. Ganal, R. Spivey, T. Wu, E.D. Earle, and S.D. Tanksley. 1993. Map-based cloning of a protein kinase gene conferring disease resistant in tomato. Science 262: 1432-1436.

Mooney, P.A., P.B. Goodwin, E.S. Ennis, and D.J. Llewellyn. 1991. Agrobacterium tumefaciencegene transfer into wheat tissues. Plant Cell, Tissue and Organ Culture 25:209-218.

Moore, G., K.M. Devos, Z. Wang, and M.D. Gale. 1995. Grasses, line up and form a circle. Current Biology 5:737-739.

Nooden, L.D. 1988. The phenomena of senescence and aging. p.1-38. *In* L.D. Nooden and A.C.

Leopold (eds.) Senescence and aging in plants. Academic Press, New York, NY.

Paterson, A.H., J.W. DeVerna, B. Lanini, and S.D. Tanksley. 1990. Fine mapping of quantitative trait loci using selective overlapping recombinant chromosomes, in an interspecies cross of tomato. Genetics 124:735-742.

Pereira, M.G., M. Lee, P. Bramel-Cox, W. Woodman, J. Doebley, and R. Whitkus. 1994. Construction of an RFLP map in sorghum and comparative mapping in maize. Genome 37:236-243.

Potrykus, I. 1990. Gene transfer to cereals: An assessment. Bio/Technology 8:535-542.

Ragab, R.A., S. Dronavalli, M.A. Saghai Marrof, and Y.G. Yu. 1994. Construction of a sorghum RFLP linkage map using sorghum and maize DNA probes. Genome 37:590-594.

Rathus, C., A.L. Adkins, R.J. Henry, S.W. Adkins, and I.D. Godwin. 1996. Progress towards transgenic sorghum. Proc. Third Australian Sorghum Conference (in press).

Rosenow, D.T., and L.E. Clark. 1995. Drought and lodging resistance for a quality sorghum crop. p.82-97. *In* Proc. of the fifieth annual corn and sorghum industry research conference 1995.

SAS Institute, Inc. 1990. SAS users guide: Statistics. SAS Institute, Gary, NC.

Santamaria, J.M., M.M. Ludlow, and S. Fukai. 1990. Contribution of osmotic adjustment to grain yield in *Sorghum-bicolor* (L.) Moench under water-limited conditions.1. Water stress before anthesis. Aust. J. Agric. Res. 41:51-65.

Stuber, C.W. 1995. Mapping and manipulating quantitative traits in maize. TIG 11:477-481.

Stuber, C.W., S.E. Lincoln, D.W. Wolff, T. Helentjaris, and S.E. Lander. 1992. Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. Genetics 132:823-839.

Tangpremsri, T., S. Fukai, K.S. Fischer, and R.G. Henzell. 1991a. Genotypic variation in osmotic adjustment in grain sorghum. I. Development of variation in osmotic adjustment under water-limited conditions. Aust. J. Agric. Res. 42:747-757.

Tangpremsri, T., S. Fukai, K.S. Fischer, and R.G. Henzell. 1991b. Genotypic variation in osmotic adjustment in grain sorghum. II. Relation with some growth attributes. Aust. J. Agric. Res. 42:759-767.

Tanksley, S.D. 1993. Mapping polygenes. Annu. Rev. Genet. 27:205-233.

Tanksley, S.D., M.W. Ganal, and G.B. Martin. 1995. Chromosome landing: A paradigm for map-based gene cloning in plants with large genomes. TIG 11:63-68.

Tao, Y.Z., C.L. McIntyre, and R.G. Henzell. 1996. Applications of molecular markers to Australian sorghum breeding programs. 1. Construction of a RFLP map using sorghum recombinant inbred lines. Proc. Third Australian Sorghum Conference (in press).

Tarczynski, M.C., R.G. Jensen, and H.J. Bohnert. 1993. Stress protection of transgenic tobacco by production of the osmolyte mannitol. Science 259:508-510.

Thomas, C.M., P. Vos, M. Zabeau, D.A. Jones, K.A. Norcott, B.P. Chadwick, and J.D.G. Jones. 1995. Identification of amplified restriction fragment polymorphism (AFLP) markers tightly linked to the tomato *Cf-9* gene for resistance to *Cladosporium fulvum*. Plant J. 8:785-794.

van Oosterom, E.J., R. Jayachandran, and F.R. Bidinger. 1996. Diallel analysis of the stay green trait and its components in sorghum. Crop Sci. 36:549-555.

Van Eck, J.M., A.D. Blowers, and E.D. Earle. 1995. Stable transformation of tomato cell cultures after bombardment with plasmid and YAC DNA. Plant Cell Reports 14:299-304.

Vos, P., R. Hogers, M. Bleeker, M. Reijans, T. van de Lee, M. Hornes, A. Frijters, J. Pot, J. Peleman, M. Kuiper, and M. Zabeau. 1995. AFLP: A new technique for DNA fingerprinting. Nucleic Acid Res. 23:4407-4414.

Walulu, R.S., D.T. Rosenow, D.B. Wester, and H.T. Nguyen. 1994. Inheritance of the stay green trait in sorghum. Crop Sci. 34:970-972.

Whitkus R., J. Doebly, and M. Lee. 1992. Comparative genome mapping of sorghum and maize. Genetics 132:1119-1130.

Woo, S.S., J. Jiang, B.S. Gill, A.H. Paterson, and R.A. Wing. 1994. Construction and characterization of a bacterial artificial chromosome library for *Sorghum bicolor*. Nucleic Acids Res. 22:4922-4931.

Xu, G.W, C.W. Magill, K.F. Schertz, and G.E. Hart.1994. A RFLP linkage map of *Sorghum bicolor* (L). Moench. Theor. Appl. Genet. 89:139-145.

Zeng, Z-B. 1994. Precision mapping of quantitative trait loci. Genetics 136:1457-1468.

Part B

Analysis of Drought Tolerance in Sorghum: Mapping of Quantitative Trait Loci and their Evaluation in Near-Isogenic Lines

M.R. Tuinstra* and G. Ejeta

Drought is the primary limitation to crop production in the world today (Boyer, 1982). The development and use of crops that are tolerant to drought may alleviate this problem. Progress toward this goal has been slow because the genetic and physiological mechanisms that mediate drought tolerance are still poorly understood (Ludlow, 1990; Bonhert, et al. 1995). We are interested in identifying mechanisms that condition adaptation of sorghum to drought environments. Several characteristics make sorghum well-suited for this research: sorghum is one of the most drought-tolerant grain crops; genetic diversity for drought tolerance has been identified in sorghum; and sorghum is an important crop in arid regions.

The development of molecular genetic markers and the use of these markers in quantitative trait loci (QTL) analysis has become a powerful approach for studying the inheritance of complex traits (Edwards et al., 1987; Paterson et al., 1988; Williams et al., 1992). Molecular markers linked to QTLs for drought tolerance could be used in breeding programs to select individuals with promising genotypes prior to field evaluation. This should increase the efficiency of selection for drought tolerance. Evaluation of QTLs associated with yield or agronomic performance in drought environments also provides a powerful and systematic approach for identifying traits that contribute to drought tolerance. Understanding the morphological and physiological mechanisms that condition the drought-tolerant phenotype should provide new insight into the biological basis of this important trait.

M.R. Tuinstra and G. Ejeta, Department of Agronomy, Purdue University, West Lafayette, IN 47907; P.B. Goldsbrough, Department of Horticulture, Purdue University, West Lafayette, IN 47907. *Corresponding author.

Phenotypic and Genetic Analysis of Drought Tolerance

Our objective is to dissect drought tolerance into individual genetic components. A population of 98 recombinant inbred (RI) lines was developed from a cross between two sorghum inbreds with contrasting drought reactions: Tx7078 (pre-flowering drought-tolerant/post-flowering drought-susceptible) and B35 (pre-flowering drought-susceptible/post-flowering drought-tolerant). The population was evaluated for response to drought in pre-flowering and post-flowering stress environments. Drought tolerance was estimated in several ways: grain yield per se measured under pre-flowering or post-flowering drought; "stability" of yield; seed set; seed weight under drought expressed as a fraction of that measured in

the fully irrigated environment; stay-green, rated on a scale from 1 to 5 in the post-flowering drought trials. Evaluation of the RI lines indicated segregation for drought tolerance during both developmental stages (Tuinstra et al., 1996a; Tuinstra, 1996b).

The RI population was also scored for the segregation of 150 RAPD markers and 20 RFLP markers. These markers were ordered into a genetic map by linkage analysis and used to determine the contribution of the parental genotypes to each of the RI lines. Single factor analysis was used to identify quantitative trait loci (QTL) associated with yield and other measures of agronomic performance under drought and non-drought conditions (Tuinstra et al., 1996a).

Several regions of the genome were associated with the expression of yield or yield components under pre-flowering and post-flowering drought, and under fully irrigated conditions (Fig. 1). QTLs on linkage groups D, F, G, and H were associated with yield and yield components under full irrigation, and with measures of agronomic performance under pre-flowering and/or post-flowering drought. In each case, the marker allele associated with higher yield under fully irrigated conditions was also associated with improved tolerance or agronomic performance under drought conditions. Two regions on linkage groups D and F were strongly associated with agronomic performance under pre-flowering drought conditions but not under fully irrigated conditions (Fig. 1). This result suggests these loci mediate the expression of pre-flowering drought tolerance independent of mechanisms that control yield. Similarly, regions of the genome on linkage groups B and F were associated with agronomic performance under post-flowering drought but not under conditions of full irrigation suggesting the effects of loci that mediate the expression of post-flowering drought tolerance, independent of yield. Several QTLs for stay green were identified on linkage groups B, F, G, H, and I. QTLs for stay green on linkage groups F, G, and H were also positively associated with grain yield under non-drought conditions (Fig. 1). This indicates there may be a physiological link between the expression of stay green under post-flowering drought and grain yield under non-drought conditions.

Near-Isogenic Lines that Differ for QTLs Associated with Drought Tolerance

QTL analysis has identified regions of the genome that influence the expression of drought tolerance. However, this analysis provides little information concerning the expression of individual QTLs. Sets of near-isogenic lines (NILs) that differ at specific QTLs can be used to carefully evaluate the phenotypic expression of individual QTLs . NILs have been developed for five QTLs associated with yield in drought environments. Initial evaluations have revealed significant phenotypic differences in agronomic performance between NILs contrasting at these QTLs.

The evaluation of QTLs in NIL can be used to address several questions. First, marker linkage to a QTL can be confirmed by examining the phenotypes of NILs that differ for individual QTLs. QTL analysis indicates regions of the genome that may

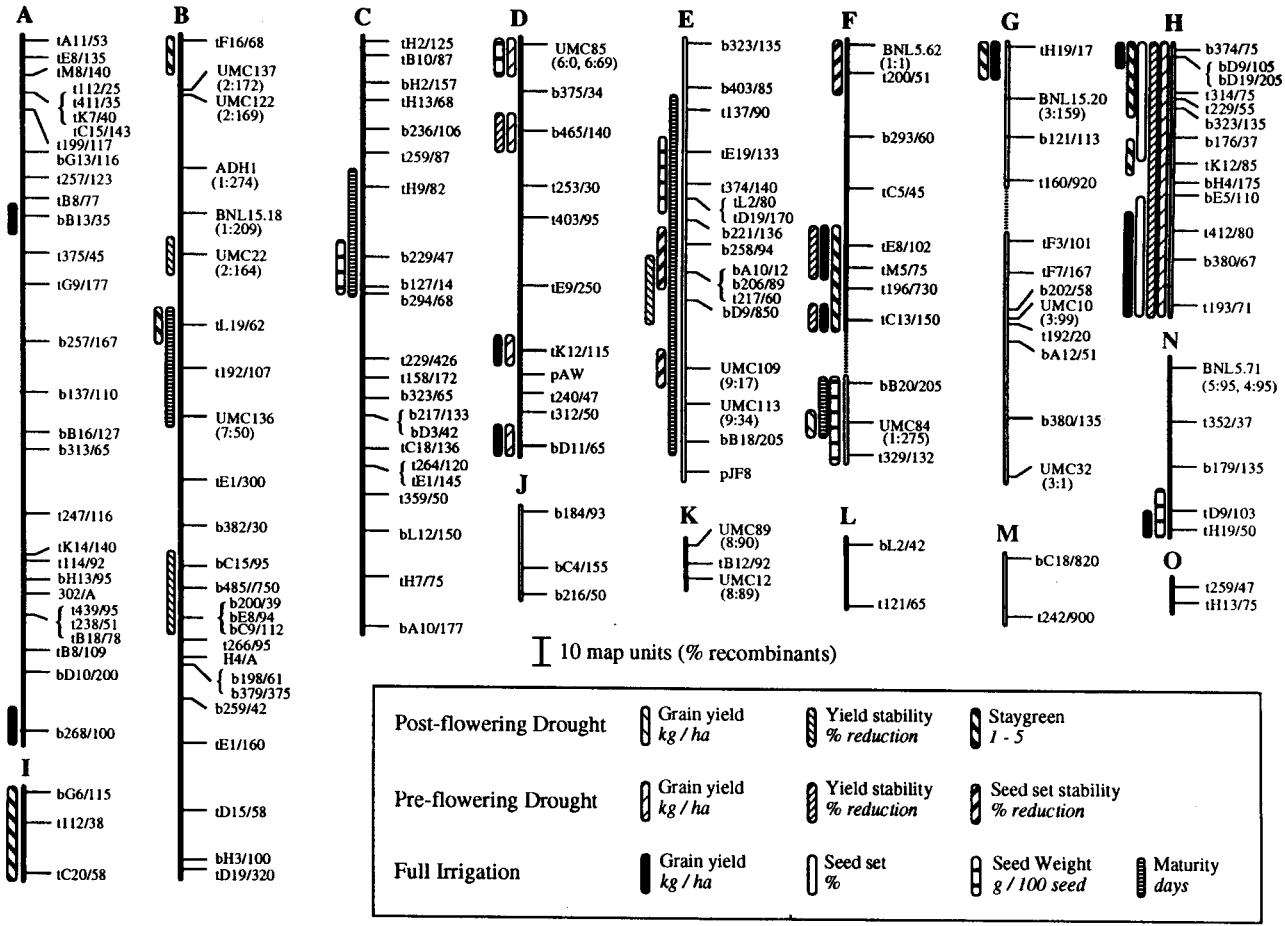


Figure 1. Sorghum genetic linkage map and QTL identified for pre-flowering and post-flowering drought tolerance and related measures of agronomic performance under non-drought conditions. A dashed line between linkage groups indicates linkage inferred from the linkage of RFLPs mapped in other populations. QTL were identified by single factor analysis and were declared significant on a per marker basis at $p<0.01$. The positions of QTL are indicated by bars on the linkage map. A significant association is indicated when a bar covers that marker. The map positions for RFLPs mapped in maize are indicated (chromosome:position).

contain QTLs but the phenotypic effects of these loci need to be confirmed. Second, NILs can be used for fine mapping of QTL. Evaluation of a series on NILs that contrast at a specific locus can be used to narrow the genetic interval known to contain the QTL (Paterson *et al.* 1990). Third, NILs that differ at a QTL can be used to characterize the expression and function of a specific locus. NILs differing for QTL associated with drought tolerance can be used to identify the specific mechanism of drought tolerance controlled by each QTL.

Future Research Objectives

NTLs have been developed for five different QTLs associated with yield in drought environments. The initial phenotypic evaluation of these NlLs suggests these loci mediate the expression of drought tolerance via different biological mechanisms. Experiments to identify and define the mechanisms of drought tolerance mediated by these loci are underway.

References

Bonhert, H.J., D.E. Nelson, and R.G. Jensen. 1995. Adaptations to environmental stresses. Plant Cell 7:1099-1111.

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443-448.

Edwards, M.D., C.W. Stuber, and J.F.Wendel. 1987. Molecular marker-facilitated investigations of quantitative trait loci in maize. I. Numbers, distributions, and types of gene action. Genetics 116:113-125.

Ludlow, M.M., and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Adv. Agron. 43:107-152.

Paterson, A.H., E.S. Lander, J.D Hewitt, S. Peterson, S.E. Lincoln, and S.D. Tanksley. 1988. Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721-736.

Paterson, A.H., J.W. DeVerna, B. Lanini, and S.D. Tanksley. 1990. Fine mapping of quantitative trait loci using selected overlapping recombinant chromosomes, in an interspecies cross of tomato. Genetics 124:735-742.

Tuinstra M.R., E.M. Grote, P.B. Goldsbrough, and G. Ejeta. 1996a. Identification of quantitative trait loci associated with pre-flowering drought tolerance in sorghum. Crop Science (in press).

Williams J.G.K., M.K. Hanafey, J.A. Rafalski, and S.V. Tingey. 1992. Genetic analysis using random amplified polymorphic DNA markers. *In*: R. Wu (ed.) Methods in enzymology. Academic Press, San Diego.

Targeting Sorghum Improvement in Drought-Prone Environments: Approaches and Progress

R.C. Muchow*, M. Cooper, F.R. Bidinger,
G.L. Hammer, A.K. Borrell and S.C. Chapman

Abstract

Grain sorghum is grown in environments of highly variable water supply, both within and between seasons. This variability, coupled with associated genotype-by-environment (GxE) interactions, results in unclear definition of both target environment(s) and traits that may be used as selection criteria, causing slow progress in breeding for drought resistance. This paper reviews new approaches to characterize environments in terms of the incidence of water deficits and to assess the value of traits for improvement of drought resistance. Sorghum simulation models are powerful tools to characterize types of environmental challenges and their frequency of occurrence at different locations. Models also are being used to assess hypotheses about trait action and their value, and to develop optimal combinations of traits for different environmental challenges. Further research involving physiologists, agronomists, and plant breeders using integrated systems analysis will realize the potential of these approaches and improve the efficiency of selection in drought-prone environments.

Rainfed production of grain sorghum is a risky enterprise due to high rainfall variability, both within and between seasons (Muchow et al., 1991; 1994). Plant breeders face considerable challenges in improving sorghum performance in these regions for two reasons: 1) climatic variability and the associated genotype-by-environment (GxE) interactions, which often result in unclear definition of the target environment(s); and 2) lack of definitive knowledge of which plant traits for drought resistance are relevant to particular environments. Consequently, progress in genetic improvement in drought-prone environments has been relatively slow (Cooper and Hammer, 1996). Important questions are: what new approaches are available to assist the plant breeder in targeting selection for drought-prone environments and what recent advances in physiological knowledge are relevant to this endeavor? Bidinger et al. (1996) set out the physiological basis of GxE interaction in crop adaptation and argue that real opportunities lie both in understanding the environmental control of crop growth and in developing simplified approaches to modeling. These approaches include better analysis of multi-environment trial (MET) data sets, better understanding of resources and challenges in target environments, and better understanding of the adaptive value of plant traits in specific environments.

Muchow et al. (1996a) recently reviewed the considerable advances in our understanding of the physiology of grain

R.C. Muchow and S.C. Chapman, CSIRO St Lucia, QLD, Australia; M. Cooper, Dept Agric, UQ, St Lucia, QLD, Australia; F.R. Bidinger, ICRISAT, Patancheru, AP India; G.L. Hammer, QDPI/APSRU Toowoomba QLD Australia; and A.K. Borrell, QDPI Warwick QLD Australia.*Corresponding author.

sorghum. In the past, physiology was viewed largely as a retrospective discipline in explaining plant function. Physiological research now tends to be more focused on providing knowledge about plant and crop processes to underpin sustainable and profitable production and assist in breeding better adapted plants. Quantitative knowledge of the physiology of yield accumulation contributes to the development of crop growth simulation models that can be used to assess improved crop management options, characterize environments, assist multi-environment testing, and evaluate potentially useful traits (Hammer et al., 1996a,b). Enhanced modelling capability and better databases, particularly of historical climatic data, have been central to recent progress in better targeting sorghum improvement in drought-prone environments.

In reviewing approaches and progress, we consider three key questions in this paper:

1) How can we best define the target environment(s)?

2) How can better characterization of environments improve the efficiency of METs?

3) How can we better evaluate which traits for improving drought resistance in grain sorghum are likely to be beneficial in different environments?

Defining the Target Environment(s)

Comstock (1977) discussed the concept of a target population of environments (TPE) for breeding programs. The TPE can be defined as the complete set of "types" of environments within the geographical area targeted by a breeding program. The types of environmental factors encountered within the TPE play a dominant role in determining crop performance, genetic variation for quantitative traits, and therefore the relative performance of genotypes. An important challenge in plant breeding is to evaluate genotypes across variable environments in a manner that allows assessment of their adaptation within the TPE. This is traditionally done using METs. One factor influencing the efficiency of this approach is GxE interaction (Cooper et al., 1993). When GxE interactions are a large source of variation, the TPE consists of a complex mixture of different types of environments. If some of these environments are repeatable and important in the TPE, then the TPE can be resolved into sub-populations. Breeding for target environments may therefore be considered as breeding for specific adaptation to those types of environments that occur frequently within the TPE. A successful example of this breeding strategy is breeding for resistance to sorghum midge (*Contarina sorghicola*) for the Australian TPE (Henzell, 1992).

Water availability is a major environmental factor responsible for GxE interactions for yield in grain sorghum. Better characterization of environments in terms of the severity and frequency of occurrence of water deficits offers the potential to improve the efficiency of selection within METs. This may lead to better choice of environments for field trials, thereby increasing gains from selection. Muchow et al. (1996b) and Cooper and Chapman (1996) outline an approach using crop simulation models coupled to

historical climatic data to define the spectrum of environmental challenges in the TPE, and then use pattern analysis to group environments in terms of types and frequency of occurrence of water deficits. This information then can be linked with spatial databases (Chapman and Baretto, 1996) to identify testing locations that either best represent the target environment(s) or present specific challenges to germplasm under test. Case studies of the approach using simulation modelling and pattern analysis to characterize sorghum environments are given below.

Muchow et al. (1996b), using 96-101 years of historical climatic data for two rainfed sorghum-growing sites in Queensland, Australia, concluded that the grouping of environments by a relative transpiration index accounted for a higher proportion of the yield variation among years than did groupings based on indices derived from a simple water balance model or direct climatic variables. Relative transpiration (RT, 0-1.0) is the ratio of actual transpiration to potential transpiration; RT values less than 1.0 indicate that water deficit is restricting crop growth. Muchow et al. (1996b) used the grain sorghum model of Hammer and Muchow (1994) to calculate daily RT using a defined cropping system (i.e., soil type, total available soil water in profile [tsw], initial available soil water [asw], cultivar, density, nutrient supply, and sowing window based on rain occurrence). The weekly RT value was calculated as the mean of the corresponding daily values to determine the weekly patterns of water deficit during the crop cycle for each year at each site. Pattern analysis (DeLacy, 1981) was used to identify the major types of water deficit pattern, and the frequency with which these types occur was then inferred by the size of the groups (Figure 1).

In the case study at Emerald, five groups of water deficit patterns were identified (Figure 1). Groups 174, 176, and 177 were of similar and higher frequency than groups 170 and 173. Groups 174 and 177 showed terminal water deficit of varying intensity, while water deficit was least in group 176. Four groups were identified at Dalby (Figure 1). Group 190 had the least water deficit but occurred most frequently, whereas groups of varying terminal water deficit occurred 49% of the time. Table 1 shows the group profiles and simulated grain yield at Dalby for the years 1985 to 1989. In field trials conducted at Dalby over the three years 1987 to 1989, the pattern analysis classified these seasons as group 190 (i.e., little water limitation, Figure 1). An important question to the plant breeder is how frequently does this environment occur. Figure 1 shows that it occurs 38% of the time, not 100% of the time, as was the case in these three years (Table 1), suggesting that genotype performance in those years would not necessarily be predictive of long-term genotype performance.

Cooper and Chapman (1996) used a similar approach to examine the patterns of water deficit at seven sites in Queensland over the historical climatic record. Out of the 660 seasons (totaled over the seven locations) that the sorghum crop was simulated, five patterns of water deficit were identified (Figure 2). In the four southern sites (Bongeen, Bowenville, Condamine, and Dalby) 60% to 90% of seasons had little or no stress (Group 507), whereas in central Queensland, less than

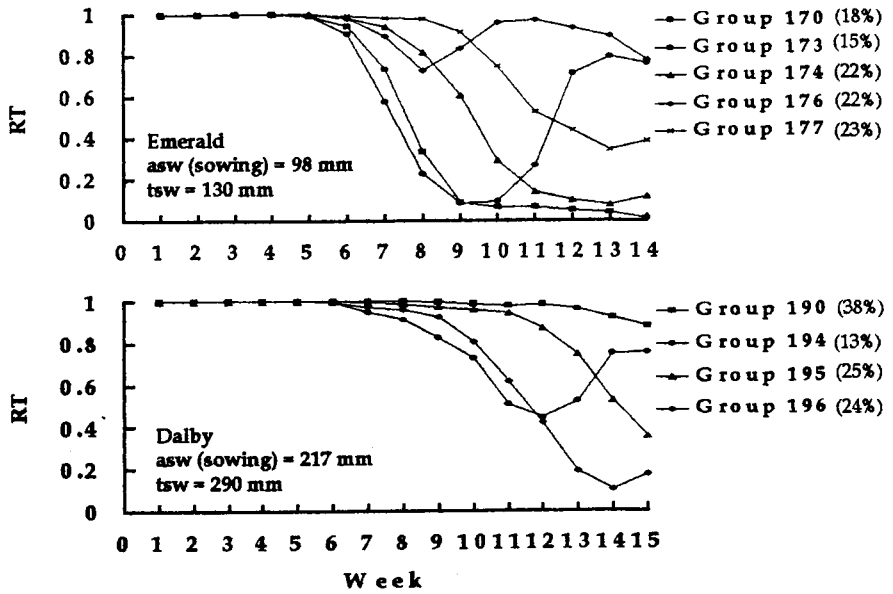


Figure 1. **Pattern of water deficit based on relative transpiration (RT) over time for two rainfed sites in Queensland, Australia. Source: Muchow et al. (1996b)**

Table 1. **Group profiles based on relative transpiration and simulated grain yield from 1985 to 1989 at Dalby, Australia.**

Year	1985	1986	1987	1988	1989
Group	196	195	190	190	190
Grain yield (t ha-^{1})	1.85	5.56	6.37	6.21	6.23

Source: Muchow et al. (1996b)

30% of seasons were characterized as no stress. Groups showing terminal stress (Groups 509 and 512) occurred to differing degrees at all locations, while mid-season water deficit (Groups 510 and 511) occurred only at the central Queensland sites (Figure 2).

Given this insight, it would seem difficult to design a MET to account for the different mixture of season types in each region. Trials in southern Queensland would tend to indicate a high frequency of low stress sites, so the results from these would probably not be relevant in central Queensland, and vice versa. Sampling would be even more difficult within central Queensland; Fernlees, for example, tends to have more mid-season water deficits, while Jambin has more terminal water deficits. Hence, the results of a MET in any single season would be unlikely to adequately sample the total TPE for central and southern Queensland.

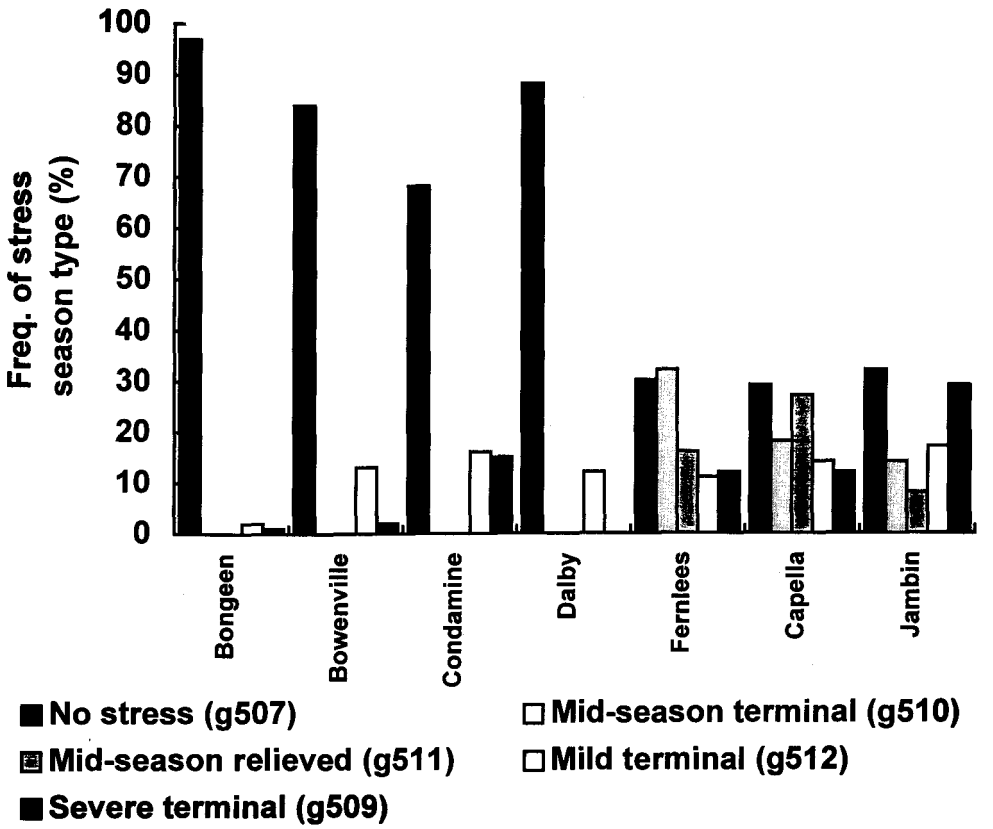


Figure 2. Frequency of water deficit season types across seven sites in Queensland's sorghum regions (Cooper and Chapman, 1996).

Cooper and Chapman (1996) also examined 17 years of METs conducted in southern and central Queensland and found that variation among sites for discrimination among cultivars was well correlated with the simulated frequency of stress seasons at any location. Assuming that the period over which the METs were conducted provided a representative sample of the possible seasons, this is strong evidence that a substantial component of the regional GxE interactions for yield in sorghum is related to the occurrence of different patterns of water deficit among the regions.

Improving the Efficiency of METs

Multi-environment trials (METs) are conducted as an integral part of a plant breeding program, with the broad objective of estimating the relative performance of genotypes in the target population of environments (TPE). Much has been discussed about the impact of GxE interactions in plant breeding and their analysis (see Cooper and Hammer, 1996), but generally less attention has been given to the issue of adequacy of the samples of environments obtained in METs. Where the TPE is considered to be heterogeneous with respect to the types of environments

encountered, most analyses of quantitative traits find significant and problematic crossover GxE interactions (Haldane, 1946).

Estimation of the importance of GxE interactions from METs is not independent of the sampling strategy used in conducting the METs (Cooper et al., 1996). Muchow et al. (1991) considered the limitations of METs in terms of their capacity to adequately sample the range of environments encountered in the TPE. Sampling variation results in the composition of environments included in any MET deviating from environments in the TPE. The consequence of this can be considered in terms of the genetic correlation between the performance of the genotypes in the MET and their expected performance in the TPE (Cooper et al., 1996). Where GxE interactions are large, relative to genotypic variation for average performance across environments, the consequence of the sampling variation is that the genetic correlation between the MET and TPE will fluctuate among successive METs; therefore, the realized response to selection in the TPE will fluctuate among successive METs.

A possible selection strategy to accommodate the MET sampling variation effect for a TPE is to use environmental characterization information from crop models to generate weights for individual selection environments based on their relevance to the TPE. Three pieces of information are required: 1) definition of the TPE (as discussed in the previous section) to give a measure of the types of environments encountered in the TPE and their frequency of occurrence; 2) characterization of the MET to give a measure of the types of environments sampled in the MET; and 3) environmental weights to give an appropriate system for weighting the information from the environments sampled in the MET.

The environments sampled in the current MET can be characterized in a manner similar to that for the TPE by establishing parameters for the cropping system, obtaining the seasonal climatic data, and running the crop simulation model for that specific season. The patterns of water deficit detected from each MET environment can then be compared to the groups of patterns obtained from characterizing the TPE to determine how well the MET sample is matched with the TPE. The difference in the environmental composition between the two provides a measure of the size of the sampling variation effect for a given MET strategy.

Where there are crossover GxE interactions among the environment types identified by the crop model characterization, and where the sample of environments obtained in the MET deviates from that in the TPE, the response to selection in the TPE from selection based on the results of the MET depends on how the selection decisions are made. For example, if the objective is to improve average performance in the TPE, selection for average performance across the MET environments will have a sub-optimal genetic covariance with average performance across the TPE (Cooper et al., 1996). Weighting procedures based on a quantitative measure of the deviation between the environments sampled in a MET and the expectation for the TPE can be used to improve the match between the environmental composition in the MET and the TPE, by down-weighting the environment types that are over sampled and up-weighting the environment types that are under sampled.

There are many ways environments could be weighted to assist selection decisions. Fox and Rosielle (1982) considered weighting strategies based on the magnitude of error, pattern analysis, and canonical correlation analysis procedures in combination with a reference set of genotypes. An alternative approach is to weight environments based on their frequency of occurrence in the TPE as measured by the crop model. For example, if the frequency of an environment in the MET deviates from its frequency in the TPE, then the expected frequency of the environment in the TPE can be used as a weight for the environments in the MET. Selection decisions would then be based on the weighted mean yield across environments rather than the mean yield based on unweighted data. There are many facets to this strategy, and these are beyond the scope of the discussion that can be developed in this paper. However, using computer-based simulated selection methodologies, it has been found that weighted selection strategies perform as well as or better than selection based on unweighted MET data (M. Cooper, personal communication). The relative effectiveness of the weighted and unweighted selection strategies depends on the inheritance of the character, complexity of the GxE interactions, MET strategy, and composition of the TPE. A lot of work is necessary in this area, but preliminary observations are promising.

This approach requires access to: a) crop modelling software and capability that can be used to characterize environments in a manner relevant to the GxE interactions encountered in the TPE; b) reliable historical climatic records; and c) climatic, soil, and crop management data from the environments sampled in METs. Sorghum simulation models are available that adequately simulate the performance of standard cultivars in water-limited environments (Hammer and Muchow, 1994). These models can easily be parameterized for new cultivars using standard field experimentation. This approach assumes water limitation is the major constraint to productivity; therefore, when another constraint (e.g., disease) interacts with water availability, caution should be exercised. A major challenge with this approach is obtaining quality historical climatic data (e.g., solar radiation, temperature, and rainfall) that encompass the spatial variation of the TPE. Furthermore, minimum data sets of soil characteristics, soil conditions at sowing, and field management operations need to be collected for each MET. Chapman and Muchow (1996) have proposed a crop-soil-climate-management database system for grain sorghum to facilitate the collection of complete datasets that can easily be linked to simulation models.

While we do not recommend this strategy as a replacement for conventional selection strategies at present, sufficient positive signals warrant its further evaluation for grain sorghum. Large GxE interactions are observed for most quantitative traits; crop modelling capability exists; water availability appears to be a major environmental factor contributing to the GxE interactions for yield; and simulated selection results suggest positive results from the weighted selection strategy. Experimental programs are underway in the field in Australia to evaluate these promising theoretical results.

Evaluating Traits For Improving Drought Resistance

Identification of major physiological or environmental factors limiting the per-

formance of existing cultivars, coupled with background physiological understanding of plant response to those limiting factors, has led to many suggestions of physiological characteristics that may be selected for by plant breeders (Donald, 1968; Ludlow and Muchow, 1990). In a recent literature survey, Jackson et al. (1996) showed that attempts to identify traits for yield improvement have been dominant in physiological research, based on the thesis that advances in crop improvement under water-limited conditions are more likely if drought resistance traits are selected in addition to yield per se.

Muchow et al. (1996a) have outlined six steps necessary for the development of germplasm containing drought resistance traits:

1) Identify traits that are likely to confer a yield advantage in drought environments.

2) Determine the extent of genetic variation in such traits.

3) Understand the physiological basis of genetic variation for a trait. Traits need to be assessed in appropriate genetic backgrounds, and molecular markers can assist in developing such populations.

4) Use simulation modelling to assess the value of the trait in a wide range of target environments.

5) Investigate the heritability of the trait. If heritability is sufficiently high, conventional breeding methods could be used to select for the trait, providing the trait is valuable and a practical means of screening can be found.

6) Seek molecular markers to improve the efficiency of trait selection if heritability is low. Drought resistance traits are generally not expressed in wetter years and therefore can only be selected for in drier years. Molecular markers would enable such traits to be selected for in all years.

Figure 3 outlines a framework for selection and evaluation of traits. If a particular trait is to improve grain yield in drought-prone environments, it must increase one or more of the following identities: amount of water transpired, transpiration efficiency (TE), or harvest index (Ludlow and Muchow, 1990). Here, we restrict our discussion to a brief treatment of the traits we feel are potentially most important: phenology, osmotic adjustment (OA), leaf area maintenance or staygreen (SG), TE, soil water and nitrogen extraction, and utilization of stem reserves for grain filling (Figure 3). A more detailed coverage is given in the recent review by Muchow et al. (1996a).

Phenology is important in adapting sorghum to drought-prone environments by matching growth duration to the available resources (Ludlow and Muchow, 1990; Muchow et al., 1996a). The association between osmotic adjustment and grain yield in drought-prone environments is not clear. While some studies found that OA was positively correlated with yield (Santamaria et al., 1990; Ludlow et al., 1990; Tangpremsri et al., 1995), others found no such correlation (Tangpremsri et al., 1991a; Krieg, 1993; Tangpremsri et al., 1995) or, in some cases, a negative correlation (Kirkham, 1988; Tangpremsri et al., 1991b). Further clarification of the physiological processes controlling OA is

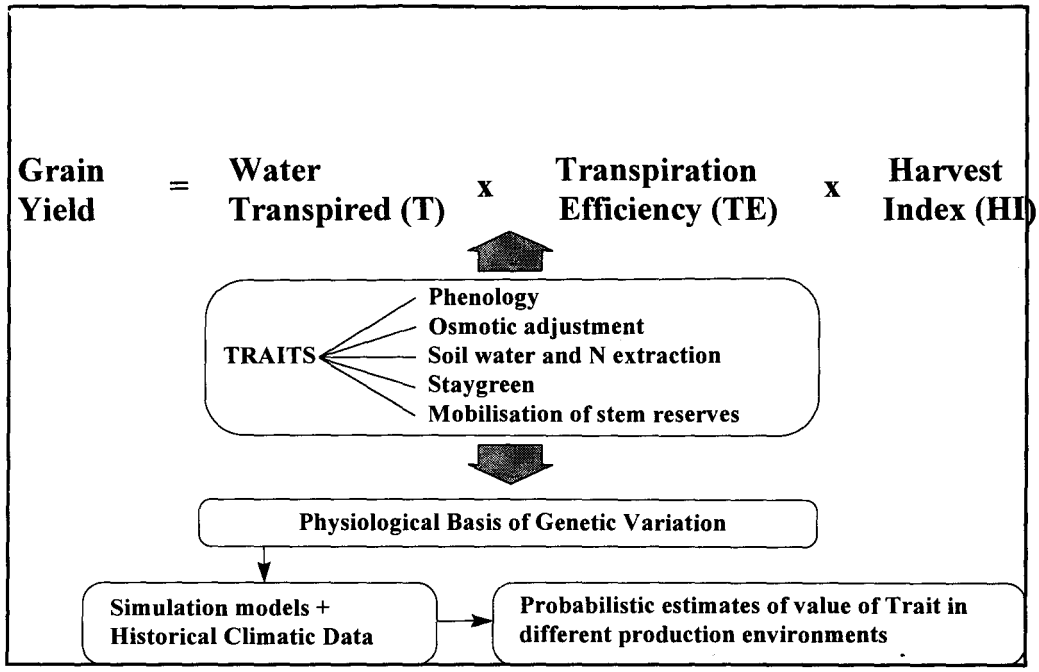


Figure 3. Framework for evaluating traits in water-limited sorghum environments.

needed before the value of this trait can be adequately assessed. It is hoped that ongoing research by Snell and Cooper (1996) will help to assess the value of this trait.

Sorghum hybrids containing the staygreen (SG) trait have been found to yield significantly more under water-limited conditions compared with hybrids not possessing this trait (Rosenow et al., 1983; Henzell et al., 1992; Borrell and Douglas, 1996). Recent research suggests that this advantage is due to maintenance of photosynthetic capacity and reduced mobilization of stem reserves to grain during the late grain-filling period, combined with lodging resistance (Borrell and Douglas, 1996). In this study, staygreen was not associated with lower harvest index as had been reported in previous studies (Rosenow et al., 1983). Further work is required to assess the extent of linkages of SG with other traits in different environments. Several studies have examined the inheritance of the SG trait (Tenkouano et al., 1993; Walulu et al., 1994; van Oosterom et al., 1996). It is difficult to select for SG because the trait is polygenic and is expressed only in drier years. Molecular markers are being developed for this trait (Tao et al., 1996) using recombinant inbred lines varying in rate of leaf senescence as a mapping population (Henzell et al., 1994).

Muchow et al. (1991) and Hammer et al. (1996a) have used simulation analysis to show that improvement in transpiration efficiency (TE) would have large benefits

in drought-prone environments. Genetic variation in TE has been observed in grain sorghum (Donatelli et al., 1992; G.L. Hammer, personal communication), but the extent of variation in TE above the value in well-adapted hybrids is relatively small. Accordingly, the scope for higher TE remains uncertain. Similarly, genetic variation in the pattern of soil water extraction (Robertson et al., 1993) and nitrogen uptake (Kamoshita et al., 1996) is small. Little progress has been made on mobilization of stem reserves to grain, beyond trait identification (Muchow et al., 1996a).

Simulation analyses provide a means to quantitatively evaluate traits in variable populations of target environments (Shorter et al., 1991; Muchow et al., 1991). Provided the physiological basis for genetic variation for a particular trait is adequately encapsulated in the model, the model can be run with historical climatic data for a specified cropping system to generate probabilistic estimates of the value of a trait in different production environments (Figure 3). Recently, Hammer et al. (1996a) simulated a MET for sorghum by introducing genetic variation for phenology, tillering, SG, and TE into the sorghum model of Hammer and Muchow (1994). They simulated ten years of experiments at three Australian sites for 24 theoretical genotypes and found that the degree of genetic variation introduced was similar to that observed among existing sorghum genotypes. While the results are specific to these environments, the analyses showed that the average response of a particular trait often was reflected in a significant advantage in a few high-yielding years, rather than superior performance in the majority of years. The power of the simulation approach is that the value of particular traits can be evaluated in a resource-efficient manner in the TPE. This approach can be extended using optimization methodology to seek an optimal combination of plant traits and crop management, given the mix of environmental challenges in the target domain (Hammer et al., 1996a).

Using a simulation approach assumes confidence in the ability of the model to simulate the effect of a particular trait. There is no reason trait consequences cannot be simulated if the crop physiological mode of action of the trait is understood and quantified, and the crop model is sufficiently detailed to simulate the interactions with growth and development generated by expression of the trait in any particular environment. In addition, as discussed earlier, adequate long-term climatic and soil databases are required. Satisfying these "ifs" requires attention to detail in focused field experiments and examination of what constitutes "sufficient detail" in modeling. On the latter, Loomis (1993) argues that more detailed models, capable of simulating processes at a level more closely aligned to gene action, are required. Others, including Shorter et al. (1991), consider that simpler crop physiological frameworks, which are more readily aligned with plant breeders' modes of action, also are required. However, the two are not mutually exclusive, and the connection is described by Shorter et al. (1991).

There is a paucity of information on the extent of genetic variation and the physiological mode of action for many traits. Such information is essential in model

development and can be obtained only by targeted experimentation. Field work on trait mode of action for SG (Borrell and Douglas, 1996; F.R. Bidinger and A.K. Borrell, personal communication), OA (Snell and Cooper, 1996), TE (G.L. Hammer, personal communication), and nitrogen use efficiency (Kamoshita et al., 1996) is underway. Comparison of simulation of a trait with the measured impact of that trait in the field will demonstrate whether existing models are adequate for the task and whether existing assumptions about trait action are valid. For example, data from field experiments on sorghum hybrids varying in SG (Borrell and Douglas, 1996) show far greater differences than those found in the simulation analysis presented by Hammer et al. (1996a). This suggests that the mechanism associated with the SG trait involves something beyond simple maintenance of leaf area. Greater differences associated with presence of SG could be associated with greater water extraction or with changes in TE (Figure 3). The interaction between research and modeling provides a sound basis to elucidate mechanisms from the field experimentation and to extrapolate their likely worth via modelling over a far more diverse set of environments than possible via direct experimentation.

Conclusions

It is generally considered that the contribution of crop physiology to plant breeding to date has been modest (Jackson et al., 1996). However, we have entered a new era in which enhanced knowledge of both the physiology of yield accumulation in grain sorghum and the physiological basis of genetic variation in drought resistance traits offers the potential for improving breeding efficiency in different target environments. Central to this thrust is enhanced modelling capability and improved databases. These tools can be used to characterize environments to assist multi-environment testing and to evaluate potentially useful traits. The use of such knowledge and tools requires a systems approach, with agronomists, physiologists, and breeders working together to raise sorghum yields in drought-prone environments.

A particularly exciting advance has been the characterization of the target population of environments (TPE), which offers to improve the efficiency of selection within multi-environment trials (MET) where GxE interactions are large. This has been used in developing a selection strategy to accommodate the MET sampling variation effect for a TPE where water limitation is considered to be the major variable influencing GxE interactions for yield of sorghum. The strategy is based on characterizing the types of water deficit environments and their frequency of occurrence using a sorghum simulation model, historical climatic databases, parameterization of the cropping system, and pattern analysis. This information is used to generate weights for environments that attempt to measure the relevance to the TPE of the environments sampled in the MET.

Research on drought resistance traits has advanced in recent years with particular emphasis on phenology, osmotic adjustment, transpiration efficiency and staygreen. Much more information is required on the physiological mode of ac-

tion of these traits and their likely value in different environments. Simulation models are important tools to assist in answering questions about trait actions and their value, and about the optimal mix of traits for particular environments. Considerable investment in physiological understanding is required to realize the potential of these approaches. Such strategic research on the physiology of grain sorghum is essential to realize future benefits to the sorghum industry.

References

Bidinger, F., G.L. Hammer, and R.C. Muchow. 1996. The physiological basis of genotype by environment interaction in crop adaptation. p.329-347. *In* M. Cooper and G.L. Hammer (eds.) Plant adaptation and crop improvement. CAB International, Wallingford Oxon.

Borrell, A.K., and A.C.L. Douglas. 1996. Maintaining green leaf area in grain sorghum increases yield in a water-limited environment. p. 315-322. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Chapman, S.C., and H.J. Barreto. 1996. Using simulation models and spatial databases to improve the efficiency of plant breeding programs. p. 563-587. *In* M. Cooper and G.L. Hammer (eds.) Plant adaptation and crop improvement. CAB International, Wallingford Oxon.

Chapman, S.C., and R.C. Muchow. 1996. A role for collaborative databases in sorghum field experimentation and modeling. p. 333-337. *In* M.A. Foale, R.G. Henzell, and J.P. Kneipp (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Comstock, R.E. 1977. Quantitative genetics and the design of breeding programs. p. 705-718. *In* E. Pollack, O. Kempthorne, and T.B. Bailey, Jr. (eds.) Proceedings of the international conference on quantitative genetics. Iowa State University Press.

Cooper, M., and S.C. Chapman. 1996. Breeding sorghum for target environments in Australia. p. 173-187. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Cooper, M., and G.L. Hammer (eds.) 1996. Plant adaptation and crop improvement. CAB International, Wallingford Oxon.

Cooper, M., I.H. DeLacy, and K.E. Basford. 1996. Relationships among analytical methods used to analyse genotypic adaptation in multi-environment trials. p. 193-224. *In* M. Cooper and G.L. Hammer (eds.) Plant adaptation and crop improvement. CAB International, Wallingford Oxon.

Cooper, M., I.H. DeLacy, and R.L. Eisemann. 1993. Recent advances in the study of genotype x environment interactions and their application to plant breeding. p. 116-131. *In* B.C. Imrie and J.B. Hacker (eds.) Focused plant improvement: Towards responsible and sustainable agriculture. Proceedings Tenth Australian Plant Breeding Conference. Vol. 1. Organising Committee, Australian Convention and Travel Service, Canberra.

DeLacy, I.H. 1981. Cluster analysis for the interpretation of genotype by environment interaction. p. 277-292. *In* D.E. Byth and V.E. Mungomery (eds.) Interpretation of plant response and adaptation to agricultural environments. Queensland Branch, Australian Institute of Agricultural Science, Brisbane.

Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Donatelli, M., G.L. Hammer, and R.L. Vanderlip. 1992. Genotype and water limitation effects on phenology, growth and transpiration efficiency in grain sorghum. Crop Science 32:781-786.

Fox, P.N., and A.A. Rosielle. 1982. Reference sets of genotypes and selection for yield in unpredictable environments. Crop Science 22:1171-1175.

Haldane, J.B.S. 1946. The interaction of nature and nurture. Annals of Eugenics 13:197-207.

Hammer, G.L., and R.C. Muchow. 1994. Assessing climatic risk to sorghum production in water-limited subtropical environments. I. Development and testing of a simulation model. Field Crops Research 36:221-234.

Hammer, G.L., D. Butler, R.C. Muchow, and H. Meinke. 1996a. Integrating physiological understanding and plant breeding via crop modeling and optimisation. p. 419-441. *In* M. Cooper and G.L. Hammer (eds.) Plant adaptation and crop improvement. CAB International, Wallingford Oxon.

Hammer, G.L., S.C. Chapman, and R.C. Muchow. 1996b. Modeling sorghum in Australia: The state of the science and its role in the pursuit of

improved practices. p. 43-60. *In* M.A. Foale and R.G. Henzell (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Henzell, R.G. 1992. Grain sorghum breeding in Australia: Current status and future prospects. p. 70-80. *In* M.A. Foale, R.G. Henzell, and P.N. Vance (eds.) Proceedings of the second Australian sorghum conference, Gatton 4-6 February 1992. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 68.

Henzell, R.G., R.L. Brengman, D.S. Fletcher, and A.N. McCosker. 1992. Relationships between yield and non-senescence (staygreen) in some grain sorghum hybrids grown under terminal drought stress. p. 355-358. *In* M.A. Foale, R.G. Henzell, and P.N. Vance (eds.) Proceedings of the second Australian sorghum conference, Gatton 4-6 February 1992. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 68.

Henzell, R.G., B.A. Franzmann, and R.L. Brengman. 1994. Sorghum midge resistance research in Australia. International Sorghum and Millets Newsletter 35:41-47.

Jackson, P.A., M.J. Robertson, M. Cooper, and G.L. Hammer. 1996. The role of physiological understanding in plant breeding from a breeding perspective. Field Crops Res. (in press).

Kamoshita, A., R.C. Muchow, M. Cooper, and S. Fukai. 1996. Influence of genotype and environment on the utilisation of nitrogen by grain sorghum. p. 391-396. *In* M.A. Foale, R.G. Henzell and J.F. Kneipp (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Kirkham, M.B. 1988. Hydraulic resistance of two sorghums varying in drought resistance. Plant and Soil 105:19-24.

Krieg, D.R. 1993. Grain sorghum for water deficient environments: A whole plant perspective. p. 133-138. *In* A bushel of potential: Grain sorghum, the crop of the future. Proceedings of the 18th Biennial Grain Sorghum Research and Utilization Conference, Lubbock Texas.

Loomis, R.S. 1993. Optimisation theory and crop improvement. p. 583-588. *In* D.R. Buxton, R. Shibles, R.A. Forsberg, B.L. Blad, K.H. Asay, G.M. Paulsen, and R.F. Wilson (eds.) International crop science I. Crop Science Society of America, Inc., Madison, Wisconsin.

Ludlow, M.M., and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Advances in Agronomy 43:107-153.

Ludlow, M.M., J.M. Santamaria, and S. Fukai. 1990. Contribution of osmotic adjustment to grain yield in *Sorghum bicolor* (L.) Moench under water-limited conditions. II Water stress after anthesis. Australian Journal of Agricultural Research 41:67-78.

Muchow, R.C., A.K. Borrell, and G.L. Hammer. 1996a. Recent advances and current needs in sorghum physiology. p. 141-157. *In* M.A. Foale, R.G. Henzell, and J.P. Kneipp (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Muchow, R.C., M. Cooper, and G.L. Hammer. 1996b. Characterising environmental challenges using models. p. 349-364. *In* M. Cooper and G.L. Hammer (eds.) Plant adaptation and crop improvement. CAB International, Wallingford Oxon.

Muchow, R.C., G.L. Hammer, and P.S. Carberry. 1991. Optimising crop and cultivar selection in response to climatic risk. p. 235-262. *In* R.C. Muchow and J.A. Bellamy (eds.) Climatic risk in crop production: Models and management for the semiarid tropics and subtropics. CAB International, Wallingford.

Muchow, R.C., G.L. Hammer, and R.L. Vanderlip. 1994. Assessing climatic risk to sorghum production in water-limited subtropical environments. II. Effect of planting date, soil water at planting, and cultivar phenology. Field Crops Research 36:235-246.

Robertson, M.J., S. Fukai, M.M. Ludlow, and G.L. Hammer. 1993. Water extraction by grain sorghum in a sub-humid environment. I. Analysis of the water extraction pattern. Field Crops Res. 33:81-97.

Rosenow, D.T., J.E. Quisenberry, C.W. Wendt, and L.E. Clark. 1983. Drought tolerant sorghum and cotton germplasm. Agricultural Water Management 7:207-222.

Santamaria, J.M., M.M. Ludlow, and S. Fukai. 1990. Contribution of osmotic adjustment to grain yield in *Sorghum bicolor* (L.) Moench under water-limited conditions. I. Water stress before anthesis. Australian Journal of Agricultural Research 41:51-65.

Shorter, R., R.J. Lawn, and G.L. Hammer. 1991. Improving genotypic adaptation in crops: A role for breeders, physiologists and modellers. Experimental Agriculture 27:155-175.

Snell, P.J., and M. Cooper. 1996. Factors influencing the repeatability of the expression of osmotic adjustment capacity of four lines of grain sorghum. p. 437-442. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proceedings of the

third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Tangpremsri, T., S. Fukai, K.S. Fischer, and R.G. Henzell. 1991a. Genotypic variation in osmotic adjustment in grain sorghum. I. Development of variation in osmotic adjustment under water-limited conditions. Australian Journal of Agricultural Research 42:747-757.

Tangpremsri, T., S. Fukai, K.S. Fischer, and R.G. Henzell. 1991b. Genotypic variation in osmotic adjustment in grain sorghum. II. Relation with some growth attributes. Australian Journal of Agricultural Research 42:759-767.

Tangpremsri, T., S. Fukai, and K.S. Fischer. 1995. Growth and yield of sorghum lines extracted from a population for differences in osmotic adjustment. Australian Journal of Agricultural Research 46:61-74.

Tao, Y.Z., C.L. McIntyre, and R.G. Henzell. 1996. Applications of molecular markers to Australian sorghum breeding programs. I. Construction of a RFLP map using sorghum recombinant inbred lines. p. 443-450. *In* M.A. Foale, R.G. Henzell, and J.F. Kneipp (eds.) Proceedings of the third Australian sorghum conference, Tamworth, 20-22 February 1996. Australian Institute of Agricultural Science, Melbourne, Occasional Publication No. 93.

Tenkouano, A., F.R. Miller, R.A. Fredrikson, and D.T. Rosenow. 1993. Genetics of nonsenescence and charcoal rot resistance in sorghum. Theoretical and Applied Genetics 85:644-648.

Van Oosterom, E.J., R. Jayachandran, and F.R. Bidinger. 1996. Diallel analysis of the stay green trait and its components in sorghum. Crop Science 36:(in press).

Walulu, R.S., D.T. Rosenow, D.B. Webster, and H.T. Nguyen. 1994. Inheritance of the staygreen trait in grain sorghum. Crop Science 34:970-972.

Breeding Pearl Millet for Drought Tolerance

V. Mahalakshmi*, E.S. Monyo, W. Payne,
S. Quattara, and F.R. Bidinger

Abstract

*Pearl millet [*Pennisetum glaucum *(L.)] is grown as a food crop under rainfed conditions in the arid and semi-arid regions of south Asia and Africa. Intra-seasonal and inter-seasonal variations in timing and intensity of rainfall result in drought stress of various intensities and durations during crop growth. Once the crop is established, it is most sensitive to drought stress in the flowering and early grain-filling periods. This paper discusses efforts to improve crop performance in these environments by 1) early flowering to provide drought escape, 2) direct evaluation of performance in natural or managed drought environments, and 3) incorporation/selection for responses of traits associated with drought tolerance. Traits and responses to drought tolerance can be effectively used in a breeding program only when there is genetic variation for the traits and the heritabilities of these traits are sufficiently high to be exploited as selection criteria. Examples of selection for grain-filling ability in stress (panicle harvest index) and its expression and relation to productivity are discussed.*

Pearl millet is one of the major rainfed crop of arid and semi-arid regions in south Asia and Africa. These environments are characterized by low and erratic rainfall resulting in drought stress during crop growth. Therefore, breeding for improved adaptation to these marginal environments has been an important objective in programs aimed at improving the productivity of this crop. Drought describes the condition in which the available soil moisture is reduced to the point that the plant cannot absorb water rapidly enough to replenish the amount transpired. Sensitivity to drought depends on the stage of crop growth; in millet once the crop is established, the flowering and early grain-filling stages are most sensitive.

Breeding for marginal environments can be approached in three ways to develop adapted crop varieties.

1. Develop cultivars with appropriate development patterns to match the water availability in the environment (assuming water availability is sufficiently predictable);

2. Select for improved yield and its stability using natural marginal/stress environments and managed stress environments by simulating naturally occurring stress patterns;

3. Select for morphological, physiological, or biochemical characteristics

V. Mahalakshmi, ICRISAT, Asia Centre, Patancheru, A.P. India 502 324; E.S. Monyo, ICRISAT, SEA, SADC/ICRISAT, Matopos Research Station, P.O. Box 776, Bulawayo, Zimbabwe; W. Payne and S. Quattra, ICRISAT Sahelian Center (ISC), BP 12404, Niamey, Niger (Via Paris); and F.R. Bidinger, ICRISAT, Asia Centre, Patancheru, A.P. India 502 324. *Corresponding author.

directly related to performance under drought conditions.

Development Patterns to Match the Resource Availability

The two major millet-growing zones of the world lie in different latitude zones, 11-17° N in west and central Africa and 15-30° N in northwest India. In both these zones, the length of the growing season varies from 10 to 18 weeks (Kowal and Kassam, 1978; Virmani et al., 1982) and is negatively related to the latitude. This relationship is more acute in west Africa, where length of the growing season changes markedly over a small range in latitude (Fig. 1). Therefore, matching development patterns to water availability has been a consistent theme in breeding programs in Asia, south and eastern Africa, and west and central Africa. This alternative is simple and can be exploited easily in a breeding program before investing major resources for drought tolerance breeding.

Early flowering is often cited as an escape mechanism in locations where end-of-season stress is a dominant feature and the inter-year variation in crop season length is minimal. With a wide range in moisture availability pattern and growing season length both in Asia and west Africa (Fig. 1), appropriate phenology of the crop rather than early flowering will ensure optimum resource use. This can be achieved by determining the required season length and patterns of drought in a location, then developing cultivars of appropriate duration and required photoperiod sensitivity. In west Africa, inter-year variation in crop season length is high, due mostly to the variation in the time of onset of rainfall, as the end of the season

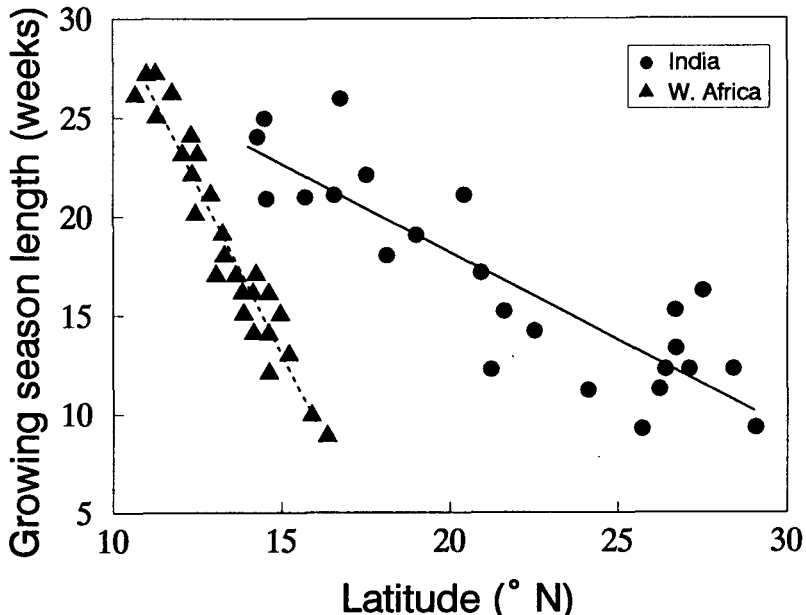


Figure 1. Relationship between latitude and season length of pearl millet growing locations in West Africa and South Asia.

is less variable (Kowal and Kassam, 1978). The approach for these environments has been to tailor cultivars through photoperiod sensitivity, providing opportunities to sow whenever the rains begin, but ensuring that flowering and grain-filling occur when the moisture regime is most favorable to overcome the end-of-season stress.

Selection for Yield and Stability

Yield has, and always will be, an important selection criterion in breeding programs. Environmental and genotype × environment variance components for grain yield, however, often exceed the genetic component of variance. The two philosophies in plant breeding for improving and stabilizing yield reflect a desire to either a) improve crop production in a specific agro-ecological environment (specific adaptation), or b) improve crop production across a wide range of environments (wide adaptation). Selecting for yield in a wide range of environments implies that the morphological and physiological plant characteristics associated with maximum yield potential are the same in the stressed environments. Initial successes in wheat and rice through breeding for wide adaptation were limited to the favorable environments; it is now recognized that improvements in rainfed marginal environments need to be addressed through specific adaptation (Cockerel, 1989). Marginal environments are highly variable both in space and time. This variability is, therefore, the real challenge to the breeders, rather than the environment per se. Two approaches used to select for specific adaptation are: a) selection for yield and stability in natural stress environments, and b) selection for yield and stability in managed stress environments.

Natural Stress Environments

In southern and eastern Africa, selection environments have been progressively refined to differentiate between terminal drought, which occurs when rains end prematurely (Mahenene-Namibia, Maun-Botswana, and Makoholi-Zimbabwe), and intermittent transient droughts of varying duration and intensity during crop growth (Matopos-Zimbabwe, Sebele-Botswana, and Mashare-Namibia). Selection for yield and stability in these environments identifies genotypes with particular adaptation to the types of droughts prevalent in these locations. It is possible to make gains in selection efficiency by appropriately differentiating between droughts occurring at particular stages of crop development (usually related to a particular phenology), effectively describing the probability of a particular drought regime in target environments, and tailoring the selection environment to match.

Using these criteria as examples, the following genotypes have been described as either resistant or tolerant to drought in their respective environments. SDMV 89001, SDMV90016, SDMV90004, SDMV91018 and Okashana-1 proved tolerant to drought in the terminal drought stress environments of Zimbabwe and Namibia and in the transient intermittent drought environment areas of Zambia (Simulumbe), Namibia (Mashare), and Malawi (Kasinthula) (Table 1). SDMV 89005, though relatively high yielding under good conditions, was not very good under terminal drought and fared the same

Table 1. Performance data of pearl millet varieties in multilocational drought stress nurseries across six SADC locations, 1991-92 growing season.

Variety	Time to 50% flowering (days)	Grain yield (t ha^{-1})						
		Matopos	Makoholi	Simulumbe	Mahanene	Mashare	Kasinthula	Mean
SDMV 89005	69	0.21	0.14	1.55	1.25	1.24	1.30	0.95
SDMV 89001	63	0.40	0.17	1.43	1.60	0.81	1.14	0.92
SDMV 90016	65	0.40	0.17	1.43	1.60	0.81	1.14	0.92
ICMV-F 86410	66	0.44	0.17	1.29	1.16	0.92	1.41	0.90
SDMV 90031	70	0.39	0.13	1.68	0.81	1.21	1.08	0.88
SDMV 90004	61	0.31	0.24	1.48	1.35	0.67	1.11	0.86
SDMV 91018	67	0.32	0.23	1.45	1.41	0.64	1.09	0.86
Okashana-1	61	0.35	0.17	1.51	1.59	0.79	0.68	0.85
Farmers' local	80	0.02	0.06	1.51	0.44	0.45	0.90	0.56
SE	-	±0.07	±0.04	±0.25	±0.21	±0.18	±0.27	-
MEAN(16)	66.9	0.34	0.16	1.42	1.21	0.81	0.99	0.83
CV(%)	-	39	56	30	24	45	55	-

as farmers' local varieties in severe terminal drought locations such as Matopos and Makoholi during the 1991/92 season. The weakness of this approach is the high degree of annual variability in available moisture, even in locations generally characterized by a specific type of drought pattern. Effective use of data from such natural stress environments requires that the actual moisture patterns of individual trials be quantified, so that differential genotype performance can be related to specific types of stress occurrence in the trial data sets, and not simply to test location. This can be done using a relatively simple soil water budgeting approach to cluster environments by stress pattern (Van Oosterom et al., 1996a). Quantification of environments in this fashion also can be a very powerful tool in the analysis of the inevitably large G × E interaction in such data sets (Van Oosterom et al., 1996b).

Managed Stress Environments

When the pattern and intensity of drought in the target environment are regular and predictable, selecting for yield and its stability in that environment should lead to better adapted material. Drought, however, is normally variable both in space and time. The former approach, therefore, can be time-consuming and the results often difficult to interpret. The alternate approach has been to select for yield and its stability in simulated stress environments. Both intensity and patterns of drought can be simulated during rain-free periods in the field to reproduce the natural stress conditions. An alternative approach possible in many tropical environments is to simulate the target drought patterns with controlled irrigation in normally rain-free periods of the year.

Such "managed" stress environments are far more repeatable than are naturally occurring environments, and they allow simulation of more than one version of the target stress pattern (e.g., differing intensities of stress at a particular stage of crop growth) (Mahalakshmi et al., 1988). As the example below illustrates, they also can allow simulation of the interaction of moisture and other management factors,

reflecting different levels of management intensity.

In west Africa, season length and total rainfall are related to the latitude (Figs. 1 and 2). Seasonal rainfall varies not only in total amount but also in the frequency and amount of rainfall during the season (Fig. 3). The variable moisture is further confounded by low soil fertility, especially low phosphate. All combinations of two fertility levels (no phosphate and 200kg SSP), two planting densities (40 x 40 cm and 100 x 100 cm), and three irrigation programs to simulate long-term rainfall patterns of 200, 300 and 600 mm, representing the 12 environments, were used to screen elite breeding materials in Niger. Stability analysis of genotypes across all 12 environments indicated that top (variety) cross hybrids had better mean grain yield and responded similarly or better than their pollinator parents to changing environmental conditions (Fig. 4). Results from such studies can help to identify better adapted material for a range of environments. An important caution in the use of such environments is the possible effects of off-season environments either directly on crop growth or development (e.g., daylength effects), or indirectly on crop × stress interactions (e.g., temperature and PET).

Selection for Traits Associated with Drought Tolerance

For any trait to be successfully used as a selection criterion in a drought breeding program, there are three major requirements.

1. The trait should be related to drought tolerance or grain yield in stressed environments.

2. There should be sufficient genetic variation for the trait to be exploited in the selection.

3. The heritability of the trait should be sufficiently high to be useful.

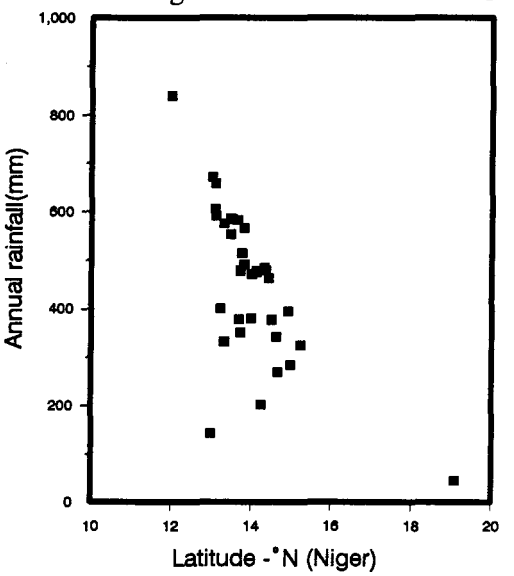


Figure 2. Relationship between latitude and total rainfall in West Africa.

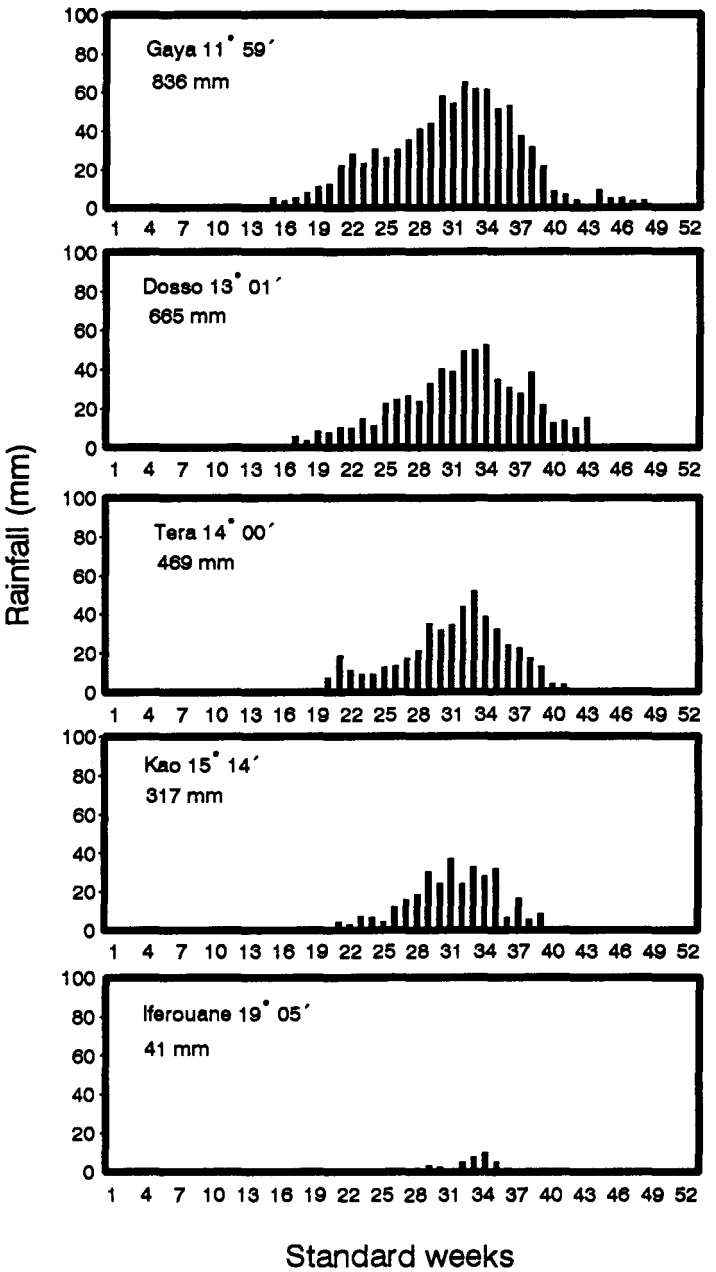


Figure 3. Rainfall distribution at selected locations in Niger.

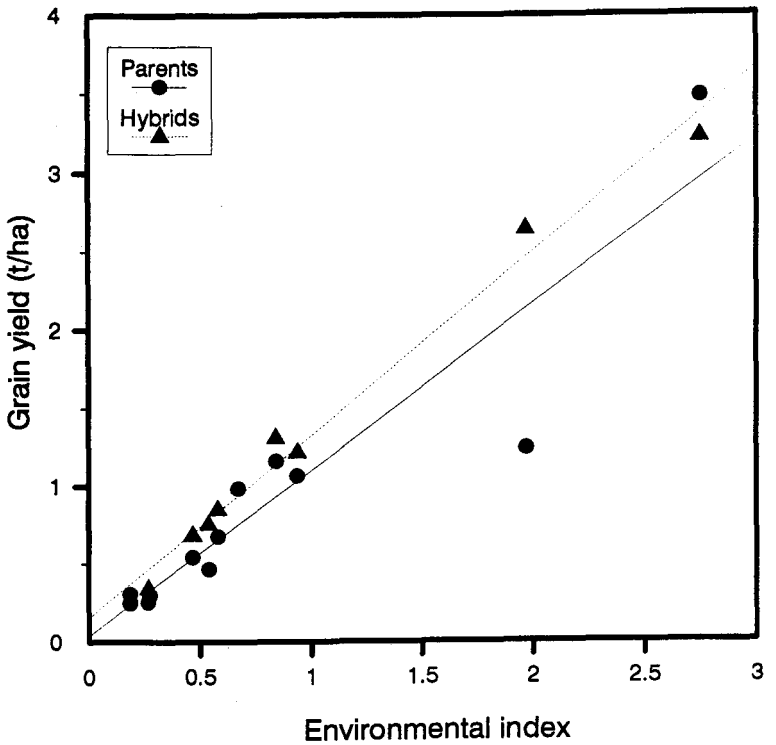


Figure 4. Performance for top (variety) cross hybrids and varieties in 12 simulated environments in Niamey, Niger during 1995.

Though many morphological, physiological, and biochemical traits have been associated with drought tolerance, the genetics of these traits are often complex and not well enough understood to allow them to be used as selection criteria in a breeding program (Bidinger and Witcombe, 1989). Considerable research has been conducted on the traits themselves, but there are few cases where an individual trait or mechanism has been shown to be sufficiently associated with yield to recommend it as a selection criterion. These traits frequently contribute to processes related to determining drought tolerance (e.g., conserving water, reducing transpiration), but pyramiding of these traits may be required to translate individual processes into grain yield.

Conceptually, traits that are heritable but not linked can be incorporated simultaneously in breeding procedures. However, cost and time involved in selection of these traits are major constraints. It is easy to use integrated traits that are directly related to drought response. The C-13 discrimination in C_3 crop, which is an integrated measure of transpiration efficiency over time, and the silking-anthesis interval under stress in maize, which ensures grain setting and filling, are examples of such traits. In pearl millet, ability to set and fill grains was found to be related to drought tolerance (Bidinger et al., 1987). Of all the responses related to drought tolerance in pearl millet, panicle harvest index (PHI), which integrates all the components of grain yield, was the

best predictor. Therefore, panicle harvest index, which integrates both setting and filling of grains, can be used as a selection criterion.

Before embarking on an ambitious program to breed for this trait, genetic variation, heritability, and response to yield under drought were examined. Genetic variation for this trait was higher under terminal stressed conditions compared to non-stressed conditions (Table 2). This would suggest that the expression of this trait is in response to drought. The other concern often expressed for traits to be used in selection is the variability associated with the measurement of the trait. Grain yield under stress is variable and, compared to grain yield, panicle harvest index is less variable (Table 2). Heritability of this trait (as measured by $s_1 \times s_2$ regression) was higher than grain yield but lower than simply inherited traits like time to 50% flowering (Fig. 5). Heritability of the trait was reported to be moderate with additive and dominance mode of inheritance (Yadav, 1994).

With this background information, we explored the possibilities of using panicle harvest index as a selection criterion to breed pearl millet for drought tolerance. The two approaches we used were: 1) varietal improvement in a population (EC87) using panicle harvest index as the selection criterion, and 2) divergent selection in restorer lines.

Varietal Improvement in a Population (EC87) Using Panicle Harvest Index as the Selection Criterion

Panicle harvest index (PHI) — ratio of grain mass to total panicle mass — is an inexpensive, but repeatable measure of the ability to both set and fill grains under moisture stress. PHI has been shown to be well correlated with estimates of terminal drought tolerance, and has potential as a selection criterion for improved ability to set and/or fill grains under terminal drought stress. PHI is being evaluated as a selection criterion in the breeding of terminal-drought-tolerant experimental varieties from populations and in the identification of terminal-drought-tolerant hybrid parents.

Table 2. Mean time to flowering, grain yield and panicle harvest index of 42 test cross hybrids in different environments.

Environments	Time to 50% flowering (days)		Grain yield $g\ m^{-2}$		Panicle harvest index (%)		
	Mean	CV	Mean	CV	Mean	CV	SD[1]
Summer 92 - Control	54	4.1	364	12.5	75.5	2.66	2.01
Summer 92 - Stress	53	4.6	214	19.4	61.8	8.89	4.16
Summer 93 - Control	55	2.6	364	11.4	76.6	3.68	1.56
Summer 93 - Stress	54	3.0	294	15.7	69.3	9.90	3.17
Summer 94 - Control	45	2.6	329	11.2	75.9	5.17	1.75
Summer 94 - Stress	44	2.3	109	21.4	55.9	10.75	4.59
Rainy 91 - Patancheru	41	2.1	358	11.0	76.5	3.07	1.4
Rainy 92 - Patancheru	41	2.6	355	10.5	78.8	2.73	1.23
Rainy 93 - Patancheru	43	1.7	466	7.8	80.3	2.56	1.4
Rainy 91 - Hisar	51	3.7	294	27.5	77.5	4.06	1.58
Rainy 92 - Hisar	49	4.3	405	23.2	70.7	5.26	2.72
Rainy 92 - Fathepur	48	4.4	299	32.2	75.8	5.28	1.92
Rainy 93 - Fathepur	54	3.4	119	34.0	64.5	9.68	2.19
Rainy 94 - Fathepur	49	3.3	265	23.0	73.0	4.91	1.67
Rainy 93 - Jodhpur	58	6.1	94	35.9	65.0	11.75	2.28

[1]SD = Standard Deviation

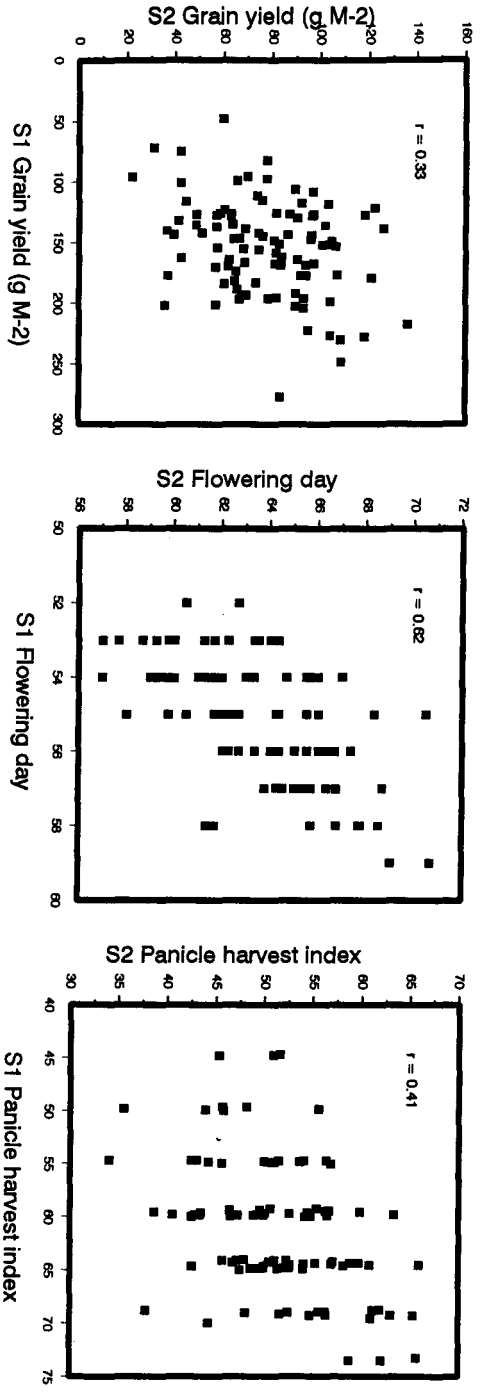


Figure 5. **Relationship between S1 progeny and S2 families: values for grain yield, time to 50% flowering, and panicle harvest index.**

We have compared selection for PHI (under stress) and selection for grain yield (under irrigation) in both single stage and two-stage (combined with yield selection) selection schemes, using the Early Composite 1987 (EC87) as the base composite. The experimental varieties based on the different selection criteria were extensively evaluated in both stressed and non-stressed test environments, including the original managed stress selection environment. One cycle of selection for PHI in a single stage scheme increased PHI in stressed environments (low PHI environments), in comparison to both a randomly selected control (1:1 line), and a control selected for grain yield (Fig. 6).

The single stage selection for PHI resulted in small yield increases in dry season test environments and a substantial increase in the rainy season stress environments in north India, compared to the population control (varieties made from a random sample of population progeny, Table 3). Compared to the selection control (selection for grain yield in the absence of stress), selection for PHI resulted in a yield advantage of 22% in the dry season stress environment, and in an ad-

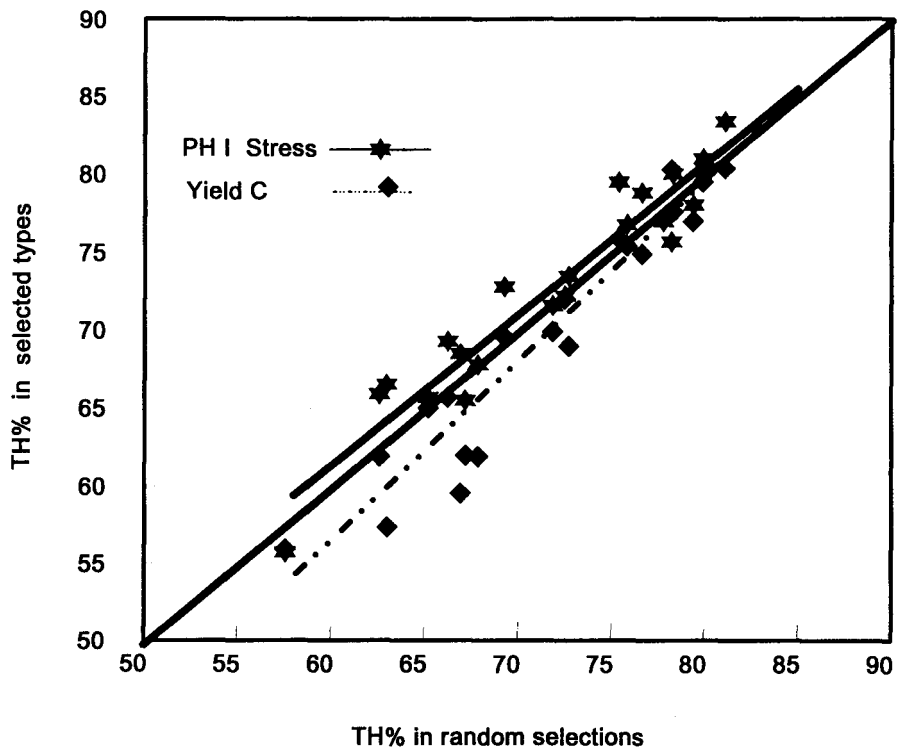


Figure 6. **Panicle harvest index of experimental varieties made on the basis of high PHI under stress and on the basis of grain yield in the irrigated control, in relation to panicle harvest index of experimental varieties made from random selections of S1 progenies (1:1 line). Data are from the test environments listed in Table 1; the drought stressed test environments are those with the low panicle harvest index.**

Table 3. **Gains/losses in grain yield of experimental varieties (as a percentage of the mean yield [gm^{-2} - column 2] of the two control varieties, made from randomly selected progenies) based on the following selection criteria: panicle harvest index in the drought nursery terminal stress treatment (PHI/DNS); grain yield in the drought nursery irrigated control treatment (YLD/DNI); panicle harvest index in the drought nursery stress plus grain yield in the rainy season (PHI/DNS + YLD/RS); and grain yield in the drought nursery irrigated treatment plus grain yield in the rainy season (YLD/DNI + YLD/RS). Test environments are coded by location (DN - dry season drought nursery; NI - north India: Hisar, Gwalior, Fathepur, and Jodhpur; SI - south India: Patancheru and Anantapur)**

Test Environ. (no.)	Random selection	PHI/DNS	YLD/DNI	PHI/DNS + YLD/RS	YLD/DNI + YLD/RS
	Grain yield $g\ m^{-2}$		Grain/loss (% over random selection)		
DN/Stress (4)	168	+2.3	-19.8	-12.9	-14.5
DN/Irrig (4)	359	+7.3	-0.8	+8.6	-5.1
NI/NonStrs (3)	352	-7.9	-1.6	+4.2	+4.7
NI/NonStrs (5)	202	-4.3	-3.5	-0.6	-4.3
NI/Stress (2)	134	+10.9	-5.9	+35.6	+2.4
S/NonStrs (4)	384	-0.6	+5.1	+5.1	-2.7

vantage of 17% in the stressed rainy season environments (Table 3). This occurred primarily because the experimental variety made from selections based on grain yield in the stress environment was significantly inferior to that made from the random selections. In ten non-stressed rainy season environments, selection for PHI reduced yield by approximately 5%, compared to the selection control (Table 3).

PHI as the first stage selection criterion in a two-stage selection scheme was less effective than in a single-stage scheme, possibly because of the reduced selection intensity for PHI in the two-stage scheme. Improvement over the population control was erratic (and negative in the selection environment), except in the rainy season stress environment. Improvement over the selection control was general, but not large, except in the rainy season stress environment (Table 3).

These results provide support for the further exploration of PHI as a selection criterion for terminal drought tolerance in the breeding of cultivars for drought-affected environments from adapted populations. The results indicate that a strong selection pressure for PHI, preferably done in the target environment, under a severe stress challenge, is likely to be the most effective application of the approach.

Divergent Selection in Restorer Lines

Test cross hybrids (on three male-sterile lines) of 49 diverse restorer (R) lines were tested for their restoration ability and performance under terminal drought conditions during 1988. Based on mean panicle harvest index of the test crosses in drought conditions, seven divergent (top and bottom) R lines from each group were selected. These were then crossed onto three diverse male-sterile lines to produce hybrids that were tested over three years in simulated drought conditions, natural drought conditions, and well-irrigated conditions (Table 2). The combined data were analyzed to test expression of the trait and genetic variation in different en-

vironments and the relationship between PHI and grain yield in different environments.

The range in panicle harvest index was higher under stressed conditions than non-stressed conditions, and the coefficient of variation was lower than grain yield in all environments. Though the two parameters — genetic variation for the trait and accuracy with which one can measure the trait — are important in the breeding procedures, the usefulness of the trait depends on its heritability. The expression of the trait was assessed in the environment where the selection was carried out, in similar environments where the trait confers advantage, and in other environments (Table 4). The selected PHI values of the R lines and their observed PHI were correlated in the summer drought stress environment where the selections were carried out and in the majority of the natural stress environments. Similarly the selected PHI values and grain yield in the stress environments in the summer were related (Table 4). Therefore, the results from these two studies would suggest that PHI could be used as a selection criterion for drought tolerance, and the chance of making bigger gains is more likely if the selections were done in the stress environment. Experiments are underway to test this hypothesis.

References

Bidinger, F.R.., V. Mahalakshmi and G.D.P. Rao. 1987. Assessment of drought resistance in pearl millet [*Pennisetum americanum* (L.) Leeke]. II Estimation of genotype response to stress. Aust. J. Agric. Res. 38:49-59.

Bidinger, F.R., and J.R. Witcombe. 1989. Evaluation of specific drought avoidance traits as selection criteria for improvement of drought resistance. p. 151-164. *In* F.W.G Baker (ed.) Drought resistance in cereals, CAB International, Wallingford, UK.

Cockerel, S. 1989. Wide adaptation: How wide? Euphytica 40:197-205.

Kowal, J.M., and A.H. Kassam. 1978. Agricultural ecology of savanna: A study of West Africa. Clarendon Press, Oxford, UK.

Mahalakshmi, V., F.R. Bidinger, and G.D.P. Rao. 1988. Timing and intensity of water deficits during flowering and grain-filling in pearl millet. Agron. J. 80:130-135.

Van Oosterom, E.J., V. Mahalakshmi, F.R. Bidinger, and K.P. Rao. 1996a. Effect of water availability and temperature on the genotype-by-environment interaction of pearl millet in semi-arid tropical environments. Euphytica 89:174-183.

Van Oosterom, E.J., F.R. Bidinger, V. Mahalakshmi, and K.P. Rao. 1996b. Effect of water availability pattern on yield of pearl millet in semi-arid tropical environments. Euphytica 89:165-173.

Virmani, S.M., M.V.K. Sivakumar, and S.J. Reddy. 1982. Rainfall probability estimates for selected locations of semi-arid India. 2nd edition. Research Bulletin No.1. International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, A.P. India.

Yadav, O.P. 1994. Inheritance of threshing percentage in pearl millet. Euphytica 78:77-80.

Table 4. Range in grain yield and panicle harvest index and correlation between panicle harvest index (selected value) and grain yield in different environments.

Environment (no. of environments)	Grain yield ($g\ m^{-2}$)	Panicle harvest index (%)	Mean correlation between selected PHI and	
			PHI	Grain yield
Selection environment (Summer Stress) (3)	109-294	56 - 69	0.59(3)	0.65(3)
Summer irrigated (3)	329 - 364	75 - 76	0.22(1)	0.57(2)
Rainy-stress (2)	94 - 119	65	0.60(2)	0.11
Rainy-nonstress (8)	464 - 466	71 - 80	0.28(1)	0.02

Discussion

Session VI - Breeding for Resistance to Moisture Stress/Drought
Session Chair: Abraham Blum
Rapporteurs - Mike Gilbert and Issoufou Kapran

Ken Kofoid -Your data shows that the stay green trait maps close to the HSP lucus. Is the stay green trait an allele of the HSP locus? Also, since drought stress is usually associated with heat stress, have you tested the stay green material in a drought stressed, non-heat stress environment?

Henry Nguyen - It is unknown until we isolate and characterize the stay green genes. It should be noted that some heat shock proteins are induced by drought (water deficit) stress and may involve cell protection under stress.

D.T. Rosenow - The stay green material has been tested in moisture stress with mild temperatures, and the genotype differential still expresses well.

R.G. Henzell - Is there any QTL for stay green in maize to compare with sorghum?

H. Nguyen - I am not aware of any public information on the genetic mapping of stay green characteristics in maize.

Koushik Seetharaman - Keep in mind that maize is a highly senescent crop - not necessarily related to sorghum.

B.S. Rana - Osmotic adjustment does not appear a stable trait. We found that RWC (relative water content of leaf) may be a better trait to characterize drought tolerant genotypes. Don't you feel that molecular characterization of RWC will be more useful in this context?

Henry Nguyen - Based on the research of Merv Ludlow and his associates in Australia, osmotic adjustment is an important trait in sorghum. The "stability" issue is a technical matter. OA and RWC are related parameters in plant water relations and both should be useful when proper measurements and stress protocols are used.

F.R. Bidinger - I believe that we should consider responses to stress or integrated traits seriously as selection criteria for drought tolerance. These are 1) a direct measurement of genotype ability to maintain the normal growth processes for the time at which the stress is occurring, 2) are readily related to overall crop performance, 3) are usually easily/economically measured, and 4) have in many cases, useful heritabilities.

B.S. Rana - 1) I have seen sorghums respond differently for stay green between the rainy and dry season. Can you explain why? 2) It seems to me that charcoal rot may be confounding stay green ratings. What is your opinion? 3) Do you feel there is a relationship between stem sugar and stay green?

D.T. Rosenow - 1) Extreme care must be taken when evaluating for stay green in the off-season due to different maturity and yield expression due to short days effects on photoperiod sensitive or even on non-sensitive types. You alsomust be sure that stay green reaction is due only to moisture stress induced senescence and not influenced by leaf diseases or natural senescence. 2) I feel that charcoal rot does not complicate stay green ratings. Charcoal rot infects only plant tissues under severe moisture stress, and therefore moisture stress comes first and results in susceptibility to charcoal rot. 3) I do not feel that high stem sugar (at least sucrose) per se contributes to stay-green. It appears that high stem sugars can result from stay green, in that green, healthy leaves produce photosynthate. Stay green can help maintain the genetic potential of stem sugars. You must be careful to not make a wrong conclusion due to the fact that sugars are low in a plant nearly dead due to moisture stress during grain fill.

R.G. Henzell - Are genotypic differences in stay green expressed more strongly among hybrids than among lines?

D.T. Rosenow - Expression of stay green in F_1 hybrids is not always the same as in parental lines. The response is expressed well in hybrids,and can be more extreme in hybrids than in lines. The stay green trait in some lines is completely recessive, while in others it is dominant. Therefore, when breeding for hybrids, breeders must evaluate the F_1s, as well as the lines themselves. For pre-flowering resistance, it appears to be dominant, and is expressed well in hybrids. In fact, heterosis of F_1 hybrids enhances resistance to pre-flowering stress.

Robert Schaffert - Is the stay green characteristic in sorghum the same as the stay green characteristic in maize, i.e., the ability to stay green after physiological maturity or is it dependent on water stress to be manifested? Is it possible to screen for evaluation trials without moisture stress?

D.T. Rosenow - The stay green trait as I use it, and I believe most other sorghum researchers use it, refers to premature leaf/plant death due specifically to soil moisture stress. I feel that any conclusion on stay green by rating natural leaf senescence in the absence of moisture stress is very risky. However, under mild stress, I feel that ratings can be useful. To my knowledge, there is no information on the relationship between stay green in sorghum and maize.

Swarnlata Kaul and B.S. Rana - There is an interest in Guineas to be used for grain mold resistance. You have shown a dwarf guinea genotype. Does it have resistance to grain mold?

D.T. Rosenow - That line, SC265, does not have grain mold resistance, but several converted guineas do have good grain mold resistance.

Oscar Rodriguez - How do you estimate or mathematically calculate the PHI?

V. Mahalakshmi - Panicle harvest index is calculated as the ratio of grain yield to spike yield.

Issoufou Kolo Abdourhamane - 1) Do you observe a difference among pearl millet genotypes with regard to harvest index? 2) I saw a slide showing yield of different pearl millet cultivars, with a local one as check. Where was the work done?

V. Mahalakshmi - 1) The variation for panicle harvest index in nonstressed conditions is very small. The trait expresses itself under terminal drought conditions. 2) This data is from Zimbabwe 1991/92 during the drought year.

Brhane Gebrekidan - Is it possible to conceive and design the dream plant (ideotype) with specific morphological and physiological characteristics, suitable for drought stress environments?

R.C. Muchow - The concept of a "dream" plant is representative of thinking two decades ago. There is no miracle plant. Today we are better able to characterize environments and target specific plant characteristics to particular environments. We also have quantitative frameworks to allow assessment of why a trait may be useful and how we might evaluate traits. I believe thinking of a "dream" plant gave physiology a poor status int the past. Now physiology is helping very much in understanding GXE interactions and providing opportunities for yield improvement in drought prone environments.

V. Mahalakshmi - There are no dream idiotypes. The plant type which will do well to pre-flowering stress (high tillering) may not be the best for post-flowering (low tillering synchronous flowering) stress. This is the very reason why specific adaptation has become the theme for marginal stress environments.

Questioner (name unknown) - How is weighting to adjust yield or comparisons of yields done?

R.C. Muchow - The TPE is characterized by running the model for 100 years of climate data at a location. Then the specific year is run with the model to characterize the pattern of stress in that year at that location. The frequency of occurrence of the pattern in that specific year in the TPE is examined. If the pattern occurs rarely the mean yield is underweighted and vice versa. On-going research is examining different weighting methodologies to realize the potential of this approach.

Swarnlata Kaul and B.S. Rana -Do you have information on genetics and physiological characterization of stay-green trait?

R.C. Muchow - There are references to the genetics of stay-green in the paper by Nguyen, et al presented at this workshop. There is current work on the physiology of stay-green in Australia by Borrell, some of which is published in the proceedings of the recent (1996) Australian Sorghum Conference.

Session VII

Breeding for Resistance to Other Abiotic Stresses and *Striga*

Session Chair: Fran Bidinger

Rapporteurs: Medson Chisi and Peter Esele

Speakers:

L.M. Gourley
J.W. Johnson
L.G. Butler
G. Ejeta
A.G.T. Babiker

Genetic Resistance to Soil Chemical Toxicities and Deficiencies

L.M. Gourley*, C.E. Watson, R.E. Schaffert, and W.A. Payne

Abstract

Breeding new crop cultivars for adaptation to stress-related phenomena due to soil chemical toxicity and deficiency is a complex process. Data from nutrient culture trials, in which seedling plants are stressed with a deficiency or excess of mineral elements, do not correlate well with those from similar field stress conditions using the same germplasm. Further, evaluating segregating populations in nutrient culture can result in little or no genetic gain due to selection. Field screening efforts are plagued with genotype × environmental interactions caused by a multitude of biotic and abiotic factors. Selecting the proper level of stress for field evaluations and maintaining this level in a dynamically changeable medium like soil can be difficult. Genetic improvement of sorghum under field conditions similar to those encountered by farmers, however, has nearly always been obtained.

Few plant breeding programs have goals of developing cultivars or hybrids specifically adapted to low-input cropping systems. Selections are generally made in highly fertile, weed-free, high plant population environments; however, many reports in the literature indicate that genes needed for achieving maximum yield in low-input or stress environments often differ from those required in high-input conditions.

The demand for cereal grains in tropical environments characterized by soils that impose mineral stresses has mandated additional breeding research to adapt sorghum and pearl millet to these environments. This paper describes some of the soil mineral stress constraints, possible plant mechanisms of tolerance or avoidance, screening methodology, and results of plant breeding efforts.

Mineral stresses are the nutrient deficiencies or toxicities of a soil that constrain crop production. Vose (1987) estimated that approximately 18% of the world's soil (over 2.4 billion ha) is acid, and approximately 25% is calcareous and liable to Fe deficiency problems. Additionally, saline and sodic soils cause mineral stresses on approximately 0.9 billion ha of land. Problem soils cause more acute crop production constraints for resource-poor tropical farmers in developing countries than for temperate zone farmers in developed countries. However, improvement in nutrient use efficiency and tolerance to toxicities would benefit all farmers.

L.M. Gourley, Department of Plant and Soil Sciences, Box 9555, Mississippi State University, Mississippi State, MS 39762; C.E. Watson, Department of Experimental Statistics, Box 9555, Mississippi State University, Mississippi State, MS 39762; R.E. Schaffert, National Maize and Sorghum Research Center (CNPMS), EMBRAPA, Caixa Postal 151, 35701-970 Sete Lagoas, Brazil; W.A. Payne, Oregon State University, Pendelton, OR (formerly with ICRISAT, Sahelian Center, Niamey, Niger). *Corresponding author.

Cation exchange sites in soils can be occupied by acidic cations, such as H^+ and Al^{3+}, and basic cations, mainly Ca^{2+}, Mg^{2+}, K^+, and Na^+. Metal cations are readily exchangeable, while H^+ is less exchangeable in the soil. The effective cation exchange capacity (ECEC) is obtained by considering only readily exchangeable cations, including Al^{3+} and the basic cations, but not undissociated H^+. Tropical soils are characterized by low levels of available N, P, and K; micro-nutrients such as Zn, B, Mo, and Cu; high P-fixation; and low ECEC. Even applications of calcium Ca and Mg in fertilizer quantities are required to make these infertile soils productive.

Soil acidification is mainly caused by the release of protons during the oxidation of C, S, and N compounds in soils. Older, more weathered soils are generally more acidic than younger soils (Helyar and Porter, 1989). Agricultural production also speeds soil acidification through crop removal, addition of acid-forming fertilizers, and incorporation of organic matter (OM), which promotes natural acidification through humification.

Toxicity of Al^{3+} — not H^+ activity — is probably the most important plant growth-limiting factor in tropical acid soils. The quantity of exchangeable Al^{3+} in the soil is generally measured as a percentage of the ECEC and expressed as percent Al saturation. Aluminum toxicity has been discussed in a number of reviews (Foy, 1988; Haug, 1984; Roy et al., 1988; Taylor, 1988); however, the physiological basis for Al tolerance remains uncertain. Acid soils also are characterized by high P-fixation of amended P. Low P-availability may be more important than Al toxicity in some acid soils.

Manganese toxicity generally occurs in acid soils, but also can occur at a pH above 5.5 in poorly drained or compacted soils (Foy, 1984). Plants take up Mn from the soil solution in the form of Mn^{2+}, and toxicity primarily affects plant shoots rather than roots. A major problem for agronomists is that a critical toxicity concentration for Mn in plant tissue has not been established (Horst, 1988).

Salinity is a problem in many tropical soils and can be caused by indigenous salt in the soil or irrigation water; a high water table in coastal areas; or greater evaporation than precipitation in semi-arid regions. Salt sensitivity in some crops has been attributed to the failure of plants to keep Na^+ and Cl^- ions out of the transpiration stream, and thus the cytoplasm of the aerial parts of the plant. Alkaline soils with pH values greater than 7.5 have unique micronutrient availability problems. Deficiencies of Fe, Mn, B, Zn, and Cu frequently occur in crop plants growing on alkaline soils (Buol and Eswaran, 1994).

Defining the Problem: Plant-Soil Interactions

Ecologists have studied the colonization, encroachment, and displacement of different species of plants on soils with severe mineral excesses or deficiencies. Each successful species had a comparative advantage over those which were not adapted to the particular stress. In evolution, plants mutate (probably the redundant genes in the genome) and adapt to changing environmental conditions through survival of the fittest. Soil microorganisms also may affect adaptation of the host plant to soil stresses in a number

of ways. Plant nutrients may be either mobilized, immobilized, or their acquisition may be altered by changes in root physiology. Nitrogen may be lost through denitrification or gained through associative N_2 fixation.

Reviews have been conducted of root responses to soil chemical factors (Foy, 1992), excess salt (Kafkafi, 1991), and excess heavy metals (Breckle, 1991). Roots generally respond to mineral excess by becoming thicker and growing more slowly (Kafkafi, 1991). O'Toole and Bland (1987) have summarized the literature on genotypic variation in crop root systems and Zobel et al. (1992) and Zobel (1994) have discussed root genetics and some of the inherent constraints to root improvement.

Nutrient use efficiency, the amount of dry matter produced per unit nutrient, was reported by Chapin (1988) to be low in wild plants adapted to acid, infertile mineral soils — obviously not a desirable strategy of adaptation to introduce into a crop species. For acid soils, Brazilian scientists define nutrient use efficiency as response to additional nutrients. Those genotypes with above-average grain production at the 50% critical level of P are deemed efficient, while those with above-average yields at the 100% critical level of P are responsive. Dvorak et al. (1991) emphasized the importance of understanding the genetic and physiological mechanisms by which plants cope with soil fertility stress in order to develop efficient strategies for breeding stress-tolerant cultivars.

Because sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R. Br.] are staple tropical crops, and because farmers' lack of resources, limited technology, and less developed management skills are more applicable to tropical than temperate zone production constraints, this paper will focus on some of the mineral stresses of tropical soils.

Problem Tropical Soils

Sanchez and Logan (1992) discussed the production constraints of the more than 4.5 billion ha of land in five agroecological regions of the tropics. The humid tropics are characterized by high and constant temperatures and a dry season of greater than 90 days. The acid savannas in Colombia, Venezuela, and Brazil are seasonal tropics defined by a dry season of three to six months and native savanna vegetation. The semi-arid tropics, characterized by a protracted dry season of six to nine months, are found in many of the Sahelian countries. The tropical steeplands are simply defined as those regions dominated by slopes steeper than 30%; wetlands are defined as regions with aquic soil moisture regimes.

The soil constraints are different among the five tropical agroecological regions (Table 1). It is important to note that more than one constraint may be associated with a particular soil in a given agroecological region. Thus, the percentages in neither rows nor columns of Table 1 add to 100%. Most of our discussion will involve the first five constraints listed in Table 1. Approximately 40% of the tropics (nearly 1.9 billion ha) is dominated by soils with low nutrient reserves, defined by Sanchez and Logan (1992) as less than 10% weatherable minerals in the sand-

and-silt fraction. Approximately one-third of the soil in the tropics (1.5 billion ha) is sufficiently acidic for soluble Al to be toxic for most crop species. This constraint is defined as greater than 60% Al saturation in the top 50 cm of soil. Acid soils with surface pH of less than 5.5, but not Al-toxic, occupy one-fourth of the tropics. Clayey soils with iron oxide/clay ratios greater than 0.2 fix large quantities of added P. This constraint, considered typical of the tropics, is found in 22% (1 billion ha) of the region. Soils with less than four cmol kg^{-1} of ECEC occupy 250 million ha, or about 5% of the tropics.

Low nutrient reserves

Approximately 40% of the soils of the tropics are highly weathered with limited capacity to supply P, K, Ca, Mg, and S. Soils with this constraint are more extensive in the humid tropics and in the acid savannas, but are locally important in the Sahel.

Acid soils with and without Al toxicity

The main mineral stress problems in tropical acid soils include deficiencies of N, P, K, Ca, Mg, Zn, and Mo; high P-fixation; and toxicities of Al and Mn (Clark, 1982; Foy, 1984; Sanchez and Salinas, 1981). Sanchez and Logan (1992) reported that Al toxicity is most prevalent in the humid tropics and acid savannas, but also occurs in large areas of the tropical steeplands. This constraint is highly correlated with low nutrient reserves. Acidity without Al toxicity is important in all agroecological zones. Although correcting soil acidity by liming might be limited to acid-susceptible crops, this constraint is generally associated with somewhat higher fertilizer requirements for these soils than those with higher pH values.

Soils with high P-fixation

This constraint is more extensive in the humid tropics and acid savannas but is also important in the steeplands. Successful management practices to overcome high P-fixation in Oxisols have been developed for the acid savannas in Brazil. This constraint is important in the steeplands and humid tropics because of the presence of allophane in volcanic soils.

Table 1. Primary chemical soil constraints in five agroecological regions of the tropics.

Soil constraint	Agroecological Zone										Total	
	Humid		Savanna		Semi-arid		Steeplands		Wetlands			
	million ha and (%)											
Low nutrient reserves	929	(64)	287	(55)	166	(16)	279	(26)	193	(34)	1854	(40)
Aluminum toxicity	808	(56)	261	(50)	132	(13)	269	(25)	23	(4)	1493	(32)
Acidity without Al toxicity	257	(18)	264	(50)	298	(29)	177	(16)	164	(29)	1160	(25)
High P fixation by Fe oxides	537	(37)	166	(32)	94	(9)	221	(20)	0	(0)	1018	(22)
Low CEC	165	(11)	19	(4)	63	(6)	2	(-)	2	(-)	251	(5)
Calcareous reaction	6	(-)	0	(0)	80	(8)	60	(6)	6	(1)	152	(3)
High soil organic matter	29	(2)	0	(0)	0	(0)	-	(0)	40	(7)	69	(1)
Salinity	8	(1)	0	(0)	20	(2)	-	(0)	38	(7)	66	(1)
High P fixation by allophane	13	(1)	2	(-)	5	(-)	26	(2)	0	(0)	46	(1)
Alkalinity	5	(-)	0	(0)	12	(1)	-	(0)	33	(6)	50	(1)
Area of five regions	1444		525		1012		1086		571		4637	

Source: Sanchez and Logan, 1992.

Soils with <4 cmol kg^{-1} ECEC

This constraint is limited to the sandier soils of the tropics, especially the Sahel. Low ECEC is not as critical in the tropics as originally thought. This is partially due to the higher-than-expected organic matter (OM) content of soils in the tropics, which provides a source of CEC. The reduction of OM after a few cycles of cropping often results in a decline in productivity. Cation leaching problems also exist in the tropics as in the temperate regions.

Scientific advances in our understanding of abiotic stresses caused by all chemical toxicities and deficiencies in soils are too numerous to review in detail and are beyond the scope of this paper. We will mention only in passing the fertility problems associated with saline, alkaline, and high OM soils. We will instead devote most of this paper to the constraints of infertile mineral soils, especially acid soils of the tropics, how plants adapt to these stresses, and discuss how plant breeders working as a part of a multidisciplinary team can assist sorghum and pearl millet farmers in these areas.

Mechanisms of Tolerance and Avoidance

Twenty-four ways in which plant species may adapt to mineral stress through tolerance or avoidance mechanisms are presented in Table 2. Definitive data are lacking on which of these mechanisms apply specifically to sorghum and pearl millet. Root function under soil stresses makes up more than the "hidden half" of the picture, although shoot growth generally reflects the overall constraints encountered by roots.

The cytoplasm of a plant must be maintained between pH 7.0 and 7.5 for normal

Table 2. Plant adaptations to mineral stress through tolerance or avoidance.

1. Ability of different types of roots to change requirements and response patterns to mineral stresses.
2. Extensive root system to exploit a larger soil volume.
3. Colonization of the root system by mycorrhizae and N-fixing bacteria.
4. High capacity for root recovery and regeneration.
5. Ability to increase root-tip mucilage and other organic carbon for binding toxic ions.
6. Ability to produce root-borne phosphatases for utilization of organically-bound P.
7. Ability of roots to modify rhizosphere to overcome low levels of nutrients.
8. Capacity of roots to increase soil pH or release chelators to overcome toxic levels of mineral elements.
9. Selective exclusion of toxic elements in the rhizosphere.
10. High uptake rate of nutrients such as P, Ca, or Mg.
11. High root to shoot ratio.
12. Lower internal demand for particular nutrients resulting in high utilization per unit of nutrient absorbed.
13. Capacity for storage, retranslocation, and reutilization of mineral nutrients during stress periods.
14. Capacity for normal metabolism at reduced tissue concentration of a nutrient.
15. High tissue tolerance to toxic elements such as Al and Mn in roots and shoots.
16. Slow growth rate to accommodate mineral deficiencies.
17. Fast growth rate to dilute effect of excess Na.
18. Aluminum compartmentation in cell vacuoles.
19. Capacity to accumulate silicon to complex toxic ions.
20. Less loss of assimilate through slower respiration rate.
21. High photosynthetic capacity.
22. Utilization of perennial growth habit to discard excess mineral elements.
23. Accumulation of seed reserves of Mo and P.
24. Variable production of phytohormones, cytokinins, and abscisic acid in response to mineral stress.

metabolic function. This is accomplished by proton pumps and coupled ion transport in rhizodermal cells even when the plant is growing on a very acid tropical soil. This difference of three to four orders of magnitude in H^+-ion concentration provides the driving force for the uptake of cations and for uptake of anions via the co-transport system (Marschner, 1991).

Plants tolerant to acid mineral soils utilize a variety of mechanisms to cope with adverse soil factors. These mechanisms can be regulated by different genes, as in the case of tissue tolerance to Al and Mn toxicity, or they may often appear to be pleiotropic, as in the case of Al tolerance and efficiency of P-acquisition. In large areas of the tropics, the P-fixing capacity of acid mineral soils is very high, and therefore, P becomes the most important nutritional factor limiting plant growth (Sanchez and Salinas, 1981; Sanchez and Logan, 1992). Avoidance of P-stress can be achieved by a large root surface area either as an inherent quality of a genotype (Fohse et al., 1988), or as root response to P deficiency (Anghinoni and Barber, 1980). Seed reserves of Mo and P also are important components of adaptation. In sorghum, excess P is stored in the seed reserves as phytic acid and can support seedling growth for some weeks with little or no uptake of P from the soil.

Plant physiologists have shown that there is genotypic variability for root system-based tolerance or avoidance of soil stresses and that plant roots respond to mineral excesses and deficiencies both morphologically and physiologically. Normal root systems are composed of at least four types of roots, and each type has distinctly different response patterns and requirements (Zobel, 1994). Further, interactions between the different types of roots and soil stresses produce the overall variability of a plant genotype.

Breckle (1991) observed that heavy metals stimulated initiation and growth of second- and third-order lateral roots, while suppressing seminal and first-order lateral roots. Zobel et al. (1992) and Waisel and Eshel (1992) demonstrated that mineral uptake differs among root types.

In the strategy of avoidance of stress factors, root-induced changes in the rhizosphere of acid mineral soils can be of key importance. They can be non-specific mechanisms such as changes in the cation-anion uptake ratio with corresponding pH changes or organic carbon release. Specific mechanisms in response to a deficiency might include enhanced exudation of organic solutes (Marschner, 1991).

Root cap cells are important sites of phytohormone synthesis and act as sensors to mechanical impedance, gravity, and environmental signals (Kutschera, 1989). Abscisic acid and cytokinins are transported into the shoots and may act as root signals when mineral stresses are encountered (Foy, 1988). Scientists at EMBRAPA have found an unidentified protein induced in the root tips of sorghum as a result of Al stress. The release into the rhizosphere of various forms of organic carbon, such as mucilage, free exudates, and sloughed-off cells, is another important component in the avoidance strategy. Sorghum roots have a high concentration of sugars, which causes an allelopathic-type response in subsequent crops by tying up microorganisms.

Mucilage is continuously being produced by growing roots of land plants, but is generally absent from most aquatic species. It is highly resistant to microbial degradation, and has a high binding capacity for polyvalent cations. Root cap mucilage is thought to protect the growing tip from desiccation, improve root-soil contact, and provide a barrier to toxic agents including metals in the soil (Bennet and Breen, 1991). It is important in acid soils for binding Al^{3+} at the rhizoplane of apical root zones and thus for protection of the root meristem (Horst et al., 1982).

Diazotrophic or N_2-fixing bacteria in the rhizosphere can aid N nutrition of the host plant, particularly in C_4 species such as sorghum, pearl millet, and corn (*Zea mays* L.) growing in soils low in available N (Boddey and Dobereiner, 1988). These organisms produce auxins that stimulate root growth and increase root surface area, effects that may favor P-acquisition and are most likely responsible for growth stimulation and yield increase in pearl millet growing in a P-deficient acid soil (Marschner, 1991). In sorghum, the capacity of diazotrophic rhizosphere bacteria for N_2-fixation may vary between genotypes by a factor of approximately 10 (Werner et al., 1989).

Vesticular arbuscular mycorrhiza (VAM) grow extensively within the root cortex and extend their external mycelia into the soil, increasing surface area and the efficiency of uptake and transport for P in P-deficient soils (Gianinazzi-Pearson and Gianinazzi, 1989). Bethlenfalvay and Franson (1989) and Pakovsky (1988) reported that infection with VAM also may decrease the risk of Mn toxicity in plants growing in acid soils, either by increasing the tolerance of the shoot tissue to elevated Mn^{2+} concentrations or by decreasing Mn^{2+} uptake.

Crop Production on Problem Soils

Infertile acid tropical soils, considered marginal for crop production, represent the largest reserve of potentially arable land in the world. In acid soils of low fertility, depletion may occur for most mineral nutrients, including Ca and Mg. Strong depletion in the rhizosphere can enhance nutrient release from so-called "non-available" fractions in the soil, e.g. non-exchangeable K (Jungk and Claassen, 1986), or organically bound P. Grain yields will, however, be very low at this level of mineral nutrition.

Helyar (1991) discussed a number of acid soil management options and emphasized that the simple prescription of "lime to a soil pH at which yields are maximum" was poor management from both biological and economic points of view. He recommended four broad approaches to the management of soil acidity: use of tolerant cultivars of different species of plants; employment of means to reduce additional soil acidification processes; application of lime and fertilizers only in quantities that improve yields and are economic; and use of other low cost ameliorants or management techniques. The appropriate mix of management inputs for a given situation depends on their relative costs and returns.

From the agronomic viewpoint, crop production on problem soils can be as recommended and practiced in developed countries, or appropriate technology and

cultivars that require minimal change to the soil can be developed. For simplicity, these two methods of improving crop production on problem soils are referred to as high-input and low-input technologies.

Eliminating Stress to Meet the Needs of the Plant

Modern agriculture in developed countries flourishes on some of the best soils where improvements such as lime, fertilizer, trace elements, and other soil ameliorants are relatively easy to obtain and technically and economically feasible to use. North America and Europe are examples of areas of high-input agriculture with high levels of production; they demonstrate the technology required to preserve soil fertility.

Considerable technology is now available for managing acid tropical soils (Helyar, 1991; Kamprath, 1984; and Sanchez, 1976). Little of this technology, however, has been adopted by farmers, and few developing countries are making any concerted research effort to develop sustainable crop production systems for these soils. A notable exception is the 12 million ha of acid soils in the savanna "Cerrado" of Brazil. This 10% portion of the Cerrado produces more than 25% of the maize, soybean [*Glycine max* (L.) Merr.], and rice (*Oryza sativa* L.) grown in Brazil. Another 35 million ha of improved pastures in the Cerrado produce 40% of Brazil's meat and 12% of its milk (Schaffert, 1994). Acid-soil-tolerant cultivars and Brazilian government subsidies on lime, fertilizer, and infrastructure investment were required for this technology adoption in the Cerrado (Sanders and Garcia, 1994). The social and economic implications behind the breakdown in technology transfer in other countries are beyond the scope of this paper; however, failure to adopt technology emphasizes scientists' responsibility not only for developing technology, but also for demonstrating and promoting to farmers the benefits and economic feasibility of the technology.

Simple solutions to complex problems, if adopted, generally end in failure. Recommendations to lime acid soils to pH 6.5, to leach and remove phytotoxic concentrations of salts from saline soils, to apply high rates of fertilizer to infertile soils, and to irrigate crops during periods of drought are all technically feasible and practiced in developed countries. To expect this technology to be directly applicable in developing countries is unrealistic. The infrastructure of roads and other transportation systems, lime and fertilizer plants, equipment dealers, financial and marketing institutions, and other agricultural supporting factors are frequently absent or not sufficiently developed to support the adoption of high-input technology in developing countries. Therefore, problem soils cause more acute crop production constraints for resource-poor tropical farmers in developing countries than for temperate zone farmers in developed countries.

Low-Input Cultural Practices

Demographic pressure in many developing countries of the tropics is forcing crop production onto marginal infertile and acid soils. Crop yields are generally low and traditional agronomic approaches to correct fertility, salinity, and acidity problems of these soils often are technically difficult and costly. Farmers in these

areas are frequently forced to use ecologically unsound methods of crop production, making agriculture unsustainable.

Several labor-intensive cultural methods are used in Africa to avoid or ameliorate the toxic effects of Al and/or Mn for sorghum production on acid soils. These methods substitute for purchased inputs of lime and fertilizer and force the farmer to abandon one site and move to a new one every two to three years. Ashes from trees and bushes, organic residue from recently buried grass, elevated ridges made from topsoil, and varying periods of fallow up to 20 years are used in these transient agricultural systems. Sanders and Garcia (1994) argued that these substitute activities for fertilizer requiring high labor or management inputs (such as residue incorporation, different rotations, and more use of manure) were never cheap solutions. Rather, the cost calculations failed to put monetary values on farmers' time and learning costs to manage sophisticated production practices. Many of these systems also promote further degradation of the environment, but the farmers in many of these areas have not been shown any superior methods of food production within their economic reach.

When lack of labor and other factors require the use of mechanization, new management technology becomes feasible. Use of acid-soil-tolerant cultivars combined with judicious quantities of lime, fertilizer, and trace elements can lead to profitable returns. Banding lime and fertilizer, planting on ridges in humid zones and in furrows in semi-arid zones, incorporation of earthworms, and pelleting trace elements or starter P fertilizer onto seeds are other agronomic practices being investigated for amelioration of acid soils.

Fertilizer quantities of dolomitic limestone (1/2 t ha^{-1}) applied to an acid Ultisol in Colombia supplied Ca and Mg, reduced Al saturation from over 80% to less than 65%, and allowed tolerant sorghum genotypes to produce good grain yields while susceptible genotypes died (Gourley, 1988). A primary reason for liming acid soils is to increase P-availability to plants. Haynes (1982) found, however, that adding P fertilizer to a freshly limed acid soil failed to increase P-availability if the soil was not first subjected to drying cycles. Lime sources in many tropical countries are scarce, and transportation costs may be prohibitive, especially to small farmers. In Brazil, for example, lime prices double for every 300 km of transportation needed.

Lime applications normally benefit the soil surface horizons but not the subsoil, because Ca in lime is not very mobile in the soil profile. Ritchey et al. (1980) showed that Ca^{2+} from the more soluble $CaSO_4$ (gypsum) moved rapidly into Brazilian acid subsoils, reducing the effect of subsoil Ca deficiency and Al toxicity on plant roots. Lund (1970) found that as the soil pH declined from 5.6 to 4.5, the concentration of Ca^{2+} in the soil solution required for maintenance of root elongation increased more than fifty fold. Since Ca^{2+} is phloem-immobile, the high Ca^{2+} requirement for root elongation has to be met by direct uptake by apical roots from the external soil solution. Exchangeable Ca^{2+} becomes deficient at levels of less than .4 cmol kg^{-1} (Ritchey et al., 1982). The use of gypsum on soils has been reviewed by Shainberg et al. (1989). The

action of these fluoride and sulphate ameliorants is based on the complexing of Al^{3+} with F^- and SO_4^{2-} to form non-toxic ionic pairs and to increase the leaching of Al as the highly mobile AlF_3^0 and $AlSO_4^+$ ions (Cameron et al., 1986).

Addition of N as anhydrous ammonia or urea, or via biological N_2-fixation, does not increase soil acidity if the added N is used by the crop. At high soil temperatures, the ammonium concentration is usually low, and nitrate is the dominant form of N supplied and taken up by roots. The preferential uptake of N as nitrate, together with high nitrate reductase activity in apical root zones (Klotz and Horst, 1988), are the main factors responsible for the increase in pH in the rhizosphere of apical root zones in acid-tolerant plant species. Removal of organic anions in harvested products without returning manure to the field increases acid production in the organic carbon cycle. Cereal grain removes fewer quantities of organic anions than hay or silage (Helyar, 1991). Plant roots can transport bicarbonate and organic anions into topsoil and subsoil layers, thus reducing soil acidity over time.

Plant breeders must make available to farmers who depend on acid soils a wide range of tolerant species and cultivars. Farmers then can practice crop rotation to improve the soil and reduce crop production constraints. Consideration must be given to ensure tolerance is used conservatively rather than for soil exploitation (Foy, 1984). Introducing a more tolerant species or cultivar can increase the farmers' returns sufficiently to favor higher amendment rates.

Management of weathered soils is further complicated because plant species and cultivars differ in nutritional requirements and sensitivities to toxicities associated with soil acidity. The sum of the individual mechanisms of tolerance that can be bred into a cultivar is important in determining the requirement of lime and fertilizer for amelioration of acid soils. Growing tolerant plants on acid soils reduces Al toxicity by binding Al to organic compounds produced by roots and by organic residue.

Genetic Diversity of Sorghum and Pearl Millet to Soil Stresses

Genetic diversity to both excess concentrations and deficiencies of many mineral elements has been demonstrated for sorghum, pearl millet, and other crops. In some cases, only a few genotypes were examined and no effort was made to determine the range of variability within the species. The breeder also must know if the variability observed for the character is due to environmental or genetic factors and must determine estimates of both heritability and expected genetic improvement in yield for the existing conditions.

Pearl millet appears to be much more tolerant of acid soil chemical toxicities and deficiencies than sorghum. Using a field screening methodology developed for sorghum in Colombia, preliminary trials showed that pearl millet had excellent adaptation to acid soils even under low-P conditions. Several pearl millet cultivars, synthetics, and populations showed potential grain yields of 2 to 3 t ha^{-1} (Clark et al., 1990; Flores et al., 1991a).

Screening Methods

Results obtained in nutrient culture for Al toxicity or tolerance often are not satisfactorily correlated with field or greenhouse studies in acid soils (Horst, 1985; Marschner, 1991; Mugwira et al., 1981; Nelson, 1983). Moreover, soil acidity stress factors vary with location, soil depth, rainfall, temperature, ECEC, natural content of essential elements, level of toxic ions, P-fixation capacity, and amount and quality of OM. Also, plants have different avoidance mechanisms, most of which are related to changes occurring at the root-soil interface. Marschner (1991) suggested that due to the wide range of stress factors to which roots may be subjected in acid soils, the results of short-term studies in nutrient solutions should be regarded with skepticism. Simply measuring Al or Mn tolerance or mineral element deficiencies one at a time as criteria for prediction of adaptation to acid soils under field conditions is unrealistic. Shifts in root growth may be only one reason for the poor correlations observed.

Examples of the chemical components of several acid soils in the humid and semi-arid tropics will demonstrate the complexity of breeding for tolerance to soil chemical toxicities and deficiencies (Table 3). The acid soils in these four countries have pH values less than 5.0 and they are in the low nutrient reserve category, but the similarity ends there. They all have their own peculiarities. The soils from the humid tropics of Colombia and Cameroon have a higher quantity of Al and a higher ECEC than the acid soils in the semi-arid countries of Niger and Mali. The major difference is in the percentage of Al saturation. Water and other nutrients being equal, Al would not be a constraint for the Mali soil and a limited or easily corrected problem for the Cameroon and Niger soils. Without some lime amendment to the Colombian soil, Al toxicity would kill the most tolerant sorghum and would probably eliminate most of the grain yield for any pearl millet genotype that survived.

A field screening technique was developed using an acid Ultisol on the CIAT substation at Quilichao, Colombia (Gourley, 1988). The soil pH was essentially unchanged after addition of 500 kg ha^{-1} of dolomitic limestone to the screening plot; however, the Al-saturation level was reduced from 80% to approximately 65%. The objective was to establish an Al-toxicity level high enough to kill sensitive sorghum genotypes, but not too high to prevent tolerant genotypes from producing a reasonable yield of grain. A simple visual rating scale was used to categorize the exotic sorghum genotypes. The world

Table 3. Chemical characteristics of acid soils in Colombia, Cameroon, Niger, and Mali.

Soil characeristics	Colombia	Cameroon	Niger	Mali
pH (H_20)	4.5	3.9	4.0	4.9
Ca (cmol kg^{-1})	0.7	1.5	0.2	0.6
Mg (cmol kg^{-1})	0.2	0.4	0.1	0.1
K (cmol kg^{-1})	0.2	0.3	0.1	0.1
Al (cmol kg^{-1})	3.9	2.9	0.6	0.1
ECEC (cmol kg^{-1})	4.9	5.3	0.9	0.9
Al saturation (%)	80	55	67	11

Adapted from Gourley (1988) and Takow et al. (1991).

collection was systematically sampled for accessions originating from acid soil areas in Africa.

At 65% Al saturation, susceptible genotypes such as Tx415 and Tx430 produced good stands and grew for approximately three weeks, after which every plant in the row died. The soil at Quilichao was uniform enough that at maturity, susceptible and tolerant genotypes planted in adjacent rows at regular spacings across the test field contained rows with no plants and rows with productive plants, respectively.

The fact that susceptible genotypes produced good plant stands in 65% Al-saturation plots cast suspicion on seedling primary root length as a screening technique. It also indicated that the seed was in some way protecting the primary root from the toxic effects of Al; however, the adventitious root system failed to penetrate the soil and the susceptible genotypes soon died. In Colombia and Brazil, it was observed that restriction of root penetration in the subsoil was often compensated by higher root densities in the topsoil, which also increased the possibility of root-induced changes in the rhizosphere of the topsoil by some sorghum genotypes.

Accumulation of Al in leaf tissue does not necessarily reflect high Al tolerance, but is most likely the result of root-induced chelation of Al in the rhizosphere and translocation of non-toxic Al into the leaf tissue (Matsumoto et al., 1976). In leaves of mature sorghum plants grown in the field on high Al soils in Colombia, Al concentrations of approximately 2,000 ug g^{-1} were observed in Al-tolerant genotypes (Gourley et al., 1991). Some, but not all, of these Al-tolerant genotypes also had high concentrations of Si. Galvez and Clark (1991) and Galvez et al. (1987) found that Si in the growth medium enabled plants to overcome Al-toxicity symptoms and enhanced shoot and root growth.

Tissue tolerance to high Mn^{2+} concentrations was increased several fold by high temperatures (Rufty et al., 1979) and high concentrations of Si (Galvez et al., 1987; Horst and Marschner, 1978). Silicon accumulator species should therefore be expected to be better adapted to high levels of exchangeable Mn^{2+} in the soil and particularly in the subsoil where the effects of liming are much less pronounced (Wright et al., 1988).

Field studies were conducted to determine mineral element concentrations in leaves of 26 sorghum genotypes that were tolerant to acid-soil conditions in Colombia (Gourley et al., 1991). Aluminum saturation levels in soils at four sites were 60% and 68% on Oxisols and 63% and 45% on Ultisols. Genetic variability among genotypes was found for the accumulation of several mineral elements. However, only P will be considered here. The ability of a genotype to accumulate P under conditions of high Al saturation or otherwise low nutrient availability is an important trait. Genotype IS 9138 accumulated 3.4 times more P on the Oxisols and genotype IS 7173C accumulated 1.8 times more P on the Ultisols than genotypes IS 8577 and 3DX57/1/1/910 (Table 4). If the differences in mineral element concentrations observed among genotypes are under genetic control, the efficiency of some genotypes to extract P

from the soil under conditions of low availability should be amenable for use in a sorghum improvement program.

Supply of soil nutrients, especially P, tends to be more limiting to pearl millet production than water supply in most of semi-arid West Africa. Payne et al. (1990) found this to be particularly true for low-input fields in Niger where substantial quantities of unused, plant-available water remained at season's end within and below root zones.

In a series of studies with pearl millet, Payne and others have shown that small quantities of P increased water use efficiency (Payne et al., 1992), P-use efficiency, and N-use efficiency (Payne et al., 1995). They concluded that moderate fertilizer application (20 kg N and 20 kg P_2O_5 ha^{-1}) and increasing plant densities from the traditional 5,000 to 10,000 hills ha^{-1} tripled water use efficiency and substantially increased grain yields. Rather than increasing farmers' risk, this system reduced the risk even in the driest years in Niger. Alagarswamy et al. (1988) suggested that differences in N-use efficiency among genotypes of pearl millet may be due to more rapid and complete retranslocation.

It is generally accepted that a dense, finely branched root system is conducive to better P-acquisition than a coarse, less branched root system. (Barber, 1984). There does appear to be genotypic variation in pearl millet root length density and P-efficiency under similar environments (Payne, 1997).

Thirty-six sorghum lines were evaluated for P-efficiency and responsiveness at the National Maize and Sorghum Research Center of EMBRAPA (CNPMS) during the 1995-96 growing season at Sete Lagoas, MG, Brazil. The screening was conducted on an acid Oxisol at 5 and 18 ug gm^{-1} P (Mehlich-1 extractor). The soil was limed to pH 5.5 to 6.0, and N and K were applied based on soil analysis. Toxic levels of Al did not occur in the plow layer but were present in the subsoil. The 36 lines included 12 traditional lines representing both tolerance and susceptibility to Al toxicity and 24 lines derived from crosses between elite B-lines and a source of tolerance to Al toxicity, IS 7173C. Twelve lines were susceptible to toxic levels of Al, and 24 lines were tolerant. Genotypes with above average grain production at the low-P level were classified as P-efficient and genotypes

Table 4. Phosphorus concentration in leaves of five sorghum lines grown in Colombia on two Al-toxic Oxisol and two Ultisol soils.

	Oxisol trials[1]		Ultisol trials[2]	
Genotype	P conc. ($mg\ g^{-1}$)	Relative[3] P conc. (%)	P conc. ($mg\ g^{-1}$)	Relative[3] P conc. (%)
IS 7173C	1.65	150	3.60	147
IS 9138	2.55	232	2.80	114
1696B	2.30	209	2.80	114
IS 8577	0.75	68	2.00	82
3DX57/1/1/910	0.75	68	2.00	82
Trial means	1.10	—	2.45	—

[1] = Two Oxisol sites had Al-saturation levels of 60.3% and 68.0%.
[2] = Two Ultisol sites had Al-saturation levels of 63.0% and 45.1%.
[3] = Genotype mean for 2 locations divided by mean of trials for 2 locations times 100.
Adapted from Gourley (1992).

with above average relative response to P were classified as responsive to P.

In the Brazilian study, average grain yield ranged from 1.76 to 3.52 t ha^{-1} at low P (mean = 2.63 t ha^{-1}) and from 1.84 to 5.39 t ha^{-1} at high P (mean = 3.68 t ha^{-1}). The relative response to applied P ranged from 0 to 93%, with a mean of 41%. The 36 entries were classified into four groups: efficient and responsive to P (ER), non-efficient and responsive (NR), efficient and not responsive (EN), and non-efficient and not responsive (NN). Tolerance and susceptibility to Al toxicity were not found to be directly related to P-efficiency and P-responsiveness. IS 7173C, the standard for tolerance to Al toxicity, was average for P-efficiency and not responsive to additional P (12%), whereas the male-sterile line BR 007B, the standard for susceptibility to Al toxicity, was average for P-efficiency and highly responsive to additional P (93%). The Al-tolerant line of a P non-efficient, near-isogenic pair for Al toxicity was more responsive to P (70%), whereas the Al-susceptible line of the pair was less responsive to P (33%). Two Al-tolerant near-isogenic recombinant lines from the cross between BR 007B and IS 7173C were average for P-efficiency and highly responsive to P (60% and 90%).

Breeding and Inheritance

Since EMBRAPA sorghum breeders reported genetic variability of sorghum for tolerance to acid soils (Schaffert et al., 1975) and the INTSORMIL sorghum acid-soil breeding project was initiated in Colombia in 1981, much progress has been made. Many good sources of Al tolerance have been identified. Tolerance appears to be dominant and conditioned by a few genes. Heterosis for tolerance to acid infertile soils also has been observed.

Of more than 6,000 sorghum genotypes from the world collection screened at Quilichao, Colombia, approximately 8% were found to tolerate 65% Al saturation, and a few of these genotypes produced greater than 2 t ha^{-1} of grain (Gourley, 1988). Many of these highly tolerant genotypes from the world collection originated in acid soil areas in Nigeria, Uganda, or Kenya, and were classified as Caudatum or Caudatum-hybrid races. Several of these lines appear to be from Dr. Hugh Doggett's breeding program at the Serere Research Station in Uganda. The open-panicled Guinea race and the hybrid Guinea-bicolor lines had a higher overall percentage of acid soil-tolerant sorghum entries than those of other races and hybrids evaluated (Gourley, 1988).

The pedigree breeding method was used to identify Al-tolerant plants in segregating populations. Planting the F_2 population in the screening plot at 65% Al saturation permitted identification of Al tolerance; however, photoperiod sensitivity, genetic plant height, or maturity could not be immediately determined. In each F_2 population of 5,000 plants, a selection intensity of 2% or less produced large numbers of Al-tolerant F_3 families. Tolerant lines later were evaluated for agronomic type in both temperate and tropical environments. As more constraints are found in the acid soil complex and as yield and other agronomic factors are added to the breeding goals, a more holistic approach to breeding can be used in the environment in which the cultivars are to be used in commercial production.

The EMBRAPA acid soil breeding program used a different approach than the INTSORMIL project in Colombia. In the Brazilian plots, the topsoil was amended with lime to approximately 45% Al saturation and, during periods of drought, the Al-susceptible or less tolerant genotypes showed an inability to penetrate and extract water from the subsoil. Results from some of the cooperative work with EMBRAPA are shown in Table 5. The Colombian-bred lines, shown as (MS), are somewhat shorter and earlier than the EMBRAPA lines, but all the tolerant lines have acceptable yields.

The performance of experimental acid soil-tolerant sorghum cultivars and hybrids has been well documented, and research continues. In newly prepared screening plots in Colombia (pH 4.4, 63% Al saturation), 18 Al-tolerant cultivars produced from 2.0 to 5.0 t ha^{-1} (400 - 1000%) more grain than a susceptible check (Gourley, 1987). Flores et al. (1988) found that six acid-soil-tolerant cultivars averaged 3066 kg ha^{-1} (943%) more grain and 4700 kg ha^{-1} (983%) more stover yield than the commercial cultivar ICA Nataima when grown on a Colombian Ultisol at pH 4.1 and 60% Al saturation.

Table 5. Grain yield, days to 50% anthesis, and plant height of ten sorghum inbred lines evaluated on acid soil at Sete Lagoas, Brazil.

Genotype[1]	Plant height (cm)	Days to 50% anthesis (days)	Grain yield (t ha^{-1})
CMSXS 208	183a	93a	4.6a
MS 109	159b	80cdef	3.8ab
CMSXS 209	152bc	85bc	3.4bc
MS 188-1	161bc	78ef	3.1bc
CMSXS 189	180a	97a	2.9bcd
MS 076	136cd	80cdef	2.8cd
MS 177	149bc	79def	2.6cde
MS 216	162bcde	81bcde	2.6cde
BR 007B (check)	93f	79def	0.6g
Tx 623B (check)	106ef	89b	0.3g
Mean	147.97	84.08	2.68

Means followed by a common letter are not different at the 0.05 level of probability according to Duncan's Multiple Range Test.
[1]Genotype designations - CMSXS and BR - inbreds developed by EMBRAPA in Brazil, MS - inbreds developed by Mississippi-INTSORMIL in Colombia, and Tx - Texas inbred. Adapted from Dos Santos et al. (1993).

Combining ability studies in Colombia (Flores et al., 1991b and 1991c), Niger (Adamou et al., 1992), and Kenya (Zake et al., 1992) compared growth and yield traits of Colombian-bred inbreds at varying Al-saturation levels in field trials. Many similar trials using EMBRAPA-developed inbreds in Brazil showed that Al tolerance was conditioned by both additive and non-additive gene action.

The Colombian National Program (ICA), in collaboration with INTSORMIL, released four photoperiod-sensitive Al-tolerant cultivars (Table 6). The first two varieties released in 1991, Sorghica Real 60 (MN 4508) and Sorghica Real 40 (156-P5-Serere 1), have consistently produced high grain yields on acid soils in both cropping seasons during the year. In 1993, ICA and the El Alcaravan Foundation, with INTSORMIL'S support, released two acid soil-tolerant sorghum cultivars, Icaravan 1 (IS 3071) and Icaravan 2 (IS 8577), which are adapted to growing conditions in Arauca in the Colombian Eastern Plains (Llanos). Icaravan 1 produced greater than 2.5 t ha^{-1} grain under low fertilization levels when the Al-saturation level was 60% or less. It also tolerates partial flooding after flowering, an essential characteristic in poorly drained savannas. Icaravan 2 has very good tolerance to Al toxicity and good agronomic characteristics when grown under

Arauca's soil and climatic conditions. Additional acid-soil-tolerant cultivars and inbreds are being released by Mississippi State University and EMBRAPA.

A fear that plants tolerant to acid soils may be low-yielding and poorly adapted to fertile soils has been expressed. The notion originated because traditional cultivars grown in acid soil areas were both acid-soil-tolerant and low-yielding when compared with modern, high-yield potential cultivars. One must remember that the traditional cultivars had not been selected for fertile soils and lacked yield stability. In the INTSORMIL-Colombia project, derivative lines were selected for the highest level of Al tolerance and fertilizer responsiveness.

Multidisciplinary Research: The Systems Approach

This paper has focused primarily on research in the tropics and omitted much of the temperate zone acid soil work. Unfortunately, many breeding lines developed on acid soils in the temperate zone do not show good tolerance in the tropics. Furthermore, seedling response to Al toxicity does not predict grain yield well. Breeders are reluctant to start breeding programs based on information collected on just a few lines using a complicated and expensive screening methodology. Such research gives the breeder no information on the range of variability or heritability, nor if the effort will change yields in farmers' fields. Assistance with these requirements is needed from plant nutritionists, biochemists, physiologists, and others before plant breeders are able or motivated to use the new technology to breed mineral element stress-tolerant cultivars.

Plant breeding by itself, however, cannot solve many of the plant mineral nutrition problems. A systems approach is required. Help is needed to evaluate breeding germplasm under different cultural practices in the field and to find rapid methods of selecting field-validated breeding lines. On-farm trials in which a range and variety of inputs are used, in addition to tolerant cultivars, are required to demonstrate feasible economic alternatives to targeted farmer clientele. The systems agronomist also must use other time-tested agronomic practices like crop rotation. Cowpea [*Vigna unguiculata* (L.) Walp.], a highly acid-soil-tolerant species, could complement low-input systems in a rotation with tolerant cultivars of sorghum and pearl millet.

Transfer of the Production System

Technology transfer characteristically has a long lag phase between development and adoption by farmers. Much of the technology to reduce or eliminate the constraints of nutrient deficiencies or toxici-

Table 6. Plant height and grain yield of five sorghum cultivars planted in acid soils with aluminum saturation levels between 40 and 60%. Mean of 12 sites in the Department of Meta, Colombia.

		Yield		
Genotype	Plant height (cm)	Semester A kg ha^{-1}	Semester B kg ha^{-1}	Mean kg ha^{-1}
Sorghica Real 60	182	3224	2994	3109
Sorghica Real 40	162	3283	2793	3038
Icaravan 1	190	2839	2421	2630
Icaravan 2	187	3312	2795	3053
ICA Nataima (check)	96	534	894	714

Adapted from Gourley and Munoz (1992).

ties of tropical soils is still in the lag phase or has been rejected by farmers for social or economic reasons. Many agricultural experts and farmers faced with these constraints agree that current production practices are neither sustainable nor environmentally friendly.

Plant breeders have developed tolerant cultivars for which a production system does not exist. In other cases, the primary constraint has not been identified and the breeding program does not exist. Much of the new soil management technology has not been integrated into a system and demonstrated to farmers to be cost effective and to minimize risk. To address most of the severe tropical soil crop production constraints, a combination of tolerant cultivars, good agronomic management practices, and modest amounts of purchased inputs are required.

In some developing countries, adaptive research programs and an effective extension service are both either lacking or ineffective. Research organizations operating in developing countries are not only responsible for developing technology, but also must collaborate with government planners and the national extension service to demonstrate and promote the benefits and economic feasibility of the technology to farmers. Improving crop production on problem tropical soils requires a multidisciplinary systems approach.

Summary

The tropics have some of the most severe mineral nutrition constraints to crop production of any agricultural area in the world. The mechanisms different plant species use to tolerate or avoid problem soil constraints are better understood now than in the past, but much more research will be required for a complete understanding. For sorghum and pearl millet, however, these proposed mechanisms, range of genetic variability of the mechanisms, and mode of inheritance generally lack verification. Tolerance to tropical acid soils appears to be an exception. Although the number and type of mechanisms responsible for the Al and Mn tolerance found in sorghum and pearl millet are still inconclusive, it is known that tolerances for the two toxicities are simply and independently inherited, and they are generally dominant or partially dominant. Genotypic variability for P-acquisition in low-P soils has been confirmed for both crops. Acid-soil-tolerant cultivars and inbreds have been released by national sorghum improvement programs in Latin America, with assistance from INTSORMIL. Sorghum and pearl millet breeders can help overcome some of these constraints by incorporating tolerance factors into cultivars and hybrids. Sanders and Garcia (1994) are correct in insisting that new technology research has important economic elements. Technologies have to function in the farmers' environment and be profitable. Cultural practices also are required to modify the constraints. Resource-poor tropical farmers need these types of economic solutions to help feed their countries' increasing populations.

Acknowledgements

The authors wish to acknowledge funding support for this research from the International Sorghum and Millet (INTSORMIL) Collaborative Research Sup-

port Program (CRSP), an initiative of the Agency for International Development, Grant No. DAN-1254-G-00-0021-00, Title XII, and the Board for International Food and Agriculture Development and Economic Cooperation (BIFADEC); Mississippi State University; the National Maize and Sorghum Research Center (CNPMS) of the Brazilian Agriculture Research Corporation (EMBRAPA); and the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) Sahelian Center.

References

Adamou, M., L.M. Gourley, C.E. Watson, S.D. Mclean, and A.S. Goggi. 1992. Evaluation of combining ability of acid soil tolerant sorghum germplasm in Niger. p. 88. *In* Agronomy Abstracts. Minneapolis, MN., 1-6 November 1992.

Alagarswamy, G., J.C. Gardner, J.W. Maranville, and R.B. Clark. 1988. Measurement of instantaneous nitrogen use efficiency among pearl millet genotypes. Crop Sci. 28:681-685.

Anghinoni, I., and S.A. Barber. 1980. Phosphorus influx and growth characteristics of corn roots as influenced by phosphorus supply. Agron. J. 72:685-688.

Barber, S.A. 1984. Soil nutrient bioavailability. John Wiley and Sons, New York, NY.

Bennet, R.J., and C.M. Breen. 1991. The aluminium signal: New dimensions to mechanisms of aluminium tolerance. Plant and Soil 134:153-166.

Bethlenfalvay, G.J., and R.L. Franson. 1989. Manganese toxicity alleviated by mycorrhizae in soybean. J. Plant Nutr. 12:953-970.

Boddey, R.M., and J. Dobereiner. 1988. Nitrogen fixation associated with grasses and cereals: Recent results and perspectives for future research. Plant and Soil 108:53-65.

Breckle, A.W. 1991. Growth under stress: heavy metals. p. 251-274. *In* Y. Waise, A. Eshel, and U. Kafkafi (eds.) Plant roots: The hidden half. Marcel Dekker, New York, NY.

Buol, S.W., and H. Eswaran. 1994. Assessment and conquest of poor soils. p. 17-27. *In* Proc. workshop on adaptation of plants to soil stresses, Lincoln, NE. 1-4 August 1993. INTSORMIL Publication No. 94-2, Lincoln, NE.

Cameron, R.S., G.S.P. Ritchie, and A.D. Robson. 1986. Relative toxicities of inorganic aluminium complexes to barley. Soil Sci. Soc. Am. J. 50:1231-1236.

Chapin, F.S., III. 1988. Ecological aspects of plant mineral nutrition. p. 161-192. *In* B. Tinker and A. Lauchli (eds.) Advances in plant nutrition 3. Praeger, New York, NY.

Clark, R.B. 1982. Plant response to mineral element toxicity and deficiency. p. 71-142. *In* M.N. Christiansen and C.F. Lewis (eds.) Breeding plants for less favorable environments. John Wiley & Sons, New York, NY.

Clark, R.B., C.I. Flores, L.M. Gourley, and R. R. Duncan. 1990. Mineral element concentrations and grain yield of sorghum (*Sorghum bicolor*) and pearl millet (*Pennisetum glaucum*) grown on acid soil. J. Plant Nutr. 13:391-396.

Dos Santos, F.G., G.V.E. Pitta, L.M. Gourley, and A.S. Goggi. 1993. Introduction and evaluation of Al-tolerant sorghum germplasm in Brazil. p. 188. *In* Agronomy abstracts. Cincinnati, OH., 7-12 November 1993.

Dvorak, J., E. Epstein, A. Galvez, P. Gulick, and J.A. Omielan. 1991. Genetic basis of plant tolerance of soil toxicity. *In* H.T. Stalker and J.P. Murphy (eds.) Proc. symp. on plant breeding in the 1990s. C.A.B. International, Wallingford, Oxon, OX10 8DE, UK.

Flores, C.I., R.B. Clark, and L.M. Gourley. 1988. Growth and yield traits of sorghum grown on acid soil at varied aluminum saturations. Plant and Soil 106:49-57.

Flores, C.I., R.B. Clark, and L.M. Gourley. 1991a. Genotypic variation of pearl millet for growth and yield on acid soil. Field Crops Res. 26:347-354.

Flores, C.I., R.B. Clark, J.F. Pedersen, and L.M. Gourley. 1991b. Leaf mineral element concentrations in sorghum (*Sorghum bicolor*) hybrids and their parents grown at varied aluminum saturations on an Ultisol. p. 1095-1104. *In* R.J. Wright, V.C. Baligar, and R.P. Murrmann (eds.) Plant-soil interactions at low pH. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Flores, C.I., L.M. Gourley, J.F. Pedersen, and R.B. Clark. 1991c. Inheritance of acid-soil tolerance in sorghum (*Sorghum bicolor*) grown on an Ultisol. p. 1081-1093. *In* R.J. Wright, V.C. Baligar, and R.P. Murrmann (ed.) Plant-soil interactions at low pH. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Fohse, D., N. Claassen, and A. Jungk. 1988. Phosphorus efficiency of plants. I. External and internal P requirement and P uptake efficiency of different plant species. Plant and Soil 110:101-109.

Foy, C.D. 1984. Physiological effects of hydrogen, aluminum and manganese toxicities in acid soil. p. 57-97. *In* F. Adams (ed.) Soil acidity and liming. ASA, CSSA, and SSSA, Madison, WI.

Foy, C.D. 1988. Plant adaptation to acid, aluminum-toxic soils. Commun. Soil Sci. Plant Anal. 19:959-987.

Foy, C.D. 1992. Soil chemical factors limiting plant root growth. Adv. Soil Sci. 19:97-150.

Galvez, L., and R.B. Clark. 1991. Effects of silicon on growth and mineral composition of sorghum (*Sorghum bicolor*) grown with toxic levels of aluminium. p. 815-823. *In* R.J. Wright, V.C. Baligar, and R.P Murrmann (eds.). Plant-soil interactions at low pH. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Galvez, L., R.B. Clark, L.M. Gourley, and J.W. Maranville. 1987. Silicon interactions with manganese and aluminum toxicity in sorghum. J. Plant Nutr. 10:1139-1147.

Gianinazzi-Pearson, V., and S. Gianinazzi. 1989. Phosphorus metabolism in mycorrhizas. p. 227-241. *In* L. Boddy, R. Marchant, and D.J. Read (eds.) Nitrogen, phosphorus and sulphur utilization by fungi. Cambridge University Press, London, UK.

Gourley, L.M. 1987. Identifying Aluminum Tolerance in Sorghum Genotypes Grown on Tropical Acid Soils. p. 89-98. *In* W.H. Gabelman and B.C. Loughman (eds.). Genetic Aspects of Plant Mineral Nutrition. Plant and Soil. Wageningen. the Netherlands.

Gourley, L.M. 1988. Breeding sorghum for acid soils of the humid tropics. p. 261-273. *In* M. Latham (ed.) Africaland - Land development and management of acid soils in Africa II. Inter. Board for Soils Research and Management (IBSRAM), Bangkok, Thailand.

Gourley, L.M. 1992. Breeding sorghum for tolerance to infertile acid soils. p. 91-99. *In* J.M. Yohe (ed.) INTSORMIL annual report 1995 - Fighting hunger with research . . . a team effort. Univ. of Nebraska, Lincoln, NE.

Gourley, L.M., A.S. Goggi, C. Ruiz-Gomez, and R.B. Clark. 1991. Mineral element concentration in 26 acid soil tolerant genotypes. p. 95. *In* Agronomy abstracts. Denver, CO., 27 October-1 November 1991.

Gourley, L.M., and G. Munoz. 1992. Sustainable production of sorghum and pearl millet in fragile, tropical acid soils. p. 51-56. *In* J.M. Yohe (ed.) INTSORMIL annual report 1995 -Fighting hunger with research . . . a team effort. Univ. of Nebraska, Lincoln, NE.

Haug, A. 1984. Molecular aspects of aluminum toxicity. Crit. Rev. Plant Sci. 1: 345-373.

Haynes, R.J. 1982. Effects of liming on phosphate availability in acid soils: A critical review. Plant and Soil 68:289-308.

Helyar, K.R. 1991. Management of acid soils. p. 365-382. *In* R.J. Wright, V.C. Baligar, and R.P Murrmann (ed.). Plant-soil interactions at low pH. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Helyar, K.R., and W.M. Porter. 1989. Soil acidification, its measurement and the processes involved. p. 61-101. *In* A.D. Robson (ed.) Soil acidity and plant growth. Academic Press Inc., San Diego, CA.

Horst, W.J. 1985. Quick screening of cowpea (*Vigna unguiculata*) genotypes for aluminium tolerance in an aluminium-treated acid soil. Z. Pflanzenernaehr. Bodenkd. 148:335-348.

Horst, W.J. 1988. The physiology of manganese toxicity. p. 175-188. *In* R. D. Graham, R.J. Hannam, and N.C. Uren (eds.) Manganese in soils and plants. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Horst, W.J., and H. Marschner. 1978. Effect of silicon on manganese tolerance of bean plants (*Phaseolus vulgaris* L.). Plant and Soil 50:287-303.

Horst, W.J., A. Wagner, and H. Marschner. 1982. Mucilage protects root meristems from aluminium injury. Z. Pflanzenphysiol. 105:435-444.

Jungk, A., and N. Claassen. 1986. Availability of phosphate and potassium as the result of interactions between root and soil in the rhizosphere. Z. Pflanzenernaehr. Bodenkd. 149:411-427.

Kafkafi, U. 1991. Root growth under stress: salinity. p. 375-392. *In* Y. Waise, A. Eshel, and U. Kafkafi (eds.) Plant roots: The hidden half. Marcel Dekker, New York, NY.

Kamprath, E.J. 1984. Crop response to lime on soils in the tropics. p. 349-368. *In* F. Adams (ed.) Soil acidity and liming. 2nd ed. ASA, CSSA, and SSSA, Madison, WI.

Klotz, F., and W.J. Horst. 1988. Genotypic differences in aluminium tolerance of soybean (*Glycine max* L.) as affected by ammonium- and nitrate-nitrogen nutrition. J. Plant Physiol. 132:702-707.

Kutschera, U. 1989. Tissue stresses in growing plant organs. Plant Physiol. 77:157-163.

Lund, Z.F. 1970. The effect of calcium and its relation to several cations in soybean root growth. Soil Sci. Soc. Am. Proc. 34:456-459.

Marschner, H. 1991. Mechanisms of adaptation of plants to acid soils. Plant and Soil 134:1-20.

Matsumoto, H., E. Hirasawa, S. Morimura, and E. Takahashi. 1976. Localization of aluminium in tea leaves. Plant Cell Physiol. 17:627-631.

Mugwira, L.M., V.T. Sapra, S.U. Patel, and M.A. Choudry. 1981. Aluminum tolerance of triticale and wheat cultivars developed in different regions. Agron. J. 73:470-475.

Nelson, L.E. 1983. Tolerance of 20 rice cultivars to excess Al and Mn. Agron. J. 75:134-138.

O'Toole, J.C., and W.L. Bland. 1987. Genotypic variation in crop plant root systems. Adv. Agron. 41:91-145.

Pakovsky, R.S. 1988. Influence of inoculation with *Azospirillum brasilense* and *Glomus fasciulatum* on sorghum nutrition. Plant and Soil 110:283-287.

Payne, W.A. 1997. Managing yield and water use of pearl millet in the Sahel. Agron. J. (in press).

Payne, W.A., M.C. Drew, L.R. Hossner, R.J. Lascano, A.B. Onken, and C.W. Wendt. 1992. Soil phosphorus availability and pearl millet water-use efficiency. Crop Sci. 32:1010-1015.

Payne, W.A., L.R. Hossner, A.B. Onken, and C.W. Wendt. 1995. Nitrogen and phosphorus uptake in pearl millet and its relation to nutrient and transpiration efficiency. Agron. J. 87:425-431.

Payne, W.A., C.W. Wendt, and R.J. Lascano. 1990. Root zone water balances of three low-input millet fields in Niger, West Africa. Agron. J. 82:813-819.

Ritchey, K.D., J.E. Silva, and U.F. Costa. 1982. Calcium deficiency in clayey B horizons of savannah Oxisols. Soil Sci. 133:378-382.

Ritchey, K.D., D.M.G. Souza, E. Lobato, and O. Correa. 1980. Calcium leaching to increase rooting depth in a Brazilian savannah Oxisol. Agron. J. 72:40-44.

Roy, A.K., A. Sharma, and A. Talukder. 1988. Some aspects of aluminum toxicity in plants. Bot. Rev. 54:145-178.

Rufty, T.W., W.W. Miner, and C.D. Raper, Jr. 1979. Temperature effects on growth and manganese tolerance in tobacco. Agron. J. 71:638-644.

Sanchez, P.A. 1976. Properties and management of soils in the tropics. John Wiley & Sons, New York, NY.

Sanchez, P.A., and T.J. Logan. 1992. Myths and science about the chemistry and fertility of soils in the tropics. p. 35-46. *In* R. Lal and P.A. Sanchez (eds.) Myths and science of soils in the tropics. SSSA Spec. Publ. 29. SSSA, Madison, WI.

Sanchez, P.A., and J.G. Salinas. 1981. Low input technology for managing Oxisols and Ultisols in tropical America. Adv. Agron. 34:279-406.

Sanders, J.H., and J.C. Garcia. 1994. The economics of stress and technology development in the Sahel and the "Cerrados" of Brazil. p. 28-47. *In* Proc. workshop on adaptation of plants to soil stresses, Lincoln, NE. 1-4 August 1993. INTSORMIL Publication No. 94-2. Lincoln, NE.

Schaffert, R.E. 1994. Discipline interactions in the quest to adapt plants to soil stresses through genetic improvement. p. 1-13. *In* Proc. workshop on adaptation of plants to soil stresses. Lincoln, NE. 1-4 August 1993. INTSORMIL Publication No. 94-2, Lincoln, NE.

Schaffert, R.E., A.J. McCrate, W.L. Trevisan, A. Bueno, J.L. Meira, and C.L. Rhykerd. 1975. Genetic variation in *Sorghum bicolor* (L.) Moench for tolerance to high levels of exchangeable aluminum in acid soils of Brazil. p. 151-160. *In* Proc. sorghum workshop, University of Puerto Rico, Mayaguez, Puerto Rico.

Shainberg, I., M.E. Summer, W.P. Miller, M.P.W. Farina, M.A. Pavan, and M.V. Fey. 1989. Use of gypsum on soils: A review. Adv. Soil Sci. 9:1-11.

Takow, J.A., M.D. Doumbia, and L.R. Hossner. 1991. Acid soil profiles of the semiarid and subhumid tropics in Central and West Africa. p. 311-320. *In* R.J. Wright, V.C. Baligar, and R.P Murrmann (eds.) Plant-soil interactions at low pH. Kluwer Academic Publishers, Dordrecht, the Netherlands.

Taylor, G.J. 1988. The physiology of aluminum tolerance in higher plants. Commun. Soil Sci. Plant Anal. 19:1179-1194.

Vose, P.B. 1987. Genetical aspects of mineral nutrition - Progress to date. p. 3-13. *In* W.H. Gabelman and B.C. Loughman (eds.) Genetic aspects of plant mineral nutrition. Martinus Nijhoff Publishers, Dordrecht, the Netherlands.

Waisel, Y., and A. Eshel. 1992. Differences in ion uptake among roots of various types. J. Plant Nutr. 15:945-958.

Werner, D., R. Berggold, D. Jaeger, A. Krotzky, H. Papen, S. Schenk, and H. Thierfelder. 1989. Plant, microbial and soil factors, determining nitrogen fixation in the rhizosphere. Z. Pflanzenernaehr. Bodenkd. 152:231-236.

Wright, R.J., V.C. Baligar, and S.F. Wright. 1988. Estimation of plant available manganese in acidic subsoil horizons. Commun. Soil Sci. Plant Anal. 19:643-662.

Zake, V.M., C.E. Watson, Jr., and L.M. Gourley. 1992. Performance of grain sorghum hybrids on infertile, acid soils in Kenya. p. 120. *In* Agronomy abstracts. Minneapolis, MN., 1-6 November 1992.

Zobel, R.W. 1994. Stress resistance and root systems. p. 80-99. *In* Proc. workshop on adaptation of plants to soil stresses. Lincoln, NE. 1-4 August 1993. INTSORMIL Publication No. 94-2, Lincoln, NE.

Zobel, R.W., L.V. Kochian, and T.G. Toulemonde. 1992. Plant root systems. p. 30-40. *In* Proc. PPI conf. on roots in plant nutrition. July 1992. Champaign, IL.

Genetic Resistance to Lodging

J. W. Johnson*, W. D. Stegmeier, D. J. Andrews,
D. T. Rosenow, R. G. Henzell, and R. L. Monk

Abstract

Lodging of sorghum and millet results in grain losses worldwide, but is especially costly in regions that harvest with machines. This paper presents a brief overview of the roles of biotic and abiotic stresses in lodging. It discusses major causes of lodging and gives sources of resistance in sorghum; including, drought induced premature leaf and plant senescence (IS 12555C, IS 12568C, NSA 440, and SC599-11E [IS 17459 derived]); charcoal rot, Macrophomina phaseolina (IS 12555C, IS 12568C, KS 19, and New Mexico 31); Fusarium stem rot (SC326-6 [IS3758 derived] and B35 [IS12555 derived]). This paper will concentrate on lodging resulting from post anthesis water stress. Techniques used in breeding for lodging resistance, including use of molecular markers to select for stay green (nonsenescence) are discussed. IS12555C had been identified as resistant to three of the major causes of sorghum lodging, suggesting that IS12555C or its appropriate derivatives would be useful in most programs that identify improved standability as a primary objective.

What are the most important characteristics of your sorghum crop? When this question is asked of farmers in the United States, they rank yield first and standability second. Standability would likely be number two in the rest of the Americas and Australia. However, in traditional farming areas of Africa and India, sorghum and pearl millet are often hand-harvested, and standability may be less important than other characteristics such as food quality.

Grain losses from lodging are not well documented. At one time, stalk rot was estimated to account for 9% of sorghum yield losses due to diseases in the United States. Of course some losses from stalk rot are not due to lodging, and some lodging losses are not due to stalk rot. Even though there is no current official estimate of grain loss due to lodging, farmers and researchers think it is significant.

It is likely that sorghum breeders have had standability in their selection index throughout the history of sorghum improvement. The need for improved stalk quality became acute with the use of the combine harvester. Karper and Quinby (1946) said that all milos are susceptible to charcoal rot, which causes plants to fall down following maturity. Quinby and Martin (1954) reported that varieties that lodge are regularly discarded in favor of stiffer-stalked varieties that yield no more or even considerably less. Karper (1945) noted that Kafir, one of the stoutest

J.W. Johnson, Director of Sorghum Research, Novartis Co., 356 Hosek Rd., Victoria, TX 77905 USA; W.D. Stegmeier, Kansas State University, Agricultural Research Center.; D.J. Andrews, Department of Agronomy University of Nebraska-Lincoln; D.T. Rosenow, Texas A&M Agricultural Experiment Station; R.G. Henzell, Department of Primary Industries, Hermitage Research Station, Warwick, Queensland, Australia; R.L. Monk, Pioneer Hi-Bred International, Inc. *Corresponding author.

stalked taller varieties, stood up well in the field for a long time after maturity, but milo was the most susceptible to charcoal rot. Today, however, Kafir is considered to possess poor standability relative to current cultivars, indicating that much progress in lodging resistance has been made since 1945.

Causes of Lodging

Sorghum and pearl millet are usually grown in harsh, water-deficient environments. The crops are normally subjected to heat and drought stress at least once before harvest. The causes of death and lodging are not well understood, but three hypotheses were proposed by Henzell et al. (1984): 1) plants die as a direct result of water deficit, i.e., a physiological breakdown due to dehydration; 2) pathogens cause death; or 3) death is due to an interaction between physiological stress and pathogens.

Lodging that occurs following a water deficit grain-filling period causes the most grain loss world-wide. When this occurs, plants senesce prematurely and then lodge due to stem collapse or breakage at or just above ground level.

Dodd (1980) reports that filling of the grain head is involved with predisposition to root and stalk rot development and suggests that size of the grain sink needs to be considered when evaluating the causes of root and stalk rot. Henzell et al. (1984) also suggest that the source-sink relationship of grain growth is implicated in lodging and stalk rots.

Diseases associated with lodging in sorghum include charcoal rot (*Macrophomina phaseolina*), fusarium (*Fusarium moniliforme*), pythium (*Pythium spp*), and anthracnose (*Colletotrichum graminicola*). Adverse abiotic conditions such as drought, wet soil, high humidity, and wind increase the effects of these diseases on lodging.

Malm and Hsi (1965) began studies of charcoal rot caused by *M. phaseolina* at New Mexico State University in 1953. Their work demonstrated variability among sorghum varieties for susceptibility to *M. phaseolina*. Plants inoculated with *M. phaseolina*- infected toothpicks two weeks after blooming developed more charcoal rot infection than did the same plants inoculated earlier in the growth cycle. Their work demonstrated that heat and moisture stress during grain fill aided the development of charcoal rot.

Rosenow et al. (1972) reported that selection for lines that could stand for extended periods following maturity identified lines with superior resistance to lodging. Evaluation criteria were root lodging, weak-neck, after-freeze stalk breakage, and charcoal rot. Nonsenescence was highly correlated with both lodging and charcoal rot resistance in tests conducted in Texas (Tables 1 and 2).

Studies in Kansas revealed a significant decrease in lodging in sorghum when adequate potassium was added to potassium-deficient soils (Murphy, 1975). The data suggested that adequate potassium reduced the incidence of stalk rot by reducing plant stress.

Insects can stress the plant and cause lodging by either predisposing the plant to pathogens or interfering with the appro-

Table 1. Relationship among stay green (LPD), lodging, and charcoal of selected sorghum lines.

	Lubbock-F403		Lubbock-F407		
Destination	LPD rating[1]	Lodging %[2]	LPD rating[1]	Charcoal rot rating[3]	Lodging %[2]
B1	2.3	0	2.9	0.7	0
B2-2	2.1	0	2.8	0.8	0
B35	2.2	0	2.7	0.5	0
BTx623	3.7	26	4.7	2.0	40
BTx625	4.7	80	4.6	3.4	38
BTx378	4.9	53	—	—	—
Tx7000	—	—	4.6	3.4	13

[1]Leaf and plant death rating: 1=all green, 3=50% leaf area dead, 5=entire plant dead.
[2]Moisture stress type lodging.
[3]Stalk rated on 1-5 scale: <1=<one internode infected, 3=3 internodes, 4=>3 internodes, 5=death, sclerotia. (Rosenow, 1977)

Table 2. Summary of agronomic, lodging, and charcoal rot data from the Statewide Lodging Test, 1975-76.

	1975				1976	
					Lodging %	
Entries	Date of 50% bloom	Lodging %	Charcoal rating	LPD rating	2/10	3/8
Res. lines (20)	8/14	9.3	1.3	2.8	0.5	13.8
Standards (5)	8/13	64.6	3.3	3.4	68.1	90.7

Rosenow, 1977

priate accumulation of carbohydrate in the stem. Common leaf- and stem-feeding insects that cause lodging are greenbugs (*Schizaphis graminum*), yellow sugarcane aphids (*Sipha flava*), and chinch bugs (*Blissus leucopterus*). Root-feeding insects such as white grubs (*Phyllophaga crinita*) and sugarcane root stalk weevils (*Anacentrinus deplanatus*) also can cause plant lodging.

It has been proposed that physiological stress per se results in rapid senescence and subsequent lodging. Henzell et al. (1984) suggested that this stress can be generated when a large "sink" for a photosynthetic assimilate, such as a rapidly growing organ (the grain), creates a high demand in relation to the assimilate supply (photosynthetic capacity). The "physiological stress" is thought to result in a shortage of available carbohydrate in the stem. Cell death occurs when the carbohydrate level is too low to support sufficient maintenance respiration. Pith disintegration then begins at the base of the plant and may extend upward several internodes as conditions worsen.

A study of 60 lines in Nebraska (Esechie et al., 1977) indicated that lodging resistance in sorghum was associated with large diameters of basal internodes and peduncles, shorter peduncles, shorter plant height and thicker rind. Schertz and Rosenow (1977) reported much variation in the internode anatomy among 12 sorghum lines selected because of their field variation for lodging percentages and stalk and peduncle strength. The most prominent differences were in number of cells with lignified walls and in wall thickness.

Random advanced lines from the sorghum population PP9 were used to study

the heritability of lodging resistance (Prest et al., 1983). Heritability estimates using S_1 progeny as the selection unit ranged from 0.46 for rind thickness to 0.85 for flowering. Rind thickness was significantly correlated (-0.46) with post frost stalk lodging, whereas internode diameter and flowering were significantly correlated (-0.31 and -0.25) with stalk lodging estimates taken before frost.

Resistant sources and breeding technology for breeding for lodging resulting from post anthesis water stress will be the basis for the remainder of this paper. Resistant sources and breeding methodologies used in combating lodging caused by diseases and insects are discussed in other papers in these proceedings.

Sources of Resistance

Kafirs had superior standability over milos when their types were popular varieties in the1940s. In the 1950s yellow endosperm types, such as the cultivar Short Kaura, provided germplasm with improved resistance to lodging caused by charcoal rot. Yellow endosperm types were used by several breeders in the U.S. KS19, a lodging-resistant restorer line used in breeding programs in Australia and the U.S., is a selection by W.M. Ross from a cross made by O.J. Webster. KS19 is one parent in several lodging-resistant lines released in Australia (Henzell et al. 1984). Maunder (1984) also reported the use of yellow endosperm lines as well as New Mexico 31, a line released by Malm and Hsi (1964), in a recurrent selections program to improve resistance to lodging caused by *M. phaseolina.*

Large genetic differences exist in sorghum for lodging caused by water deficits. Unfortunately, most genotypes are susceptible. Table 3 lists some lines that are lodging-resistant in Australia and the U.S.

Table 3. Lodging resistant sources.

Designation	Probable source of resistance
KS19	Short Kaura
QL10	KS19
QL27	KS19
QL41	B35
B35	IS 12555
SC35-14E	IS 12555
SC56-14E	IS 12568
SC599-11E	IS 17459
NSA 440	-

One of the lodging resistant cultivars, IS 12568C (SC56-14E), was included in a program to examine the genetic and environmental control of rooting patterns in sorghum (Jordan and Monk, 1980). Their observations provided evidence that the roots of IS 12568C grew deeper than those of the other cultivars studied and that deep rooting is an effective means of utilizing stored water. IS 12568C was effective in producing a deep rooted hybrid with Tx622, a shallow-rooted cultivar. Deep roots could be one explanation for lodging resistance of IS 12568C and its hybrids. Sorghum root lodging can occur in wet soil accompanied by wind. Lines with resistance to root lodging are presented in Table 4.

Evaluation and Selection Techniques

The primary approach to improve lodging resistance used in Texas (Rosenow and Clark, 1995) utilizes the naturally occurring low-rainfall conditions of West Texas for selection. Germplasm is evaluated in field nurseries under limited irri-

Table 4. Sorghum lines resistant to root lodging.

Designation	Name, pedigree, group, or derivation
BTx399	Wheatland
B35	IS 12555 der./SC35 der.
BTx638	(?*BTx624)
Tx2862	(Tx2783*GR2-39)
Tx2896	(80C2241*Tx430)
Tx2894	(SC120*Tx7000(2))
SC1177C	Doc-Sub
SC1201C	Guin-Caud
IS 12652C	Nig-Dur-Sub
IS 2856C	Caffrorum
IS 6920C	Cau-Kaf
IS 3515C	Nigr
IS 12556C	Durra
IS 12609C	Zerazera
IS 12658C	Dur-Bic
IS 12685C	Doc-Leoti

gation where yield potential is expressed but post-flowering stress commonly occurs. Large field screening nurseries are established at several locations with different planting dates. This approach helps to insure stress during and after grain fill. Irrigation is applied during the early growth stages to produce good growth and yield expression. Irrigation is terminated prior to anthesis, allowing moisture stress to develop after flowering and to intensify during grain fill. In these nurseries, entries are visually rated for premature leaf and plant death. Ratings on a 1 to 5 scale (1 = completely green, 3 = 50% of leaf area dead, 5 = death) are normally made at or soon after physiological maturity, but can be made any time that differences appear among genotypes. Visual rating of leaf death is an excellent method of evaluating actual percentage of greenleaf area (Wanous et al., 1991).

Nurseries are often left standing for an extended period following maturity to allow lodging to occur. Lodging notes are taken periodically throughout the season on the percentage of lodged plants and the type of lodging, whenever significant lodging occurs. Notes on flowering, plant height, and head exertion are taken on all entries. Knowledge of maturity is critical because sorghum is most susceptible to post-flowering stress just prior to physiological maturity. Plants a few days earlier or later in maturity may show little premature senescence. Flowering notes are taken on all plots, and comparisons are made only among entries of similar maturities.

In field screening nurseries, standard checks with contrasting reaction to post-flowering drought and different types of lodging are used every five to ten plots. Single row plots, six meters in length, are used in most screening nurseries.

Results in Australia are similar to those reported by Rosenow in Texas: a significant positive association exists between nonsenescence and lodging resistance. Most breeding programs in Australia take a similar approach to evaluating lodging resistance. Hybrids rather than inbred lines are evaluated because the low grain yields of inbreds tend to make them lodging-resistant. The genotypes under test are grown at a number of sites at which grain yield, maturity, nonsenescence, and lodging are measured if differences are expressed. Several sites are used to increase the chances of encountering lodging conditions. Then selection is made for resistance to lodging within maturity and yield classes.

Because the most prevalent type of lodging in Australia is expressed only in plants that undergo water deficits during grain filling, some control over the environment is desirable. Rain-out shelters have been used to study specific aspects of lodging and stalk rots, but they are

obviously of limited use in a breeding program. Very effective use has been made, however, of a dry-season (winter) planting in tropical Australia. This environment has an extremely predictable dry season, and lodging induced by water deficits can readily be achieved by manipulating irrigation.The programs in Australia are currently using only stay green to address the lodging problem. Current sources of stay green are B35, SC35C, SC56C, QL12, and E36.

Lodging and Yield Potential

Henzell et al. (1992) reported that hybrids with at least one parent derived from B35 had superior lodging resistance and equal grain yield to three check hybrids that were earlier in maturity than the lodging-resistant hybrids. Borrell et al. (1996) studied nine hybrids varying in rate of leaf senescence in a water-limited environment. He found that leaf senescence was negatively associated with grain dry mass but positively associated with the amount of stem reserve mobilized.

Sixteen trials were examined which contained A35 hybrids and had recorded lodging from the Grain Sorghum Performance Tests in Texas (published by the Texas Agricultural Experiment Station) for the period of 1985-1994 (Table 5). The trials used had an average of 80 hybrids (most of them commercial hybrids); the A35 hybrids were made with several male parents. The A35 hybrids lodged significantly less than other hybrids, and average yield of the A35 hybrids was higher than the trial average.

In an attempt to compare similar maturing stay green and senescencing hybrids for yield in the absence of lodging, three hybrids — one stay green and two senesecing — were selected for study from the Kansas Performance Tests With Grain and Forage Sorghum Hybrids (published by the Kansas Agriculture Experiment Station). The time period for the study was chosen because 1990-1995 were the only years that the stay green hybrid was entered in the Kansas trials. The senescencing hybrids were selected because they had public pedigrees, were similar in maturity to the stay green hybrid, and were known to be above average in yield potential and lodging resistance. Molecular markers indicate that the stay green hybrid has three of the major genes associated with nonsenescence in B35.

The stay green hybrid averaged more grain yield and had less lodging than either of the senescencing hybrids (Table 6). More importantly, when trials in which the senescencing hybrid had no lodging were averaged, the stay green hybrid maintained a yield advantage over each of the senescencing hybrids. These data indicate that competitive hybrids can be produced that have improved lodging resistance as a result of the stay green trait.

Marker-Assisted Selection

The stay green trait in B35 has been shown to increase resistance levels to

Table 5. Yield rank and percent lodging of A35 hybrids from 16 selected TAES Grain Sorghum Performance Trials in Texas 1985-1994.*

Average number of hybrids in trials	Average yield rank of A35 hybrids	Average % lodging of A35 hybrids	Average % lodging of non A35 hybrids
80	33	2.3	16.6

* Average of 16 locations that had significant lodging during the period studied.

Table 6. Yield, maturity and lodging of stay green and senescencing hybrids selected from the Kansas Performance Tests with Grain and Forage Sorghum Hybrids, Kansas Agricultural Experiment Station, 1990-95.

Hybrid*	Yield kg/ha	Days to bloom	Lodging %	Yield from trials without lodging
Stay green hybrids	7270[1]	64	8	8220[3]
ATx399 x Tx2737	6700	66	13	7710
Stay green hybrids	6700[2]	63	2	6840[4]
ATx399 x RTx430	6270	64	6	6520

* Stay green hybrid: RFLP markers indicate that the major stay green genes present in B35 are present in this hybrid. Pedigree of the hybrid is unknown to the authors.

[1] 27 trials (1994-95)
[2] 47 trials (1990-93)
[3] 11 trials (1994-95)
[4] 20 trials (1990-93)

lodging caused by charcoal rot, Fusarium stalk rot, wind, after-freeze stalk breakage, and water deficiency during grain fill, while not significantly reducing grain yield potential. More information is needed on the inheritance of various drought and lodging resistance traits. Walulu et al. (1994) reported that the stay green trait in B35 was controlled by one or two major dominant genes. RFLP markers tightly associated with the QTLs for stay green have been identified (Nguyen and Rosenow, 1993; Xu et al., 1995). These markers are being utilized to facilitate a backcrossing program to transfer the stay green trait to improved agronomic types. Molecular markers permit the identification of plants containing the stay green trait without providing a water stress environment after flowering.

Pearl Millet

Muuka (1989) found two main types of lodging due to senescence in pearl millet: basal and peduncle. Basal lodging was due to collapse of the stem just above the ground. Root lodging was not a factor. Peduncle lodging was involved in collapse of the peduncle, usually just above the last node, letting the head hang down. These pendant heads are often harvestable, but wind will eventually break the peduncle at the point of collapse. Among the 18 genotypes studied, peduncle lodging was about twice as important as basal stem lodging. Genetic variation was found for resistance to both types of lodging. Resistance to both was positively correlated to stem and peduncle diameter and rind thickness. A thick, long flag leaf sheath reduced peduncle lodging. Grain yield, plant height, and head number all increased lodging.

The University of Nebraska pearl millet breeding program has selected strongly for resistance to both types of lodging, developing short parental lines that have thick stems and peduncles that give relatively short hybrids (1.2 to 1.5 m) with erect tillers. Lodging scores in hybrid tests and the Regional Trials vary considerably with conditions, but when susceptible hybrids lodge 50%, lodging of resistant hybrids will be 10% or less.

Lodging of millet can be caused or influenced by several factors: diseases and insects, root lodging in clay or hardpan soils, reduced secondary and brace root development, nodal abscission layers, and shriveling and disintegration of parenchyma tissues in the stalk peduncle

and internodes when the plant is drought-stressed as it approaches physiological maturity. Root lodging is observed only in tall landrace accessions whose root systems spread horizontally and penetrate poorly into the B-horizon of the soil. These plants are easily uprooted in severe wind storms. Breakage at a stalk node appears to be inherited as a simple recessive trait and can be eliminated by selection in early segregating generations. Crown lodging associated with stalk diseases such as charcoal rot occurs frequently in this environment. The post-flowering drought stress necessary for charcoal rot development is present in varying degrees in nearly all growing seasons. This provides an opportunity to select for reduced incidence and severity of charcoal rot and improved lodging resistance in nearly every generation in the development of lines and populations.

In Kansas, lodging resulting from parenchyma tissue shrinkage and detachment from the stalk rind, when millet is stressed during the late seed-fill period, continues to be a severe problem. At Fort Hays, Kansas, it is closely associated with improved seed set and grain yield. Materials with seed sets of 10 to 30 percent seldom lodge, but lodging percentages rapidly increase as seed set levels of 80 to 100 percent are obtained and as grain yield levels increase.

Crosses involving IP2789, an early-maturing, club-headed line from Mauritania (via the ICRISAT germplasm repository) have produced early-maturing progenies in which parenchyma tissues remain intact and attached to the stalk rind. Superior progenies have been crossed and backcrossed to elite maintainer and fertility restorer lines. Lodging resistance in F_2 and F_3 progenies appears to be controlled by a recessive factor, but good data sets have not been obtained. Some of the hybrid combinations of susceptible X-resistant lines have intermediate levels of lodging, indicating the factor conditioning lodging resistance may act as a partial dominant trait in some genetic backgrounds.

Conclusion

Lodging-resistant germplasm has been identified using large multilocation field screening nurseries, timely irrigations, and subjective scoring. The approach was successful in identifying improved lines with lodging resistance from segregating families and identifying sources that transferred resistance to F_1 hybrids. The stay green trait derived from IS 12555 can increase standability while maintaining competitive grain yield potential. The use of molecular markers will likely increase and accelerate the use of stay green by eliminating the need for water-stressed breeding nurseries. Progress has been made in identifying pearl millet germplasm resistant to several types of lodging and in transferring resistance to improved types.

References

Borrell, A.K., and A.C.L. Douglas. 1996. Maintaining green leaf area in grain sorghum increases yield in a water-limited environment. p. 315-322. *In* Proceedings of the Australian sorghum conference, Tamworth, 20-22 February, 1996, Australian Institute of Agricultural Science, Melbourne, Occasional Publication No.93.

Dodd, J.L. 1980. The photosynthetic stress-translocation balance concept of sorghum stalk rots. p. 300-305. *In* Sorghum diseases, a world review: Proceedings of the international workshop on

sorghum diseases, sponsored jointly by Texas A&M University, USA, and ICRISAT, Patancheru, A.P. 502 324, India.

Esechie, H.A., J.W. Maranville, and W.M. Ross. 1977. Relationship of stalk morphology and chemical composition to lodging resistance in sorghum. Crop Science 17: 609-612.

Henzell, R.G., R.L. Dodman, A.A. Done, R.L. Brengman, and E.P. Mayers. 1984. Lodging, stalk rot, and root rot in sorghum in Australia. p. 209-218. *In* Sorghum root and stalk rots: A critical review. Proceedings of the consulative group discussion on research needs and strategies for control of sorghum root and stalk rot diseases, 27 November - 2 December 1983, Bellagio, Italy. ICRISAT, Patancheru, A.P. 502 324 India.

Henzell, R.G., R.L. Brengman, D.S. Fletcher, and A.N. McCosker. 1992. Relationship between yield and non-senescence (stay green) in some grain sorghum hybrids grown under terminal drought stress. p. 355-359. *In* Proceedings of the 2nd Australian sorghum conference, Gatton, 4-6 February 1992.

Jordan, W.R., and R.L. Monk. 1980. Enhancement of drought resistance of sorghum: Progress and limitations. p. 185-204. *In* Proceedings of the 35th annual corn and sorghum research conference, Am. Seed Trade Assn. Chicago, IL.

Karper, R.E. 1945. Combine sorghums. Southern Seedsman USA. May 1945.

Karper, R.E., and J.R. Quinby. 1946. The history and evaluation of milo in the United States. Journal American Society of Agronomy 38: 441-453.

Malm, N.R., and B.C.H. Hsi. 1965. Charcoal rot studies in New Mexico. pp 51-53. *In* Proceedings of the fourth biennial grain sorghum research and utilization conference. Grain Sorghum Producers' Association (GSPA), Abernathy, Texas, U.S.

Maunder, A.B. 1984. Breeding for stalk rot resistance as a component of acceptable agronomic performance. p. 219-224. *In* Sorghum root and stalk rots. A critical review. Proceedings of the consulative group discussion of research needs and strategies for control of sorghum root and stalk rot diseases, 27 November - 2 December 1983, Bellagia Italy. ICRISAT, Patancheru, A.P. 502 324 India.

Murphy, L.S. 1975. Fertlizers efficiency for corn and grain sorghum. p. 49-72. *In* Proceedings of the thirteenth annual corn and sorghum research conference.

Muuka, F.P. 1989. Genotypic differences in lodging and mechanical strength in stalks and peduncles of pearl millet (*Pennisetum glaucum* [L.] R.Br.), MS thesis, Department of Agronomy, University of Nebraska, Lincoln, Nebraska.

Nguyen, H.T., and D.T. Rosenow. 1993. Identification of molecular genetic markers linked to drought resistance traits in grain sorghum. p. 127-132. *In* Proceedings of the 18th biennial grain sorghum research and utilization conference, Feb. 28 - March 2, 1993, Lubbock, TX.

Prest, T.J., R.P. Cantrell, and J.D. Axtell. 1983. Heritability of lodging resistance and its association with other agronomic traits in a diverse sorghum population. Crop Sci 23:217-221.

Quinby, J.R., and J.H. Martin. 1954. Sorghum Improvement. Adv. in Agronomy VI:305-359.

Rosenow, D.T., J.W. Johnson, R.A. Frederiksen. 1972. Selection for lodging resistance in grain sorghum. p. 18. *In* Agronomy abstracts, American Society of Agronomy, Madison, Wisconsin, U.S.

Rosenow, D.T. 1977. Breeding for lodging resistance in sorghum. p. 171-185. *In* Proceedings of the 32nd annual corn and sorghum research conference, Dec. 6-8, Chicago, IL.

Rosenow, D.T., and L E. Clark. 1995. Drought and lodging resistance for a quality sorghum crop. Proceedings of the 50th annual corn and sorghum research conference. Dec. 6-7, 1995, Chicago, IL. p. 82-87.

Schertz, K.F., and Rosenow, D.T. 1977. Anatomical variation in stalk internodes of sorghum. Crop Science 17:628-631.

Walulu, R.S., D.T. Rosenow, D.B. Wester, and H.T. Nguyen. 1994. Inheritance of the stay green trait in sorghum. Crop Sci. 34:970-972.

Wanous, M.K., F.R. Miller, and D.T. Rosenow. 1991. Evaluation of visual rating scales for green leaf retention in sorghum. Crop Sci. 31:1691-1694.

Xu, W., O. Crasta, D.T. Rosenow, J. Mullet, and H.T. Nguyen. 1995. Major QTLs for post-flowering drought resistance in grain sorghum. p.22. *In* Proceedings of plant genome III conference, January 1995, San Diego, CA.

Striga-Host Relationships and Their Role in Defining Resistance

L. Butler*, G. Ejeta, A.G. Babiker, and D.E. Hess

Abstract

The parasitic weed Striga hermonthica *has become the greatest biological constraint on cereal production in much of sub-Saharan Africa. Prevailing drought conditions and low soil fertility, coupled with increased production pressure, have led to the introduction and intensive monocropping of new genotypes, most of which have proved to be highly susceptible to* Striga, *causing infestation levels far beyond those observed with traditional farming practices.*

The problem is so severe it requires consideration of every possible control approach. Innovative research should focus on methodologies targeting early developmental stages which will have an immediate impact on the Striga *seed bank. One of the most practical approaches for subsistence farmers, for whom expensive technological inputs are not available, is the development of adapted crop cultivars with enhanced levels of resistance to the parasite. A good beginning has been made using this approach, with the recent release and wide distribution in Africa of eight new* Striga*-resistant sorghum cultivars developed in our research program at Purdue University. However, much more work on host plant resistance remains to be done. Only one well-defined mechanism of resistance, low stimulant production, has been exploited thus far in cereals. Experience has shown that durable resistance requires multiple resistance mechanisms (Parker, 1983). This paper summarizes what is known of the complex relationship between host and parasite, with particular emphasis on features that offer opportunities for development of as yet unexploited mechanisms of host resistance.*

Requirements for Parasitism by *Striga*

As a hemiparasite, *Striga* cannot survive without the services and resources provided by its host. The host must satisfy a series of several rather stringent requirements in order for *Striga* to complete its life cycle, produce viable seeds, and perpetuate itself (Worsham, 1987).

Recognition of Host vs Non-host

Striga has very specific requirements for initiation of germination, including a chemical signal produced by the roots of hosts as well as non-hosts such as cotton (Cook et al., 1966). Host specificity cannot be explained on the basis of current information about the nature of root exudate composition of hosts vs. non-hosts (Riopel and Timko, 1992). With

L.Butler (Deceased), Department of Biochemistry, Purdue University, West Lafayette, IN 47907; G. Ejeta, Deparment of Agronomy, Purdue University, West Lafayette, IN 47907; A.G. Babiker, Agricultural Research Corporation, Gezira Agricultural Research Station, Box 126, Wad Medani, Sudan; and D.E. Hess, Research Institute for Arid Tropics, Sahelian Center, B.P. 12404, Niamey, Niger. *Corresponding author.

respect to attachment to host roots after germination, *Striga* is non-specific, attaching to inert materials such as glass as well as roots of non-hosts (Nickrent et al., 1979). The mechanisms by which *Striga* recognizes a host root, overcomes its defenses, penetrates and parasitizes it remain unknown.

There are reports of host-specific "strains" of *Striga* (Riches and Parker, 1995; Vasudeva Rao and Musselman, 1987; Bharathalakshmi et al., 1990, Freitag et al., 1996). When sorghum is introduced into primarily millet-producing areas, or vice versa, *Striga* often does not infest the newly introduced crop in the first few years (Riches and Parker, 1995). Adaptation to the other host generally occurs within a few seasons, although it is not clear whether adaptation involves introduction of the alternate "strain" of *Striga* from elsewhere or whether the *Striga* specific for one host somehow adapts to the alternate host. Detailed research on the mechanisms by which *Striga* recognizes hosts could produce new insights into host resistance and new opportunities for controlling the parasite.

Integration/Coordination of Host and Parasite Life Cycles

Striga's complete dependence upon a host for survival requires close coordination of its life cycle with that of the host. Because *Striga* seeds are minute (200 microns) with limited stored resources, a germinating seed can survive only about three days unless it finds and attaches to a host root (Riopel and Baird, 1987). It is not surprising, therefore, that germination of *Striga* seeds is under close control of the host via labile chemical signals exuded by host roots, so that germination usually occurs only when a suitable host root is available. Less expectedly, evidence is accumulating that later stages in the life cycle of *Striga* also are under the control or influence of the host, thus ensuring synchrony of the entire life cycles of host and parasite, and enhancing the likelihood of parasite survival.

The Life Cycle of *Striga*

Subsequent to germination, *Striga* attaches to and penetrates host roots and establishes vascular connections with the host. As much as half of *Striga*'s life cycle is subterranean, growing completely at the expense of its host. Much of the damage to the host crop occurs during the subterranean growth stages, before the parasite is accessible for removal by hand pulling or for treatment with contact herbicides. After emergence, *Striga* flowers and sets seed rather quickly, so its life cycle is generally complete by the time a healthy host plant matures and senesces. A heavily infested host plant may fail to complete its development, even to the point that the parasite development may be negatively affected.

Germination

Newly ripened *Striga* seeds are effectively dormant. A period of "after-ripening" by storage of the seeds in dry conditions lowers the moisture content and breaks dormancy (Mohamed et al., 1996). Yet germination does not occur until the after-ripened seeds have been exposed to warm, moist conditions for several days

to several weeks, and then to a specific exogenous chemical signal exuded from host roots (Riopel and Timko, 1992). These requirements put *Striga* germination not only under control of the host, but also under the influence of seasonal conditions. The dormancy of newly produced seeds prevents suicidal germination at the end of a crop season when no suitable host would be available for completion of the *Striga* life cycle. The moisture conditioning requirement delays *Striga* germination until early seasonal rains have resulted in germination and growth of the host to a degree that the parasite can be supported.

Initiation of Haustorium

Striga seeds germinated *in vitro* with purified germination stimulants fail to develop beyond the formation of a radicle (Riopel and Timko, 1995). *Striga* seeds germinating close to host roots develop a specialized organ of attachment, the haustorium, in response to another root-derived chemical signal, described below. This haustorial initiation signal and the germination stimulant have no cross-reactivity and are independently inherited (Weerasuriya, 1995). Roots of many non-hosts exude chemicals which initiate haustorium formation, so host-nonhost specificity cannot be explained on the basis of exudation of haustorial initiation factors exclusively by host roots (Riopel and Timko, 1995). Haustorial initiation in response to the signal is the most rapid multicellular morphogenetic event known in the plant kingdom (J.L. Riopel, 1996, personal communication). Within a few hours of receiving the initiation signal from a host root, the cell extension plane of the *Striga* radicle shifts 90 degrees, producing a complex structure with characteristic hairs (Riopel and Timko, 1995). Until this stage, *Striga* seedling development occurs primarily due to cell elongation rather than cell division (Okonkwo, 1987).

Attachment

Like its response to germination stimulant and haustorial initiator, *Striga* is non-specific with respect to attachment. Indeed, *Striga* has been reported to attach to plastic surfaces more readily than to host roots (Riopel and Timko, 1995). Attachment may involve surface papillae composed of sticky hemicelluloses (Baird and Riopel, 1985).

Penetration and Establishment

Details of the rapid penetration of *Striga* to the host xylem, including probable involvement of lytic enzymes, are provided by Riopel and Timko (1995). According to Riopel (1996, personal communication), the complexity of the haustorium is underappreciated. This morphological bridge undergoes further development, from parenchyma cells in the cortex to a complex organ with a population of cells that go directly to host vascular tissue, to establish xylem-to-xylem connections, presumably guided by signals provided by the complex internal chemistry of the host. Non-hosts and some resistant host genotypes manage to prevent establishment or diminish its frequency. Defense responses (not all have been shown to occur in response to *Striga*) include localized necrosis (hypersensitive response), suberization, callose deposition and wall lignification, and synthesis of defensive proteins (Riopel and Timko, 1995).

Plumule Formation

Under natural conditions, *Striga* seedlings do not form a shoot until the radicle has penetrated the host root (Okonkwo, 1987), suggesting that plumule formation, like other developmental stages, is under host control. On a minimal artificial medium of mineral salts and sucrose, Okonkwo (1987) was able to get full but relatively slow development of *Striga hermonthica*, indicating that *Striga* is able to synthesize all required developmental signals. Nevertheless, there is good evidence that the normally rapid shoot formation and *Striga* plant development on host roots require developmental signals provided by the host (Cai et al., 1993).

Metabolic Adaptation

Little is understood how *Striga*, a dicot, metabolically adapts to growth on its monocot host, but a profound adaptation would seem to be necessary. Grafting of a dicot onto a monocot host would not be expected to be successful, but establishment of *Striga* on a cereal host appears to be functionally equivalent to successful grafting.

Growth

Striga spends a relatively large proportion of its life cycle growing holoparasitically in a subterranean mode, undetectable except for its deleterious effects on the host. The rate of the parasite's development is undoubtedly influenced not only by host signals/metabolites but also by growth conditions. During the subterranean stage, *Striga* does much of its damage to the host. To prevent significant damage to the host, it is imperative to control the parasite at its early developmental stages. Control is difficult, however, because the subterranean stage is unavailable for treatment with contact herbicide or for hand pulling or cultivation.

Flowering and Seed Production

It may be presumed that *Striga* flowering and seed production also are under host control, timed to occur during host seed maturation. However, emerged *S. hermonthica* plants can complete their life cycle on the root system of a dead host.

Host-Derived Signals Controlling *Striga* Development

Germination

Striga seeds commit their slender resources to germination only when a series of specific requirements have been met (Worsham, 1987). In order to germinate, freshly harvested *Striga* seeds must undergo an after-ripening period, in which dormancy is broken by lowering moisture content, followed by pre-treatment in moist, warm conditions prior to exposure to an exogenous germination stimulant. In nature, germination stimulants are chemical signals generally exuded from host and non-host roots. Several classes of chemicals have been shown to be active as *Striga* germination stimulants (Butler, 1995).

In terms of controlling *Striga* germination in the field, the most important of the host root-derived stimulants are the strigolactones, a group of sesquiterpene analogs produced and exuded in varying ratios by roots of host plants (Butler,

1995). The strigolactones are active as germination stimulants at concentrations far too low to be detected by chemical assays (Siame et al., 1993). Mangnus and Zwanenburg (1992) reported that activity of strigolactones depends on an intact lactone D ring, and proposed a molecular mechanism. Siame et al. (1993) provided corroborating evidence for the role of the lactone ring by demonstrating that esterase/lactonase enzymes readily inactivate strigolactones.

The first strigolactone identified was strigol, found in the root exudate of cotton, which is not a host for *Striga* (Cook et al., 1966). Strigol was later shown to be the major strigolactone exuded from roots of maize and proso millet, and a minor component of sorghum root exudate (Siame et al., 1993). The major strigolactone exuded by sorghum roots is sorgolactone (Hauck et al., 1992). Another strigolactone, alectrol, is the major *Striga* germination stimulant exuded by roots of cowpea (Muller et al., 1992).

Another unique group of compounds, the sorgoleones, also have been identified from sorghum root exudate and have been shown to stimulate *Striga* seed germination (Netzly & Butler, 1986; Chang et al., 1986). The sorgoleones differ in the number of carbon atoms and double bonds in their hydrocarbon chain (Netzly et al., 1988). The sorgoleones are exuded as oily droplets at the tips of sorghum root hairs (Netzly and Butler, 1986). They are produced in the hydroquinone form, which can stimulate germination, but are readily oxidized to the quinone form, which is not only inactive (Chang et al., 1986), but appears to be a strong selective inhibitor of *Striga* seed germination (A.M. Mohamed et al., 1996, personal communication). The major sorgoleone component has been synthesized (Sargent and Wangchareontrakul, 1990). Certain simpler synthetic quinones can either inhibit or stimulate *Striga* seed germination, depending on concentration and other conditions (D.E. Hess, A.M. Mohamed, and L.G. Butler, 1996, personal communication). Host roots exude germination inhibitors as well as stimulants (Weerasuriya et al., 1993). In addition to stimulating and inhibiting *Striga* germination, the sorgoleones are powerful contact allergens (Netzly and Butler, 1986), as might be expected from their structural similarity to urushiol; they also are selective herbicides, inhibiting electron transfer in mitochondria and chloroplasts (Nimbal et al., 1996).

Production of strigolactones and sorgoleones by sorghum roots is influenced by environmental conditions. Strigolactones are produced under growth conditions of excess moisture, essentially hydroponically. Their production is regulated by day length, with as much as a million-fold more produced under short (two-hour) days than long (16-hour) days (Weerasuriya et al., 1993). In contrast, the sorgoleones are produced and exuded only under drying conditions; excess moisture prevents the appearance of the oily droplets on the tips of root hairs (Netzly and Butler, 1986).

Ironically, the highly water-soluble strigolactones exuded under high moisture condtions correlate best with sorghum susceptibility to *Striga* (Hess et al., 1992). The hydrophobic sorgoleones, with their limited solubility in water, are produced under drying conditions charac-

teristic of the cropping conditions under which sorghum is usually planted. But the amount of sorgoleones produced does not correlate with susceptibility to *Striga*. All sorghum tested, irrespective of susceptibility to the parasite, produced similar amounts of sorgoleones (Hess et al., 1992). In contrast, resistant and susceptible sorghum genotypes differ by as much as a billion-fold in the amount of strigolactones they exude (Weerasuriya et al., 1993). Sorghum from China, where *Striga* is not yet recognized as a problem, produces extremely high levels of strigolactones and is highly susceptible to *Striga* (Weerasuriya et al., 1993). Some African sorghum produces extremely low levels of stimulant and generally exhibits useful levels of resistance to *Striga* (Hess et al., 1992). Some, such as SRN 39 and others that are high stimulant producers yet somewhat resistant, presumably have additional resistance mechanisms.

Screening for low germination stimulant production, the only trait contributing to *Striga* resistance that has been well characterized, has been facilitated by use of a simple agar gel assay (Hess et al., 1992). This assay, combined with field assessment, has provided strong evidence that low stimulant production is controlled by a simply inherited recessive gene (Hess and Ejeta, 1992; Vogler et al., 1996). This gene, along with others controlling various other traits, is being mapped on the sorghum genome (Weerasuriya, 1995).

The first detectable response of conditioned *Striga* seeds to germination stimulants such as strigol is production of ethylene (Babiker et al., 1993). Ethylene is such a potent germination stimulant that it is used to treat infested fields in the U.S. to induce suicidal germination and thereby lower the degree of infestation (Sand and Manley, 1990). Treatment of *S. asiatica* seeds with a combination of thidiazuron, a cotton defoliant with cytokinin-like activity, and selected auxins such as 2,4-D has been reported to stimulate endogenous ethylene production and germination, warranting consideration as an effective method for cleaning up infested fields (Babiker et al., 1994).

Haustorial Initiation

Like germination, initiation of the haustorium, the specialized structure that represents the beginning of parasitic expression for *Striga*, is under control of host-derived signals (Nickrent et al., 1979). A large number of phenolic compounds and cytokinins have been shown to induce haustorial initiation (Riopel and Timko, 1995). In particular, the simple quinone, 2,6-dimethoxy-p-benzoquinone (2,6-DMBQ), is quite active in this regard, although it is not found in sorghum root exudate unless the roots have been mechanically damaged. Weerasuriya (1995) reported involvement of a natural signal exuded by undamaged sorghum roots. The signal, the structure of which has not been elucidated, is less stable than 2,6-DMBQ. A more complete discussion of various features of haustorial initiation is presented by Riopel and Timko (1995).

A host genotype that produces normal levels of germination stimulant but only very low levels of haustorial initiation factor would be valuable. It would not only be minimally parasitized by *Striga* but would tend to clean up infested fields by stimulating suicidal germination. The

agar gel assay for production of germination stimulant (Hess et al., 1992) has been modified to screen for low production of haustorial initiation factor (Weerasuriya, 1995). Regrettably, variation of the amount of this signal produced within sorghum (Weerasuriya, 1995) and maize (Reda, et al., 1994) genotypes appears to be relatively small, compared to the large differences in germination stimulant production by sorghum genotypes (Hess et al., 1992). To our knowledge, no crop genotype producing satisfactorily low levels of haustorial initiator has been identified.

Subsequent Stages of Development

Although there is evidence from *in vitro* culture studies that *Striga* developmental stages beyond haustorial initiation are under control of signals obtained directly from the host through vascular connections (Cai et al., 1993), these presumed signals have not been characterized or identified.

Timing of Signal Production and Response

Effective coordination of the life cycle of *Striga* with that of the host requires controlled, brief periods of release of short-lived signals, and timely responses to signals. For sorghum, maximum strigolactone production occurs four to eight days after seed germination (Weerasuriya et al., 1993). Even if *Striga* seeds are already conditioned when the crop is planted, this timing permits establishment of the crop seedling without interference by *Striga*. A similar time frame applies to sorgoleone production (Netzly et al., 1988). The time frame for host root production of haustorial initiation factor has not been reported, but in agar gels it appears to be a few hours slower than germination stimulant production.

The first detectable response of *Striga* to germination stimulant is increased production of ethylene, in as little as four hours (Babiker et al., 1993). Germinating *Striga* seeds also respond rapidly (within four hours) to the haustorial initiator signal. The response includes cessation of cell elongation, radial expansion of cortical cells, initiation of haustorial hairs, and development of densely staining hairs at the haustorial apex (Riopel and Timko, 1995).

Although subsequent signals exchanged directly through vascular tissue between host and parasite are not yet known, it is clear that all signals controlling parasite and/or host development must be short-lived in order to establish an appropriately limited time frame for each developmental stage. This inherent instability in the natural host-parasite interaction environment may account for some of the difficulty in characterizing and identifying these signal molecules. Moreover, unstable signals with short lifetimes in soil are not attractive targets for synthesis for application to soil to disrupt parasite-host development (for example, to induce suicidal germination).

Modes of Signal Transmission

Germination and haustorial initiation signals are necessarily transmitted through the soil. Subsequent signals are apparently transmitted through vascular connections. The mechanism of action of these signals is essentially unknown be-

yond the observation that germination stimulants turn on ethylene production (Babiker et al., 1993), and the haustorial initiator shifts the dimension of cell expansion and initiates cell division and differentiation (Riopel and Timko, 1992).

Metabolic Inputs from the Host and Their Metabolic Cost

Striga is completely dependent upon its host for water and minerals, having no roots of its own. *Striga* damage to the host is most severe under drought and low fertility conditions, in which the host plant is under stress (Boukar et al., 1996). *Striga* does not close its stomata unless water deprivation is severe (Press and Stewart, 1987)

Although *Striga* is photosynthetic, it is partially heterotrophic, with the proportion of host-derived carbon varying between 5% and 35% (Cechin and Press, 1993a). *Striga* infestation inhibits host photosynthesis up to 40% in laboratory studies (Smith et al., 1995) and to a similar extent in field studies (Gurney et al., 1995). It has been suggested that the capacity to maintain normal rates of photosynthesis when infected may be an important correlate of host tolerance to *Striga* (Cechin and Press, 1993a).

The loss in host productivity associated with *Striga* parasitism is greater than can be accounted for by loss of host metabolic resources to the parasite (Press and Stewart, 1987). This pathological effect may be due to the *Striga*-induced inhibition of host photosynthesis (Graves et al., 1990) and/or to disruption of host hormonal balance. Drennan and El-Hiweris (1979) reported drastic reductions in cytokinins and gibberellins and an appreciable increase in abscic acid and farnesol in the xylem sap of *S. hermonthica*-infested sorghum.

Striga-host relationships are strongly influenced by availability of nitrogen to the host, with increased levels of nitrogen fertilizer usually resulting in decreased levels of *Striga* infestation (Sherif and Parker, 1986). The chemical form of the nitrogen transferred from the host to *Striga* has not been reported. It may differ with the level and source of nitrogen available to the host.

Host Defenses Against *Striga*

Hosts such as sorghum and millet that have co-evolved with *Striga* are more likely to have developed effective defenses than hosts such as maize that were introduced relatively recently into *Striga*-endemic areas.

Avoidance

Some sorghum genotypes minimize *Striga* infestation by avoidance, either distributing their roots unusually deep away from *Striga* seeds, which mainly occur in the upper 10 cm of soil (Cherif-Ari et al., 1990; Olivier and Leroux, 1992), or by producing such low levels of germination stimulant that relatively few *Striga* seeds germinate.

It has been suggested that low stimulant production is of limited utility in protecting host crops against *Striga*, possibly due to wide availability of stimulant from other plant sources. But if this were the case, there would be no coordination of *Striga* germination with the presence of a

suitable host. Under these conditions, timely germination of *Striga* seeds appropriately positioned near a host root so that attachment could occur would be rare, and almost all *Striga* seeds germinated would simply die. This would result in rapid depletion of the *Striga* seed population in the soil, contrary to the observed longevity of *Striga* infestations (Doggett, 1988). Presumably most *Striga* germination is in response to host-produced germination stimulant.

Resistance

We define host resistance to *Striga* as a crop genotype which supports significantly fewer *Striga* plants and has a higher yield than susceptible genotypes grown under the same infested conditions (Ejeta et al., 1992). Among the cereals, resistant genotypes have been identified mainly in sorghum; some of these are also low stimulant producers (Weerasuriya, 1995).

Two mechanisms of resistance have been proposed. Mechanical protection by enhanced lignification or suberization of host root tissue was reported by Maiti et al. (1984). Alternatively, resistance due to metabolic chemical protection (e.g., antibiosis) has been reported for cowpeas resistant to *Striga gesneroides* (Lane et al., 1993) and in wild sorghum (*S. versicolor*) resistant to *S. hermonthica* (Lane et al., 1994). *Striga* attachment to, or subsequent development on, cowpea roots may be delayed, or may result in necrosis and death of the attached *Striga* plantlets (Lane et al., 1993). Slow development of *S. hermonthica* tubercules on roots of a Kenyan accession of *S. arundinaceum* was reported (Lane et al., 1994). In addition, most parasite seedlings attached to the roots of *Sorghum versicolor* accessions died following penetration. Those that survived exhibited slowed development (Lane et al., 1994). The metabolic/chemical basis for this resistance has not been elucidated. An association of high levels of phenolic acids with host resistance in sorghum has been reported (El Hiweris, 1987), but could not be confirmed in our laboratory.

Phytoalexins are an important resistance factor to *Orbanche* spp. in both sunflower (resistance in cv. 81-14 to *O. cumana*) and chickpea (resistance in cv. ILC 280 to *O. crenata*) (Wegmann et al., 1991). Phytoalexins are low molecular weight secondary metabolites, synthesized after pathogen attack, that serve in plant self-defense. However, at present no evidence of their involvement in host resistance to *Striga* has been reported.

Tolerance

Tolerant crop genotypes support as many *Striga* plants as do susceptible genotypes, without a concomittant reduction in productivity (Ejeta et al., 1992). In contrast to resistant genotypes, production of tolerant genotypes increases the number of *Striga* seeds in the soil. Tolerance is therefore a less desirable trait than resistance.

In maize, several tolerant genotypes have been reported (Kim, 1994) but resistant maizes have been more difficult to identify. At IITA, sources of resistance to *Striga* were identified in some African landraces and the wild relative, *Zea diploperennis*. Introgression into improved genetic backgrounds is underway.

The physiological basis for tolerance to *Striga* is not known. It is possible that tolerant crop genotypes are able to sequester their nutrients more successfully against loss to *Striga* than susceptible genotypes, but this explanation seems inadequate because metabolite loss to *Striga* cannot account for the loss of productivity of *Striga*-infested hosts (Press and Stewart, 1987). It seems more likely that *Striga*-derived materials such as inhibitors of host photosynthesis are less toxic to tolerant crop genotypes than to susceptible genotypes.

Host-Parasite Incompatibility

One of the most puzzling aspects of the *Striga*-host relationship is the apparent compatibility of host and parasite. The dicotlyedenous parasite differs so greatly from its monocotyledenous cereal host with respect to morphology, development, and metabolism that it is difficult to accept, much less understand, how the completely host-dependent parasitism is maintained and perpetuated. In susceptible hosts, discrimination between self and non-self must be circumvented somehow so the parasite is not rejected. One would not expect grafting between *Striga* and cereal hosts to be successful (perhaps it would be useful to investigate this possibility), but normal establishment and propagation of *Striga* on host roots would appear to be functionally equivalent to a graft. Proposed studies on hosts vs. non-hosts may eventually lead to a satisfactory resolution of these problems.

It has been suggested (Graves et al., 1989), that although the major flow of 14C labeled metabolites is from host to *Striga* (Rogers and Nelson, 1962), a *Striga*-derived "toxin" might account for the major loss in productivity of *Striga*-infected hosts not accounted for by competition for metabolic resources. We have shown that materials quite toxic to *Striga* hosts can be extracted from *Striga* plants (Bell-Lelong et al., 1994). Depending on how the materials are applied to host seedlings, symptoms include wilting, leaf curling and chlorosis, resembling effects of *Striga* infestation in the field. Although *Striga* extracts are rich in phenolic compounds, the toxic material does not purify with any of the major phenolics. Two toxic components of *Striga* extract have been purified but not yet identified. It is not yet clear to what extent these toxic materials are unique to *Striga* or other parasitic plants.

We are not aware of any necessity or benefit for *Striga* to negatively affect its hosts beyond the sharing of host metabolites, moisture and minerals. In fact, it would seem to be in the best interest of *Striga* to have a fully productive host. We can therefore only speculate on the possible role of the *Striga* toxin. The toxin might modify host metabolism to stimulate production of metabolites required by *Striga*, or it might limit host leaf development to permit better access of *Striga* to sunlight. The sorgoleones are powerful inhibitors of photosynthetic electron transport (Nimbal et al., 1996); induction or introduction of this type of compound in photosynthetic tissue as a consequence of *Striga* infestation might account for the observed *Striga*-induced reduction in photosynthesis (Graves et al., 1990). Alternatively, the so-called toxin could be a normal *Striga* metabolite, somehow incompatible with host metabolism, toxic because of accessibility to the host by

Babiker, A.G.T., T. Cai, G. Ejeta, L.G. Butler, and W.R. Woodson. 1994. Enhancement of ethylene biosynthesis and germination with thidiazuron and some selected auxins in *Striga asiatica* seeds. Physiol. Plantarum 91:529-36.

Baird, W.V., and J.L. Riopel. 1985. Surface characteristics of root and haustorial hairs of parasitic Scrophulariaceae. Bot. Gazette 146:63-9.

Bell-Lelong, D., G. Ejeta, D. Hess, and L.G. Butler. 1994. Do phenolics from the parasitic weed *Striga* inhibit host growth? Acta Hort. 381:683-686.

Bharathalakshmi, J., C.R. Werth, and L.J. Musselman. 1990. A study of genetic diversity among host-specific populations of the witchweed *Striga hermonthica* in Africa. Pl. Sys. Evol. 172:1-12.

Boukar. I., D.E. Hess, and W.A. Payne. 1996. Dynamics of moisture, nitrogen, and *Striga* infestation on pearl millet transpiration and growth. Agronomy J. 88:545-549.

Butler, L.G. 1995. Chemical communication between the parasitic weed *Striga* and its crop host. p. 158-168. *In* Inderjit, K.M.M. Dakshini, and F.A. Einhellig (eds.) Allelopathy: Organisms, processes and applications, ACS Symposium Series #582, Washington, American Chemical Society.

Cai T., A.G. Babiker, G. Ejeta, and L.G. Butler. 1993. Morphological response of witchweed (*Striga asiatica*) to *in vitro* culture. J. Exp. Botany 44:1377-84.

Cechin, I., and M.C. Press. 1993a. Nitrogen relations of the sorghum-*Striga hermonthica* host-parasite association: Growth and photosynthesis. Plant, Cell and Environment 16:237-47.

Cechin, I., and M.C. Press. 1993b. Nitrogen relations of the sorghum-*Striga hermonthica* host-parasite association: Germination, attachment and early growth. New Phytol. 124:681-687.

Chang, M., D.H. Netzly, L.G. Butler, and D.G. Lynn. 1986. Chemical regulation of distance: Characterization of the first natural host germination stimulant for *Striga asiatica*. J. Am. Chem. Soc. 108:7858-60.

Cherif-Ari, O., T.L. Housley, and G. Ejeta. 1990. Sorghum root length density and the potential for avoiding *Striga* parasitism. Plant Soil 121:67-72.

Cook, C.E., L.P. Whichard, B. Turner, M.E. Wall, and G.H. Egley. 1966. Germination of witchweed (*S. lutea Lour.*): Isolation and properties of a potent stimulant. Science 154:1189-90.

Doggett, H. 1988. Coordination of *Striga* research. p. 126-33. *In* S.K. Kim (ed.) Combatting *Striga* in Africa. Proceedings, International Workshop Organized by IITA, ICRISAT and IDRC, Ibadan, Nigeria, 1991.

Drennan, D.S.H., and S.O. El-Hiweris. 1979. Changes in growth substances in *Sorghum vulgare* infected by *Striga hermonthica*. p. 144-55. *In* L.J. Musselman, A.D. Worsham, and R.E. Eplee (eds.) Proceedings second international symposium on parasitic weeds, Raleigh, North Carolina State University, Raleigh.

Ejeta, G., L.G. Butler, and A.G.T. Babiker. 1992. New approaches to the control of *Striga*. *Striga* research at Purdue University. Bulletin RB-991, Ag. Res. Station, Purdue University.

El Hiweris, S.O. 1987. Nature of resistance to *Striga hermonthica* (Del.) Benth. parasitism in some sorghum cultivars. Weed Research 27:305-11.

Freitag, J., D.E. Hess, H.G. Welz, and H.H. Geiger. 1996. Pearl millet and sorghum specific races of *Striga hermonthica* in Niger. p. 472-78. *In* M.T. Moreno, J.I. Cubero, D. Berner, D. Joel, L.J. Musselman, and C. Parker (eds.) Advances in Parasitic Plants Research, Sevilla, Direccion General de Investigicion In Agraria.

Graves, J.D., M.C. Press, and G.R. Stewart. 1989. A carbon balance model of the sorghum-*Striga hermonthica* host-parasite association. Plant, Cell and Environment 12:01-07.

Graves, J.D., A. Wylde, M.C. Press, and G.R. Stewart. 1990. Growth and carbon allocation in *Pennisetum typhoides* infected with the parasitic angiosperm *Striga hermonthica*. Plant, Cell and Environment 13:367-73.

Gurney, A.L, M.C. Press, and J.K. Ransom. 1995. The parasitic angiosperm *Striga hermonthica* can reduce photosynthesis of its sorghum and maize hosts in the field. J. Exp. Botany 46:1817-23.

Hauck, C., S. Muller, and H. Schildknecht. 1992. A germination stimulant for parasitic flowering plants from *Sorghum bicolor*, a genuine host plant. J. Plant Physiol. 139:474-78.

Hess, D.E., and G. Ejeta. 1992. Inheritance of resistance to *Striga* in sorghum genotype SRN39. Plant Breeding 109:233-41.

Hess, D.E., G. Ejeta, and L.G. Butler. 1992. Selecting sorghum genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga*. Phytochemistry 31:493-97.

Kim, S.K. 1994. Genetics of maize tolerance of *Striga hermonthica*. Crop Science 34:900-07.

Lane, J.A., J.A. Bailey, R.C. Butler, and P.J. Terry. 1993. Resistance of cowpea [*Vigna unguiculata* (L.) Walp.] to *Striga gesnerioides* (Willd.) Vatke, a parasitic angiosperm. New Phytol. 1993:405-12.

Lane, J.A., T.H.M. Moore, J. Steel, R.F. Mithen, J.A. Bailey. 1994. Resistance of cowpea and sorghum germplasm to *Striga* species. p. 356-64. *In* A.H. Pieterse, J.A.C. Verkleij, and S. terBorg (eds.) Biology and management of *Oro-*

banche: Proceedings of the third international workshop on *Orobanche* and related *Striga* research, Royal Tropical Institute, Amsterdam .

Mangnus, E.M., and B. Zwanenburg. 1992. Tentative molecular mechanism for germination stimulation of *Striga* and *Orobanche* seeds by strigol and its synthetic analogs. J. Agric. Food Chem. 40:1066-70.

Maiti, R.K., K.V. Ramaiah, S.S. Bisen, and V.L. Chidley. 1984. A comparative study of the haustorial development of *Striga asiatica* (L.) Kuntze on sorghum cultivars. Annals of Botany 54:447-57.

Mohamed, A.M., M. Foley, G. Ejeta, L.G. Butler, and T.L. Housley. 1996. Moisture content and dormancy in *Striga asiatca* seeds. Weed Science. In press.

Muller, S., C. Hauck, and H. Schildknecht. 1992. Germination stimulants produced by *Vigna unguiculata* Walp cv Saunders Upright. J. Plant Growth Regul. 11:77-84.

Netzly, D.H., and L.G. Butler. 1986. Roots of sorghum exude hydrophobic droplets containing biologically active components. Crop Science 26:775-78.

Netzly, D.H., J.L. Riopel, G. Ejeta, and L.G. Butler. 1988. Germination stimulants of witchweed (*Striga asiatica*) from hydrophobic root exudate of sorghum. Weed Science 36:441-46.

Nickrent, D.L., L.J. Musselman, J.L. Riopel, R.E. Eplee. 1979. Haustorial initiation and non-host penetration in witchweed (*Striga asiatica*). Ann. Bot. 43:233-36.

Nimbal, C.I., J.F. Pedersen, C.N. Yerkes, L.A. Weston, and S.C. Weller. 1996. Phytotoxicity and distribution of sorgoleone in grain sorghum germplasm. J. Agric. Food Chem. 44:1343-1347.

Ogborn, J.E.A. 1987. *Striga* control under peasant farming conditions. p.145-158. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture, CRC Press, Boca Raton.

Okonkwo, S.N.C. 1987. Developmental studies on witchweeds. p. 63-75. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture, CRC Press, Boca Raton.

Olivier, A., and G.D. Leroux. 1992. Root development and production of a witchweed (*Striga* spp.) germination stimulant in sorghum cultivars. Weed Science 40:542-45.

Parker, C. 1983. *Striga*: Analysis of past research and summary of the problem. p. 9-16. *In* Proceedings of the second international workshop on *Striga*, 1981. IDR/ICRISAT, Ouagadougou, Upper Volta., ICRISAT, Patancheru, AP, India.

Parker, C., and C.R. Riches. 1993. Parasitic weeds of the world: Biology and control, CAB International, Wallingford UK.

Press, M.C., and G.R. Stewart. 1987. Growth and photosynthesis in *Sorghum bicolor* infected with *Striga hermonthica*. Annals Botany 60:657-62.

Reda, F., L.G. Butler, G. Ejeta and J.K. Ransome. 1994. Screening of maize genotypes for low *Striga asiatica* stimulant production using the agar gel technique.African Crop Science J. 2: 173-177.

Riches, D.R., and C. Parker. 1995. Parasitic plants as weeds. p. 226-55. *In* M.C. Press and J.D. Graves (eds.) Parasitic plants. Chapman and Hall, London.

Riopel, J.L., and W.V. Baird. 1987. Morphogenesis of the early development of primary haustoria in *Striga asiatica*. p. 107-25. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. CRC Press, Boca Raton.

Riopel, J.L., and M.P. Timko. 1992. Signals and regulation in the development of *Striga* and other parasitic angiosperms. p. 493-507. *In* D.P.S. Verma (ed.) Molecular signals in plant-microbe communications, CRC Press, Boca Raton.

Riopel, J.L., and M.P. Timko. 1995. Haustorial initiation and differentiation. p. 39-79. *In* M.C. Press and J.D. Graves (eds.) Parasitic plants. Chapman and Hall, London.

Rogers, J., and R. Nelson. 1962. Penetration and nutrition of *Striga asiatica*. Phytopathology 52:1064-70.

Sand, P.F., and J.D. Manley. 1990. The witchweed eradication program: Survey, regulatory and control. p. 141-50. *In* P.F. Sand, R.E. Eplee, and R.G. Westbrooks (eds.) Witchweed research and control in the United States. Weed Science Soc. of America, Champaign, IL.

Sargent, M.V., and S. Wangchareontrakul. 1990. The synthesis of the first natural host germination stimulant for *Striga asiatica* (witchweed). J. Chem. Soc. Perkin Trans. 1:1429-1434.

Sherif, A.M., and C. Parker. 1986. Effect of nitrogen sources and organic matter on *Sorghum bicolor* L. Moench and *Striga hermonthica* Benth. Ethiopian J. Agric. Sci. 8:19-35.

Siame, B.A., Y. Weerasuriya, K. Wood, G. Ejeta, and L.G. Butler. 1993. Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. J. Agric. Food Chem. 41:1486-91.

Smith, L.H., A.J. Keys, and M.C.W. Evans. 1995. *Striga hermonthica* decreases photosynthesis in *Zea mays* through effects on leaf cell structure. J. Exp. Botany 46:759-65.

Vasudeva Rao, M.J., and L.J. Mussleman. 1987. Host specificity in *Striga* spp. and physiological "strains." p. 13-25. *In* L.J. Mussleman (ed.) Parasitic weeds in agriculture. CRC Press, Boca Raton.

banche: Proceedings of the third international workshop on *Orobanche* and related *Striga* research, Royal Tropical Institute, Amsterdam .

Mangnus, E.M., and B. Zwanenburg. 1992. Tentative molecular mechanism for germination stimulation of *Striga* and *Orobanche* seeds by strigol and its synthetic analogs. J. Agric. Food Chem. 40:1066-70.

Maiti, R.K., K.V. Ramaiah, S.S. Bisen, and V.L. Chidley. 1984. A comparative study of the haustorial development of *Striga asiatica* (L.) Kuntze on sorghum cultivars. Annals of Botany 54:447-57.

Mohamed, A.M., M. Foley, G. Ejeta, L.G. Butler, and T.L. Housley. 1996. Moisture content and dormancy in *Striga asiatca* seeds. Weed Science. In press.

Muller, S., C. Hauck, and H. Schildknecht. 1992. Germination stimulants produced by *Vigna unguiculata* Walp cv Saunders Upright. J. Plant Growth Regul. 11:77-84.

Netzly, D.H., and L.G. Butler. 1986. Roots of sorghum exude hydrophobic droplets containing biologically active components. Crop Science 26:775-78.

Netzly, D.H., J.L. Riopel, G. Ejeta, and L.G. Butler. 1988. Germination stimulants of witchweed (*Striga asiatica*) from hydrophobic root exudate of sorghum. Weed Science 36:441-46.

Nickrent, D.L., L.J. Musselman, J.L. Riopel, R.E. Eplee. 1979. Haustorial initiation and non-host penetration in witchweed (*Striga asiatica*). Ann. Bot. 43:233-36.

Nimbal, C.I., J.F. Pedersen, C.N. Yerkes, L.A. Weston, and S.C. Weller. 1996. Phytotoxicity and distribution of sorgoleone in grain sorghum germplasm. J. Agric. Food Chem. 44:1343-1347.

Ogborn, J.E.A. 1987. *Striga* control under peasant farming conditions. p.145-158. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture, CRC Press, Boca Raton.

Okonkwo, S.N.C. 1987. Developmental studies on witchweeds. p. 63-75. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture, CRC Press, Boca Raton.

Olivier, A., and G.D. Leroux. 1992. Root development and production of a witchweed (*Striga* spp.) germination stimulant in sorghum cultivars. Weed Science 40:542-45.

Parker, C. 1983. *Striga*: Analysis of past research and summary of the problem. p. 9-16. *In* Proceedings of the second international workshop on *Striga*, 1981. IDR/ICRISAT, Ouagadougou, Upper Volta., ICRISAT, Patancheru, AP, India.

Parker, C., and C.R. Riches. 1993. Parasitic weeds of the world: Biology and control, CAB International, Wallingford UK.

Press, M.C., and G.R. Stewart. 1987. Growth and photosynthesis in *Sorghum bicolor* infected with *Striga hermonthica*. Annals Botany 60:657-62.

Reda, F., L.G. Butler, G. Ejeta and J.K. Ransome. 1994. Screening of maize genotypes for low *Striga asiatica* stimulant production using the agar gel technique.African Crop Science J. 2: 173-177.

Riches, D.R., and C. Parker. 1995. Parasitic plants as weeds. p. 226-55. *In* M.C. Press and J.D. Graves (eds.) Parasitic plants. Chapman and Hall, London.

Riopel, J.L., and W.V. Baird. 1987. Morphogenesis of the early development of primary haustoria in *Striga asiatica*. p. 107-25. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. CRC Press, Boca Raton.

Riopel, J.L., and M.P. Timko. 1992. Signals and regulation in the development of *Striga* and other parasitic angiosperms. p. 493-507. *In* D.P.S. Verma (ed.) Molecular signals in plant-microbe communications, CRC Press, Boca Raton.

Riopel, J.L., and M.P. Timko. 1995. Haustorial initiation and differentiation. p. 39-79. *In* M.C. Press and J.D. Graves (eds.) Parasitic plants. Chapman and Hall, London.

Rogers, J., and R. Nelson. 1962. Penetration and nutrition of *Striga asiatica*. Phytopathology 52:1064-70.

Sand, P.F., and J.D. Manley. 1990. The witchweed eradication program: Survey, regulatory and control. p. 141-50. *In* P.F. Sand, R.E. Eplee, and R.G. Westbrooks (eds.) Witchweed research and control in the United States. Weed Science Soc. of America, Champaign, IL.

Sargent, M.V., and S. Wangchareontrakul. 1990. The synthesis of the first natural host germination stimulant for *Striga asiatica* (witchweed). J. Chem. Soc. Perkin Trans. 1:1429-1434.

Sherif, A.M., and C. Parker. 1986. Effect of nitrogen sources and organic matter on *Sorghum bicolor* L. Moench and *Striga hermonthica* Benth. Ethiopian J. Agric. Sci. 8:19-35.

Siame, B.A., Y. Weerasuriya, K. Wood, G. Ejeta, and L.G. Butler. 1993. Isolation of strigol, a germination stimulant for *Striga asiatica*, from host plants. J. Agric. Food Chem. 41:1486-91.

Smith, L.H., A.J. Keys, and M.C.W. Evans. 1995. *Striga hermonthica* decreases photosynthesis in *Zea mays* through effects on leaf cell structure. J. Exp. Botany 46:759-65.

Vasudeva Rao, M.J., and L.J. Mussleman. 1987. Host specificity in *Striga* spp. and physiological "strains." p. 13-25. *In* L.J. Mussleman (ed.) Parasitic weeds in agriculture. CRC Press, Boca Raton.

Vogler, R.K., G. Ejeta, and L.G. Butler. 1996. Inheritance of low production of *Striga* germination stimulant in sorghum. Crop Science 36 (in press).

Weerasuriya, Y. 1995. Construction of a molecular linkage map, mapping of quantitative trait loci, characterization of polyphenols, and screening of genotypes for *Striga* resistance in sorghum. PhD thesis, Purdue University, 177pp.

Weerasuriya, Y., B.A. Siame, D. Hess, G. Ejeta, and L.G. Butler. 1993. Influence of conditions and genotype on the amount of *Striga* germination stimulants exuded by roots of several host crops. J. Agric. Food Chem. 41:1492-96.

Wegmann, K., E. von Elert, H-J. Harloff, and M. Stadler. 1991. Tolerance and resistance to *Orobanche*. p. 318-21. In K. Wegmann and L.J. Musselman (eds.) Proceedings, international workshop on *Orobanche* research, Obermarchtal, Germany, 1989. Eberhard-Karls-Universitaet Tuebingen, Germany.

Worsham, A.D. 1987. Germination of witchweed seeds. p. 45-61. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. CRC Press, Boca Raton.

Breeding for *Striga* Resistance in Sorghum

Gebisa Ejeta*, L.G. Butler, D.E. Hess,
Tunde Obilana, and B.V. Reddy.

Abstract

Genetic variation for resistance to Striga, *though limited, is available in sorghum germplasm, making host plant resistance a feasible control measure. The conventional approach to selection for resistance to* Striga *has involved evaluation of sorghum germplasm in* Striga*-infested plots. This approach has not been widely successful owing to the complexity of the biology of the host-parasite relationship and its interaction with other environmental factors. Future approaches to breeding for* Striga *resistance will need to be based on a better understanding of the basic host-parasite biology and selection for host genotypes that lack an essential signal(s) for successful parasitism. A mix of conventional and non-conventional approaches may have to be employed in the future in breaking down* Striga *resistance into simpler components that can be exploited for developing crop genotypes with durable resistance. This paper outlines the state of the art in host plant resistance to* Striga, *assesses some of the accomplishments to date, and suggests feasible approaches for future efforts in breeding* Striga*-resistant sorghum cultivars.*

Striga spp. are obligate parasitic weeds of significant economic importance. They parasitize many important food crops in much of Africa and Asia but are particularly severe on sorghum [*Sorghum bicolor* (L.) Moench], pearl millet (*Pennisetum glaucum* L.), maize *(Zea mays* L.), and cowpea [*Vigna unguiculata* (L.) Walp]. *Striga* may have become one of the greatest biological constraints to food production in these parts of the world, probably a more serious agricultural problem than insects, birds, or plant diseases (Ejeta and Butler, 1993). Yield losses from damage by *Striga* are often very significant, the range of estimates varying from 10-70% depending on crop cultivar and degree of infestation (Doggett, 1988). Crop losses due to *Striga* infestation are often higher in Africa than in India. Annual cereal grain losses in Africa from damage by *Striga* have been estimated at about 40% (Lagoke et al., 1991). In many places in Africa, the *Striga* problem has reached epidemic proportions, presenting a rather desperate situation to small subsistence agriculture in these regions.

Striga is a member of the Scrophulariaceae family. The genus *Striga*, although parasitic, produces normal green leaves with brightly colored (pink, red, white or purple) flowers. Botanically, it is characterized by opposite leaves, irregular flowers with a corolla divided into a

Gebisa Ejeta, L.G. Butler and D.E. Hess, Purdue University, Departments of Agronomy and Biochemistry, West Lafayette, IN 47907-1150, U.S.; Tunde Obilana and B.V. Reddy, ICRISAT, Patancheru, Andhra Pradesh 502 324, India.. *Corresponding author.

tube and spreading lobes, herbaceous habit, small seeds, and parasitism (Musselman, 1987). *Striga* seeds are very small, some 0.30 mm long and 0.15 mm wide. Depending on the species and the environmental conditions for plant development, each *Striga* plant may produce 40,000 to 90,000 seeds.

Striga seeds require after-ripening, conditioning, and stimulation by chemical compounds exuded by hosts and pseudo-hosts before they can germinate to successfully parasitize a host plant (Doggett, 1988; Patterson, 1987). The organ of parasitism, the haustorium, also is produced in response to yet another chemical signal produced by host roots (Edwards, 1979; Okonkwo, 1966; Lynn and Chang, 1990). The haustorium provides *Striga* seedlings with an attachment mechanism to the host roots, thereby forming a morphological and physiological bridge between them. Numerous *Striga* plants may penetrate and attach to a single individual host plant, thereby dictating degree of infestation and extent of crop damage.

Striga is native to the grasslands of the Old World tropics, reaching its greatest diversity in sub-Saharan Africa. The genus *Striga* includes 50-60 species, all of which are said to be parasitic (Patterson, 1987). However, three obligate parasitic species are recognized as the most economically important because of their impact as yield reducers. The species affecting cereal crops, *Striga hermonthica* (Del.) Benth., *Striga asiatica* (L.) Kuntze, and *Striga forbesi* are found in both Africa and Asia. *Striga gesneroides* (Wild.) Vatke is deleterious to cowpeas and tobacco, also in both Africa and Asia. *Striga hermonthica* is an obligate outcrosser, whereas the other three species are highly self-pollinating (Musselman and Hepper, 1986).

Striga was first recognized as an important weed early in the turn of the century, first in India (Barber, 1904) and soon after in South Africa (Burtt-Davy, 1905). Experimental work on methods to alleviate the *Striga* problem have been underway for several decades, resulting in several potential control measures (Burtt-Davy, 1905). However, many of these methods, including the use of chemical herbicides, nitrogen fertilization, and soil fumigation, have been costly and beyond the range of conventional methods available to poor subsistence farmers. Eradication of *Striga* may not be a feasible goal because of the unique adaptation of *Striga* to its environment, the complexity of the biological relationships between the parasite and its hosts, and the influence of external factors on this relationship.

Given sufficient resources, however, control of *Striga* species is possible with innovative and integrated farming practices. Combining several approaches may be necessary. Cultural practices that conserve soil moisture and nutrients have been known to lessen the vulnerability of host plants to *Striga*. Chemical inputs specifically directed to weaknesses of *Striga* may prove to be effective and feasible for African farmers. Host plant resistance is the most practical and economically feasible means for reducing crop losses to *Striga* and is central to an integrated control approach.

Definition of Terms

Ejeta et al. (1991) defined *Striga resistance* as the capacity of a host plant to support fewer emerged *Striga* plants and to yield more grain than a susceptible crop

plant grown under similar infestation. In contrast, *susceptible* genotypes support a large number of *Striga* plants and show proportional and significant reductions in yield and overall performance. *Tolerant* genotypes are those which may germinate and support as many *Striga* plants as do susceptible genotypes, without showing a concomitant reduction in grain production or overall plant productivity. A host genotype that is totally free of *Striga* when grown under infested conditions would be termed *immune*.

Specificity of Resistance

The genus *Striga* is parasitic to a wide diversity of plant species. The host range of the four economically important species is also broad. Among the Poaceae, sorghum, millet, maize, rice (*Oryza sativa*), and sugarcane (*Saccharum spp.*) are often heavily affected. *S. gesneroides* parasitizes dicot species, primarily cowpea, tobacco (*Nicotiana tabacum*), and sweet potato (*Ipomoea batatas*). Host specificity is thought to be based on satisfying the requirements for germination, attachment, penetration, and the overall nutritional requirements of the parasite. *Striga* also may depend on host plants for its supply of essential compounds such as hormones (kinetin, IAA), in addition to water and minerals, although *in vitro* studies have shown that *Striga* spp. may vary in these requirements. Exogenous compounds may be essential in some parasitic species and not in others.

Gene Action in *Striga* Resistance

An understanding of gene action associated with both resistance in host plants and virulence in the parasite is essential for successful development and deployment of host plant resistance as a feasible measure of *Striga* control. Published reports on the genetics of host plant resistance to *Striga*, however, have been limited. Several reasons are cited for this lack of genetic information on *Striga* resistance (Ejeta et al., 1991). The lack of an effective and reliable germplasm screening technique and the overall paucity of germplasm with strong levels of *Striga* resistance are major hindrances to establishment of a clear mode of inheritance. Because field evaluation of crop germplasm for *Striga* resistance in artificially or naturally infested experimental plots tends to be cumbersome and unreliable and confounds several factors, it is inefficient. Genetic differences for resistance among host genotypes, in either initial screening of raw germplasm or separation of segregating populations in deliberate crosses, also may be obscured by apparent diversity and changing population of the parasite. The performance of some host cultivars tends to vary with geographical area of testing, perhaps because of strain variability. This is a particularly important constraint in the more obligate outcrossing species of *Striga*.

Host Plant Resistance

Results of inheritance studies based on field evaluation of *Striga* resistance have been somewhat inconsistent. An early report by Saunders (1993) suggested that resistance to *Striga asiatica* in sorghum was recessive in two crosses and partially dominant in a third. Both additive and non-additive gene action were found to be responsible for resistance, with additive components being more predominant. Kulkarni and Shinde (1985) found field

tolerance to *Striga asiatica* to be governed by non-additive gene action. Obilana (1984), defining resistance as "low total number of *Striga* per sorghum plant," reported gene action to be non-additive with over-dominance of susceptibility; he estimated that two to five genes controlled resistance to *Striga hermonthica* in sorghum. Ramaiah (1987) reported that in three out of five sorghum parents studied, susceptibility was dominant over resistance; in one parent, resistance was dominant; and in the other parent resistance was partially dominant. Hess and Ejeta (1992), using a pot study, established that in an elite source of genotype (SRN39), *Striga* resistance was inherited as a recessive trait controlled by one or two genes.

A simple genetic control for *Striga* resistance in sorghum emerged as specific components of resistance were investigated. One of these mechanisms is low production by host roots of compounds that *Striga* seeds require for germination. Methods for separating genotypes on their level of production of germination stimulants have been developed (Parker et al., 1977; Hess et al., 1992). Using these methods, qualitative inheritance of *Striga* resistance in certain genotypes was clearly demonstrated (Ramaiah et al., 1990; Vogler et al., 1996). Similarly, as simple screening methods that can be conducted under controlled conditions are developed for other mechanisms of resistance, it is expected that clear genetic information about *Striga* resistance will likely emerge (Ejeta et al., 1991). The development of new simple assays will facilitate further genetic analysis through both conventional Mendelian genetics as well as molecular marker studies. Such information will be invaluable to breeding efforts in the development of host plant resistance to *Striga* in sorghum and other major crops.

Genetics of Striga *Virulence*

In addition to more complete genetic information on host genotypes, effective exploitation of host plant resistance may require good knowledge of the nature of genetic variation in the parasite population and its interaction with host genotypes. Unfortunately, however, genetic information on *Striga* populations is generally lacking. Yet in an obligate outcrossing species such as *Striga hermonthica*, increased virulence in the parasite can be associated with inherent phenotypic changes in the parasite population. Hence a more definitive study on host-parasite genetic interaction would require testing of a host genotype against a specific strain of *Striga*. Pure genetic stocks of "strains" of *Striga hermonthica* have not been developed by research scientists, and they are not likely to exist in nature. Development of pure stocks of *Striga* populations would require inbreeding through selfing or sib mating for several generations of *Striga* populations, each maintained on a specific and uniform host genotype. Strains developed through such a procedure could then be tested against an array of host differentials, which can then distinguish the *Striga* strains. Host differentials and pure *Striga* strains, once developed, could be used to characterize new sources of *Striga* and host variants and more definitively classify genes for *Striga* resistance. Such a catalog of virulence genes or a definition of gene-to-gene resistance in *Striga* can greatly facilitate sequential release of individual genes as well as pyramiding of multiple resistance

genes for a more efficient management of host plant resistance to *Striga* in sorghum as well as in other crops.

Mechanisms of Resistance

Striga resistance in sorghum results from one or a combination of several recognized mechanisms that influence the development of parasitism (Ejeta et al., 1991). These can be generally classified into four categories:

1. Production of Few or No Chemical Signals Required for Eliciting Germination and/or Haustorial Formation in Striga

One of the better characterized mechanisms of resistance against *Striga* is the host root's low production of chemical compounds that *Striga* seeds require as stimulants for germination (Worsham, 1987). Stimulation of *Striga* seeds to germinate initiates the potential relationship between the host and the parasite and hence provides the first opportunity for resistance to *Striga* infestation. Host plants that produce low amounts of stimulants will cause fewer *Striga* seeds to germinate and thus will be subject to less severe attack. The production of germination stimulants is relatively simple to assay. Extensive genetic variation exists among roots of both host and non-host plants for levels of production of chemical exudates that are effective as germination stimulants. There may have been considerable, though not deliberate, selection for stimulant production among landraces of sorghum. Weerasuriya et al (1993) reported a 10-fold difference in stimulant activity produced by two different sorghum cultivars that evolved under different environmental conditions. This variation was presumed to be responsible for the *Striga* resistance found in some sorghum cultivars (Hess et al., 1992).

Following successful germination, roots of *Striga* develop the haustorium, an organ of attachment, forming a morphological and physiological bridge between the host and parasite. The formation of haustoria also is elicited in response to yet another chemical signal produced by the host root (Edwards, 1979). Crop genotypes that produce normal levels of the germination signal but lack the signal that encourages haustorial formation should not only be resistant to *Striga* but also should deplete the *Striga* seed population in the soil by promoting suicidal germination. This hypothesis could not be tested, however, since assays for measuring amounts of the haustorial factor have not been developed, and genetic variants of sorghum for the trait have yet to be identified.

2. Chemical and Non-chemical Barriers Discouraging Attachment and Penetration

Striga also may depend on additional host factors for its further growth and development beyond attachment and penetration. Cai et al. (1993) found that *Striga asiatica* cultured *in vitro* can readily be regenerated into non-parasitic type plantlets without haustoria or development of a primarily plumule. However, regeneration into parasitic type plantlets typical of growth on host roots required other unidentified factors produced by host plants, suggesting that *Striga* depends on additional factors from its hosts for further differentiation and development.

Host and non-host crop plants also may protect themselves against parasitism through other chemical and non-chemical means that discourage attachment and penetration by *Striga* on host tissue. The host plant may produce mechanical barriers that impede invasion of cortical cells by haustoria. It has been postulated that lignified pericycle cells and endodermal cells thickened with silica deposits physically obstruct attachment of haustoria to roots of sorghum genotypes known to have good field resistance (Saunders, 1933; Maiti et al., 1984).

3. Chemical Defense (Antibiosis) Against Growth and Development of the Parasite

Crop plants also may produce chemical compounds that discourage subsequent development of a germinated *Striga* seedling. Non-host plants clearly exhibit such a mechanism of resistance, and it is plausible that host plants with a strong hypersensitive resistance mechanism also can be found, provided suitable assays are made available for the screening of appropriate germplasm. This remains to be a very promising area of research.

4. Avoidance Mechanisms

Host plants with diminished root volume and root length density in the upper soil profile, where much of the *Striga* inoculum is found, have been implicated as having an avoidance mechanism of resistance (Dixon and Parker, 1984; Cherif et al., 1990). Research in this area, while promising, could not advance because of difficulties assessing and measuring roots under laboratory or field conditions.

Breeding Methods and Strategies

Advances in the development of selection methods and strategies for improving sorghum for *Striga* resistance have been hampered partly as a result of limited research in elucidating the genetics and/or the specific mechanisms associated with expression of resistance against parasitic weeds. As we understand host-parasite interactions better, develop appropriate assays, and characterize our crop germplasm properly, we should be able to employ, with minor modification, breeding methods that have been used effectively for other traits (Ejeta and Butler, 1993). Characterization of source germplasm, development of simple and efficient screening techniques, and a well-planned selection strategy for yield and other traits of importance in subsistence agriculture are the bare essentials for embarking on breeding for *Striga* resistance. We describe below research efforts and investments that have been placed on each of these essential areas during the last several decades.

Source Germplasm

Since Saunders (1933) first reported his ground-breaking work on *Striga lutea* (Lour), considerable gains have been made in understanding *Striga* parasitism. Some of these efforts included identification and characterization of source germplasm in major crops of the semi-arid tropics, including sorghum. There appears to be an overall paucity of genes for *Striga* resistance in these crops, as suggested in our earlier report (Ejeta et al., 1991). It is indeed astonishing that, in contrast to the extent and spread of the *Striga* problem and the opportunities for natural and deliberate selection in environments where the host and the parasite

have co-evolved, there has been a lower level of genetic variability for *Striga* resistance in these crops.

It is quite probable, however, considering the apparent complexity of the trait and the strong genotype × environment interaction associated with inheritance of field *Striga* resistance, selection efforts (particularly natural selection forces) may have favored tolerance to resistance since stability of performance often is the criterion for selection in subsistence agriculture. However, though very rare, *Striga*-resistant genotypes have been found among African sorghum landraces. The preponderance of tolerant genotypes among African landraces may not be noticed until one examines sorghum germplasm that evolved in *Striga*-free environments. Chinese kaoliangs are the only known sorghum types that evolved in the northern hemisphere where *Striga* has not been endemic. Invariably, kaoliangs are highly susceptible to *Striga*, presumably because they have not been selected against *Striga* infestation in their area of adaptation. As a breeding objective, however, development of tolerant genotypes may have limited value since the use of tolerant genotypes will continue the build-up of the *Striga* seed inoculum in the soil. A number of sorghum genotypes have been found to possess resistance or tolerance to *Striga* in different parts of the world. The following genotypes have been extensively evaluated with mixed results: IS9830, IS3167(Framida), IS8577(Dobbs), IS7777, SRN39, Tetron, P967083, and 555.

Screening Techniques

Successful breeding efforts require efficient methods for separating among genotypes. Highly heritable traits with easily recognizable phenotypes are often easily selected, and responses to selection for such traits have been excellent. In contrast, evaluation of host plant resistance to *Striga* under field conditions has been slow and inefficient, and assessment of inheritance for *Striga* resistance in the field has been inconsistent. Screening a large number of genotypes in *Striga*-infested fields also has been difficult due to the complex interactions among host, parasite, and an array of environmental factors that affect the establishment of the parasite as well as the response of the host (Ejeta and Butler, 1993). As a result, selection efforts in breeding sorghum varieties with *Striga* resistance, strictly based on field evaluation of variants, have not been very successful.

Field *Striga* infestation is rarely (if ever) uniform. Even when the *Striga* seed inoculum in the soil is high, the seed age and moisture level could be different, possibly responding differentially to the stimuli required for germination and the subsequent initiation and development of the haustoria. A number of field screening techniques, ranging from developing a *Striga* sick plot (artificially infesting experimental plots with the same batch of *Striga* seeds) to a more structured experimental layout and statistically powerful designs (Rao, 1985), have been suggested to improve the reliability of field screening for *Striga* resistance. These improvements in field plot techniques have greatly facilitated multilocation testing of finished varieties. However, in evaluating *Striga* resistance in a large number of genotypes or a breeding nursery with segregating progeny rows, it has been difficult to determine with any certainty which of the segregating plants is infested or free from *Striga*. Development of simple, ac-

curate, and rapid laboratory procedures that can predict field resistance to *Striga* on a per plant basis is crucial to a *Striga* resistance breeding program. Although several such procedures have been attempted (Rao, 1985), only two — the double plot technique (Parker et al., 1977) and the agar gel assay (Hess et al., 1992) — have proven useful for screening a large number of breeding progenies with reliable results. When informative laboratory procedures such as these are made available, germplasm is properly characterized, genetic information is clearly presented, and selection for useful variants is easily implemented. In this regard, a powerful screening procedure is an indispensable tool to a plant breeding program.

Selection for Yield, Adaptation, and Grain Quality

Not unlike many other pest and disease resistance genes, the factors responsible for *Striga* resistance also have been found in landraces that often have several agronomic weaknesses that need to be fixed through further breeding. Most source germplasm for *Striga* resistance has been poor-yielding, photoperiod-sensitive, tall in height, late in maturity, limited in adaptation range, and often lacking in evident grain quality. As a result, a deliberate breeding effort to combine these essential agronomic attributes with *Striga* resistance often is required. Many of these agronomic traits can be selected for under field conditions in a conventional breeding program, but the process of incorporating genes for *Striga* resistance will require supplemental assays.

ICRISAT (1983) reported the development of new sorghum lines through such an effort, providing the first group of improved *Striga*-resistant cultivars resulting from a deliberate breeding effort. Although these improved lines (SAR1 through SAR34) possess good evident grain quality, they have limited yield potential. More significantly, selection of these lines was undertaken for *Striga asiatica* in India, and the resistance of many of these lines did not hold up when exposed to the more virulent *Striga hermonthica*. Many of the lines had poor adaptation under African conditions.

The recent release by Purdue University (Ejeta, 1995) of eight *Striga*-resistant sorghum cultivars (P9401 through P9408) that combine *Striga* resistance with high yield potential, grain quality, leaf disease resistance, and broad adaptation made for a significant breakthrough in *Striga* research on sorghum. The breeding effort resulting in the improved sorghum cultivars combined the use of laboratory procedure (agar gel assay) with multilocation field testing in the United States, as well as in a number of African counties. Because of their high yield and excellent broad adaptation, these lines could be grown even in *Striga*-free environments without any comparative yield loss. Seeds of these cultivars were multiplied and distributed for commercial cultivation in *Striga*-endemic areas of ten African countries in 1995. World Vision, a Christian non-governmental organization, has since expanded the demonstration and diffusion of these cultivars to more farm communities in these countries.

Breeding Methods

Once a source germplasm is identified and a suitable assay is developed, incorporation of *Striga* resistance into improved genetic backgrounds becomes a

routine plant breeding procedure. Although a number of alternative breeding methods could be utilized, the following breeding methods have been suggested as the most promising and likely to yield good results (Ejeta et al., 1991):

Early generation testing. Pedigree breeding is the most commonly employed plant breeding method in most field crop improvement programs. Complementary traits from two or more parents are combined into one genetic background through genetic recombination acted upon by artificial selection. This breeding method allows the breeder to use his/her skills to estimate field performance from single plant behavior. An effective pedigree breeding procedure in selecting for *Striga* resistance requires the availability of a non-destructive assay that can serve as a signal for the presence of the factors of resistance on a single plant basis. The alternative is to select early generation breeding progenies for agronomic and grain quality traits and defer selection for *Striga* resistance until homozygous progenies are derived after several generations of selfing. This is necessary because selecting for field *Striga* resistance in unreplicated segregating progenies on a per plant basis is rather uninformative.

F_1 hybrids. To date the use of F_1 hybrids of sorghum has been limited to countries where agriculture is fairly well developed and there is a functional seed industry for production and regular distribution of reliable good quality seed. In many of these countries, *Striga* is not endemic. As a result, the elite sorghum germplasm pool shared by the international research community for development of parental lines for hybrids does not contain genes for *Striga* resistance. Efforts have been underway both at ICRISAT and Purdue University to incorporate genes for *Striga* resistance into seed parents of experimental hybrids. We believe grain sorghum and maize hybrids that combine yield potential, adaptation, and grain quality with a good level of *Striga* resistance will make a significant contribution to sorghum agriculture in the *Striga*-endemic semi-arid tropics (Ejeta and Butler, 1993).

Recurrent selection schemes. A population improvement approach using a cyclical selection scheme in a carefully synthesized random mating population should be appropriate to concentrate genes for *Striga* resistance from several sources into one common background. Unfortunately, not much effort has been made to use population improvement for *Striga* resistance in sorghum. A random mating sorghum population has been developed at Purdue University (Ejeta and Butler, 1993). Unfortunately, applied plant breeders practicing in *Striga*-endemic areas have not shown overwhelming interest in its use. However, if such a population can be run through repeated cycles of selection and random mating at an experimental site with *Striga* infestation, elite progenies can be drawn that may possess a more broad-based, horizontal resistance to *Striga*. Effort is required to produce empirical evidence for such a hypothesis, however.

Marker-assisted backcrossing. The advent of molecular marker technology has introduced a powerful approach to learning the genetic basis of trait expression in crop plants. Growing evidence indicates that molecular markers also would be useful for manipulating complex traits that have been rather difficult to handle through phenotypic selection. *Striga* re-

sistance is one such trait. Field resistance to *Striga* in some backgrounds has been shown to be quantitatively inherited. Use of molecular marker technologies has demonstrated that the phenotypic variability of quantitatively inherited complex traits can be accounted for by relatively few quantitative trait loci (Tanksley, 1993; Edwards et al., 1987; Patterson et al., 1988). Markers are being used in many agronomic crops to elucidate the genetic basis of inheritance and to enhance the efficiency of selection of economically important traits (Tanksley et al., 1996). Efforts also are underway in a number of programs to develop an exhaustive linkage map of sorghum and to identify molecular markers associated with quantitative trait loci (QTLs) involved in the inheritance of complex traits, including resistance to *Striga*.

Research efforts at Purdue University in the United States and at University of Honeheim, Germany, have been targeting the identification and eventual exploitation of QTLs associated with *Striga* resistance. Once identified, these markers will need to be tested for their power of detection across different genetic populations and environmental conditions, before being used as markers in backcross breeding. Alternatively, advanced backcross QTL analysis (AB-QTL), using the same backcross populations for both mapping and selection, has been proposed as a more efficient approach for marker-assisted selection (Tanksley and Nelson, 1996). Using the AB-QTL approach, markers linked to an important QTL such as *Striga* resistance can be used to identify genotypes in the same mapping populations that contain the favorable introgressed chromosomal segment. These lines can subsequently be backcrossed to the agronomically elite recurrent parent.

Current and Future Approaches

In general, conventional approaches to the control of *Striga* have not been very successful. A mix of control strategies that exploit the basic biological relationships between *Striga* and its hosts needs to be developed. Host plant resistance is central to an effective *Striga* control strategy. However, as has been stated earlier, phenotypic selection for *Striga* resistance under field conditions has been slow and inefficient. Because of the complex nature of the *Striga* problem, efforts in *Striga* resistance breeding need to be methodical and based on a better understanding of the basic biology of *Striga* and its association with its hosts. Current efforts initiated along these lines and in combining an array of biotechnological approaches for the control of *Striga* (Ejeta and Butler, 1996) will need to be further advanced. Future approaches in breeding for *Striga* resistance may need to focus on the following major areas.

Dissecting Striga Resistance into Simpler Components

Field resistance to *Striga* is the eventual expression of a series of interactive relationships between *Striga* and its hosts and is therefore inherited as a quantitative trait. As a result, selection for resistance under field conditions has been slow and difficult. Successful *Striga* parasitism depends on a series of intricate inter-relationships involving exchange of vital signals produced by the host. Many of these signals are chemical compounds that, when absent or produced in low amounts, prevent establishment of parasitism. Resistance also could be due to chemical defense (antibiosis), morphological barriers, or other mechanisms conferring tolerance. Interruption of one or more of these

signals and inter-relationships between *Striga* and its host may lead to resistance.

Striga resistance, therefore, can be dissected into simpler components through better understanding of the basic host-parasite biology. Characterization of the vital signals exchanged between host and parasite could lead to development of an appropriate assay that can separate resistant and susceptible genotypes. Resistance based on presence or absence of a specific signal is likely to be under simple genetic control. Such an approach has several advantages. Powerful assays that detect the presence or absence of these signals could be developed. The availability of a simple assay allows routine screening of a crop germplasm which can be readily catalogued on the basis of a specific mechanism. Genetic differentials of the host can be established to help select for resistance and to monitor virulence. Conventional plant breeding as well as new techniques (e.g. molecular markers) can be used to combine more than one mechanism of resistance into one genetic background. Methodical dissection of *Striga* resistance into simpler components has been proposed by Ejeta and Butler (1993), and the basic rationale and assumptions for effective implementation of the approach have been described.

Exploiting Existing Variability

The intricate inter-relationships between *Striga* and its host described above may have resulted from co-evolution of *Striga* with host crops in the Old World. This should have led to germplasm diversity, which may remain undetected to date because of lack of suitable assays to separate sorghum genotypes on the basis of specific, simply inherited genetic variations. Until now, the best characterized mechanism of *Striga* resistance is the one based on low production of the chemical signal required for germination. Appropriate assays have been developed (Parker et al., 1997; Hess et al., 1992) and landraces of sorghum germplasm have been sufficiently screened (ICRISAT, 1978; Weerasuriya, 1994).

As appropriate assays are developed for signals required for initiation of haustoria or attachment and penetration and for hypersensitive type resistance (antibiosis), sorghum landraces need to be thoroughly screened. An invaluable source of genetic variation for *Striga* resistance could very well be available in wild and related species of sorghum. Wild sorghum has not hitherto been thoroughly evaluated for *Striga* resistance, but needs to be evaluated for exhaustive exploitation of the sorghum germplasm.

Induction of New Mutations

Availability of an appropriate assay will allow exploitation of newly derived mutations. Sorghum germplasm has been successfully improved through artificial mutation for a number of traits. It is plausible that genetic mutations for *Striga* resistance can be generated through chemical or energy mutations based on interruption of one or more of the vital signals exchanged between *Striga* and its host. If a series of assays were developed, initial effort could be directed to screening populations that previously have been mutated for other traits, before embarking on a deliberate mutation breeding effort.

Pyramiding of Striga Resistance Genes

Once appropriate assays for specific signals exchanged between *Striga* and its host are developed, germplasm properly

sorted out, and genetic differentials clearly established, genes for multiple mechanism of resistance can be incorporated into one elite genetic background using several feasible methods. *Striga* resistance resulting from a combination of such mechanisms is expected to be more durable and stable across ecological zones and across *Striga* strains than the single gene resistance sources from which they were derived. While the pyramiding of these genes can be done through conventional backcrossing, marker-assisted selection would facilitate and speed up the process of obtaining elite sorghum genotypes with multiple resistance sources. Such an approach should result in a more precise assessment of sources as well as movement of genes into an array of genetic backgrounds.

References

Barber, C.A. 1904. Diseases of Andropogon sorghum in the Madras Presidency (India). Madras Dep. Agric. Bull. 2: 273-288.

Burtt-Davy, J. 1905. Botanical notes: Witchweed. Transvaal Agric. 3:130.

Cai, T., A.G.T. Babiker, G. Ejeta, and L.G. Butler. 1993. Morphological response of witchweed (*Striga asiatica*) to *in vitro* culture. J. Exp. Botany 44:1377-1384.

Cherif-Ari, O., T.L. Housley, and G. Ejeta. 1990. Sorghum root length density and potential for avoiding parasitism. Plant and Soil 121:67.

Dixon, N.H., and C. Parker. 1984. Aspects of resistance of sorghum varieties to *Striga* species. p. 123-132. *In* Parker et al. (eds.) Proc. third international symposium on parasitic weeds. Aleppo, Syria.

Doggett, H. 1988. Sorghum (2nd ed.). John Wiley & Sons, New York, NY.

Edwards, M.D., C.W. Stuber, and J.F. Wendel. 1987. Molecular marker-facilitated investigations of quantitative trait loci in maize. I. Numbers, distribution, and types of gene action. Genetics 116:113-125.

Edwards, W.G.H. 1979. Orobanche and other plant parasite factors. p. 235-248. *In* J.B. Harborne (ed.) Phytochemical ecology. Academic Press, New York.

Ejeta, G. 1995. Development and enhancement of sorghum germplasm with sustained tolerance to drought, *Striga* and grain mold. INTSORMIL Ann. Rept. 82-87.

Ejeta, G., and L.G. Butler. 1996. Biotechnological approaches for understanding mechanisms of resistance to *Striga*. p.567-573. *In* Moreno et al. (eds.) Advances in parasitic plant research. Proc. Sixth International Parasitic Weed Symposium, 16-18 April 1996.

Ejeta, G., and L.G. Butler. 1993. Host plant resistance to *Striga*. p. 561-569. *In* D.R. Buxton et al. (eds.) 1993 international crop science I. International Crop Science Congress. Crop Science Society of America, Madison, WI.

Ejeta, G., L.G. Butler, D.E. Hess, and R.K. Vogler. 1991. Genetic and breeding strategies for *Striga* resistance in sorghum. p. 539-544. *In* Ransom et al. (eds.) Proc. fifth international symposium on parasitic weeds. Nairobi, Kenya.

Hess, D.E., and G. Ejeta. 1992. Inheritance of *Striga* resistance in sorghum genotype SRN39. Plant Breeding 109:233-241.

Hess, D.E., G. Ejeta, and L.G. Butler. 1992. Selecting sorghum genotypes expressing a quantitative biosynthetic trait that confers resistance to *Striga*. Phytochemistry 31:493-497.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1978. ICRISAT Annual Report 1977-78. Hyderabad, India.

ICRISAT (International Crops Research Institute for the Semi-Arid Tropics). 1983. ICRISAT Annual Report 1982-83. Hyderabad, India.

Kulkarni, N., and V.K. Shinde. 1985. Genetics of grain yield in sorghum under *Striga* stress. Ind. J. Genet. 45:21-24.

Lagoke, S.T., V. Parkinson, and R.M. Agunbiade. 1991. Parasitic weeds and control methods in Africa. p. 3-15. *In* S.K. Kim (ed.) Combatting *Striga* in Africa. Proc. International Workshops organized by IITA, ICRISAT and IDRC, 22-24 August 1988. IITA, Ibadan, Nigeria.

Lynn, D.G., and M. Chang. 1990. Phenolic signals in cohabitation: Implication for plant development. Ann. Rev. Plant Physiol. 41:497-526.

Maiti, R.K., K.V. Ramaiah, S.S. Bisen, and V.L. Chidley. 1984. A comparative study of the haustorial development of *S. asiatica* on sorghum cultivars. Ann. Bot. 54:447.

Musselman, L.J. 1987. Taxonomy of witchweeds. p. 3-12. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. Vol. 1. CRC Press, Boca Raton, FL., USA.

Musselman, L.J., and F.N. Hepper. 1986. The witchweeds (*Striga*, Scrophulariaceae) of the Sudan Republic. Kew. Bull. 41:205.

Obilana, A.T. 1984. Inheritance of resistance to *Striga* (*Striga hermonthica* Benth.) in sorghum. Prot. Ecol. 7:305-311.

Okonkwo, S.N.C. 1966. Studies on *Striga* senegalensis. I. In vitro culture of seedlings. Effect of various sugars and glutamine. Am. J. Bot. 53:687-693.

Parker, C., A.M. Hitchcock, and K.V. Ramaiah. 1977. The germination of *Striga* species by crop root exudates. Techniques for selecting resistant crop cultivars. Proc. 6th Asian-Pacific Weed Sci. Soc. Conf. Indiana, Indonesia 1:67.

Patterson, A.H., E.S. Lander, J.D. Hewitt, S. Peterson, S.E. Lincoln, and S.D. Tanksley. 1988. Resolution of quantitative traits into Mendelian factors by using a complete linkage map of restriction fragment length polymorphisms. Nature 335:721-726.

Patterson, D.T. 1987. Environmental factors affecting witchweeds growth and development. p. 27-41. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. Vol. 1. CRC Press, Boca Raton, FL, USA.

Ramaiah, K.V. 1987. Breeding cereal grains for resistance to witchweed. p. 227-242. *In* L.J. Musselman (ed.) Parasitic weeds in agriculture. Vol. 1. CRC Press, Boca Raton, FL, USA.

Ramaiah, K.V., V.L. Chidly, and L.R. House. 1990. Inheritance of *Striga* seed germination stimulant in sorghum. Euphytica 45:33-38.

Rao, Vasudeva M.J. 1985. Techniques for screening sorghums for resistance to *Striga*. p. 18. *In* Information Bulletin No. 20. International Crops Research Institute for the Semi-Arid Tropics, Patancheru, A.P. 502 324, India.

Saunders, A.R. 1933. Studies on phanerogamic parasitism with particular reference to *S. lutea*. S. Afr. Dept. Agric. Bull. 128.

Tanksley, S.D. 1993. Mapping polygenes. Annu. Rev. Genet. 27:205-233.

Tanksley, S.D., S. Grandillo, T.M. Fulton, D. Zamir, Y. Eshed, V. Petiard, J. Lopez, and T. Beck-Bunn. 1996. Advanced backcross QTL analysis in a cross between an elite processing line of tomato and its wild relative L. pimpinellifolium. Theor. Appl. Genet. 92:213-224.

Tanksley, S.D., and J.C. Nelson. 1996. Advanced backcross QTL analysis: A method for the simultaneous discovery and transfer of valuable QTLs from unadapted germplasm into elite breeding lines. Theor. Appl. Genet. 92:191-203.

Vogler, R.K., G. Ejeta, and L.G. Butler. 1996. Inheritance of low production of *Striga* germination stimulant in sorghum. Crop Sci. 36:1185-1191.

Weerasuriya, Y.M. 1994. The construction of a molecular linkage map, mapping of quantitative trait loci, characterization of polyphenols, and screening of genotypes for *Striga* resistance in sorghum. Ph.D. thesis. Purdue University.

Weerasuriya, Y., B. Siame, D.E. Hess, G. Ejeta, and L.G. Butler. 1993. Influence of conditions on the amount of *Striga* germination stimulants exuded by the roots of several host crops. J. Agric. Food Chem.

Worsham, A.D. 1987. Germination of witchweed seeds. p. 45-61. *In* Musselman, L.J. (ed.) Parasitic weeds in agriculture. Vol. 1. *Striga*. CRC Press, Boca Raton, FL.

Integrated Use of *Striga*-Resistant Sorghum Varieties with Cultural and Chemical Control

A. G. T. Babiker

Abstract

The complementary effect of cultural and chemical control of Striga *was evaluated on resistant and local varieties of sorghum. Emergence of the parasite was earlier and more intense on the local than on the* Striga*-resistant varieties SRN 39 and IS 9830. Early hand-pulling of* Striga *was ineffective, irrespective of crop variety. Late hand-pulling did not affect the parasite on Dabar, but good control (75%) was attained on SRN 39. Intercropping reduced* Striga *emergence, growth, and capacity to produce seeds on all crop varieties. Urea, dicamba, or their combination effected good to satisfactory control of* Striga *on resistant varieties, but performed inconsistently on the local ones. Chlorsulfuron and its tank mix with dicamba, irrespective of the preceeding urea treatment, suppressed* Striga *on all varieties. Unrestricted* Striga *parasitism reduced straw and grain yield of all varieties. SRN 39, unlike Dabar, evaded early damage by* Striga *and outyielded the local varieties, although often not significantly. Chlorsulfuron and its tank mix with dicamba, irrespective of the preceding urea treatment or crop variety, increased yield significantly. Dicamba alone did not affect yield. Dicamba, applied subsequent to urea, significantly increased yield of Gadam El Hamam (G/H), but not of SRN 39. Two* Striga *control options were identified. One, based on resistant varieties and involving use of low level inputs, is suitable for subsistence farmers with limited resources. The second option is based on use of high level inputs of local varieties with high yield potentials and is suitable for high-input farming systems.*

Witchweeds, *Striga* spp., present serious constraints to the production of major cereal crops such as sorghum [*Sorghum bicolor* (L.) Moench], pearl millet [*Pennisetum glaucum* (L.) R. Br.] and maize (*Zea mays* L.) in arid and semi-arid tropical Africa. The two most important *Striga* species on cereals are *S. hermonthica* and *S. asiatica*. About 21 million hectares of the grain-producing area in Africa are estimated to be infested, and grain production on 44 million hectares is potentially endangered (Sauerborn, 1991). Grain losses due to *Striga* damage were estimated at about 40% when averaged across the continent (Lagoke et al., 1991). Total crop failures, which are not uncommon under heavy *Striga* infestations, have in some cases resulted in relocation of villages (Doggett, 1965).

Sorghum is the most important grain crop in the Sudan. The crop is produced under three farming systems: irrigated, traditional, and mechanized. The area under the crop constitutes 74% of the total area under cereals and 45% of the total cultivated acreage. The bulk of the crop is grown mainly in the Central Clay Plains.

A.G.T. Babiker, Agricultural Research Corporation, P.O.Box 126, Wad Medani, Sudan

Over 90% of the crop is under rains and most of that is mechanized (Ejeta, 1985). Yield of sorghum is generally very low and is further reduced or threatened by *S. hermonthica* (Hamdoun and Babiker, 1988).

Traditionally *Striga* was controlled in African farming systems by prolonged crop rotation with bush fallows, trap crops, and hand-weeding. However, because of population pressure and the attendant need for food, most of these methods have gone into disuse. Available evidence indicates that the *Striga* problem has grown to be epidemic (Ejeta et al., 1993). The recent flare up and spread of the parasite are associated with low soil fertility, unreliable rainfall, and intensive monocropping of susceptible hosts (Butler, 1993).

The need to contain, control, and discourage spread of the parasite is urgent. Most of the modern control methods, which utilize herbicides and other chemical control measures, have been developed specifically for high-input advanced agricultural systems. Because of economic constraints, these control measures seem unlikly to be of use to subsistence farmers, for whom *Striga*-resistant cultivars should provide the simplest, best, and cheapest solution. However, there is always the possibility of a good resistant variety losing its resistance or not displaying resistance when considered across seasons and over locations (Parker, 1983). Therefore the most promising approach is an integrated one, comprising resistant varieties and complementary agronomic and cultural practices.

The primary objective of this study was to develop an integrated *Striga* management strategy suitable for subsistence farming systems. The investigation, which was undertaken on both irrigated and rainfed sorghum, focused on the influence of complementary agronomic practices on relative performance of two resistant varieties, SRN 39 and IS 9830, and some selected local cultivars under *Striga* infestation.

Materials and Methods

Irrigated Sorghum

A series of experiments was undertaken at the Gezira Research Station during the 1988 - 1991 seasons. Sorghum was planted in a *Striga* sick plot on ridges 80 cm apart at a within-row spacing of 15 cm. The emerged seedlings were later thinned to two plants per hill. Plots (3x7m) were arranged in randomized complete blocks with four replicates. Treatment effects were assessed by periodic count of *Striga* and by determining sorghum grain and/or straw yield at harvest. Yield data, collected from the middle two rows, were examined by the analysis of variance. Details of individual experiments are given below.

Hand-pulling

The sorghum varieties SRN 39 and Dabar were employed. Treatments were no hand-pulling and hand-pulling once at 45, 60, or 75 days after crop emergence.

Intercropping

SRN 39 and Gadam El Hamam (G/H) were used. Dolichous beans (*Lablab purpureus* L.) were planted in holes (two seeds per hole) 15 cm apart, midway between sorghum planting holes, on the same ridge as sorghum. They were then

thinned to one seedling per hole 15 days after emergence.

Fertilizers and herbicides

SRN 39 and G/H were used. Urea was applied at planting at rates of 0 and 190 kg ha^{-1}. Superimposed on the urea treatments were the herbicides chlorsulfuron (2.4 g ha^{-1}), dicamba (0.3kg ha^{-1}), and their tank mix, applied 30 days after planting as soil-directed sprays.

Rain Grown Sorghum

Experiments were undertaken at Gadaref, Umsagattah, and Tozi, traditional farming areas with medium rainfall (400-600mm), and at Simsim, a mechanized farming area with medium to high rainfall (600-800 mm). All experiments were conducted under natural *Striga* infestation.

Traditional Farming

Sorghum was planted in hills on rows 90 cm apart at a within-row spacing of 30 cm. The crop was later thinned to two plants per hill. Treatments were arranged in randomized complete blocks with four replicates. Treatment effects on *Striga* and sorghum were assessed as previously described.

Gadarif

Four sorghum varieties, SRN 39 and the local cultivars Korakolo, Abdella Mustafa (A/M), and Safra, were employed. Urea was broadcast by hand at planting at rates of 0 or 95 kg ha^{-1} Superimposed on the urea treatments was a tank mix of chlorsulfuron (2.4 g ha^{-1}) and dicamba (0.3 kg ha^{-1}), applied as a soil-directed spray four weeks after crop emergence.

Umsagattah

Sorghum varieties SRN 39, IS 9830, and Wad Akar were planted in 6x6m plots. Plots sown to Wad Akar received urea at planting at rates of 0, 95, and 190 kg ha^{-1}. Plots planted to the other cultivars did not receive urea.

Tozi

Three sorghum varieties, SRN 39, IS 9830, and Feterita Korakolo, were planted in 6x6m plots. Urea was applied at planting at rates of 0 and 95 kg ha^{-1}.

Mechanized Farming

An experiment was conducted at Simsim. The crop was sown with a press drill in rows 90 cm apart. Urea was applied before seeding at the rate of 47.6 kg ha^{-1}. Chlorsulfuron alone or in a tank mix with dicamba was applied 30 days after sowing, as a soil-directed spray, with a tractor-mounted sprayer. Plots (8x50m) were arranged in randomized blocks with four replicates. *Striga* count was undertaken in ten quadrants (1 m^2 each) selected at random in each plot. Sorghum grain yield was determined at harvest.

Results

Irrigated Sorghum

Effects on Striga

Striga population density varied with season and crop variety. In general, emer-

gence of the parasite was earlier and more intense on the local varieties than on the *Striga*-resistant varieties SRN 39 and IS 9830 (Tables 1-4). Hand-pulling, irrespective of time, did not reduce *Striga* population on Dabar. Early hand-pulling, 45 and 60 days after crop emergence, had a negligible effect on *Striga* on SRN 39. However, hand-pulling 75 days after crop emergence resulted in a low *Striga* count 15 days later (75% control) (Table 1). Intercropping reduced *Striga* shoots by 42 to 96%, *Striga* dry weight by 89 to 92%, and number of fertile capsules by 100% (Table 2).

Urea, dicamba, and their combination effected satisfactory to excellent control (62-92%) of *Striga* on SRN 39. However, on G/H, inconsistent performance was displayed. Chlorsulfuron and its tank mix with dicamba effectively controlled the parasite (77-100%) on both SRN 39 and G/H. The activity of the herbicide mixture and combinations with urea was not different from that of each of the single products (Table 3).

Effects on sorghum

Unrestricted *Striga* parasitism reduced straw yield of all varieties (Tables 1 and 4). Hand-pulling of *Striga* at 45 and 60 days after crop emergence increased straw yield of Dabar by 86% and 93%, respectively. The corresponding increases in SRN 39 yield were 44% and 67%. Hand-pulling 75 days after crop emergence was ineffective on Dabar. However, it increased SRN 39 yield by 48% (Table 1). Intercropping considerably decreased time to flowering, and increased number of heads and straw yield of the susceptible variety G/H. However, with SRN 39, only negligible effects were displayed (Table 5).

Table 1. Efficacy of hand-pulling on *Striga* on sorghum as influenced by time and crop variety.

Variety	Hand-pulling time (in days)	*Striga*[1] (plants/m^2)	Straw yield (t ha^{-1})
Dabar	Not pulled	7	1.4
Dabar	Pulled 45 DAS[2]	10	2.6
Dabar	Pulled 60 DAS	6	2.7
Dabar	Pulled 75 DAS	6	1.3
SRN-39	Not pulled	5	2.7
SRN-39	Pulled 45 DAS	4	3.9
SRN-39	Pulled 60 DAS	4	4.5
SRN-39	Pulled 75 DAS	1	4.0

[1] *Striga* count was undertaken 90 days after crop emergence.
[2] DAS = days after crop sowing

Table 2. Influence of intercropping with *I. Purpureus* on *Striga* population density, dry weight, and seed production capacity.

Treatment	*Striga* (plant/m^2)		*Striga* dry weight (g/m^2)	Fertile capsules/plant
	50 DAS[1]	120 DAS		
SRN 39	12	9	24.6	7
SRN39 + L[2]	4	1	1.8	0
G/H[3]	50	46	97.2	15
G/H + L	21	3	3.6	0

[1] DAS = days after sowing
[2] +L = + *Lablab purpureus* intercropping
[3] G/H = Gadam El Hamam

Table 3. Effect of urea and herbicide on *Striga* emergence and sorghum yield (1991).

	Striga (plants/m^2)		Grain yield (t ha^{-1})	
Sorghum	G/H[1]	SRN 39	G/H	SRN 39
Treatments	60 DAS[2]	60 DAS		
Untreated control	50	34	0.21	0.40
Urea (U)[3]	52	6	1.15	1.38
Dicamba (D)[4]	21	6	0.92	0.86
D + U	5	3	2.02	1.31
Chlorsulfuron[5]	2	0	2.05	1.73
Ch + U	2	0	3.96	2.11
Ch + D	2	0	1.99	1.45
Ch + U + D	2	0	3.86	1.94
S.E. ±			0.325	

[1]G/H = Gadam El Hamam
[2]DAS = days after sowing
[3]Urea - 190 kg ha^{-1}
[4]Dicamba - 300 g ha^{-1}
[5]Chlorsulfuron - 2.4 g ha^{-1}

Table 4. Influence of crop variety and urea on *Striga* incidence (60 DAS[1]) and sorghum growth (GRS-1988).

Treatment	*Striga* (plants/m^2)	Straw yields (t ha^{-1})
SRN-39	12	4.9
SRN-39 + U[2]	14	8.1
SRN-39 + U*[3]	8	11.6
IS 9830	26	3.3
IS 9830 + U	8	11.1
IS 9830 + U*	7	11.3
Dabar	26	1.2
Dabar + U	35	4.6
Dabar + U*	42	5.7

[1]DAS = Days after sowing
[2]U = urea at 95 kg ha^{-1}
[3]U* = urea at 190 kg ha^{-1}

Table 5. Influence of intercropping with *L. purpureus* on number of sorghum heads of *Striga*-infested irrigated sorghum (000 ha^{-1}).

	Time after planting (in days)		
Treatment	40	70	100
SRN 39	89	102	105
SRN 39 +L[1]	90	96	102
G/H[2]	2	13	27
G/H + L	43	71	71
S.E.±	6.3	8	6.3

[1]+ L *Lablab purpureus* intercropping
[2]G/H = Gadam El Hamam

Results from a detailed experiment using G/H and SRN 39 showed that unrestricted *Striga* parasitism reduced grain yield of all varieties (Table 3). Urea at 190 kg ha^{-1} effected a significant increase in yield of G/H. Chlorsulfuron, irrespective of the preceding urea treatment, increased yield significantly. Dicamba alone had a negligible effect. Dicamba preceded by urea or applied as a tank mix with chorsulfuron effected a consistent and significant increase in yield (Table 3).

Untreated and urea-treated SRN 39 outyielded the corresponding G/H treatments, albeit not significantly. Dicamba alone, and when preceded by urea, effected non-significant increases. Chlorsulfuron and its tank mix with dicamba, irrespective of the preceeding urea treatment, effected a significant increase in yield (Table 3).

Rain Grown Sorghum

Effects on Striga

Striga incidence varied with site, season, and crop variety. The resistant varie-

Table 6. Effects of urea and herbicide on *Striga* on sorghum (Gadarif, 1994).

Treatment and crop variety	*Striga* (Plant/m^2)			
	Untreated	U[1]	Ch[2]+D[3]	Ch+D+U
Korakolo	370	150	14	50
A/M[4]	217	215	52	58
Safra	248	204	58	50
SRN 39	52	26	6	15

[1]U=urea (47.6 kg ha^{-1})
[2]Ch=chlorsulfuron (2.4 g ha^{-1})
[3]D=dicama (300 g ha^{-1})
[4]A/M=Abdella Mustafa

ties, IS 9830 and SRN 39, sustained between 25% and 93% less *Striga* than the local cultivars (Tables 6-9). At Gadarif, urea at 47.6 kg ha^{-1} reduced *Striga* emergence by 20-59% on Korakolo, Safra, and SRN 39. However, it had a negligible effect on A/M. The corresponding reductions at Simsim were 17% on G/H and 42% on SRN 39 (Tables 6 and 7). At Tozi, urea at 95 kg ha^{-1} suppressed *Striga* emergence by 56%, 50%, and 25% on IS 9830, SRN 39, and Korakolo, respectively (Table 8). At Umsagattah, urea at 95 kg ha^{-1} increased *Striga* emergence on the local variety, Wad Akar, by over one fold (Table 9).

Chlorsulfuron and its tank mix with dicamba reduced *Striga* emergence by 74-96% on all varieties at both Gadarif and Simsim. Herbicide-urea combinations were as effective or slightly less effective on *Striga* as sole herbicide treatments (Tables 6 and 7).

Effects on grain yield

With a single exception, the untreated *Striga*-resistant SRN 39 and IS 9830 outyielded the local varieties (Tables 6-9). At Simsim and Tozi, no yield was realized from the untreated local varieties, Korakolo and G/H. However, the resistant varieties, SRN 39 and IS 9830, yielded 0.48 to 0.95 t ha^{-1} (Table 7 and 8). At Simsim,

Table 7. Effects of herbicide and urea on *Striga* and sorghum grain yield (Simsim, 1994)

Treatment and crop variety	*Striga* (plants/m^2)[1]	Grain yield kg ha^{-1}
G/H	300	0.00
G/H+CH[2] .4 g	30	0.95
G/H+Ch 3.57 g	30	0.95
G/H U[3]	250	0.63
G/H+U+Ch 2.4 g	60	1.48
G/H+U+Ch 3.57 g	40	1.94
SRN 39	120	0.41
SRN+Ch 2.4 g	20	0.80
SRN+Ch 3.57 g	10	0.39
SRN+U	70	0.73
SRN+U+Ch 2.4 g	20	0.85
SRN+U+Ch 3.57 g	10	0.79

[1]*Striga* count was made 70 days after sowing
[2]Ch=chlorsulfuron
[3]U=urea at 47.6 kg ha^{-1}

Table 8. Effects of crop variety and nitrogen on *Striga* incidence and sorghum grain yield (Tozi, 1988)

Sorghum variety	*Striga* (plants/m^2)	Grain yield (t ha^{-1})
SRN 39	6	600
IS 9830	9	480
Korakolo	12	0
SRN 39+U[1]	3	700
IS 9830+U	4	550
Korakolo+U	9	630

[1]U=urea at 95 kg ha^{-1}

Table 9. Effects of variety and nitrogen on *Striga* incidence and sorghum yield (Umsagattah, 1987)

Sorghum variety	*Striga* (plants/m^2)	Grain yield (t ha^{-1})
IS 9830	4	760
SRN 39	4	290
Wad Akar	22	220
Wad Akar+U[1]	54	400
Wad Akar+U*[2]	37	430

[1]U=urea at 90 kg ha^{-1}
[2]U*=urea at 190 kg ha^{-1}

urea at 47.6 kg ha^{-1} substantially increased yield of both SRN 39 and G/H (Table 7). At Tozi, urea at 95 kg ha^{-1} slightly increased yields of SRN 39 and IS 9830. However, a considerable yield increase was realized from the local variety Korakolo (Table 8).

At Gadarif, a tank mix of chlorsulfuron and dicamba increased yields of all varieties. Yield increases over the corresponding urea treatment were highest (121% to 143%) for the local varieties and lowest (13%) for SRN 39 (Table 6). At Simsim, chlosulfuron at 2.4 and 3.57 kg ha^{-1} increased the yield of G/H over that of the untreated control. The herbicide at the low rate gave more yield than at the high rate. G/H yield was increased further when the herbicide was preceded by a urea treatment, with more yield (31%) realized at the high rate (Table 7). Chlorsulfuron at 2.4 kg ha^{-1} increased yield of SRN 39 by 97% over the respective untreated control. Increasing the chlorsulfuron rate to 3.75 g ha^{-1} decreased yield. Chlorsulfuron, irrespective of rate, when preceded by urea, increased yield considerably. However, the attained yield was comparable to that of the corresponding sole urea treatment (Table 7).

Discussion

It is evident from the results that control of *Striga* is modulated by crop variety, season, and site. This is consistent with various reports associating *Striga* incidence with environmental variables (Pieterse and Pesch, 1983). No single treatment provides adequate and reliable control. Adequate, reliable, and acceptable *Striga* control requires development of a management strategy that takes into account both the technical and socio-economic aspects of the problem.

Though far from providing an ideal solution to the problem, the study identifies two control options. The first option involves use of *Striga*-resistant varieties and low inputs and is suitable for subsistence farmers with limited resources. Under low inputs, SRN 39 outyielded the local varieties, sustained low *Striga* infestation, and evaded early damage by the parasite. These findings indicate the potential of SRN 39 as a component in an integrated measure to combat *Striga* under subsistence farming conditions.

Implementation of supportive treatments such as crop rotation, hand-pulling of *Striga* at flowering, intercropping, nitrogenous fertilizers, and spot spraying with post-emergence herbicides will further curtail seed production, enhance demise of the viable seed bank, and may curtail development of more virulent *Striga* strains that are capable of overcoming resistance. It has to be borne in mind that *S. hermonthica* is an out-crossing species.

The second option stems from the finding that chlorsulfuron or chlorsulfuron in a tank mix with dicamba effected good control of the parasite on local *Striga* susceptible varieties but with high yield potentials. In addition to increasing yield, such treatments ensure rapid depletion of *Striga* seed reserves. Chlorsulfuron does not inhibit *Striga* seed germination (A.G.T. Babiker, unpublished). This option offers fewer restrictions on crop variety and, hence, less interference with farmers' and consumers' preferences. However, it requires high inputs and is

suitable only for large-scale commercial mechanized farming with adequate rainfall, and under irrigation where proper crop husbandry practices could be implemented and high yields are expected. The high yield attained, together with long-term benefits arising from enhancement of *Striga* seed demise, will offset, at least in part, the added cost of the treatment.

Acknowledgments

This work is supported by the Agricultural Research Corporation of the Sudan and INTSORMIL (International Sorghum and Millet [CRSP]). The author is indebted to Dr. John M. Yohe, INTSORMIL Program Director, and Dr. Darrell T. Rosenow, Chair of the Organizing Committee of the International Conference on Genetic Improvement of Sorghum and Millet, for inviting him to attend and present this paper.

References

Butler, L.G. 1993. Chemical communication between the parasitic weed *Striga* and its crop host. A new dimension in allelochemistry. p. 158-168. *In* K.M. Inderjit, M. Dakshini, and F.A. Einhelling (eds.) Allelopathy, organisms, processes and applications, 1-5 Aug. Ames, IA. ACS, Washington, DC.

Doggett, H. 1984. *Striga hermonthica* on sorghum in East Africa. J. Agric. Sci. 65:183-194.

Doggett, H. 1988. Sorghum (2nd ed.). John Wiley & Sons, New York, NY.

Ejeta, G. 1985. Current status of sorghum improvement research and development in the Sudan. p. 11-18. *In* G. Ejeta (ed.) Hybrid sorghum for Sudan. Workshop Proceedings, 5-8 Nov., 1983, Gezira Research Station, Wad Medani, Sudan. Agricultural Research Corporation, Wad Medani, Sudan.

Ejeta, G., L.G. Butler, and A.G.T. Babiker. 1993. New approaches to the control of *Striga*. *Striga* research at Purdue University. Agricultural Experiment Station Research Bulletin No. 991. Purdue University, West Lafayette, IN.

Hamdoun, A.M., and A.G.T. Babiker. 1989. *Striga* in the Sudan. p. 80-91. *In* T.O Robson and H.R. Broad (eds.) *Striga*: Improved management in Africa. Proceedings FAO/OAU All-African Government Consultation for *Striga* Control, 1986. FAO Plant Production and Protection Paper 96, FAO, Rome.

Lagoke, S.T.O., V. Parkinson, and R.M. Agunbiade. 1991. Parasitic weeds and control methods in Africa. p. 3-14. *In* S.K. Kim (ed.) Combating *Striga* in Africa. Proceedings of an International Workshop, 1988, Ibadan, Nigeria. IITA, Ibadan, Nigeria.

Parker, C. 1983. *Striga* analysis of past reseach and summary of the problem. p. 9-16. *In* K.V. Ramaiah, and M.J. Rao (eds.) Proceedings of the second international workshop on *Striga*, 1981, Ouagadougo. ICRISAT, Patancheru.

Parker, C., and R.C. Riches. 1993. Parasitic weeds of the world: Biology and control. CAB International, Wallingford, UK.

Pieterse, A.H., and C.J. Pesch. 1983. The witchweeds (*Striga* spp): A review. Abst. Tropic. Agric. 9:9-37.

Sauerborn, J. 1991. The economic importance of the phytoparasites *Orabanche* and *Striga*. p. 137-143. *In* J. K. Ransom, L. J. Musselman, A. D. Worsham, and C. Parker (eds.) Proceedings, 5th international symposium on parasitic weeds, 1991, Nairobi. CIMMYT, Nairobi.

Discussion

Session VII - Breeding for Resistance to Other Abiotic Stresses and *Striga*
Session Chair: Fran Bidinger
Rapporteurs - Medson Chisi and Peter Esele

Brhane Gebrekidan - 1) What has been the contribution of ICRISAT's long term highland sorghum breeding program in Mexico to the highland sorghum improvement programs of eastern Africa? 2) What is the explanation for the predominance of high tannin and brown sorghums in very high altitudes of eastern and central Africa?

S.Z. Mukuru - 1) ICRISAT's highland sorghum program in Mexico developed cold tolerant improved sorghum varieties but these are poorly adapted in eastern Africa. Grain yields of these are low and they are highly susceptible to leaf blast and anthracnose. However, these are being used in crosses with selected adapted germplasm to improve their adaptation and leaf disease resistance. 2) It is true that high tannin brown sorghums are dominant at high altitude. In fact, in Uganda, Rwanda and Burundi, all the high altitude sorghum cultivated by farmers are high tannin brown type. I believe the farmers have selected these because they are less damaged by birds.

Brhane Gebrekidan - Support for highland sorghum research should continue because of the importance of these sorghums in the region. Introgression of desirable traits from lowland sorghums to highland materials has not been very effective.

S.Z. Mukuru - I agree with your comment that research on sorghum should be continued. Sorghums in the highlands of eastern Africa are extremely important to small-scale, poor resource farmers who depend on these for food and drink. I also agree, introgression of yield component traits for low elevation sorghum into highland sorghums has not been effective. However, I think it should be possible to introgress other useful plant and grain traits from the lowland into highland types. It should also be possible to transfer disease and insect pest resistances available in lowland germplasm into highland types.

Jeff Dahlberg - Are the highland sorghums showing any seedling cold tolerance?

S.Z. Mukuru - Yes, highland sorghums have good levels of seedling cold tolerance. The seedlings of cold tolerant sorghums grow upright and have greater seedling vigor than susceptible types.

Oscar Rodriguez - Has your program done any research on iron deficiency in sorghum?

L.M. Gourley - Neither Mississippi State University nor EMBRAPA has done so.

J.W. Johnson - Texas A&M University did this about 10 years ago.

Brhane Gebrekidan - Since *Striga* is a massive problem for cereal production in Africa, it should take a massive research response commensurate with the

problem. How much effort is ICRISAT putting into solving this problem in addition to what others are doing?

Fran Bidinger - I know field resistance has been frustrating and ICRISAT is maintaining staff in West Africa working on this problem and is also collaborating with Purdue University on this same problem.

Ranajit Bandyopadhyay - ICRISAT continues to have a major emphasis on research on sorghum *Striga* which has been given the highest priority among the sorghum themes in ICRISAT's Medium Term Plan (1993-98). Most of ICRISAT research on *Striga* is centered at Samanko in Mali and is led by Dr. D.E. Hess. Research is also being conducted in India, Kenya, Nigeria and Zimbabwe. Current research includes: 1) inheritance of resistance; 2) development of molecular markers (in collaboration with the University of Hohenheim); 3) biological control (in collaboration with the University of Giessen); 4) breeding for *Striga* resistance at all locations; 5) development/refinement of methods to screen for components of *Striga* resistance; and, 6) soil and crop management practices for managing *Striga* using an integrated approach to include resistant varieties, hand pulling, intercropping, herbicides, and fertilizers. Recently, ICRISAT formalized a working group approach to form a multilocational, multidisciplinary team of breeders, plant pathologists, agronomists, molecular biologists and economists for conducting research on *Striga*. As indicated earlier, much of ICRISAT research on *Striga* is conducted in collaboration with NARS and advance research institutes. During the next few years, ICRISAT plans to further intensify *Striga* research by infusing more resources. A recent review of *Striga* research in ICRISAT suggested that pearl millet germplasm has not been screened carefully for *Striga* resistance. Therefore, there is a strong need to evaluate pearl millet germplasm for *Striga* resistance before emphatic conclusions are made that no *Striga* resistance exists in cultivated pearl millet.

D.S. Murty - You have presented three or four mechanisms of possible resistance to *Striga* on sorghum. Do you have examples other than those for low stimulant mechanism? This has bearing on our progress in gene pyramiding.

Gebisa Ejeta - Our work so far had focussed on low stimulant production. We are just getting into looking at attachment and penetration mechanisms. As soon as we optimize our protocol, we will begin to screen germplasm. We have a collection of sorghum lines known to have resistance — and those will be screened first. We are hopeful.

H.M. Saadan - Many farmers growing sorghum are poor resource farmers. If these farmers have to use chemicals and fertilizer to control *Striga,* is the cost involved in purchasing these inputs covered on the sale of the crop, or, in other words, does the yield obtained off-set the cost of using agro chemicals?

A.G.T. Babiker - Poor resource farmers have to use resistant varieties and low rates of urea. It may be advisable that they go for hand-pulling or spot treatment. Use of resistant varieties should be coupled with an additional practices, otherwise stability and durability of their resistance may be challenged.

A.B. Obilana - In relationship with IPM of *Striga* using chemical and inter-

cropping, our SADC/ICRISAT SMIP research activities in southern Africa is in close collaboration with the NARS and farmers in Tanzania (with Dr. Mbwaga) and Zimbabwe (Mr. Mabasa). Use of Dicamba has been found to be not too successful in the dry sorghum farming areas of Zimbabwe so it has been dropped in favor of intercropping. Use of cowpeas in intercropping with sorghum is proving effective in controlling *Striga* in Tanzania. However, the problem of cowpea being affected by Alectra, another parasitic weed, is a constraint in the use of cowpeas. We can start looking into genotypes of cowpeas to see if resistance and morphology of the cowpea plants are important in controlling *Striga* and Alectra.

A.G.T. Babiker - Intercropping should be done with a variety which covers the soil surface. Moreover, it is more effective with tolerant and/or resistant sorghum varieties. Under *Striga* infestation, stress susceptible varieties will compete less with the intercrop. To be effective, the intercrop must be planted on the same row as the main crop.

Issoufou Kollo - We have found Dicamba to be ineffective on millet in the control of *Striga* in rainfed conditions. What are the toxicity problems with this chemical?

A.G.T. Babiker - Even in our trial, Dicamba alone gave moderate control of the parasite. The product has to be applied four weeks after crop emergence as a soil directed spray. Moreover, you have to adjust your rate. I prefer Dicamba in combination with very low rate of chlorsylforan or Dicamba after a urea treatment. Please note it is more effective on resistant varieties.

Issoufou Kollo - In one experiment, we got a quadratic response in using nitrogen as a way of control on *Striga*. You need to use high levels of nitrogen to get the desired results. What is your comment?

A.G.T. Babiker - Yes, that is true. The effect of nitrogen depends on variety, initial soil fertility and nitrogen rate. It is more effective on resistant varieties.

Bourema Dembele - 1) As most Malian farmers grow Guinea type sorghum cultivars, is there a progress in *Striga* research on those types of sorghum? 2) What are the results adopted by farmers in Sudan?

Gebisa Ejeta - We have not done any work on incorporating *Striga* resistance into the local Guineas. I think it is better to do that in Mali.

A.G.T. Babiker - To a limited extent, resistant varieties have been adopted by commercial companies. We are still pushing herbicides in the rainfed areas.

David Andrews - Since there must be many instances when numerous *Striga* seeds germinate, and possibly attach to a sorghum plant, but only few emerge, what is it that retards or otherwise controls the growth of the remaining seeds/attached *Striga* seedlings. Could it be that they are sensitive to toxins produced by older seedlings — a type of cuckoo effect?

L.G. Butler - I don't know why so few attached seeds continue to develop to emergence, and I doubt if anyone else knows. I would not be surprised if different sorghum genotypes give different degrees of development beyond attachment.

If so, this would be consistent with a host-derived signal controlling this developmental step.

David Andrews - No cultivated pearl millets have been reported to have *Striga* resistance. Have other Pennisetum species been tested for their reaction to *Striga*, particularly those from which it has been shown gene/genome transfer might be possible? (P. *purpureum*, P. *squamulatum*, P. *orientale* — even wild pearl millets P. *glaucum* spp. *violaceum/fallax*, syn. *monodii*).

Gebisa Ejeta - Either through library search or through personal contacts, I have not come across a confirmed source of resistance in wild relatives of pearl millet. The only report I had heard about was that of a shibrah type at the ISC; but upon later observations was found out to be susceptible.

Session VIII

Breeding for Improved Quality and Utilization

Session Chair: Tim Lust

Rapporteurs: Senait Yetneberk and Aissata Bengaly Berthé

Speakers:

B.R. Hamaker
J.F. Pederson
L.W. Rooney
D.S. Murty
N. Nicholsen

Nutritional Quality of Sorghum

Bruce R. Hamaker* and John D. Axtell

Abstract

Sorghum grain generally has somewhat lower nutritional quality than other cereal grains. The lysine content of sorghum is lower due to a higher level of the lysine-deficient prolamin proteins and lower amounts of non-prolamins. Protein and energy digestibility also is slightly lower in sorghum than in other cereals for livestock and can be significantly lower in humans. High lysine sorghum was identified or developed in the early 1970s and, in recent trials, ranged from 0.30 to 0.49% lysine on a flour basis. Sorghum lines with high protein digestibility, both uncooked and cooked, were recently discovered. The high protein digestibility results from abnormally shaped protein bodies where the main storage protein, α-kafirin, is readily accessible to proteases. Among these lines a unique kernel trait also was found that has dense floury endosperm, often with the presence of a vitreous (hard) core.

Sorghum and pearl millet grains are consumed as human food, mostly by the rural poor in semi-arid developing countries. Consumption frequently represents such a high proportion of total caloric intake that quality, amount, and availability of nutrients from the grains are important to the nutritional status of these populations. For animals, sorghum and (to a lesser extent) pearl millet are important feed grains in developed countries and may in the future be utilized more for feed in developing countries. In general, the nutritional quality of sorghum grain for human food is somewhat lower than that of other cereals, and its nutritional quality is slightly lower for animal feed in its unprocessed form. Pearl millet is comparable to other cereals in nutritional quality and digestibility, and, in some cases, is better in protein quality and quantity.

Starch content of both sorghum and pearl millet is about 70% (whole grain). Crude protein content is about 11% (flour weight basis, 12% moisture), higher than in comparable cereals like maize (Klopfenstein and Hoseney, 1995). Lysine is the limiting amino acid in sorghum and pearl millet for humans and non-ruminant animals. The lysine content of normal sorghum cultivars — about 2.0% of total protein or about 0.25% of flour weight — is lower than that of normal maize (Axtell and Ejeta, 1990), due, in part, to sorghum's approximately 10 to 15% higher prolamin content (Hamaker et al., 1995), and lower amounts of the high lysine-containing non-prolamin proteins. Prolamins, the storage proteins of these cereals, are nearly devoid of lysine. Pearl millet has better protein quality than sorghum, with the limiting amino acid, lysine, at approximately 3.0-3.5% of total protein (Serna-Saldivar and Rooney, 1995).

Energy and protein digestibility of unprocessed sorghum grain (tannin-free), compared to other cereal grains, is generally lower in humans, especially children

Bruce R. Hamaker, Department of Food Science, Purdue University, West Lafayette, IN 47907; John D. Axtell, Department of Agronomy, Purdue University, West Lafayette, IN 47907.*Corresponding author.

(MacLean et al., 1981). For livestock, energy and protein digestibility of sorghum is only slightly less than that of maize, at about 95% of the value (Bramel-Cox et al., 1995). Pearl millet, on the other hand, has been reported to have very good utilization in humans or livestock. The following discussion focuses on recent improvements in protein quality and digestibility of sorghum for humans and livestock.

High Lysine Sorghum

Two sources of high-lysine sorghum now exist. The first is the naturally occurring Ethiopian mutant identified by Singh and Axtell (1973) from the World Sorghum Collection, with lysine levels of 3.1% and a total crude protein content of 15-17% (Axtell et al., 1974). On a flour weight basis, lysine content is 0.50%. The second high-lysine gene mutation in sorghum was induced using chemical mutagenesis by Axtell and colleagues (Mohan, 1975; Axtell and Ejeta, 1990). The P721 opaque mutant (designated P721Q) resulted in a 60% increase in lysine content. The mutant is controlled by a single gene that is simply inherited as a partially dominant factor. Selections in the 1994 crop year from a high-lysine population developed at Purdue University ranged from 0.30 to 0.49% lysine, flour basis, compared to normal sorghum cultivars that contain about 0.24 % lysine. Yield in this group ranged from 6775 to 8709 lb/acre.

Protein Digestibility of Sorghum Grain

Digestibility of sorghum protein and energy in children have been reported to be low, compared to other cereals. MacLean et al. (1981) found that young Perúvian children who consumed four sorghum porridges made from different cultivars had a mean apparent nitrogen absorption (protein digestibility) of 46%. This was 57% of the digestibility of a control casein diet which was assumed to be completely digested. Also, a comparatively high percentage (21%) of dietary energy intake was recovered in the feces. Kurien et al. (1960) showed that when a rice diet was incrementally replaced with sorghum, apparent protein digestibility dropped from 75% to 55%. On the other hand, protein and energy digestibilities dramatically increased when sorghum foods were processed. Extruded, decorticated sorghum protein was 81% digestible (apparent) in children (MacLean et al., 1983) and fermented sorghum protein was 79% digestible (apparent) (Graham et al., 1986). Likewise, digestible energy increased in both these processed products, as evidenced by the presence of only about 8% of ingested energy in the feces.

Both *in vivo* and *in vitro* studies show that digestibility of sorghum protein, unlike most food proteins, oddly decreases on simple cooking in water (Axtell et al., 1981; Mertz et al., 1984; Eggum et al., 1983; Mitaru et al., 1985). Reduction in protein digestibility reflects a decrease in digestibility of the kafirin proteins, the storage prolamins of sorghum (Eggum et al., 1983; Oria et al., 1995a). Because of the low quality of sorghum kafirins, an increase in digestibility of these proteins is associated with a decrease in biological value when sorghum is eaten as the sole source of protein (Eggum et al., 1983). However, sorghum is rarely consumed without other sources of protein. Increasing digestibility of sorghum protein is im-

portant for humans who consume mixed sorghum-based diets with marginal protein levels; it also could mean reductions in protein supplements for sorgum-fed livestock. Nutritionally superior sorghum grain would ideally have high lysine content and high protein digestibility.

Hamaker et al. (1987) found that the addition of various reducing agents to cleave disulfide bonds increased *in vitro* pepsin digestibility of uncooked and cooked sorghum to the level of digestibility in other cereals. This effectively negated the decrease normally seen with cooking, suggesting that disulfide bond formation or interchange during cooking causes enzyme-resistant complexes to be formed.

Kafirin Proteins

Sorghum kafirins are synthesized in the endosperm at the rough endoplasmic reticulum, where they aggregate and accumulate in membrane-bound protein bodies (Taylor et al., 1985). We recently showed, using a new extraction method, that sorghum grain has a 10 to 15% higher prolamin content than does maize, and that both cereals contain slightly higher prolamin amounts than previously thought (Hamaker et al., 1995). Normal sorghum cultivars contained approximately 70% kafirin in the whole grain and 80% kafirin in the endosperm.

Sorghum kafirins were assigned the same nomenclature given to analogous zeins — α, ß, and γ — based on differences in extractability, molecular weight, and structure (Shull et al., 1991). Shull et al. (1992) showed that the major kafirin, α, is located in the central region of the protein body, and the high cysteine ß (5 mol%) and γ (7 mol%) fractions are found in the dark-staining regions located mostly at the periphery of the protein body. α-Kafirin (M_r 25,000 and 23,000) makes up about 80% of the total kafirin and about 65% of the total kernel protein; ß-kafirin (M_r 20,000, 18,000, and 16,000) comprises about 5-10% of the total kafirin, and γ-kafirin (M_r 28,000) comprises about 10-15% of the total. Figure 1 shows the sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) profiles of kafirin and non-kafirin proteins and a cross-section of typical protein bodies of sorghum.

We theorize that a high concentration of disulfide-bonded kafirins on the outer shell of the protein body makes sorghum protein bodies hard to digest (Oria et al., 1995a,b). Unpublished studies in our laboratory showed that isolated native (unreduced) α-kafirin was highly digestible in both uncooked and cooked sorghum when mixed with a starch carrier. Therefore, in terms of digestibility, sorghum protein bodies represent a barrier to digestion of α-kafirin. Cooking, we believe, promotes sulfhydryl-disulfide interchange among the peripheral protein body proteins, making the protein bodies even less digestible.

A Highly Digestible Sorghum Cultivar

In the process of screening a number of sorghum cultivars to establish the variability in *in vitro* protein digestibility, we recently discovered two experimental lines that had substantially higher protein digestibility than normal sorghums, both uncooked and cooked (Table 1). Protein digestibility did not decrease appreciably in these lines upon cooking. The highly digestible lines were found in the high-lysine population developed by Axtell and

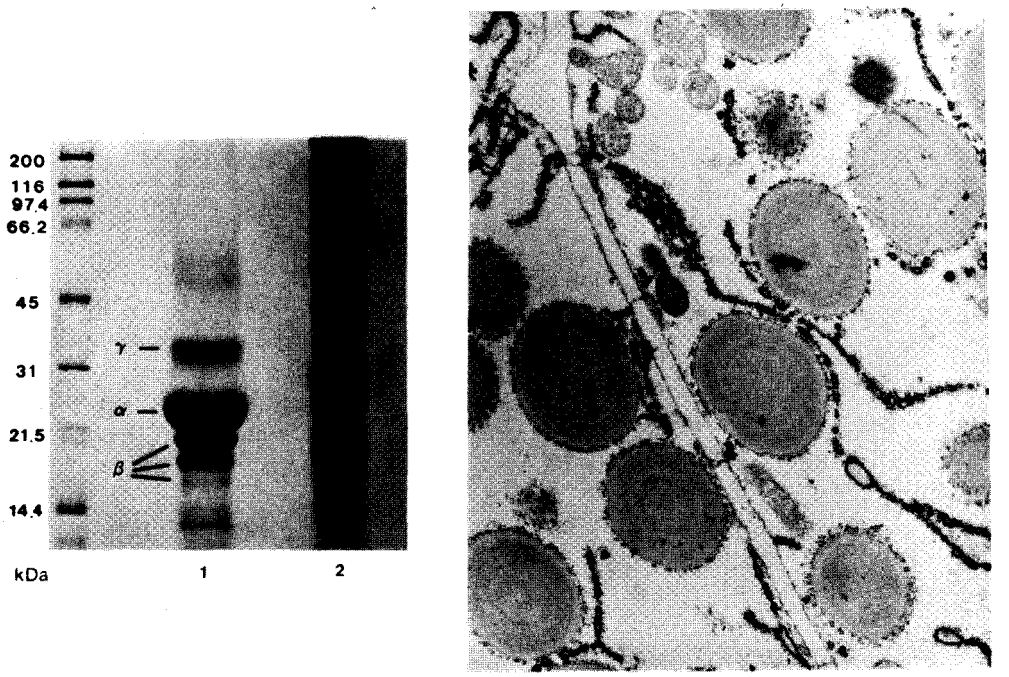


Figure 1. **SDS-PAGE protein profiles of sorghum α-, ß-, and γ-kafirins (lane 1) and non-kafirins (lane 2) and a transmission electron micrograph of sorghum endosperm showing protein bodies.**

colleagues from the original chemically derived mutant, P721Q (Mohan, 1975). In further studies, many lines within the high-lysine population were found to contain this trait. Although digestibility of the highly digestible lines still varied somewhat over three crops, it was consistently higher than *in vitro* protein digestibility of maize and normal sorghum cultivars.

Using a three-enzyme (trypsin, chymotrypsin, peptidase) *in vitro* digestibility method (Pedersen and Eggum, 1983), which monitors the number of peptide bonds hydrolyzed by titrated NaOH, we found that initial rates of digestion were much higher for the highly digestible lines compared to normal sorghum (Figure 2). Higher digestibility was accounted for by a more rapid digestion of the α-kafirin protein as revealed by a time course digestion visualized by SDS-PAGE and quantified by an enzyme-

Table 1. ***In vitro*** **protein digestibility using pepsin of normal and highly digestible sorghum genotypes.**

	Uncooked	Cooked
Normal	%	%
P721N	77.9	58.0
SAFRA	65.8	57.8
Sepon 82	80.8	66.3
SC283-14	75.3	70.2
Dabar	73.6	55.8
Hageen Dura 1	77.8	59.3
Highly Digestible		
P851171	87.0	80.8
P850029	87.8	78.7

linked immunosorbant assay (ELISA), which we developed using α-kafirin rabbit antiserum.

When viewed by transmission electron microscopy (TEM), the protein bodies of the highly digestible cultivar appeared remarkably different from normal (Figure 3). Protein bodies were abnormally shaped with deep invaginations. Using an immunolocalization technique with γ-kafirin antiserum, we showed that γ-kafirin in the mutant was located in discrete dark-staining regions within and at the base of folds instead of at the protein body periphery. This indicated that α-kafirin, in this case, was more accessible to digestive enzymes and not encapsulated by enzyme-resistant proteins.

We recently developed an ELISA-based protein digestibility screening assay for sorghum, based on reduction in α-kafirin following a short predigestion step. In this method, extracted undigested proteins are measured by ELISA for remaining α-kafirin. Following digestion the highly digestible sorghum lines contained much less α-kafirin than did normal lines (Figure 4). We currently are working on improving the precision and shortening the time of the assay, and will compare a large number of sorghum cultivars using the ELISA-based assay and the standard pH-stat protein digestibility assay.

Grain Quality of Highly Digestible Sorghum Culivars

In a study of 40 sorghum lines from Axtell's high-lysine population, we analyzed grain for kernel hardness characteristics (density and visual appearance of

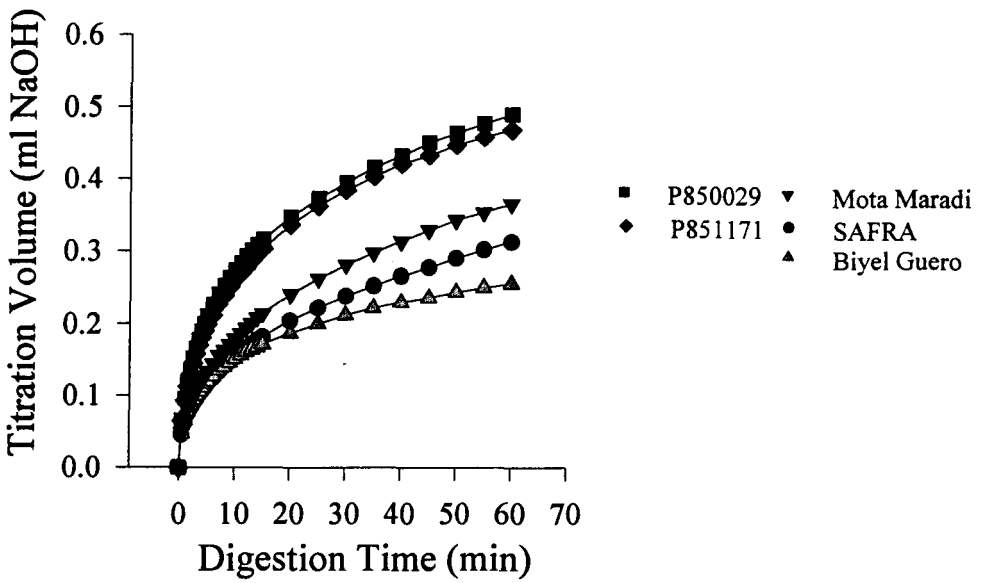


Figure 2. Titration curve by pH-stat method for 60 min. comparing digestion of uncooked flours of three normal sorghum cultivars and two highly digestible cultivars (P850029 and P851171).

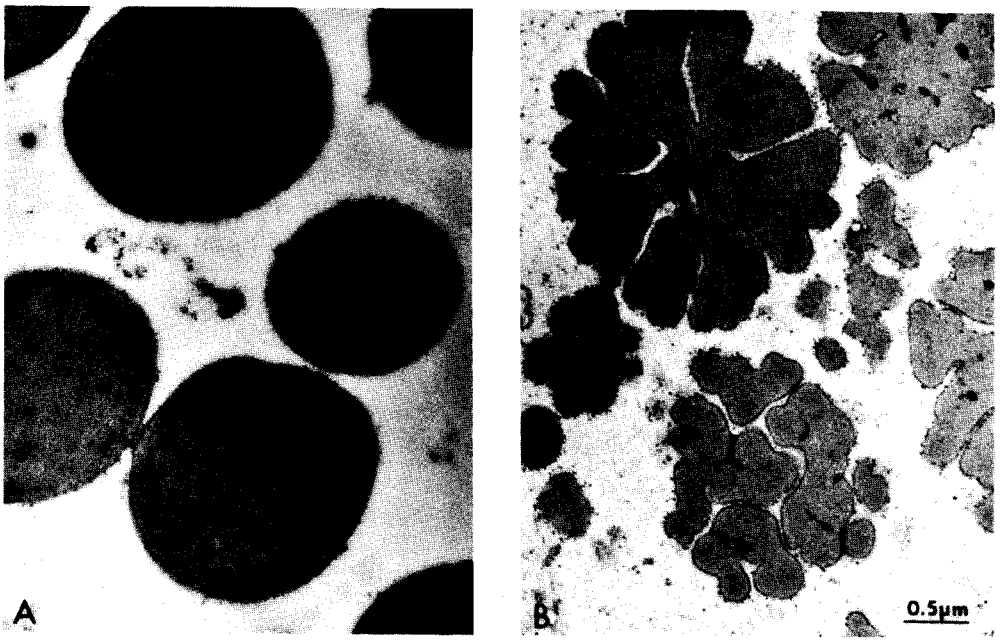


Figure 3. Transmission electron micrographs of a normal sorghum cultivar (P721N) (A) and a highly digestible cultivar (P851171) (B), showing protein bodies in developing (30 days after half bloom) sorghum endosperm.

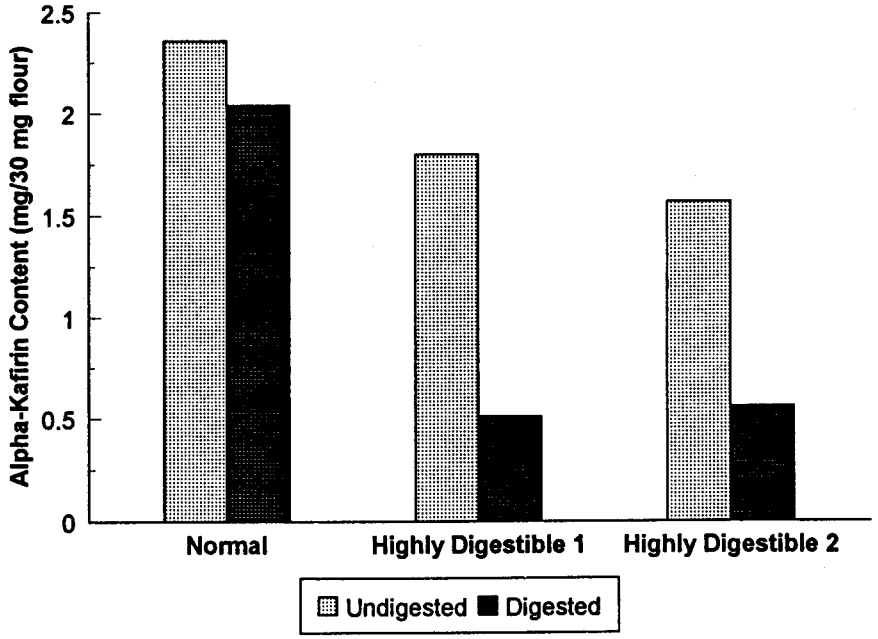


Figure 4. Basis for a new ELISA-based protein digestibility screening assay for sorghum grain. α-Kafirin is digested much faster in the highly digestible sorghum cultivars than in the normal cultivar.

cross-sections), lysine content, and protein digestibility. A novel endosperm type was found within this group which we have called "dense floury." The kernel density of this floury type grain is just below that of typical vitreous grains. Its endosperm contains a partially translucent, vitreous-appearing central portion (or central ring) surrounded by a floury-appearing region radiating outward to the kernel periphery (Figure 5). Inspection of the vitreous portions of these unique grains by scanning electron microscopy reveals densely packed starch granules within a discontinuous protein matrix. Conversely, vitreous endosperm often is defined as having starch granules tightly packed into a continuous protein matrix. We speculate that the dense floury grain may have application in animal feed as the starch may be more available than the starch in normal vitreous sorghum grains. The traits of high protein digestibility and high lysine content were found combined in lines with the dense floury characteristic; however, the two traits do not appear to be linked, as lines also were found containing only one or the other trait.

Acknowledgements

This research was supported in part by a grant from the U.S. Agency for International Development, INTSORMIL CRSP LAG-1254-G-00-6009.

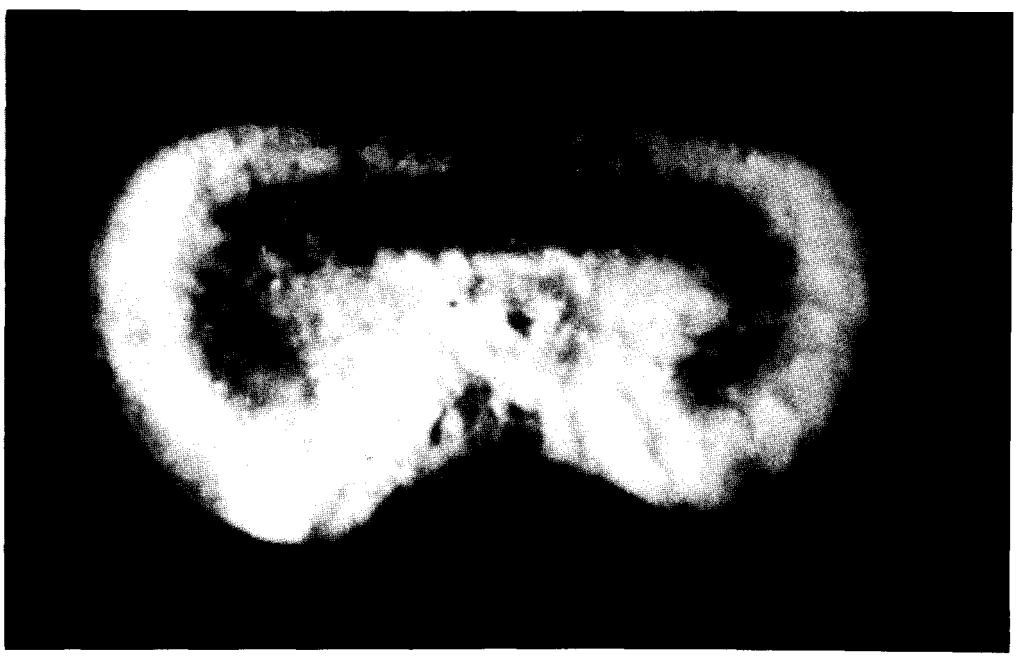


Figure 5. Cross-section of a kernel of a dense floury sorghum line containing a central vitreous region.

References

Axtell, J.D., and G. Ejeta. 1990. Improving sorghum grain protein quality by breeding. p. 117-125. *In* Ejeta, G. (ed.) Proceedings of the International conference on sorghum nutritional quality. Purdue University, West Lafayette, IN.

Axtell, J.D., A.W. Kirleis, M.M. Hassen, N. de Croz-Mason, E.T. Mertz, and L. Munck. 1981. Digestibility of sorghum proteins. Proc. Natl. Acad. Sci. USA 78:1333-1335.

Axtell, J.D., D. Mohan, D. and D. Cummings. 1974. Genetic improvement of biological efficiency and protein quality in sorghum. p. 29-39. *In* Proceedings, 29th annual corn and sorghum research conference, Chicago. American Seed Trade Association, Washington, D.C.

Bramel-Cox, P.J., K.A. Kumar, J.D. Hancock, and D.J. Andrews. 1995. Sorghum and millets for forage and feed. p. 325-364. *In* Dendy, D.A.V. (ed.) Sorghum and millets: Chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Eggum, B.O., L. Monowar, K.E.B. Knudsen, L. Munck, and J.D. Axtell, J.D. 1983. Nutritional quality of sorghum and sorghum foods from Sudan. J. Cereal Sci. 1:127-137.

Graham, G.G., W.C. MacLean, E. Morales, B.R. Hamaker, A.W. Kirleis, E.T. Mertz, and J.D. Axtell. 1986. Digestibility and utilization of protein and energy from *nasha*, a traditional Sudanese fermented sorghum weaning food. J. Nutr. 116:978-984.

Hamaker, B.R., A.W. Kirleis, L.G. Butler, J.D. Axtell, and E.T. Mertz, E.T. 1987. Improving the *in vitro* digestibility of sorghum with reducing agents. Proc. Natl. Acad. Sci. USA 84:626-628.

Hamaker, B.R., A.A. Mohamed, J.E. Habben, C.P. Huang, and B.A. Larkins. 1995. Efficient procedure for extracting maize and sorghum kernel proteins reveals higher prolamin contents than the conventional method. Cereal Chem. 72:583-588.

Klopfenstein, C.F., and R.C. Hoseney. 1995. Nutritional properties of sorghum and the millets. p. 125-168. *In* Dendy, D.A.V. (ed.) Sorghum and millets: Chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Kurien, P.P., M. Narayanarao, M. Swaminathan, and V. Subrahmanyan, V. 1960. The metabolism of nitrogen, calcium, and phosphorus in undernourished children: The effect of partial or complete replacement of rice in poor vegetarian diets by kaffir corn (*Sorghum vulgare*). Br. J. Nutr. 14:339-345.

MacLean, W.C., G. Lopez de Romaña, A. Gastanaduy, and G.G. Graham. 1983. The effect of decortication and extrusion on the digestibility of sorghum by preschool children. J. Nutr. 113:2171-2177.

MacLean, W.C., G. Lopez de Romaña, R.P. Placko, and G.G. Graham. 1981. Protein quality and digestibility of sorghum in preschool children: balance studies and plasma free amino acids. J. Nutr. 111:1928-1936.

Mertz, E.T., M.M. Hassen, C. Cairns-Whittern, A.W. Kirleis, L. Tu, and J.D. Axtell. 1984. Pepsin digestibility of proteins in sorghum and other major cereals. Proc. Natl. Acad. Sci. USA 81:1-2.

Mitaru, B.N., R.D. Reichert, and R. Blair. 1985. Protein and amino acid digestibilities for chickens of reconstituted and boiled sorghum grains varying in tannin contents. Poultry Sci. 64:101-106.

Mohan, D. 1975. Chemically induced high-lysine mutants in *Sorghum bicolor* (L.) Moench. Thesis, Purdue University, West Lafayette, IN, 110 pp.

Oria, M.P., B.R. Hamaker, and J.M. Shull. 1995a. Resistance of sorghum α-, ß-, and γ-kafirins to pepsin digestion. J. Agric. Food Chem. 43:2148-2153.

Oria, M.P., B.R. Hamaker, and J.M. Shull. 1995b. *In vitro* protein digestibility of developing and mature sorghum grain in relation to α-, ß-, and γ-kafirin disulfide crosslinking. J. Cereal Sci. 22:85-93.

Pedersen, B., and B.O. Eggum. 1983. Prediction of protein digestibility by an *in vitro* enzymatic pH-stat procedure. Tierphysiol. Tierernaehr. Futtermittelk De. 49:265-277.

Serna-Saldivar, S. and L.W. Rooney. 1995. Structure and chemistry of sorghum and millets. pp. 69-124. *In* Dendy, D.A.V. (ed.) Sorghum and Millets: Chemistry and Technology. American Association of Cereal Chemists, St. Paul, MN.

Shull, J.M., J.J. Watterson, and A.W. Kirleis. 1991. Proposed nomenclature for the alcohol-soluble proteins (kafirins) of *Sorghum bicolor* (L.) Moench based on molecular weight, solubility, and structure. J. Agric. Food Chem. 39:83-87.

Shull, J.M., J.J. Watterson, and A.W. Kirleis. 1992. Purification and immunocytochemical localization of kafirins in *Sorghum bicolor* (L.) Moench endosperm. Protoplasma 171:64-74.

Singh, R., and J.D. Axtell. 1973. High-lysine mutant gene (hl) that improves protein quality and biological value of grain sorghum. Crop Sci. 13:535-539.

Taylor, J.R.N., L. Schussler, and N. Liebenberg v.d W. 1985. Protein body formation in endosperm of developing *Sorghum bicolor* (L.) Moench seeds. S. Afric. J. Bot. 51:35-40.

Breeding Sorghum And Pearl Millet For Forage And Fuel

J. F. Pedersen

Abstract

*Sorghum [*Sorghum bicolor *(L.) Moench] and pearl millet [*Pennisetum glaucum *(L.) R. Br.] are unique species in their ability to be used in many forage/livestock system roles. Such flexibility has made prioritizing breeding objectives difficult and has even contributed to contradictory opinions on appropriate forage breeding objectives. Few breeding projects identified in the USDA-ARS, USDA-CREES, or at ICRISAT had forage sorghum or forage pearl millet as their sole research assignment. In the United States, it can be argued that breeding resources committed to forage sorghum improvement are probably declining. A new forage sorghum and forage pearl millet project recently considered by INTSORMIL did not receive high enough priority to receive funding from available resources.*

This paper discusses: new technologies, including automated harvesting systems, statistical methods, and forage quality assessment methods, that allow considerable increases in the scale and efficiencies of forage sorghum and millet breeding programs; examples of genes coding for characters known to impact forage quality; the status of the ethanol industry in general; the prospect for ethanol from biomass; and production of paper from stover. Due to limited resources, forage sorghum and millet breeding programs will have to focus on narrow, high impact objectives and utilize the best available technology.

Methods of breeding sorghum and pearl millet for forage and fuel are essentially the same as for any other targeted markets. This paper will focus on the breeding objectives, problems, and opportunities facing forage sorghum and forage millet breeders. Thorough reviews of the literature on the genetics and breeding of forage sorghums and forage millets have recently been published by Andrews and Kumar (1992) and Bramel-Cox et al. (1995).

J. F. Pedersen, USDA, ARS, NPA Wheat Sorghum and Forage Research, Department of Agronomy, University of Nebraska-Lincoln, Lincoln, NE 68583-0937. Joint contribution of the USDA-ARS and the Nebraska Agricultural Experiment Station.

Review of Current Status

Importance of Forage Sorghum and Forage Millet

When grown primarily as forage crops, these two species are unique. They are productive warm season annuals, are readily established using conventional equipment and cropping, and have much lower water requirements than maize grown for silage. These characteristics provide considerable flexibility for for-

age/livestock producers in managing their resources and responding to the critical forage needs of their livestock. However, such flexibility of use makes identification of breeding objectives difficult. Even the growth stage of the final sorghum or millet product varies.

Many forage/livestock systems suffer from periods of low forage productivity. Forage sorghum and pearl millet are commonly used in the vegetative stage to fill summer forage production needs through direct grazing. They also can be preserved at various maturities as hay or as silage to fill winter forage production voids. Grazing or preservation of the stalks and leaves remaining after grain harvest are common practices with grain sorghums in the United States and dual-purpose sorghums grown elsewhere. Producers also have required particular physical parameters (for example, height or seed color) to meet the definition of a "forage" in political programs. Such diversity in the use of these two species as forages has contributed to diverse and sometimes contradictory opinions on appropriate forage breeding objectives.

In the United States, only 142,000 ha of forage sorghum were harvested for silage in 1993 (U.S. Agricultural Statistics, 1994). Based on the 1985 ratio of hectares of forage sorghum harvested for silage to hectares of other forage sorghum harvested or grazed (these estimates were discontinued after 1985), approximately 24,300 additional ha of forage sorghum were harvested or grazed in 1993. This figure, however, may be a considerable underestimate. A seed industry source indicates that hectares of forage sorghum for hay may be three times greater than hectares of forage sorghum grown for silage (A. Armburst, Sharp Brothers Seed Co., 1996, personal communication). When combined with the resulting small individual target markets for each specific forage product, the diversity of breeding objectives has resulted in a limited commitment of resources to any single objective and a consequent limited impact in the marketplace.

Current Breeding Objectives

A 1988 survey of 26 public and private forage sorghum breeders (Kalton, 1988) indicated that the primary objectives of the majority of the breeders were: increased total yield, standability, disease resistance, and insect resistance. Few breeders identified improvement of forage quality as an objective.

A current search of the USDA Research (CRIS) data base (1996) using the search strings "sorghum and forage and breeding" and "millet and forage and breeding" identified a variety of current research objectives. Broad breeding objectives include:

- Evaluate introductions and wild species for genetic potential
- Efficiently utilize genes from exotic germplasm
- Create additional diversity by hybridization and tissue culture
- Develop superior genetic stocks and germplasms
- Breed better cultivars.

Specific breeding objectives include:

- Improved yield
- High yield for silage

- Improved quality
- Improved disease resistance
- Improved insect resistance
- Improved drought resistance
- Tolerance to acid soil
- Tolerance to aluminum and manganese toxicity
- Efficiency of phosphorous utilization
- Reduction of harmful substances
- Conversion of Burkina Faso pearl millet landraces to short, day-neutral pearl millet lines.

Basic research objectives include:

- Determine the constraints to superior forage sorghums
- Establish taxonomic and cytogenetic relationships
- Develop more efficient breeding methods
- Develop methods for converting and transferring genetic characters to cultivated materials
- Develop interspecific transfer methods for gene(s) controlling apomixis
- Develop RFLP methodology to enhance plant breeding effectiveness
- Clone and characterize stem elongation genes
- Determine chemical composition of sorghums carrying brown midrib genes
- Evaluate expression of lignin-associated genes for molecular understanding
- Isolate and characterize lignin-associated genes for genetic engineering
- Understand the control and inheritance of apomixis
- Understand development of genetic diversity in apomictic genotypes
- Understand development and molecular aspects of two pearl millet mutants with tendencies towards apomixis
- Map gene(s) for apomixis in interspecific hybrid.

Few projects had forage sorghum or forage millet as their sole research assignment. Most were grain projects with some commitment to forages, or forage projects that included additional species. A similar search of the ICRISAT Global Research Portfolio (ICRISAT, 1996) data base showed three pearl millet projects and five sorghum projects, but none had stated objectives of forage improvement.

Breeding Approach/Products

According to Kalton (1988), most forage sorghum breeders are developing improved hybrids. Based on the above objectives, it appears that forage sorghum and millet breeders use most of the previously discussed methods. Anticipated products from breeding programs include hybrids, parental lines, varieties, populations, genetic stocks, and cloned genes, as well as a wealth of scientific knowledge.

Current Resources

Total fiscal commitment or scientist year commitment to forage sorghum and millet breeding is difficult to determine since most such efforts represent portions of larger projects with grain or other forage crop objectives. However, in the United States, it can be argued that breeding resources committed to forage sorghum improvement are probably declining. Total USDA/ CREES/ ARS research dollars committed to grain sorghum re-

search have declined from $3.02 million in 1986 to $2.70 million in 1996 (T. Lust, National Grain Sorghum Board, 1996, personal communication). At the same time, private sector sorghum breeding programs have been eliminated by some companies and reduced in size by others. It appears that forage sorghum breeding programs suffered similar reductions during this period, as well.

Plot harvesting equipment available to current forage sorghum and millet breeders varies, but can be as crude and labor-intensive as machetes and hanging scales. While many forage grass breeding programs include laboratory quality assessment of breeding materials and actual grazing evaluation of advanced lines, such data often is available to forage sorghum and millet breeders only on a fee basis. These limitations severely restrict the numbers of breeding lines that can be harvested and evaluated; they also restrict forage breeding objectives to characters that can be readily observed or measured.

Define State of the Art

Measuring Yield (Forage Harvest Technologies)

Harvest systems that reduce labor needs, increase capacity of programs, and provide a safe working environment for operators are essential. Such systems are in use at several public and private research locations and are based on commercially available silage harvesters. One such harvest system recently described by Pedersen and Moore (1995) has been used on both forage sorghum and pearl millet and can harvest and weigh approximately one plot/minute. Data can be collected electronically. Forage is finely chopped and easily subsampled for moisture and quality analysis. When combined with state of the art forage quality technology, quantitative yield and quality data can be obtained on greatly increased numbers of breeding lines.

Statistical Methods

The ability to increase the number of breeding lines, and the amount of data collected on each line, affects design and analysis of experiments. Non-uniformity of fields becomes more important as the ability to identify uniform blocks decreases. Unbalanced data sets become more probable as the number of lines evaluated increases. In a recent review of yield trial design and analysis, Johnson et al. (1992) point out that recent developments in computer technology have greatly enhanced our ability to utilize complex statistical models. They demonstrate that mixed linear model methodology (MLMM) can enhance analysis of combined data and/or unbalanced data, adjust for spatial variation, identify specific genotypic by environmental interactions, as well as estimate or predict genetic effects. In one example using MLMM, standard errors between entries were halved when entries and blocks were assumed to be random (the situation most plausible biologically) rather than fixed.

Nearest neighbor analysis (NNA) has been used successfully by small grain breeders (Besag and Kempton, 1988; Gleeson and Cullis, 1987) to increase experimental precision. Although Johnson et al. (1992) reported little or no benefit of

NNA in maize (*Zea mays* L.) yield trials, they concluded that NNA may be more useful in yield trials conducted in non-irrigated, stress environments. These are precisely the environments that forage sorghum and millet have traditionally occupied.

A unique problem facing forage breeders is how to interpret data from multiple harvests of the same plot throughout a growing season. Forage sorghum breeders attempting to improve sudangrass are often faced with multiple harvest data. Pedersen et al. (1991) described a concise and easily interpreted method to help breeders interpret such data. With this method, yield is regressed against an index associated with harvest dates, resulting in a single regression coefficient descriptive of cultivar response over all harvest dates. The practical value of such a technique increases as the number of lines evaluated increases.

Forage Quality Technologies

The "gold standard" for determining the quality of a forage is feeding it to cattle and measuring animal response in either weight gain (for beef cattle) or milk production (for dairy cattle). This "gold standard" has been used successfully in the final testing phases of several forage programs. However, such forage quality assessments are far too costly and require too much forage material to be practical in early generation forage breeding. Therefore, a number of laboratory assays that predict cattle performance have been developed.

One of the most (if not the most) widely accepted laboratory assays for forage quality is *in vitro* dry matter disappearance (IVDMD), originally developed by Tilley and Terry (1963). This procedure utilizes actual rumen fluid as a digestive agent with results very similar to *in vivo* digestion. However, because the procedure requires a surgically fistulated donor animal, many biological, environmental, and procedural variables can influence the final results. Marten and Barnes (1980) have summarized and presented standardization techniques for some of the many variations that have developed from the original procedure.

Shortly after the IVDMD procedure was developed, Goering and Van Soest (1970) described a forage fiber analysis system that utilizes chemical rather than biological degradation of forages. It breaks down forages into cell solubles, hemicellulose, cellulose, lignin, and ash fractions. This system is attractive because results are not so readily affected by biological, environmental, and procedural variables. Results reveal information about the structural/chemical makeup of forages, but do not imitate actual digestion by ruminants. Results also are used to predict relative feed value (RFV) of alfalfa and are used routinely for commercial alfalfa hay analysis; however, RFV would be of questionable value for forages such as sorghum and millet.

Two relatively new modifications of the *in vitro* dry matter disappearance procedure show great promise in simplifying and/or expanding the information derived from the procedure. The first is a commercially available system from ANKOM Technology Corporation (140 Turk Hill Park, Fairport, NY) that utilizes rumen fluid, sealable sample bags, and bulk di-

gestion vials, and is currently being utilized by our lab. Initial results indicate good agreement in ranking of sorghum genotypes with traditional IVDMD results, and greatly enhanced ease of operation and sample handling. The system also is adaptable to digestion kinetics studies.

An *in vitro* procedure developed by Schofield et al. (1994) also utilizes rumen fluid, but goes one step further in providing digestion kinetics data. The rumen fluid is placed in a sealed digestion vessel, and pressure sensors measure gas production, continuously outputting data until the digestion process is stopped.

Another technology of great value is near infrared reflectance spectroscopy (NIRS). It is well described in a handbook edited by Marten et al. (1989). This technology utilizes near infrared spectral data to predict wet lab forage quality parameters. It requires collection of reference laboratory data and the development of complex prediction equations (through the use of relatively user-friendly software). Once these steps are accomplished, multiple lab values can be predicted from a single NIRS scan, which can be accomplished in approximately one minute. This technology can make measurement of forage quality data economically possible for some forage breeding projects.

Forage Quality Genes

Although most forage quality parameters appear to be quantitatively inherited (Andrews and Kumar, 1992; Bramel-Cox et al., 1995), several simply inherited qualitative characters have significant impact on forage quality. Examples include brown midrib in sorghum (Fritz et al., 1981) and pearl millet (Cherney et al., 1988) and the presence or absence of tricomes in pearl millet (Hanna et al., 1977). Other characteristics, including plant color, sweetness, juiciness, and even seed pericarp color may affect forage quality. Kalton (1988) proposes that an ideal silage sorghum would include the following traits, presumably for quality enhancement:

- Red seeded
- Yellow endosperm
- No testa layer
- Brown midrib
- Tan plant color
- Juicy stalk
- Moderate to low HCN-p
- High IVDMD
- Good protein content
- Good leafiness and green leaf retention

Genes controlling simply inherited characters that affect quality are available, more so than for most other forage grasses. The genetic knowledge base of forage sorghum and millet is high compared to other forage grasses. However, incorporating all of these, plus high yield and agronomic acceptability, into hybrids would be an ambitious effort by forage sorghum and millet breeders.

Exploring the Future

U.S. land area committed to overall sorghum production has decreased. Land area committed to forage sorghum production is relatively small and appears to have decreased as well. The number of sorghum breeders and research projects in both the private and public sector are de-

clining. It appears that either major changes in markets available for forage sorghum and millet will have to occur and research resources committed to them increase drastically, or the "ambitious effort" needed will have to become "narrow" and "efficient" to continue breeding progress under the status quo. New technologies that may create large new markets for sorghum and millet biomass could be on the horizon. I will begin exploration of the future assuming current research and market trends.

Future Resource Allocation

Forage sorghum and millet research will continue, primarily as a portion of larger sorghum or millet projects or larger forage projects. In many cases, such research may be "bootlegged," or accomplished without any resources officially being committed to forage research. An INTSORMIL example illustrates this trend. Within INTSORMIL itself, five new projects were proposed during the past several months, including one on forages. However after funds were allocated to projects based on need and impact, as determined by an external evaluation committee, the forage project was not funded (D. Walters, INTSORMIL, 1996, personal communication). Increased resources for forage sorghum and millet cannot be expected under the status quo.

Narrow Breeding Objectives

Given very limited, or even borrowed resources, emphasis in forage breeding should be placed on objectives with the highest potential impact. Widely diverse objectives targeted at equally diverse growth stages, morphological types, and markets dilute meager resources even more. Based on land area committed, maximum impact in the U.S. appears to be probable in silage sorghum improvement. Priority should be given to enhancing silage yield and quality.

An example of the need for more focused or concentrated effort might be the incorporation of the brown midrib trait into an acceptable commercial hybrid. Brown midrib has been known in maize since at least 1926 (Eyster, 1926). Brown midrib mutants were originally induced and described in sorghum18 years ago (Porter et al., 1978) and millet in 1988 (Cherney et al.). The clear increase in forage quality (Fritz et al., 1981) resulting in increased animal performance (Lusk et al., 1984; Grant et al., 1995) has been researched and described. Yet, a commercial brown midrib hybrid was not available to growers in 1996. This will soon be accomplished (J. O'Rear, Garrison & Townsend, Inc. 1996, personal communication). Why has it taken so long?

Technology: Do More With Less

Forage sorghum and millet breeding programs will have to acquire (by some means) and utilize the best state of the art technology in order to increase impact. Few fully funded forage programs can afford these technologies alone. Because of limited resources available for forage sorghum and millet breeding, enhancing collaborations among breeders is necessary. Automated plot harvesting equipment is essential for yield testing. Enhanced NIRS capabilities, including "global" prediction equations, will be-

come essential for quality assessment. Both technologies substantially increase the number of lines that can be evaluated, while lowering time and/or funds committed. Development and use of molecular markers for selection will become important for forage parameters as they become available and affordable.

New Technologies/Markets/Industries

Astute readers will have noted that although the title of this paper included the topic of breeding for "fuel," it has not yet been addressed. Because starch is easily converted to sugar and then fermented, a large ethanol industry has developed in the United States, utilizing grain as its primary raw substrate. Midwestern U.S. newspapers routinely report on expansion of already large industrial ethanol projects. On Thursday, Sept. 12, the *Lincoln Journal Star* reported that "High Plains Corp. has announced a $17 million contract to produce industrial-grade ethanol in its York (NE) plant" (Russo, 1996). Considerable effort has been spent developing sweet sorghum lines for ethanol production. A bibliography compiled by Duncan (1993) shows over 100 references related to this topic. At the present time, a fuel industry has failed to develop around sweet sorghum in the United States.

Recent research emphasis has begun to shift from sugar to biomass. Starch is made up of D-glucose units bound in $\alpha(1\rightarrow4)$ linkages (amylose) or $\alpha(1\rightarrow4)$ chains with $\alpha(1\rightarrow6)$ branch points (amylopectin). Plant cell walls are made primarily of cellulose, linear polymers of D-glucose in $\beta(1\rightarrow4)$ linkage. Hemicelluloses, polymers of pentoses, are also common cell wall components (Lehninger, 1977). If technologies could be developed to make the glucose in cellulose available, and to make the pentoses in hemicellulose available and fermentable, abundant biomass could become an economical raw substrate for the ethanol industry.

Advances in fermentation technology accomplished with molecular biology are making the above scenario economically possible. Research permitting efficient breakdown of cellulose and hemicellulose to simple sugars is underway (Vogel, 1996). Zhang et al. (1995) have produced recombinant bacteria that can ferment glucose and xylose and produce high (86% of theoretical) ethanol yields. Wyman (1992) indicates that the cost of producing ethanol from biomass in 1992 was $0.38 L ($1.35/gal) and predicted that it may be feasible to produce ethanol for $0.16 ($0.60/gal) by the year 2010, making ethanol from biomass equivalent to $25/barrel crude oil. If this industry develops, our challenge will be developing sorghum and pearl millet forages that can provide biomass that is competitive economically, at acceptable environmental, political, and cultural costs compared to other potential biomass species.

Other developing industries also could utilize sorghum stover as raw substrate. These include industries that produce construction materials, such as fiberboard, and the paper industry. A plan to build an $89 million pulp plant in central Nebraska was recently announced (Daib, 1996). Initial estimates indicate this single plant will need 60,000 to 73,000 ha of corn stalk stover for substrate. Harvest, transportation, and storage technologies are currently being worked out. An imme-

diate challenge is to determine if it is possible to develop sorghum or millet stover that is superior to corn. If so, narrow breeding objectives could be established to develop hybrids with this market as a target.

Conclusion

Forage sorghum and millet breeding programs exist in an era of limited resources. Unless markets for these products grow or are developed, breeders will have to become more efficient and focused to continue serving their current clientele. To close on a positive note, forage sorghum and millet breeders do have a wealth of genes and genetic knowledge to work with that is not available to breeders working with many other forage species. We may be envied by some of our forage breeding colleagues because of the availabilty of such tools in producing varieties and hybrids that meet livestock producers' needs. These tools also should enable focused and rapid response to the needs of new industrial markets as they continue to develop.

References

Andrews, D.J., and K.A. Kumar. 1992. Pearl millet for food, feed and forage. Adv. Agron. 42: 89-139.

Besag, J.E., and R.A.Kempton.1988.Statistical analysis of field experiments using neighboring plots. Biometrics 42:231-251.

Bramel-Cox, P.J., J.D. Hancock, K.A. Kumar, and D.J. Andrews. 1995. Sorghum and millets for forage and feed. p. 325-364. *In* D.A.V. Dendy (ed.) Sorghum and millets: Chemistry and technology. American Association of Cereal Chemists, Inc., St. Paul, MN.

Cherney, J.H., J.D. Axtell, M.M. Hassen, and K.S. Anliker. 1988. Forage quality characterization of a chemically induced brown-midrib mutant in pearl millet. Crop Sci. 28:783-787.

Daib, J. 1996, September 13. Farmers lend an ear to plan that turns old cornstalks into paper. Lincoln Journal Star, p. 7B.

Duncan, R.R. 1993. Sweet sorghum bibliography. Sorghum Newsletter 34:81-87.

Eyster, W. H. 1926. Chromosomes VIII in maize. Science 64:22.

Fritz, J.O., R.P. Cantrell, V.L. Lechtenberg, J.D. Axtell, and J.M. Hertel. 1981. Brown midrib mutants in sudangrass and grain sorghum. Crop Sci. 21:706-709.

Gleeson, A.C., and B.R. Cullis. 1987. Residual maximum likelihood (REML) estimation of a neighbor model for field experiments. Biometrics 43:277-299.

Goering, H.K., and P.J. Van Soest. 1970. Forage fiber analyses. USDA Agric. Handb. No. 379.

Grant, R.J., K.J. Moore, and J.F. Pedersen. 1995. Brown midrib sorghum silage for midlactation dairy cows. J. Dairy Sci. 78:1970-1980.

Hanna, W.W., W.G. Monson, and G.W. Burton. 1977. Morphological and anatomical factors affecting forage quality. Ga. Agric. Res. 18:17-21.

ICRISAT. 1996. ICRISAT Global Research Portfolio [On-line]. Available: Internet: http://www.cgiar.org/icrisat/research.htm.

Johnson, B., S. Rodriguez-Herrea, and W. Stroup. 1992. Recent developments in design and analysis of corn and yield trails. p. 177-187. *In* Proc. 47th Ann. Corn and Sorghum Industry Res. Conf., Chicago, IL.

Kalton, R.R. 1988. Overview of the forage sorghums. Proc. Am. Seed Trade Assoc. Annu. Corn Sorghum Res. Conf. 43:1-12.

Lehninger, Albert L., 1977. Biochemistry, 2nd ed. Worth Publishers, Inc., New York.

Lusk, J.W., P.K. Karau, D.O. Balogu, and L.M. Gourley. 1984. Brown midrib or corn silage for milk production. J. Dairy Sci. 67:1739-1744.

Marten, G.C., and R.F. Barnes. 1980. Prediction of energy digestibility of forages with *in vitro* rumen fermentation and fungal enzyme systems. p. 61-71. *In* W.G. Pidgen, C.C. Balch, and Michael Graham (eds.) Standardization of analytical methodology for feeds. Publ. IDRC-134e Int. Res. Dev. Ctr., Ottowa, Ont., Canada.

Marten, G.C., J.S. Shenk, and F.E. Barton. 1989. Near infrared reflectance spectroscopy (NIRS): Analysis of forage quality. USDA, ARS Agriculture Handbook No. 643.

Pedersen, J.F., and K.J. Moore. 1995. An automated plot harvest system for use with a commercial forage harvester. Agron. J. 87:605-607.

Pedersen, J.F., K.J. Moore, and E. van Santen. 1991. Interpretive analysis for forage yield trial data. Agron. J. 83:774-776.

Porter, K.S., J.D. Axtell, V.L. Lechtenberg, and V.F. Colenbrander. 1978. Phenotype, fiber composition, and *in vitro* dry matter disappear-

ance of chemically induced brown midrib (*bmr*) mutants of sorghum. Crop Sci. 18:205-208.

Russo, E. 1996, September 12. Big ethanol contract goes to York. Lincoln Journal Star, p. 7B.

Schofield, P.R., R.E. Pitt, and A.N. Pell. 1994. Kinetics of fiber digestion from in vitro gas production. J. Anim. Sci. 72:2980.

Tilley, J.M.A., and R.A. Terry. 1963. A two-stage technique for the *in vitro* digestion of forage crops. J. Br. Grassl. Soc. 18:104-111.

United States Department of Agriculture. 1994. Agricultural Statistics. National Agricultural Statistics Service. United States Government Printing Office, Washington, D.C.

United States Department of Agriculture. 1996. USDA Research CRIS Database [On-line]. Available: Internet: http://cos.gdb.org/best/fed-fund/usda/usda.form.html.

Vogel, K.P. 1996. Energy production from forages (or American agriculture - back to the future). J. Soil and Water Conserv. 51:137-139.

Wyman, C.E. 1990. The DOE/SERI Ethanol for biomass program. Ethanol from biomass annual review meeting - draft proceedings, Sept. 12, 1990, Lincoln, NE. National Renewable Energy Lab, Golden, CO.

Zhang, M., C. Eddy, K. Deanda, M. Finkstein, and S. Picataggio. 1995. Metabolic engineering of a pentose metabolism pathway in ethanologenic Zymomonas mobilis. Science 267:240-243.

Overcoming Constraints to Utilization of Sorghum and Millet

L.W. Rooney*, R.D. Waniska, and R. Subramanian

Abstract

Sorghum and pearl millet are used in a wide variety of traditional foods in the semi-arid tropics. However, their use as food is declining in urban areas as wheat, rice, and maize products become more plentiful. Lack of a reliable supply of high quality grain for processing severely limits the acceptance of sorghum and pearl millet. Shelf-stable products are in short supply because the grains available for processing are of inferior quality. Technology is available for processing sorghum and pearl millet; however, major extension and improved cultivars are needed. Other constraints to the use of sorghum and pearl millet include their image as "second class" crops, the tannins in sorghum, low cost imported wheat, rice, and maize, and government policies. Breeders must work diligently to develop new cultivars, targeting total units of useful food or feed per hectare. Improved end-use quality will allow value-added processing, which could improve farm income from identity-preserved grain.

Sorghum and pearl millet are important food crops in the dry tropical areas of the world. They have good composition and can be made into a wide array of products, such as fermented and unfermented breads, beverages, porridges, snacks, rice-like products, and couscous. Significant reviews on the chemistry, quality, nutritional value, and technology of sorghum and millets have been published (Hulse et al., 1980; Rooney et al., 1980, 1982, 1986; Hoseney et al., 1987; Rooney and Serna-Saldivar, 1991; Serna-Saldivar et al., 1991; Dendy, 1995).

The purpose of this paper is to critically evaluate the major constraints to sorghum and millet use and to determine what can be done to enhance and expand use of sorghum and millet because of their relative advantages in hot dry environments. We do not intend to review all the literature, but we have included a bibliography of critical references.

Lloyd W. Rooney and R.D. Waniska, Cereal Quality Laboratory, Texas A&M University, College Station, Texas; and R. Subramanian, ICRISAT, Hyderabad, India. *Corresponding author.

Constraints on the Use of Sorghum and Millet as Food

Use of sorghum and millet as human food has decreased during the last two decades for many reasons. Lack of a consistent supply of good quality grain for processing is a tough obstacle to overcome. The image of sorghum and millet as "poor people's food" has led to avoidance by upper and middle class consumers. In addition, governments often provide subsidies for wheat, rice, or maize-based foods that are denied to sorghum and millet processors. Industrialized countries export inexpensive wheat flour,

maize meal, and rice to sorghum- and millet-producing countries, which means local sorghum and millet products cannot compete economically. Urban consumers want food products that deliver convenience, taste, texture, color, and shelf-stability at an economical cost, but sorghum and millet products usually cannot meet these requirements. Grain molds, weathering, and head bugs are major problems in many sorghum-producing areas.

In our experience, it is possible to produce outstanding products from sorghum and millet cultivars that have good processing quality. However, disaster strikes when products must be made with samples from the regular grain markets. It is not possible to compete with rice when 10% of the "white" sorghum kernels have a purple testa, resulting in a dark-colored product. This mixture of grains makes it difficult (if not impossible) to produce acceptable products. Locally grown maize also has problems, but in many countries the maize is grown by larger farmers and the quality is more uniform for processing. The lack of a consistent supply of good quality sorghum grain often precludes pilot plant production trials of new products.

The alleged poor nutritional quality of sorghum, especially due to tannins and poor protein digestibility, often is detrimental to its acceptance. Some key nutritionists and others believe that all sorghum contains tannins, thereby scaring away potential users. For example, a poultry nutritionist from India told me that he "would only feed sorghum if it was priced at 60 to 70% the value of maize." Upon further discussion, I learned he was afraid of the tannins in sorghum, even though most, if not all, Indian sorghum does not contain condensed tannins.

The "poor-feed" image of sorghum discourages food product development, even though good prototype products have been made by several multinational research and development centers. Usually such projects are killed by the marketing people who do not relish an up-hill battle to convince consumers to buy the product.

Environmental conditions during grain maturation greatly affect the appearance of the grain because the sorghum head is exposed to insects, molds, and moisture. The kernels are often attacked by grain-feeding bugs, and the damaged areas are ideal for attack by fungi. A hot and humid environment during and after maturation negatively affects grain quality. Molds discolor the grain, break down the endosperm, and significantly deteriorate processing qualities. Mold-damaged or weathered grain cannot be decorticated; the flour or grits are badly discolored and cannot be used for food. Moldy sorghums are impossible to malt for use in beer. The major fungi involved are *Fusarium*, *Alternaria,* and *Curvularia* species. Sorghum mold and weather damage are the most important limitations to sorghum improvement worldwide.

Strategies for Overcoming Constraints

The image of sorghum and millet as poor people's food must be overcome. We need to develop highly improved products from new sorghum that have attractive, more socially acceptable names. A new name, along with identity-preserved production schemes, would lead to improved acceptability. In our lab, we have used the term *JOWAR* to refer to special food sor-

ghums to circumvent the undesirable image of sorghum or milo that exists in the U.S. The marketing of new grains calls for imagination along with new superior food types. This is a difficult task to accomplish, but if sorghum and millet are to be used in value-added products, it is necessary.

Development of Value-Added Products

The best strategy for developing convenient, shelf-stable sorghum and millet foods is to use identity-preserved grains to produce high-value products that can be priced slightly lower than imported products. The targets should be middle class and wealthy people where sufficient profits can be gleaned to allow for developing the industry. There is no need to develop low-cost, inferior quality foods. It is necessary to develop high value foods that appeal to the wealthy urban consumers who will pay for convenience, acceptable taste, and texture. An array of decorticated products, instant couscous, flours, grits, snacks, and others could be targeted. Rice is considered a convenience food in many areas because it is ready for cooking. Similar products, e.g., grits, flours, and meals, could be made from sorghum and millet.

Development of value-added products should follow this general procedure: 1) identify upscale products and niche markets (supermarkets); 2) develop sorghum and millet products using low-input technologies and identity-preserved grain (specify variety and hybrids); and 3) educate farmers and producers.

Identity-Preserved Production

The maize and soybean industries are rapidly expanding value-enhanced marketing of grains, where varieties or hybrids are grown specifically for enhanced nutritive or processing properties. The grain is identity-preserved and sold to the end user. High oil corn, waxy maize, white corn, and special soybean varieties for processing are some examples. These markets will continue to grow because they are cost-effective as long as all parties make a reasonable profit. Where will sorghum be? Unless significant effort is made to improve sorghum quality, the crop will continue to lose market share and will be less valuable than other grains.

We believe that sorghum and millet must be grown under identity-preserved systems if they are to be used for value-added food products. Such systems are difficult to promote in sorghum and millet producing areas because there must be control of seed quality, production, harvesting, storage, handling, processing, and marketing. An identity-preserved system can work best for relatively small-scale processors who have access to grain supplies and to local markets in which logistics and marketing are controllable. For example, modern large-scale milling systems for sorghum and millet installed in Nigeria and the Sudan failed due mainly to lack of a consistent quality grain supply and high costs of transporting finished products from the central milling location across the country. In contrast, the introduction of small mills in Botswana has been successful because they are adapted to local conditions.

Improvement of Grain Quality

Sorghum and millet breeding objectives should be aimed toward useful products per hectare, value-added characteristics, economic grain yields and quality, mold/head bugs/weathering resistance, and available screening methods. Plant breeders should consider yield

in terms of useful quantities of food produced per unit of land. Breeding for yield without regard for quality is a mistake. Farmers in the semi-arid tropics have not planted improved sorghum varieties because they are susceptible to weathering and head bugs and have unacceptable processing and food properties. We reported years ago that a thin pericarp sorghum is unacceptable because the work required to dehull it by hand-pounding in a mortar and pestle is increased by 50% or greater. Therefore, sorghum breeders must recognize that food quality in many areas is critically important and is an essential part of grain yield. This has proven true in Honduras where Sureno, an improved sorghum, has been readily adopted by farmers because it has good tortilla-making qualities and a sweet juicy stalk that improves its forage quality.

In West Africa, a major priority should be to develop improved local varieties that are resistant to molds, weathering, and head bugs and have photosensitivity and good food quality (tan plant, straw color glumes). Such varieties could be utilized for identity-preserved sorghum production for value-added products. Until we obtain superior quality grains consistently (bright white or red color, no pigmented testa), sorghum and millet food use in urban areas is doomed. There are white and yellow seeded millets that have outstanding milling properties (hardness, spherical shape, white endosperm) and produce light color products. These might be preferred over purple or slate grey for use in specific value-added products.

Overcoming the Effects of Tannins in Sorghum

Sorghum and maize grains contain equal amounts of total phenols. Often laboratories apply general phenol assays to measure tannins, resulting in erroneously high values, even for sorghum that does not contain tannins. Tannin sorghum (brown sorghum) has a definitive pigmented testa caused by the combination of dominant B_1-B_2-S-genes. Such sorghum has significant levels of condensed tannins and some resistance to birds and grain molding. Sorghum tannins are catechins that cause reduced feed efficiency ranging from 10 to 30%, depending upon feeding systems, livestock species, and processing of the grain.

General phenol analysis methods often are used to determine tannins. All sorghum and other cereals contain many phenolic compounds that give a reaction for general phenols. Thus, Southeast Asian buyers often complain that U.S. sorghum contains high levels of tannins. In every instance, the analysis used is a general phenol assay which gives erroneous information.

The Vanillin-HCL method is the best test for tannin analysis in sorghum because it measures only condensed tannins, not total phenols. It uses catechin as a standard. Blanks should be subtracted from the readings since some indigenous compounds interfere with the assay. The catechin values arrived at by this method are only relative values since the standards are not sorghum tannins. Sometimes, tannic acid values are reported for sorghum, especially in the early literature. We now understand that sorghum does not contain any tannic acid. Thus, studies with tannic acid in animal feeding trials are irrelevant.

The effects of tannins can be overcome by adding formaldehyde in trace levels, malting, alkaline processing, and simply

adding extra protein to the ration. Animals fed rations containing high-tannin sorghum will usually consume more of the ration to produce similar weight gain. However, the concern that animals will not consume brown sorghum is unfounded.

Feed Utilization of Sorghum and Millet

Sorghum is a good feed grain as long as it is supplemented properly for the particular species being fed. The nutritive value of sorghum for food and feed is misunderstood by potential users who think that all sorghum contains tannins and that high-tannin sorghum cannot be used as livestock feeds. Sorghum without a pigmented testa has 95% or greater the feeding value of yellow dent maize for all species of livestock. Pearl millet has outstanding feed value for poultry and swine because of its higher fat and improved amino acid content. The digestibility of sorghum is improved significantly by proper processing of the grain prior to feeding. Sorghum and millet are ground finely for use in swine and poultry rations, while a wide array of methods are used for ruminant feeds, including popping, steam flaking, rolling, reconstituting, and grinding. Steam flaking is a preferred way of processing grain for the feedlots.

Traditional Food Use of Sorghum and Millet

The proper sorghum and millet cultivars can be processed into a wide variety of acceptable commercial food products. These grains can be extruded to produce a great array of snacks, ready-to-eat breakfast foods, instant porridges, and other products. The flakes of a waxy sorghum obtained by dry heat processing can be used to produce granola products with excellent texture and taste. Tortillas and tortilla chips have been produced from pearl millet and sorghum alone or with maize blends. The sorghum products have a bland flavor while pearl millet products have a unique flavor and color. The critical limitation is the lack of cost-efficient, reliable supplies of grain.

Three classes of sorghum based on endosperm texture have been proposed: 1) hard — suitable for thick porridges and couscous, 2) intermediate — suitable for unfermented breads, boiled rice-like products, malting and brewing, and 3) soft — suitable for fermented breads. Thus, plant breeders selecting for food quality within a specific food category can visually select for certain kernel characteristics and texture. In general, within each hardness group, the preferred sorghum should have a white pericarp and tan plant color without a pigmented subcoat; however, there are exceptions. For example, the preferred pericarp color of sorghum for beer is red; a dominant intensifier gene gives a very bright, clear red kernel with an intermediate to soft texture without a pigmented testa.

Plant breeders can use grain hardness, density, and ease of pericarp removal for early generation selection for sorghum and millet quality. Then laboratory milling and cooking tests can be conducted in advanced generations followed by large-scale processing and cooking trials for advanced breeding materials. The assays that should be applied for each food category have been summarized by Rooney et al. (1986) and Murty and Kumar (1995).

Special processes are used to convert brown or high-tannin sorghum into foods. In some areas, brown sorghum is steeped in wood ashes, germinated, and used to produce thick porridges. Brown sorghum is preferred for traditional opaque beer production. Sometimes special porridges made from brown sorghum are given to new mothers or are consumed by farmers doing strenuous work. Brown sorghum porridge is said to "stay with" the farmer longer, possibly because the condensed tannins affect digestibility. In some areas, brown sorghum products are preferred over white products. In East Africa, brown sorghum is added to opaque beer made from maize to improve the color and acceptability. In some areas, brown sorghum porridges are preferred. Malting and fermentation tend to improve the digestibility/nutritional value of brown sorghum.

Neither sorghum nor millet has gluten proteins. To produce yeast-leavened breads, sorghum or millet flour is usually substituted for part of the wheat flour in the formula. The level of substitution varies depending upon the quality of the wheat flour, the baking procedure, the quality of the sorghum or millet flour and the type of product desired. In biscuits, up to 100% of the flour can be sorghum or millet flour. The non-wheat flour tends to give a drier more sandy texture, so modifications to the formula must be made. The use of sorghum and millet in composite flours depends upon the cost and availability of acceptable quality flour. Sorghum has a definite advantage over maize in composite flours because of its bland flavor and white color. Unfortunately, high quality sorghum flour is usually unavailable because acceptable quality grain is lacking.

Dry Milling Quality

The milling quality of sorghum and millet is determined mainly by kernel size, shape, density, hardness, structure, presence of a pigmented testa, pericarp thickness, and color. Kernels with outstanding dehulling properties have a high proportion of hard endosperm, a thick white pericarp, and no pigmented testa. Soft floury kernels disintegrate during dehulling and cannot be milled efficiently. For hand dehulling, a thick starchy mesocarp (zz) reduces labor 50% or more. Long, slender pearl millet kernels have very poor dehulling properties, while white kernels have the highest yields of the preferred light color flour.

In general, abrasive milling techniques are effective. The barley pearler, Kett Mill, TADD, and Satake Rice Pearler have been used to determine milling properties of sorghum and millet (Reichert et al., 1988; Munck, 1995) in the breeding program. In effect, these techniques are similar with varying degrees of force applied to the grain to abrasively remove the pericarp. Good milling cultivars retain their integrity and allow the pericarp to be removed to produce high yields of white decorticated kernels. Hardness and density are strongly positively related to good milling properties. Adequate techniques to select for food quality are currently available for use in breeding programs.

Improving Sorghum Digestibility

In our research program, we have tried for thirty years to improve the digest-

ibility of sorghum through breeding. Invariably, types that have high digestibility according to *in vitro* tests also have soft, floury endosperm characteristics. Attempts to develop white or red sorghum with high digestibility have resulted in hybrids with poor yields and greater susceptibility to attack by molds and weathering. It is difficult to improve digestibility without enhancing the susceptibility of the grain to deterioration, because sorghum kernels are exposed to ambient conditions during maturation and are prone to attack by molds and insects.

Digestibility for ruminants and possibly swine is improved with waxy sorghum, but that improvement is accompanied by poor seed emergence and viability. Current waxy sorghum hybrids have lower yields of grain, although yields could be improved by greater breeding and selection efforts. A heterowaxy hybrid, where one parent is waxy and one nonwaxy, may provide a high-yielding sorghum with some improvement in digestibility. Some of the yellow endosperm hybrids thought to be more digestible have seed vigor and emergence problems. Therefore, we must be careful in the quest to develop highly digestible sorghums. The most efficient way may be to develop improved, more efficient processing techniques for sorghum grains bred to resist the molds and post-harvest weathering that occurs during sorghum production in most areas.

Reducing Effects of Molds, Insects, and Weathering on Grain Quality

Problems with grain molds, weathering, and head bugs in many sorghum producing areas can be overcome most quickly by the production of white, tan plant sorghum with straw-colored glumes. This is critically important in West Africa, where the new improved types have been significantly devastated by head bugs and mold. For example, N'Tenimissa has been recently released in Mali as the first tan plant local sorghum. It has some agronomic problems, but it definitely has improved grain characteristics for processing into food products. In the meantime, it is hoped that head bug and mold resistance can be obtained in adapted sorghum with higher yields.

Sorghum with open panicles, thin pericarp, condensed tannins, corneous endosperm, and large, tight glumes is generally considered more resistant to molds and weathering (Waniska et al., 1992). Antimicrobial proteins found in sorghum may lead to the production of white sorghum with more tolerance to molds. Weathering and molding of pearl millet does occur, but it is not usually a significant problem.

Sorghum does not develop aflatoxins prior to harvest like maize does. Sorghum contains A. flavus and other species, but, apparently the exposure of the grain to the atmosphere prevents significant levels of aflatoxin formation. Sorghum containing aflatoxin was present in 1996 in some areas of South Texas; however, the aflatoxin developed after harvest during storage of high moisture grains. In addition, sorghum does not produce significant amounts of fumonisin. This must be confirmed, but the relative resistance of sorghum to field contamination by these mycotoxins is a major advantage for sorghum over maize. As maize is grown under more marginal conditions, the risk of increased levels of mycotoxins must be considered.

Future of Sorghum and Millet

It is possible for consumption of sorghum and pearl millet to increase, as is the case in Nigeria where a change in government policy has greatly expanded the use of sorghum for brewing and in a wide array of malt beverages, malt extracts, biscuits, and other confectionary products. The use of sorghum would not have occurred without the change in government policy. Still, acquiring sufficient quantities of sorghum of good quality for processing is a major problem in Nigeria. In some cases maize is used instead of sorghum because more uniform supplies of consistent quality are available. Industry is slowly increasing special sorghum varieties with improved malting properties. Developing identity-preserved grains is important if sorghum and millet are to be accepted in urban foods.

Greater utilization of sorghum and pearl millet can occur through use of improved varieties, improved technologies, and government policy changes that promote indigenous cereals. The economics that are true today may quickly become obsolete when one of the above components changes. In 1996, the price of wheat increased rapidly, and interest in potential use of sorghum flours rose significantly. This interest has decreased rapidly, however, as the price of wheat flour has decreased. Thus, the major goal of sorghum and pearl millet research activities should be to develop the best quality, highest yielding cultivars possible to take advantage of whatever markets are economically viable. For example, sorghum in composite flour for bread is significantly better than maize flour, but unfortunately insufficient sorghum flour is available, so maize is often used. The bland flavor and white color of sorghum flour is a distinct advantage of sorghum over maize. Yet today in Mali, yellow corn flour is proposed for incorporation into composite breads. It is critically important that research continue to develop superior sorghum and pearl millet cultivars which will provide the grain required when new processes or old technologies become economically important. Sorghum and millet utilization as food will continue to decrease in urban areas until new convenient shelf-stable products are developed.

Sorghum and millet play important roles where maize production is marginal or likely to be contaminated with aflatoxin and fumonisins. The challenge to improve sorghum and millet utilization is great. Progress can be made but we must carefully evaluate our strategy. Clearly improved quality for food, feed, and industrial use must be a part of it.

Acknowledgment

I want to thank Ms. Pamela Littlejohn for word processing assistance. I thank my colleagues in the Texas A&M Sorghum Improvement Program for 30 years of wonderful cooperation and collaboration on sorghum quality research. Finally, I appreciate the long-term financial support from The Texas Agricultural Experiment Station and The United States Agency for International Development Collaborative Research Support through the International Sorghum and Millet Program (INTSORMIL).

References (Works Cited)

Dendy, D.A.V. 1995. Sorghum and millets chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Hoseney, R.C., D.U. Andrews, and H. Clark. 1987. Sorghum and pearl millet. *In* R.A. Olson and K. Frey (eds.) Nutritional quality of cereal grains: Genetic and agronomic improvement. Ameri-

can Society of Agronomy, Inc., Crop and Soil Science Societies of America, Inc., Madison, WI.

Hulse, J.H., E.M. Laing, and O.E. Pearson, O.E. 1980. Sorghum and the millets: Their composition and nutritive value. Academic Press, San Francisco, CA.

Munck, L. 1995. Milling technologies and processes. p. 223–81. *In* D.A.V. Dendy (ed.) Sorghum and millets chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Murty, D.S., and K.A. Kumar. 1995. Traditional uses of sorghum and millets. p. 185–221. *In* D.A.V. Dendy (ed.) Sorghum and millets chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Rooney, L.W., C.F. Earp, and M.N. Khan. 1982. Sorghums and millets. *In* I.A. Wolf (ed.) CRC handbook of processing and utilization in agriculture. CRC Press, Boca Raton, FL.

Rooney, L.W., M.N. Khan, and C.F. Earp. 1980. The technology of sorghum products. *In* E. Inglett and L. Munck (eds.) Cereals for food and beverages: Recent progress in cereal chemistry. Academic Press, New York, NY.

Rooney, L.W., A.W. Kirleis, and D.S. Murty. 1986. Traditional foods from sorghum: Their production, evaluation and nutritional value. *In* Y. Pomeranz (ed.) Advances in cereal science and technology, Vol. VIII. American Association of Cereal Chemistry, St. Paul, MN.

Rooney, L.W., and S.O. Serna-Saldivar. 1991. Sorghum. p. 233-270. *In* K.J. Lorenz and K. Kulp (eds.) Handbook of cereal science and technology. Marcel Dekker, New York, NY.

Serna-Saldivar, S.O., C.M. McDonough and L.W. Rooney. 1991, The millets. p. 271–300. *In* K.J. Lorenz and K. Kulp (eds.) Handbook of cereal science and technology. Marcel Dekker, New York, NY.

Waniska, R.D., G.A. Forbes, and B. Bandyopadhyay. (1992) Cereal chemistry and grain mold resistance p. 265–72. *In* W.J. deMilliano, et al. (eds.) Sorghum and millet diseases, a second world review. International Crops Research Center for the Semi–Arid Tropics, Patancheru, India.

Bibliography of Related Works

Butler, L.G. 1989. Effects of condensed tannins on animal nutrition. p. 391-402. *In* R.W. Hemingway and J.J. Karchesy (eds.) Chemistry and significance of condensed tannins. Plenum Press, New York.

Butler, L.G. 1990. The nature and amelioration of the antinutritional effects of tannins in sorghum grain. p. 191-205. *In* Proceedings of the international conference on sorghum nutritional quality, 26 Feb.-1 March 1990, Purdue University, West Lafayette, IN.

Creelman, R.A., L.W. Rooney, and F.R. Miller. 1982. Sorghum. p. 395-426. In Y. Pomeranz and L. Munck (eds.) Cereals: A renewable resource, theory and practice. American Association of Cereal Chemists, Minneapolis, MN.

Daiber, K.H., and J.R.N. Taylor. 1995. Opaque beer. p. 299–323. *In* D.A.V. Dendy (ed.) Sorghum and millets chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Hagerman, A.E.. and L.G. Butler. 1989. Choosing appropriate methods and standards for assaying tannin. Journal of Chemical Ecology 15:1795-1810.

Hallgren, L. 1995. Lager beers from sorghum. p. 283–97. *In* D.A.V. Dendy (ed.) Sorghum and millets chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Knabe, D.A. 1990. Sorghum as swine feed. *In* Proceedings of international conference on sorghum nutritional quality, 26 Feb. - 1 March, 1990, Purdue University, West Lafayette, IN.

McDonough, C.M., and L.W. Rooney. 1989. Structural characteristics of *Pennisetum americanum* using scanning electron and fluorescence microscopies. Food Microstructure 8:137-49.

Mwasaru, M.A., R.D. Reichert, and S.Z. Mukuru. 1988. Factors affecting the abrasive dehulling efficiency of high tannin sorghum. Cereal Chemistry 65:171-74.

Rooney. L.W., and C.M. McDonough. 1987. Food quality and consumer acceptance of pearl millet. *In* J.R. Witcombe and S.R. Beckerman (eds.) Proceedings of the international pearl millet workshop. ICRISAT, Patancheru, India.

Rooney, L.W., and F. Miller. 1982. Variation in the structure and kernel characteristics of sorghum. p. 143. In L.W. Rooney and D.S. Murty (eds.) International symposium on sorghum grain quality. ICRISAT, Patancheru. A.P., India.

Rooney, L.W., and R.L. Pflugfelder. 1986. Factors affecting starch digestibility with special emphasis on sorghum and maize. Journal of Animal Science 63:1607-23.

Seitz, L.M., R.L. Wright, R.D. Waniska, and L.W. Rooney. 1993. Contribution of 2–acetyl–1–pyrroline to odors from wetted ground pearl millet. Journal of Agriculture and Food Chemistry 41:955–58.

Serna–Saldivar, S.O., and L.W. Rooney. 1995. Structure and chemistry of sorghum and millets. p. 69–124. *In* D.A.V. Dendy (ed.) Sorghum and millets chemistry and technology. American Association of Cereal Chemists, St. Paul, MN.

Status and Breeding Requirements for Sorghum Utilization in Beverages in Nigeria

D.S. Murty*, S.A. Bello, and C.C. Nwasike

Abstract

*Sorghum [*Sorghum bicolor *(L.) Moench] grain has traditionally been used in Nigeria for malting and brewing opaque beers such as pito and burukutu on a domestic scale, while the beverage industries depended completely on imported barley malt. Since the imposition of a ban on imported barley and other cereals in 1988, beverage industries have successfully substituted barley malt with sorghum grain as malt and adjunct in the production of lager beer and non-alcoholic malt drinks. Industrial use of sorghum as adjunct requires cultivars with uniform grain size and shape (round or oval), hard endosperm, higher extract and soluble proteins, lower polyphenol or tannin and fat contents, and low gelatinization temperatures. Grains required by the malting industry should possess fast water uptake and high germinability, higher malt extract and enzyme (β-amylase) activities, soft endosperm, low polyphenol/tannin content, and less mold and rootlet activity during germination. Choice of appropriate cultivars, locations, and growing conditions could improve the quality of industrial raw material. Increased collaboration between research and industry is required.*

Nigeria is the foremost country in Africa in both total area cultivated with sorghum and sorghum production (4 million t; FAO, 1994). Commonly called *dawa*, sorghum is the staple cereal in northern Nigeria and is consumed in traditional foods such as *tuwo* (thick porridge), *ogi* (thin fermented porridge), *kunu tsamia* and *massa*. Traditionally, sorghum is also used in some parts of Nigeria in the production of opaque beers such as *burukutu*, *pito* and *otika* by the small cottage industry. Until the 1970s, however, the food and beverage industries in Nigeria totally depended on imported barley malt, wheat, maize, and other cereal products as raw materials (ICRISAT, 1990).

During the 1980s, the government of Nigeria introduced a Structural Adjustment Program (SAP) with emphasis on the local sourcing of raw materials to save foreign exchange and increase self-reliance. Earlier research and development efforts in Nigeria on the prospective use of local cereals such as sorghum came to light, and the Nigerian beverage industries made a strong and successful effort to substitute imported barley malt with local sorghum. It has been estimated through specific surveys in Nigeria that about 120,000 metric tons of sorghum were used per year by the industries (Forson and Ajayi, 1995). The objective of this paper is to summarize the current use of sorghum by the various Nigerian food and beverage industries, review the grain quality requirements for such end uses, and discuss their implication in breeding.

D.S. Murty, ICRISAT, B.P. 320, Bamako, Mali; S.A. Bello, Guinness (Nig.) PLC, PMB 21071, Ikeja, Lagos, Nigeria; and C.C. Nwasike, Department of Plant Science, Institute for Agricultural Research PMB 1044, Zaria, Nigeria. *Corresponding author.

Current Status of Utilization

Lager Beer

The potential use of sorghum as grain and/or malt in lager beer production was under investigation by researchers in Nigeria during the 1970s and early 1980s (Aisien, 1982; FIIRO, 1976; Okafor and Aniche, 1980; Okon and Uwaifo, 1985; Olaniyi, 1984; Skinner, 1976). Encouraging results led to pilot production trials in 1984 (Koleoso and Olatunji, 1992). However, the brewing industry was not obliged to use sorghum grain and malt in lager beer production until January, 1988, when the ban on barley imports became effective. The breweries have subsequently modified their brewing processes and equipment to a considerable extent to suit sorghum processing and brewing.

Currently several brands of lager beer and stout, such as *Star, Gulder, Satzenbrau, Harp, 33 Export, Trophy, Rock* and *Kronenburg,* are being produced and marketed with a major proportion of their cereal extract derived from sorghum. Several of these are produced by using 50-80% sorghum and 50-20% maize as the cereal source. Preferences for the form of sorghum used in lager beer production vary with brewers. It is used either as raw grain (broken pieces or fine grits) or malt. Different brewers use different proportions of sorghum malt, sorghum grits, and maize grits. For example some brewers use 40% sorghum malt, 40% sorghum grits, and 20% maize grits. However, all the breweries are using significant quantities of external enzymes such as α-amylase, neutral protease, β-glucanase, cellulase, and amyloglucosidase to obtain complete saccharification and wort clarification during the brewing process (Aisien, 1990). Bogunjoko (1992) estimated that one ton of sorghum grain could produce 70 hL of lager that would require 4 kg of exogenous enzymes. Hallgren (1995) described the clear beer brewing procedures required for sorghum substitution mixtures and their associated problems.

During the early 1980s, the sorghum cultivar SK5912, developed at the Institute for Agricultural Research (IAR), was identified as suitable for brewing and malting (Andrews, 1970; Curtis, 1967; Koleoso and Olatunji, 1992; Obilana, 1985). Due to insufficient supply of this grain, however, brewers have been using local Kaura and Farafara grains procured from the markets. The grains of SK5912 and Kaura have yellow endosperm while Farafara has normal white endosperm. The brewers are not satisfied with the grain lots available in the local market because they frequently represent a mixture of different cultivars with similar grain color, and impurities are high. Some breweries have invested in large agricultural farms, where they could grow sorghum and maize cultivars of their choice and obtain uniform and dependable raw material. Guinness (Nig.) PLC has undertaken a contract grower scheme for grain procurement of another recently bred early maturing white grain sorghum cultivar, ICSV400.

The qualities of sorghum malt available to brewers in the Nigerian market vary from lot to lot, and non-uniform grain lots and malt affect their milling and brew house performance (ICRISAT, 1990). The sorghum malting technology

in Nigeria is in its infancy and undergoing constant improvement. Only a few companies can supply sorghum malt in commercial quantities; some breweries have acquired their own malting facilities. Floor malting is still widely used, while box malting and various other locally modified methods are upcoming. Problems encountered during industrial malting in Nigeria include molds, cyanogenesis, high malting losses (up to 20%), insufficient modification, and non-uniform germination (Ikediobi, 1990). There also is a shortage of good quality brewers' grits in the market, and some brewers use a coarse meal of whole sorghum grain obtained by hammer milling. The milling quality of the grain available in the market and the milling process are not satisfactory; as a result, millers are able to achieve only a maximum of 50% extraction of grits after dehulling (Hallgren, 1995).

Non-Alcoholic Malt Drinks

The production of lager beer by the brewing industry in Nigeria has declined considerably over the years (ICRISAT, 1990). In 1995, most breweries operated at 50% of their installed capacity and unofficial estimates of total beer produced that year are around only 4 million hL, compared to the original installed production capacity of 18 million hL in 1988 (Bogunjoko, 1992). However, the production of non-alcoholic malt drinks by the same breweries is apparently increasing. A variety of malt drinks with brand names such as *Malta, Maltina, Amstel Malta* and *Evamalt* are being increasingly and successfully marketed.

The production process for malt drinks is similar to that for lager beer until the wort separation stage; alcoholic fermentation is avoided. The wort is further boiled; flavor and coloring agents are added before bottling. Since the ban on imported barley came into effect, the breweries have successfully substituted sorghum grain and malt for barley malt and other adjuncts used in malt drinks. The use of sorghum malt for production of non-alcoholic malt drinks and other food drinks appears to be much more widespread than for production of lager beer. There seem to be no major problems in consumer acceptance and marketing of these malt drinks, which are highly popular and liked across various religious communities. However, problems related to the acquisition of good quality sorghum malt and adjunct by the breweries are the same as those mentioned for lager beer production.

Weaning Food Drinks

Malt cocoa-based weaning food drinks are highly popular in Nigeria. The industries in this sector traditionally used barley malt extract as the base material. However, since 1988, these industries also have successfully substituted sorghum malt or grain extract for barley. The production process involves the preparation of a clear wort, concentration of the wort to a syrup, addition of cocoa, whey, and other nutritive ingredients, and preparation of a dry cake followed by packaging in a granulated form. Several malt cocoa drinks, such as *Milo* and *Bournvita,* are being marketed with considerable sorghum extract contents. The quality of sorghum malt extract is, in general, similar to that of barley malt extract; therefore, locally sourced sorghum malt extract can substitute for imported barley malt in a

range of weaning foods at a cheaper price, and some Nigerian companies are selling sorghum malt extract (Solabi, 1990). Recently baby food formulations also have been supplemented with sorghum malt extract.

Sorghum for Malting

Sorghum has traditionally been malted for centuries in Africa to make alcoholic and non-alcoholic beverages. Industrial malting of sorghum based on scientific principles and modern technology has been well established in South Africa, but is only a recent enterprise in Nigeria (Daiber and Taylor, 1995; Ikediobi, 1990; Novellie, 1968). Sorghum can be malted by soaking clean grain in water at 25-30°C for 24-48 hours, then draining the excess water, and allowing germination and growth for about 5 to 6 days at 25-30°C (Palmer, 1992). The moisture level of the grain is kept high (>40%) by frequent sprinkling of water. The germinating grains are frequently turned and aerated, and a high level of humidity is maintained. Microbial infection can be reduced by using 0.1% formaldehyde during the steeping process. The malted grain is dried rapidly at 50°C for about 24 hours to a moisture level of about 10%. In Nigeria, the dried malt is agitated and derooted by screening. Unlike barley, the application of gibberillic acid during steeping of sorghum doesn't trigger enzyme synthesis (Palmer, 1989). Sorghum grain used for malting must meet more stringent and specific requirements than that used for food, feed, or adjunct. However, no official standards of sorghum malt quality have been established in Nigeria, but the following grain and malt characters are desired by the maltsters and brewers.

Clean and Mold-Free Grains

Sorghum grains for malting should be generally clean and free from molds and bacteria. Grain molds are the major problem in sorghum malting, and, in spite of treatment with formaldehyde, fungi located in the endosperm could create mold problems on the malting floor under high humidity and warm temperatures. Sorghum grains produced under hot and humid conditions are ideal for development of fungi such as *Aspergillus flavus* and *Fusarium* spp on the grain surface and can pose mycotoxin problems in the malt (Dufour and Melotte, 1992). Although grain mold-resistant cultivars are desirable, molded grain can be avoided by choosing production environments less prone to mold attack.

High Germinability (95%)

The importance of good germinability of grains used for malting should not be overemphasized. Germinability must be assured by harvesting grain at complete maturity and appropriate moisture content (<12%) and storing it under clean and dry conditions to protect the grain from insect and microbial attack.

Uniform Grain Size and Fast Water Uptake

Uniform grain size is desired in malts for lager brewing because the undersized grains potentially yield lower extract, albeit relatively more protein due to the improved embryo to endosperm ratio. Fast water uptake by the grain is also desired for rapid mobilization of enzyme activity, increased soluble protein, and endosperm modification (Dufour and Melotte, 1992; Ikediobi 1990).

Low Malting Loss

One disadvantage of sorghum as a source of malt is the relatively higher malting loss compared to barley. Malting losses of about 18 to 28% were reported by different researchers after 96 hours of germination, and there were significant differences between cultivars (Illori et al., 1990; Jayatissa et al., 1980; Subramanian et al., 1995). Average malting losses of 20% may have to be tolerated in sorghum while selection for relatively lower malting loss continues.

High Malt Extract (80%)

Percentage of total malt extract is the most important trait considered by lager brewers since it is the net result of enzyme activity, endosperm modification, and solubilization. In opaque beer production, complete solubilization is not required, so percentage of total extract is of secondary importance to diastatic enzyme activity. Palmer (1989) and Dufour and Melotte (1992) suggested improved three-step mashing procedures to obtain higher percentage of malt extracts in sorghum. Swanston et al. (1992 and 1993) observed wide differences between sorghum cultivars for percentage of total extract. Large grain size is important for obtaining a higher percentage of total malt extract.

High Diastatic Power

Diastatic power is the inherent ability of the malt to enzymatically hydrolyze carbohydrates. Diastatic power of sorghum malt is due to the joint activity of α-amylase and β-amylase, both of which are synthesized *de novo* during germination in the embryo and scutellum (Daiber and Taylor 1995; Novellie, 1984). The diastatic power of sorghum malt is much lower than that of barley malt. Also in contrast to barley, in sorghum malt α-amylase is the major component (60-80%) and β-amylase is the minor. The methods employed to measure and express diastatic power by various workers have varied. The joint activity of the two enzymes has frequently been measured and expressed in Sorghum Diastase Units (SDU/g dry malt); one SDU is roughly equivalent to 0.5° Lintner.

The diastatic power of sorghum is widely recognized to vary between cultivars (Novellie, 1984; Daiber, 1988; Jayatissa et al., 1980; Subramanian et al., 1995). The activity of one amylase could be determined by the inactivation of the other. Munck and Mundy (1984) identified two α-amylase isozymes and a homogeneous α-amylase. The saccharification power of malted sorghum is restricted mainly because of limited β-amylase (Nout and Davies, 1982). However, some cultivars can develop significantly higher levels of β-amylase during germination (Palmer, 1989). Munck and Mundy (1984), Swanston et al. (1992), and Dufour and Melotte (1992) analysed sorghum grains from a large number of cultivars and found highly significant differences for β-amylase activity. The α-amylase activity levels were found to be generally acceptable for brewing and sometimes even higher than those found in barley. It is therefore important to select sorghum cultivars with relatively higher levels of β-amylase or a higher ratio of β-amylase to α-amylase.

High Free Alpha-Amino Nitrogen (Fan) Content

During malting, the grain proteins are hydrolysed by the proteolytic enzymes to yield soluble peptides and free a-amino

nitrogen (FAN). The ratio of FAN to total nitrogen of the malt naturally indicates the proteolytic activity. In germinating grains, FAN supports the growing seedling, while in brewing, FAN is critical for rapid multiplication of the yeast followed by normal fermentation of the wort (Pickerell, 1986; Taylor, 1983; Taylor and Boyd, 1986). Normally an optimal level of 130-150 mg/L of FAN is required for satisfactory growth of yeast (Hallgren, 1995). Variation due to cultivars and environments has been recognized to be equally important for FAN of malted sorghum (Daiber, 1988 ; Daiber and Taylor, 1995; Chitsika and Mudimbu 1992; Subramanian et al., 1995). Good monitoring and selection of sorghum cultivars with a favorable FAN ratio and optimal fertilization of production fields is required.

Low Polyphenol or Tannin Content

In clear or lager beer production, only white or cream colored grains free from tannins or polyphenols are used for malt and adjunct. Grains of local white grain cultivars procured from Nigerian markets exhibit impurities with brown grains containing testa. White grains with red or purple spots on the pericarp could leach pigment into the endosperm. The polyphenolic compounds not only inhibit enzyme activity, but also lead to color problems in the wort. White grains from tan plant types cause the least color problems of the wort.

Medium to Soft Endosperm Texture

Sorghum malt is relatively hard and less friable than barley malt; therefore endosperm cell wall breakdown is relatively poor and slow during the malting process, which leads to wort clarification and separation problems in lager brewing (Palmer, 1992). During the malting of barley, endogenous β-glucanases degrade the cell walls rapidly, while in the malting of sorghum, endosperm cell walls do not break down, but develop portals through which starch and protein-degrading enzymes pass to access the cell reserves (Palmer, 1991). It has been suggested that sorghum endosperm cell walls might require application of β-glucanases and cellulases to obtain improved modification and wort separation (Etok Akpan, 1993).

Since the peripheral corneous endosperm resists complete modification, Ikediobi (1990) identified loosely packed starch granules and easily accessible protein bodies as desired properties for improved malting. Swanston et al. (1992) found a close relationship between malt milling energy and percentage of total extract. Rooney et al. (1986) suggested that sorghum grains with intermediate texture could be suitable for beer products. Palmer (1989) felt that grains with mealy endosperm may be required by maltsters. Since soft and floury endosperm types are generally known to be vulnerable to molds and storage insects, medium endosperm texture types with a limited peripheral corneous layer and a relatively large central floury area might be suitable for malting.

Sorghum as Adjunct

Sorghum is used by the lager beer industry, as well as the non-alcoholic beverage and baby food industries in Nigeria, as an adjunct or a source of cereal extract. It is used either as a coarse meal or uniform grits, depending upon availability and price. Because of either the lack of well-established industrial sorghum mill-

ing technologies or insufficient supply of grain of uniform and consistent quality, there is a shortage of sorghum brewers' grits in the market. Hallgren (1995) discussed the problems associated with brewing a sorghum meal of non-uniform particles, particularly when the flour content is high. Therefore, for sorghum grain to be used as an adjunct, the dehulling and milling qualities are most important. Various grain quality characters that affect milling quality and brewers' grits are considered below.

Uniform Size and Shape

It is now well established that uniform size and symmetrical (oval or round) shape of the sorghum grain are important for mechanical dehulling and processing to grits with minimum milling losses (Murty, 1992).

Low Phenols and Tannin Content

Polyphenols and tannins in the adjunct impart an off color and astringency problems to the extract, in addition to causing enzyme inhibition. In general, grains with testa exhibit poor milling qualities. Therefore grains with white or yellow pericarp (and endosperm) free from colored spots are preferred for milling.

Hard Endosperm Texture

Grains with hard endosperm texture are suitable for dehulling and gritting. Hardness of the grain could be evaluated through various tests: resistance to abrasive dehulling or pearling, flotation, milling energy determination, particle size index (psi) of milled products, milling time/Stenvert hardness measurement, etc. (Hallgren and Murty, 1983; Pomeranz, 1986). All these methods are useful to breeders, although flotation in sodium nitrate and Stenvert hardness tests require small sample size and simple equipment. A combination of the Stenvert hardness test with psi determination of the milled product might yield complete information to select for grain hardness. Hallgren (1995) suggested particle size index determination to evaluate the quality of grits.

Higher Extract (90%) and Soluble Nitrogen

High starch content in the sorghum grits is important for yielding the desired extract (90% on dry basis). The protein content of the grits should be around 8-9%, but more importantly, the grits should possess a favorable ratio of soluble to insoluble nitrogen.

Low Fat Content

The oil content of sorghum grits used as adjunct in lager beer should be less than 1%, because oil reduces the shelf life of the grits and leads to poor foam stability of the beer (Hallgren, 1995). Normally oil, ash, and fiber contents of the grits and other flour products are routinely evaluated. Efficient degermination and milling techniques applied to hard grain sorghum should yield grits with acceptable low fat content.

Low Gelatinization Temperature

The gelatinization temperature (GT) of sorghum starch can be observed by the loss of birefringence in the hot stage microscope. Normally the GTs in sorghum

vary between 68-76°C and are higher than those of barley (Hallgren, 1995). Brewers need to follow modified mashing procedures for sorghum and thus incur extra energy costs. Therefore, sorghum grains with lower GTs and better cooking properties are desired by brewers, although the problems are not insurmountable.

Breeding Implications

For millers to produce a good adjunct and for maltsters to produce malt required by the various industries, sorghum grain quality considerations are generally the same except for the relatively soft endosperm texture and higher diastatic power needs of maltsters. Laboratory methods to evaluate the various physical and chemical parameters desired by the industries are straightforward and simple except for the enzyme assays. Sorghum cultivars suitable for producing adjunct must have white or yellow grains (no testa or phenols) of an optimum size (30g/1000) and shape (round or oval) and a highly corneous texture to permit higher extraction of pearled and gritted products. These traits can be achieved by selecting for increased density and hardness of the grain and high recovery from pearling.

In view of the positive correlation of endosperm hardness and mold resistance among white grain types (Jambunathan et al., 1992), simultaneous progress could be made for improved mold resistance. However, maltsters' requirements suggest selection of medium or soft endosperm types, which are unfortunately known to be vulnerable to grain molds in wet and humid environments. In general, the grain protein content of sorghum is fairly adequate and not a serious limitation for industrial use, provided the production environments are properly managed. It might therefore be practical to choose suitable cultivars and environments less prone to molds for producing grain for malting.

Except for grain color and shape, most of the quality traits desired for malting and brewing are affected by genotype × environment interactions. On the other hand, there is a considerable limitation of enzyme activity levels in sorghum required for satisfactory conversion and solubilization during the malting and brewing of lager beer. In view of reports on significant genetic variation for α- and β-amylase activities in sorghum, breeders should pursue selection for a higher β-amylase component in germplasm and breeding collections. The need for sorghum grains with low gelatinization temperatures and lack of endosperm cell wall-degrading enzymes has been mentioned. It is suggested that mutation breeding techniques could possibly be applied to search for such desired sorghum mutants.

Future

Sorghum utilization by the industries in Nigeria is currently less than 5% of total sorghum production, but is widespread in various beverage, food drink, and baby food industries. Observed market prices in the last decade have generally shown sorghum to be marginally cheaper than maize. If this trend continues into the future, it is expected that sorghum utilization by industries in Nigeria will increase. The problems of procuring sorghum grain of consistent quality would be resolved by

intervention of the agrobased industries in seed multiplication of sorghum and contract farming in suitable agroecological production zones. The Nigerian experience during the last decade in the industrial application of locally produced cereals is remarkable and could set the trend in other countries of the continent.

Sorghum is probably the only tropical cereal with increased potential for use in malt-based products in the future. Therefore research should focus on improved knowledge of sorghum malting, assessment and use, and methods to reduce local production costs. It would be profitable to fully explore the sorghum germplasm for malting traits. Further advances in technology for malting and brewing of sorghum, coupled with genetic enhancement, could brighten the prospects for industrial use of sorghum. More intensive collaboration between research and industry is called for.

References

Aisien, A.O. 1982. Enzymatic modification of sorghum endosperm during growth and malting. J. Sci. Food Agric. 33:754-759.

Aisien, A.O. 1990. Utilization of sorghum in brewing lager beer in Nigeria. p. 24. *In* Industrial utilization of sorghum. Summary proceedings of a symposium on the current status and potential of industrial uses of sorghum in Nigeria, 4-6 Dec, 1989, Kano, Nigeria. ICRISAT, Patancheru, 502 324 (A.P.), India.

Aisien, A.O., and G.C.J. Muts. 1987. Microscale malting and brewing studies of some sorghum varieties. J. Inst. Brew. 93:328-331.

Aisien, A.O., G.H. Palmer, and J.R. Stark. 1983. The development of enzymes during germination and seedling growth in Nigerian sorghum. Starch/Staerke 35:316-320.

Andrews, D.J. 1970. Breeding and testing dwarf sorghums in Nigeria. Expl. Agric. 6:41-50.

Bogunjoko. J.S.T. 1992. Industrial uses of sorghum in Nigeria. p. 115-119. *In* Utilization of sorghum and millets. ICRISAT, Patancheru, 502 324 (A.P.) India.

Chitsika, J.M., and M.W. Mudimbu. 1992. Quality criteria for opaque beer in Zimbabwe. p. 151-155. *In* Utilization of sorghum and millets. ICRISAT, Patancheru, 502 324 (A.P.), India.

Curtis, D.L. 1967. A review of the sorghum breeding programme in Nigeria. Samaru Miscellaneous Paper No. 18, p. 14. ABU, Samaru, Nigeria.

Daiber, K.H. 1988. Malted and treated sorghum for the industrial production of beer, feed and food. p. 15-30. *In* Proceedings 4th quadrennial symposium on sorghum and millet. Lausanne, Switzerland, ICC, International Association of Cereal Science and Technology.

Daiber, K.H., and J.R.N. Taylor. 1995. Opaque beers. p. 299-323. *In* D.A.V. Dendy (ed.) Sorghum and millets: Chemistry and technology. AACC. Minn. USA

Dufour, J.P., and L. Melotte. 1992. Sorghum malts for the production of a lager beer. ASBC Journal 50:3, 110-119.

Etok Akpan, O.U. 1993. Enzyme degradation and nature of the endosperm cell walls of germinating sorghums and barley. J. Sci. Food Agric. 61:389-393.

FAO. 1994. Agrostat data base. Food and Agricultural Organization of the UN., Rome

FIIRO (Federal Institute of Industrial Research, Oshodi). 1976. Production of malt from Nigerian sorghum. Technical Information Bulletin for Industries (FIIRO). 1976 (5) 1-4.

Forson, J.B., and O. Ajayi. 1995. Industrial utilization of sorghum in Nigeria: Implication of evidence and distributive impacts for research. p. 7-18. *In* Processing and industrial utilization of sorghum and related cereals in Africa. OAU/STRC-SAFGRAD, Ouagadougou, Burkina Faso.

Glennie, C.W. 1984. Endosperm cell wall modification in sorghum grain during germination. Cereal Chem. 61:285-289.

Hallgren, L. 1995. Lager beers from sorghum. p. 283-297. *In* Sorghum and millets: Chemistry and technology, AACC. Minn. USA.

Hallgren, L., and D.S. Murty. 1983. A screening test for grain hardness in sorghum employing density grading in sodium nitrate solution. J. Cereal Sci. 1:265-274.

Ikediobi, C.O. 1990. Industrial production of sorghum malt in Nigeria. p. 32. *In* Industrial utilization of sorghum. ICRISAT, Patancheru, 502 324, (A.P.) India.

Illori, M.O. 1991. The use of sorghum for beer brewing in Nigeria. Technovation 11:1, 27-37.

Illori, M.O., J.O. Akingbala, G.B. Oguntimein, and J.O. Ogundiwin. 1990. Effect of grain bed thickness, duration of steeping and germination on the malting properties of improved Nigerian sorghum varieties. Lebensm. Wiss.U. Technol. 23, 505-512.

Jambunathan, R., N.S. Kherdekar, and J.W. Stenhouse. 1992. Sorghum grain hardness and its relationship to mold susceptibility and mold resistance. J. Agric. Food Chem. 40:1403-1408.

Koleoso, O.A., and O. Olatunji, 1992. Sorghum and millet adjunct replacement in clear (lager) beer: Policy and practice in Nigeria. p. 41-46. In M.I. Gomez, L.R. House, L.W. Rooney, and D.A.V. Dendy (eds.) Utilization of sorghum and millets. ICRISAT, Patancheru (AP) 502 324, India.

Munck, L., and J. Mundy, 1984. Sorghum malting studies. p. 56-58. *In* Proceedings of the symposium, the processing of sorghum and millets: Criteria for quality of grains and products for human food. ICC. Vienna, Austria, 4-5 June 1984.

Murty, D.S. 1992. The breeder's role in crop utilization. A perspective. p.157-163. *In* Utilization of sorghum and millets. ICRISAT, Patancheru 502 324 (A.P.), India.

Murty, D.S. (ed.). 1990. Industrial utilization of sorghum: Summary of proceedings of a symposium on the current status and potential of industrial use of sorghum in Nigeria, 4-6 Dec., 1989, Kano, Nigeria. ICRISAT, Patancheru (A.P.) India.

Nout, M.J.R., and B.J. Davies. 1982. Malting characteristics of finger millet, sorghum and barley. I. Inst. Brew. 88:157-163.

Novellie, L. 1968. Kaffir beer brewing, ancient art and modern industry. Wallerstein Lab. Commum. 31:17-32.

Novellie, L. 1984. Sorghum quality for malting and brewing. *In* Proceedings of the symposium, the processing of sorghum and millets: Criteria for quality of grains and products for human food. ICC. Vienna, Austria. 4-5 June 1984.

Obilana, A.B. 1985. Sorghum breeding and selection for brewing industry in Nigeria. National Symposium on the brewing industry: Now and in the 21st century. Problems-challenges and prospect. 29 May-1st June, 1985, Owerri, Nigeria.

Okafor, N., and Aniche. 1980. Brewing a lager beer from Nigerian sorghum. Brewing and Distillation International 10:32-35.

Okon, E.U., and A.O. Uwaifo. 1985. Evaluation of malting sorghums. I. The malting potential of Nigerian varieties of sorghum. Brewers Digest 24-29.

Olaniyi, O.A. 1984. Cereal in brewing industry. A paper presented at the 8th Annual Conference of the Nigerian Institute of Food Technology. Obafemi Awolowo University. Ile Ife, November, 1984.

Palmer, G.H. 1989. Cereals in malting and brewing. p. 61-242. *In* G.H. Palmer (ed.) Cereal science and technology. Aberdeen, Aberdeen University Press.

Palmer, G.H. 1991. Enzymatic degradation of the endosperm cell walls of germinated sorghum. World Journal of Microbiology and Biotechnology 7:17-21.

Palmer, G.H. 1992. Sorghum and food beverage and brewing potentials. Process Biochemistry 27:145-153.

Pickerell, A.T.W. 1986. The influence of free alpha-amino nitrogen in sorghum beer fermentations. J. Inst. Brew. 92:568-571.

Pomeranz, Y. 1986. Comparison of screening methods for indirect determination of sorghum hardness. Cereal Chem. 63:36-38.

Rooney, L.W., Kirleis, A.W., and D.S. Murty, 1986. Traditional foods from sorghum: Their production, evaluation and nutritional value. p. 317-353. *In* Y. Pomeranz (ed.) Advances in cereal science and technology. AACC. St. Paul, Minn., U.S.

Skinner, K. 1976. Tropical lager beer brewing with sorghum malt. Brewing and Distilling International 6, 26-27.

Solabi, G.A. 1990. Uses of sorghum in malted and fermented foods and drinks. p. 37. *In* Industrial utilization of sorghum. ICRISAT, Patancheru, 502 324 (A.P.), India.

Subramanian, V., Murty, D.S., Rao, N.S., and R. Jambunathan, 1992. Chemical changes, and diastatic activity in grains of sorghum (*Sorghum bicolor*) cultivars during germination. J Sci. Food Agric. 58:35-40.

Subramanian, V., N. Sambasiva Rao, R. Jambunathan, D.S. Murty, and B.V.S. Reddy. 1995. The effect of malting on the extractability of proteins and its relationship to diastatic activity in sorghum. Journal of Cereal Sci. 21:283-289.

Swanston, J.S., K. Taylor, and D.S. Murty, 1992. Grain and malt milling energies in sorghum and their relationships with extract and diastatic power. J. Inst. Brew. 98(2):129-131.

Swanston, J.S., K. Taylor, N.S. Rao, V. Subramanian, and D.S. Murty. 1993. The use of rapid screening tests to compare changes during malting in sorghum. J. Inst. Brew. 99:(G) 483-486.

Taylor, J.R.N. 1983. The effect of malting on the protein and free amino nitrogen composition of sorghum. J. Sci Food Agric. 34:885-892.

Taylor, J.R.N., and H.K. Boyd. 1986. Free amino nitrogen production in sorghum beer mashing. J. Inst. Brew. J. Sci Food Agric. 37:1109-1117.

Sorghum and Millet for Food: Current Situation and Future Needs in Southern Africa

N.F. Nicholson* and J.R.N. Taylor

Abstract

In Southern African Development Community (SADC) countries, there is increasing poverty and malnutrition. Sorghum and pearl millet, which once were the traditional crops, have lost ground to maize and are now marginalized as subsistence crops. A limited number of sorghum products are marketed, but growth is stagnant. This paper presents some ideas on methods of re-establishing sorghum and pearl millet as important cereal crops.

If one looks at the socioeconomic data for sub-Saharan Africa (Table 1) it is difficult to be optimistic about the future. The three percent annual population growth rate continues to be the highest in the world, in sharp contrast to the growth rate of 1.8% in Asia and Latin America. The population of sub-Saharan Africa is forecast to increase from 540 to 862 million in the year 2010, and may grow to 1.3 billion people by 2025. Considering that per capita food production in Africa dropped by 12% between 1961 and 1995, there would appear to be little chance of meeting the future demand for food.

Sub-Saharan Africa is rapidly growing poorer. During the 1980s, the area's per capita Gross National Product declined by more than one percent a year as the population soared, except in Botswana, where growth rates have consistently been above five percent. Still, it is estimated that 55% of the population in Botswana live below the Poverty Datum Line (PDL). In the rural areas, 66% live below the PDL, while 30% of the urban population lives in poverty. Compared to most of Africa, Botswana is a wealthy country, but the wealth is not distributed evenly. If the Botswana percentage (55%) for population living below the PDL is applied to the rest of sub-Saharan Africa's 540 million people, close to 300 million would be living in extreme poverty. In reality, however, far more than 300 million people are extremely poor. Because poverty leads to malnutrition, and because two-fifths of all Africans are under age 15, the consequences are frightening. How can this deterioration be arrested? Improvements in sorghum and millet may provide the answer.

Sorghum Utilization in Southern Africa

Sorghum is grown in all countries of southern Africa, and, except in South Africa, is cultivated almost exclusively by small-scale peasant farmers. According to FAO figures for 1994 (Tables 2, 3, and 4), total production was 1.34 million tons. Tanzania was the largest producer with

N.F. Nicholson, Managing Director, Foods Botswana (Pty) Lbl., Serowe, Botswana; J.R.N. Taylor, Head, Department of Food Science, University of Pretoria, South Africa. *Corresponding author.

Table 1. Some socioeconomic data for sub-Saharan Africa.[1,2]

Region or Country	Land (1993)		Population				GDP 1993			Foreign debt 1993 $m
	Area sq.km^2	Agricultural land as % of total	1993 millions	Urban as % of total in 1993	2010 forecast millions	% under 15 1992	GDP $ bn	Agricultural Output as % of total	GDP per hd. $	
SADC[3]	6911980	5.5	128.5	34	194.9		147.4	15.0	1147	54299
Angola	1246700	2.0	9.9	27	17.1	45.3	6.0	6.1	548	9655
Botswana	600370	2.4	1.3	27	2.2	44.6	3.6	5.0	2590	674
Lesotho	30355	10.5	1.8	61	2.7	41.0	1.3	14.0	660	512
Malawi	118480	25.3	10.3	12	14.7	46.8	2.0	35.0	220	1821
Mozambique	801590	4.0	15.1	30	27.4	43.7	1.4	33.1	80	5263
Namibia	824290	1.0	1.5	29	2.4	44.0	2.6	12.0	1660	300
South Africa	1184825	11.0	40.7	50	56.9	37.8	118.1	14.0	2900	17300
Swaziland	17360	9.3	0.8	28	1.2	47.8	0.9	13.1	1080	226
Tanzania	945090	6.0	27.9	22	42.8	47.0	2.5	61.4	100	7522
Zambia	752610	7.0	8.6	42	13.0	57.6	3.2	28.6	370	6788
Zimbabwe	390310	7.0	10.6	30	14.5	44.6	5.8	14.4	540	4168
E. & Central Africa[4]	10696715	5.9	216.3	22	352.3		58.5	31.3	270	61743
Sudan	2505810	5.0	26.7	22	42.7	44.4	4.3	28.7	160	16560
Ethiopia	1221900	13.0	53.1	13	92.5	47.7	6.0	47.8	100	4729
Chad	1284000	2.0	5.9	34	9.7	42.9	1.2	43.6	200	757
W. Africa[5]	5310172	12.4	195.2	35	314.7		72.4	35.3	371	76480
Nigeria	923850	34.0	104.9	37	164.1	46.9	33.0	35.0	315	32531
B. Faso	274200	13.0	9.5	17	16.3	46.3	2.9	43.0	300	1144
Mali	1240000	1.7	9.8	25	15.9	47.8	2.7	45.0	300	2650
Sub-Saharan Africa[d]	22918867	7.3	540.0	30	861.9		278.3	23.7	515	192522

[1] Data from United Nations and World Bank Publications
[2] Sub-Saharan Africa consists of 48 out of 54 countries in Africa
[3] SADC - Southern African Development Community - 12 countries. Figures for Mauritius not included.
[4] 20 Countries - Figures for Equatorial Guinea, Sao Tome & Principe, Seychelles, Comoros, Madagascar not included.
[5] 16 Countries - Figures for Cape Verde not included.

Table 2. Production of sorghum, millet and maize (000t) in sub-Saharan Africa.[1,2]

	Sorghum			Millet			Maize		
	1979-81[6]	1994	% Increase/ (Decrease)	1979-1981	1994	% Increase/ (Decrease)	1979-1981	1994	% Increase/ (Decrease)
Southern Africa (SADC)[3]	1452	1344	(7.5)	647	540	(16.5)	18038	19352	7.3
Angola	na	na	na	49	53		286	201	
Botswana	21	38		2	3		12	8	
Lesotho	59	60		na	na		112	175	
Malawi	20	17		7	10		1275	1040	
Mozambique	161	184		5	29		383	528	
Namibia	6	10		34	59		31	45	
South Africa	540	432		15	10		11322	11811	
Swaziland	1	na		na	na		85	64	
Tanzania	543	478		360	218		1762	2159	
Zambia	16	35		22	63		941	1021	
Zimbabwe	85	90		153	95		1829	2300	
East, Central Africa[4]	5144	6416	24.7	1523	2166	42.2	4772	7837	64.2
West Africa[5]	5100	7359	44.3	5495	8043	46.4	2131	5211	144.0
Sub-Saharan Africa[2]	11696	15119	29.2	7665	10749	40.2	24941	32400	29.9

[1] Data from FAO (1994).
[2] Sub-Saharan Africa consists of 48 out of 54 countries in Africa.
[3] SADC - Southern African Development Community - 12 countries. Figures for Mauritius not included.
[4] 20 Countries - Figures for Equatorial Guinea, Sao Tome & Principe, Seychelles, Comoros, Madagascar not included.
[5] 16 Countries - Figures for Cape Verde not included.
[6] Average for the three years.
na = not available.

Table 3. Harvested areas of sorghum, millet and maize (000 ha) in sub-Saharan Africa.[1,2]

	Sorghum			Millet			Maize		
	1979-81[6]	1994	% Increase/ (Decrease)	1979-1981	1994	% Increase/ (Decrease)	1979-1981	1994	% Increase/ (Decrease)
Southern Africa (SADC)[3]	1570	1660	5.7	1059	1332	25.8	9867	10340	4.8
Angola	na	na		80	399		600	702	
Botswana	98	100		12	6		42	20	
Lesotho	58	50		na	na		116	103	
Malawi	30	54		11	24		1077	1128	
Mozambique	268	383		20	74		673	940	
Namibia	15	14		77	80		25	33	
South Africa	215	161		22	22		4298	3901	
Swaziland	2	na		na	na		66	80	
Tanzania	713	684		450	340		1350	1629	
Zambia	31	39		34	72		523	496	
Zimbabwe	140	174		353	315		1097	1308	
East, Central Africa[4]	5986	9394	57.0	2257	4431	96.3	4079	5334	30.8
West Africa[5]	5758	9730	69.0	8237	12446	51.0	2293	4634	102.0
Sub-Saharan Africa[2]	13248	20784	57.0	11553	18209	57.6	16239	20308	25.0

[1] Data from FAO (1994).
[2] Sub-Saharan Africa consists of 48 out of 54 countries in Africa.
[3] SADC - Southern African Development Community - 12 countries. Figures for Mauritius not included.
[4] 20 Countries - Figures for Equatorial Guinea, Sao Tome & Principe, Seychelles, Comoros, Madagascar not included.
[5] 16 Countries - Figures for Cape Verde not included.
[6] Average for the three years.
na = not available.

Table 4. Yield of sorghum, millet and maize (kg ha^{-1}) in sub-Saharan Africa.[1,2]

	Sorghum			Millet			Maize		
	1979-81[6]	1994	% Increase/ (Decrease)	1979-1981	1994	% Increase/ (Decrease)	1979-1981	1994	% Increase/ (Decrease)
Southern Africa (SADC)[3]	925	810	(12.5)	611	405	(33.7)	1828	1872	2.4
Angola	na	na		612	133		477	286	
Botswana	214	380		167	500		286	400	
Lesotho	1017	1200		na	na		966	1699	
Malawi	667	318		636	417		1184	921	
Mozambique	601	480		250	392		569	561	
Namibia	400	714		442	737		1240	1363	
South Africa	2511	2683		682	455		2634	3027	
Swaziland	500	na		na	na		1287	800	
Tanzania	762	698		800	641		1305	1325	
Zambia	516	897		647	875		1799	2058	
Zimbabwe	607	517		433	302		1667	1758	
East, Central Africa[4]	859	682	(20.6)	675	489	(27.5)	1169	1469	25.7
West Africa[5]	886	756	(14.7)	667	646	(3.1)	929	1125	21.1
Sub-Saharan Africa[2]	883	727	(17.7)	663	590	(11.0)	1536	1595	3.8

[1] Data from FAO (1994).
[2] Sub-Saharan Africa consists of 48 out of 54 countries in Africa.
[3] SADC - Southern African Development Community - 12 countries. Figures for Mauritius not included.
[4] 20 Countries - Figures for Equatorial Guinea, Sao Tome & Principe, Seychelles, Comoros, Madagascar not included.
[5] 16 Countries - Figures for Cape Verde not included.
[6] Average for the three years.
na = not available.

478,000 tons and an average yield of 698 kg/ha, followed by South Africa with 432,000 tons and an average yield of 2683 kg ha^{-1}. In South Africa, large-scale commercial farmers grow most of the sorghum, mainly red hybrids supplied by four seed companies. Not more than 20,000 tons per year are produced by peasant farmers. It is tempting to conjecture about the effect on food security in the region if sorghum farmers outside South Africa could achieve South African yields.

Sorghum has two major food uses in the region — as a meal (flour) to make porridge and a malt to brew opaque beer. Less than 30% of the region's total sorghum production is processed by industry for food use, the majority of which is in South Africa. Table 5 details industry usage of sorghum in South Africa.

Sorghum for Meal

Porridge made from the meal of maize, sorghum, or pearl millet is the major staple food of southern Africa. Mechanized processing of sorghum for meal takes place in South Africa, Botswana and, to a limited extent, Zimbabwe. In South Africa and Botswana approximately 60,000 tons of sorghum are processed each year by some 70 mills (mostly cottage industry type) into sorghum meal for sale in wholesale/retail outlets. The meal is consumed largely in rural areas in the form of soft porridge (fermented or unfermented). Because there are no standard specifications for production of sorghum meal, meal quality is extremely variable. Outside South Africa and Botswana, meal is still produced in the traditional way by hand-pounding with a pestle and mortar.

Most stiff (thick) porridge is made from white maize rather than sorghum. Maize is the giant of southern Africa cereals, representing 77% of all cereals produced during the 95/96 crop season (Table 6). Sorghum and millet combined represented 10% of the total. There are large maize milling plants in all countries of the region and maize meal is available everywhere. In South Africa alone, some 1.6 million tons of maize meal are produced yearly by milling companies, compared to 30,000 tons of sorghum meal.

Sorghum for Brewing

A large proportion of the sorghum produced in South Africa is used for malting to brew traditional African beer. To those familiar only with conventional European lager-type beer, their first encounter with African beer, otherwise known as sorghum beer or opaque beer, can be rather disconcerting. Opaque beer is so-named because it contains semi-suspended solids of starch, cereal, and yeast. It is generally pinkish-brown in color. Unlike conventional beer, opaque beer is consumed in an active state of fermentation. But, perhaps most surprising is the taste. Opaque beer is not bittered with hops, but is sour like yogurt, due to lactic acid fermentation. The alcohol content of opaque beer is low compared to many lager beers, up to 3% (w/w).

Opaque beer is produced in the home and in industrial breweries throughout southern and eastern Africa. Total regional commercial production is difficult to quantify, but is probably between 20 and 30 million hectolitres per year. This contrasts with 24 million hectolitres per year of lager type beer produced in South

Table 5. Industry usage of sorghum in South Africa (metric tons of raw sorghum per product).

Year	Malt indoor	Malt floor	Meal	Rice/Grits brewing	Rice/Grits human	Other	Total human	Animal feed	Total
1987	40217	78068	13069	986	1645	7622	141607	254264	395871
1988	48914	90839	20879	5985	931	5170	172718	174139	346857
1989	49995	97049	17830	7184	64	2275	174397	167379	341776
1990	56541	102307	27050	6520	124	1115	193657	121696	315353
1991	55104	105776	29437	4140	236	522	195215	50060	245275
1992	53385	103623	38485	2222	946	235	198896	43945	242841
1993	56736	98489	42177	1647	582	66	199697	87114	286811
1994	53444	88931	37817	3594	234	54	184074	226098	410172
1995	39957	94615	43304	3894	506	293	182569	120426	302995
Average	50477	95522	30005	4019	585	1928	182536	138346	320882

Data from Sorghum Board of South Africa

Table 6. Production of cereals (000t) in SADC countries for 1995-96 crop season. [1,2]

	Maize	Wheat	Rice	Millet/Sorghum	All cereals
Angola	398	0	0	102	500
Botswana	22	0	0	59	81
Lesotho	111	18	0	16	145
Malawi	1946	2	34	63	2045
Mozambique	947	0	91	288	1326
Namibia	16	4	0	64	84
South Africa	10038	2400	0	465	12903
Swaziland	107	0	1	0	108
Tanzania	2638	61	373	1391	4463
Zambia	1409	50	9	90	1558
Zimbabwe	2609	325	0	218	3152
SADC total	20241	2860	508	2756	26365
% of all cereals	76.8	10.8	1.9	10.5	100.0
Domestic Surplus/ (Shortfall)	1496	(735)	(252)	401	910

[1] Data from Food Security Quarterly Bulletin June/July 96 - SADC Regional Early Warning Unit.
[2] Figures for Mauritius not included.

Africa alone. Home-brewed opaque beer production is even more difficult to estimate, but is probably at least twice as great as industrial production. Total production of sorghum malt in southern Africa is around 200,000 tons. Today, sorghum malting is almost exclusively a large-scale commercial operation. The grain is either malted outdoors on concrete (floor malting) or in modern indoor (pneumatic) maltings, similar to those used for barley.

The particular characteristics of the traditional southern African sorghum varieties have given opaque beer its unique character, and hence dictate the quality attributes sought in the selection of modern sorghum cultivars for opaque beer brewing. Table 7 summarizes the properties of sorghum malt and pearl millet malt, compared to barley malt.

Sorghum malt has low amylase activity (diastatic power). More strictly speaking, the level of beta-amylase is low (Novellie, 1960), approximately 20-25% of the level in barley malt (Taylor and Robbins, 1994). The level of alpha-amylase is similar to the level in barley. Because amylases are required to hydrolyze starch into sugars during brewing, the most important quality criterion in the selection of sorghum cultivars for malting is their diastatic power (DP). DP is a measure of the joint alpha- and beta-amylase activity of sorghum malt. The assay for sorghum malt DP was developed by the late Dr. Lawrence Novellie of the Council for Scientific and Industrial Research (CSIR) in South Africa (Novellie, 1959), and for many years has been a recognized standard method (South African Bureau of Standards, 1970). Recently, the CSIR published a slightly revised and improved version of the assay, which has been approved by sorghum maltsters and brewers throughout southern Africa (Dewar, Taylor, and Joustra, 1995). A level of around 30 Sorghum Diastatic Units (SDU/gram) is generally considered adequate for opaque beer brewing. As this specification cannot be consistently achieved by industrial maltsters, new cultivars with high DP potential are constantly sought.

A quality criterion of secondary importance is the free amino nitrogen (FAN) content of sorghum malt. FAN comprises amino acids and small peptides. In brewing, these are needed by the yeast as a source of nitrogen for growth during fermentation. FAN is of particular importance in opaque beer brewing, as a large proportion of unmalted cereal adjunct is used in the grist. Since this adjunct contains little FAN, industrial opaque beer brewers generally set a minimum specific for FAN in sorghum malt. The assay for FAN in sorghum malt (Dewar, Taylor, and Joustra, 1995) is a modification of the

Table 7. Some grain and malt properties of sorghum and pearl millet compared to barley (from Daiber and Taylor, 1995).

Property	Sorghum	Pearl Millet	Barley
Starch gel. Temp. Range (°C)	68-78	62-78	51-60
Opt. Malting temp. (°C)	24-28	(25-30)[a]	14-18
Malting loss (%)	10-20	High	7
Diastatic power (SDU/g)	20-60	(20-60)[a]	150-200
α-amylase (% of DP)	60-80	(60-80)[a]	18-50
Extract at 60°C	Medium	No information	High
Extract at 45-70°C	High	No information	High

European Brewery Convention ninhydrin method (Lie, 1973). A level of 110mg FAN/100 gram sorghum malt is considered adequate. The amino acids and small peptides comprising FAN are products of proteolysis during malting. Hence grain that germinates well (High Germinative Energy) will generally produce malt containing good levels of FAN.

The color of opaque beer is related to the pericarp color of the grain. For this reason, reddish-brown sorghum cultivars are selected. On occasion, such colored sorghum has not been available and brewers have had to resort to adding red coloring to the beer. It need hardly be stated that this is not a desirable strategy.

Some industrial sorghum maltsters and opaque beer brewers (in Botswana and Zimbabwe, for example) prefer malt made from high-tannin sorghum cultivars. High-tannin sorghum generally produces malt of slightly higher DP and FAN, but more importantly, the grain is more resistant to mold infection during malting. The moist (approaching 100% rh) warm conditions (25-30°C) of sorghum malting are highly conducive to mold growth. Further, a number of molds associated with sorghum malt produce mycotoxins, in particular aflatoxins (Rabie and Thiel, 1985). Aflatoxin contamination of sorghum malt is an ever-present threat against which sorghum maltsters and brewers must be vigilant.

The drawback of producing malt from high-tannin sorghum is that unless the grain is treated, the tannins will inactivate the malt amylase enzymes when the milled malt is mixed with water during brewing. Industrially, this problem is solved by steeping the high-tannin grain in a highly dilute solution (approx. 0.04% v/v) of formaldehyde. The process, which was invented by Dr. Klaus Daiber of the CSIR (Daiber, 1975), is used widely by industrial sorghum maltsters. It is, however, unsuitable for use by home maltsters. Thus, the selection of low-tannin (condensed tannin-free), mold-resistant sorghum cultivars for malting should be a major priority. For mold resistance, hard endosperm types seem to be advantageous (Kumari and Chandrashekar, 1994).

In Africa in recent years, there has been considerable interest in brewing conventional lager-type beer using sorghum malt (Palmer, Etokakpan, and Igyor, 1989). Much of this interest stems from a ban imposed by Nigeria in the late 1980s on the importation of barley. This ban forced brewers in that country to make use of locally grown grain (sorghum and maize) and industrial enzymes to produce beer. Interest in brewing with sorghum malt is strong because, like barley malt, it is a source of enzymes, but unlike barley, sorghum grows well in tropical Africa. In Nigeria raw sorghum meal milled by hammer-mill is used by one of the major breweries as the sole cereal ingredient of the grist at a level in excess of 70%. Industrial enzymes are used in place of malt. White or yellow sorghum is preferred to red. Sorghum is preferred over maize, because the lipid content is lower and less convertible to extract; more of the lipids are removed with the spent grain during filtration. Most of the literature on using sorghum in conventional beer brewing presents results of laboratory-scale brewing tests. A successful pilot-scale brew was carried out in Japan using a 66:34

blend of sorghum and barley malts (Demuyaker and Ohta, 1994).

In conventional beer brewing, the most important parameter of malt quality is extract. In essence, extract is a measure of the proportion of malt (essentially starch) that will go into solution during the brewing process; the higher the extract, the better the malt. As Table 7 shows, the quantity of extract obtained from sorghum malt at 60°C (a normal brewing temperature) is low in comparison with barley. In contrast, the quantity of extract obtained when brewing temperature is raised to 70°C is comparable to that obtained from barley malt. This difference between sorghum malt and barley malt is explained by the fact that the gelatinization temperature of sorghum starch is considerably higher than that of barley — 68-78°C compared to 51-60°C (Table 7). The starch must be gelatinized before it can be hydrolyzed into soluble dextrins and sugars by the malt enzymes. The problem with the high gelatinization temperature of sorghum starch is that the malt amylase enzymes, particularly beta-amylase, are rapidly inactivated at this temperature. The result is incomplete starch solubilization during brewing (Taylor, 1992). In opaque beer this is not a major problem. In fact, it may be somewhat desirable since a characteristic of opaque beer is semi-suspended starch. However, such starch is, of course, most undesirable in conventional beer. Extract, therefore, is not a major parameter of sorghum quality for opaque beer brewing, but is extremely important for lager brewing. Thus, if sorghum malt is to become a viable alternative to barley malt for conventional beer brewing, the breeding of sorghum cultivars with lower starch gelatinization temperature would be of considerable value.

Although traditional African beer is referred to as sorghum beer, at least 70% of the grist in industrial brewing is provided by maize grits or maize meal. Very limited quantities of sorghum grits (an average of 4,000 mt/pa) are used in South Africa. More sorghum could be used if sorghum grits of low fat content (1%) were available commercially at a competitive price with maize.

Pearl Millet Utilization in Southern Africa

Pearl millet is grown in most countries of southern Africa. It is known by a number of names (for example, *mahungu* in Namibia and *mhunga* in Zimbabwe). It is cultivated almost exclusively by small-scale peasant farmers. According to FAO figures (Table 2), 540,000 mt of millet were produced in 1994 in the SADC region. The types of millet are not indicated, but it is realistic to assume that at least 70% of the total would be pearl millet. Tanzania is the largest producer of millet in the region.

Pearl millet has two major food uses in the southern African region: for malting to brew opaque beer, and to make meal for porridge. According to Dendy (1995), Keyler (1993, 1994) found that consumers in northern Namibia greatly prefer porridge made from pearl millet to porridge made from maize. But they often have to eat the latter because it is all that is available, especially in times of shortage during extreme droughts, because maize can be imported but pearl millet cannot. The effects of these droughts are illustrated by the wild fluctuations in pearl millet production. In 1991, production in

Namibia was 65,000 tons, whereas in 1992 it was only 20,000 tons.

Pearl Millet for Meal

Meal from pearl millet is still produced in the traditional way by hand pounding with a pestle and mortar. This is a two-stage process; first the outer layers of the grain, the pericarp and germ, are removed (dehulling), then the endosperm is reduced to a meal. Increasingly, the milling process is being mechanized. The grain is dehulled using locally produced and adapted versions of the Prairie Research Laboratory (PRL) dehuller. The machine works on the principal of abrasion. It consists of a number of abrasive discs mounted on a shaft. The discs rotate at a high speed (approx. 2800 rpm) within a cylindrical box (Dendy, 1995). The bran produced by abrasion is drawn off by a cyclone fan, also operating at high speed. The abraded grain is then milled to meal of the desired particle size, using a hammer mill (Dendy, 1995).

The milling proportions of different pearl millet varieties vary greatly (Dendy, 1993; Gomez, Monyo, Lechner, and Bidinger, 1993). The data summarized in Table 8 indicate a significant variation ($p \leq 0.001$) between varieties for all the parameters measured: kernel size, 100 grain weight, percentage "floaters," visual hardness, water absorption, and dehulling loss. Pearl millet with a large, hard endosperm kernel is generally selected for meal production, as these characteristics will maximize the yield of clean (free of germ and pericarp) endosperm. However, there is some evidence that grain that is too large may require excessive effort to reduce it to a meal by hand pounding (Dendy, 1993), making it less popular with those who have to perform this physically demanding task.

An important quality criterion that may be neglected in the selection of varieties, is porridge-making quality of the meal. The consumer judges porridge consistency, color, and flavor. As porridges are traditionally eaten with the hand, porridge stiffness is an important quality criterion. There is evidence, in the case of sorghum, that porridge firmness is related to the amylose content of the starch (Fliedel, 1994). Creamy-white pearl millet porridge is preferred in northern Namibia over greyish colored porridge (Dendy, 1993). Porridge color is related to both intrinsic endosperm color and the effects of weathering. During weathering (or conditioning of the grain for dehulling), pigments may migrate from the testa into the endosperm (Dendy, 1993).

In regard to flavor, there is some evidence that pigments in the testa layer of certain pearl millet varieties can migrate into the endosperm during grain-conditioning, making the resulting porridge slightly bitter and less acceptable (Dendy, 1993). This would suggest that pearl millet varieties without pigmented testa layers should be selected for meal production.

Pearl Millet for Brewing

In contrast to sorghum malting, pearl millet malting is generally a home industry, although industrial malting is sometimes done in Zimbabwe. As is the case with sorghum malt, the DP (amylase activity) of pearl millet malt is low. Over 22

cultivars, a range of 22-57 SDU/g has been found (Gomez, Monyo, Lechner, and Bidinger, 1993) (Table 8), much the same as for sorghum malt (Table 7). Thus, pearl millet varieties should be selected for opaque beer brewing primarily on the basis of DP. As with sorghum malt, optimum germination temperatures are high, 25-30°C (Table 7). Thus, mold infection and mycotoxin production during malting are potential problems. Selection of mold-resistant pearl millet varieties for malting should be a priority. In this context, hard endosperm and polyphenol-rich varieties could be of value.

Some research has been carried out into brewing conventional beer using pearl millet malt (Nzelibe and Mwasike, 1995). However, the high proportion of germ and, therefore, high fat content in pearl millet mitigates against economic levels of starch extract and good beer flavor stability. Thus, it is unlikely that conventional beer brewing using pearl millet malt will ever be a commercial proposition.

The Future of Sorghum and Millet as a Food in Southern Africa

Looking at the data in Tables 2 to 6, one could conclude that sorghum and millet have no future in southern Africa, other than as subsistence crops. The figures show that the production of sorghum and millet is declining. Maize production is increasing. Although the accuracy of the statistics is limited, particularly with regard to millet, they do provide a rough indication of what is happening. It is obvious that sorghum and millet are far less important cereal crops in southern Africa than in east/central Africa and west Africa. Also, industrial usage of sorghum in SADC countries is stagnant; there has been no growth in the last ten years. In South Africa and Botswana, cottage industries involved in mechanized processing of sorghum into meal have proliferated, but there has been no overall increase in market volume. In South Africa the large industrial sorghum beer industry is in disarray, and it is apparent that small entrepreneurs are opening breweries with resulting decline in quality of beer. Sorghum brewing could well become a cottage industry in the future. Sorghum and millet are becoming marginalized in the region's agroeconomies. Industry profits from sorghum are declining. Wheat and maize are more profitable to process. What little industrialization of sorghum has taken place in the last thirty years in southern Africa may well disappear.

Can the decline of sorghum and millet be halted? We believe it can, but only if

Table 8. Quality evaluation of 22 pearl millet genotypes (from Gomez, Monyo, Lechner and Bidinger, 1993).

Quality attribute	Mean	Maximum	Minimum
100 grain mass (g)	1.03	1.56	0.82
Specific gravity <1.3 (%)	46	81	20
Visual hardness 1=soft, 5=hard	3.0	3.8	2.0
Water absorption (%)	18.6	23.1	13.3
Dehulling loss (%)	11.2	14.5	9.9
Malt diastatic power (SDU/g)	36.3	56.5	21.5

there is constructive collaboration between all parties concerned, particularly seed breeders, seed companies, food processing companies, farmers, and government. In southern Africa this may be wishful thinking, but the need is obvious. Increasing instability in weather patterns is producing more drought. We have had two in the last five years, including the worst in living memory in 1991-1992. Statistical evidence in Zimbabwe shows that the country is likely to experience two severe droughts in every ten years and that four seasons in every ten would experience below normal rainfall (Unganai, 1996). In most of the last ten years, the region has been in a cereal deficit situation. Except for Botswana, most countries have serious shortages of foreign exchange and limited ability to pay for large imports of cereals.

Politics holds the key to whether sorghum and millet can be re-established on a large scale in the region. Unfortunately, maize being the dominant cereal influences most government decisions. For example, in times of drought, importation of maize of any quality and color has been permitted. Large importation could be avoided if governments initiated policies to force milling companies to use a percentage of sorghum in maize meal or bread flour. It also would help if United Nations bodies such as UNICEF and the World Food Program would change their anti-sorghum stance, particularly with regard to its use in extruded infant food. Governments must demonstrate that they have the political will to promote sorghum as a substitute to maize. This is particularly vital in the case of seed breeding, multiplication, and marketing. Much of the seed industry in the region is government-controlled. It should be privatized. Sorghum and millet breeding stock should be made available as soon as possible to private companies. The multiplication of hybrid seed and subsequent distribution to small-scale peasant farmers is urgent. After all, if hybrid maize is used by the majority of peasant farmers why not hybrid sorghum?

Any attempts by governments to promote sorghum and millet will encounter strong resistance from the maize lobby. The influence of this lobby is insidious. For example, we understand that in Botswana CIMMYT has instituted a program, with cooperation from the Botswana government, to promote a new drought-resistant maize suitable for growing in regions with 300 mm rainfall per year without fertilizers. Is this possible? Table 9 shows that over a recent five-year period in Botswana, the area planted to maize has averaged in excess of 20% of total area planted. Given the climatic conditions, the government should surely not encourage the distribution of any maize seed.

This year Foods Botswana purchased a small amount of white hybrid sorghum BSHI from a farmer in Botswana. The yield of this sorghum was around 1500 kg/ha, compared to the average yield of 196 kg/ha (Table 9). This particular seed was released by ICRISAT to Botswana in 1991. Tests by our laboratory indicated good processing characteristics. Five years later, there is still no grain. The hybrid seed has not been successfully multiplied.

Industry (food processing companies) has a major role to play. Sorghum breed-

Table 9. Production of maize and sorghum in South Africa and Botswana.

	South Africa						Botswana					
	Maize			Sorghum			Maize			Sorghum		
Year	Area planted (000 ha)	Production (000t)	Yield (kg ha^{-1})	Area planted (000 ha)	Production (000t)	Yield (kg ha^{-1})	Area planted (000 ha)	Production (000t)	Yield (kg ha^{-1})	Area planted (000 ha)	Production (000t)	Yield (kg ha^{-1})
1987	4129	7068	1712	317	477	1504	44	4	91	161	16	100
1988	3729	6731	1805	313	474	1514	46	3	65	210	18	86
1989	3806	11552	3035	182	472	2593	54	7	130	279	94	337
1990	3502	8342	2382	138	288	2086	88	7	80	266	53	199
1991	3322	7826	2356	118	241	2042	80	12	150	206	38	184
1992	3487	2955	847	135	100	740	na	na	na	na	na	na
1993	3663	9077	2478	168	428	2547	na	na	na	na	na	na
1994	3904	12026	3080	161	441	2739	na	na	na	na	na	na
Average	3692	8197	2220	192	365	1901	62	7	112	224	44	196

Data from governments of South Africa and Botswana agricultural statistics.
na = not available.

ers must listen to our requirements. In southern Africa, except for malting, we need white food grade sorghum, not a selection of red, yellow, brown, or grey sorghum. The latter are not suitable for processing into products that can compete with maize meal or maize grits. In addition we need hybrid sorghum that offers the same return to farmers as maize hybrids.

At present there is no standard definition of a white food-grade sorghum hybrid. It should be a tan plant sorghum with a thin white pericarp, hard white endosperm, whose parents are both genetically white. Our company has already demonstrated that this type can produce excellent white sorghum flour, as either a replacement or an extender for maize. We also have produced whole meal flour for use as soft porridge, which can compete favorably with existing commercial sorghum meals made from dehulled red sorghum. Unfortunately, limited supplies of white sorghum, including some imported from Texas, have prevented us from marketing these products. We believe contract growing with farmers is necessary to secure our needs. Several farmers in the region have expressed considerable interest. Last year we contracted 9000 hectares in northern Botswana for growing Kuyuma, a white Zambian variety developed by Dr. Verma. Excessive rainfall (300% above normal) wiped out 8000 ha, leaving 1000 ha that produced 2000 tons of excellent white food grade sorghum.

Conclusion

In southern Africa the odds are stacked against the successful revitalization of sorghum and pearl millet. It will be a long haul. Time is not on the side of the millions of people living in poverty in rural and urban areas. We hope that biotechnology will provide one of the keys to unlock the door to a desperately needed green revolution for sorghum and millet.

References

Daiber, K.H. 1975. Treatment of cereal grain. S. Afr. Patent 75/4957.

Daiber, K.H., and J.R.N. Taylor. 1995. Opaque beers. p. 299-323. *In* D.A.V. Dendy (ed.) Sorghum and millets: Chemistry and technology. American Association of Cereal Chemists, St. Paul.

Demuyaker, B., Y. Ohta, K. Nakatani, N. Fukui, and K. Kanagwa. 1994. Brewing of beer with sorghum vulgare malt with minimal barley malt blending. J. Am. Soc. Chem. 52(3): 111-115.

Dendy, D.A.V. 1993. Report on a visit to Namibia to assist in the improvement of pearl millet processing and products at the Namibia Development Corporation, Musese, Kavango. Natural Resources Institute, Chatham Maritime.

Dendy, D.A.V. 1995. A study of millet (mahangu) processing in Namibia: The way forward. p. 4, 7-13. Grains After Harvest. Upton, Oxfordshire.

Dewar, J., J.R.N. Taylor, and S.M. Joustra. 1995. Accepted methods of sorghum malting and brewing analyses. CSIR Food Science and Technology, Pretoria.

Fliedel, G. 1994. Evaluation de la qualite' du sorgho pour la fabrication du to. Agriculture et Developpement (4)12-21.

Gomez, M.I., E.S. Monyo, W.B. Lechner, and F.R. Bidinger. 1993. Crop-product quality and utilization. p. 36-37. *In* SADC/ICRISAT southern Africa programs. Annual Report 1992. SADC/ICRISAT Sorghum and Millet Improvement Program, Bulawayo.

Kumari, S.R., and A. Chandrashekar. 1994. Relationships between grain hardness and contents of prolamin and three anti-fungal proteins. Journal of Cereal Sciences 20:93-99.

Lie, S. 1973. The EBC-ninhydrin method for determination of free α-amino nitrogen. Journal of the Institute of Brewing 79:37-41.

Novellie, L. 1959. Kaffircorn malting and brewing studies. III. Determination of amylases in kaffircorn malts. J. Sci. Food Agric. 10:441-449.

Novellie, L. 1960. Kaffircorn malting and brewing studies. VI. The extraction and nature of the insoluble amylases of kaffircorn malts. J. Sci. Food Agric. 11: 457-463.

Nzelibe, H.C., and C.C. Nwasike. 1995. The brewing potential of "acha" (*Digitaria exillis*) malt compared with pearl millet (*Pennisetum typhoides*) malts and sorghum (*Sorghum bicolor*) malts. Journal of the Institute of Brewing 101:345-350.

Palmer, G.H., O.U. Etokakpan, and M.A. Igyor. 1989. Review: Sorghum as a brewing material. MIRCEN J. 5:265-273.

Rabie, C.J., and P.E. Thiel. 1985. Toxigenic fungi and mycotoxins in sorghum malt. p. 252-256. *In* proceedings of the first scientific and technical convention. Institute of Brewing, Central and Southern Africa Section, Johannesburg.

South African Bureau of Standards. 1970. Standard test method for the determination of the diastatic power of malts prepared from kaffircorn (sorghum) including bird-proof varieties, and from millet. South African Bureau of Standards, Pretoria.

Taylor, J.R.N. 1992. Brewing with malted grain sorghum. J. Amer. Soc. Brew. Chem. 50:13-18.

Taylor, J.R.N., and D.J. Robbins. 1994. Factors influencing beta-amylase activity in sorghum malt. J. Inst. Brew. 99:413-416.

Unganai, L.S. 1996. Regional climatic trends and the state of seasonal to interannual forecasting in southern Africa. Drought Monitoring Centre, Harare, Zimbabwe.

Discussion

Session VIII - Breeding for Improved Quality and Utilization
Session Chair: Tim Lust
Rapporteurs -Senait Yetneberk and Aissata Bengaly Berthe

Robert Schaffert - Has any work been done on sorghum to see if a higher percentage of gamma-kafirin protein increases quality for composite flours for bread making?

Bruce Hamaker - We have not done any work in this area. However, we have observed differences in gamma-kafirin content among sorghum cultivars, so it would be useful to look at this. At EMBRAPA-Brazil, it was shown that Quality Protein Maize, which contains a higher level of gamma-zein, could be added at a higher level to wheat than normal maize, and still get a good quality bread loaf.

Fred Miller - In describing the population for higher protein quality and the evaluation of dense floury endosperm types — what is the milling loss of these potentially high use sorghums, when compared to normal endosperm densities?

Bruce Hamaker - We have not yet looked at milling characteristics of the dense floury sorghums.

B.S. Rana - Comment on J.F. Pederson presentation. There is a lot of optimism in your talk towards ethanol production from stover of sorghum through digestion of cellulose. I would like to further add more to the potential value of sorghum. We have released a variety (SSV89) with sweet stalk (19% Brix) and high juice yield. We have recently developed another sweet stalk variety with high biomass and grain yield. These are more useful for ethanol production than non-juicy and nonsweet sorghums. We have also developed the techniques for the production of ethanol from stalk as well as from grain to maximize the whole plant use.

Robert Schaffert - Research at EMBRAPA has indicated that silage quality is inferior for silages made from sweet sorghums as opposed to dry stalk sorghums.

P. Esele - Are there any significant differences in nutritional qualities between brown/red sorghums and white sorghums, save for the presence of tannins in the brown sorghums? This is in view of the resistance of the brown sorghums to grain mold. If there are no significant nutritional quality differences, then I would advocate production of brown sorghums. The tannins could be removed either by dehulling or hydrolysis.

L.W. Rooney - In certain environments, brown (high tannin) sorghums must be grown to escape birds/molds. Methods have been developed to process the brown grain into various foods which are very acceptable and nutritious when supplemented with other foods in the diet. I have drank delightful beer made from brown (red) sorghums. It is clear that

brown sorghum does contain condensed tannins that do adversely affect nutritional value. However, brown sorghum is consumed by animals readily in feed rations with weight gains equivalent to no tannin sorghum, but the feed efficiency is reduced significantly.

A.B. El Ahmadi - I would like Dr. Rooney to elaborate a little bit on the suitability of using waxy endosperm sorghums in making food products, especially Sudanese "Kisra".

L.W. Rooney - I cannot recall any data on the use of waxy endosperm in Kisra or Injera. Waxy sorghum, when cooked, is extremely sticky and difficult to handle so it is not useful in many products.

J.N. Mushonga - What is your experience with white sorghum vs. brown in terms of diastatic activity? I found some white sorghums which had very high diastatic activity.

D.S. Murty - There are white sorghums as good as brown sorghums with respect to diastatic activity. Further, screening of germplasm and breeding stocks is recommended. Published literature indicates good variability even in white sorghums for diastatic power.

David Andrews - While biotechnology may well help to improve end uses in many ways, the reality of the situation in Southern Africa is that varieties/hybrids have been bred and released that meet end processing requirements. The problem is (as Mr. Nicholsen said) is that there is no consistent production of these. The problems are currently 'downstream' from breeding research, in on-farm production, consistency of product and marketing. These bottlenecks must be addressed by SADC governments.

N. Nicholsen - The problem is primarily political. Despite the desperate need for white food grade varieties/hybrids, government agricultural research organizations have no motivation to address this need — this must come from the politicians.

J.N. Mushonga - I think you have not given a completely correct account of the situation in the Southern Africa region. You appear to speak about Botswana and South Africa. There are white sorghum grown in Southern Africa, but companies don't bulk enough grain. Zimbabwe has a very large opaque beer industry.

Session IX

Plenary Session

Session Chair: John Yohe

Rapporteurs: Phil Warren and Aliya Kasakova

Speakers:

Stephen Smith
A.B. Maunder
S.B. King
Dennis Avery

Germplasm and the Biodiversity Treaty

Stephen Smith* and H.L. Shands

Abstract

More effective use of plant genetic resources is crucial for the sustainable production of food in a healthy environment. U.S. sorghum breeders have made extensive use of adapted exotic germplasm, and much enhanced elite germplasm has subsequently been transferred from the U.S. to developing countries. Greater efforts are required to conserve and utilize genetic diversity in sorghum. The Convention on Biological Diversity (CBD) heralds a change in the hitherto informal international exchanges of germplasm. The FAO International Undertaking on germplasm access and the sharing of benefits between germplasm users and donors is being revised in accordance with the CBD. In the current international environment, many developing countries aspire to receive significant additional funding and technologies in return for providing access to genetic resources. However, significant new funds may not be forthcoming. Details of new arrangements to better conserve and utilize plant genetic resources, as agreed upon in the framework Global Plan of Action, are yet to be worked out. The most immediate and controversial issues are financing and benefit sharing. A greater sense of reality of the worth of exotic unadapted germplasm and greater public investment in the conservation and evaluation of these resources will be needed to forestall a possible breakdown in negotiations and consequent barriers to germplasm exchange that may then arise.

It is a very great honor and privilege to be among you, to visit with you, and to learn from you. Your work, by its practical results, presents new possibilities for the future health of humankind by improving agricultural productivity and creating a cleaner, more diverse, and more sustainable environment through the more effective deployment of genetic resources. By working together, in a true spirit of sharing and collaboration across national, economic, and political boundaries, you carry forward the essential, millennia-old multinational dependencies of agriculture upon the transfer, recombination, and evaluation of germplasm into the next century and beyond.

Most genetic resources have not been evaluated, and many new genetic combinations remain to be made and tested in many environments. New possibilities exist to help improve productivity for farmers of every nationality, geographic location, husbandry type, economic level, or farm size. The character and quality of the world will be determined by the effectiveness of plant breeders to better provide for growing populations and protect the environment by bringing forth new,

Stephen Smith, Pioneer Hi-Bred International Inc., Johnston, Iowa; H.L. Shands, USDA-ARS, Beltsville, Maryland. *Corresponding author.

better adapted, and more productive varieties.

As plant breeders, you are intuitively aware of the impact of environment and its confounding effects upon the agronomic performance of varieties and achievement of genetic gain.

It is my responsibility here today to bring to your attention another kind of environment, one that must concern you — the political and economic environment that affects your capabilities to continue effectively as plant breeders. This environment is undergoing fundamental change. Public funding is declining for applied plant breeding. The private sector is becoming more involved in plant breeding and applied research. Public funding is declining for international programs; for example, the U.S. is cutting its funding of the Consultative Group for International Agricultural Research (CGIAR) system that includes centers as IRRI, CIMMYT, and ICRISAT. Intellectual Property Protection is becoming the norm with different rules on transfer and use of technologies and germplasm. In the developed world 98% of the population lives remote from the land, both geographically and intellectually. Provided with a diverse abundance of readily available, cheap, convenient and nutritious food, many in the U.S. and Europe, for example, have forgotten their former and ultimate dependence upon agriculture.

Consequently, public investments in the future of agriculture will be extremely difficult to obtain in this environment. Genetic resources are in imminent danger of becoming hostages as many developing countries perceive that these resources can be used as bargaining chips to obtain immediate and significant funds from developed countries. But unevaluated genetic resources cannot result in benefits in terms of improved agricultural productivity. Exotic genetic resources have little immediate tangible economic worth in their current unevaluated and unenhanced state.

The stage is set for a stormy environment resulting in reduced funding coupled with additional barriers to exchange and utilization of germplasm. Further confounding these difficulties is the lack of understanding and appreciation of your work by many governmental and other delegates at international fora (e.g., the CBD) that will mold national and international policies and funding. A significant body of diverse non-governmental organizations are openly hostile to IPP, plant breeding, high yield agriculture, the Green Revolution, and "western" science. These groups, many of which do not understand agriculture and use the issues to play politics, will, by their effective lobbying of government delegates, further damage the environment in which you operate as breeders. It is therefore imperative that your activities and contributions be more vocally and visibly brought to the attention of the public and government.

The public must be reacquainted with its dependence upon agriculture and its responsibilities to provide for the future infrastructure of agriculture. Dependence upon genetic resources, their conservation, enhancement, and breeding are key subjects now on the international agenda.

Your critics must be challenged to show how they would obtain greater real

public support for the conservation of genetic resources and how they would feed a world where the population may double its present size in 50 years while also protecting the environment.

Agricultural Revolutions

The invention of agriculture thousands of years ago did not lead to a magical panacea. "Until the last two centuries in every part of the world nearly everyone lived on the edge of starvation" (Ponting, 1991). The 18th Century in France was the second worst for famines in the country's recorded history, with sixteen outbreaks. In Fourteenth Century Europe, "the poor were dying in large numbers or turned to robbery in attempts to get food; and huge bands of starving peasants swarmed across the countryside....Bread would be mixed with pigeon and pig droppings, and animals that had died of disease were eaten....In Ireland....bodies were dug up from graves to provide food and in Silesia executed criminals were eaten" (Ponting, 1991).

A second agricultural revolution began after 1800 based upon improved crop nutrition and husbandry (England, the Netherlands), with an expansion of land under cultivation (the U.S., Canada, Australia) and increasing capitalization. A third revolution began in the 1930s in northern Europe, the U.S, Canada, and Australia. There were productivity gains due to plant breeding, improved disease, pest, and weed control from chemical applications, mechanization (one quarter of U.S. agricultural output had previously gone to feeding horses), and further capitalization. Approximately half of yield improvement for major crops grown in these countries came from genetic change alone. During the 1960s, genetic, chemical, and husbandry changes brought about the Green Revolution in Asia; the second half of the 20th Century often known as the Scientific Revolution.

It was only during this third revolution that the processes of crop domestication and locations of crop genetic diversity initiated by Nicolai Vavilov began to be appreciated. However, dynamics affecting genetic diversity were not of interest before the 1960s. Concern about the erosion of genetic resources in landraces led to the construction of several gene banks (e.g., the International Agricultural Research Centers [IARCS] such as IRRI, CIMMYT, CIAT, CIP) and other national genebanks (e.g., Fort Collins). However, Duncan et al. (1995) notes that "genetic erosion in areas of germplasm diversity continues to plague the world sorghum industry."

Some lessons from this history are:

1) Genetic resources are of critical and increasing importance to the future of world food and environmental security.

2) Useful genetic diversity, not genetic resource diversity alone, is the critical issue.

3) Useful genetic diversity requires identification of sources of a range of diversity, coupled with the ability to recombine that diversity into new varieties that are better adapted to the needs of the farmer.

4) Genetic resource diversity must be increasingly conserved *ex situ* as pres-

sures increase for farmers to grow the most productive varieties. There is evidence that landrace use is persisting in many regions; however, this usage will increasingly become fragile, and backup conservation *ex situ* must be provided.

5) Plant breeding requires an ever increasing source of intellect, improved knowledge about the relationships between genes and traits of agronomic importances, and improved abilities to identify, manipulate, and more effectively recombine new genetic varieties.

6) The rapid application of new knowledge and technological capabilities can help improve conservation, evaluation, enhancement, and breeding.

7) The private sector cannot operate without strong Intellectual Property Protection (IPP), nor can it serve farmers in regions without a base level of market infrastructure and a sound business environment.

8) There is a crucial dependence upon basic activities such as research, conservation, and prebreeding, which are too long term and too risky for private sector investment. Given the broad public good of these activities, public funding is the only means of meeting these financial needs.

9) Improved productivity has bought and paid for the funds necessary to secure and further explore basic genetic resources. A productive agriculture generates an annual food dividend that is reflected in the low percentage of personal consumption directed toward food.

10) More than adequate funds are available to provide for basic research and the conservation and prebreeding of exotic germplasm. It requires political will to make the necessary investments from monies already earned from investments by prior generations.

The Environment Prior to the Convention on Biological Diversity (CBD)

Prelude to the "Gene Wars"

Resources needed to sustain advances in agricultural productivity are not evenly distributed around the globe. Most sites of crop genetic diversity are found in so-called "southern" countries that are still developing industrially. More financial and technological resources are located in "northern" industrialized societies. Here farmers concentrate on market-oriented production agriculture. Genetic diversity is arrayed differently in this environment, and most diversity is seen not in or among farmers' fields, but within and among breeding programs. Germplasm is arrayed geographically and in time, rather than in place, as is the case with heterogeneous landrace varieties. Plant breeding programs represent tertiary centers of diversity complementing the primary and secondary Vavilovian centers. Tertiary centers contain well-characterized and productive diversity. Programs in these centers depend for the long term on basic research and infusions of exotic germplasm from other centers of diversity, including collections stored in *ex situ* genebanks. However, until exotic collections have been adapted, enhanced, and well evaluated, they cannot represent tangible assets for significant investments of effort by the private sector. Consequently, contributions from governments and foundations have supported conservation.

Most stored collections were freely available as the "common heritage of humankind." Exceptions were late generation materials in private breeding programs and parental inbred lines of hybrids.

Then a new perspective appeared. Agriculture originated in the developing world, which has a vast store of rich diversity. Farmers in the south have been improving and conserving this diversity for 10,000 years and for centuries have given it away free to the north. The north has gotten rich off the genetic resources of the south and has given nothing back. This diversity is in demand by the industrialized north, which simply sells back to the south pirated germplasm at high prices. Thus, the north maintains control over germplasm in the genebanks and locks up germplasm for further breeding by IPP.

The "Gene Wars"

This perspective led to confrontations known as the "north-south gene wars" and resulted in the FAO International Undertaking on Plant Genetic Resources in 1983. Key articles of the IU are:

Article 1 acknowledges plant genetic resources as a heritage of mankind and consequently should be available without restriction (the term "common heritage" was not used until Annex Resolution 4/89), to ensure that plant genetic resources....particularly for agriculture, will be explored, preserved, evaluated, and made available for plant breeding and scientific purposes.

Article *2* includes landraces, wild and weed species, and relatives of cultivated varieties, newly developed and other cultivars, obsolete cultivars, and special genetic stocks (breeders' lines and mutants).

The IU was "a product of sometimes acrimonious debate" largely as a reaction to the unbalanced terms of access which existed to "raw germplasm" on the one hand (which was freely available) and to "improved germplasm" on the other (which was subject to proprietary restrictions) (Cooper, 1993). The level of passion and acrimony can be gauged from the following statement by Tewolde Berhan G. Egziabher. "If the South continues to be outsmarted, it will continue to smart from the millennium-old hurt. Those who are hurt will bash about in pain. Who knows which bash will produce a magnified Bosnia, unwittingly flinging its weight of chaos at the North? If the North wants stability to enjoy its ill-gained wealth, it had better keep its greed within set limits."

The IU could not be adopted by consensus, as private industry could not attract private funding if proprietary germplasm were freely available. Therefore, a second resolution (c 4/89) was adopted that "recognized that Plant Breeders' Rights were not necessarily inconsistent with the Undertaking" while simultaneously recognizing a concept known as Farmers' Rights. The concept of Farmers' Rights is stated as "rights arising from the past, present, and future contributions of farmers in conserving, improving, and making available plant genetic resources."

According to Annex II of the IU "these rights are vested in the International Community in order to:

a) ensure that the need for conservation is globally recognized and that sufficient funds for these purposes will be available;

b) assist farmers and farming communities, in all regions of the world, but especially in the areas of origin/diversity of plant genetic resources, in the protection and conservation of their plant genetic resources, and of the natural biosphere;

c) allow farmers, their communities, and countries in all regions, to participate fully in the benefits derived, at present and in the future, from the improved use of plant genetic resources, through plant breeding and other scientific methods."

Resolution 5/89 noted that "the majority of....plant genetic resources come from the developing countries,"and "the contribution of....farmers has not been sufficiently recognized or rewarded." A third resolution (c 5/91) "reaffirmed the sovereign rights of nations over their genetic resources and agreed in principle that (the concept of) Farmers' Rights should be implemented through an international fund that will support plant genetic conservation and utilization programs, particularly, but not exclusively, in the developing countries."

However, the concept of Farmers' Rights has since become exceedingly nebulous, with a range of interpretations. Some say it means:

- a moral principle acknowledging the historical contribution of farmers;
- a political strategy to balance the growth of intellectual property rights;
- a right or mechanism for compensation for what farmers have done in the past;
- a right or mechanism for compensation for what farmers do now and will do in the future
- an extension of the right to save seed;
- an extension of the right to sell seed;
- a new form of intellectual property protection;
- a mechanism for funding and promoting the conservation of agricultural biodiversity;
- the provision of land rights for indigenous people;
- the rights to self determination for indigenous people;
- provision of subsidies to maintain current lifestyles;
- provision of subsidies to conduct *in situ* conservation;
- provision of resources for greater farmer participatory breeding;
- provision of resources to capacity build breeding programs and market infrastructure;
- provision for *ex situ* conservation; and
- provision of resources to fund more plant breeding.

Neither NGOs, industrialized countries, nor the private sector have yet provided a clear set of goals or programs that could be enacted supporting conservation or utilization of plant genetic resources and, therefore, be seen as progress in fulfilling the concept of Farmers' Rights. This inaction has left a void that has been filled with a growing multiplicity of

vague, sometimes contradictory, and often controversial, concepts. The diversity of foci and the evolving broad social and political goals now make the concept of Farmers' Rights a sticking point in achieving consensus on genetic resource issues.

Real Signs of Progress — at Last?

During the past two years, the FAO has surveyed the State of the World's (SOW) genetic resources. Reports were received from 154 countries. Eleven regional and sub-regional meetings were held. The SOW report represents a historical landmark, providing the first comprehensive global evaluation of *in situ* and *ex situ* conservation and plant breeding. A Global Plan of Action (GPA) was prepared by the FAO from the SOW. The GPA is a framework with 20 priority action areas (see Appendix I). In June, 1996, over 100 nations agreed to the GPA. Most of the action areas (*ex situ* conservation, genetic enhancement, capacity building) will improve the effective utilization of germplasm and should be funded. However, none of the details regarding implementation or funding of the GPA has been agreed upon.

Biodiversity and the Convention on Biodiversity (CBD)

Broader concerns about reductions of global biodiversity well beyond the realm of agriculture the FAO focuses on, initiated the Convention on Biodiversity (CBD). Economic and technological issues of concern primarily to developing countries, also became integral. The CBD entered into force on December 29, 1993, as a legally binding treaty. It prescribes national goals and international responsibilities for the conservation and sustainable use of biodiversity; including plant genetic resources for food and agriculture.

The three main objectives of the Convention are the conservation of biodiversity at the genetic, species and ecosystems levels; the sustainable use of its components; and the fair and equitable sharing of benefits derived from the use of genetic resources.

Key provisions of the CBD

Article 15 is a key element heralding a landmark change in ownership of genetic resources; resources that prior to the Convention were considered as the "common heritage of humankind".

Article 15-1 recognizes "the sovereign rights of States over their natural resources, the authority to determine access to genetic resources rests with the national governments and is subject to national legislation". Article 15-4 and 15-5 prescribe that access to genetic resources should be granted on "mutually agreed terms" and "shall be subject to prior informed consent". Article 15-7 states that "Each Contracting Party shall take legislative, administrative, or policy measures....through financial mechanisms with the aim of sharing in a fair and equitable way the results of research and development and the benefits arising from the commercial and other utilization of genetic resources with the Contracting Party providing such resources. Such sharing shall be upon mutually agreed terms."

Other important Articles relevant to plant breeding and agriculture include:

Article 16: "to provide and facilitate access for and transfer of technology (including biotechnology). ....Access shall be provided....under fair and most favorable terms, including on concessional and preferential terms....In the case of technology subject to ....intellectual property rights, such access and transfer shall be provided on terms which recognize and are consistent with the adequate and effective protection of intellectual property rights."

Article 16-5: "The Contracting Parties, recognizing that patents and other intellectual property rights may have an influence on the implementation of this Convention, shall cooperate in this regard subject to national legislation and international law in order to ensure that such rights are supportive of and do not run counter to its objectives."

Article 19: "Each Contracting Party shall take all practicable measures to advance priority access on a fair and equitable basis, especially (to) developing countries, to the results and benefits arising from biotechnologies based upon genetic resources...."

Article 20: "The developed country Parties shall provide new and additional financial resources to enable developing country Parties to meet the agreed full incremental costs to them of implementing measures which fulfill the obligations of this Convention....The extent to which developing country Parties will effectively implement their commitments....will depend on the effective implementation by developed country Parties of their commitments under this Convention related to financial resources and transfer of technology."

The Convention began to examine agricultural biodiversity in 1996. Meanwhile, the FAO's IU is being revised in accord with the CBD. Agreements made within the IU are among nations. These agreements only affect private industry if a nation chooses to enact specific provision into national law. However, the IU may eventually become an annex or a protocol to the CBD. Agreements made within the sphere of the CBD will have legally binding authority upon the public and private sectors for nations that ratify the Convention and which are signatories to those provisions. However, even though the U.S. has not ratified the CBD, its public and private sectors cannot be immune from agreements made by other nations, for those agreements will condition the environment in which the U.S. must source germplasm, conduct research and product development, and sell agricultural products throughout the world.

Characteristics of the CBD

The agenda has exhibited a marked propensity to broaden its focus to encompass a great complexity of biological, ecological, sociological, economic and political issues. For example, discussions on biosafety have encompassed liability for biological impacts and also for economic displacement attributed to new technologies through to the fundamental utility of biotechnology itself. Agendas of other issues, such as access to genetic resources, agricultural biodiversity, intellectual property rights and technology could similarly broaden. The scientific advisory body (SBTTA) also has had difficulties in preparing scientifically sound and balanced papers for discussion by delegates. For example, the paper on biodiversity in agriculture was heavily criticized by many delegations.

Liabilities of Non-Participation in the CBD process

The U.S. has not ratified the CBD, and so has limited "observer" status. Many developing countries have positions that differ from industrialized countries due to respective economic, sociological and technological capacities. Consequently, the CBD could produce binding protocols that would affect many technological, economic, sociological, IPP and liability elements that relate to agriculture. Non-Governmental Organizations (NGOs), that are often highly critical of private industry, have a high profile at meetings and influence many country delegations. Industry had been slow to attend or to provide input to the CBD, but this situation was rapidly reversed when the issue of biosafety arose.

The U.S. could ratify the CBD and so be a full participant, but this is highly unlikely to happen in the near future. The U.S. could threaten a cessation of funding to the UN until the CBD supports policy based on scientific principles that is in accord with "good" science and free trade (Miller, pers. com.). Third, the U.S. could fail to ratify the Convention and be faced with events shaped more by other nations and NGOs. The option, after ratification, to engage in improving the scientific basis of policy making, is, arguably, the most effective course to follow.

Convergence of the FAO International Undertaking and the Convention on Biodiversity

The FAO International Undertaking and the CBD converge or overlap for at least three reasons. First, both involve responses not only to scientific issues, but also to economic, sociological and political pressures. For example, Raustiala and Victor (1996) note: "For industrialized countries, the goal was to promote conservation....For developing countries, the goal was broader: the sustainable use of biological resources, financial and technological transfers to assist in biodiversity protection, and the equitable distribution of the economic benefits of biological resources....a central aim of the developing countries has been to channel Northern interest in natural resources toward the creation of mechanisms for wealth and technology redistribution." Second, both focus upon agriculture; the impact of agriculture upon the environment inevitably attracts the attention of the CBD. Third, the CBD represents a forum for countries to make agreements that may not have been reached in the revision of the IU, but are legally binding by virtue of the authority of the Convention.

The CBD has just turned its attention to biodiversity in agriculture. The Convention draft on agricultural diversity sparked great controversy. Most developed countries saw it as an unscientific, unbalanced attack on modern agriculture that failed to comprehend the limitations of traditional agricultural practices to provide levels of productivity that would be necessary to sustainably feed increasing populations and to protect fragile lands from inefficient cultivation. Most countries recommended that the FAO deal with agriculture and the CBD focus on outstanding issues (e.g. soil microbial diversity, diversity of pollinator organisms). If the FAO does not soon reach resolutions on access to germplasm, benefit sharing and financing that are accept-

able to many developing countries, these issues will all return to the agenda of the CBD.

Future Prospects

Problems of defining and realizing the concept of Farmers' Rights and insistence that northern industrialized countries commit significant new funds, (up to $300 million annually) to put the GPA into effect, and for which no specific projects have been outlined or costed, remain major sticking points in agreeing to terms on conservation, access and more effective utilization of plant genetic resources for food and agriculture.

The CBD's immediate role in agriculture remains unclear, but it will exert great influence upon discussions at the FAO. Countries will turn to the legal authority of CBD if their expectations are not met by the FAO. The next round of debate at FAO (December, 1996) will center around access and exchange of germplasm and the CBD sets the context. Consequently, a new system will seek to promote access to genetic resources from collections by providing a standard set of conditions regulating access and benefit sharing from users to the donors of germplasm. Funding could come from either an access fee and/or the sharing of royalty streams following commercialization. The CBD requirement for prior informed consent and equitable benefit sharing could be accommodated in an appropriate agreement.

Royalty flows from the use of exotic genetic resources generally will be small due to low profit margins in the seed industry and the relatively small, yet often significant, contribution that exotic germplasm makes to an improved variety. Unadapted and poorly evaluated plant genetic resources for food and agriculture are best suited to a multilateral system of access that is internationally funded by governments. The only alternative to a multilateral system for these collections would be a multiplicity of bilateral agreements. Bilateral agreements can be effective for crops such as rubber or spices that have high value and limited distribution, and they can be instrumental in promoting investments in evaluation, prebreeding and enhancement of other staple crops. However, bilateral agreements are unlikely to occur for germplasm that is not well known by plant breeders, which is the case of the majority of *ex situ* collections and *in situ* landraces of the major crop species. If negotiations on a multilateral system are protracted or get bogged down in complicated formulae for benefit sharing based on detailed pedigrees or from evidence provided by molecular data, then bilateral arrangements will be the inevitable alternative. However, to reiterate, bilateral agreements will be unlikely to help conserve the vast bulk of unadapted and uncharacterized germplasm collections of major crop species. The immediate goals of a revised multilateral system should be to provide a foundation for conservation with greater access to enable additional opportunities for germplasm enhancement to occur. Bilateral arrangements could provide additional means to attract resources into global access and germplasm enhancement. Access, evaluation and prebreeding are prerequisites before any potential, but hidden, benefits can be revealed.

The CBD notes that it "recognizes the special nature of agricultural biodiversity, its distinctive features, and problems requiring distinctive solutions." However,

many arguments over access to genetic resources and the role that intellectual property and the private sector can play in genetic resource conservation have occurred precisely because realities of utilizing exotic genetic diversity for food and agriculture were not understood. Exotic germplasm represents a long term and high risk component of a breeding program. It requires long periods of prebreeding and enhancement before it can usefully enter a breeding program that is geared to product development.

Conservation and much of prebreeding do not fit into the scope of business that a privately funded organization can support, nor do they frequently generate products that have an intellectual property component. The conservation of genetic resources is very largely a public good. Consequently, battles that are fought over intellectual property protection and access and benefit sharing from exotic germplasm are misdirected. IPP provides a framework for benefit sharing and can thus encourage investment, but it cannot lead to conservation or encourage preliminary evaluation of exotic germplasm unless opportunities for commercialization can be identified. Conservation and much of prebreeding, therefore, must currently be funded in the public domain.

Fledgling prebreeding and enhancement programs (such as the Genetic Enhancement of Maize [GEM] project) are critically important to foster. New useful genetic resources will emanate from these programs and eventually will be incorporated in proprietary and public breeding programs. The genetic introductions will show, by example, the worth of further private investments in sourcing exotic germplasm. New technologies should also enable more effective sourcing of a broader, more exotic germplasm base and thus the future framework of IPP will encourage more private investment into prebreeding and germplasm enhancement programs. Developing countries misjudge the strength of their position when they threaten to prevent access to exotic germplasm. As a result, genetic resources become hostages between parties that cannot agree on their value. All suffer when programs to evaluate and enhance a broader base of germplasm are reduced because tertiary centers of diversity (breeding programs) geared to produce new varieties are reduced in their capabilities.

The GPA provides frameworks for positive actions on genetic resource conservation and utilization. By focusing on technical needs and solutions, the GPA opens up possibilities for positive progress. However, details still need to be worked out. Funding will be required to support the priority action areas. In budgetary terms, the funds are small (total of $300 million per year) but they will require strong public support.

U.S. agriculture, backed by previous generations of plant breeding and basic research, has effectively generated funds to provide this nation's share of conserving plant genetic resources. For example, an 8.7 billion bushel corn crop selling at $3 per bushel generates $26 billion at the farm gate. Conservatively, $10.4 billion (40%) of this annual farm gate value comes from genetic changes made during the past 60 years. As a result of earlier public and private investments, U.S. agriculture generates a food dividend that is realized in a low percentage of personal

outlay for food. It will require public understanding and political will to reinvest some of these dividends for the future of agriculture. Those investments should include capacity building in plant breeding, conservation, and genetic enhancement on an international scale. Private industry can bring additional intellectual and technological capabilities to bear through mutually agreed bilateral programs that can further help evaluate and enhance genetic resources on a global scale.

References

Cooper, D. 1993. The international undertaking on plant genetic resources. Plant Genetic Resources 2:158-166.

Duncan, R.R., P.J. Bramel-Cox, and F.R. Miller, 1991. Contributions of Introduced sorghum germplasm to hybrid development in the USA. pp 69-102 *In* H.L. Shands, and L.E. Wiesner (eds.) Use of plant introductions in cultivar development. Part 1. CSSA Spec. Publ. 17. CSSA, Madison, WI.

Duncan, R.R., J. Dahlberg, and M. Spinks. 1995. International activities in sorghum germplasm acquisition during the past thirty-five years. pp. 117-134 *In* R.R. Duncan (ed.) International germplasm transfer: Past and present.CSSA Spec. Publ. 23. CSSA, Madison, WI.

Ponting, C. 1991. A Green History of the World; The environment and the collapse of great civilizations. Penguin Books, NY.

Raustiala, K. and D.G. Victor. 1996. Biodiversity since Rio: The future of the Convention on Biological Diversity. Environment 38:16-45.

Stephens, J.C., F.R. Miller and D.T. Rosenow. 1967. Conversion of alien sorghums to early combine genotypes. Crop Sci. 7:396.

Appendix I.

Priority Activities and Long Term Objectives of the GPA (disagreed text as of June 10th in parentheses).

Note: Preliminary per annum cost estimates are given; lowest amount is for basic or rudimentary action; intermediate is moderate; highest is more ideal and comprehensive.

A) *In Situ* Conservation and Development

1) Surveying and Inventorying Plant Genetic Resources for Food and Agriculture

To identify, locate, inventory, and assess any threats to those species, ecotypes, cultivars, and populations of plants relevant to food and agriculture. $2.1m $3.0m $7.3m

2) Supporting On-farm, Management and Improvement of Plant Genetic Resources

To better understand and improve the effectiveness of existing on-farm conservation , management, improvement, and use of plant genetic resources for food and agriculture. To achieve a better balance between *in situ* and *ex situ* conservation. To encourage concrete recognition of (the concept of) Farmers' Rights. To promote the equitable sharing of benefits from plant genetic resources as called for in the CBD. To foster the future emergence of public or private seed companies and encourage cooperative enterprises as an outgrowth of successful on-farm selection and breeding. To encourage traditional seed exchange and supply systems. $6.3m $10.5m $16.7m

3) Assisting Farmers in Disaster Situations to Restore Agricultural Systems

To support farmers' and rural peoples' livelihoods and sustainable agricultural options through the rehabilitation of agricultural systems based on locally adapted plant genetic resources, including the restoration of pre-existing germplasm in cases of disaster-induced loss of plant genetic resources. $4.7m $5.1m $5.3m

4) Promoting In Situ Conservation of Wild Crop Relatives and Wild Plants for Food Production

To promote conservation of genetic resources of wild crop relatives and wild plants for food production in protected areas and on other lands not explicitly listed as protected areas. $3.9m $5.6m $9.9m

B) *Ex Situ* Conservation

5) Sustaining Existing Ex Situ Collections

To give high priority to safeguarding as much existing unique and valuable diversity as possible in *ex situ* collections. (To ensure the observance of the sovereign rights of the countries of origin.) $25.2m $38.6m $55.0m

6) Regenerating Threatened Ex Situ Accessions

To complete the first safe world-wide regeneration of accessions in *ex-situ* conditions, under conditions designed to preserve the genetic integrity of the materials. To create in the process the institutional linkages and experiences to regenerate materials as it becomes necessary in the future. $4.4m $6.0m $9.2m

7) Supporting Planned and Targeted Collecting of Plant Genetic Resources for Food and Agriculture

To collect those species, ecotypes, farmers varieties, or other cultivars, and associated information, that are under threat or are of anticipated use. $1.1m $2.1m $3.0m

8) Expanding Ex Situ Conservation through Botanic Gardens and Use of New Technologies

To conserve and make available for improvement and use the full range of plant genetic resources for food and agriculture. $3.0m $5.0m $12.3m

C) Utilization of Plant Genetic Resources

9) Expanding Evaluation and Increasing the Number of Core Collections to Facilitate Use

To increase and improve the ease of use of conserved plant genetic resources. To Facilitate innovative progress in plant breeding through promoting the identification of useful accessions or their component genes for introduction into genetic enhancement and plant breeding programs. To promote plant breeding that results in higher levels of genetic diversity in crops and agricultural systems. To identify germplasm of potential value for direct use by farmers in on-farm programs. $9.0m $14.4m $25.0m.

10) Increasing Genetic Enhancement and Base-Broadening Efforts

To increase food security and improve farmers livelihoods through the development of better plant varieties. To reduce genetic uniformity in crop varieties. To increase sustainability and the capacity for adaptation to unexpected environmental changes. $25.7m $26.3m $42.3m

11) Promoting Higher Levels of Diversity in Crops to Reduce Genetic Vulnerability

To reduce genetic erosion and possible genetic vulnerability and promote sustainable productivity by facilitating use of genetic diversity in crops. $3.7m $7.9m $16.7m

12) Promoting Under-Utilized Crops and Species

To contribute to agricultural diversification, increased food security and improved farmers' livelihoods. To promote the conservation and sustainable management of under-utilized species and their genetic resources. $1.7m $4.1m $8.2m

13) Supporting Seed Production and Distribution

To increase the availability of good quality seed of a wider range of plant varieties. $3.2m $5.5m $10.3m

14) Developing New Markets for Local Varieties and "Diversity-Rich" Products

To establish stronger demand and more robust market mechanisms for farmer-varieties and related agricultural products.$1.8m $2.5m $6.0m

D) Institutions and Capacity Building

15) Building Strong National Programs

To identify and meet national needs through instituting rational, sustainable, effective and equitable approaches to the conservation and use of plant genetic resources for the benefit of present and future generations. $3.6m $5.3m $10.5m

16) Promoting Networks for Plant Genetic Resources

To ensure that all countries are served by an active regional network and an appropriate complement of crop-based, thematic, and *in situ* oriented networks. $6.7m $10.4m $12.9m

17) Constructing Comprehensive Information Systems for Plant Genetic Resources

To facilitate increased access to and better management and utilization of plant genetic resources through the assembly, exchange and provision of useful information. $9.1m $12.6m $17.3m

18) Developing Monitoring and Early Warning Systems for Loss of Plant Genetic Resources

To minimize genetic erosion and its impact on sustainable agriculture by monitoring key elements of genetic resource conservation and the various factors causing genetic erosion, and assembling information to enable remedial or preventive action to be taken. $1.5m $2.4m $4.3m

19) Expanding and Improving Education and Training

To make available to every country according to their needs and priorities, training in all the relevant functions of conservation and utilization as well as management and policy. $9.8m $14.0m $22.0m

20) Promoting Public Awareness of the Value of Plant Genetic Resource Conservation and Use

To communicate the impact of genetic resource activities to key target audiences in order to generate and sustain political action. $4.1m $6.9m $9.5m

Total Funding per Year over 10 Years

$130.6m, $188.2m or $303.8m, depending on whether the minimal, moderate, or optimal plans are pursued.

Additional Priority Areas Raised at the preparatory Rome meeting (April, 1996)

- benefits derived from the use of plant genetic resources and mecha-

nisms for benefit sharing for the realization of farmers' rights
- technology transfer
- biotechnologies and associated benefits and risks
- national, regional and global agricultural policies
- the state of diversity in the major centres of diversity
- research for on-farm plant genetic resources management, including definitions of appropriate methodologies
- studies on new approaches to plant breeding
- local and under-utilized crops
- international crop-related networks
- current expenditures on plant genetic resource conservation and utilization activities

Existing Sources of Financing

- bilateral official development assistance (including the EU and a portion of the CGIAR)
- World Bank
- Global Environmental Facility (including funds administered in conjunction with the CBD)
- FAO
- UNDP
- UNEP
- other specialized UN funds
- International Fund for Agricultural Development
- regional development banks
- non-governmental organizations (e.g., World Wildlife Fund)
- foundations
- universities and research institutes
- investments or loans from private sector, from governments, etc.
- internal national funding to support national plant genetic resources for food and agriculture programs.

Possible New Sources of Funding

- realization of the concept of Farmers' Rights
- new fund managed by GEF; governments would make special allocations
- special trust fund, voluntary or mandatory; consideration might be given to opening such a fund to contributions by the private sector.

Role of Private Sector

A. Bruce Maunder

Abstract

The hybridization of pearl millet and sorghum led to more than the benefits of heterosis. With an opportunity to sell seed annually, as well as maintain a reasonable degree of protection of the germplasm, the private sector entered this element of the seed industry as early as 1949, some seven years before the first hybrid seed was sold. Whereas commercially produced sorghum hybrids spread rather quickly throughout the Western Hemisphere, much of the African and Asian market is only now giving serious consideration to this form of the crop, with India reporting 50% of the millet and sorghum area planted to hybrids. An obvious need of agriculture in developing countries is technology transfer from national or international research improvement programs to the producer, both the subsistence farmer as well as the large operator. For millet and sorghum, dependable markets, relatively large areas of cultivation, and the farmers' desire to increase yields through cultural and varietal changes (e.g., moving to hybrids) suggests farmers will benefit from the presence of private seed firms. Likely reasons for success would be dependable supply with acceptable quality/purity, and hopefully, but not necessarily, an improved level of production.

Public plant breeding research is an asset to private seed firms. Small, indigenous seed firms, in particular, depend on public plant research institutions for advanced breeding materials, even new varieties or hybrids. According to a recent survey, currently in India 71% of hybrid sorghum and 32% of hybrid millet being sold may very well be of public origin or non-proprietary. A strong public plant breeding program is essential for long-range success of the private seed industry, whether it be in developed or developing countries.

Generally, the outlook for the private sector in developing countries is bright. In the Western Hemisphere, the Mexico sorghum picture is most optimistic, with favorable cost of production and strong performance resulting in a return per hectare comparable or superior to the return for maize. The U.S. and Argentina, with reduced areas planted to sorghum, have seen research budgets curtailed, causing a need for re-prioritization of research efforts.

For the future, besides private sector research dollars, scientists need and must share a free flow of genetic resources from all geographic areas and political philosophies. Subsidies of public seed products must be abolished to level the playing field. A thriving

A. Bruce Maunder, Retired Senior Vice President, DEKALB Genetics Corporation, 4511 Ninth St, Lubbock, TX 79416

private sector will lead to more investment in developing countries. Of greatest significance, however, will be the unified approach of both public and private scientists working toward an essential goal of improved millet and sorghum hybrids.

The hybridization of pearl millet and sorghum led to more than the benefits of heterosis. With an opportunity to sell seed annually, as well as maintain a reasonable degree of protection of the germplasm, the private sector entered this element of the seed business (a small part of the 50 billion dollar seed industry) in the early stage of hybrids. In fact, Quinby (1974) notes that the DEKALB Agricultural Association located a sorghum breeding program near Spade, Texas (northwest of Lubbock) in 1949, and was able to sell proprietary hybrid seed in 1956, a year ahead of the rest of the industry. This activity, he concludes, "hastened the release of parents of hybrids by the Experiment Stations and caused other seed companies to start hybrid sorghum breeding programs." Additionally, the hybridization of sorghum often led the way for international expansion of multinationals into countries such as Mexico, Argentina, and India, to name but a few.

For clarification, the private sector currently plays a major role in breeding sorghum and millet, but is by no means exclusive in this function. Certainly producers and consumers depend on the public sector to develop cultivars where there is insufficient market potential for private sector investment in breeding. For example, private sector breeding of sorghum or millet varieties doesn't have the same market potential as development of hybrids. Also, market size influences the degree of effort expended by the private sector. Finally, the farmer or producer benefits more than anyone from strong competition in the seed industry.

Private Sector in Developing Countries

The private sector is critical to productive agriculture worldwide because it meets special needs and provides critical impact in developing countries. A survey of the sorghum and millet industry in India led Pray et al. (1991) to suggest that private companies can profitably conduct research on "poor peoples' crops" in competition with public research institutions. They further encouraged the consideration of policies aimed at fostering private breeding research. Seventeen firms had Research and Development (R & D) programs, spent an average four percent of seed sales revenue on research (similar to the percentage spent on research in the U.S.), and employed 31 Ph.D. and 45 M.S. degree graduates. Table 1 indicates private sector involvement in crops with greatest emphasis on millet, sorghum, and sunflower. With current reductions in private sector activities in the U.S., these numbers may very well exceed or at least equal U.S. private research investment and number of programs. The availability of privately labeled hybrids to many U.S. companies that do not conduct research themselves tends to confuse the actual research effort, with perhaps 50 companies marketing sorghum hybrids with parental lines obtained from the public sector.

The results of a survey of several countries, designed to calculate areas planted in sorghum and millet and the percentage of each area planted in hybrids, may be

Table 1. R&D programs in India and expenditures by crop.

	Number of companies with R&D	R&D expenditure by crop (Rs million)
Pearl millet	12	3.7
Sorghum	10	3.4
Sunflower	10	3.5
Cotton	9	2.1
Corn	6	2.1

Source: Pray et al. (1991).

Table 2. Area (ha) of sorghum/millet and percent hybrid seed for specific countries.

Country	Area planted (1000 ha)		% Hybrid	
	Sorghum	Millet	Sorghum	Millet
India	12,800	10,200	40	46
Australia	1,000	10	100	75
Nigeria	4,000	5,050	1	0
Niger	1,000	3,038	0	0
Sudan	6,234	1,250	6	0
Mexico	1,650	—	100	—
Argentina	674	—	100	—
U.S.	4,940	—	100	

seen in Table 2. If several responses were received from one country (such as India), averages are included. Currently in India, nearly 50% of the millet and sorghum area is planted in hybrids. K.R. Chopra (1996, personal communication) suggests that value-wise, the private sector has captured 60% of the formal seed market. To the contrary, D.S. Murty (1996, personal communication) indicates that of the 17 sorghum growing countries in West and Central Africa, only Nigeria and Niger have formally released sorghum hybrids; however, the area currently planted in hybrids does not exceed 1000 hectares. Egypt, Sudan, Zimbabwe, and South Africa are exceptions, with hybrid sorghum usage ranging up to 95% in South Africa. Throughout Africa pearl millet production is generally limited to varieties. The Gezira irrigation project in Sudan is now striving for 100% hybrid sorghum by 1996. Hageen Dura-1, released in 1983, has stimulated the movement away from local varieties. At a conference announcing hybrids for Sudan, Mufti (1983) stated that there is no seed industry in the country to meet the growing need for good quality seed, which will effectively increase production of the most important food crop of the nation.

An obvious need in agriculture in developing countries is technology transfer from national or international research improvement programs to producers, both subsistence farmers as well as large operators. For millet and sorghum, the existence of dependable markets, relatively large areas of cultivation, and farmers' desire to increase yields through cultural and varietal changes (likely moving to hybrids) indicate that farmers will benefit from the presence of private seed firms. Norman Borlaug believes, however, that in some cultures, yield increases of as much as 50% may be required to achieve movement away from traditional landrace cultivars. Certainly, profit to farmers should be great enough that they can afford to pay a higher price for quality seed. First hand reports from Sudan, however, suggest a willingness to pay more for seed from a multinational company rather than a local vendor, just on the basis of purity and quality.

Lack of substantive knowledge of a viable seed business or industry will likely require input from those experienced in seed enterprises; such input should be readily available from programs like the ASSIST program at Iowa State University. There are three principal

advantages and likely reasons for success (Duvick, personal communication): 1) dependable supply, 2) acceptable quality/purity, and 3) hopefully, but not necessarily, an improved level of performance. Any one of these advantages would lead to increases in profit to farmers. In brief, commercial seeds are best suited to profitable crops in favorable farming regions.

To attract the development of seed firms, a nation's government should be politically stable and its infrastructure, particularly transportation, adequate for the delivery of goods and services to the farming community. To attract seed firms, an opportunity for a reasonable return on investment without government restriction is essential, since capital risk will be required. Private but indigenous seed enterprises may be a logical first step, but their inability to cope with fluctuating exchange rates and lack of sufficient funds for research often has put them at a serious disadvantage in competition with multinationals — Argentina being a good example. These entrepreneurial indigenous companies likely will require outside training and perhaps some subsidy early on, but there are in every country individuals capable of such activity. A supply of trained indigenous agriculturists will be indispensable in operating the seed firms. There also should be evidence that markets for both seed and crop are relatively stable, without undue interference from government regulations or private-market manipulators.

The presence of public plant breeding research is an asset to private seed firms. Small, indigenous seed firms, in particular, depend on public plant research institutions for advanced breeding materials or even new varieties, as well as for knowledge of new agronomic techniques applied to the new varieties or hybrids. Currently in India, the survey suggests 71% of the hybrid sorghum and 32% of the hybrid millet being sold may very well be of public origin or non-proprietary, whereas in the U.S., Mexico, and Argentina, the great majority of sorghum pedigrees are, in fact, proprietary. A strong public plant breeding program is essential for long-range success of the private seed industry, whether it be in developed or developing countries. By the same reasoning, public plant breeding researchers must accept the need for, and presence of, the private sector, since in most third world scenarios this will be the only way their efforts will affect the agricultural economy and, subsequently, the national economy. The private sector accomplishes, beyond research, what the extension and public foundation seed organizations are not currently doing. US/AID, in recognition of this approach and opportunity, has been encouraging more commercial involvement in developing countries.

Intellectual property laws are not the first requirement for building a commercial seed industry in a country. In fact seed firms often start out by handling hybrid crops such as millet and sorghum with built-in property protection because the seeds must be purchased for each subsequent planting. Seed firms also may provide better seed quality or purity, which again lessens the need for intellectual property laws early on.

Opportunities for the Private Sector

Developing Countries

In Sub-Saharan Africa, Sanders et al. (1996) suggest that "sustainable" means reversing crop yield declines in some of the low input systems and increasing yield

gains in moderate input systems. Obviously, with only 34% of the world's acres using high technology or modern seed, bringing in a private sector component to step up research makes sense. As competition increases, the share of private sector activity likewise increases. Bringing in private sector activity, however, is somewhat evolutionary and not an immediate transition. The government of India, for example, has recognized the capabilities of the private sector to breed, produce, and market proprietary and publicly bred materials more efficiently. With control of 60% of the market now, the private sector unanimously suggests things will be better business-wise and the future seems bright. Much open pollinated area means potential hybrid business. The combination of all three components — research, production, and marketing — promotes greater efficiency in the private sector. Public sector R & D will be most effective if private research is not regarded as competition to be met with suspicion, but as a partnership worthy of recognition and support.

ICRISAT's investment and success in improvement of pearl millet is a classic example of multidisciplinary teamwork and research partnership. The impact is felt in farming communities in real production environments. An ultimate opportunity will center around the export of seed or surplus grain. In West Central Africa, the private seed industry is very weak, with Niger, for example, badly in need of support to produce and distribute AND-1, its first sorghum hybrid. Markets can be developed when national governments have policies that encourage the private sector and provide adequate legal protection of proprietary germplasm. Not to be overlooked is the critical ability of the private sector to more effectively provide adequate stocks of high quality seed, a problem often encountered by the public sector in less developed countries.

Environmental and economic conditions (e.g., water supply and cost of inputs) also will give rise to greater demand for sorghum. Some see this as a likely scenario in China, which could stimulate a private sector seed industry for both crops.

Developed Countries

Where the private sector has been well established (as it has in Europe, Australia, and the Western Hemisphere), the high percentage of proprietary hybrids suggests that the level of improvement depends primarily on available budget. Unless subsidized from other crops, funding available for hybrid research must come from seed volume of hybrid sorghum. With a significant downward trend in area planted in sorghum in both the U.S. and Argentina (which previously planted 7.2 and 3.0 million hectares, respectively, but are now down to perhaps 4.9 and .67 million hectares), some breeding programs have been dropped and others have been reduced significantly. The multinational seed companies affected have, in turn, had an adverse effect on smaller programs worldwide. As in any business venture without outside funding, market size related to number of participants is critical. Currently, Mexico appears to be an exception, with favorable cost of production and performance of sorghum resulting in a return per hectare comparable or superior to the return for maize. Unfortunately, breeding programs cannot be stopped and started as can programs in an

industrial factory, which means there will be a significant time lag when adjusting to market size. Fortunately, this deficiency can be modified or reduced by input from the public sector.

The private sector companies must concentrate on activities they do best, considering funding limits. Their infrastructures support applied breeding of lines and hybrids, followed by extensive testing over wide geographic areas. They can best accomplish these activities by:

- being more efficient and flexible
- better understanding market requirements
- interacting with new agronomic practices
- concentrating on a holistic approach for improvement
- working larger numbers in selection and testing
- being concerned about seed cost in evaluating inbreds
- placing greater emphasis on short or medium term breeding programs
- ensuring less crop vulnerability.

Currently, commercial breeders work closely with entities within the public sector, whether they be state or federal, and with the IARCs. The U.S. Sorghum Germplasm Committee, which advises the National Plant Germplasm System in the U.S., is made up of half private and half public sorghum scientists. Likewise, the private sector actively lobbies through various organizations to establish or maintain public sorghum research positions. Members participate in the Sorghum Improvement Conference of North America and have the opportunity to be chosen for the Grain Sorghum Producers Award. The U.S. private sector handles large winter or off-season programs with frequent support for the public sector, which provides nursery rows and some pollinating. The private sector in past years has volunteered to increase plant introductions where short-day sites and non-U.S. locations were required. Over the next several years, those commercial programs of sufficient size to support biotechnology research on maize are likely to see spin-offs affecting sorghum and millet.

Limitations or Restrictions

Developing Countries

Hybrids and a well-developed private seed sector would be farther along were it not for government restrictions in many developing countries. Hybrid registration requirements as well as phytosanitary restrictions may delay or prevent release of otherwise improved hybrids, as well as the movement of same or basic germplasm essential for research. In countries where government agencies keep a part of all breeding or parent lines that come into the country, the private sector has limited legal protection for proprietary germplasm. The same concerns exist where plant variety protection does not exist. Hopefully UPOV rules will be accepted in more of these situations.

Economically, the private sector can be restricted not just by market size but by percent of the market in hybrids. Both world price and within-country price, in relation to maize, can be critical to market size, as in Mexico, where maize has received specific incentives with price support.

Similar effects are seen in countries where public hybrids are subsidized by the government, giving unfair price competition. Production costs for both seed and the commercial crop also will affect customer acceptance of the crop or, more specifically, hybrids of the crop. Finally, a frequent problem with many developing countries has been low demand or price instability in years of above average crop production, which results in loss of producer incentive. Limited or no access to an export market further exacerbates this weakness, greatly inhibiting development of an "after the farm gate" market.

Research in the private sector depends on sales; however, limitations on the sale of seed other than that certified by government agencies severely restrict the sale of proprietary hybrids. India, for example, has a multiplicity of central and state government acts, which sometimes constrain the production and marketing of sorghum and pearl millet seeds. The government needs to regulate the seed trade through a single central seed act.

Developed Countries

Plainly stated, in areas where private sector companies have a long history, limitations will be pretty much self-inflicted. Generally, exceptional human resources and adequate financial resources, as well as effective research, should overcome any limitations. We, however, cannot disregard the probability of closer government control of new transgenic traits, such as plant-produced pesticides, when they become part of the sorghum/millet industry. Certainly to maintain the financial input needed for adequate research activity, it is critical that the industry, both private and public, do a better job of promoting a crop sometimes considered "a poor man's food," but of proven worth, to: insure production under abiotic stress; generate significant farm income; limit erosion; enhance crop rotation; have essentially equal feed value to maize; provide a second principal feed grain; and be backed by a tremendously valuable world collection to handle future opportunities. Not to be forgotten, this is a crop known to be readily adaptable to genetic engineering.

Future Needs

A free flow of genetic resources to be shared and utilized by scientists from all geographic areas and political philosophies also requires a united effort to facilitate long-term collection and maintenance. Distance involved, the lack of trained curators, the cost of operations, the need for user-friendly descriptors, and the necessity for derived benefits from germplasm, all emphasize the need for international cooperation on plant genetic resources as part of our global heritage to sustain and improve agriculture. Future improvement in germplasm cooperation will most likely result from more scientist-to-scientist relationships (Maunder, 1995). For conserved germplasm to be user-friendly, essential descriptive and screening work must be conducted, and, where feasible, limited to prebreeding of crops. Finally, the private sector must increase its willingness to deposit germplasm resources in publicly available banks and to provide valuable descriptors of this material. Control must exist, however, if materials going into a country are to be shared with unknown third parties or if the germplasm involves enhancement or breeding expense with no control under UPOV. The private sector has developed in India, not from support by national programs, but rather because

of free distribution of germplasm and encouragement from the International Center, ICRISAT.

Subsidies of public seed products must be abolished to level the playing field. Apparently there are no restrictions on prices in India, but, under inflationary controls in Argentina, fixed pricing nearly eliminated the private sector when faced with mandated wage increases. Market development is a major requirement whether for a new or existing private sector company. Since research is driven by seed sales, the sorghum and millet industry in general must be united in promoting these crops as essential to feeding a world population that will possibly double by 2040. Those involved must talk to customers, they being producers, livestock feeders, and, ultimately, consumers. Certainly situations exist where government and other donors should help develop a seed industry and its related infrastructure.

The private sector in the U.S. always has a long list of early generation genetic resources or finished lines of known and proven value, depending on the magnitude of their research. Current concerns relate to the potential impact of ergot throughout the Western Hemisphere. The poultry industry would like more areas planted to similar light-colored grain of the food sorghum category, but would accept non-tan material if enough white, cream, or yellow could not be assembled under some sort of contract. As in most sorghum areas, more tolerance to abiotic stress will be of real value. Mexico's surge in sorghum area and productivity points out the value of both high yields and yield stability compared to corn, not to mention rotational advantages. The likelihood of continued higher sorghum prices in North America and a new farm program in the U.S. will lead to increased area planted to sorghum. This in turn will be reflected by greater funding for private sector research.

A thriving private sector will lead to more investment in developing countries. Additional funds will allow for research on nutritional characteristics, agronomic management studies, and longer term breeding approaches. The private sector has the capability to fund graduate programs, provide grants, and give time in support of worthwhile public programs. Of greatest significance, however, will be the unified approach of both public and private scientists working toward the common goal of developing improved millet and sorghum hybrids.

Acknowledgment

The author is greatly indebted to those millet and sorghum scientists responding from some six continents, who provided current crop statistics and described the present activities of the private sector in their respective countries.

References

Maunder, A.B. 1995. The need for international cooperation in germplasm activities. p. 83-93. *In* R.R. Duncan (ed.) International germplasm transfer: Past and present. CSSA Special Publication 23.

Mufti, M.A. 1983. The role of seed business in increasing productivity. p. 86-88. *In* G. Ejeta (ed.) Hybrid sorghum seed for Sudan. Purdue University, West Lafayette, IN.

Pray C.E., S. Ribeiro, R.A.E. Moeller, and P.P. Rao. 1991. Private research and public benefit: The private seed industry for sorghum and pearl millet in India. p. 315-324. *In* Research policy 20. Elsener Science Publishers B.V.

Quinby, J.R. 1974. Sorghum improvement and the genetics of growth. Texas A&M University Press, College Station, TX.

Sanders, J.H., B.I. Shapiro, and S. Ramaswamy. 1996. The economics of agricultural technology in semiarid Sub-Saharan Africa. Johns Hopkins University Press, Baltimore, MD.

International Research Perspective

S.B. King and K.F. Nwanze

Abstract

Since the Rockefeller Foundation embarked on a wheat improvement program in Mexico in the early 1940s, international agriculture research has grown considerably and contributed significantly toward bringing hope to the task of feeding the ever increasing world population. Many countries and donor agencies have supported this expansion effort, which has, among other things, witnessed the development of a network of international centers of agriculture research under, auspices of the CGIAR. Today, international research finds itself facing reduced funding in real terms. This has resulted in a number of changes in emphases, including a more careful identification of research priorities, increased collaboration among an array of partners (NARS, IARCs, ARIs, extension services, farmers, and agribusiness), and greater emphasis on more targeted training, expanded information exchange and management, and more effective communications.

Historical Background

Past difficulties in transferring technologies, especially those immediately relevant to agricultural production, from developed to developing countries have concerned researchers and developers from as early as colonial periods. These technologies did not fit into the agro-ecological and socio-economic environments of the countries for which they were destined. Essentially, experience has shown that only technologies either indigenous or suited to local environments can foster agricultural development. This occurs in two ways: 1) through the importation of expatriate staff, i.e., the transfer of intellectual expertise in order to bring together a critical mass of agricultural scientists (as a short-term measure), and 2) through the enhancement of the indigenous research capacity, i.e., human capital or resource development (as a long-term measure). These measures enable such countries to access the advances in knowledge available in the global scientific community and embody that knowledge in technology suited to their own resources and cultural endowments.

The process of broader and systematic international involvement in a developing country's agriculture, with direct relevance to food crops as opposed to cash crops (the latter often being a feature of a past colonial era), was initiated by the Rockefeller Foundation in collaboration with Mexico in the early 1940s. Focus was mainly on wheat production, although maize also benefited from this collaboration. Scientists posted in Mexico at the request of that country's government

S.B. King, Formerly ICRISAT, 1448 Hampton Circle, Goshen, IN 46526 and K.F. Nwanze, WARDA, 01 B.P. 2551, Bouake, Cote d'Ivoire. *Corresponding author. ICRISAT Conference Paper No. CP 1306.

developed improved cultivars using the available world collection of wheat germplasm, catapulting yields under irrigated and fertilized conditions. Additionally, Mexican scientists and technicians were trained within and outside the country. By the 1960s, wheat production had improved to the extent that Mexico, which had been a wheat-importing country, began to export wheat.

The Rockefeller Foundation subsequently extended its international collaborative activities on maize and wheat to other countries of Latin America and Asia. The Ford Foundation also was active in helping developing countries increase their agricultural production through research and strengthening of human resources. These two foundations jointly established the International Rice Research Institute (IRRI) in 1960, which became the first international institute mandated with food crop and global responsibilities. The success of IRRI gave rise to three other international centers: the International Center for Improvement of Wheat and Maize (CIMMYT) in Mexico in 1966; the International Center of Tropical Agriculture (CIAT) in Colombia in 1967; and the International Institute of Tropical Agriculture (IITA) in Nigeria in 1967.

Apart from the Rockefeller and Ford Foundations, several other organizations became active (and continue to be active) in fostering international partnerships with researchers, extension agents, and administrators in developing countries. Although several donor agencies (governments of developed countries, foundations, and aid agencies) had previously provided bilateral support for agricultural research and development, the impact of the first group of international research centers dedicated to long neglected food crops had within a few years gained considerable credibility. This success generated a world-wide demand for similar research centers on other commodities and in other geographic regions. The internationalization of research begun by the Rockefeller and Ford Foundations received a major boost with the development of the miracle rice variety, IR-8, released by IRRI in 1966. By 1968, it had covered millions of hectares of farm land in Asia. Improved rice varieties and wheat varieties, which responded to high inputs of fertilizer and water, formed the backbone of the green revolution of the 1960s and 1970s. A donor consortium known as the Consultative Group on International Agricultural Research (CGIAR) was formed in 1971 under the sponsorship of the World Bank, the FAO, and the UNDP, and with support from several governments and other banking institutions. The CGIAR expanded the development of international research centers; the network now consists of 16 autonomous centers headquartered in 15 countries with mandates ranging from food crops to livestock, fisheries, agro-forestry, and institutional development. Regional and national sub-stations of these centers are today distributed worldwide.

Shift in Research Environment

Most of the first two decades of the CGIAR was a period of growth with the addition of more centers and expansion of existing centers and their research agendas. One of these, ICRISAT, was established in 1972. Funds were ample and virtually always certain to support most or

all the research planned by centers. Other mechanisms to promote additional international agricultural research were developed outside the CGIAR. For example, the Collaborative Research Support Program (CRSP) concept was created by USAID and the Board for International Food and Agriculture Development (BIFAD), under the auspices of Title XII of the Foreign Assistance Act of the U.S. Government. The Sorghum and Millet Collaborative Research Program (INTSORMIL) is one of several CRSPs established in the late 1970s and early 1980s to mobilize the land grant universities of the U.S. into the international food and agricultural research mandate of the U.S. Government. Governments of other developed countries provided additional mechanisms to support agricultural research to fight the anticipated dire consequences of insufficient food supplies for rapidly growing populations in Asia, Africa, and Latin America.

During the past decade, however, the environment for international research has been shifting from one of expanding effort and funding to one of declining funding in real terms, often accompanied by diminishing research agendas and increasing uncertainty. Many centers and organizations/institutes are seeking innovative ways to deal with the problem. Largely as a result of funding uncertainty and in the interests of developing a more flexible way to deal with the current research environment, ICRISAT has reorganized its research portfolio into a series of multidisciplinary, largely global projects based on the 92 core research themes developed through a year-long process of developing the 1994-98 Medium Term Plan (MTP). These research themes were operationalized into 22 projects relating to the 29 production systems toward which ICRISAT's work is targeted. ICRISAT has recently reduced the number of projects from 22 to 12, and now it is working on its MTP for the years 1998-2002. Throughout this process of organizing and reorganizing, ICRISAT has made a concerted effort to involve the NARS and other partners.

There have been a number of other shifts in the international agricultural research environment in recent years. One of these is today's greater emphasis on activities associated with the transfer of technologies generated by research to farmers and the farming community. In fact, half the budget of the SADC/ICRISAT Sorghum and Millet Improvement Project (SMIP) is now allocated to technology transfer activities. Many technologies generated by research on crop improvement still sit on the shelf, never having been tested or promoted at the farmer level.

The integration of crop research with research on livestock is gaining increasing attention, because many farming systems, particularly in developing countries, integrate both aspects. Certainly sorghum and pearl millet production areas are characterized by integrated crop/livestock systems. Recent initiation of the Systems-Wide Livestock Initiative of the CGIAR signifies the increased emphasis on this area. Government policies that affect agriculture also are gaining greater recognition by international research. These policies have a significant effect on agricultural production, but unfortunately, a negative one in many developing countries.

Partnerships in Research Collaboration

Effectively meeting the challenges of international agricultural research requires making the most of limited resources and opportunities. Forming partnerships in which the comparative advantages of the various players are exploited is almost always an essential ingredient of success.

A good example of a successful research partnership is the project on breeding for resistance to downy mildew in pearl millet, a disease that has posed a serious production constraint during most of the 30 years since pearl millet hybrids were introduced into commercial cultivation in India. In 1990, ICRISAT, the India National Program on Pearl Millet Improvement, the University of Wales (Bangor), the John Innes Centre (Norwich), and the Overseas Development Administration (UK) formed a partnership to develop marker-assisted selection for improving downy mildew resistance in pearl millet hybrids in India. By 1993, QTLs for downy mildew resistance had been identified, and it is anticipated that by the end of 1996 resistance will be transferred to elite, seed parent backgrounds using marker-assisted selection. This success in research would not have been possible in such a short time without effective collaboration among the national research program of a less developed country, advanced research institutes and funding of a developed country, and an international center. The project succeeded in part because it was built on the comparative advantages of each partner.

NARS as Partners

The national agricultural research systems (NARS) have the major responsibility for research in developing countries. Significant differences exist among NARS in their strength and capacity to do research. Also, national research programs often are characterized by heavy reliance on donor funding to support research.

A number of efforts by donors and NARS themselves to strengthen NARS nationally, have failed, and the NARS remain weak. Sometimes NARS have improved research facilities and more and better trained scientists, but their operating budgets remain dismally low for effective research. Innovative means of rasing money for research are required, and those who make policy, especially Ministries of Planning and Finance, should be sensitized to the needs of research so as not to lose the advantage of good research facilities and highly trained scientists. Sometimes efforts of various programs within a country are not coordinated well enough to solve problems related to agricultural research. Agricultural research institutes, universities, appropriate NGOs, private agribusinesses, and farmer organizations can all make vital contributions as partners. Collaboration among NARS of different countries to solve common problems within a region also could be an effective and less expensive approach to problem solving.

NARS are the major partners of IARCs and other advanced research institutes (ARIs) to assist with agricultural research in developing countries. Greater interaction between NARS and the CGIAR is needed, and steps are being taken to enhance this partnership. The major area of priority setting links closely with the Technical Advisory Committee (TAC) of

the CGIAR. As a first step, the NARS are working to agree on their regional priorities through their regional fora. Hopefully this area of joint or aligned priority setting will expand in the near future. There has been a history of partnerships between NARS and IARCs; some have been excellent and others have left much to be desired. Developing good partnerships requires a conviction of their value, the will and determination to make them work, and the necessary time and attention to nurture them.

Extension Services as Partners

Extension services are the logical agents to transfer research-developed technologies to the farming community. However, in many less developed countries, extension services are poorly managed and funded, having low levels of motivation, training, and understanding of farmer needs. By themselves, they are often ineffective in the transfer of research-generated technology. However, they can be useful partners in some cases, and it is essential that efforts to transfer technologies to farmers recognize the mandated role of extension services in this area.

NGOs as Partners

In much of Africa, and perhaps in many developing countries on other continents, a transition in thinking is occurring, from the idea that government should do everything to the idea that things should be done by others, including private enterprise. Non-governmental organizations (NGOs) are rapidly stepping in to fill the void.

The importance of NGOs as players in the development process of less advanced countries has grown considerably in recent years. NGOs are especially active today in fields of agriculture, natural resources, and the environment, and many are involved in technology generation and transfer. NGOs work closely with rural communities and with farmers. They often are closely tuned to farmers views, aspirations, and problems, and NGO employees often are recruited from communities in which they work. NGOs tend to work in a concentrated way in specific areas. They often have the confidence of farmers and can therefore be influential with them. Researchers are not in this position, nor are extension services in many cases. NGOs can be an intermediate avenue for researchers to meet farmers, and a good avenue for exposing farmers to new technologies. They also can be involved as intermediaries in getting farmers involved in participatory aspects of research. They can be of great assistance in the implementation of on-farm trials.

Donors have perceived the important role NGOs play in development and consequently are directing more support toward NGOs. To best use the dwindling financial resources now available to agriculture research, it is paramount that collaboration increase between NGOs, NARS, and IARCs. By late 1994, 12 of the 16 IARCs had already established collaborative activities with over 300 NGOs, ranging from local to international. Five years earlier, this number probably did not exceed 30.

ICRISAT is working with a number of NGOs and is seeking more avenues to

allow collaboration with NGOs to result in clear comparative advantage and complementarity. One area we believe is especially well-suited is small-scale seed production, particularly for sorghum, millets, and groundnut. Although generally there is little incentive for commercial production of seeds of open-pollinated varieties, in India, at least with pearl millet, past commercial activity in this area has been considerable. NGOs can be stimuli for getting things done at the local level, preferably in collaboration with NARS.

Farmers as Partners

Systems generally used in developed countries to generate and transfer technologies to farmers may not be appropriate for use in less developed countries. For example, while it is about right to take six to ten years to breed a variety and another four to six years to test it on-farm in developed countries, we believe it is not practical (in fact, wrong) to take this long in developing countries. In contrast to farmers in developed countries, farmers in developing countries have very few options available to them regarding the crop varieties they grow. They do not know, as do those of us in research, about the vast range of genetic variability among the thousands of accessions of these crops available in genebanks. Farmers in developing countries often are not aware of traits such as earliness, shorter plant stature, grain color, ease of threshing, etc., which may not be available in the landrace varieties they currently grow. We researchers often hold the view that we know what plant type is best for the farmer, developing these views with little, if any, interaction with the farmers who grow the crop in the targeted area. This is certainly one reason, though not the only one, why new releases have not always been adopted by farmers.

Perhaps we are now seeing a shift away from this type of thinking. But have we gone far enough to involve farmers in our research, or should we go even farther? Are we willing to involve farmers in the actual selection of progenies in our breeding nurseries? Are we willing to accept the fact that for farmers yield may not be the most important trait, but may rank second, third, or even fifth in priority? Are we willing to allow farmers to become genuine partners in deciding what our breeding programs produce? We do not believe farmers should determine the methodology of breeding to be used because they do not have the necessary training, but they certainly must have the opportunity to educate crop improvement scientists on what they believe is best for them. In some instances, this may involve, at least for the short term, allowing farmers to select materials we have in our breeding program or making it possible for them to see and test materials that come directly from other breeding programs. We must not lose sight of the fact that farmers should be treated as extremely important partners in our breeding programs.

Agribusiness as a Research Partner

The private sector is an important research partner in agricultural production in developed countries, but it is seldom acknowledged as such. However, if agriculture is to go beyond the subsistence level in developing countries, it is essential that researchers be aware of the interests and potential interests the private sec-

tor may have in production and use of the crop. For starters, increased production is going to require markets that in turn may require new uses for farm products.

Making Collaboration Work

If international research partnerships are to be effective, they will require efforts in training, information exchange, and communication.

Training

Research of necessity depends on trained staff; therefore, training has been an important component of international research efforts. Both the INTSORMIL and ICRISAT training programs for sorghum and pearl millet researchers and support staff have contributed enormously to the capacity of NARS to conduct research on these crops. It is doubtful that the national programs of many countries would be of sufficient strength to conduct research on these crops today were it not for the emphasis these two organizations have placed on training.

INTSORMIL and ICRISAT have taken somewhat different approaches in the past to training, but their programs have complemented each other well. The INTSORMIL program has emphasized advanced degree training (over 80% of the 818 participants have gained MSc or PhD degrees; see Table 1), and the ICRISAT program has emphasized in-service training of technician-level support staff (about two-thirds of the over 1600 participants in sorghum and pearl millet research; see Table 2). In 1984, ICRISAT contracted with INTSORMIL to develop and manage the advanced degree program for the SADC/ICRISAT Sorghum and Millet Improvement Project (SMIP). Ninety-six participants from nine SADC countries received advanced degrees through this program

Both programs have rightfully stressed training of participants from Africa, with INTSORMIL's second regional emphasis (aside from the U.S.) on Latin America and ICRISAT's on Asia. About 30% of INTSORMIL trainees have come from the U.S. and 2% from other developed countries, whereas only about 5% of those in the ICRISAT program have come from developed countries. Training people from developed countries is an important contribution, however, because it provides a way of sensitizing people in these countries to international agriculture. Many of the participants of these training programs have gone on to careers that include international research. Emphasis of both programs has been in breeding

Table 1. Numbers of participants trained in INTSORMIL's training program by type of training and region of origin, 1980-1996 (July).

Type of training	Region of origin					Total
	Africa	Asia	Latin America	U.S.	Other	
PhD	115	50	62	110	10	347
MSc	134	30	48	113	4	329
BSc	13	1	9	15	0	38
Post Doctorate	5	10	4	11	0	30
Visiting Scientist	11	3	3	0	2	19
Short Term	25	10	15	2	2	55
Total	304	106	141	251	18	818

Table 2. Numbers of participants trained in sorghum and pearl millet improvement and production techniques at ICRISAT Asia Center by training category and region of origin, 1974 to 1996 (July 1).[1]

Type of training	Region of origin				Total
	Africa	Asia	Latin America	Other	
Research Scholars	20	53	4	14	91
Research Fellows	6	6	1	29	42
Visiting Scholars	64	108	6	0	178
In-Service Participants	700	135	24	1	860
Short Term Participants	58	54	1	3	116
Apprentices	0	10	1	32	43
Total	848	366	37	79	1330

[1]Figures do not include several hundred participants who received training at ICRISAT locations other than ICRISAT Asia Center.

followed by agronomy, plant pathology, and entomology, with food quality and utilization ranking second in the INTSORMIL program. There is increasing emphasis on training of women; to date about one in four participants in INTSORMIL's program and about one in eight in ICRISAT's program have been women.

In the future, we believe responsibility for training should shift from developed countries and IARCs to developing countries using local institutions. For sustained development, it is essential that this transition occur. Certainly the capacity to support in-country training is available in a number of developing countries and a greater reliance on these institutions for training should quickly identify the good ones and strengthen their capabilities as training centers. We believe donors would like to assist training institutions that are doing a good job in developing countries.

Information Exchange and Management

An enormous array of genetic materials and evaluation data have been generated by sorghum and pearl millet improvement programs worldwide. However, this information cannot be fully utilized unless it is efficiently managed and accessible. Several of the IARCs are working together to address this need, exploiting major advances in database software capabilities, to develop an International Crop Information System (ICIS).

The specific objectives of ICIS are to enable unique identification of all genetic materials, document the nature and chronology of genetic resource use and development, and manage and provide access to performance information and evaluation environment data. This system would provide a powerful new research tool, enabling assessment of genetic diversity or similarity, answering queries on the performance of specific genetic material, identifying material with target performance, and assessing patterns of genotype × environment interaction.

ICIS is expected to provide a generalized scheme by which specific systems for sorghum and pearl millet can be developed. Thus with the eventual development of an International Sorghum Information System and an International Pearl Millet Information System, sorghum and pearl millet researchers worldwide would have a tool not only to document and manage their own pedigree, genotypic

performance, and evaluation environment data, but also to gain access to this information globally.

Communications

Good communications are essential for effective collaboration, especially in developing collaboration among NARS and between IARCs and NARS. Efforts are being made on a number of fronts to establish electronic networking among partners. This is already happening within individual consortia/initiatives such as the Consorcio para el Desarrollo Sostenible de la Ecoregion Andina (CONDESAN) in Latin America and the African Highlands Initiative of East and Central Africa. Hopefully it can rapidly develop further.

Conclusion

It is safe to conclude that institutions, organizations, and people involved in international agricultural research have come a long way since the early days of this business. There have been a number of success stories for which we as a research community can be proud. There have also been some failures, including some big ones. And a number of research outcomes have been neither successes nor failures. This category includes research results which may prove vital to the success of some future venture in international research, which may make a difference in the lives of citizens of the less developed countries.

Certainly international research, like most any research, requires resources, innovative thinking, fresh ideas, and collaboration. It also requires much good will, teamwork, and a conviction that success can be achieved in a reasonable time frame with good cooperation. It requires a desire to share credit.

International agricultural research is a noble cause that has already positively affected the lives of many of the most disadvantaged people of the world. If given opportunities to continue in this endeavor, we believe international research will play a key role in the lives of millions of the world's citizens in future.

Agricultural Research and Extension: The Only Way to Feed the World *and* Save Its Wildlife for All Time

Dennis T. Avery

Dennis T. Avery is Director of Global Food Issues for the Hudson Institute of Indianapolis. He was formerly the senior agricultural analyst for the U.S. Department of State. He grew up on a Michigan dairy farm and studied agricultural economics at Michigan State and the University of Wisconsin. Hudson has recently published his book, Saving the Planet With Pesticides and Plastic: The Environmental Triumph of High-Yield Farming, which is available for $19.95 postpaid. For review copies or book purchases, call the Center for Global Food Issues at 800/876-8011.

This speech was adapted from a presentation to the annual meeting of the American Association for the Advancement of Science, invited by the AAAS Panel on Environment and Sustainability, for its session on The Limits to Agricultural Productivity, Baltimore, MD, Feb. 10, 1996.

What if a far-sighted United Nations Environmental Commission in 1947 had asked a panel of world farming experts to develop *an environmentally-sustainable model for world agriculture*? What would that environmentally-ideal agriculture look like today? How would it go about preserving the natural resources, wildlife species, ecosystems, and the quality of planetary life?

The answer is that the best possible agriculture for the environment would look amazingly like modern, high-yield, technologically-supported farming — only more so. (Africa, for example, needs to use much more fertilizer and high-yield seeds to protect its unique wild species from habitat loss.)

High-yield agriculture is the best available model — and the only proven environmental success — for a world that must triple its farm output over the next 45 years, and whose largest demonstrated environmental threat is loss of wildlife habitat.

The first and foremost issue of agricultural sustainability is preventing the plow-down of the world's remaining wildlands for low-yield food production.

Our environmentally-ideal agriculture must use monocultures, potent new seed varieties, irrigation, fertilizers, and pesticides to get high yields. It must do this because high yields are the most critical factor in preserving millions of square miles of wildlife habitat from being plowed down for low-yielding crops. These technologies are already protecting at least ten million square miles of wildlands from the plow. Organic farming as a global model might cost us 20-30 million square miles of wildlife habitat by the time world population peaks in 2040.

Our environmentally-benign agriculture must use modern medicines to keep livestock and poultry healthy and productive. It also must develop the best livestock and poultry genetics. Both increase feed conversion efficiency so people can get the vital amino acids they cannot synthesize themselves from meat, milk, and eggs — without losing millions more square miles of wildlife habitat to pastures and feed crops.

Environmentalists should be honoring veterinary medicines on two counts. First, they are able to relieve or eliminate needless suffering among domestic animals and poultry. Very few human parents brag that they raise their children without vaccines or medications to deal with life's inevitable pests and diseases. Second, they lower poultry and livestock death rates. Otherwise, farmers would have to start with at least fifty percent more birds and animals to produce today's meat, milk, and eggs. That would mean far higher feed tonnages, requiring far more land, in addition to more suffering by dumb creatures.

The environmental impact of modern livestock and poultry production can be seen, in fact, from these two small examples:

Researchers at Cornell University have calculated that if New York State produced milk today the way it did in 1960, the state would need an additional 1.9 million acres to produce the current milk supply. That is about nine times the land area of New York City (D. Bauman, Dairy Science Department, Cornell University, 1995, personal communication. His calculation did not take the potential of BST into account). Europe's dairy industries have developed a similar pattern of producing more milk per acre of land over recent decades.

If Ontario, Canada, produced its chickens on free range, it would need another 1.2 million acres, or ten times the land area of the city of Toronto *taken from wildlife* (G. Surgeoner, Department of Environmental Biology, University of Guelph, Ontario, 1995, personal communication). Free-range hogs would be even more land-extensive and cause significantly more soil erosion.

Research is the largest component of agricultural sustainability under human control. The more we invest in knowledge of how to raise crop and livestock productivity, the more of it we get — and the more wildlands we can protect.

Our environmentally-ideal agriculture would be pursuing agricultural research more aggressively than we are doing today, because the world is beginning its biggest-ever surge in food demand. It often takes decades to develop and extend key new technologies. This is public investment in science to save wildlands from the plow.

Biotechnology research must be high among research priorities, for its potential environmental benefits. Nothing else on our shelf of existing knowledge promises so much for future crop and livestock yields increased, wildlife habitat saved, and pollution avoided.

Since no plant or livestock genetics are immune from pest evolution, our environmentally-ideal agriculture must use ge-

netics and chemistry to keep crop and livestock varieties evolving faster than the pests can adapt. Sustainability lies in the research process, not the individual genetic strains. As an example, an international research consortium has recently created a genetic block against a new strain of barley striped rust which has been moving northward from Colombia. Researchers used both standard plant breeding and biotechnology to create a resistance in three to four years, a feat that would have taken 20-30 years with traditional plant breeding, and perhaps hundreds of years with farmer-saved seeds.

The second most serious threat to farming sustainability is the ancient enemy, soil erosion. High-yield farming is the soil-safest agriculture mankind has ever developed, far surpassing organic farming in its broad-gauge ability to prevent erosion, improve soil tilth and quality and prevent both runoff and erosion from fields.

When we tripled the yields on the world's best and safest cropland over the past 35 years, we cut erosion per ton of the food produced by at least two-thirds. We also avoided extending farming to more highly-erodible land, cutting erosion per ton still further.

Today, conservation tillage systems are cutting those already-lowered erosion rates by another 65-95 percent, *with chemicals*. We are controlling weeds with herbicides rather than with "bare-earth" farming systems like plowing and fallow. These new conservation farming systems also deliver more soil tilth, more earthworms, and more soil bacteria.

Conservation tillage is already being used on hundreds of millions of acres of land in the U.S., Canada, Western Europe, Brazil, Argentina, Australia, and even Africa. It is probably a key to sustainable farming for most of the world.

High-yield farming outshines both organic and traditional farming in terms of monocropping, waterlogging, salinization, and most other aspects of sustainability.

Monocropping and its high yields do far more to protect the wildlands than organic farming, so long as it is adequately backed with genetic diversity in breeding lines and gene banks. Waterlogging and salinization can be forestalled with better water pricing, better drainage, and high-efficiency irrigation systems. Soil compaction can be forestalled with low-pressure tires, tracked equipment, and other prevention techniques.

Modern agriculture has very little depleting impact on resources. Organic farming would rapidly deplete the world's wildlands and topsoil resources instead of slowly depleting petroleum or phosphate resources that extend for centuries. Only agriculture's use of petroleum as chemicals can be charged against its environmental account, not its use of diesel fuel.

There is no valid excuse for diverting good cropland from production, or for letting the sunlight and rainfall which descend on it in a year disappear without benefit to people or wildlife.

Mother Nature is grateful that the travesty of cropland set-aside has been almost completely eliminated from U.S. farm

policy. There has been no European or U.S. farm surplus, just an excess of farm trade barriers. Gradually, our "conservation reserve" now can be reduced and targeted at wildlife conservation, instead of mythical efforts to raise the prices of farm crops. The cropland diverted by governments has produced neither food nor real wildlife habitat; the remaining diverted land should be turned back into permanent wildlife habitat, or released for its highest use in forestry, forage, or cropping.

The world needs to use its best and safest farmland to feed the larger, more affluent population it will have in the 21st century. This urgently requires the elimination of farm trade barriers, to eliminate the pointless emphasis on "food self-sufficiency" featured for reasons of rural politics in so many countries.

The world's good farmland is inequitably distributed to supply the food needs of many countries in the 21st century. Free trade will not put good farmers or farmland out of business, but rather guide our investments for expanded food production. The poorest quality land supports the most wildlife species, all over the world. We must protect the *poor* land from the plow.

The impacts of pesticides on both humans and wildlife are almost entirely beneficial.

Our panel of environmental farming "wise men" would be honoring pesticides for their contribution to *cutting human cancer rates*. Pesticides suppress natural toxins in our crops and enable us to produce ample supplies of low-cost fruits and vegetables, which can cut our total cancer risks in half. The impact of modern pesticides is confined almost entirely to the crop fields, where biodiversity is neither environmentally important nor economically desirable.

Still Short of Environmental Perfection

Of course there are still environmental shortcomings in modern high-yield agriculture. For example, we need still more effective pesticides that are even safer for applicators. We need more attention to soil compaction and preserving water quality. However, it says a lot about our progress that hog odors are one of our major farm policy problems.

The panel of experts might even have avoided some of high-yield farming's real-world environmental mistakes. They would not have set high price supports to tempt high-tech farmers into maximum yields that aggravated pollution and erosion. They would have encouraged more crop rotation and a wider range of crops than the subsidy structures have done. They would have priced irrigation water at its real cost, permitting the irrigation of much larger acreages with far less waterlogging and salinization.

Tripling the Crop Yields Again

The naturalists and ecologists are telling us the big environmental threat is neither population nor pesticides, but the *loss of wildlands* with their unique species, food webs, and contributions to climate patterns.

Agriculture dominates the world's land use. Cities take only 1.4 percent of the earth's land area, and will occupy less than four percent in 2030 (Crosson and Anderson, 1992). Agriculture (with pastures) takes about one-third of the land area, and its high yields have kept another third for forests — on the land left over after we have "enough" food.

The world's population is likely to restabilize at roughly nine billion people, about the year 2040. Most of these people will be affluent, demanding much more meat and milk, along with more fruits, vegetables, and cotton. Thus the world's agricultural output must increase by at least 250 percent, and may need to triple (McCalla, 1994).

Moral concerns aside, famine is not an option for saving the environment. Poor people in the newly-emerging countries are clearly willing to chop down forests and kill wildlife to get adequate calories — or even to get high-quality protein. India is trying to produce its own milk, even though it has to steal one-third of its dairy fodder from the forests and much of the rest from its crop residues. Indonesia is clearing tropical forest to grow low-yielding soybeans for chickenfeed. And it plans to drain one of the world's largest freshwater wetlands to grow rice it could buy at less cost from Thailand.

Forest requirements will rise even more sharply than food needs. Industrial wood demand is likely to rise ten-fold, unless we shift toward more environmentally-damaging wood substitutes such as steel and concrete (Sutton, 1995).

Land Is the Scarcest Natural Resource

The world's population today is 80 percent bigger than it was in 1960. The environmental wonder of the 20th Century is that today's farmers are feeding better diets to almost twice as many people from *virtually the same cropland base.* We used 1,394 million hectares of land for crops in 1961 — and only 1,441 million hectares in 1992 to get twice the grain and oilseeds (FAO Yearbook, 1974). Most of the expansion was on productive and sustainable lands in places like Canada, Australia, Paraguay, eastern Bolivia, and Brazil. This is not, however, to excuse the unnecessary expansion of cropland in some rain forests (Ecuador, Indonesia, Brazil) or other fragile environments.

In addition, the average Third World citizen is getting 28 percent more calories, including 59 percent more vegetable oil (twice the resource cost of cereal calories) and 50 percent more animal calories (three times the resource cost of cereals) (FAO Yearbook, 1992).

Producing today's world food supply with 1960 crop yields would probably require an additional 10.9 million square miles of land, or more than the total land area of Europe and the U.S. combined! This is no precise estimate — but it underscores the enormous environmental importance of continuing to raise crop and forest yields if we are to have wildlands in the future.

In forestry, Roger Sedjo of Resources for the Future (1992 and 1996, personal communication) says the world should be able to provide the industrial wood needs

for nine billion people from less than six percent of the current wild forest area, planted to high-yield tree plantations. But eco-activists oppose "unnatural" monocultured forests, and we aren't planting enough tree plantations for the wood we will need when today's tree seedlings are ready for harvest in 20 years.

The Best Land Has the Fewest Species

For biodiversity, it is even more important to save poor-quality land than prime cropland. Ecologist Michael Huston (1994) points out in his book *Biological Diversity* that the poorest lands harbor the greatest variety of wildlife species, all over the world. Good quality land typically has thriving populations of a *few* wild species. In rain forests and swamps, the tough conditions force wildlife into narrow niches — producing lots of species.

Huston notes that America cleared about 100,000 square miles of wild forest in Ohio and Indiana during the 19th century, and apparently lost no wildlife species. Neither Ohio nor Indiana today harbor any unique native plant species. In contrast, Florida has 385, Texas 389 and California 1517 — because those states have lots of poor-quality land.

The world's *big* reservoir of biodiversity is the tropics, where tropical forests harbor 60-80 percent of the world's various wild species. (Estimates of tropical species keep rising.) This is hugely important for agricultural policy, because the world's big food gap is in the fast-growing, densely-populated tropic countries. Asia will have eight to nine times as many people per acre of cropland in 2030 as North America (FAO yearbook, 1992; Urban and Nightengale, 1992). Moreover, Asia currently averages only about 15 grams of animal protein per person per day, compared to 71 in the U.S. and 55 in Japan (FAO yearbook, 1992). By 2030, Asia will almost certainly demand Japan's current 55 grams of animal protein per day, for four billion people instead of 2.8 billion.

What About Organic and Alternative Agriculture?

Data from eight countries endorse the experience of a British farm manager who told me his 50,000-acre farm is "lucky to get half as much yield" from its organic fields as from its chemically-supported crops. Worse, the world lacks the organic nitrogen to support *current* crop output organically, let alone tripling it for the future. The U.S. apparently has less than one-third of the organic nitrogen which would be needed today. Targeting all of America's sewage sludge for farm use would make up for only two percent of the current chemical nitrogen being used. The rest of the world has less organic nitrogen per capita than America.

The only realistic way to get huge increases in organic nitrogen is to clear more forests to grow lots more clover, trading wildlife for legumes. Low-input farming is either organic farming gone wrong, or high-tech farming without enough confidence to conserve wildlife.

Sustainability from Technology

Agricultural research is the most important sustainability component under humanity's direct control — and we are

failing to make the appropriate investments. Remember, we don't have to keep tripling farm output every 50 years into the future. We only have to do it once more.

Can we realistically expect to triple farm productivity again? The accepted expert on the theoretical crop yield limit is C.T. deWit of Wageningen University in the Netherlands. He estimated the limit at about 15-22 metric tons per hectare of cropland. The top U.S. corn yields are already over 20 tons per hectare. However, the current world average crop yields are far lower — only about 2.6 tons per hectare of wheat, 3.5 tons per hectare of rice, and 3.7 tons per hectare of maize. Crop yields in the Third World have lately been rising by about 3.5 percent annually and in the U.S. by more than four percent per year.

We can expect that biotechnology and other technologies will continue to raise the yield potential of more of the world's lands toward their full potential. Moreover, as more countries become more affluent, we can expect more of the land to be supported with the capital, fertilizer menus, and intensive management which have already produced high yields in the U.S., Europe, and China.

DeWit saw agriculture not as a matter of diminishing returns but as the serial elimination of constraints. When we can plant early in the season, using seeds with high potential, provide the complete roster of nutrients, eliminate weed competition, control insects and diseases, and take fuller advantage of the sunlight and moisture, then a high proportion of the world's cropland should come far closer to deWit's maximums.

To show how this plays out in the real world, new U.S. corn hybrids can tolerate being crowded at 50,000 plants per acre, five times as densely as we used to plant. This raises yield potential to 19 tons per hectare (300 bushels per acre). It also helps shade out weeds and reduce soil erosion. The new varieties have shorter stalks that put more of their energy into grain. They also "flex" —in dry years they produce smaller ears instead of barren stalks. At such high yields, researchers are finding they must add more chlorine; the chlorine that normally comes with the phosphate is not enough (Gogerty, 1996).

When we can feed the resulting ample supplies of grain and forage to livestock and poultry that have added growth hormone, comfortable surroundings, and protection from diseases, the resulting feed efficiency will have the effect of raising crop yields still further. Bovine growth hormone will safely increase the world's dairy feed efficiency, making it possible to provide more milk for India without plowing down wildlife. Pork growth hormone will cut feed grain requirements per pound of lean pork by more than 25 percent. This is exactly what a more crowded and affluent planet will need!

For those worried about providing grain imports for China's meat consumption (now rising at four million tons per year) be reassured that we could produce another 250 million tons of grain per year *at current yields* just from the underused cropland in the U.S. and Argentina.

For those truly worried about producing enough meat, milk, and eggs for nine billion affluent people in the world of 2040, biotechnology is the strongest reason to hope we can save the wildlife habitat. Hybrid seeds and fertilizer are still powerful tools, but by themselves they would probably not be enough to triple crop yields again. Biotechnology is our best reason to believe that we can not only bring more of the world's croplands up to deWit's theoretical maximum — but indeed to raise the theoretical maximum.

Pesticides and Sustainability

Pesticide use is one of the most hotly-debated farm sustainability issues. However, the assertion that farm chemicals damage the environment and reduce long-term sustainability is refuted by the ever increasing yields on our fields. Pest damage worldwide has increased dramatically despite pesticide use — but that is mainly a factor of redoubled production. How high would crop and livestock losses have mounted *without* the pesticides? Pest resistance is a sustainability issue, but we can develop new pest resistance in crops and livestock, pesticides with new modes of action, and prudent ways to slow the development of resistance.

I am hugely pleased by the new biotech seeds, but not because they will enable us to produce high yields with fewer chemical sprays. I do not see reduction in the current use of safe, closely-regulated farm chemicals as any particular benefit to people or the environment. I do see the new bred-in pesticides as a way to reduce the perennial problems with pest tolerance, because they should offer far fewer opportunities for pests to develop pesticide tolerance. I also see the new biotech-produced varieties of herbicide-tolerant seeds as a way to let us use more of our safest weed killers with an absolute minimum of risk to the environment.

The positive impacts of pesticides on human health are huge. Their potential risks are tiny.

I recently debated a Greenpeace staffer, who declared angrily that "Captan causes cancer." I noted that Captan is about one ten-millionth as carcinogenic as safe drinking water — and asked how much wildlife Greenpeace is willing to plow down for cancer risks so small. The reality is that the natural chemicals in our foods — such as limonene in orange juice and caffeic acid in most green vegetables — carry 10,000 times as much cancer risk as the pesticide residues. Yet eating five fruits and vegetables per day cuts a family's cancer risk in half, no matter how they were grown. We can't produce enough low-cost, attractive fruits and vegetables without pesticides.

Our cancers today are the result of living longer, smoking, fat in our diets, alcohol, AIDS, and sun-tanning. (Better detection has created the appearance of increase in breast and prostate cancers.) One person in four dies of cancer in the First World because we have eliminated most other causes of death.

The impacts of biotechnology on human health also will be strongly positive. One of its first impacts will be to produce pork (with porcine growth hormone), which will have half the carcass fat of current hogs, making it easier for people to maintain appropriate weights without

fad diets. Over time, we can expect biotechnology to produce a myriad of agricultural advances which will enable us to protect human health more effectively than we can today.

The impacts of farm chemicals on wildlife are almost entirely beneficial.

Today's high-specific, low-volume and short-lived pesticides do not "wreak havoc" on the wildlife. The newest compounds are no more toxic than aspirin or table salt; a couple of ounces treats a whole hectare; and the compound has biodegraded within weeks. The safety of modern pesticides is so great that eco-activists today have been reduced to lumping pesticides with PCBs (never used as pesticides), DDT (banned for decades), and such toxic heavy metals as lead and mercury — to achieve guilt by association. This is no more valid than lumping garter snakes with cobras.

In America, the Wallace Institute for Alternative Agriculture recently denounced the "myth" that high-yield farming will be able to feed so many people and still preserve wildlands and wildlife biodiversity. (Actually, we cannot guarantee high-yield farming *will* be able to do it; however, it is clear that low-yield farming *won't*.) The Wallace Institute cited two pieces of evidence on the "dangers" of high-yield farming for wildlife (Hewitt and Smith, 1995):

Chesapeake Bay oyster populations have fallen 96 percent in 100 years, and the Bay receives an overabundance of nitrogen and phosphate. But the Wallace Institute fails to mention the MSX virus, which has ravaged the Bay's oysters in recent decades. Nor does it point out that the cities and suburbs are the most serious (and growing) sources of nutrient pollution.

Researchers found six percent of the bald eagles in Virginia's James River area were being killed by secondary pesticide poisoning in 1991. The Wallace Institute didn't know, or didn't mention, that the eagle poisonings ended with elimination of one granular soil insecticide in 1992.

Can these tiny and poorly-founded criticisms offset millions of square miles of wildlands saved with safety-tested chemicals?

Other Sustainability Questions

Monocropping has been labeled "unsustainable" because big fields of identical plants are more susceptible to disease. However, the big monocropped fields are also much more productive. Turning the whole world's agriculture into a gene museum would be a disaster for the environment. We save the most genes, the most wildlife, and the most environmental quality by getting high yields in monocrop fields — and defending against diseases by keeping a broad genetic base in our gene banks, in our breeding, and in our breeding technologies.

Land-race seed varieties are mistakenly seen as an important sustainability issue by some eco-activists. However, Canadian researchers recently tested newer corn hybrids against 30-year-older varieties; they found 80 percent higher yields in the new ones, and the *biggest yield differences came under stressed conditions* such as high plant density,

drought, and low nitrogen levels! There are no "magic" old varieties; we just need to keep breeding new ones that are even tougher and more productive. We also need more comprehensive seed and gene banking efforts.

Biotechnology, in fact, is one of the best ways to guarantee the salvation and use of the world's natural genes. Without biotechnology, only a few of the genes in the rain forest (or any other wild environment) are useful to humans. That's because only close cousins can be married with our traditional cross-breeding techniques. With biotechnology, almost any gene in the world is potentially useful, and we are already seeing a global pattern of First World researchers helping to fund Third World conservation efforts to ensure that the world's genes will be available. The research thrust is, in turn, making it easier for the world to save the wild genes with higher-yielding crops, higher-productivity poultry and livestock, and faster-growing plantation trees, to supply human needs from fewer acres.

Soil quality cannot possibly be maintained in today's world without high-tech methods. Fertilizers — plant nutrients — are essential to maintaining soil fertility, structure, and organic content. High yields mean more crop residues, which are critical in building structure and organic content. Long-term studies show that soil carbon and nitrogen levels are highest when we combine conservation tillage, crop rotation, and adequate fertilizer. Incidentally, plants absorb all their nitrogen fertilizer in mineralized (inorganic) form, so the organic farmers' insistence on organic nitrogen apparently sprang from the historic experience that manure was important for retaining soil tilth. Today, however, we can produce better soil tilth by combining effective manure usage with conservation tillage — and making up nutrient shortfalls with chemical fertilizer.

Soil degradation is another of the charges against high-yield farming. However, the evidence from long-term field studies says the productivity of the fields continues to increase as long as the soil structure and quality remain high. These factors are impacted most heavily by tillage and nutrient management, not pesticide use (Zaborski and Stinner, 1995). (Earthworms and soil bacteria hate being plowed more than anything.)

The threat to water quality is one of the most valid charges against high-yield farming. Runoff from our fields and feedlots has carried nitrogen, phosphate, and pesticide traces into our water. Even here, however, the story is far better than the environmental movement has painted it — and better than our regulators seem to understand. Regulators on both sides of the Atlantic have set ten parts per million as the limit for nitrogen/nitrates in drinking water. But the only health threat associated with nitrogen is the famous "blue-baby" syndrome, and it takes over 150 ppm of N to trigger "blue-baby." (The increasingly rare cases are almost always traced back to leaking septic tanks and cracked well casings.)

The pesticide traces in our groundwater are rarely found in parts per thousand, which was all we could detect when our regulatory frameworks were established. We now routinely detect pesticide traces at parts per billion — a million times more

dilute! Our new U.S. standard for pesticide safety is one additional death per million lifetimes; but a person is five times more likely than that to be killed by a crashing plane — while standing on the ground!

There is no real reason why runoff from our farms has to represent a long-term problem for the environment. Conservation tillage systems reduce runoff from the fields by up to 90 percent. Farmers are also beginning to broadly implement precision application of the chemicals (using navigation satellites and microcomputers), managing their fields square meter by square meter according to soil type, slope, plant population, hydrology, and nearness to waterways. Livestock and poultry operations can be sufficiently dispersed so their manure is an asset, and it can be effectively managed without posing serious threats to the environment. (To the degree that activists tighten effluent limits unrealistically, they will sacrifice wildlife habitat, and they will still not bring back the old peasant villages.)

Resource depletion is another charge leveled at high-yield agriculture, but it is another false one. In phosphate, the world has a good 250 years of high-grade ore remaining, and after that we'll have to find more economic ways to mine the world's big deposits of low-grade ores. (The answer may be biological recovery using genetically-engineered bacteria.)

In petroleum, farming uses only a tiny proportion of human consumption. (In the U.S., it is two percent). Moreover, agriculture tends to use the same energy systems as the rest of society. When our economy was horse-powered, so was agriculture. When our society moves to hydrogen, hydro-power, and/or nuclear power, so will agriculture. Agriculture could be self-powered again, but somewhere in the world we would have to convert millions of square miles of wildlands to provide the fodder for draft animals or biofuels. Our overall sustainability would suffer needlessly. (If global warming is demonstrated to represent a serious problem, we will have to spend trillions of dollars to shift our entire energy system from fossil fuels; there is no good reason to start early on agriculture.)

The "small family farm" has been the holy grail of Western farm policy for 60 years. But with technology, one farmer can produce more now than in 1933. That releases another to produce the TV sets, computers, and other things we want that didn't exist in 1933. Moreover, in a world that needs to triple its farm output, there will be plenty of jobs for farmers. In fact, if our farmers have to triple food output and save our wildlands from being plowed down for low-yield crops, we may need to put the living museum for the 15th century peasant village somewhere else.

Hormone risks have been high on the EU's list of political issues for decades. The EU has taken the lofty position that it will not permit hormone risks to its consumers, and has banned them all. But a woman would have had to eat one million pounds of beef liver — in one sitting — to get as much estrogen exposure as is contained in one morning-after birth control pill (Whalen and Stare, 1975). Now a huge proportion of the EU's meat supply is produced *with black-market hormones not tested for safety nor approved for human consumption.* The World Trade Or-

ganization and the scientific community agree the EU hormone ban is an unwarranted trade barrier which will have to change.

The Environmental Impacts of Western Farm Subsidies

It is time now to recognize that the farm price supports of the OECD countries are 1) financially regressive for the countries which offer them; 2) socially counterproductive because they encourage larger farms more than smaller ones; and 3) environmentally perverse because they discourage the world from using its safest and most productive land for meeting the 21st century food challenge. Most of Europe's environmental complaints about high-yield farming are due directly to the Common Agricultural Policy, not to technology.

High yields are good, but maximum yields cannot be achieved without high levels of nutrient runoff and terrible problems with surface and coastal waters. The Aegean Sea turns green in the summer because of subsidies, not technologies. The EU has huge concentrations of hogs, poultry — and manure — around its cities because of its grain price supports, not technology. Grain prices were set too high, so the meat producers located near the ports where they could import cheap non-grain feeds.

The EU's farmers tore out their ancient stone fences and hedgerows because the prices for crops were so high. If the EU had been making direct payments to small producers, most of the fences and hedgerows would still be there, surrounding high-yield crops. The EU's farm technology should have contributed to the economy and created additional jobs. Instead, because of trade barriers and subsidies, the EU's farm productivity started a trade war and raised its tax burden.

The time has come for the U.S. and the EU to end the trade war defending farm policies that no longer make sense for either. When high-tech farmers can drown any government price support with surplus, it is time to start offering the farm subsidies as direct income payments, and liberalizing farm trade for its environmental benefits.

America is reining in the growth of its government spending, and this is moving the country toward a more trade-oriented farm policy. Western Europe also finds itself at a farm policy turning point. Its old policy of farm export subsidies is now untenable due to international negotiations and budget pressures. In the years just ahead, the Eastern expansion of the EU is likely to triple the number of EU farmers. Poland, Hungary and Czech Republic have more than four million farmers. Turkey has nearly 12 million, along with 27 million acres of cropland and a huge new irrigation project in the Upper Euphrates Valley. Poland, Hungary, Turkey, France, Holland, and Denmark will need farm markets outside Europe. The world should want their farm products.

Saving Wildlife With Free Farm Trade

The world needs to use its best and safest cropland to meet the 21st Century food challenge. That will take the fewest acres, displace the fewest wild species and cause the least erosion. North America

and Europe both have more than their share of the world's best and safest farmland for the decades ahead.

But if today's pervasive farm trade barriers persist, densely-populated Asian countries will try to maintain national food self-sufficiency to placate big farm populations made restless by urban income gains. China is the most vivid case in point: its population is nearly stabilized, but its meat consumption is rising by four million tons per year. Chinese farmers are already using high-yield seeds, and double or triple-cropping their land. China needs to pursue still-higher yields — but it also needs to consider the economic and environmental benefits of importing part of its diet improvement from high-yield farmers with export potential, such as the U.S., Argentina, France, Brazil, Poland, and Turkey.

India's consumers are getting more income, and would like to have two million additional tons of milk per year. But India's farmers are producing only one million addition tons of milk despite stealing one-third of their dairy feed from their forests (thus endangering wild species) and another third from the crop residues that should protect their soil. Milk prices are two and three times the world market level. Should India import milk? Should it use BST? Or should it endanger the Bengal tiger by converting its habitat to subsistence agriculture?

The Real Threat to the Environment

Sustainability is a major, legitimate concern for a world with a rising human population and the ability to modify its long-term behavior through research and investment. *Our analysis clearly indicates, however, that the environmental movement has never really examined farming sustainability.* The activists apparently started with an opposition to pesticides, and added whatever charges against high-yield farming that seemed to resonate with a public largely ignorant about farming. They added the charge that high-yield farming was "unsustainable" when they found the word was almost as powerful as "cancer" in a press release.

The alternative agriculture movement seems to have done little objective research on the sustainability and sustaining capabilities of various farming systems. It cites no research or long-term field studies offering productivity for the future. It offers no evidence of rising organic yields or progress in raising nitrogen use efficiency. Critics of high-yield farming have simply leveled unsubstantiated charges at the farming system which has already prevented the greatest loss of wildlife in the modern history of the planet, as if by doing so they could prevent more people from being born.

The real danger to the environment today — especially to its wildlands and wildlife — is the myth that low-yield farming is environmentally sustaining. The agricultural policy of the environmental activists is not sustainability. It is rather a retreat into fantasy.

The activists present the fantasy that the world's population can be magically and painlessly returned to two or three billion lucky persons. They offer an alternative fantasy that the world will become vegetarian, even though the world has never in history had a voluntarily vegetar-

ian country or culture, even as Third World countries ravage wildlands to get meat and dairy products.

They attach the fantasy label "sustainable" to farming systems which cannot feed people adequately, cannot protect them from cancer, cannot protect topsoil, cannot preserve soil quality, and cannot prevent the plow-down of 20 million square miles of wildlands and wild species.

They fantasize that organic and alternative farming can somehow achieve substantially higher yields per acre, to meet already expanding global needs, without chemicals, petroleum, or chemical fertilizers. This defies recent experience and 10,000 years of farming history. Fantasy cannot serve humanity or the environment if it leads us to ignore realities that must be headed off with research and development programs that take years or decades.

The danger to wildlife now includes the entire leadership of Greenpeace, which seems more interested in terrorizing the public with trivial chemical risks than with saving either wildlife or human lives. Coincidentally, such chemical terror campaigns have been the environmental organizations' most effective fund-raising technique for decades. Environmental groups may now raise nearly as much money from vilifying pesticides as chemical companies net from making them. (And the environmental groups' return on investment is far higher.)

The danger to wildlife includes Lester Brown, the famous famine forecaster who for 25 years has discouraged public investments in agricultural research and public acceptance of its successes. He has told us to put our faith in "population management." But population management has nothing to offer a China which has virtually restabilized its population but wants millions of tons more meat. How much of the future plow-down of forests for food should be credited to the communications genius and flawed analysis of Lester Brown?

The memory of Rachel Carson and her brilliantly-flawed masterpiece *Silent Spring* are unfortunately now a danger to the environment. Ms. Carson was terribly wrong about the cancer risks of pesticides to both people and wildlife, so her eloquence and sincerity continue to push us in the wrong direction for environmental sustainability. She did not understand in 1965 that the world would have to choose between high crop yields and lost wildlife habitat.

The wildlife dangers even include some scientists at reputable agricultural research institutions who have either not understood the global environmental importance of high farm productivity or were willing to overlook it in pursuit of research grants. Because of sincere but wrong-headed efforts by these and other eco-activists, the world is *not* making the investments in agricultural research to ensure that we can protect the world's wildlands with still higher farm yields in the next century. We are *not* actively extending high-yield agriculture to Africa on behalf of its unique wealth of species and genes. We are *not* planting the tree plantations that should be harvested 20 years from now to protect 95 percent of the world's wild forests from intensive logging. We are *not* eliminating the farm

trade barriers which could prevent densely-populated tropical countries from destroying hundreds of thousands of tropical species in a destructive quest for national food self-sufficiency.

High-yield farming is our only proven path to saving most of the world's natural environment in a world that will inevitably have more people and more food demand. Unfortunately, the environmental movement has convinced much of the public that high-yield farming is the danger, not the solution. Can the "green" movement now truly begin to "think globally and act locally" instead of thinking locally and saying "not in my back yard?" Can environmental activists afford to embrace high yield farming and farm chemicals — even if those are the only ways to save the planet's wildlands and wildlife?

References

Crosson, P.R., and J.P. Anderson. 1992. Resources and global food prospects. World Bank Technical Paper 184.

FAO Production Yearbook. 1976. Table 1, Land Use.

FAO Production Yearbook. 1992a. Table 3, Population; Table 6, Calories; Table 108, Fat. Vol. 46.

FAO Production Yearbook. 1992b. Table 107, Protein. Vol. 40.

Gogerty, R. 1996. More plants, more corn. p.7-8. *In* The Furrow. Deere & Co., Moline, IL.

Hewitt, T., and K.R. Smith. 1995. Intensive agriculture and environmental quality: Examining the newest agricultural myth. Henry Wallace Institute for Alternative Agriculture, Greenbelt, MD.

Huston, M. 1994. Biological diversity. Cambridge University Press.

McCalla, A. October 1994. Agricultural and food needs to 2025: Why we should be concerned. Crawford Memorial Lecture. Consultative Group on International Agricultural Research. World Bank, Washington, D.C.

Sutton, W.R.J. 1995. The need for planted forests and the example of radiata pine. Paper presented at the symposium Planted Forests — Contributions to Sustainable Societies, Portland, OR, 28 June, 1995.

Urban, F., and R. Nightengale. 1993. World population by country and region, 1950-90, and projections to 2050, USDA/ERS.

Whelan, E., and F. Stare. 1975. Panic in the pantry. Atheneum, New York.

Zaborski, E.R., and J.L. Stinner. 1995. Impacts of soil tillage on soil fauna and biological processes. *In* Farming for a better environment. White paper prepared by the Soil and Water Conservation Society, Ankeny, IA.

Discussion

Session IX - Plenary Session
Session Chair: John Yohe
Rapporteurs - Robert Schaffert and A.S. Kasakova

Lee House - Scientists are generally modest people, highly trained, enthusiastic about our research, and evaluated by accomplishments in our projects. We not only fail to expose our work to the public, we don't know how. You tell us what we should do, do you have any comments about how we can do it?

Dennis Avery - Our research has and is leading to a productive agriculture. Because of increasing production, area required for agriculture is less than if the same amount of food would be produced at lower productivity levels. The realization that highly productive agriculture is important to preservation of forests and habitats for flora and fauna is real and important and in the current climate environmental protection/preservation is valuable to include in our justification for and in selling of our research accomplishments.

John Witcombe - What do you think about environmentalists and biotechnology?

Dennis Avery - Environmentalists take the high moral ground of saving wildlife. We must play the environmental card. We are saving land and wildlife. Environmentalists cannot argue against that and may finally admit that the real concern is population. Biotechnology is the biggest piece of unexploited science in the world.

B.S. Rana - Comment on Dennis Avery's presentation. The stronger thought may carry the audience and they may forget where they are sailing. I understand from your talk that if in China, people become nonvegetarian they will require more animals for food and also creating a greater requirement for feed. If deforestation is being done in India to promote milk production, we must produce more nutritive forages to support the dairy industry; if petrol/gasoline will be in short supply, we must produce sufficient sorghum for ethanol production to run the cars in the future. We also understand that biotechnology is a powerful tool in the future and that it may become a strong technology for genetic improvement in the future. Sorghum hybrids may be the answer for quick impact. I appreciate your thoughts and believe that it will become a reality in the future.

Poster Abstracts

Genetic Variability in Sorghum for P Efficiency and Responsiveness

V.M.C. Alves, R.E. Schaffert*,
A.F.C. Bahia F°, G.V.E. Pitta,
EMBRAPA/CNPMS, CP 151, 35701-970
Sete Lagoas, MG, Brazil;
F.G. Santos and C.A. de Oliveira,
Fellowship/CNPq/CNPMS

Thirty six sorghum lines were evaluated for P efficiency and responsiveness at the National Maize and Sorghum Research Center of EMBRAPA/CNPMS during the 1995/96 growing season at Sete Lagoas, MG, Brazil. The experiment was conducted on a Dark Red Latosol under savanna vegetation soil at 5 and 18 ppm P (Mehlich-1 extractor). The soil was limed to raise the pH to a range between 5.5 and 6.0. Triple superphosphate was broadcast and incorporated to reach the desired P levels as determined by an incubation curve. N and K were applied based on the soil analysis. The 36 lines included 12 traditional lines representing both tolerance and susceptibility to Al toxicity and 24 lines derived from crosses between elite B-lines and a source of tolerance to Al toxicity, SC 283-14 E (IS7173C). Twelve lines were susceptible to toxic levels of Al and 24 lines were tolerant. Toxic levels of Al did not occur in the plow layer but were present in the subsoil. Genotypes with above average grain production at the low P level were classified as P-efficient and genotypes with above average relative response to P were classified as responsive to P. Average grain yield ranged from 1.76 to 3.52 t/ha at low P with a mean of 2.63 t/ha and from 1.84 to 5.39 t/ha at high P with a mean of 3.68 t/ha. The relative response to applied P ranged from less than zero to 93% with an average of 41%. The 36 entries were classified into four groups, efficient and responsive to P (ER), nonefficient and responsive to P (NR), efficient and not responsive to P (EN), and nonefficient and not responsive to P (NN). Tolerance and susceptibility to Al toxicity was not directly related to P efficiency and P responsiveness. The standard for tolerance to Al toxicity, SC 283-14 E, was near average for P efficiency (2.70 t/ha at low P) and not responsive to additional P (12%), whereas the standard for susceptibility to Al toxicity, the commercial male sterile line BR 007B, was near average for P efficiency (2.60 t/ha at low P) and highly responsive to additional P (93%). The Al-tolerant line of a P-non efficient near-isogenic pair for Al toxicity was more responsive to P (70%), whereas the Al susceptible line of the pair was less responsive to P (33%). Two Al tolerant near-isogenic recombinant lines from the cross between BR 007 and SC 283-14 E were near average for P efficiency and highly responsive to P (60 and 90%).

Identification and Characterization of the Ma_5 and Ma_6 Maturity Loci in Sorghum.

S. Aydin*, W.L. Rooney and F.R. Miller,
Department of Soil and Crop Sciences,
Texas A&M University, College Station, Texas

The genetics of maturity in sorghum have been well documented for many years, and it has become a model for research concerning the factors that affect maturity or photoperiodic response in tropical cereals. Since Quinby[1] (1974) first identified and characterized the Ma_1, Ma_2, Ma_3, and Ma_4 loci in sorghum, maturity in sorghum has been defined by the alleles at those loci and their interaction. Recently, an extremely photoperiod-sensitive hybrid was discovered from the cross of 90T190 and RTx430. When planted in early April, hybrids from this cross are extremely photoperiod-sensitive and they will not flower until mid-October (up to 180 days in Central Texas). This "ultralate" phenotype is not caused by known combination of alleles at the four *Ma* loci currently characterized. The objective of this research was to determine the genetic inheritance of this ultralate (photoperiod-sensitive)

phenotype obtained from the cross of two photoperiod insensitive genotypes.

Accession 90T190 was hybridized to three different U.S. adapted inbred lines or germplasm (RTx2858, VG153, and Tx2785). 90T190 is a breeding line of Argentina descent that flowers in approximately 70-75 days in Central Texas. The U.S. adapted germplasms or lines had flowering dates between 65-85 days. F_1 hybrids from these crosses were grown in Puerto Rico to produce the F_2 generation. All three F_2 populations, F_1's and the parents were planted in College Station, TX on April 15, 1996. The flowering dates of individual F_2 plants were recorded until July 27. After this date no vegetative plants exhibited any floral initiation and were declared "ultralate". Based on initial results, two phenotypic classes were created; those that flowered (photoperiod insensitive) and those that did not (photoperiod sensitive or ultralate). Chi-Square tests were completed to test to goodness-to-fit to segregation ratios expected for possible modes of inheritance.

Several modes of inheritance for this trait may be hypothesized: (1) A single gene inheritance in which the heterozygote is ultralate and either homozygous genotype is of normal maturity. (2) A two-gene system in which the ultralate phenotype is caused by duplicate dominant epistasis. In option 1, an F_2 population should segregate 1:1 ultralate:normal. In option 2, an F_2 population should segregate 9:7 ultralate:normal. For each population, segregation fit a 9:7 ratio and only one population fit a 1:1 ratio. (Table 2). Combined data across all three populations also fit a 9:7 ratio.

Based on these preliminary results, we proposed that this phenotype is controlled genetically by two previously uncharacterized maturity loci herein designated Ma_5 and Ma_6. We assume that these are different genes from Ma_1-Ma_4 because (1) such an ultralate phenotype has not been previously documented in sorghum, and (2) the ultralate phenotype was derived from a cross of two photoperiod-insensitive types. Additional evaluation of the $F_{2:3}$ generation is needed to confirm these initial observations and the genetic inheritance of the ultralate phenotypes. We are also working to determine the allelic composition of U.S. germplasm at Ma_5 and Ma_6 and to identify molecular markers linked to these loci. Efforts to develop U.S. adapted breeding material to utilize these loci are underway.

Table 1. Expected segregation ratios for different genetic inheritance schemes.

Inbred line, germplasm or generation	Putative genotype	Phenotype
Option 1 - Single gene inheritance of ultralate		
Tx2858, VG153, Tx2785	Ma_5Ma_5	Normal
90T190	ma_5ma_5	Normal
F_1	Ma_5ma_5	Ultralate
F_2	1 Ma_5Ma_5	1 Ultralate
	2 Ma_5ma_5	1 Normal
	1 ma_5ma_5	
Option 2-Two gene model: Duplicate dominant Epistasis		
Tx2858, VG153, Tx2785	$Ma_5Ma_5ma_6ma_6$	Normal
90T190	$ma_5ma_5Ma_6Ma_6$	Normal
F_1	$Ma_5ma_5Ma_6ma_6$	Ultralate
F_2	9 $Ma_5\_Ma_6$	9 Ultralate
	3 Ma_5 — ma_6ma_6	7 Normal
	3 ma_5ma_5 Ma_6 —	
	1 ma_5ma_5 ma_6ma_6	

Table 2. F_2 segregation within four populations putatively segregations for Ma_5-Ma_6

Cross	Number of F_2 plant			X^2	
	Flowering	Non-flowering	Total	9:7	1:1
RTx2858*90T190	66	114	180	3.664	12.8**
VG153*90T190	62	72	134	0.6438	0.7462
Tx2785*90T190	53	94	147	3.54	11.44**
Total	181	280	461	3.82	21.3**

**$P(X^2_{1df}>6.64) <0.01$

References

Quinby, J.R. 1974. Sorghum Improvement and the Genetics of Growth Texas A&M University Press, College Station TX. 108 pp.

The Couscous Quality of Different Grains Used in Mali

A.B. Berthé*, Laboratoire de Tehnologie Alimentaire, Institut D'Economie Rurale, Mali; C.M McDonough, L.W. Rooney R.D Waniska, Texas A&M University, College Station, TX

Couscous was produced from sorghum (*Sorghum bicolor*), corn (*Zea mays*) and fonio (*Digitaria exilis*) using a laboratory procedure. Protein and starch contents were quite similar. However, fonio starch had 41% amylose in the starch compared to 28% for corn and sorghum. The waxy sorghum had less than 2% amylose. The grains were decorticated using an abrasive milling procedure followed by grinding the decorticated grain into flour with a Udy grinder. The decortication yields were 78.7, 77.7, 66.7 and 50.1% for normal sorghum, waxy sorghum, corn and fonio, respectively. The fonio kernels were soft and tended to break during decortication. The sorghums were white, tan plant food types with an intermediate to hard texture.

The highest yields of couscous were obtained from fonio flour (218%). Sorghum and corn had couscous yields of 156 and 164% respectively. The color of the sorghum couscous was lighter than couscous from corn or fonio. Sorghum couscous had a bland flavor while that from corn had a typical maize flavor. Both products were acceptable. The waxy sorghum processed significantly different from the other grains and would be difficult to use in couscous preparation because of its sticky characteristics during steaming.

The Effect of Decortication Time on Pearl Millet Dégué (Fermented Couscous) Quality

A.B. Berthé* , D. Dramé, S. Maiga, K. Tangara, and A. Konaté
Laboratoire de Technologie Alimentaire, Institut D'Economie Rurale (Mali)

The relationship between pearl millet dégué and decortication time was investigated. Cooking, and physico-chemical parameters were strongly correlated to dégué quality. Decortication yield affected dégué color, texture and flavor as well as protein and ash content. Dégués prepared from non dehulled pearl millet were chewier than those prepared from decorticated pearl millet.

Identification of RAPD Markers Tightly Linked to a Gene for Resistance to Anthracnose in Sorghum

Khazan Singh Boora*, Richard A. Fredricksen and Clint W. Magill, Dept. of Plant Pathology and Microbiology, Texas A&M University, College Station, TX

Resistance to anthracnose in the sorghum cultivar SC 326-6 has been shown to be inherited as a single gene recessive trait in a cross to the susceptible cultivar, BTx623. Progeny tests made for 115 selfed F_2 plants identified 20 homozygous recessive (resistant) plants, 65 that were segregating for resistance, and 30 that were homozygous susceptible. Bulked segregant analysis was conducted using RAPD primers that had revealed differences in the PCR amplification products of the parents. Two primers, OPF7 and OPL 4, have been identified that amplify bands that appear to be closely linked to the recessive resistance allele, and primer OPK 16 amplifies a fragment that is less closely linked tc the dominant susceptible allele. These RAPD markers, when used as RFLP probes, hybridized at several fragments with parents and bulks restricted with Eco R1, Eco RV, Hind III and Bam HI en-

zymes. RAPD probe OPL 4 showed a single RFLP in the resistant parent and resistant bulk with Bam HI. These markers will be cloned and sequenced to generate codominant sequence tagged sites. Since resistance in this case is recessive, the RAPD bands could be very helpful in identifying heterozygotes, making the task of incorporating this gene in to breeding or commercial accessions much easier.

Effect of Inoculation on Antifungal Proteins in Sorghum Caryopses

F. Bueso*, K. Seetharaman, R. D. Waniska and L.W. Rooney,
Cereal Quality Lab, Texas A&M University, College Station, TX 77843-2474

Grain mold is a condition resulting from the field deterioration of sorghum grains as a result of fungal infection occurring at or near anthesis. The sorghum plant esponds to fungal attack by a complex of defense mechanisms including the synthesis of an assortment of proteins commonly referred to as antifungal proteins (AFP). Chitinase, sormatin and glucanase are detectable in naturally infected sorghum caryopses at 10 days after anthesis (DAA), their level of synthesis peaked around physiological maturity (30 DAA) and then decreased at harvest (50 DAA).

The objective of this study was to determine the changes in AFP levels following inoculation by grain molding pathogens.

Two sorghum cultivars, a moderately resistant (Malisor 84-7) and a susceptible (RTx430), were grown in a greenhouse and inoculated at anthesis and 15 DAA with a mixture of conidial suspensions of *Fusarium moniliforme* Sheldon ($5x10^5$ spores/ml) and *Curvularia lunata* (Wakker) Boedjin ($5x10^5$ spores/ml), in a complete random design with two replications. The inoculated plants were covered with a plastic bag for 24 hours to promote mold growth. Control plants were sprayed with water and also covered with a plastic bag for 24 hours. Plants inoculated at anthesis were sampled at 5, 10, 15, 23, 30 and 50 DAA, while plants inoculated 15 DAA were sampled 18 DAA. Proteins were extracted and immunologically assayed (western blots) for chitinase, sormatin and glucanase.

AFP levels were not different between control and treated sorghum caryopses sprayed at anthesis. AFPs were detected 30 DAA and decreased 50 DAA in both cultivars. AFP levels in control plants sprayed 15 DAA were detectable 18 DAA, and peaked 30 DAA. However, AFPs were not detectable in treated caryopses until 30 DAA and their levels increased up to 50 DAA.

These data suggest that caryopses AFP levels are influenced by the date of inoculation and therefore may have implications in understanding the role of AFPs in defending caryopses against grain mold infection.

Relationship Between Sorghum Spikelet Morphology and Resistance to Sorghum Midge

Niamoye Yaro Diarisso, Bonnie B. Pendleton, and George L. Teetes,
Department of Entomology, Texas A&M University, College Station, TX 77843-2475

Sorghum midge, *Stenodiplosis sorghicola* (Coquillett), is an insect pest that, without appropriate management measures, can severely limit grain yield of sorghum. Sorghum is vulnerable to attack by sorghum midge only when sorghum spikelets are flowering. Adult sorghum midge lay eggs between the glumes of flowering spikelets of sorghum. Larval feeding on the sorghum ovary prevents the kernel from developing.

Field experiments to investigate the relationship between the time of day spikelets of resistant sorghum flower and resistance to sorghum midge were conducted during 1993, 1994, and 1995 at the Texas A&M University Research Farm in College Station. Spikelet morphology was studied in the laboratory to determine differences between resistant and susceptible sorghums. Sorghums studied were resistant lines ATx2755 and RTx2767, resistant hybrid ATx2755 x RT2767, susceptible lines ATx2752 and RT430, susceptible hybrid ATx2752 x RTx430, and resistant by susceptible hybrid ATx2755 x RTx430. The spikelet flowering process was divided into six stages, and the proportion of spikelets in each stage on selected rachis branches was assessed hourly from spikelet opening (approximately 0100 hours) to closing (approximately 1100 hours) during every other night of the flowering period. Adult sorghum midge abundance also was assessed hourly by counting the number of sorghum midges on the sorghum panicles from which flowering data were collected and on additional panicles. Temperature and relative humidity measurements were collected hourly and used to detect the effect of weather on time of sorghum flowering and presence of sorghum midges. Samples of spikelets were collected from tagged panicles and examined by using a microscope to see how spikelets of resistant sorghums differed morphologically from susceptible sorghums. The number of kernels that failed to develop because of sorghum midges was counted when the kernels were in the hard-dough stage.

Most spikelets of resistant sorghums flowered in the middle of the night and reached peak flowering at 0500 or 0600 hours, when few sorghum midges were present. By flowering early, resistant sorghum escaped sorghum midge oviposition and thus damage. Spikelets of susceptible sorghums flowered after daylight, when sorghum midges were more abundant than when the resistant sorghums flowered. Also, glumes of spikelets of some resistant sorghums were open for a shorter time than were those of more susceptible sorghums. Stigmas of susceptible sorghums were either hairier or longer than those of resistant sorghums and were not stuck to the lemma of the spikelet. Stigmas, styles, and anthers of susceptible sorghums were significantly longer (1.5, 1.5, and 1.7 mm, respectively), and ovaries smaller (1.3 mm) than those of resistant sorghums (1.4 mm). Mean damage during the three years ranged from 16.8-23.5% to the resistant sorghums and 49.9-56.2% to the susceptible lines and hybrid.

Influence of Nitrogen Sources on Induction and Growth of Embryogenic Callus of Sorghum

L.A.Elkonin and N.V.Pakhomova, Volga-Region,
Institute of Biotechnology, 410020 Saratov, Russia

In order to optimize the composition of the medium for growth of embryogenic sorghum cells, we studied the influence of different sources of nitrogen on induction and proliferation of embryogenic callus (EC) of several cultivars of grain sorghum.

Fragments of young panicles were cultured on MS medium and its 8 modifications with different levels and ratios of NH_4^+ (370, 1130, 2250 mg/l) and NO_3^-(2500, 4500, 8200) ions, with or without organic nitrogen (1-asparagine 1 g/l and l-proline 2 g/l). The differences in NH_4^+ and NO_3^- concentrations were obtained by changing the concentrations of KNO_3 and NH_4NO_3 in the basal MS medium. All the media contained 3% of sucrose and 1.0 mg/l of 2,4-D.

It was revealed that addition of amino acids to basal MS medium is significantly more effective than increase of concentration of inorganic nitrogen. The medium with redoubled concentration of NO_3^- (in comparison with MS) trebled concentration of NH_4^+, and addition of organic nitrogen (M2AP medium) was the most effective in stimulation of EC growth, exceeding both the MS and the MS with amino acids. The stimulating effect of inorganic nitrogen composition of M2AP medium was evident only after addition of both amino acids - asparagine and proline. Further increase of inor-

ganic nitrogen was less effective. The increase of concentration of NO_3^- only or NH_4^+ only in the media supplemented with organic nitrogen was also less effective in stimulation of EC growth. This fact demonstrates that both sources of inorganic nitrogen (NH_4^+ and NO_3^-) and optimal NH_4^+/NO_3^- ratio are important for EC growth in sorghum.

The medium M2AP with increased inorganic nitrogen and addition of amino acids was favourable for induction of EC in different sorghum cultivars. It should be noted that proportion of EC in total callus was extremely high in cultures grown on all media with increased NH_4^+ level and addition of amino acids. However, for subculturing of induced EC, MS medium with 2,4-D and 6-BAP or N6 medium with 2,4-D, asparagine and proline were superior than M2AP.

EC developed on all the media tested in these experiments was compact. Evidently, changes in the level of inorganic nitrogen and the NH_4^+/NO_3^- ratio in the MS medium, as well as the addition of asparagine and proline, cannot result in formation of friable embryogenic callus that can be obtained in sorghum on the N6 medium supplemented with the same amino acids.

Induction of Male Sterility Mutations and Fertility Reversions of Sorghum in Tissue Culture Conditions and in Vivo

L.A.Elkonin, T.N.Milovanova and M.I. Tsvetova, Volga-Region,
Institute of Biotechnology, 410020 Saratov, Russia

The objective of this research was to elaborate on the approaches to reconstruction of genetic systems that control male fertility of sorghum plants, using tissue culture methods and mutagenesis.

The male-sterile mutants were regenerated from callus cultures obtained from leaves and panicles of haploid and diploid lines of Milo-145. The mutants were obtained in two independent experiments and appeared with a high frequency (66-90% of regenerants). The mutants were characterized by partial or complete male sterility in self-pollinated semi-sterile mutants, and a non-Mendelian segregation of sterile, semi-sterile and fertile plants was observed. Similar segregation was observed in testcrosses with parental lines. Progenies of different tillers of the same semi-sterile mutants differed by the ratio of sterile and fertile plants. This indicated somatic segregation of genetic factors conditioning male sterility. In the testcrosses of sterile mutants with different fertility-restorers of A1, cytoplasm induced mutation was expressed either as nuclear recessive or nuclear dominant. After pollination of sterile plants with sterility-maintainers of A1 cytoplasm a partial restoration of fertility was observed. It was concluded that induced sterility was the result of cytoplasmic mutation; the differences in the results of testcrosses were due to interactions of the mutant cytoplasm with different restorer genes.

We have also shown the possibility for regeneration of male sterile mutants after callus treatment with streptomycin - an efficient cytoplasmic mutagen. The frequency of regeneration of male-sterile mutants was 50-100% and exceeded 20-30 times the frequency of induction of sterile and semisterile plants in the M1 after seed treatment with the same streptomycin concentration. Maternal inheritance of male sterility observed in one of the mutants confirmed the CMS mutation. However, in advanced backcross generations a partial or complete reversion to fertility was observed.

We have also studied the possibility of obtaining revertants to male fertility from callus cultures obtained from sorghum plants with CMS. A partial restoration of male fertility has been revealed in three of 20 regenerants from a callus line obtained from the panicle fragments of male steriles plant that were chosen in the F_2 of the hybrid A1 Saratovskoye-3 x S-752. From one of these regenerants the AS-1 line was obtained. The AS-1 line is characterized by variable expression of male fertility varying in different plants in each generation. Different panicles of the same plant often had different pollen fertility levels and seed set. Considerable variation was observed between the samples from different parts of the same panicle. Fertility level also varied in the same family grown in different

years, indicating the possibility that environmental factors influence the expression of male fertility. Male fertility of the AS-1 line was transmitted through the pollen in crosses with progenitor CMS line A Saratovskoye-3, indicating a nuclear location for the genetic factor which caused fertility.

A similar line with variable expression of male fertility was obtained from another plant with CMS without application of tissue culture methods. This plant chosen was in the F_2 of the hybrid A1 Saratovskoye-3 x KVV-124. It was transferred to the greenhouse. After 5-6 months, fertile tillers developed on this plant, and their formation was observed in greenhouse conditions and outdoors. The fertility was inherited for four generations under self-pollination and was transmitted through the pollen in crosses with progenitor CMS line A1 Saratovskoye-3. This confirmed the nuclear location of the genetic factor that conditioned male fertility. Line AS-2 was characterized by highly specific expression of male fertility: the main tiller was sterile or, rarely, semisterile, and the next tillers were semifertile or fertile. Similar expression of male fertility is peculiar for environmentally sensitive male-sterile mutants of rice. Thus, we have apparently isolated a male-sterile sorghum mutant with environmentally regulated male fertility.

Nuclear-cytoplasmic Interactions in Fertility Restoration on Different CMS-inducing Cytoplasms of Sorghum

L.A. Elkonin, V.V. Kozhemyakin and A.G.Ishin, Volga Region,
Institute of Biotechnology, 410020 Saratov, Russia

Restoration of male fertility on different CMS-inducing cytoplasms in sorghum was established to be controlled by one or a few dominant nuclear genes that interact specifically with cytoplasmic genes. However, in some nuclear-cytoplasmic combinations we have observed several phenomena that cannot be explained by this scheme.

Using successive backcrosses, the nuclear genomes of several early-maturing A1 restorer lines of grain sorghum were transferred into the A_2, A_3, A_4 and '9E' CMS-inducing cytoplasms; the donors of these cytoplasms were isonuclear lines with the nuclear genome of Tx398 (the seeds were kindly supplied by Dr. K.F. Schertz).

In some hybrid combinations, a restoration of male fertility conditioned by 1-2 dominant genes was observed in the F_1s. In many cases, the F_1 was recorded as male sterile. In some combinations, it was stably inherited through backcross generations up to BC3-BC7. However, during backcrossing of a number of lines (Milo-10, S-723, KVV-28, KVV-181) to the different cytoplasms, considerable genetic instability was observed: all the hybrids in the F_1 exhibited male sterility, in the BC1 a few fertile and partially fertile plants appeared, whereas in BC2-BC3 fertile plants made up to 50% of population. This phenomenon was observed frequently on the A_2 and A_4 cytoplasms. Such a reversion to fertility is thought to be the result of recessive nuclear-restorer genes or frequent cytoplasmic mutations under certain nuclear genomes. Indeed, fertile plants appeared in the BC2 of Milo-10 on A_2 cytoplasm were homozygous and didn't segregate male sterile plants. Fertile revertants appeared in the BC2 of S-723 on A_4 cytoplasm that had an unusual mode of inheritance: their self-pollinated progeny was predominantly semisterile and sterile. Fertility was not transmitted through the pollen in testcrosses with sterile siblings.

Another interesting phenomenon was revealed on the '9E' cytoplasm: two isocytoplasmic CMS lines on this cytoplasm expressed a different reaction on the same tester-line. The line KVV-114 is a restorer for ['9E'] Tx 398 and a maintainer for another line, ['9E'] Milo-10, that was obtained by consecutive backcrosses from the first one. The genetic mechanisms underlying this phenomenon are under investigation.

Thus, the same CMS-inducing cytoplasm may express different systems of fertility restoration depending on the nuclear genotype of the CMS line.

Selection for a High Frequency of Aposporous Structures in the Ovules in Sorghum Line AS-1 Derived from Tissue Culture

N.Kh. Enaleeva, E.V. Belayeva, L.A.Elkonin, Volga-Region,
Institute of Biotechnology, 410020 Saratov, Russia

A sorghum line, AS-1, with elements of apomixis was obtained after self-pollination of a partially fertile regenerant from the tissue culture of plants with CMS (Enaleeva et al., 1994; Elkonin et al., 1995). A donor plant was chosen in the F2 of the A1 hybrid Saratovskoye-3 X Feterita (S-752). A1 Saratovskoye-3 is characterized by tendency to form additional (aposporous) structures in the ovules with a low frequency (2.5%). These structures are the large cells with single nucleus or multinuclear formations that developed alongside the common meiotic embryo-sacs (ESs); Feterita (S-752) had no deviations in female generative structures. In AS-1, the frequency of aposporous structures (APS) in the ovules increased significantly: up to 21.2% in one family of the R4 generation, varying in different plants from 4%-31%. In this line, APS sometimes resembled ES with normal or abnormal differentiation. Rarely, cases of parthenogenesis were observed in such aposporous or meiotic ESs.

In order to increase and stabilize the expression of apomictic potentials in AS-1, we have begun direct selection of plants that show a high APS frequency. For four generations seed progenies of such plants were selected and used for reproduction. The progenitor plant (8% of APS) was taken from the R4 generation. In the progeny of this plant a twin was revealed; one of its seedlings was grown through anthesis. The APS frequency in this plant was 11.5% . The next cycle of selection redoubled the APS frequency: In the R6 generation the mean number was 24.5% and any number of plants the frequency of multinuclear APS reached 16%. The maximum value observed in a given plant was 45.5%. From the seeds of this plant the R7 generation was grown. The mean frequency of APS in its progeny was increased up to 35.7% with a maximum value in some plants of 66%. In an AS-1 derivative that was not selected for APS, the mean frequency of additional structures in the ovules of plants grown in the same year was 7%.

In the last generation, along with additional structures, apomictic embryos were observed in the ESs in 2 out of 12 investigated plants. The frequency of such ESs in these plants was 2% and 6%. The embryos have the appearance of globular multicellular formations, however, traces of pollen tube penetration were absent. The polar nuclei were either intact or degenerated. It was not possible to determine whether these ESs were meiotic or aposporous. No apomictic embryos was revealed in the progenitor plant and in plants from previous generations of selection.

Thus, direct selection for APS frequency resulted in a 4-8 time increase of quantified expression of this trait. Moreover, selection increased apomictic potentials of the AS-1 line that resulted in autonomous development of embryos from meiotic or aposporous ESs.

Genetic Improvement of Sorghum in Uganda

J. Peter Esele, Plant Pathologist and Director, Serere Agricultural
and Animal Production Research Institute, P.O. Soroti - Uganda

Grain yields in sorghum have remained low and static in Uganda, averaging 1200 kg/ha for the last 10 years. Low yielding varieties, in addition to some biotic and abiotic constraints, contribute significantly to this low yield output. Progress is being made towards development of hybrids to improve on yield per unit area. A and B lines were introduced from the Texas A&M program. Crosses were made with elite Ugandan cultivars and evaluated. The F_1s have outyielded Uganda developed hybrids such as Himidi, Hibred and Hijack. ATx632 is a promising male-sterile for hybrid development

in Uganda. The grain mold complex is one of the major biotic constraints to sorghum production in Uganda. Development of resistant varieties is being pursued based on the utilization of genes for resistance. Inbred lines SC103-12E and Sureño from the Texas A&M program are being utilized. SC103-12E contributes genes $\overline{B}_1\overline{B}_2$ and R-Y-for testa and grain color, respectively; while Sureño contributes intensifier genes. These genes have important attributes for grain mold resistance. Drought stress is an important abiotic constraint to sorghum production in Uganda. Much of the country where sorghum is produced receives low rainfall. Efforts are being made to develop early maturing sorghum cultivars.

Occurrence of Sorghum Ergot Disease in Argentina and Bolivia

L.M. Giorda, EEA.INTA Manfredi, 5988 Manfredi-Cordoba, Argentina;
M.J.Martinez, Lab. de Fitopatologia, Fac. de Ciencias Agropecuarias-UNC;
S.Palacios and M.Nasetta, CEPROCOR, 5000 Cordoba-Argentina.

In the Americas, ergot disease was reported first in Brazil in 1995 and later was observed in Uruguay, Paraguay and Bolivia. In Argentina, it was first observed during March/April 1996 in commercial fields of grain and forage sorghum F_1 hybrid seed production. It was also observed on johnsongrass type plants and in sorghum production fields where weather conditions affected anther dehiscence and pollen activity, predisposing to sterility. In addition, volunteer plants of diploid and tetraploid maize varieties, growing near an ergot diseased sorghum nursery, were affected by the sugary disease. Copious exudation of honeydew containing macro- and microconida typical of *Sphacelia sorghi* McRae was observed from the spikelets of sorghum plants. This honeydew did not ooze from maize ovaries containing fungal stromata and conidia, but from the panicles.

Pseudo sclerotia and honeydew exuding profusely from infected spikelets of sorghum male sterile lines were collected from Bolivia and Argentina and mantained under 10 and -15 °C for analysis and Koch's postulate studies. Artificial inoculations were done under field conditions on offspring of female lines and on sorghum A/B lines growing in the greenhouse. Panicles were inoculated at anthesis by spraying honeydew, containing the conidia,and those from the field experiment bagged for 10 days. Plants in the greenhouse were maintained at 19-22 °C and a relative humidity about 85% from 15 days prior to inoculation until 15 days after inoculation(DAI). Within 5-8 DAI, depending on the cultivar and environmental conditions, symptoms and signs of *S. sorghi* resembling those described by Reiss et al. were observed. Under field conditions, the honeydew exudates could only be observed early in the morning when humidity was high. Subsequent, warm and dry conditions dried the honeydew, forming a hard crust on the spikelets commonly covered by fungal contaminations, mainly *Cerebella spp.*, *Fusarium spp.*, and *F.moniliforme*.

Pseudo sclerotia and honeydew extracts from Argentina and Bolivia were used to perform thin layer chromatography on silica-gel developed with methanol/chloroform (1:4). After spraying with p-dimethylamine-benzaldehidein sulfuric acid/ethanol, spots exhibiting the typical bluish color from ergoline-type alkaloid derivatives were observed. The presence of this type of alkaloids is characteristic of *Claviceps africana*, according to Frederickson et al. (2).

References

Reis, E.M. et al. Plant Dis.80:463,1996. (2) Frederickson et al. Mycol. Res.95:1101,1991.

New Sources of Yellow Endosperm and ß-Carotene in Pearl Millet

C.T. Hash, A.G. Bhaskar Raj, ICRISAT Asia Center, Patancheru 502 324, AP, India;
S. Appa Rao, Lao-IRRI Project, P.O. Box 4195, Vientiane, Laos and
Umaid Singh, ICRISAT Asia Center, Patancheru 502 324

Millions of people in the semi-arid tropics (SAT) depend on pearl millet [*Pennisetum glaucum* (L.) R. Br.] for their staple food. Many suffer from vitamin A deficiency. Consumption of pearl millet grain having yellow endoperm that contains ß-carotene could partially address this problem. Yellow endosperm grain containing carotenes was reported previously from the late-maturing, photoperiod-sensitive dauro landrace from central Nigeria. However, seed of these previously described materials is no longer available.

At ICRISAT Asia Center, the yellow endosperm trait was recently detected segregating in several accessions from the World Collection of pearl millet germplasm. This trait was stabilized in selections from two lines, IP 15533 and IP 15536, both originating in Burkina Faso. These selections were evaluated for their ß-carotene content, with yellow maize and three pearl millets having more common non-yellow endosperm colors as controls. High performance liquid chromatography (HPLC) with standard ß-carotene was used for this. Nutritionally significant levels of ß-carotene were detected in the yellow grain pearl millet selections from IP 15533 (137 µg/100 g) and IP 15536 (61 µg/100 g), as well as the yellow maize (480 µg/100 g), but no ß-carotene was detected in grain samples of white (SADC White Grain Composite), light grey (Lubasi late variety), and dark grey (ICMV 221) pearl millets tested. The levels of ß-carotene observed in the yellow grain pearl millet and maize in this study were very similar to those previously reported.

Mapping of Quantitative Trait Loci for Seedling Thermotolerance and Other Traits in Pearl Millet

Catherine Howarth, Graeme Cavan, Kirsten Skot, Rattan Yadav, Institute of Grassland and Environmental Research, Aberystwyth, SY23 3EB, U.K.; Eva Weltzien R., Tom Hash, International Crops Research Institute for the Semi-Arid Tropics, Andhra Pradesh 502 324, India

High temperatures and drought stress cause a failure of seedling establishment, altered crop quality and reduced seed set in many parts of the world. A wide genetic range in the response to these conditions is found both within and between species. Pearl millet [*Pennisetum glaucum* (L.) R. Br.] is an important cereal grain and fodder crop in many parts of the semi-arid tropics, grown particularly by subsistence farmers in marginal areas. Research is being conducted to identify selection criteria and molecular markers for tolerance to these stresses, to understand the underlying mechanisms and to develop improved varieties and elite parents. This project involves an integrated approach of breeding and physiology at ICRISAT, field trials in Rajasthan, India, and physiology, biochemistry and molecular biology in the UK funded by the UK Overseas Development Administration.

Molecular methods such as restriction fragment length polymorphism (RFLP) analysis can be used to identify and map the quantitative trait loci (QTL) involved in stress tolerance. Mapping potential physiological and biochemical components of a trait provides information on their involvement in that trait and is a new way to elucidate the mechanisms of plant response to the environment. Genetic mapping not only shows in a much clearer fashion how traits are genetically correlated but how they are linked on the chromosome. This provides precise information on the effectiveness of multi-trait selection and the potential to avoid undesirable correlated responses to selection.

The first molecular marker map of pearl millet has recently been constructed making available RFLP probes to facilitate the mapping of new

crosses where stress tolerance can be subjected to QTL analysis. In this poster we describe the approach being used in this project, the selection of material for mapping, the screening systems developed and the results so far obtained. In each cross, the RFLP genotype of 150 random F_2 plants has been determined, and F_4 seed derived from these F_2s used to assess all traits. These traits include 1000-seed weight, germination, emergence, seedling vigor, panicle characteristics, time to flowering and downy mildew resistance in addition to stress tolerance and its components. 32 probes were used to map cross 1 and 23 for cross 2; these covered all 7 linkage groups with a spacing of approximately 16 cM. The skeleton map obtained was suitable for identifying QTLs for all target traits. Cross 1: ICMP 451 x H 77/833-2: Both parents are pollinators of agronomically elite hybrids currently cultivated in Rajasthan, India; ICMP 451 is the male parent of a long-duration, dual-purpose grain and fodder/stover hybrid, ICMH451, that is widely grown in higher rainfall areas (>400 mm mean annual precipitation). H 77/833-2 is the male parent of the extra-early, thermotolerant grain hybrid HHB 67. The parent H 77/833-2 shows a much higher average combining ability for thermotolerance in hybrids, while ICMP 451 exhibits the poorest average combining ability for this character among the six elite inbreds tested. Cross 2: H 77/833-2 x PRLT2/89-33. The PRLT2/89-33 parent is an inbred derived from the ICRISAT Bold Seeded Early Composite, which is based largely on landrace material from Togo and Ghana whose seedlings show very poor heat tolerance. It differs from H 77/833-2 in many growth characters (reduced nodal and basal tillering, larger seeds, thicker panicles, broader leaves) and is superior to h77/833-2 for grain filling under terminal drought stress. Cross 2 segregates for tolerance to terminal drought stress and this is now being mapped. Both yield characters and putative component physiological traits (e.g., rate of senescence, osmotic adjustment, tillering and fate of tillers, flowering time) are being measured in the drought nursery at ICRISAT. Fine mapping of the seedling thermotolerance QTLs (in collaboration with the John Innes Centre, Norwich), of genes showing differential gene expression during stress and marker-assisted selection is also underway with this material.

Development and Assessment of Methods for Evaluating Seedling Thermotolerance in Pearl Millet.

Catherine Howarth, Kirsten Skot, Institute of Grassland and Environmental Research, Aberystwyth, SY23 3EB, U.K.; Eva Weltzien R. and Fran Bidinger, ICRISAT, Andhra Pradesh 502324, India

High temperatures result in seedling establishment failure in many species and consequent catastrophic crop failure. In this study, a number of potential methods for screening thermotolerance have been developed and assessed in a selection experiment with seedlings of pearl millet [*Pennisetum glaucum* L. (R.Br.)]. In India, pearl millet is the principal grain and fodder crop in arid and semi-arid areas bordering on the Thar desert in the states of Rajasthan, Haryana, and Gujarat. Although pearl millet shows considerable environmental adaptation to these marginal areas, its yield there is not only low but also highly variable. Seed and biomass yields are severely constrained by extremes of temperature prevalent at the start of the growing season and by unreliable and irregular rainfall.

Genetic variability for seedling thermotolerance was detected using a field screening technique, and the environmental parameters of the field environment were extensively characterized (Peacock et al. 1993). Two populations were chosen for further study based both on these field results and also on detailed laboratory analyses: IP 3201, a landrace accession from Rajasthan with good seedling thermotolerance and ICMV 155, a high yielding, released open-pollinated variety but with low seedling thermotolerance. Over 200 fullsib progenies were produced from a random mated population cross combining these two. Screening for thermotolerance has now been conducted by three different methods over two cycles of bi-directional selection to assess the applicability of the different screening techniques. The methods used were (a)

field screening in Rajasthan; (b) sand bed screening tank; (c) electrolyte leakage.

The aim of the sand bed screening tank was to simulate the field conditions in Rajasthan in a controlled manner. Temperature cycling commenced three days after sowing when full emergence had occurred and continued for a subsequent eight days when the run was finished. The air temperature was maintained at a constant 30°C and the maximum temperature of the soil surface each day was 58°C. Electrolyte leakage provides an indirect measure of membrane thermostability; the more damage caused by the stress, the more solutes will leak into the bathing medium. In this research, intact two day-old seedlings were used, and preliminary experiments were conducted using a thermal gradient bar to determine the critical temperatures to use for screening. The greatest difference between entries (and highest correlation with field performance) was found with seedlings that had been acclimated for 2h at 43°C immediately prior to treatment at 48°C for 2h.

Cycle 1 screening was conducted on an identical set of fullsibs for all three methods and so the screening results could be compared directly. All three screening methods were able to successfully identify tolerance/susceptibility to seedling heat stress among the progenies, with the sand bed screening tank having the broadest range in progeny response. The sand bed screening tank also had the highest genetic variance and the highest genetic coefficient of variation. The field evaluation had the highest experimental error, and the electrolyte leakage test was the most precise, as judged by the magnitude of error variances and coefficients of error variation. Heritability was also highest with the electrolyte leakage test. The correlations among the three tests, based on mean progeny rating in each test were all significant. Nearly half of the progenies selected as tolerant or susceptible to heat stress by the individual tests were common. The good relationship between the field and the sand bed screening tank is very encouraging, as it indicates that in both environments seedling death or survival is caused by the same or similar factors. The relationships between these two tests and the test for electrolyte leakage are rather different, suggesting that membrane stability may be only a component of seedling tolerance to heat stress. Selections for high and low thermotolerance were made from each of the three sets of screening results in cycle 1. These were recombined to produce six sets of fullsib progenies and were then screened by all three methods for cycle 2 selection. Again bi-directional selection was conducted. 12 population bulks have been produced of this selected material, along with the initial C0 bulk, their testcrosses, parental populations and other controls. These have undergone preliminary evaluation by all three selection techniques to assess the results of selection and the results obtained will be reported here.

Reference

Peacock, J.M., P. Soman, R. Jayachandran, A.U. Rani, C.J. Howarth, and A. Thomas. 1993. High soil surface temperature effects on seedling survival in pearl millet. Experimental Agriculture 29, 215-225.

The financial support of the Overseas Development Administration of the UK (ODA) for the laboratory studies, of the Deutsche Gesellschaft für Technische Zusammenarbeit (GTZ), and the United Nations Development Programme (UNDP) for the breeding work are gratefully acknowledged.

Variation in Physical Seed Characters Significant in Grain Mold Resistance of Sorghum

S.Indira and B.S.Rana, National Research Centre for Sorghum, Hyderabad 500 030, India

In sorghum, grain mold susceptibility during the rainy season causes economic losses that make it monetarily less competitive compared to other crops. The resistance to grain mold has previously been reported to be correlated with grain hardness, water absorption rate and plant type. In the present study additional characters e.g., test weight, volume and density, floater and germination have been

studied in 10 parents and 45 crosses among them in diallel design without reciprocals (Table 1).

Grain hardness was determined as breaking strength in kg and the grain density as a ratio of weight/volume. The volume of 100 grains was calculated by putting the 100 grains into a known volume of water, the difference being the grain volume. The floater seeds % was calculated by putting grain in the solution of Sodium nitrite ($NaNO_3$) of sp gr 1.3.

Grain mold score in the field (1=Res - 5=Susc) ranged from 1.6 to 4.1 in parents and 1.42 to 2.75 in hybrids. After threshing, the grain mold score was reduced to 0.98 -3.55 in parents and 0.88 to 2.75 in hybrids. The grain mold incidence was low (0.98 -1.25) in K 24-1, SPV 475, SPV 351 and SPV 603 and crosses based on these lines.

The 100 grain weight ranged from 1.58 to 3.28 g in hybrids and 1.9 to 3.13 g in parents. Grain hardness was more in parents ranging from 4.65 to 11.42 kg than in hybrids (3.75 to 9.61 kg). Similarly, density of grain was more in parents ranging from 0.61 to 2.16 g/cm^{-3},than in hybrids. The volume of 100 grains was 5.5 to 9.0 ml in parents and 5.3 to 10.3 ml in hybrids. Only two parents IS 3922 and SPV 232 showed a higher volume of grains (9.0 and 9.43 ml). The range of floaters % was 19.1 to 31.5% in parents and 1.75 to 40.5% in hybrids. As a lower percentage of floaters is desirable, some hybrids may have high density grains but, other hybrids may have lighter grain than all the parents. The floater % was lowest in three crosses viz. SPV 351 x SPV 232, SPV 475 x SPV 456 and SPV 603 x 296 B ranging from 1.75 to 4.75.

The germination was higher in hybrids (13 - 74%) than in parents (8 to 64%). The parents K 24-1, SPV 351, SPV 603, SPV 232 and IS 3443 and some of their crosses, K 24-1 x SPV 475, SPV 475 x SPV 603, SPV 603 x SPV 232 and SPV 351 x IS 3443, were found to be higher in germination percent i.e., up to 74%.

The hybrids were superior to their parents for resistance to grain molds as well as 100 grain weight, volume and germination %. The grain hardness and water absorption of hybrids was less than the parental mean (Table 1). The average heterosis was negative for grain mold resistance indicating that hybrids had 17% better resistance than parents. On average, 100 grain weight and germination % had marginal superiority of 8-10% over parents. For the remaining traits individual heterosis was important.

The weight of 100 grains was positively and significantly correlated with volume of grains (r = 0.90**) and grain hardness (r = 0.138) and negatively correlated with percent floaters. The volume and density of grain was not correlated with mold incidence and other characters. However, hardness of grain was found to be negatively correlated with percent floaters (r = 0.156) and grain mold incidence (r = 0.30*). Therefore, grain mold incidence would be low in those varieties which had hard grains (X4) and low floaters (X5). The multiple regression of grain mold susceptibility (Y1) for these traits was: Y1 = 2.332 - 0.1186** X4 + 0.0189** X5. Thus, less floater % and more hardness contribute to grain mold resistance and provide a selection criteria for resistance breeding.

Table 1. Mean grain mold grade (1 Res. - 5 Sus.) and physical characteristics of grain

	Grain molds (1-5)	100 grain wt. (g)	Grain hardness (kg)	Grain volume (ml)	Density (g/cm^{-3})	Floaters (%)	Percent Germination
Parents	2.27	2.29	7.09	7019	0.82	24.41	40.78
Hybrids	1.90	2.49	6.82	7.36	0.69	23.79	45.04
SE±	0.42	0.27	0.55	0.44	0.29	4.28	8.57
Av. heterossis %	16.83	8.46	-3.41	2.36	0.66	-3.11	10.45
r	0.78	-0.10	-0.30*	0.01	-0.03	0.45**	

r = Correlation with grain mold resistance
* = Significant at 5% ; ** Significant at 1%

Genetics of Stem Sweetness and Seed Yield in Pearl Millet (*Pennisetum glaucum* [L.] R. Br.)

N. Jayaraman, S.R. Sree Rangasamy and S. Juliet Hepziba, Department of Millets, School of Genetics, Ramil Nadu Agricultural University, Coimbatore-641 003, India

High grain yield and quality straw are two features desired in pearl millet. To identify superior cross combinations and evolving breeding strategies for the improvement of stem sweetness and grain yield in pearl millet, a 7 X 7 diallel cross including reciprocals was generated. A comparative study of F_1 hybrids and their parents performance was made over three seasons. Genetic and graphical analyses, estimation of GCA and SCA, and studies of phenotypic stability were carried out to assess various genetic parameters. Combining ability analysis indicated the importance of both additive and non-additive gene action in the expression of yield and yield components, while the stem brix value at different growth stages was chiefly additive in nature. However, genetic and graphical analyses suggested the influence of dominance and non-allelic interaction. Stem sweetness was low in the vegetative phase, reached maximum during flowering and was reduced slightly at grain maturity. The stem sweetness at maturity, plus yield of grain and straw, were at maximum in summer as compared to *kharif* and *rabi* seasons.

Sink-Source Relationship in the Grain Sorghum Plant: Its Role in Grain Yield and the Possible Ways to Improve It.

A.S. Kasakova, All-Russia Research Institute for Sorghum, Zernograd, Rostov-on-Don Region, Russia

Grain sorghum genotypes were studied during ten years of field experiments to estimate the influence of environment on yield and the sink-source relationship. Dry mass accumulation and distribution during vegetative and generative growth stages were more stable under water stress conditions with short- and mid-season varieties. With the method of partial (50% of upper or lower leaves) or total defoliation it was shown: 1) genotypes differ in the role of upper or lower leaves in grain filling; and 2) the more ecologically stable genotypes have more intensive reutilization of storage and structure elements during stress.

Molecular Analysis of Resistance to Greenbug in Sorghum

C.S. Katsar, Dept. Entomology, Texas A&M University, College Station, TX; A. H. Paterson Dept. Soil & Crop Sciences, Texas A&M University, College Station, TX; G.C. Peterson, Dept. Soil & Crop Sciences, Texas A&M University Agricultural Research and Extension Center, Lubbock, TX; and G.L. Teetes, Dept. Entomology, Texas A&M University, College Station, TX

The greenbug, *Schizaphis graminum* (Rondani), is a major insect pest of sorghum, *Sorghum bicolor* (L.) Moench. In Texas alone, losses due to greenbug damage are estimated to be $21.3 million. Sorghum populations segregating for resistance to biotypes C, E and I were developed at the Texas A&M University Agricultural Research and Extension Center at Lubbock, TX for the purpose of identifying molecular markers diagnostic of sorghum resistance to greenbug biotypes.

A segregating sorghum population consisting of 195 F_3 families from a cross of sorghum lines RTx430*PI550607 was phenotyped under green-

house conditions for their reaction to greenbug biotypes E and I. The number of genes segregating for resistance was determined by Chi-squared analysis. A single dominant gene appeared to be segregating for biotype E resistance, while three resistance genes appeared to be segregating for biotype I. A recently published RFLP map of sorghum was used to identify DNA markers linked to greenbug resistance in this and other sorghum populations. A molecular marker from this map was found which accounted for 16% of the biotype E resistance ($\alpha=10^{-5}$) and a marker, mapping to a different linkage group, also cosegregates with biotype I resistance ($\alpha=0.02$). When analyzed concurrently, these two markers account for approximately 14% of the phenotypic variation in biotype I resistance ($\alpha=10^{-3}$).

Selective genotyping is a strategy used to expediate mapping monogenically inherited traits whereby the most susceptible and resistant phenotypes are genotyped prior to genotyping an entire segregating population. Phenotypic analysis of resistance to biotype E greenbug in 220 F_3 families of the cross Tx2783*SC283-14E suggested this resistance is simply inherited. Selective genotyping was used to determine the location of a biotype E resistance gene in this cross. A DNA marker, accounting for approximately 46% of the total phenotypic variation ($\alpha=10^{-4}$), was identified. This marker maps to an altogether different locus than either of the two molecular markers previously identified.

Currently, efforts are being made to identify other DNA markers diagnostic of greenbug biotypes C, E and I in these and other sorghum populations.

Components of Plant Height and Internodal Patterns Determining Dwarfing Systems in Sorghum

Swarnlata Kaul, National Research Centre for Sorghum, Hyderabad, India.; V.P.Singh, and B.S.Rana, National Research Centre for Sorghum, Hyderabad, India. *Reader, Dept. of Plant Science, Rohilkhand University, Bareilly, India;

Sorghum has vast variability for plant height which effects the plant canopy, harvest index and yield potential. Dwarf genotypes are suitable for combine harvest while dual purpose types are required in the tropics. A nonlinear relationship exists between grain yield and plant height. However, early flowering and leaf number, the characteristics of dwarf plants, are advantageous for grain yield (Rana et al 1984).

MATERIAL: An experiment was conducted to study the internodal patterns of 25 sorghum genotypes. Among dwarfs, IS 24373 was extremely dwarf. Five temperate genotypes from USA SGIRL-MR-1, CK 60B, IS 84, SC 108, and BTx 623 and derivative lines 168, CS 3541, 296 B, 2077 B were dwarf genotypes. E 12-1, E 35-1, SRN 4841 were African tall genotypes while Aispuri, M 35-1 and improved Ramkel were Indian tall genotypes. Three high yielding hybrids CSH 5, CSH 6, CSH 9 and four varieties CSV 9, CSV 10, SPV 462, CSV 13 and E 36-1 derived from temperate x tropical crosses formed the intermediate group between temperate dwarfs and tropical talls.

All genotypes were grown in the rainy season in a randomized block design replicated three times over two years. Data were recorded on length of individual internodes (IL), total number of internodes (NI), stem thickness (ST) and plant height of five plants per genotype.

RESULTS: Plant height was sub-divided into three components: stalk length (SL), peduncle length (PDL) and panicle length (PL). The SL was 55.8 - 111.5 cm in temperate and derived dwarfs, 143.6 - 164.8 cm in medium tall genotypes and 211.0 -247.0 cm in African and Indian tall cultivars.

The number of internodes was 11 - 14 in dwarfs, 11 - 15 in medium tall, 10 - 16 in tall cultivars, 14 in extreme dwarf and thus comparable in different height groups. However IL varied from 4.4 - 5.9 cm in temperate dwarfs, 4.9 - 6.25 cm in derived

dwarfs, 8.0 - 12.4 in medium tall and 10.5 - 21.0 cm in talls while in the extreme dwarf genotype it was 2.4 cm. Thus, IL was distinctly short in dwarfs. The PDL was 11.1 cm in extreme dwarfs, 19.5 - 40.0 cm in dwarfs, 29.1 - 50.3 cm in medium and 12.3 - 35.9 cm in tall cultivars. Thus short peduncle length induced dwarfness in IS 24373 while its elongation added to the height in the dwarf and medium genotypes. Plant dry weight (DW) was 24.9 - 111.9 g in dwarfs, 77.0 - 163.3 g in medium and 90.9 - 282.0 g in talls. The CV for SL, NI and PDL was 39.4, 29.2 and 34.8% respectively but was high for DW (55%), thickness of stalk (67%) and average internode length (100%).

Plant height (PHT) was positively correlated (r = 0.94**) with IL but not significantly with PDL, PL, NI and ST. The length of each individual internode was positively correlated (r = 0.73** to 0.94**) with plant height. The multiple regression equation to determine plant height (Y) was:

$$Y = 75.44 + 1.48^{**} X_1 + 2.79^{**} X_2 + 5.52^{**} X_3 + 6.84^{**} X_4 - 3.07^{**} X_5 + 4.63^{**} X_6 \ (R^2 = 0.98)$$

Where X_1 = PDL, X_2 = PL, X_3 = NI, X_4 = III internode length, X_5 = V internode length, and X_6 = VII internode length.

The III and VII internodes were significantly and positively correlated with plant height while V internode had a negative influence on plant height. Hence condensation of III and VII internodes in particular effectively induced dwarfing in sorghum though reduction in all the nodes would make the plant extremely dwarf, as in IS 24373. PDL and PL were direct components of PHT and any increase in them would add to plant height, though it was not necessary that long stalk would bear long PDL or long PL.

The dwarf groups showed a slow increase and condensation in the middle internodes followed by a slow increase. In tall genotypes, the elongation of basal internodes had been very fast. The following patterns (P1-P5) of internode elongation determined the plant height in sorghum.

P-1	Double parabolic (Two peaks) (condensed internodes)	IS24373 (84 cm)
P-2	Accelerated-retarded-Accelerated (Short internodes)	168, CS 3541, SC 108, 2077B (119-145 cm)
P3	Accelerated-Static-accelerated	SGIRL-MR-1, CK 60B,
	a) Short internodes	IS 84 (115-133cm)
	b) Medium internodes	CSH5, CSH6, CSV13 (175-180 cm)
	c) Long internodes	CSV10, Y75 (201-275 cm)
P-4	Parbolic (negative skewed)	
	a) Short internodes	296 B (125 cm)
	b) Medium internodes	CSH 9 (175 cm)
P5	Parbolic (positive skewed)	
	a) No re-elongation of last internodes	BTx 623, E 36-1 (119-162 cm)
	b) Re-elongation of last internodes	i) CSV 9, SPV 462 (211-225 cm) ii) E 35-1, E 12-1 SRN 4841 (211-236 cm) iii) Aispuri, Imp. Ramkel, M 35-1 (252-291 cm)

CONCLUSION: The plant height was determined by the internodal length rather than internode number. Shortening of the III and VII internodes was an effective indicator of dwarfing. Four different patterns of internode elongation coupled with short length represented the dwarfing system in sorghum.

Rana, B.S.; B.C.Barah; H.P.Binswanger and N.G.P.Rao. 1984. Breeding optimum plant type in sorghum. Indian J. Genet. 44:14-27.

Downy Mildew Resistant and High Yielding Pearl Millet Hybrid JKBH 26 for the Low Rainfall Zones of India

C. Rama Krishna, Senior Manager - Research, J.K. Agri-Genetics, A Division of J.K. Industries Ltd., Secunderabad, A.P. India

Pearl millet (*Pennisetum glaucum* [L.] R. Br.) locally known as *bajra*, is an important cereal crop in India with an estimated area of 11 million ha in the arid and semiarid regions of the country. This represents 30% of the world pearl millet area. Nearly 75% of this is grown in the states of Rajasthan, Gujarat, Maharashtra and Uttar Pradesh. The states of northwestern India, i.e., Rajasthan, Gu-

jarat, Haryana, Uttar Pradesh, Delhi, Punjab and Madjya Pradesh, are grouped under Zone A by the All India Pearl Millet Improvement Project (AICP-MIP). JKBH is well suited for this zone.

JKBH 26, a single-cross hybrid, was developed by crossing an early male-sterile line with a medium maturing, medium tall restorer line. JKBH 26 was tested as MH 595 in the Zone A trials of AICPMIP during 1993 to 1995. In these years, it exhibited stable grain yield performance. Its mean yield for three years was 2.30 t ha^{-1}, compared to 1.98 t ha^{-1}, 1.97 t ha^{-1} and 2.14 t ha^{-1} for the national checks - MH 338 (HHB 67), MH 169 (Pusa 23) and MH 179 (ICMH 451), respectively. Fodder is equally important in this zone. Because of its tall height (160-200 cm), JKBH 26 gave high mean fodder yields of 5.3 t ha^{-1} meeting the farmers' requirements. JKBH 26 is a medium-maturing hybrid taking 50-53 days for 50% flowering and maturing in 78-83 days. The plants have well exerted, compact, non-bristled panicles. This hybrid has grey colored bold grain (12.8 g per 1000 grains) and recorded 9.62% protein compared to 7.87% for national check MH 169. It is highly resistant to lodging as was evident from demonstration plots in farmers' fields in northern India (Zone A) during the 1994 rainy season. The hybrid is highly resistant to downy mildew (*Sclerospora graminicola*), the most widespread and destructive disease of pearl millet. It was the only hybrid to record 0.0% incidence 60 days after sowing in the 1994 AICP-MIP trials under sick plot conditions where susceptible check HB 3 had recorded 87.6%. Further, no incidence was recorded under natural conditions during 1993. JKBH 26 responds well to nitrogenous fertilizers, having shown an increase of 34.9% in grain yield when nitrogen level was increased from 0 kg ha^{-1} to 30 kg ha^{-1}. The hybrid is suitable for cultivation as a dryland crop during the rainy season in low rainfall zones of northwestern India. Having completed three years of testing in AICP-MIP trials successfully, a proposal for its identification has already been submitted to the project.

During the rainy season of 1996, JKBH 26 occupied an area of about 76,000 ha and is expected to be grown on 150,000 thousand ha in 1997.

High Yielding Grain Sorghum Hybrid JKSH 22 for Peninsular India

C. Rama Krishna, Senior Manager - Research, J.K. Agri-Genetics,
Division of J.K. Industries Ltd., Secunderabad, A.P. India

Sorghum (*Sorghum bicolor* [L.] Moench), locally known as *jowar*, is cultivated in India in both rainy and post rainy seasons for food and fodder. In the rainy season, it is grown in an area of about 6.5 million ha, mostly in the states of Maharashtra, Madhya Pradesh, Andhra Pradesh, Karnataka and Tamil Nadu in peninsular India. About 80% of sorghum seed produced for the rainy season is sold in Maharashtra and Karnataka.

Genetic improvement for productivity and quality of produce are the major objectives of breeding for rainy season sorghum. The spread of high yielding hybrids has significantly improved productivity of rainy season sorghums, especially in the states of Maharashtra and Karnataka. JKSH 22 [tested as JKSH 161 in the All India Coordinated Sorghum Improvement Project (AICSIP) trials], has both high yield potential and improved grain quality and has been successfully cultivated in peninsular India. It was developed by crossing a bold seeded short male-sterile line with a medium tall restorer line. JKSH 161 was tested in the AICSIP trials during 1993 to 1995. Results indicated that its mean grain yield was 4.0 t ha^{-1} compared to 3.7 t ha^{-1} for the national check. In 1993, JKSH 161 ranked first in both rainfed and irrigated trials with a mean grain yield of 4.8 t ha^{-1} and 7.5 t ha^{-1} respectively, showing its noninteractive nature. It is a medium maturing hybrid taking 65-72 days to 50% flowering and maturing in 103-111 days. It has a very large, open panicle, an ideal feature for rainy season sorghums. Grains are bold (35.8 g per 1000 grains) with pearly white color for which farmers receive better prices. The flour of JKSH 161 gives soft, cream colored *roti* (bread) that puffs well and has fair keeping quality (AICSIP report, rainy season 1994). When the monsoon is delayed shoot fly

(*Atherigona soccata*) pressure increases and can cause substantial economic damage. JKSH 161 is tolerant to shoot fly with an average of 48.4% dead hearts compared to 62.9% for the national check. JKSH 161 responds well to fertilizers and was superior at the national level for both grain and fodder yields at various levels of nitrogen and phosphorus (Agronomy Trial 1 (K), AICSIP 1995). Having completed the required three years testing in AICSIP trials, a proposal for its identification has been submitted to the project.

For most present-day sorghum hybrids parental lines should be staggered at sowing to synchronize flowering. However, with JKSH 22 there are no seed production problems since the parents nick perfectly and can be sown simultaneously in hybrid seed production plots. This facilitates attaining high seed yields, which attracts seed producers to take up its production on a large scale.

JKSH 22 has been well accepted by farmers due to its unique phenotypic and agronomic features. During the rainy season of 1996, JKSH 22 occupied about 120,000 ha in the sorghum growing areas of peninsular India and is expected to be grown on about 400,000 ha in 1997.

Pearl Millet (Okashana No.1) Farmer-Based Seed Production in Namibia

W.R. Lechner, Ministry of Agriculture, Water and Rural Development,
Omahenene Research Station, Box 144, Oshakati, Namibia

After the 1991-92 severe drought, the Government of the Republic of Namibia (GRN) realized that seed of important food crop varieties for small scale farmers must be produced "in country."

In 1992 a small-scale farmer seed project for pearl millet, the major food cereal of northern Namibia was launched by GRN with funding assistance by FAO and the European Union (EU). Pearl millet open pollinated variety (OPV) OKASHANA No. 1 was released in 1990 and the first 50 kg of seed obtained from the SADC-ICRISAT program at Matopos, Zimbabwe.

The table below shows how small-scale farmer involvement has grown rapidly, as their understanding of seed production requirements grew, and the financial advantages of being seed producers were realized. This has led to the formation in 1996 of the Northern Namibia Farmers Seed Growers Co-operative (NNFSGC). Small-scale seed producers must register and use GRN foundation seed. Only seed which has passed the requisite field inspections conducted by Agricultural Extension seed inspection officers of the Directorate of Extension and Engineering Services is accepted. Each year all seed processed has been sold out.

The 1995-96 intake price for clean seed is N$ 2.00 per kg and the retail price of treated bagged seed to farmers is N$ 3.00/kg - the grain price is about N$ 1.20/kg.

Pearl millet (Okashana No. 1) seed production (tons)

Year	1992-93	1993-94	1994-95	1995-96
Grn production	37	38	46	17
Farmers production	21	35	74	214
Total production	58	73	120	231

The cleaned seed is treated with Thiulin slurry and sealed in 2kg labeled plastic bags, the seed rate for one hectare.

With a total production of 231 metric tons, a seed rate of 2 kg ha^{-1} and assuming a replanting rate of 25%, approximately 86,000 ha will be planted with new Okashana No. 1 seed in the 1996/97 season. This is about 25% of Namibia's pearl millet crop which, according to FAO's Early Warning System, is about 350,000 ha.

Farmer education has been critical to the success of this multiplication scheme, both in how to produce seed, and their willingness to buy quality seed of a good variety at a price that generates sufficient income to operate the process.

Phenotypic Diversity of Sorghum Landraces in China

Yu Li and Cuizhen Li, Institute of Crop Germplasm Resources,
Chinese Academy of Agricultural Sciences, Beijing 100081, PR China

Sorghum [*Sorghum bicolor* (L.) Moench] was one of the most important crops in China in the past and is still an important crop in northern China today. During long-term domestication, this cereal has accumulated a great deal of genetic variation, and many landraces have formed in various local environments. For the total number of sorghum accessions preserved in the Chinese Genebank (16874), landraces (10386) account for about 61.5%. Based on the analysis of some morphological characters including seedling sheath color, midrib color, panicle compactness, panicle shape, kernel covering, glume color, kernel color and tillering ability, a high degree of phenotypic diversity for Chinese origin sorghum landraces could be found. Shandong, Liaoning and Neimenggu, the regions most suitable for sorghum cultivation in China have highest diversity. These regions also have long history of sorghum production.

Great variability exists in Chinese sorghum landraces for some quantitative characters such as plant height, diameter of stalk base, panicle length, peduncle length, grain weight per panicle, 1000-grain weight and days to maturity. Disease and pest resistance, stress tolerance and quality traits were evaluated in the past decade and elite germplasm with specific characters have been identified.

Germplasm Evaluation in Forage Sorghum

G.P. Lodhi, Department of Plant Breeding, CCS Haryana
Agricultural University, Hisar-125 004, India

Evaluation and characterization of germplasm of any crop species must precede crop improvement program. Since useful genes may be available in a multitude of lines or populations, information on parameters of genetic variability is of immense value in recombination breeding.

CCS Haryana Agricultural University, Hisar - Department of Plant Breeding, shares at the national level, major responsibilities for collecting, maintaining, evaluating and cataloging the forage sorghum germplasm. A total of 11000 germplasm lines were evaluated for various attributes and a data base developed.

Considerable genetic variability has been observed for morphological or physiological traits related to performance, adaptation, nutritive value, digestibility, toxic constituents, and resistance to pests and diseases. This is exemplified by the range of variation observed for days to flowering (38-93 days), plant height (39-328 cm), leaf number (3-20), leaf length (49-85 cm), leaf breadth (3.6 to 8.6 cm), stem girth (3.6 -6.4 cm), leaf weight per plant (8.3 - 90.0 g), stem weight per plant (61 - 430 g), leaf : stem ratio (0.1 - 0.7), green fodder yield per plant (12.0 - 1510.0 g) and dry matter yield per plant (5.7 - 417.0 g). Because of intrinsic complexities in recombination breeding and handling of multiparent crosses, it is worthwhile to identify genetic stocks that contain more than one trait related to per se performance and end-use quality. In that context the following lines were found to be good for fodder yield and should be extensively exploited in the breeding of ideal forage sorghum varieties: IS 1044, IS 18580, IS 18578, PS 14413, PJ 7R, HC 136, S 285, S 308 and HFS 566. Due to the farmer's preference and need for multicut varieties, progress has been made to identify genetic stocks possessing inherent genetic potential for regeneration and tillering without an exogenous supply of growth promoting hormones. Multicut types that can be involved in crosses to transfer genetic potential for regeneration and faster growth include: SSG 59-3, HFS 566, J 69, M.P. Chari, IS 3214, 3240, 3274, 3374, G I, G 46 and G 48.

Production potential of forage sorghum lines is of less value if they do not possess good nutritive value, digestibility, and low content of antimetabolites/constituents like HCN and tannin. A large range of variation has been found for HCN (70-600 ppm), tannin (0.5 to 6.3%), protein (3.01 - 8.75%), IVDMD (40 to 66%), NDF (57 to 70%), ADF (31 to 43%), cellulose (21-33%) and lignin (4-7%). From the lines analyzed, 12 and 9 lines appeared to possess low HCN and tannin content, respectively. The promising lines are IS 1059, IS 3247, JS 29/1, IS 4776 and NS 256. Low HCN and tannin content are assumed to be dominant. Sorghum genotypes, Impi Jowar and S 520 had high protein (more than 7%) while IS 4770, IS 8312 and IS 6880 have higher digestibility (more than 55%). HC 136 and HC 171 possess high protein content, high *in vitro* dry matter digestibility and very low content of toxic constituents. Lines G 40, IS 8087, IS 3380, SPV 98, S 171, S 260 and S 435 showed resistance to most foliar diseases. Lines IS 5469 and IS 2123 show resistance to stem borer and shotfly and are also good in other fodder traits.

Breeding value of elite germplasm lines is best indicated by general combining ability and stability over environments. Lines found to be good combiners include IS 1049, IS 6090, PJ 7R, C 406-8, T30 and PC6 for plant height and leaf characters; G10, HC 136, PSV 102, SPV 98 and JS 263 for fodder yield; *S. roxburghii* for IVDMD and tannin; IS 4776 for protein and HCN; and IS 1049 for protein and IVDMD. Use of these lines in breeding programs to accumulate a constellation of favorable alleles in a dynamic population, and to develop genetic maps using molecular markers, would be worthwhile.

Sorghum Crop Improvement Research in Zimbabwe

N. Mangombe, Sorghum and Millet Unit, Matopos Research Station, P. Bag K5137, Bulawayo, Zimbabwe; S. Mabasa, Weed Research Team, Henderson Research Station, P. Bag 2004, Mazoe, Zimbabwe; and L.T. Gono, Sorghum and Millet Unit, Matopos Research Station, P. Bag K5137, Bulawayo, Zimbabwe

Small holder farmers in Zimbabwe's marginal rainfall (450 - 650 mm) regions III, IV and V grow more than 90% of white and brown sorghum under rainfed conditions. The sorghum cultivars are predominantly open pollinated varieties. A few large-scale commercial farmers in these regions grow DC75, a brown sorghum hybrid, under dryland conditions. White sorghum is generally used for food, whereas brown sorghum is used for brewing opaque beer.

The yield gap between improved open pollinated varieties (2.71 t/ha) and small holder farmers' yields (0.32 t/ha) is high. However, for large-scale commercial farmers, yields of 2.72 t/ha are close to the potential of the hybrid, DC75 (3.61 t ha^{-1}), because of use of the improved hybrid and proper management practices. The large gap for small-holder farmers is caused by lack of improved varieties which can tolerate drought, diseases, pests, insects, and low soil fertility.

Genetic improvement is currently focussing on developing varieties with the following qualities: disease resistance, drought tolerance, pest and insect resistance, good grain quality and *Striga* tolerance. Low grain yields and quality are being improved through crosses involving NL 330, NL 499, SV-1 and SV-2 which are higher yielding varieties.

Screen ing of Sorghum for Resistance to Ergot (*Claviceps africana*)

N.W. McLaren and W.G. Wenzel, ARC-Grain Crops Institute, Private Bag X1251, Potchefstroom, 2520, Republic of South Africa

Ergot of sorghum, caused by *Claviceps africana* was first reported in Africa in 1965. It has subsequently spread throughout sub-Saharan Africa and, within the last two years to Brazil, Argentina

and Australia. Concern has been expressed about its spread into the U.S.

The disease is characterized by a sticky exudate that develops on the tips of infected florets. Infection may range from a few florets to the entire panicle. Since the fungus colonizes the ovary, infected florets produce no grain. During 1995/96, losses in South Africa ranged from 20-60%. Although most severe in seed production fields, the disease is also prevalent in cooler commercial production areas.

The disease is favored by cool, humid conditions during early anthesis. The optimum temperature for infection is ±20°C and disease incidence is negligible above 28°C. High humidity during the infection period facilitates disease development.

Despite *Claviceps spp* occurring on many graminaceous crops, there is no consistent evidence of genetic sources of physiological resistance that ensures protection against the particular *Claviceps spp* that parasitizes that crop plant. As a result, emphasis in screening and selection studies has been placed on floral characteristics that promote disease escape. Since florets are only susceptible to infection from floret opening to fertilization, emphasis has been on pollination-based escape-resistance.

Pre-flowering cold conditions (minimum temperature <12°C) 23-27 days prior to anthesis reduce pollen viability with a concomitant reduction in seed set under pollination bags and increased ergot susceptibility in artificially inoculated screening trials. Reduced pollen viability was evident by a large increase in starchless pollen grains in low temperature susceptible genotypes. In sequential planting date evaluations, cold tolerance was expressed as increased seed set and escape resistance compared with cold susceptible genotypes at equivalent temperatures.

Due to the close correlation between climate, predisposition to ergot and infection, small variations in flowering date and associated weather during early anthesis in screening trials can affect disease severity. This raises the question as to whether observed differences in disease severity between genotypes is weather or genetic based. A non-linear regression analysis technique that determines the relationship between mean expected ergot severity (as percentage infected florets) associated with a specific flowering date in a 200-entry sorghum nursery (termed the ergot potential) and observed ergot incidence in genotypes was used to quantify ergot escape resistance. Subsequent modeling of ergot development in large nurseries in relation to pre-flowering cold stress and maximum daily temperature and humidity during early anthesis has enabled the disease potential to be mathematically computed. The disease potential required to induce ergot in a genotype (termed ergot breakdown point) is used as criterion to quantify escape resistance. Disease potentials required to induce ergot in sorghum lines ranged from near 0 in male-sterile lines to 48% in IA38.

Components of escape resistance were studied and are illustrated. These include pollen viability associated with levels of cold stress, pollen x donor:female incompatibility, rate of flower opening, pollen shed and fertilization. All floral characteristics which delayed pollination were associated with an increase in ergot severity. Genotypes which tend towards cleistogamy are least prone to infection.

Yield Stability of Twelve Pearl Millet Populations in Semi-Arid Kenya

L. M'Ragwa, C. Kamau, J. Gitari and E. Njirum,
KARI, Katumani, P.O. Box 340, Machakos, Kenya

The goal of a breeder is to develop varieties that have high yield potential and stability when grown in different and variable environments. Stability is important because varieties with predictable performance are more desired by farmers.

Twelve pearl millet populations were tested in the randomized complete block national performance trials (NPT) with four replications from 1983 to 1993. The objective was to compare grain yield stability across the possible release environments. The mean grain yield, linear regression coefficient (b), coefficient of determination (R^2) and coefficient of variation (cv) were used to determine grain yield stability.

The mean grain yield ranged from 1267.9 kg ha^{-1} to 2261.9 kg ha^{-1}. KAT/PM-1 (2261.9 kg ha^{-1}) and KAT/PM-2 (1926.6 kg ha^{1}), the two cultivars recommended for cultivation in Kenya, had significantly ($P<0.05$) greater grain yields than others. Local populations, including ex-Coast coll. #164, Gatunga local and cross derivative Px8, had the lowest grain yield. There were no significant differences among the ex-ICRISAT populations WC-K77, ICMS 7703, ICMS 7818 and IVS 5454. These varieties appear to have lost their original identity due to selection over several cycles.

Grain yield stability parameters: b values, R^2 and cv indicated that KAT/PM-1 was more variable and adapted to good environments than KAT/PM-2. Varieties WC-K77, KAT/PM-2 and IVS 5454 were more stable than others in the seven environments. Populations ex-Gatunga, Sounga Bukina, Px8, ex-Coast coll. # 164 and ICMS 7818 appeared to be adapted to poor environments and less stable than others. Therefore, these varieties were withdrawn from the1996 long rains NPT and substituted with four varieties from ICRISAT.

Genetic Improvement of Sorghum Malting Qualities

J.N. Mushonga, Research and Special Services, Harare, Zimbabwe

Eighty-five sorghum genotypes, composed of 13 lines, 5 testers, 65 F_1 hybrids and 2 controls were planted at Muzarabani, Zimbabwe for two seasons, 1986-87 and 1987-88, to study combining ability and heterosis for diastatic activity expressed as sorghum diastatic unit (SDU) per gram of malt in 1989 at Matopos, Zimbabwe. Differences between sorghum lines, testers, crosses and total entries were significant for diastatic activity in both seasons. The mean SDU g^{-1} malt for crosses varied from 20.5 to 67.2 for the 1986-87 season and 13.3 to 48.9 for the 1987-88 season. Nonadditive gene action was primarily responsible for diastatic activity. The highest positive general combining ability effects were observed for 4HA85S and tester 120A. Significant positive specific combining ability effects were observed for cross 120A x D-38073-2 in both seasons. This is the only cross which had positive heterobeltiosis in both seasons. Most of the crosses had negative heterobeltiosis.

The Study of Sorghum Apomixis in China

T.T. Niu, F.Y. Zhang, S.B. Wu, C.G. Meng, X.M. Han, X.M. Yan,
J.X. Wang, J.B. Zheng, Y.J. Shang, J.A. Ping, L.X. Wang, Y.M. Wei,
and Y. Sun, Shanxi Academy of Agri. Sci, Taiyuan, Shanxi, P.R. China 030031

An apomictic line, SSA -1, was created by multiple crossing with R473 as one parent.

Various approaches including a crossing test, progeny test and embryogenesis test were used to study the autonomous seed set of SSA-1. The results showed that SSA-1 had no pollen abortion, no cross sterility in the sexual spiklets and could produce seed autonomously. Frequency of autonomous seed setting is 13.3-32.7%. The trait of autonomous seed setting is controlled by two recessive genes. The frequency of apomixis is 25.5-52.2%, indicating facultative apomictic properties. No crossing sterility was observed in SSA-1. The

frequency of apomixis of SSA-1 was not dependent upon factors such as methods of pollination or types of pollinators. It is, therefore, a good line for apomixis studies and the fixation of heterozygosity.

Another sorghum apomictic line 296B was identified, and the embryological study on it is discussed in the article "The Morphological Characteristics of Apomictic Embryo in Sorghum".

References

S.B. Wu, X.M. Han, J.X. Wang, F.Y. Zhang, C.G. Meng, X.M. Yan, and T.T. Niu. 1993. Apomictic symptoms in the embryology in a sorghum line 296B. Acta Agriculturae Boreali-Sinica. 1993. 8 (Suppl.) : 10-15.

S.B. Wu, Y.J. Shang, X.M. Han, J.X. Wang, T.T. Niu, F.Y. Zhang, Y.M. Wei, C. G. Meng, X.M. Yan, and J.B. Zheng. 1994. Embryological study on apomixis in a sorghum line SSA-1. Acta Botanica Sinica. 36 (11) : 833-837.

F.Y. Zhang, C.G. Meng, X.M. Yan, J.B. Zheng, J.A. Ping, L.X. Wang, Y.M. Wei, T.T. Niu, and S.B. Wu. 1996. Studies on the apomixis property and genetic behavior of the sorghum line SSA- 1. Acta Agronomica Sinica (in press).

Screening New Sorghum Hybrids for Resistance to the Stemborer, *Chilo partellus*, and for Grain Yield

A.M. Nour and K.N. Saxena, International Centre of Insect Physiology and Ecology (ICIPE), P.O. Box 30, Mbita, Kenya

Ten sorghum hybrids were evaluated for resistance to the stem borer, *Chilo partellus* (Swinhoe) and grain yield during the short rainy season of 1990 and the long rainy season of 1991, at Mbita Point Field Station. Significant differences were detected among these hybrids for deadheart, stem tunnelling, larval and pupal population density, number of tillers per plant, plant height, and grain yield.

All hybrids showed resistance for at least one resistance parameter. However, three hybrids, namely ATx623 x IS-1044, 1441 A x Serena and 1441A x IS-1044, showed resistance against deadheart and stem tunnelling and were considered as resistant hybrids. These were identified as high-yielding sorghum hybrids with a good level of resistance.

The percent stem tunnelling and deadheart were negatively and significantly correlated with plant height. All hybrids gave grain yields significantly higher than either local check. The resistant check IS-1044, gave the lowest grain yield of 4.98 t/ha^{-1}.

Pearl Millet Improvement in Ghana: Past, Present and Future

S.K. Nutsugah, D. K. Atokpte and P.B. Tanzubil, Savanna Agricultural Research Institute (SARI), Council for Scientific and Industrial Research (CSIR), P.O. Box 52, Tamale, Ghana

Pearl millet (*Pennisetum glaucum*), is one of the most important staple cereal food crops in Northern Ghana. It is grown for grain on about 220,000 ha in the savanna agroecological zones, covering the Upper West, Upper East and Northern Regions. These regions cover 41% of the total land area of the country. Millet has hardly been exploited genetically for grain production despite its importance as a staple crop with high nutritional value and resistance to adverse conditions.

Research into the improvement of pearl millet is mandated to the Savanna Agricultural Research

Institute (SARI) at Nyankpala, near Tamale, in northern Ghana.

The general objective of the pearl millet improvement program is to develop high-yielding varieties with specific adaptation to different ecological zones of the savanna. Specifically, the research program seeks to identify and develop early, medium and late maturing varieties with high grain yield, good grain quality and resistance to downy mildew, smut, ergot, stemborers and head insects.

In order to achieve these stated objectives, several activities are undertaken in the form of projects. These include (A) Germplasm Enhancement: (i) Introduction, collection and conservation of pearl millet germplasm, (ii) Breeding for resistance to *Striga hermonthica,* (iii) Breeding for resistance to downy mildew (DM), smut and head insects, (iv) Breeding for food quality, (v) Variety testing, regional and international trials, (vi) Breeder seed production; (B) Pathology: (i) Screening for host plant resistance to DM, smut and ergot, (ii) Reselection of pearl millet varieties utilizing residual variability for DM reaction and (iii) Survey of disease/pest problems in the mandate area; and (C) Entomology: (i) Studies on distribution and damage potential of key insect pests, (ii) Bioecology of head insects and borers, and (iii) Development of IPM packages for the key insects, especially stemborers and head insects.

The millet improvement program commenced in 1980 in SARI (then Nyankpala Agricultural Experiment Station). However, due to high turnover of research staff, the millet improvement programs lagged behind in research implementation and output due to lack of program continuity. In spite of this constraint, the focus is on early millet which is very important for the subsistence farmers in the major millet growing areas of the Upper East Region. The late millet has not been given serious recognition in research work because it produces straw at the expense of grain. Furthermore, it serves as a reservoir for asexual spores of *Sclerospora graminicola* and diapausing larvae of the stemborer, *Coniesta ignefusalis,* in infected debris during the off season.

The millet pathology research program commenced in 1992 in collaboration with ICRISAT, Niger, under the West and Central Africa Millet Research Network (WCAMRN). The work involves screening of introductions and local genotypes for their resistance to DM, smut and ergot. The resistance-screening techniques used at ICRISAT in India and Niger have been modified to suit our working conditions. Some selections have been identified to possess multiple resistance to DM, smut and ergot during 1993-95 rainy seasons and have been incorporated into our breeding programs. These selections were MDN 88, Ex-Borno, Sosat C-88 and SE 360.

Entomology research has identified stemborers and head insects (*Caryna spp., Dysdercus volkeri* and *Heliocheilus albipunetella*) as key pests that deserve attention. Partial burning of stalks at harvest is recommended for stemborer control while hand picking and the use of botanical pesticides, especially those from Neem (*Azadiracta indica*) are promising against the head feeders.

The purpose of this poster is, therefore, to provide a background to the principal constraints to millet improvement in Ghana and give a synopsis of the results so far obtained. The future program will focus on a logical progression of systematic testing and selection process in improving the crop. The emphasis will be on population improvement, recurrent selection approach, development of sustainable plant protection, and production systems.

Inheritance and Physiology of Chilling Tolerance in Grain Sorghum

J. P. Ouma, C. E. Watson, L. M. Gourley, and J. O. Garner
Dept of Agronomy, Mississippi State University, Mississippi State, MS.

Four cold-tolerant sorghum inbreds collected from high altitude locations in Eastern Africa, three cold-susceptible brown mid-rib (BMR) lines, and their F_2 and F_3 progenies were grown on a high altitude site at Lanet, Kenya in 1994 and 1995. Cold tolerance was measured as the ability to set seed under low night temperatures. There were significant differences for percent seed set among inbreds, F_2's, and F_3's. Seed set of the F_2 generation was intermediate between the cold-tolerant and cold-

susceptible parents. Significant additive and dominance genetic variances were observed. Additive x additive epistasis was noted in some crosses. Dominance was toward the cold-tolerant parent. The estimated minimum number of genes segregating was 1 to 3. Cold-tolerance during flowering appeared to be determined by a few genes with additive and non-additive genetic effects. Broad-sense heritability was high, but narrow sense heritability was low to moderate. Thus improvement of cold tolerance at flowering will require breeding methods which minimize environmental variation.

In the greenhouse, visual symptoms of chilling stress were observed among genotypes during the vegetative stage. Observations were made on the second leaf from the top. Mean growth temperature in the greenhouse was 16.8 / 9.7°C (day/night) . Symptoms of chilling injury included slow growth, loss of chlorophyll, and wilting in the chill-susceptible genotypes. Tropical highland cultivars, S-92, N-17, and Nyundo, were chill-tolerant. Among the temperate genotypes, BMR989 was the more susceptible to cold damage than BMR986 and RTx430. When plants were transferred from 30°C to constant 10 or 24°C in the growth chamber, leaves of N-17 were observed to develop purple pigmentation under 24°C. At 10°C, loss of chlorophyll was observed in the newly developed leaves of all genotypes. This reaction was more pronounced in the cold-susceptible temperate genotypes.

For electrolyte leakage and differential thermal analysis, genotypes, BMR989, RTx430, LAN6 (F_2 progeny of S-92 x BMR989), and S-92, were used. For electrolyte leakage, three 1-cm diameter leaf disks were incubated at 6 , 15 or 30°C for a period of 30, 60, 120, or 180 min. Electrolyte conductivity of each tissue sample was measured. There was a significant temperature x stress duration interaction. Highest electrolyte conductivity occurred with 6°C and 180 min. Cultivar differences were insignificant, but a consistent trend was observed among genotypes. The LAN6 genotypes had lower electrolyte leakage than their parents. In order of increasing conductivity, genotypes were ranked LAN6 RTx430 S-92 BMR989.

Differential thermal analysis was carried out using leaf lamina and leaf cross sections. The final temperature was set at -20° C with a chilling rate of 1°C per hour. Low temperature exotherms generally occurred at -10.9°C. Tropical parent S-92 had a significantly higher freezing temperature than the temperate parent. The F_2 progeny had a temperature exotherm similar to the tropical parent. Ranking of genotypes by their low temperature exotherms was not in agreement with results of electrolyte leakage or visual observations.

The changes in fatty acid composition of leaf polar lipids of N-17,RTx430, and BMR989, were analyzed using gas chromatography. Plants at the 6-leaf stage were subjected to air temperatures of 24 or 10°C for 7 d in the growth chamber. Unsaturated fatty acid content of phosphatidyl ethanolamine was significantly higher than that of other lipid classes at 10°C. Palmitic acid (16:0) and stearic acid (18:0) contents did not differ among lipid classes. Unsaturated fatty acid content of total polar lipids was significantly higher at 10°C than at 24°C. Saturated fatty acid content of leaf extract differed with lipid classes but not temperature. Linolenic acid (18:3) content was significantly higher at 10°C than at 24°C, but did not differ among lipid classes. At 10°C, N-17 showed a slightly higher degree of unsaturation than RTx430 or BMR989.

Integrated Crop Management in Sorghum: Comprehensive Manual and Model

Bonnie B. Pendleton, Department of Entomology, Texas A&M University, College Station, TX 77843-2475; Richard A. Frederiksen, Department of Plant Pathology and Microbiology, Texas A&M University, College Station, TX 77843-2132; and George L. Teetes, Department of Entomology, Texas A&M University, College Station, TX 77843-2475

Escalating awareness of potential pesticide effects on the environment and human health, and the need for increased crop production efficiency, dictate a greater role for alternative management tactics for crop protection. Because non-chemical pest management tactics are preventative in nature, they must be a planned part of the total crop production system. Integrated pest management has not been implemented to the desired level in agriculture

because crop protection strategies have not been fully incorporated into crop production systems.

Sorghum grown on several million acres in Texas is vital to the economy of the state. Sorghum could be the most environmentally compatible and economically viable crop grown in Texas if growers adopted existing integrated crop management strategies for weeds, insects, plant pathogens, fertilization, irrigation, tillage, and crop rotations. However, to maximize implementation of an integrated pest management system for sorghum, growers must have immediate access to all information required to grow a crop that will provide the most optimum economic return.

More than 30 scientists from The Texas A&M University System developed an integrated production system for producing high and sustainable yields of sorghum while minimizing detrimental effects caused by pests and the overuse of pesticides. Agronomic components such as developmental time between plant growth stages, amount and timing of fertilizer applications, dates of planting, cultivar selection, crop rotation, and crop refuse destruction interact to affect disease, insect, and weed abundance and dynamics, and ultimately crop yield. Multiple management tactics for insect pests of sorghum include such practices as crop rotation, crop refuse destruction, use of insect-resistant varieties, elimination of weed hosts, conservation of natural enemies, escape from insect pests through the use of proper planting date and early maturing varieties, and use of insecticides when necessary. Similarly, weed management could be significantly improved by incorporating cultivation and rotation practices with herbicides. Finally, disease management should rely on cultural tactics such as plant resistance, crop rotation, crop-refuse and weed-host destruction, and application of fungicides should be based on need.

Information is being compiled into a comprehensive sorghum production and protection manual entitled "Integrated Crop Management in Sorghum." Chapters of the comprehensive sorghum crop management manual include crop production; plant health; weeds; diseases; insect and mite pests; vertebrate pests; abiotic constraints to production; storage of grain; pesticide laws, safety, application, and record-keeping; integration; computer simulation modeling; new technologies; environmental advantages; and economic factors affecting sorghum production.

Prospects of Inter-population Hybrids in Pearl Millet

K.N. Rai and A.S. Rao, ICRISAT Asia Center, Patancheru, Andhra Pradesh 502 324, India

Recent yield trials at Sador, and Bengou in Niger have shown inter-population hybrids of pearl millet [*Pennisetum glaucum* (L.) R. Br.] out yield their higher-yielding parental populations by 25-81%. Commercial prospects of such hybrids will depend on (1) their demonstrated yield advantage over popular open-pollinated varieties (OPVs) in on-farm trials, (2) the feasibility of developing male-sterile populations for use as seed parents, and (3) cost of seed production and farmers' acceptance of phenotypically variable hybrid cultivars. We evaluated the feasibility of developing a male-sterile population using the A_4 system of cytoplasmic-nuclear male sterility (CMS) and a dwarf Nigerian Composite (NCD2) as a test case. Two cycles of recurrent selection for male sterility of 81 A_4 hybrids at ICRISAT Asia Center was effective in developing a completely maintainer version of NCD2, as reflected in complete sterility of the topcross hybrid made from NCD2 C2 and 81A4. This progress occurred without any significant changes in grain yield and agronomic traits. Results from a sidecar method of conversion of NCD2 into a male-sterile population showed that 97% of the plants in BC_1 and all plants in BC_2 populations were male-sterile, indicating how rapidly NCD2, and perhaps any other population, can be converted into a male-sterile population using the A_4 CMS system. Seed production of inter-population hybrids can be expected to be quite economical, owing to higher seed yield of male-sterile populations as compared to male-sterile inbred lines (used in single-cross and topcross hybrids). Also, inter-population hybrids will be phenotypically no more

variable than OPVs, and are expected to be equally stable for grain yield and resistance to downy mildew [*Sclerospora graminicola* (Sacc.) Schroet.]. These features of inter-population hybrids, coupled with their grain yield advantage over OPVs, can make them more acceptable than OPVs to farmers in western Africa.

Development of Allotriploid Fodder Sorghum through Interspecific Hybridization and Somaclonal Variation

M. Raveendran, S.R. Sree Rangasamy and N. Senthil, 15 Shastri Street, P.N. Pdur, Coimbatore 641 041, Tamil Nadu, India

Wide hybridization plays a major role in the development of multicut fodder sorghum for the transfer of desirable characters like perenniality, disease and pest resistance, etc. The present study was undertaken with an aim to synthesize a perennial, vigorous sterile triploid sorghum with more biomass yield. To achieve this, F_1 hybrids were developed between a diploid fodder sorghum variety, Co 27, and the tetraploid wild species *S. halepense* and evaluated. Further, to get more variability for selecting better fodder types, F_2 (both open- and self-pollinated) populations and somaclones (through F_1 inflorescence culture) were evaluated.

The F_1 hybrids showed a pollen fertility of 26%. They were intermediate between the parents in biomass yield (27.4% relative heterosis). The F_1s showed superiority over Co 27 in their amenability to propagate vegetatively through stem cuttings (52%) and rooted slips (35%).

In the F_2, both open- and self-pollinated populations showed transgressive segregation for all the characters. Populations had high values for mean, variability and heritability and low genetic advance, for all the characters except biomass yield and HCN content. The F_2 ratoon crop showed an increase over the main crop for many characters. The sterile (pollen fertility <30%) F_2 plants were more vigorous than the fertile plants.

The study of somaclones (Scl generation) indicated the possibility of adding variability to the population through *in vitro* culture.

Hence there is a possibility of isolating the targeted sterile allotriploid high-yielding fodder sorghum types comparable to that of Cumbu-Napier hybrid (2n = 21).

Value Addition of Sorghum Through Genetic Improvement and Post-harvest Processing

S. Bala Ravi, P.K. Biswas and C.V. Ratnavathi, National Research Centre for Sorghum, Hyderabad 500030, INDIA.

Sorghum is grown in India during two crop seasons. Rainy season (kharif) sorghum occupies about 56% of the area and contributes about 68% of the production. The remaining area and production is accountable to the post-rainy season (rabi) crop. Post-rainy season sorghum is characterized by the wider use of traditional and low-yielding cultivars which have low harvest index, excellent grain quality and adaptation to receding soil moisture. Its grain is valued for food and stalk for fodder. High-yielding hybrids and varieties are widely used during the rainy season. This crop often suffers from grain mold and deterioration of grain quality which cause lower economic return to the producer despite high productivity. This together with lower preference of rainy season grain for food is causing a steady replacement of the crop with other competitive rainfed crops. Hence research as

value addition of rainy season sorghum through genetic improvement and post harvest processing was undertaken at The National Research Centre for Sorghum, Hyderabad with a goal to enhance profitability and demand. This paper reports on value addition of kharif grain through post-harvest processing and malting, its demand enhancement by use in industrial alcohol production and development of genotypes combining high grain, biomass production and stalk sugar content for enhanced profitability.

Diastatic ability of eighty six genotypes comprising elite breeding lines and germplasm accessions were assayed in accordance with the procedure of Ratnavathi and Bala Ravi (1991) and Novellie (1959). Thirteen of these genotypes were also evaluated for their hot water extract (HWE), content of protein and alpha-amino nitrogen (AAN) in the extract. Grain samples molded at different levels were studied for their hardness using a Kiyo hardness tester, loss during processing in a mini-dehuller and starch and protein content. Studies on sweet stalk sorghum involved evaluation of 90 hybrids derived from 6 lines x 15 testers for seven key characters following Kempthorne (1957). Derivatives of these breeding lines were selected for favourable agronomic attributes including biomass yield and brix and developed as male sterile and restorer lines.

Variability in diastatic activity ranged from 9 to 151 SDU and malting loss from 8.5 to 34%. IS 14384, a red grain African accession, and SPV 824, a white grain elite Indian breeding line, showed high SDU. Restriction of malting loss to around 15% or below was possible by reducing malting temperature and regulating grain moisture. Genotypes also showed variability in HWE yield, protein content and AAN content. HWE yield ranged from 5.34 to 9.93%, and AAN from 64 to 185 mg/100 g protein. Thus certain genotypes are more suitable for malting and others as brewing adjunct.

Studies on partitioning of dry matter (DM) and pattern of sugar accumulation in the stalk of the grain type and sweet-stalk sorghum revealed that high grain yield may not always preclude sugar accumulation in the stalk. Genetic capability for rapid DM accumulation, its appropriate partitioning and slow foliar senescence may encourage high grain and sugar yield simultaneously. Among the seven characters studied in the Linex Tester experiment, high heterosis was found for grain yield followed by biomass with little heterosis for stalk brix. Additive variance was highest for biomass. Crosses between grain types and sweet-stalk types provide excellent derivatives for developing A and R lines. Sweet stalk sorghum hybrids were capable of yielding 3-4 t/ha grain and 40-50 t/ha fresh stalk with brix 16 or above. Such hybrids may yield at least 50% additional return to the producer in comparison with high yielding grain sorghum.

Studies with grain affected by mold showed that the value of mildly affected samples could be increased by milling or scrubbing in water. Further, damaged grain is a competitive raw material for industrial alcohol production.

References

Kempthorne, O. 1957. An Introduction to Genetical Statistics, Wiley, New York.
Novellie, L. 1959. J. Sci. Food Agric. 10:441.
Ratnavathi, C. V.and Bala Ravi,S. 1991. J. Cereal Science 14:287.

Genetic and Molecular Characterization of Kafirins in Lysine-rich Cultivars of Sorghum

N.P. Eswara Reddy, M. Vauterin, Laboratorium voor Plantengenetica, Vrije Universiteit Brussel, B-1640, Sint-Genesius Rode, Belgium; G. Bauw, Laboratorium Genetika,Vakgroep Molekulaire Genetika, Universiteit Gent, K.L.Ledeganckstraat 35, B-9000 Gent, Belgium; and M. Jacobs, Laboratorium voor Plantengenetica, Vrije Universiteit Brussel, B-1640, Sint-Genesius Rode, Belgium

Kafirins from naturally occurring lysine-rich cultivars of sorghum selected for their resistance to (S)-2-aminoethyl-L-cysteine (Vernaillen et al., 1993) were analyzed at the genetic and molecular level and compared with the low-lysine cultivar, White Martin, and a chemically induced high-ly-

sine mutant, P 7210 (Mohan and Axtell, 1975). SDS-PAGE analysis of kafirins showed the absence of both 25.3 kD and 25.9 kD proteins in lysine-rich cultivars, IS 21702, G 1058 and CVS 365, and only presence of the 25.3 kD protein in G 205, compared with White Martin and P 7210. Previously we have reported that these missing bands belong to α-kafirin group (Reddy and Jacobs, 1995).

Genetic Analysis

The genetic variability of kafirins in low-lysine and lysine-rich cultivars of sorghum was investigated by isoelectric focusing (IEF) and reversed-phase high-performance liquid chromatography (RP-HPLC). Isoelectric focusing pattern of reduced-alkylated kafirins indicated significant differences showing a microheterogeneity of the kafirins among the cultivars. The variability of kafirins was further confirmed by densitometric analysis of the IEF scanned gels. This indicated that the kafirins consist of at least eight to ten polypeptides with different isoelectric points varying among the cultivars. The isoelectric point for the 25.3 kD and 25.9 kD proteins was determined as 6.8 and 7.0 respectively. The qualitative and quantitative differences could be determined mainly in the region of pH 7.0-8.0. The RP-HPLC offers an alternative method for separation and characterization of the kafirins since the characterization depends mainly on hydrophobicity rather than charge. Although, kafirins from the different cultivars display similar electrophoretic mobility on SDS-PAGE, the RP-HPLC yielded significantly different elution profiles indicating differences at the polypeptide composition and showing the genetic diversity among the cultivars. The partially purified 25.3 kD and 25.9 kD proteins from White Martin has given unique peaks when analyzed by RP-HPLC which were absent in the chromatograms of the other cultivars including P721o.

The lysine-rich cultivars G 1058 and G 205 were crossed with the low-lysine cultivar White Martin for breeding purposes and to assess the genetic basis for the 25.3 kD and 25.9 kD proteins. The SDS-PAGE of kafirins from F_1 hybrids shows a pattern representing both parental bands as expected. In F_2 progenies, the observed band pattern indicated that at least two genes were involved in the control of the 25.3 kD and 25.9 kD proteins. Since the kafirins are coded by a multigene family, we presume that these proteins are encoded by more than one gene which segregated independently.

Molecular Analysis

The analysis of changes in kafirins during seed development in White Martin showed the accumulation of these proteins steadily reaching a plateau 20 days after pollination, where as the synthesis of non-kafirin fractions continued till maturity. These results were further confirmed by northern blot analysis using a 955 bp of α-kafirin fragment as probe derived from the cDNA clone pSKR2 (De Rose et al., 1989).

About 200 bp of the gene coding for the 25.3 kD protein has been cloned and sequenced from White Martin by the PCR technique using degenerated primers derived from the protein sequence. Homology level was determined by comparison with already known genomic and cDNA clones coding for kafirins (De Rose et al., 1989)). The data base search showed about 80% homology with the genomic clones pGK1 and pGK4 and the cDNA clone pSK8. Ninety per cent homology was determined with the cDNA clone pSKR2. Based on sequence and restriction analyses, we presume that the gene encoding the 25.3 kD protein is different from previously characterized kafirin genes. Polymorphism was not detected among these cultivars when the 200 bp PCR cloned fragment was used as probe, which supports the existence of high genetic uniformity within *Sorghum bicolor* as already reported (Tao et al., 1993). We assume that the gene coding for the 25.3 kD protein is present in all cultivars but its expression may be down regulated in some of them. Currently experiments are in progress to clone the full coding sequence and promoter by IPCR using internal primers.

References

Vernaillen S., F. Laureys, and M. Jacobs. 1993. Plant Breeding. 111, 295-305.

Mohan, D.D. and J.D. Axtell. 1975. Proceeding of the 9th Biennial Grain Sorghum Research and Utilization Conference, Lubbock, Texas.

N.P.E.Reddy and M. Jacobs. 1995. Proceedings of the FAO/IAEA International Symposium on the Use of Induced Mutations and Molecular Techniques for Crop Improvement, Vienna, Austria, IAEA-SM-230/184P.

De Rose R.T., D.P. Ma, I.J. Kwon, S.E. Hasmain, R.C. Klassy and T.C. Hall. 1989. Plant Mol. Bio. 12: 245-256.

Tao Y., J.M. Manners, M.M. Ludlow and R.G. Henzell. 1993. Theor.Appl.Genet. 86: 679-688.

Protecting American Agriculture
Implications of a Sorghum Ergot in the Western Hemisphere

Scott C. Redlin and Jeffry N. L. Stibick

Sorghum is one of the world's major food crops. In 1991, a new ergot of sorghum was described which occurs in Africa, Asia and Australasia. It has now been found in Brazil and other parts of South America.

The U.S. sorghum seed industry is concerned that infested seed could be imported into the United States. Plant Protection and Quarantine is collaborating with EMBRAPA and Texas A&M University to determine the extent of the South American outbreaks and the biology of the ergot, its dissemination and control. Options are being considered to reduce the risk of the introduction of this fungus to the United States.

Generation Mean Analysis of Grain Mold Resistance in Sorghum

R. Rodriguez , W. L. Rooney, Dep. of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843; D. T. Rosenow, Texas A&M University, Agricultural Research and Extension Center, Rt. 3, Lubbock, TX 79401; R. A. Frederiksen. Dep. of Plant Pathology and Microbiology, Texas A&M University, College Station, TX 77843; A. J. Bockholt, Dep. of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843; and R. D. Waniska, Dep. of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843

Sorghum (*Sorghum bicolor* L.) grain mold is caused by a complex of fungi including *Fusarium moniliforme* and *Curvularia lunata*. It becomes an important disease when plant flowering and grain maturation coincides with rainy or humid conditions and warm temperatures. While genetic variation for grain mold resistance has been identified, effective transfer and utilization has been difficult. Therefore, more research into the genetic control of grain mold resistance is needed. This study was undertaken to evaluate the effect of genetic variances and heritability for grain mold resistance and determine the number of genes contributing to grain mold resistance.

One method to estimate relative importance of different genetic effects is generation means analysis. Generation Means Analysis (GMA) is an application of weighted least-squares analysis that estimates relative genetic effects from the means of different generations. This method is used by breeders and geneticists to assess additive, dominance, and epistatic variation in inheritance studies.

The inbred lines RTx430 and Sureño were used to study grain mold resistance. RTx430 is a line with excellent combining ability, and is used as a restorer line in the seed production of different hybrids. However, it is susceptible to grain mold. Sureño is a dual-purpose food grain and forage variety with moderate resistance to grain mold. In 1995, an experiment that included RTx430, Sureño, their F_1 , F_2 and 134 unselected $F_{2:3}$ families was planted at Beeville and College Station TX, with two replicates arranged in a randomized complete block design. The nurseries were not inoculated as significant levels of grain mold occur naturally at both locations. Days to 50 % flowering and grain mold were measured (1-5 rating) on a total-plot basis for $F_{2:3}$ families and on a single plant basis for parents, F_1 and F_2 generations. Combined analysis of variance was used for data from $F_{2:3}$ families and parents. GMA was completed using data from all generations. The number of genes contributing to grain mold resistance was calculated as follow (Das and Griffey, 1994):

$$\text{No. Of Genes Estimated} = \frac{(GR)^2}{5.33[\sigma^2_{F2:3}-(\sigma^2_{ps}/2 - \sigma^2_{pr})]}$$

Where GR is genotypic range, estimated as the difference between the mean response of two par-

ents :σ^2_{ps}, σ^2_{pr}, and $\sigma^2_{F2:3}$ are variances of susceptible (RTx430) and resistant (Sureño) parent and $F_{2:3}$ respectively.

Significant differences were found for locations, $F_{2:3}$ families and parents. In both locations the susceptible parent was severely affected by grain mold with a rating of 4.5. Transgressive segregation (both high and low) for grain mold resistance was detected in the $F_{2:3}$ families. At least three genes are estimated to contribute to grain mold resistance in the cross of RTx430 x Sureño. Broad-sense heritability on a single plot basis for the 134 $F_{2:3}$ families was high (0.79). However, GMA estimated that the order of genetic effects was as follows: dominance x dominance > additive x additive > dominance > additive. The order of genetic effects at Beeville was dominance x dominance > additive x additive > additive. Therefore, while broad-sense heritability was high, selection for grain mold resistance may be difficult because much of the genetic variability is due to dominant gene action.

References

Das, M. K. and C.A. Griffey. 1994. Heritability and Number of Genes Governing Adult-Plant Resistance to Powdery Mildew in Houser and Red Coat Winter Wheats. Phytopathology 84 (4): 406-409.

Sorghum Conversion Program

D.T. Rosenow, Texas Agricultural Experiment Station (TAES), Route 3, Box 219, Lubbock, TX 79401-9757; J.A. Dahlberg,USDA-ARS-TARS, Box 70, Mayaguez, PR 00681; L.E. Clark, Texas Agricultural Experiment Station, 11708 Hwy 70 South, Vernon, TX 76385; and G.C. Peterson, Texas Agricultural Experiment Station (TAES), Route 3, Box 219, Lubbock, TX 79401-9757

Sorghum [*Sorghum bicolor* (L.) Moench] is a native of tropical Africa. Most of the diversity in the species is found in indigenous sorghums in tropical Africa and Asia. Most of these sorghums are tall, photoperiod sensitive types which will not flower under the long summer day lengths in the U.S. and other temperate zones, making them very difficult to evaluate and use in these regions of the world. Access to and utilization of genetic diversity and access to new and improved sources of desirable traits is critical to sorghum improvement worldwide.

The Sorghum Conversion Program is a cooperative germplasm utilization project between the Texas Agricultural Experiment Station of The Texas A&M University System, and the United State Department of Agriculture of the Agriculture Research Service (USDA-ARS), Mayaguez, Puerto Rico. The objective is to transform tall, late-maturing exotic sorghums into shorter, non-photoperiod sensitive earlier types which can easily be utilized in the U.S. and other sorghum improvement programs. Maturity and height in sorghum are controlled largely by a few major genes. The Conversion Program utilizes backcrossing to transfer a few major desired height and maturity genes into converted genotypes.

Short winter days in Puerto Rico (where all sorghums flower early) are used for making crosses, backcrosses, and growing F_1's and the long summer days in Texas are used for growing F_2's and selection of short, early plants. A 4-dwarf B-line is used in the initial cross as the source of desired recessive height and maturity genes. The F_2 of approximately 1000 plants is planted at Chillicothe, Texas, where segregation for height and maturity occur. A single short, early plant is selected from each population, and the seed is returned to Puerto Rico for backcrossing to the original exotic using the F_3 as the female and growing the F_1 of that backcross, with the BCF_2 seed again sent to Texas, to repeat the cycle. At the third backcross, the exotic is used as the female in order to recover the cytoplasm of the exotic.

After four backcrosses, most converted versions are sufficiently similar to original exotics and are then released to all public and private researchers as converted lines with a "C" added to the original IS number to designate the converted line. A new

policy now also provides for the release and distribution of a BC_1 Bulk (from short, early plants selected at the BC_1 stage) from each exotic.

At present, 583 fully converted lines have been released along with 293 partially converted bulks. Currently, an additional 40 new converted lines and 50 BC_1 partially converted bulks have been submitted to USDA-ARS for final release approval. It is anticipated that 30 to 50 new fully converted lines and partially converted bulks will be released each year.

Converted lines are relatively pure for easy maintenance and preservation. At the time of release, seed is available from Texas A&M University. Seed of all converted lines is deposited at the NSSL at Ft. Collins, Colorado for long term permanent storage. Each converted line receives a new PI in the GRIN system and seed is maintained at the USDA Regional Plant Introduction Station at Griffin, Georgia.

Converted lines are of a height and maturity readily usable in the U.S. and other temperate zones as well as in tropical, short-day conditions. They can be easily evaluated under field or other conditions for various traits. The converted lines have been very useful in broadening genetic diversity and providing sources of desirable traits used extensively in both public and private sorghum improvement programs. Especially important have been sources of disease resistance (head smut, downy mildew, anthracnose, grain mold/weathering, charcoal rot), insect resistance (midge, aphids, chinch bug), lodging resistance, drought resistance (both pre- and post-flowering), improved grain and food quality traits, high yield, and wide adaptation.

The original exotic lines entered into the Conversion Program were selected as elite and/or diversity by the late I.E. Stokes (SC1-92) or J.C. Stephens (SC93-228) former sorghum researchers at Meridian, MS and Chillicothe, TX, respectively, and by Dr. L.R. House (SC229-240). The Modified Nursery, as selected by K.O. Rachie et al., from the World Sorghum Collection in 1963-64, was the next large group of exotics entered (SC 241 to SC 950). The Modified Nursery included representatives of each classification group as described by Murty and Govil, lines representing major variation in each group, and other variations of possible breeding value, as selected from the World Sorghum Collection as it existed when assembled in the mid-1960's in India. The SC numbers from SC951 upward have been entered only for specific reasons such as new diversity of type, diversity of (or new) location of collection, specific known or suspected traits, or specific recommendations of sorghum researchers. New candidates for conversion are solicited and welcomed from sorghum researchers worldwide.

Conclusion

Conversion of selected elite and unique tropical sorghums in the cooperative Texas A&M/USDA-ARS Sorghum Conversion Program provides new exotic germplasm in a readily usable form for efficient evaluation and utilization. This program has been successful in enhancing the use of exotic sorghum germplasm, broadening the genetic diversity, and providing new sources of desirable traits to the sorghum industry. Converted lines have provided many of the best sources of desirable traits available to sorghum researchers.

The backcross procedure has worked well. Major height and maturity genes segregate well and independently. Four backcrosses have generally been sufficient to recover the important traits of the exotic line in a shorter and earlier converted form. Biotechnology applications using molecular markers for maturity and height genes are being initiated to improve conversion efficiency.

Performance of New Cytoplasmic Male Sterile Sorghum Lines Developed for Tolerance to Toxic Levels of Aluminum in Acid Soils.

R.E. Schaffert, V.M.C. Alves, A.F.C. Bahia F°, and G.V.E. Pitta, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil; F.G. Santos and C.A. de Oliveira, Fellowship/ CNPq/CNPMS

The fertility non-restoring line from the Texas A&M/USDA Sorghum Conversion Program, IS 7173C (SC 283-14E), a genetic source for tolerance to Al toxicity in acid soils, was used to incorporate this trait into various sources of non-restoring lines with the objective of developing commercial male-sterile lines tolerant to Al toxicity. The susceptible male-sterile B-lines, BR 007, Redlan, Wheatland, Dwarf Redlan, and SC 566 were crossed with SC 283-14E. Several hundred head to row F_4 families visually selected for desirable agronomic traits were selected for Al tolerance under acid soil conditions (45% Al saturation) at the National Maize and Sorghum Research Center (CNPMS) of the Brazilian Agriculture Research Corporation (EMBRAPA). Progenies were selected for root development based on their reaction to moisture stress during prolonged periods without rain. Turgid plants were assumed to have a better developed root system than moisture stressed plants and were classified as having Al tolerance. Selected F_7 progenies were backcrossed to a source of cytoplasmic male sterility to develop respective A lines for each selected B-line progeny. The B-lines of 55 selected A/B-line pairs were evaluated for tolerance to Al toxicity using relative seminal root growth (RSRG) of seedlings in nutrient solution with 4ppm of Al for seven days as the indicator. The average RSRG of the tolerant (SC283-14E) and susceptible (BR 007B) checks were 50.6% and 6.6% respectively. The RSRG of the 55 selected progenies from 16 family groups ranged from 2.8% to 75.5%. Twelve progenies from four family groups were susceptible and 43 progenies from 14 family groups were tolerant. Tolerant progenies selected from families derived from Redlan and Dwarf Redlan crosses had slightly lower RSRG than tolerant progenies from families derived from BR 007 and Wheatland. Head to row progenies from three groups segregated for tolerance and susceptible reaction, confirming three near-isogenic (96.9%) pairs for this trait. The relatively high frequency of segregation after the S5 generation suggests that one or a few major genes control this characteristic. The average grain production of 172 test cross hybrids involving four male testers and the 43 tolerant female lines was 5.7 t ha^{-1} compared to 4.59 t ha^{-1} for the 48 test cross hybrids involving the 12 susceptible females and four testers in a fertile soil observation trial at CNPMS.

Performance of Near-Isogenic Sorghum Lines and Hybrids for Tolerance to Toxic Levels of Exchangeable Aluminum

R.E. Schaffert, V.M.C. Alves, G.V.E. Pitta, A.F.C. Bahia F°, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil, and C.A. de Oliveira, Fellowship CNPq/CNPMS

Near isogenic sorghum lines developed at the National Maize and Sorgum Research Center (CNPMS) of the Brazilian Agriculture Research Corporation (EMBRAPA) for tolerance to Al toxicity in acid soils and their hybrids were evaluated for tolerance to Al toxicity. Three near-isogenic pairs of sorghum lines with cytoplasmic male sterility, four restorer lines (three susceptible (S) and one tolerant (T) to Al toxicity), and their respective (TxT), (TxS), (SxT), and (SxS) hybrids, were evaluated for tolerance to Al toxicity using relative seminal root growth (RSRG) of seedlings in nutrient solution with 4ppm of Al for seven days as the indicator. The average RSRG of seedlings of the tolerant line of the three near-isogenic pairs was 5.8 times greater than the susceptible line. The average RSRG values for the four tolerant and six susceptible lines were 51.7% and 7.8% respectively. Average RSRG values for the (TxT), (TxS), (SxT), and (SxS) hybrids were 59.7%, 47.8%, 48.3% and 11.2% respectively. The (TxS) and (SxT) hybrids had RSRG equivalent to the tolerant parent demonstrating a complete dominant mode of inheritance. A dominant mode of inheritance for tolerance to Al toxicity in sorghum has also been observed under field conditions at CNPMS.

Induction of Root Proteins in Near Isogenic Sorghum Lines Tolerant and Susceptible To Toxic Levels of Exchangeable Aluminum

R.E. Schaffert, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil; M.A. Lopes, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil; F.T. Carvalho, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil, and Fellowship/ CNPq/CNPMS; R.S. Portugal, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil, and Fellowship/ CNPq/CNPMS; G.M. Cançado, EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil, and Fellowship/ CNPq/CNPMS; M.J. Vascocelos, and E. Paiva EMBRAPA/CNPMS, CP 151, 35701-970 Sete Lagoas, MG, Brazil

The soils of the acid savannas or "Cerrado" of Brazil are commonly characterized by low pH, low phosphorus availability, high P fixation, low fertility, and toxic aluminum. Plant cultivars with tolerance to Al toxicity are essential for sustainable production in these acid savannas. The development of improved cultivars for these conditions is dependent on adaptive mechanisms genetically transmitted. These adaptive mechanisms are related to factors that impede the entrance of toxic Al into the root cells and the interaction of Al with polypeptide root exudates. The objective of this research was to identify proteins in the root tips induced as a result of Al stress. Seeds of a near-isogenic pair of sorghum lines were germinated for three days in water and placed in a nutrient solution with zero and 60 μM Al for 96 hours. Root tips (1.5 mm) were excised, ground with 6.8 pH buffer extraction solution in a 1:1 proportion and centrifuged at 120,000g. The pellet was resuspended in sample buffer. The material was run on an SDS-PAGE gel electrophoresis. The results indicate formation of a protein band at approximately 95 KD in the root tips with Al stress. The band was not observed in the root tips without Al stress. These results indicated that proteins are induced in the microsomal membrane fraction of the root tip under Al stress. Preliminary results indicated that the Al-tolerant line produced a larger quantity of this protein and may be a factor contributing to Al tolerance.

Regeneration of Plants from and Transient Gene Expression in Mesophyll Protoplasts of Sorghum

N. Seetharama and R.V. Sairam
ICRISAT Asia Center, Patancheru, A.P. 502324, India

The development of efficient and reproducible techniques for regeneration of fertile plants from protoplasts opens up opportunities for genetic transformation by direct DNA uptake. It also facilitates the production of somatic hybrids between sexually incompatible species. Xu and Wei (1993) reported success in regenerating plants from protoplasts isolated from the inflorescence-derived calli of two sorghum cultivars. However, the leaf is the most suitable source of plant protoplasts because it allows isolation of a large number of relatively uniform protoplasts without destroying the plant.

We have developed a protocol for regeneration of plants from mesophyll protoplasts of sorghum seed parent 296B. The sixth leaf (with ligule fully emerged) from 18-day old plants (grown in dark for 2 days before harvesting) proved to be the most suitable source of viable protoplasts. The protoplasts regenerated a cell wall within 24 hours of embedding in KM8 agarose medium. The first division was observed after 6 days after plating, and the second after 10 days. Microcolonies were visible after 15-20 days, which resulted in microcalli after 25-30 days. Plants were obtained after 4-5 weeks of culture of the microcalli on MS medium supplemented with 0.2 mg l^{-1} kinetin and 2 mg l^{-1}

BAP. The frequency of regeneration of microcalli was 12.8%. Regenerated plants were transferred to a glasshouse where they grew normally and set seed. Plants grown in the field from these seeds also showed normal growth.

We studied direct DNA uptake by the protoplasts using two methods: (i) adding equal volume of polyethylene glycol (M. wt. 4000, initial concentration 40%) to the fresh protoplast suspension, and (ii) electroporation using the equipment and protocol of the manufacturer (BTx Inc., CA 92121, USA: *Electro cell manipulator*$^{(R)}$ 600). Plasmid pJS108 from Drs. Jin Su and Ray Wu, Cornell University, containing *gus* and *bar* genes was used as the source of foreign DNA. The putative transformants were monitored periodically for *gus* activity. Intense blue staining was observed after 24 hours, especially with the electroporated protoplasts. The dividing cells and microcalli also exhibited *gus* activity. We are now attempting the regeneration of plants after transformation.

Reference

Xu Z and Wei Z. 1993. Regeneration of plants from protoplasts of *Sorghum vulgare*. *In:* You C and Chen Z (eds) Biotechnology in Agriculture, pp. 403-406. Kluwer Academic Publishers, Dordrecht.

Haploidy in Pearl Millet: Where Are We?

N. Seetharama, T. Shyamala and T.H. Rao
ICRISAT Asia Center, Patancheru, 502 324, A. P., India

Production of haploids through anther or microspore cultures is an intermediary biotechnological tool for breeders, geneticists, and map makers. This technique is a useful tool for rapid development of inbreds, and isolation of mutants and protoplasts for somatic hybridization or genetic transformation. We are working on the development of suitable techniques for the production of haploids in pearl millet using a variety of explants and culture media.

Spikelet cultures: The developing spikelets (with microspores at uninucleate stage) were cultured in solid, activated charcoal containing YP medium under red light. Within 10 days, anthers emerged from some of the spikelets. About 15% of such anthers contained dividing microspores. They were used for anther culture (below), and the spikelet cultures continued for up to 3 months in the same petriplates. The ovaries of some (up to 50% in some pertriplates) enlarged, and single plants arose from them. Such seedlings were transferred to MS medium. In a few plantlets, the root tip squashes showed only 7 chromosomes (haploid number). We grew some of these to maturity in the glasshouse. Seeds from glasshouse-grown plants were sown in the field.. Tissue samples (young leaves from 5 plants bulked) from each row were subjected to isozyme and RAPD analyses. There were minor differences between samples. RFLP analysis with multi-locus probes are underway. Anatomical studies showed meristamatic activity at the chalazal end of the embryo sac. Further studies are required to confirm haploid origin of plants from spikelet cultures.

Anther culture: Anthers emerging from spikelet cultures (above) were plated on solid YP medium. Profuse proembryoid-like structures were obtained from each anther, which continued growth in MS medium, but failed to differentiate further.

Microspore culture: Anthers showing androgeneic response (above) were ground or crushed to release developing microspores. About 3 ml of responding microspores (1.7×10^5 microspores L^{-1}) were mixed with a callus-induction (CI) medium containing 2 mg L^{-1} 2-4,D and 0.6% low-melting point agarose, and poured into petriplates. The microspores embedded in agarose medium continued to grow and form callus masses of varying sizes (microcalli). About 0.008% of the plated microspores responded. We are yet to succeed in regenerating whole plants from such cultures, but have observed satisfactory growth and establishment of polarity in microcalli.

Conclusions: Isolated microspore cultures offer a more reliable system for haploid production than spikelet or anther cultures. It eliminates the possibility of selecting plants regenerating from the diploid cells of anther or ovary wall. Therefore, we will initially culture spikelets and collect the emerging anthers with dividing microspores. Next, we will isolate and culture such developing microspores under a variety of culture conditions in several media to optimize conditions capable of inducing faster differentiation of calli into plantlets.

In Vitro Bioactivity of Antifungal Proteins Purified from Sorghum Caryopses Against Grain Molding Fungi

K. Seetharaman, E. Whitehead, R. D. Waniska and L.W. Rooney,
Cereal Quality Lab, Texas A&M University, College Station, TX 77843-2474

The role of sorghum antifungal proteins (AFPs) in inhibiting sorghum grain molding was investigated. Several AFPs, such as sormatin, chitinases, glucanases and ribosome inhibiting proteins (RIP), have been identified in sorghums .

AFPs from sorghum seeds were extracted, purified using 55% ammonium sulfate precipitation and eluted from a CM-Sephadex column using a 10-500mM salt gradient and four fractions collected. One fraction (Fraction G4) contained sormatin, chitinase, glucananse and ribosome-inactivating protein (RIP). Individual proteins were eluted and antibodies raised against these proteins in rabbits.

The fractions were also tested for bioactivity against *Fusarium moniliforme*, *Curvularia lunata*, *Aspergillus flavus* and *Aspergillus parasiticus*, using hyphal rupture, hyphal extension and spore germination methods.

A fraction containing several AFPs was inhibitory against *F. moniliforme* and *C. lunata*. *F. moniliforme* exhibited hyphal rupture at the growing tip and other regions of mycelium at protein levels as low as 20:g. *C. lunata* required higher protein levels (20-100:g) and ruptured only at hyphal tips. Spore germination was completely inhibited by <100:g protein in both species. Spore germination was not inhibited when the protein fraction was boiled, suggesting the involvement of proteins.

The AFP fraction completely inhibited spore germination in both *Aspergillus* species tested. However, spore germination *A. parasiticus* was also inhibited when the boiled fraction was tested. Both *Aspergillus* species did not exhibit hyphal disruption when treated with AFPs.

Inhibitory effects of a mixture of AFPs, as opposed to individual AFPs, is promising as a means to increase the overall resistance of a plant against several pathogens.

Utilization of Non-Milo Source of Cytoplasms by Restorer Identification and Substitution of Cytoplasm in Desirable Nuclear Background

N. Senthil and A.K. Fazlullah Khan, School of Genetics,
Tamilnadu Agricultural University, Coimbatore 641 003, India

The majority of commercial hybrids of sorghum are milo cytoplasm based. Alternate cytoplasm based hybrids are needed to avoid disease and environmental hazards and to add nuclear diversity. Studies on the identification of restorers in non-milo cytoplasm are very limited. Hence, the present

study was aimed at identifying suitable restorers for non-milo cytoplasm and to develop alloplasmic male sterile lines in a well adapted nuclear base by substitution of cytoplasm. One hundred and forty-four F_1s developed by crossing 12 diverse, non-milo male-sterile lines and 12 diverse testers were screened for fertility restoration during kharif 1994. Out of 144 F_1s, 22 crosses were identified as fertile showing possibilities for commercial exploitation. From the remaining F_1s that showed 100% sterility, 52 were backcrossed with their respective male parents in order to substitute its cytoplasm. The above 52 BC_1F_1 materials were raised during the 1995 summer along with recurrent parents and a second backcross was affected by the paired cross method. The BC_2F_1 raised during the summer of 1996 was backcrossed again. The substitution work will be continued further up to the BC_6 in order to substitute the cytoplasm in the desirable recurrent parent nuclear background for further utilization.

Mapping in an Australian Sorghum Recombinant Inbred Line Population.

Yuezhi Tao, CSIRO Division of Tropical Crops and Pastures, 306 Carmody Rd, St Lucia Q 4067; David Jordan, CSIRO Division of Tropical Crops and Pastures, 306 Carmody Rd, St Lucia Q 4067 and Department of Agriculture, University of Queensland, St Lucia Q 4067; Robert Henzell, QDPI Hermitage Research Station, Warwick Q 4370; and Lynne McIntyre, CSIRO Division of Tropical Crops and Pastures, 306 Carmody Rd, St Lucia Q 4067

A genetic map between 2 elite sorghum lines, QL39 and QL41, has been developed using 160 Recombinant Inbred Lines (RILs). Both elite lines were developed by the Queensland Department of Primary Industries and have been used widely in Australian sorghum breeding programs. Four hundred probes, including sorghum genomic, maize cDNA and genomic and sugarcane cDNA and genomic clones were screened. Ninety-four loci have been mapped onto 10 linkage groups, covering approximately 980cM. The cross is segregating for many morphological traits and traits of agronomic interest, such as height, maturity, awns, seedling color, head shape, organophosphate reaction, rust, and bacterial leaf blight. Associations between markers and all traits have been found and are reported here.

Map and Pedigree Based Approaches to Developing Molecular Markers for Midge Resistance and Stay Green in Sorghum.

Yuezhi Tao, CSIRO Division of Tropical Crops and Pastures, 306 Carmody Rd,St Lucia Q 4067; David Jordan, CSIRO Division of Tropical Crops and Pastures, 306 Carmody Rd, St Lucia Q 4067 and Department of Agriculture, University of Queensland, St Lucia Q 4067; Robert Henzell, QDPI Hermitage Research Station, Warwick Q 4370; Ian Godwin, Department of Agriculture, University of Queensland, St Lucia Q 4067, and Lynne McIntyre, CSIRO Division of Tropical Crops and Pastures, 306 Carmody Rd, St Lucia Q 4067

A genetic map between 2 elite sorghum lines, QL39 and QL41, has been developed using 160 Recombinant Inbred Lines. QL39 is a senescent, midge-resistant line, while QL41 is a non-senescent line with a low level of midge resistance. Ninety-four loci have been mapped onto 10 linkage groups and associations between markers and both these traits have been found. Data from pedigree analysis has enabled one region for each trait to be traced to the original source of the trait, providing supporting evidence for the location of a QTL at this location.

Sorghum Midge-Resistant Hybrids for the 21st Century

George L. Teetes, Department of Entomology, Texas A&M University, College Station, TX 77843-2475; Gary C. Peterson, Texas A&M University Agricultural Research and Extension Center, Route 3, Box 219, Lubbock, TX 79401-9757 Roger Anderson, Department of Entomology, Texas A&M University, College Station, TX 77843-2475; Kenneth Schaefer, Texas A&M University Agricultural Research and Extension Center, Highway 44 West, Route 2, Box 589, Corpus Christi, TX 78406-9704; and Jerry W. Jones, Texas A&M University Agricultural Research and Extension Center, Route 3, Box 219, Lubbock, TX 79401-9757

Sorghum, *Sorghum bicolor* (L.) Moench, hybrids were evaluated for resistance to sorghum midge, *Stenodiplosis sorghicola* (Coquillett), at Corpus Christi, Texas, with high sorghum midge abundance, and at College Station, Texas, with moderate sorghum midge abundance. Sorghum at Corpus Christi and College Station was planted on 7 and 29 April 1995 in rows spaced 96.5 and 76.2 cm apart, respectively. Evaluated in a three-replication randomized complete block design were 17 F_1 hybrids with experimental A lines crossed to released R lines, and three resistant, two resistant x susceptible, and four susceptible standard checks. A scale of 1 = 0-10, 2 = 11-20, to 9 = 81-100% kernels failing to develop was used to rate sorghum at physiological maturity for damage caused by sorghum midge. Grain yield ($kgha^{-1}$) was assessed.

Damage ratings were higher at Corpus Christi (mean damage rating 4.5), indicating more damage by sorghum midge than at College Station (mean damage rating 2.3). Relative differences between hybrids were similar between locations. Superior experimental resistant hybrids sustained much less damage than did susceptible or resistant checks. Hybrids with superior resistance (damage rating less than 3.0) at Corpus Christi were less damaged at College Station. At both locations, hybrids reached 50% flowering within an eight-day period, and susceptible hybrids sustained more damage for a specific day of flowering than did resistant hybrids.

Mean grain yield at Corpus Christi and College Station ranged from 360 to 4,527 and 1,740 to 5,488 kg ha^{-1}, respectively. Experimental hybrids yielded 3,767 and 4,910 kg ha^{-1}, standard resistant checks yielded 3,674 and 4,219 kg ha^{-1}, resistant x susceptible checks yielded 2,913 and 5,201 kg ha^{-1}, whereas susceptible checks yielded 1,176 and 2,990 kg ha^{-1} at Corpus Christi and College Station, respectively. Resistant hybrids had lower damage ratings and usually produced more grain. Damage was of sufficient magnitude to identify sorghums with superior grain yield potential and resistance. Experimental hybrids produced significantly more grain than did susceptible hybrid checks. Although most differences between experimental resistant hybrids and standard resistant or resistant x susceptible checks were not significant, experimental sorghums produced more grain. Experimental sorghums with female parents A91-6, A92-3, and A93-6 produced superior hybrids during at least two previous years and will be released to the commercial seed industry. Hybrids with female parents designated A94 were evaluated for the first time and will be evaluated further to determine suitability for commercial production.

The Potential of Local Cultivars in Sorghum Improvement in Mali

A. Toure, IER, CRRA-Sotuba, BP 438, Bamako, Mali, West Africa; K. Traore, IER, CRRA-Cinzana, BP 214, Segou, Mali, West Africa; J.F. Scheuring, Novartis Seeds AG, R-1008.8.06, CH-4002, Basel, Switzerland; D.T. Rosenow, Texas A&M University, Agricultural Research and Extension Center, Route 3, Lubbock, TX 79401-9757; and L.W. Rooney, Texas A&M University, Department of Soil and Crop Science, College Station, TX 77843-2474

Over 1300 accessions of sorghum were collected in the different regions of Mali during several germplasm collections from 1979 to 1990. Each germplasm collection was evaluated to exploit the breeding potential inherent in local germplasm which for the most part has remained under utilized by breeders. Each of the germplasm collections was evaluated systematically at the

main sorghum stations (Sotuba 12°39'N, Cinzana 13°17'N, Samé 14°26'N, Longorola 12°21'N, Béma, 15°02'N, and Baramandougou 13°35'N). Each entry was planted at 3 planting dates at each location with 15 days between planting dates. Cultivars were evaluated for photoperiod sensitivity, maturity, genetic traits, yield, agronomic desirability, and grain for food desirability.

Three major races exist in the country: guinea, durra and caudatum. The guinea race represents about 70% of the germplasm in the country and is divided into two important groups: Kéninké (54%) and Kendé (16%). They are the most diversified race in Mali. The durra sorghums are the second most important race and represent 17% of Malian germplasm. The evaluation of the germplasm provides information on the identity of each cultivar and prediction of the different phenotypes of progenies in crosses. Different sources of resistance to various abiotic and biotic constraints have been identified. Screening in charcoal pits during the hot off-season at Cinzana indicated that local cultivars showed more resistance to drought and heat at the seedling stage (CSM 205). Many cultivars (Séguétana) showed good tolerance to *Striga hermonthica* during evaluation in large field nurseries at several locations. Malisor 84-7, an improved cultivar, has been identified to posses excellent tolerance to head bugs (*Eurystylus maginatus*) which can be genetically transferred to its progeny. The local guinea sorghums have shown quite good resistance to the panicle feeding bug/grain mold complex. Inheritance of head bug resistance is quantitative and primarily recessive.

A significant amount of information about key characteristics of the local cultivars has been accumulated that goes into successful agronomic and organoleptic Malian adaptation. For leaf disease in the guinea sorghums, lower leaves are readily attacked by an array of leaf diseases, but the top leaves, especially the top three, are practically free of all leaf disease symptoms. Most of the traditionally grown cultivars are sensitive to photoperiod. These sorghums have been selected to flower at the end of the wet season, so that the grains ripen under dry conditions. With photoperiod-sensitive sorghums, seed number tends to decrease with planting date. This decrease causes a 34 to 58% reduction in seeds per panicle for 15 to 30 days delay of planting. Poor grain quality has been a major problem in development of new products with value added. A series of decortication trials was performed to test the effect of kernel texture and shape on recovery rates. Local guineas recovery rates were consistently around 70%, while experimentals varied from 35% to 68%. The local guinea sorghums showed a kernel weight typically between 20 and 24g/1000 kernels. Many improved and exotic cultivars showed kernel size levels that are below 20g/1000 kernels, which is the lower end of most local guineense cultivars.

White-seeded, tan-plant guinea-type breeding lines have been developed from the direct cross of guinea with Zerazera, Malisor 84-7 and Sureño. Progenies showed a large seed number without having to use a compact, bug-filled panicle. They also showed long glumes and vitreous grain. N'ténimissa (Bimbiri soumalé* Zerazera), a new tan plant and straw glume color breeding progeny, possesses excellent guinea traits and yield potential. New tan-plant, guinea-type breeding materials offer an opportunity to develop new food products, and industrial products, which could enhance demand and stabilize prices. These value-added sorghum cultivars will be the basis for identity preserved production for use in processing into higher value products. In this manner, many of the genes of the elite variety are kept while some qualities of the locally adaptation cultivar are retained. These results indicate that great potential exists for improving yields and other consumer preferred traits through utilization of local cultivars in breeding programs. These findings suggest it would be useful to pursue a full exploitation of the local landraces for sustainable cultivar development for the country.

Sorghum Breeding in Zambia, its Impact and Future Needs

B.N. Verma and M. Chisi, Zamseed, P.O. Box 35441, Lusaka, Zambia

Past social and political developments when coupled with the neglect of crop improvement programs marginalized the importance of sorghum, a traditional food crop of Zambia. Over time, maize replaced sorghum in developed parts of the country, including areas that were not suitable for its

cultivation. However, changing rainfall patterns has made production of maize highly unreliable, causing critical food shortages and a heavy import burden on the already strained economy of the country. Recognizing the problem of over-dependence on a single crop, the Government of Zambia initiated a series of measures to diversify its agriculture. This included a crop improvement program to improve traditional drought-resistant food crops like sorghum and millets for small-scale farmers. The Swedish International Development Authority (SIDA) joined in the Government's initiative by providing technical and financial support for seed research.

Taking advantage of improved germplasm from all over the world, the program has developed a series of widely adapted, early maturing high yielding varieties and hybrids for different purposes over a relatively short period of time. Initially, research teams faced a great deal of resistance and criticism against improved cultivars from various organizations responsible for the transfer of technology to farmers. This resistance was mainly caused by a widely-held perception in different sections of the agricultural sector that sorghum farmers, being resource-poor and small scale, have no capacity to invest in seed and the accompanying management that is necessary for realizing high yields of improved cultivars. In order to overcome this hurdle, research teams began a vigorous variety-promotion campaign by directly working with the farmers on a pilot basis in one district. The campaign was extremely rewarding. It attracted attention of many developmental agencies who quickly picked up the initiative from the team. The improved cultivars have now started moving in, not only in the country but also across countries in the region. With the increasing demand of seed from farmers, the entire seed industry is getting sensitized and, at present sorghum is recognized to be the most viable alternatives in the crop diversification program not only of Zambia but the entire SADC region. If different policy matters relating to crop utilization, seed, and grain marketing are handled carefully by the policy makers, sorghum has a great future in the region.

Physiology of Stay Green Trait in Sorghum

D.M. Vietor, C.M. Sowder, Lee Tarpley, Dale Pawlak, W.L. Rooney, and F.R. Miller, Department of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843

Rationale. Phenotypic and yield differences among cultivars differing in preflowering and postflowering-tolerance to water stress have been identified in *Sorghum bicolor* L. (Moench). Variation in components of carbon and water exchange are associated with these cultivar differences in stress response. Leaf CO_2 exchange rates of postflowering-tolerant lines can be more stable than preflowering-tolerant lines as water stress develops (Peng et al., 1991). The CO_2 exchange rates of hybrids that were comprised of the postflowering-tolerant female B35 ranged up to 50% less than hybrids comprised of the preflowering-tolerant female RTx430 at relatively large stomatal conductance, but rates were comparable among hybrids at low stomatal conductance (Kidambi et al., 1990). Yet, consistent differences in osmotic adjustment capability and in relationships between leaf pressure potential and leaf water potential have not been observed between cultivars differing in preflowering and postflowering tolerance to water stress (Ackerson et al., 1980). Reductions in rates of ^{14}C-assimilate export from leaves have been reported for hybrids of preflowering- and postflowering-tolerant lines under increasing water stress (Sung and Krieg, 1979). Photoassimilate retention in leaves could maintain positive turgor in sorghum, but osmotic adjustment has been shown to increase to a maximum after stomatal conductance and CO_2 exchange rate have begun declining under diurnal increases in water stress. Observations that leaf ^{14}C-assimilate export is less sensitive to declining leaf water potential than CO_2 exchange rate (Sung and Krieg, 1979) indicate leaf photoassimilate would be depleted rather than accumulated after CO_2 exchange rate begins declining under water stress (Girma and Krieg, 1992a). Reports of osmotic adjustment while CO_2 exchange rate de-

clined suggest that solute accumulation in sorghum leaves was due, in part, to reductions in assimilate unloading in vegetative and storage organs rather than the direct effect of increasing water stress on leaf photoassimilation and export during a diurnal cycle (Girma and Krieg, 1992b). This relationship between osmotic adjustment and assimilate partitioning to grain is consistent with observations that high grain yields under well-watered conditions have been associated with susceptibility to postflowering water stress among sorghum cultivars (Rosenow and Clark, 1981).

The objective of this research was to compare CO_2 exchange rate, carbohydrate concentrations, sucrose synthesis rate, and ^{14}C-assimilate partitioning in radiolabeled leaves among preflowering- and postflowering-tolerant sorghum lines and the F_1 hybrid thereof.

Methods. The physiological indicators of carbon exchange and partitioning were monitored for the penultimate leaf of well-watered and water-stressed plants under field conditions. Well-watered plants were grown in plots in a silty-clay-loam soil and water-stressed plants were grown in pots of fritted clay that were inserted into the soil within rows of well-watered plots. The sorghum lines B35 and RTx430 and the F_1 hybrid thereof were main plots and were split between two growing seasons in a split-plot design. Leaves of single plants within each of four replications were exposed to $^{14}CO_2$ and monitored for 3 h under steady-state conditions during preboot, anthesis, and grain-filling. Average xylem pressure potentials in stressed plants were 1134 kPa, 1247 kPa, and 1426 kPa at the respective stages. Sucrose, glucose, fructose, and starch were extracted from subsamples of leaf blades during both years (Hendrix, 1993) and from upper stems in 1993. Aliquots of extracts were assayed using enzyme-linked colorimetric assays (Tarpley et al., 1993). The ^{14}C-assimilate in labeled leaves was extracted and separated into sucrose, hexose, and starch components and counted using liquid scintillation spectroscopy (Tarpley et al., 1993). Radioactivity in blade sucrose, CO_2 assimilation, and the specific radioactivity of $^{14}CO_2$ were used to compute sucrose synthesis rates during the 3-h labeling period.

Results. Although stem dry weights of B35 were comparable to or greater than RTx430 at all three growth stages under well-watered conditions, grain dry weights of B35 were significantly (P=0.05) smaller during grain filling. Unlike dry weights, the rates of leaf CO_2 exchange, sucrose synthesis, and ^{14}C-assimilate export of B35 were significantly (P=0.05) slower than RTx430 or the F_1 hybrid at all three sampling stages of well-watered plants. Leaf starch concentrations of B35 were significantly (P=0.05) greater than RTx430 and the hybrid at all three stages, but leaf sucrose concentrations did not differ among the lines and hybrid under well-watered conditions. Similarly, the percentage of ^{14}C-assimilate in leaf starch was significantly (P=0.05) greater than RTx430 during grain filling, and the percentage of ^{14}C-assimilate in leaf sucrose was significantly larger in RTx430 than in B35 and the hybrid at anthesis. Stem sugar and starch concentrations did not differ among the two lines and the hybrid under well-watered conditions. Water stress diminished differences among B35, RTx430, and the F_1 hybrid. In addition to plant dry weight; rates of leaf CO_2 exchange, sucrose synthesis, and ^{14}C-assimilate export; sucrose concentrations; and partitioning of ^{14}C-assimilate among leaf sugars and starch was similar between B35 and Tx430 after water stress was imposed during preboot, anthesis, and grain filling.

Discussion: Relatively slow rates of CO_2 exchange, sucrose synthesis, and ^{14}C-assimilate export for B35 were associated with greater concentrations and radiolabel recoveries in leaf starch in B35 than in the preflowering-tolerant line, RTx430, during grain filling. The smaller capacity of the grain of B35 could have limited leaf export of ^{14}C-assimilate in B35, compared to RTx430. Yet, the absence of greater stem biomass and carbohydrate concentrations in RTx430, compared to B35 during preboot and anthesis precluded a hypothesis that low assimilate unloading rates in vegetative and reproductive organs under well-watered conditions were contributing to cultivar differences in leaf traits and stress tolerance. Consistent differences between B35 and RTx430 under well-watered conditions suggested that regulation in leaf blades contributed to cultivar differences in the observed leaf traits. Yet, it is not clear whether the cultivar differences in leaf traits under well-watered conditions are relevant to stress tolerance. It may be possible to select for postflowering tolerance to water stress while avoiding alleles that exhibit relatively slow rates of leaf CO_2 exchange, sucrose synthesis, and ^{14}C-assimilate export under well-watered conditions.

References

Ackerson, R.C., D.R. Krieg, and F.J.M. Sung. 1980. Crop Sci. 20:10-14.
Girma, F.S., and D.R. Krieg. 1992a. Plant Physiol. 99:83-88.
_____. 1992b. Plant Physiol. 99:577-582.
Hendrix, D.L. 1993. Crop Sci. 33:1306-1311.
Kidambi, S.P., D.R. Krieg, and H.T. Nguyen. 1990. Euphytica 50:139-146
Peng, S., D.R. Krieg, and F.S. Girma. 1991. Photosynthesis Research 28:1-7.
Rosenow, D.T., and L.E. Clark. 1981. p. 19-29; 36th corn and sorghum research conf.
Sung, F.J.M., and D.R. Krieg. 1979. Plant Physiol. 64:852-856.
Tarpley, L., J.A. Dahlberg, D.M. Vietor, and F.R. Miller. 1993. Crop Sci. 33:338-341.

Biochemical and Genetic Studies on Male Sterile Lines in Pearl Millet [*Pennisetum glaucum (l.) R. Br.*]

C. Vijayalakshmi, N. Jayaraman and S. Juliet Hepziba, Department of Millets, School of Genetics, Tamil Nadu Agricultural University, Coimbatore-641 003. India

The anthers of eleven diverse male sterile lines and their maintainers of pearl millet were analyzed for total protein content. Electrophoresis of protein extracts, followed by silver staining, was carried out. The male-sterile lines showed fewer fractions of polypeptides, while B lines had more high molecular weight polypeptides. Fourteen different polypeptides were present in the male-sterile lines and thirteen in their maintainers. Distinct differences existed between male-sterile lines and their maintainers, and also among different male-sterile lines and maintainers. The polypeptides of molecular weights 34,600 *daltons* and 28,800 *daltons* were absent in all the B lines, while those of 52,500 *daltons* and 40,700 *daltons* were present only in B lines. Combining ability analysis was conducted on eleven diverse male-sterile lines and five testers of pearl millet in a Line X Tester method. This indicated that both additive and non-additive genetic variances were significant. Among lines, 405A was the best combiner for yield, tallness and late flowering, and among testers, PT 1890 and PT 3095 were good combiners for grain yield. The hybrid combination 405A X PT 1890 showed the highest per se performance and *SCA* effects for grain yield, offered scope for exploitation of heterosis.

An Outlook on the Sorghum Genetic Improvement Research Program in Northern Mexico

Hector Williams-Alanis, M.Sc. Industrial Crops Program researchers. Sorghum. INIFAP-Rio Bravo Experiment Station, Apdo. Postal 172, CP 88900, Rio Bravo, Tam. Mexico; J. Heriberto Torres-Montalvo, Texas A&M University Doctoral Student. Department of Plant Pathology and Microbiology, College Station, Texas 77843-2132; and Noe Montes-Garcia, M.Sc. Industrial Crops Program researchers. Sorghum. INIFAP-Rio Bravo Experiment Station, Apdo. Postal 172, CP 88900, Rio Bravo, Tam. Mexico

The state of Tamaulipas, situated in northeastern Mexico is the most important grain sorghum production area nationwide. About 800,000 ha are planted annually with an average production of 1.7 million tons. The main problems of the crop in northern Mexico are drought, inadequate management of plant and soil (in this case for soil conservation moisture), and diseases such as charcoal rot *(Macrophomina phaseolina)*, head smut *(Sporisorium reilianum)*, and grain molds.

The sorghum improvement program at the Rio Bravo Experiment Station started in 1974. Up to this date, six grain sorghum hybrids (RB 2000, RB

2010, RB 2020, RB 3006, RB 3030 and RB 4000) have been released. The goal of this program is to develop high-yielding hybrids with wide adaptation, adaptation to both irrigated and rainfed conditions, with excellent agronomic characteristics, and tolerance to diseases.

The first sorghum hybrids released by this program in 1976 were obtained from crosses between male-sterile Mexican lines by restorer lines from INTSORMIL with characteristics for tropical adaptation. These hybrids showed adaptation to the main sorghum areas in Mexico. In 1989, a hybrid (100% Mexican) derived from germplasm of INTSORMIL was released.

Currently the sorghum improvement program at Rio Bravo is the only one in INIFAP (Mexican Agricultural Research Service) and we have developed studies to compare tan plant with red plant characteristics, studies with different cytoplasm types (A_1 and A_2), and sterilization of restorer lines.

We consider that the perspectives are favorable for our program if the economic resources are available. It has been demonstrated that the germplasm obtained in this program has adaptation to all sorghum regions in Mexico. Additionally, there is an outstanding staff of researchers trying to form a group of excellence. Two members of the Sorghum Improvement Program are in Doctoral studies at Texas A&M University with the main objective to increase their knowledge about the new techniques needed to solve the problems present in our region.

Survey of Anthracnose Resistant Sorghum Germplasm Lines to Identify Additional Resistance Genes

C.C. Wiltse, W.L. Rooney, Department of Soil and Crop Sciences, Texas A&M University, College Station, TX 77843; R.A. Frederiksen, Department of Plant Pathology and Microbiology, Texas A&M University, College Station, TX 77843; and D.T. Rosenow, Texas A&M University, Agricultural Research and Extension Center, Rt 3, Lubbock, TX 79401

Anthracnose, caused by the fungus *Colletotrichum graminicola* (Ces.) Wils., is one of the most common and destructive diseases of grain sorghum, *Sorghum bicolor* (L.) Moench. The disease is most serious in the warm, humid sorghum growing regions of the world. Breeding for stable resistance has met with limited success due to the variation in pathogenicity and virulence of several *C. graminicola* isolates and the lack of knowledge pertaining to the host/pathogen interaction. Several attempts to determine the inheritance of resistance to anthracnose have resulted in conclusions including a single dominant multiallelic gene (Tenkouano, 1993), a single recessive gene (K.S. Boora and R.A. Frederiksen, 1996, personal communication), at least 2 independent dominant genes (Jones, 1979), and 2 linked dominant genes, each conferring resistance to different phases of the disease (Coleman and Stokes, 1954).

Several sorghum germplasm accessions in the TAMU/USDA Sorghum Conversion Project have been identified as having good resistance to anthracnose. Before these lines can be effectively utilized in sorghum breeding programs, information regarding the genetic control of resistance in these lines is needed. An experiment is being conducted to determine whether or not resistance is conferred by one or more genes. Thirteen resistant lines (SC155-14E, SC120-14E, SC647-14E, SC166-14E, SC84-14E, SC414-12E, SC748-5, SC991-14E, SC689-14E, SC326-6, SC176-14E, SC701-14E, and SC137-14E) were used to make 16 different resistant-by-resistant crosses. The $F_{2:3}$ generations from each family are currently growing during at the Texas A&M University Research Farm near College Station, TX. The experiment was artificially inoculated with the *C. graminicola* isolate TX430BB85 and was watered periodically with an overhead sprinkler in an attempt to create a suitable environment for disease development and spread. Each row was evaluated for foliar symptoms of anthracnose to determine if the row was resistant, susceptible, or segregating for resistance and susceptibility.

To date, segregating and susceptible rows have been identified in 6 of the 13 $F_{2:3}$ populations. These data indicate that resistance to anthracnose is conferred by more than one gene. Due to the extreme drought conditions during the 1996 summer and subsequent lack of adequate disease pressure, the data thus far do not clearly indicate the number of different genes segregating within the populations. Further evaluation of the 16 $F_{2:3}$ families will be continued during the remainder of the summer.

References

Coleman, O.H., and I.E. Stokes. 1954. The inheritance of resistance to stalk red rot in sorghum. Agron. J. 46:61-63.

Jones, E.M. 1979. The inheritance of resistance to *Colletotrichum graminicola* in grain sorghum, *Sorghum bicolor*. Ph.D. Diss. Purdue Univ., West Lafayette, IN.

Tenkouano, A. 1993. Genetic and ontogenic analysis of anthracnose resistance in *Sorghum bicolor* (L.) Moench. Ph.D. Diss. Texas A&M Univ., College Station, TX.

The Morphological Characteristics of Apomictic Embryo in Sorghum

Shubiao Wu, Xuemei Han, Yongjin Shang, The Department of Biotechnology, Shanxi Academy of Agricultural Sciences, Taiyuan, Shanxi, China 030031; Tiantang Niu, Shanxi Academy of Agricultural Sciences, Taiyuan, Shanxi, China 030006; and Fuyao Zhang, Sorghum Research Institute, Shanxi Academy of Agricultural Sciences, Yuci, Shanxi, China 030610

The embryo structure of two apomictic lines 296B and SSA-1 is discussed in this paper. The apomictic embryo has the characteristic of lacking suspensor in sorghum, otherwise, the sexual embryo has a long suspensor in the same species. This character is an index of judgement on apomxis. The asexual embryos in the lack of suspensor suggests that there are some relationships between non-zygotic embryos.

Rainfed Sorghum Landraces: The Germplasm Structure in the Sudanian Zone of Chad

N.D. Yagoua, CIRAD-CA Station de Bébédjia, BP 31, Moundou, Chad

The Challenge

Sorghum [*Sorghum bicolor* (L.) Moench] is a staple cereal for human consumption in Chad. As a consequence of ecological changes, (i) many landraces no longer fit their environment, and (ii) farmers need new varieties withstanding new constraints, plus stable yields, while preserving good grain qualities.

The Germplasm Structure

A better understanding of local cultivars is a prerequisite for accurate biological adjustments being conducted in order to match the challenge. For that purpose, 76 sorghum populations represented by 4416 panicles have been collected throughout the Sudanian zone of Chad and analyzed.

Results

1) Taxonomic and genetic patterns

(i) Four out of the five basic races (Harland and de Wet's classification) and their hybrids are represented;

(ii) As expected, the Kafir race and its relatives are not represented;

(iii) About 65% of the cultivars are entirely or predominantly hybrid between the races (caudatum-guinea, guinea-caudatum, caudatum-durra and guinea-bicolor);

(iv) Caudatum constitutes the dominant race in basic race composite cultivars; no population entirely constituted by the caudatum race was identified.

2) Genetic erosion

(i) Almost one third of the cultivars known during the last thirty years are increasingly abandoned due to *Striga* [*Striga hermonthica* (Del.) Benth.] pressure and an unfit vegetative cycle. Durra and guinea-durra sorghum are the least competitive.

(ii) The caudatum race (38.3% of basic races represented in the germplasm), contributes to more than 85% of the hybrids, which means this race has a good general combining ability.

3) Vegetative cycles

(i) 50% flowering duration lies between 70 and 155 days if sowing occurs the last of May.

(ii) Landraces with intermediate cycles (90-120 days) are scarce.

4)Grain productivity

Caudatum, caudatum-guinea, guinea-caudatum and durra-caudatum sorghums produce the most grain (50-65 g per panicle).

As A Consequence

(i) Sorghum germplasm in the Sudanian zone of Chad is one of the most diversified in sub-Saharan Africa. Since genetic erosion is important, saving the landraces should be a priority.

(ii) Hybrid landraces, i.e., caudatum-guinea, guinea-caudatum, caudatum-durra should be exploited by mass selection since they exhibit high variability.

(iii) The caudatum race combines well with other races and should be used as much as possible.

(iv) For sustainably filling the gap of unadapted landraces, biological adjustments should aim at reduce down to 90-120 days the cycle of the long season cultivars preferred for storage grain qualities and palatability and improve resistance to *Striga* and/or midge (*Stenodiplosis sorghicola* (Coq.).

The Methodology Study on the Sorghum Germplasm Evaluation for Sterile Tolerance

Z.P. Yu, G.X. Zhang, Y.P. Gao, and H.S. Yu
Shanxi Academy of Agricultural Sciences, Taiyuan, Shanxi, P.R. China 030031

To utilize low-fertility-tolerant germplasm in sorghum breeding, 6364 Chinese sorghum entries and 3140 exotic introduced entries were evaluated between 1982 and 1995. Three hundred seventy-eight entries were identified as grade I tolerant lines. The evaluation methodology and related topics are discussed in the paper.

The Study and Utilization of Alternative Sorghum Cytoplasms in China

F.Y. Zhang, T.T. Niu, Y.M. Wei, Z.L. Bai, G.X. Zhang, C.G. Meng, X.M. Yan, J.A. Ping, L.X. Wang, and Y. Sun, Shanxi Academy of Agri. Sci, Taiyuan, Shanxi, P.R. China 030031

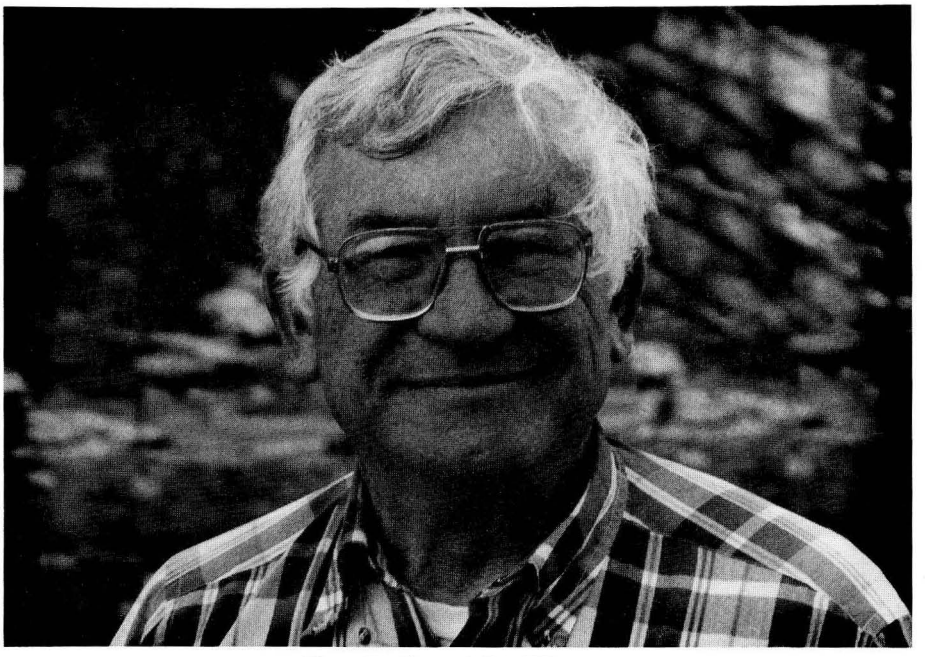
The test crosses showed that most kaoliang A_1 R-lines produced maintainer responses for both A_2 and A_3 cytoplasms. The ease of the cytoplasms to restore fertility was determined to be, $A_1 \rightarrow A_2 \rightarrow A_3 \circledR A_4 \rightarrow 9E \rightarrow A_{3D}$. A commercial A_2 cytoplasic male-sterile line, V_4A was released as a seed parent and two hybrids made with it have been grown on fields of about 100,000 ha. The pollen abortion characteristics of the cytoplasm sources are described.

Award Presentation

to

Dr. Leland R. House

Presenter: Dr. Gebisa Ejeta



Dr. Leland R. House

Dr. Gebisa Ejeta, on behalf of the International Sorghum Research Community, presented Dr. Leland R. House with a plaque and the following tribute commemorating his lifelong service and dedication to the improvement of the sorghum crop around the world.

Dr. Leland R. House has been the leading contributor to sorghum improvement around the world for over 35 years. He has been involved in essentially all aspects of developments in sorghum improvement programs in Asia, the Middle East and in many parts of Africa for the past three decades. His contributions have been in many areas, ranging from germplasm development and exchange, sorghum breeding, to training and regional program development. His efforts led to very significant increases in sorghum production in several countries including India, Sudan, and Zambia.

Dr. House began his career in International Agriculture when he joined the Rockefeller Foundation program for maize improvement in India in 1959. In 1961, he assumed responsibility for the Rockefeller Foundation Indian Sorghum Improvement Program. Working with his Indian counterpart, Dr. N.G.P. Rao, he was jointly responsible for development of the All India Coordinated Sorghum Improvement Program. This program has been exceptionally productive and served as a model for similar programs in other crops in India, and for crop improvement programs in other parts of the world. One of his primary objectives has always been to develop crop improvement teams through close scientific collaboration with scientists in other

disciplines. The All India Coordinated Sorghum Program is a wonderful example of his success in this regard. He gave his time unselfishly to help in the professional development of his Indian colleagues resulting in major achievements in Indian sorghum production.

During the time that the first sorghum hybrids were being developed in India, Dr. House was actively involved in the development of a seed industry to support hybrid seed production. He helped establish hybrid seed programs in government organizations and to stimulate development of a private seed sector through his contacts with Indian seedsmen. Some of these private companies have become well established in India. Throughout these developments, Dr. House has been a constant and unselfish advisor to both public and private sector seedsmen.

In 1971 Dr. House began a regional sorghum program at the Arid Lands Agricultural Development Office (ALAD) in Beirut, Lebanon. During the next five years he fostered extensive germplasm development and training programs in several countries of the Middle East and Africa. Several of the scientists trained at ALAD have gone on to assume key positions in crop improvement programs in the region. One of his principal accomplishments was the initiation of a hybrid sorghum program in Sudan in cooperation with Sudanese scientists in the Agricultural Research Corporation. His stimulation of interest in hybrid sorghum for Sudan led to the development several years later, by his colleague Dr. Gebisa Ejeta, of Hageen Dura-1. This hybrid is currently producing yield increases from two to five times that of local varieties, under both irrigated and rainfed conditions. This is a major contribution to the country of Sudan, especially in view of the current drought-induced food crisis in that part of Africa. In Zambia, working with his colleague, Dr. Bhola Nath Verma, they laid the foundation for a successful sorghum research program that developed varieties and hybrids for different uses in the country. They also established the value of the new cultivars and insured the abundance of seeds. This effort in Zambia is an excellent example of a development activity growing out of a research program.

Dr. House was one of the principal organizers of key International Sorghum Symposia in the world. He was instrumental in organizing "Sorghum in the Seventies" in 1971, and co-editor with Dr. Rao, of the proceedings published in 1972. This was the first major international sorghum research symposium ever held and Dr. House was instrumental in initiating, organizing, and publishing the symposium. A sequel was held in 1981 after Dr. House joined ICRISAT as Program Leader for sorghum improvement. Again, he was the driving force behind "Sorghum in the Eighties", which was published in 1982. Dr. House also initiated the early discussions and efforts that led to this meeting. In 1984, Dr. House assumed leadership of the Southern Africa Regional Sorghum/Millet Improvement Project in Bulawayo, Zimbabwe, having been assigned as its first Executive Director. He was responsible for the oversight of the many activities of the Center ranging from assembly of germplasm, experiment station development,

establishment of laboratory facilities, and coordination of training efforts to mobilizing emergency seed production efforts, which was widely hailed as meeting critical needs of poor farmers in the Southern Africa region.

Dr. House contributed unselfishly to the professional development of numerous sorghum scientists around the world. His approach on research teams has always been to work quietly, but steadily, behind the scenes to motivate others to higher levels of achievement. His impact on sorghum production around the world has been amplified by his ability to motivate others. A good example is the publication of a sorghum breeding handbook, that not only provides the basic principles of sorghum breeding in a very direct and practical manner, but also is clearly illustrated with an excellent set of "how to" photographs.

Dr. House epitomizes the ideal example of the role of an expatriate scientist in Third World Agricultural Development. As a leader he is a catalyst, a member of a team, and a contributor. He builds trust and loyalty among his staff. He builds confidence with young professionals. He directs but does not dictate. He has an amazing ability to identify with people across cultures. He is gifted with the ability for seeing problems from the perspective of the locals. Throughout his long and distinguished career, he worked quietly, but with a great sense of purpose. He accomplished goals by excellent organization, keen intelligence and hard work. His dedication to science and sorghum improvement provides inspiration and motivation for others around him. His encouragement, support and able technical assistance, strengthened numerous national sorghum and millet improvement programs. Among his many contributions, is his involvement in the promotion and development of the seed industry in developing countries, his untiring effort in mobilizing the development and free movement of improved sorghum germplasm around the world, and his inspiration and encouragement in the professional development of young scientists, that will remain his legacy. He has been exceedingly successful in all of these areas. His effectiveness is clearly demonstrated by the tremendous respect and high esteem which his colleagues around the world have for him.

Conference

Participants


FOUNTAIN COURT

Conference Participants

Argentina

Laura M. Giorda
EEA. INTA Manfredi
5988 Manfredi - Cordoba
Argentina

Eliseo S. Juncos
Morgan - Criadero y Semillero
Maipu 942 - ler piso (1340)
Buenos Aires, Argentina

Eduardo E. Teyssandier
Cargill Seeds
Alem 623
Perjamino, Argentina

Vicente Trucillo
NIDERA S.A.
C.C. 6
Venado Tuerto, Argentina

Australia

Hugh Campbell
Hylan Seed Co.
A.C.N. 009 806 151
P O Box 315
Kingaroy, Q 4610, Australia

Francis Coe
Hylan Seed Co.
A.C.N. 009 806 151
P.O. Box 315
Kingaroy, Q 4610, Australia

Rodney Coe
Hylan Seed Co.
A.C.N. 009 806 151
P.O Box 315
Kingaroy, Q 4610, Australia

B.A. Franzmann
Queensland Dept of Primary Industries
P.O. Box 102
Toowoomba 4350, Queensland, Australia

Brian Hare
Pacific Seeds
P.O. Box 337
Toowoomba, Qld, Australia

R.G. Henzell
Hermitage Research Station
Queensland Dept Primary Industries
Warwick, Queensland, Australia

Lynne McIntyre
CSIRO Div of Tropical Crops & Pastures
306 Carmody Rd, St Lucia
Brisbane, Qld, Australia

Russell C. Muchow
CSIRO Div of Tropical Crops & Pastures
306 Carmody Rd.
St Lucia, Q., Australia

Neil Muller
Pacific Seeds P/L
P.O. Box 337
Toowoomba 4350, QLD,
Australia

Bruce John Winter
Grainco Seeds
P.O. Box 136
Toowoomba, QLD, Australia

Belgium

N.P. Eswara Reddy
Vrije Universiteit Brussel
Institute for Molecular Biology
65, Paardenstraat; B-1640,
St. Genesius-Rode
Brussels, Belgium

Botswana

Nigel Nicholsen
Foods (Botswana) (PTY) LTP.
P.O. Box 1131
Serowe, Botswana

Brazil

Gabriel Maciel
IPA - AV - GAL.
San Martin - 1371
Bomji - Recife - PE, Brazil

Paulo Ribas
Sementes AGROCERES S/A
KM 25, Rod. Mgt. 154, C. P. 81
38.360.000 Capinopolis, MG
Brazil

Robert E. Schaffert
EMBRAPA/CNPMS
Caixa Postal 151
35701-976 Sete Lagoas, MG, Brazil

Cameroon

Richard Kenga
Institute of Agronomic Research (IRA)
B.P. Box 33
Maroua, Cameroon

Chad

Ndjekounkosse Djool Yagoua
WCASRN Representative
Station CIRAD-CA de Bebedjia, BP 764
Ndjamena, CHAD

China

Yu Li
Inst. Of Crop Germplasm Resour., CAAS
30 Bai Shi Qiao Rd.
Beijing 100081, China

Cote D'Ivoire

Karim Traore
WARDA
01 B.P. 2551
Bouake 01, Cote D'Ivoire

Egypt

Elhamy El-Assiuty
ARC
Plant Pathology Research Institute
9 Gamaa Street
Giza, Egypt

Osman El-Nagouly
ARC
Field Crops Research Institute
Giza, Egypt

El Salvador

Rene Clara Valencia
Centro Nacional de Technologia
Agricola de El Salvador
Apartado Postal 885
San Salvador, El Salvador

Ethiopia

Aberra Debelo
Institute of Agricultural Research
P.O. Box 2003
Addis Ababa, Ethiopia

Girma Tegegne
c/o Deputy Director
Institute of Agricultural Research
P.O. Box 2003
Addis Ababa, Ethiopia

Senait Yetneberk
c/o Deputy General Director
Institute of Agricultural Research
P.O. Box 2003
Addis Ababa, Ethiopia

Ghana

S.K. Nutsugah
Savanna Agricultural Research Institute
P.O. Box 52
Tamale, GHANA

Guatemala

Antonio J. Cristiani B.
Cristiani Burkard, S.A.
Ave. La Reforma 13-70, Zona 9
Guatemala City, Guatemala

Sandra Cristiani B.
Cristiani Burkard, S.A.
Ave. La Reforma 13-70, Zona 9
Guatemala City, Guatemala

Honduras

Francisco Gomez
Departamento De Agronomia
Escuela Agricola Panamericana
Zamorano, Honduras

Alejandro Palma
DeKalb CA
Col. Miraflores B 15, C#2516
Tegucigalpa, Honduras

India

S.K. Bhatnagar
All India Coordinated Pearl Millet Improvement Project India. ICAR
Agricultural Research Station
Mandore, Jodhpur, 342 304 India

F.R. Bidinger
ICRISAT Asia Center
Patancheru PO
Andhra Pradesh 502 324
Hyderabad, India

Ranajit Bandyopadhyay
ICRISAT Asia Center
Crop Protection Div., Patancheru PO,
Andhra Pradesh 502 324
Hyderabad, India

Khazan S. Boora
CCS Haryana Agricultural University
Plant Breeding Dept
Hisar 125004, India

Paula Bramel-Cox
ICRISAT
Patancheru P O
Andhra Pradesh 502 324
Hyderabad, India

D.E. Byth
ICRISAT
Patancheru P O
Andhra Pradesh 502 324
Hyderabad, India

S.G. Mutalik Desai
Cargill Seeds India Ltd.
308 Sophia's Choice
St. Mark's Road
Bangalore, India

O.P. Govila
Indian Agricultural Rsch Institute
Division of Genetics
New Delhi-110012, India

Suresh K. Gupta
Proagro Seed Co. LTD
8-1-39, Tolichowki
Hyderabad, 500008, A.P., India

C. Tom Hash
ICRISAT
IAC, Genetic Enhancement Division
Patancheru 502 324 Andhra Pradesh, India

S. Indira
Indian Council of Agriculture Rsch
National Research Center
Hyderabad 500030, A.P.,
India

N. Jayaraman
Tamil Nadu Agricultural University
Department of Millet, School of Genetics
Coimbatore-641 003.
India

Swarnlata Kaul
National Research Centre for Sorghum
Rajender Nagar
Hyderabad, A.P. 500030
India

C. Rama Krishna
J.K. Agri-Genetics
9-1-87 Sarojinidevi Rd, Adj. to
Sangeet Theatre
Secunderabad, Andhra Pradesh, India

G.P. Lodhi
CCS Haryana Agricultural University
Plant Breeding Dept
Hisar 125004, India

V. Mahalakshmi
ICRISAT Asia Center
Patancheru 502324,
Andhra Pradesh, India

H.D. Patil
Proagro Seed Co. LTD.
N-2/Ah-2/23,
Probodhankar Thakre Nagar, CIDCO
Aurangabad, 431003, India

K.N. Rai
ICRISAT Asia Center
Patancheru 502 324,
Andhra Pradesh, India

B.S. Rana
National Research Centre for Sorghum
Rajendranagar, Hyderabad
500 030 A.P., India

H. Frederick W. Rattunde
ICRISAT
Patancheru 502 324
Andhra Pradesh, India

S. Bala Ravi
Indian Council of Agriculture Research
National Research Center
Hyderabad 500030, A.P., India

Belum V S Reddy
ICRISAT
Patancheru 502 324
Andhra Pradesh, India

Satish C. Sawe
Maharashtra Hybrid Seeds Co Ltd.
4th Flr, Resham Bhavan, 78,
Veer Nariman Road
Bombay 400 020, India

Nadoor Seetharama
ICRISAT
Patancheru P.O. 502 324
Andhra Pradesh, India

N. Senthil
15, Shastri Street, P.N. Pudur
Coimbatore 641 041, Tamil Nadu
India

John W. Stenhouse
ICRISAT
Patancheru P.O.
Andhra Pradesh 502 324, India

V. Subramanian
ICRISAT
Patancheru P.O. 502 324
Andhra Pradesh, India

Ram P. Thakur
ICRISAT Asia Center
Patancheru PO,
Andhra Pradesh 502 324
Hyderabad, India

Prakash N. Tupekar
Maharashtra Hybrid Seeds Co, Ltd.
4th Floor, Resham Bhavan, 78,
Veer Nariman Road
Bombay 400020, India

Paresh K. Verma
Proagro Seed Co. Ltd
8-1-39, Tolichowki
Hyderabad, 500008, A.P., India

Israel

Abraham Blum
Institute of Field Crops
Volcani Centre
P.O. Box 6
Bet Dagan, Israel

Kenya

Chagema John Kedera
Kenya Agricultural Research Institute
P.O. Box 67070
Nairobi, Kenya

Stan King
ICRISAT Country Representative
P.O. Box 39063
Nairobi, Kenya

Riungu M'Ragwa
Kenya Agricultural Research Institution Katumani,
Box 340
Machakos, Kenya

S.Z. Mukuru
ICRISAT
P.O. Box 39063
Nairobi, Kenya

Joseph Ochieng
Asst Director of Food Crops
Kenya Agricultural Research Institute
Nairobi, Kenya

Mali

Berthe Aissata Bengaly
IER
B.P. 438
Bamako, Mali

Jacques Chantereau
CIRAD
B P 320
Bamako, Mali

Adama Coulibaly
Cinzana Research Station
B.P. 214
Segou, Mali

Sidi Bekaye Coulibaly
Institut D'Economie Rurale
B.P. 214
Segou, Mali

Bourema Dembele
IER
CRRA Sotuba, B.P. 438
Bamako, Mali

Yacouba Doumbia
Sotuba Research Station
B.P. 438
Bamako, Mali

D.S. Murty
ICRISAT
B P 320
Bamako, Mali

Salimata C. Sidibe
Sotuba Research Station
B.P. 438
Bamako, Mali

Abdoul Wahab Toure
Sotuba Research Station
B.P. 438
Bamako, Mali

Mexico

Andres Encinas
SEHIMEX
5 de Febrero 256
Irapuato, 36500, Mexico

Edgar Haro
HiBridos Pioneer De Mexico
KM 21 Carr. Guad-More #8601
Guadalajara, Mexico

Juan M. Munoz
Organizacion 1001,
Cd de los Ninos
Guadalajara, 45040, Mexico

Armando Rodriguez
Asgrow Mexicana S.A. De C.V.
Av. Mariano Otero 2347 200
Piso Colonia Verde Valle
Guadalajara, Jalisco, Mexico

Enrique Romo
CERES Internacional de Semillas
S.A. de C.V.
Rincon del Crepusculo #133
Irapuato, Gto., Mexico

Javier Simental
Sandoz Servicios, S.A. De C.V.
Av. Lapizlazuli 2568, 1 Piso A,
Col. Boxques De La Victoria, C.P. 4454
Guadalajara, Jalisco, Mexico

Hector Williams-Alanis
Campo Experimental Rio Bravo INIFAP
Apdo. Postal 172
Rio Bravo, Mexico

Francisco Zavala-Garcia
Universidad Avtonoma de Nvevo Leon
2928 Playa Monalo Col. Primavera
Monterrey, N.L., Mexico

Myanmar

U. John Ba Maw
Central Agriculture Research Inst.,
Ye in, Pyimnana,
Myanmar

Namibia

Sheehama-Ndje Aludhilu Ipinge
Okashana Research Station
Ministry of Ag., Water & Rural Dev.
P.O. Box 217
Tsumeb, Namibia

Wolfgang Richard Lechner
Mahanene Research Station
Box 144
Oshakati, Namibia

Niger

Ouendeba Botorou
INRAN
B.P. 429
Niamey, Niger

Issoufou Kapran
INRAN
B.P. 60
Kollo, Niger

K. Anand Kumar
ICRISAT
B P 12404
Niamey, Niger

Moussa Oumarou
INRAN
B.P. 429
Niamey, Niger

Seyni Sirifi
INRAN
B.P. 60
Kollo, Niger

Nigeria

S.C. Gupta
ICRISAT
PMB 3491
Kano, Nigeria

Paraguay

Wilhelm Wiebe Giesbrecht
Ingeniero Agronomo
C.d.c. 883 Asuncion
Loma Plata Chaco, Paraguay

Puerto Rico

Jeff Dahlberg
USDA-ARS-TARS
Box 70
Mayaguez, Puerto Rico 00709-0070

Russia

L.A. Elkonin
Volga-Region Institute of Biotechnology
Selectsiony pr., 5. 410020
Saratov, Russia

Aliya S. Kasakova
All-Russia Rsch Institute for Sorghum
19, Lenin Street
Zernograd, Rostov-on-Don, 347720
Russia

Senegal

Amadou Fofana
CRZ/ISRA
B.P. 53
Kolda, Senegal

South Africa

N.W. McLaren
Grain Crops Institute
Private Bag X1251
Potchefstroom, South Africa

Sudan

Abdel Gabar Babiker
Agricultural Research Corporation
P.O. Box 126
Wad Medani, Sudan

Abdel Latif M Nour
ARC
P.O. Box 126
Wad Medani, Gezira, Sudan

Tanzania

Hamis Saadan
National Sorghum & Research Program
Research & Training Dpt. P.O. Box 2066
Dar es Salaam, Tanzania

Thailand

Julee Tippayaruk
Field Crops Research Institute
Department of Agriculture
Jatuchak Bangkok 10900
Bangkok, Thailand

Uganda

J. Peter Esele
Serere Agric & Animal Prod. Rsch Instit.
P.O. Soroti
Serere, Uganda

United Kingdom

K.M. Devos
Norwich Research Park
Colney Norwich, UK NR4 7UH
Norwich, Norfolk, United Kingdom

David Harris
University of Wales
Centre for Arid Zone Studies
Bangor, Awynnedd, United Kingdom

Catherine J. Howarth
Instit of Grassland & Environmental Rsch
Plas Gogerddan
Aberystwyth, Wales, United Kingdom

John R. Witcombe
University of Wales
Centre for Arid Zone Studies
Bangor, Gwynedd, North Wales llS72UW
United Kingdom

United States

John R. Abernathy
Texas A&M Agricultural Experiment Stn.
Rt. 3, Box 219
Lubbock, TX 79401

Adam Aboubacar (Mali)
Purdue University
Food Science Dept
West Lafayette, IN 47907

David Andrews
University of Nebraska
Agronomy Dept
328 Keim Hall
Lincoln, NE 68583-0915

Art Armbrust
P.O. Box 140
Healy, KS 68750

Don Ator
Texas Seed Trade Assn.
P.O. Box 1430
Pflugerville, TX 78691

Dennis Avery
Center for Global Food Issues
P.O. Box 202
Churchville, VA 24221

John D. Axtell
Purdue University
Agronomy Dept
West Lafayette, IN 47907

Selahattin Aydin (Turkey)
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Mulu Ayele (Ethiopia)
Texas Tech University
Plant Molecular Genetics Lab
Mail Stop 2122
Lubbock, TX 73403

Elizabeth Banset
INTSORMIL/Editor
University of Nebraska
300 Agricultural Hall
Lincoln, NE 68583-0709

Jimmy Barber
Mycogen Seeds
7918 Vicksburg
Lubbock, TX 79424

J.L. Bennetzen
Purdue University
Biological Science Dept
West Lafayette, IN 47907-1392

Admasu Melake Berhan (Ethiopia)
Purdue University
Biochemistry Dept
West Lafayette, IN 47907

Nathan R. Boardman
Crosbyton Seed Company
P.O. Box 429
Crosbyton, TX 79322

Ray L. Brengman
Kansas State University
Agronomy Dept./ Throckmorton Hall
Manhattan, KS 66506

Francisco Javier Bueso (Honduras)
Texas A&M Univeristy
Soil & Crop Sciences Dept.
College Station, TX 77840

Larry Butler
Purdue University
Biochemistry Dept
West Lafayette, IN 47907

Ricardo A. Carranza
Ingeniero Agronomo
1212 Hwy 25 South, Apt. 48
Starkville, MS 39759

Carlos Carvalho (Brazil)
Purdue University
Agronomy Dept
West Lafayette, IN 47907

Surinder Chopra
Iowa State University
2204 Molecular Biology
Ames, IA 50010

Larry Claflin
Kansas State University
Plant Pathology Dept
Manhattan, KS 66506

Lewis E. Clark
Texas A&M University
P.O. Box 1658
Vernon, TX 76385

Somkid Clarke
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Leon Clement
Northrup King Co.
356 Hosek Road
Victoria, TX 77905

Cloyce G. Coffman
Texas A&M University
348 Heep Center
College Station, TX 77843-2474

Delroy Collins
Texas A&M University
Plant Pathology & Microbiology Dept
College Station, TX 77843-2132

Yunxing Cui (China)
Texas A&M University
Plant Pathology Dept
College Station, TX 77843

Tom Davee
Cargill Hybrid Seeds
RR 2, Box 82
Lockney, TX 79241

Rex DeLong
Pioneer Hi-Bred Int'l Inc.
501 East Pioneer Rd.
Plainview, TX 79072

Niamoye Y. Diarisso (Mali)
Texas A&M University
Entomology Dept.
College Station, TX 77843-2475

Mamourou Diourte (Mali)
Kansas State University
300 Jardine Terr., Apt. M#1
Manhattan, KS 66502

Steve A. Eberhart
USDA, ARS
National Seed Storage Laboratory
1111 S. Mason St.
Ft. Collins, CO 80521-4500

Jack Eberspacher
National Grain Sorghum Producers
P.O. Box 530
Abernathy, TX 79311

Gebisa Ejeta
Purdue University
Agronomy Dept
West Lafayette, IN 47907

Joan Frederick
INTSORMIL
University of Nebraska
114 Biochemistry Hall
Lincoln, NE 68583-0748

Richard A. Frederiksen
Texas A&M University
Plant Pathology & Microbiology Dept
College Station, TX 77843-2132

Brhane Gebrekidan
Virginia Polytechnic Institute State Univ
1060 Litton Reaves Hall
Blacksburg, VA 24061-0334

Mike Gilbert
Cargill
P.O. Box 5645
Minneapolis, MN 55440

Patricio F. Gutierrez (Ecuador)
University of Nebraska
Agronomy Dept
Lincoln, NE 68583-0817

Boukary Hama (Niger)
Mississippi State University
Box 9810
Mississippi State, MS 39762

Bruce Hamaker
Purdue University
Food Science Dept, Smith Hall
West Lafayette, IN 47907

W.W. Hanna
USDA/ARS SAA-
Georgia Coastal Plain Exper. Stn.
P.O. BOX 748
Tifton, GA 31793

Gary E. Hart
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843

Brad Helton
West Texas A&M University
Box 998
Canyon, TX 79016

Mark Hood
Pioneer Hi-Bred Int'l, Inc.
P.O. Box 67
Clarkedale, AR 72325

Leland R. House
Rt. 2, Box 136 A-1
Bakersville, NC 28705

Temam Hussien (Ethiopia)
Kansas State University
Plant Pathology Dept
Manhattan, KS 66506

Yahia Ibrahim (Sudan)
Purdue University
Agronomy Dept., Lilly Hall
West Lafayette, IN 47907

John Jaster
Pioneer Hi-Bred International, Inc.
P.O. Box 97
Taft, TX 78390

Stanley G. Jensen
USDA/ARS
University of Nebraska
422 Plant Science
Lincoln, NE 68583-0722

Jerry W. Johnson
Northrup King
356 Hosek Road
Victoria, TX 77901

Jerry Jones
Texas A&M Experiment Station
Route 3, Box 219
Lubbock, TX 79401

Robert R. Kalton
Iowa State University
Plant Breeding Dept
1202 Agronomy Hall
Ames, IA 50010

Catherine S. Katsar
Texas A&M University
Entomology Dept
College Station, TX 77843-2475

Yilma Kebede
Pioneer Hi-Bred International
1724 Hayes Drive
Manhattan, KS 66502

Babrak Khaleeq
3401 Garland Street
Plainview, TX 79072

Kenneth Kofoid
Kansas State University
Agricultural Research Center-Hays
1232 240th Ave.
Hays, KS 67601

Issoufou Kollo (Niger)
Texas A&M University
Plant Pathology & Microbiology Dept
College Station, TX 77843-2132

Terry Lemming
Purdue University
Agronomy Dept, Lilly Hall
West Lafayette, IN 47907

Lee Leonard
Cargill Hybrid Seeds
RR2, Box 82
Lockney, TX 79241

John F. Leslie
Kansas State University
Plant Pathology Dept
4002 Throckmorton Plant Sciences Ctr
Manhattan, KS 66506-5502

Tim Lust
National Grain Sorghum Producers
Box 560
Abernathy, TX 79311

Clint Magill
Texas A&M University
Plant Pathology Dept
College Station, TX 77843

Daniel Mandel
NC+ Hybrids
207 E. Wichita
Colwich, KS 67030

A. Bruce Maunder
DeKalb Genetics Corp.
Rt 2 Box 56
Lubbock, TX 79415

Marilyn McDonald
INTSORMIL
University of Nebraska
113 Biochemistry Hall
Lincoln, NE 68583-0748

Dan Meckenstock
3107 Thunderbird Dr.
Hays, KS 67601

Barry Miller
Pioneer Hi-Bred Int'l, Inc.
501 East Pioneer Rd
Plainview, TX 79072

Fred Miller
6417 Zak Road
Bryan, TX 77808

Raymond Miller
Pioneer Hi-Bred Int'l, Inc.
501 East Pioneer Rd.
Plainview, TX 79072

Abdella Mohammed (Sudan)
Purdue University
Agronomy Dept, Lilly Hall
West Lafayette, IN 47907

Roger Monk
Pioneer Hi-Bred Int'l, Inc.
P.O. Box 97
Taft, TX 78390

John Mullet
Texas A&M University
Crop Biotechnology Center
College Station, TX 77843

Linus M Muriithi (Kenya)
Kansas State University
Plant Pathology Dept
Manhattan, KS 66506-5502

Dario Narvaez (Colombia)
Kansas State University
Plant Pathology Dept
4004 Throckmorton Hall
Manhattan, KS 66506

Lexingtons Nduulu (Kenya)
Purdue University
Agronomy Dept, Lilly Hall
West Lafayette, IN 47907

Henry T. Nguyen
Texas Tech University
Plant & Soil Sciences Dept
Lubbock, TX 79409

Mike Northcutt
Production Plus
Box 1106
Plainview, TX 79073-1106

Gary Odvody
Texas A&M University
Plant Sciences Dept
Route 2 - Box 589
Corpus Christi, TX 78410

Jerry D. O'Rear
Garrison & Townsend, Inc.
P.O. 2420
Hereford, TX 79045

James Osborne
NC+ Hybrids
207 E. Wichita
Colwich, KS 67030

Josephine P. Ouma (Kenya)
Mississippi State University
Box 9555
Mississippi State, MS 39762

George Pechacek
Crosbyton Seed Co.
P.O. Box 429
Crosbyton, TX 79322

Jeff Pedersen
USDA-ARS
University of Nebraska
344 Keim Hall
Lincoln, NE 68583-0915

Bonnie B. Pendleton
Texas A&M University
Entomology Dept
College Station, TX 77843-2475

Gary Peterson
Texas A&M Agric. & Rsch Center
Route 3, Box 219
Lubbock, TX 79401

James M. Phillips
Triumph Seed Co., Inc.
P.O. Box 1050
Ralls, TX 79357

Shankar Podduturi
Pioneer Hi-Bred Int'l Inc.
501 East Pioneer Rd.
Plainview, TX 79072

Kay Porter
Pioneer Hi-Bred International, Inc.
501 East Pioneer Road
Plainview, TX 79072

Edwin Price
Texas A&M University
International Agricultural Programs
Administration Bldg., Room 12
College Station, TX 77843-2477

Daryl R. Pring
USDA-ARS, University of Florida
Plant Pathology Dept,
1453 Fifield Hall
Gainesville, FL 32611

Hector Quemada
Asgrow Seed Co.
2605 East Kilgore Road
Kalamazoo, MI 49002

Joe Raab
DeKalb Genetics Corporation
Route 2, Box 373
Bishop, TX 78343

John Rajewski
University of Nebraska
Agronomy Dept
KCR Room 105
Lincoln, NE 68583-0817

Keerti Rathori
Texas A&M University
Crop Biotechnology Center
College Station, TX 77843

Oscar Rodriguez
G.E. Pogue Seed Co., Inc.
P.O. Drawer 389
Kenedy, TX 78119

Raul Rodriguez
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Bill Rooney
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Lloyd W. Rooney
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Darrell T. Rosenow
Texas A&M Agric. Experiment Station
Route 3, Box 219
Lubbock, TX 79401

E.C.A. Runge
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843

Keith Schertz
3806 Oaklawn
Bryan, TX 77801

Koushik Seetharaman (India)
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843

Peter Setimela (Botswana)
University of Nebraska
328 Keim Hall
Lincoln, NE 68583-0915

Roberta Smith
Texas A&M University
Soil & Crop Science Dept
College Station, TX 77843

Rodney Smith
Cargill Hybrid Seeds
RR2, Box 82
Lockney, TX 79241

Stephen Smith
Pioneer Hi-Bred Int'l Inc.
7300 NW 62nd Ave.
Johnston, IA 50131

Matt Sowder
Crosbyton Seed Co.
306 East Main
Crosbyton, TX 79322

William D. Stegmeier
Kansas State University
Agricultural Research Center-Hays
1232 240th Ave
Hays, KS 67601

Jeffrey N.L. Stibick
USDA/APHIS
4700 River Road
Riverdale, MD 20737

Dorothy Stoner
INTSORMIL
University of Nebraska
108 Biochemistry Hall
Lincoln, NE 68583-0748

Donnie Swink
Crosbyton Seed Co.
306 East Main
Crosbyton, TX 79322

George L. Teetes
Texas A&M University
Entomology Dept
College Station, TX 77843-2475

Niaba Teme (Mali)
Texas A&M Agricultural Experiment Stn.
RR 3, Box 219
Lubbock, TX 79401

Geoffrey L. Thomas
Asgrow Seed Co.
P.O. Box 1945
Plainview, TX 79073

Ronald Thomason
West Texas A&M University
Box 998
Canyon, TX 79016

Gary H. Toenniessen
Rockefeller Foundation
420 Fifth Avenue
New York, NY 10018

Aboubacar Toure (Mali)
Texas A&M Agricultural Research Stn.
Route 3, Box 219
Lubbock, TX 79401

Mitch Tuinstra
Purdue University
Agronomy Dept, Lilly Hall
West Lafayette, IN 47907

Donald M. Vietor
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Ralph Waniska
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Karl Wardlow
Coffey Seeds
Route 1, Box 253B
Plainview, TX 79072

W. Phillip Warren
USAID/G/EG/AFS
SA-2, Room 401
Department of State
Washington, DC 20523-0214

Clarence Watson
Mississippi State University
Box 9653
Mississippi State, MS 39762

Curtis Wiltse
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Charles Woodfin
Texas A&M Agric Experiment Station
Rt 3, Box 219
Lubbock, TX 79401-9757

Norman Wuthrich
Texas A&M Agric. Exper Stn./Halfway
Box 117
Plainview, TX 79041

John M. Yohe
INTSORMIL Program Director
University of Nebraska
115 Biochemistry Hall
Lincoln, NE 68583-0748

Haiyan Zhao (China)
Texas A&M University
Soil & Crop Sciences Dept
College Station, TX 77843-2474

Hugo L. Zorrilla
Pioneer Hi-Bred International
1724 Hayes Drive
Manhattan, KS 66502

Venezuela

Alvaro E. Munera
Cargill De Venezuela C.A.
Av. Intercommunal Santiago Marino
Sector La Providencia, Parcela No. 7
Turmero 2101, Aragua, Venezuela

Zambia

Medson Chisi
Mt. Makulu Research Station
Private Bag 7
Chilanga, Zambia

Bhola Nath Verma
c/o Zambia Seed Co.
P.O. Box 35441
Lusaka, Zambia

Zimbabwe

Nicholas Mangombe
Crop Breeding Institute
Box CY 550, Causeway
Harare, Zimbabwe

Emmanuel S. Monyo
SADC/ICRISAT
P.O. Box 776
Bulawayo, Zimbabwe

Joseph Mushonga
Research & Specialist Services
Box CY594, Causeway
Harare, Zimbabwe

A. Babatunde Obilana
SADC/ICRISAT SMIP
Matopos Research Station
P.O. Box 776
Bulawayo, Zimbabwe

About INTSORMIL

The collaborative research support program (CRSP) concept was created by the U.S. Agency for International Development (USAID) and the Board for International Food and Agriculture Development (BIFAD), under the auspices of Title XII of the Foreign Assistance Act, as a long term mechanism for mobilizing the U.S. Land Grant Universities in the international food and agricultural research mandate of the U.S. Government. The CRSPs are communities of U.S. Land Grant Universities working with USAID and USAID Missions, other U.S. Federal Agencies, developing country National Agricultural Research Systems (NARS), developing Country Colleges and Universities, International Agricultural Research Centers (IARCs), private agencies, industry, and private voluntary organizations (PVOs). INTSORMIL, the Sorghum and Millet Collaborative Research Support Program (CRSP) was established in 1979 and is one of nine CRSPs currently in operation. The universities active in the INTSORMIL CRSP are Kansas State University, Mississippi State University, University of Nebraska, Purdue University and Texas A&M University.

The INTSORMIL mission is to use collaborative research as a mechanism to develop human and institutional research capabilities to overcome constraints to sorghum and millet production and utilization for the mutual benefit of U.S. and LDC agriculture.

Collaborative research sites are maintained in the agroecological zones of western, southern, and eastern Africa, and in Central America. These sites support the general goals of building NARS institutional capabilities, creating human and technological capital for solving sorghum and millet constraints with sustainable global impact, promoting economic growth, enhancing food security, and encouraging entrepreneurial activities.

About ICRISAT

The semi-arid tropics (SAT) encompasses parts of 48 developing countries including most of India, parts of southeast Asia, a swathe across sub-Saharan Africa, much of southern and eastern Africa, and parts of Latin America. Many of these countries are among the poorest in the world. Approximately one sixth of the world's population lives in the SAT, which is typified by unpredictable weather, limited and erratic rainfall, and nutrient-poor soils.

ICRISAT's mandate crops are sorghum, pearl millet, finger millet, chickpea, pigeonpea, and groundnut; these six crops are vital to life for the ever-increasing populations of the semi-arid tropics. ICRISAT's mission is to conduct research which can lead to enhanced sustainable production of these crops and to improved management of the limited natural resources of the SAT. ICRISAT communicates information on technologies as they are developed through workshops, networks, training, library services, and publishing.

ICRISAT was established in 1972. It is one of 18 nonprofit, research and training centers funded through the Consultative Group on International Agricultural Research (CGIAR). The CGIAR is an informal association of approximately 50 public and private sector donors; it is co-sponsored by the Food and Agriculture Organization of the United Nations (FAO), the World Bank, and the United Nations Development Programme (UNDP).