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SARP Research Proceedings

Applications of systems approaches in plant breeding

Proceedings of the SARP Applications Workshop held at the
International Rice Research Institute (IRRI), Los Baños, Philippines,
18 April - 6 May, 1994

P.K. Aggarwal, R.B. Matthews, M.J. Kropff & H.H. van Laar
(Editors)

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DLO-Research Institute for Agrobiology and Soil Fertility, Wageningen
WAU-Department of Theoretical Production Ecology, Wageningen
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Preface

Crop simulation models integrate interdisciplinary knowledge on the effect of climatic, edaphic and physiological factors, and biotic and abiotic stresses on crop growth, development and yield. These have been used for optimizing water and nutrient usage in cropping systems, for determining economic thresholds for pest management, for determining production potentials, and for agro-ecological zoning. There is now an increasing awareness of their potential in aiding the plant breeding process which, from selection of suitable parent lines through the release of a superior cultivar, takes a long time, sometimes upto ten years or more. Methods that improve the efficiency of the process will have a large impact on breeding programmes and their outputs.

A workshop was organized by the SARP project in April 1994 at the International Rice Research Institute (IRRI) to focus on the applications of crop models and other system tools in increasing the efficiency of plant breeding programmes. Plant breeders, physiologists, agronomists, soil scientists, statisticians, modellers and crop protection specialists of IRRI, National Agricultural Research Systems (NARS) and Wageningen participated in this meeting. This volume contains the papers presented at this workshop.

The papers presented are grouped into four sections. The first section provides a general introduction to the theme of the workshop and a framework for the applications of crop models in plant breeding. The next section documents views and expectations of breeders, statisticians and agronomists from crop modelling. The third section describes a number of case studies where applications of the framework are described in relation to (*i*) designing new plant types for increased yield potential, for greater weed competitiveness, and for mitigating climate change effects, (*ii*) increasing the efficiency of multi-location trials and the evaluation of large germplasm collections, and (*iii*) assisting in determining the suitable planting dates in the hybrid rice seed production programmes. Some papers document the level of variability available in major crop inputs related to main physiological traits. These papers present the first results of the on-going case studies. More complete details of these studies will become available later. The last section summarizes the major areas and the methodologies for use in each of these areas.

We acknowledge the invaluable help of Say Calubiran-Badrina in preparing all the figures, and Cecilia V. Lopez assisting in finalizing several papers.

Los Baños, Wageningen The Editors
May, 1995

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Systems approach to understanding genotype by environment interactions

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The success with the approach to solving food production problems in the 1960s and the 1970s of the International Rice Research Institute and other CGIAR centres is well known. At that time the imperative - the goal - was to increase the pile of rice. The concept to achieve that goal was based on a relatively simple model.

According to the fundamental model of applied genetics, the expression of phenotype - in this case, the yield of rice - is a function of three factors:

- the genotype (G),
- the environment (E), and
- the interaction of the genotype and environment (G × E).

In the 1960s, the objectives were:

- to increase the yield potential of the genotype,
- to develop host plant resistance to major pests,
- to enhance and minimize variation on the environment with water, fertilizer and chemicals to control pests, and
- to minimize G × E and identify technologies suitable to wide areas of adaptation.

The result was the 'green revolution', and the unprecedented increase in rice productivity, which resulted in adequate supplies of rice at prices affordable to the urban and rural poor.

Today, however, our goals have broadened. They include not just the well-being of present rice farmers and consumers, but also the generations to come, and particularly those with low income. In addition, we have a concern for the global environment.

Our simple model can still meet these new objectives, but we must change emphasis.

The genetic component

- * We must continue the search to increase basic yield-determining factors. In IRRI's mega project *Raising the irrigated rice yield plateau*, we targeted an increase in yield potential of up to 50%. The 'new plant type' combined with heterosis in tropical hybrid rice should increase irrigated rice yield potential to 15 t ha^{-1} in the dry season in the tropics.

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- We must provide more durable tolerance to biotic stresses by broadening the genetic base, and enhancing the diversity of the system at the level of genes, cultivars and species.

Thus, we envisage a continuation of our effort in the genetic improvement of rice and we add to that the use of new tools in biotechnology and the understanding of pest/host interactions. We also see an increasing concern for biodiversity. Nowhere is that more pronounced than in pest management, where IRRI research is concerned as much with the diversity of the biological agents that influence the resilience of the system, as to the diversity of the 'genes' and their deployment to minimize, in a durable manner, economic losses from pest damage.

The environmental component

- We must ensure the permanency of the resource base of the intensive food systems - the irrigated rice and the rice/wheat systems. We were able to intensify these systems because of early maturing, high yielding varieties, extended growing season (with irrigation), provision of external nutrients to support the increased demand of the cropping systems, and increased productivity of labour and decreased 'turnaround' time between crops. There are now disturbing signs about the long-term sustainability of these systems. We must understand the effect of the intensification on the processes that determine the capacity of the resource base to maintain the productivity of these systems.

The genotype × environment component

The wide adaptation concept - the need to minimize G × E (and maximize G) was successful for the rapid adoption of the seed-based technology of the 'green revolution' of the 1960s. But is it appropriate today? And is it appropriate for the more variable rainfed ecosystems, the rainfed lowlands and the uplands?

If we examine the relative contribution of G, E and G × E to total variance, we see a shift from a dominance of G in the uniform, irrigated environment, to G × E accounting for most of the variance in the rainfed ecosystems.

Now, instead of ignoring or attempting to reduce the G × E variability, we have to find ways to capture the favourable and repeatable G × E. We must not only utilize the G but also the favourable G × E which will provide for the efficient use of resources in a sustainable manner. There is a need to measure and characterize the resources of the ecosystems, and to understand how to maximize the capture and minimize their loss. The efficiency of use of these resources by the genotype(s) in the system must be increased.

The key, I believe, is to understand the processes and the traits that determine G × E. We must change from thinking globally and acting globally, to thinking globally (i.e. understanding processes) and acting locally (i.e. adapting to local resources).

This move from global to local adaptation needs a different approach - a systems approach - to conceptualizing and conducting research. Simulation models can be instrumental in this respect.

Systems approach

A new frontier in agricultural science is in the way we think, analyse, conceptualize and conduct our research. The new model and the new objective require a new approach - a systems perspective where the understanding of the whole is linked with the knowledge of the component parts. In a shift to a systems approach, however, we must remember that science is traditionally a reductionist process, and deals with the component pieces; it requires focus on the underlying processes and mechanisms. The systems approach will require more knowledge-based technologies - an integration of the component parts as, for example, in integrated pest management - than has been the experience in the past.

We can divide our research activities into four broad areas - four M's of research: Measurement, Mechanisms, Models and Methods.

I believe that in the 'seed-based', wide adaptation model, we were able to move quickly from Measurement - (the measurement of the variation in a segregating rice population) to Method (technique) the release of a selected cultivar. The central two components of understanding Mechanisms and Processes, and the ability to Model and predict their impact, were not needed for widespread adoption.

The focus on Measurement and Method has not been so successful for more complex technologies - for example our cropping and farming systems work, or for developing varieties for the variable environments. We need to match global knowledge with local applications. This will require an understanding of the mechanisms and processes that influence the use of resources and the use of models at all levels:

* Conceptual models as in the ideotype for higher yield - why not an ideotype for a system, a watershed?

* Process models that look at the interactions of processes, that ask the 'what if' question.

* Predictive models that will allow us to think globally and act locally.

Thus, in IRRI's medium term plan, there is a shift in research activities from the Measurement of resources, toward understanding of Mechanisms and processes and to the development of Models. There is less emphasis on Methods (new technologies) at IRRI, because these are being taken up by collaborating scientists in the National Agricultural Research Systems (NARS), who also participate in various networks.

In summary, the 1990s and beyond will see an extension of our model - a 'green evolution' where IRRI scientists are concerned as much about the environmental component of the base model as the genetic component. We must continue only with good science, but move to thinking globally and acting locally. There is a need for knowledge-based methods, rather than single, 'technology-based' ones, requiring more interdependence and less independence in our science.

We are pleased that this new approach of understanding Mechanisms and using Models has found a sound basis at the National Agricultural Research Systems as well through the SARP project. Through this collaborative effort a 'green evolution' will not be just an IRRI initiative, but a joint effort of the NARS, IRRI and the Wageningen systems group. It is of great significance that modelling, breeding and understanding of G × E are becoming integrated research activities through initiatives like this workshop.

A framework for applications of crop growth simulation models in plant breeding

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Abstract
A systems framework has been developed to use crop models and other quantitative tools, experiments, and data bases in plant breeding programmes in the project Simulation and Systems Analysis for Rice Production (SARP). In this paper, we document the specific objectives and the methodology being used in this programme.

Introduction

Systems analysis and crop growth simulation are relatively recent techniques that offer a means of quantitative understanding of the effects of climatic, edaphic and agronomic management factors on crop growth and productivity in different environments. Since crop models integrate the effects of different factors on productivity they provide a unique opportunity to supplement results of field trials. The models can also be used to evaluate the effect of numerous combinations of factors e.g. years (climatic variability) × cultivar × regions × water availability × sowing time in a relatively short time. Such models are increasingly being used for environmental characterization and agro-ecological zoning, defining research priorities, technology transfer, estimating production potentials, evaluating the interaction effects of fertility, planting dates, soil type and climatic variability on crop productivity, strategic and tactical decision making and for predicting the effects of climatic change and climatic variability (Penning de Vries et al., 1993). In the past, there have been a limited number of applications of crop models in crop improvement programmes but recent studies indicated their potential in increasing the efficiency of plant breeding.

The framework

A systems framework has been developed to use crop models and other tools, experiments, and data bases in plant breeding programmes (Fig. 1) in the project Simulation and Systems Analysis for Rice Production (SARP, ten Berge et al., 1994). In this introductory paper, we

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document briefly the specific objectives, the crop simulation model ORYZA1 (Kropff et al., 1994a), other tools and methodologies being used in the plant breeding application programme of the SARP project.

Objectives of the SARP programme on crop breeding

The objective of the crop breeding programmes is the development of improved breeding lines/varieties for a specific product with a defined quality for target environments. For most crops this breeding process involves a time investment of 10 - 15 years. Two major activities in this process are - (*i*) conceptualizing plant type design, identification of suitable parents and their hybridization, and (*ii*) the multi-location evaluation for determining genotype by environment interactions (Hunt, 1993). Some kind of conceptual design has always been used in breeding through the identification of parents with complementary traits which were expected to improve existing cultivars when combined. An example of an improved plant type design that had a major impact on agricultural production is the short stature design for cereals that was developed in the 1960s.

The issue of designing ideotypes now needs a fresh initiative in the context of the large increase in food production required to feed the growing population. A systems approach may help in optimizing local agricultural production systems. This approach will involve not only improved crop management systems, but also new crop types. Crop ideotype designs should then be based on sound physiological understanding of the system and its interaction with edaphic, climatic, biotic and management factors. Donald (1962) identified the importance of

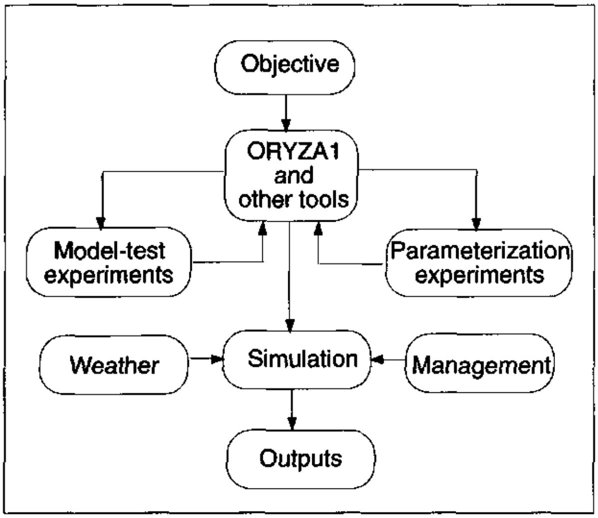

Figure 1. A framework for the application of crop models in plant breeding.

basic knowledge on the processes driving the production of dry matter, and economic yield formation. This led to a design driven breeding approach (Donald, 1968). In a recent review, however, Hunt (1993) concluded that only a few breeding programmes have adopted the concept of a formal ideotype design as a major breeding activity. With the advancement of ecophysiological systems modelling of crops in the past decades, the potential to integrate physiological/morphological process level knowledge to design new plant types has emerged. Few examples of such an approach in rice are now available (Dingkuhn et al., 1991; Penning de Vries, 1991; Kropff et al., 1994b; Aggarwal et al., 1995).

The second important activity in plant breeding programmes is the multi-location evaluation of plant breeding lines. This is a laborious, time consuming and expensive process. Crop models that are sensitive to varietal differences can be used together with historical weather data to simulate genotype by environment interactions and thus speed up the efficiency of multi-location evaluation.

Crop model

ORYZA1 is the model used in the SARP application programme on plant breeding. The model is based on INTERCOM (Kropff & van Laar, 1993), SUCROS (Spitters et al., 1989), and the MACROS module L1D (Penning de Vries et al., 1989). The model framework relies on input of detailed ecophysiological information, that is crucial for theoretical evaluation of plant types for increased yield potential.

The general structure of the ORYZA1 model is presented in Fig. 2. Under favourable growth conditions, light and temperature are the main factors determining crop growth rate. From the leaf area index, the vertical distribution of leaf area and light profile within the canopy are calculated. Single leaf photosynthesis is calculated based on leaf N concentration and light intensity, and the photosynthesis profile of the full canopy is obtained from the light and N canopy profiles. The maximum rate of CO_2 assimilation at high radiation levels (the asymptote; A_m) depends upon the leaf N concentration. The relationship between A_m and the leaf N concentration is linear and shows little variation across environments and species.

In the model, leaf N content is expressed on a leaf area basis. The vertical distribution of N in the canopy profile is accounted for by a generic exponential distribution derived from the detailed data sets of our recent experiments. Total daily CO_2 assimilation is then obtained by integrating the instantaneous rates of CO_2 assimilation over the LAI on a daily time-step. Net daily growth rate (kg ha^{-1} d^{-1}) is obtained after subtraction of respiration requirements and accounting for energy losses in the conversion of carbohydrates into structural dry matter.

The accumulated dry matter is partitioned among the various plant organs. Phenological development rate is tracked as a function of ambient mean daily air temperature. When the canopy is not yet closed, leaf area development is calculated from mean daily temperature. When the canopy closes, the increase in leaf area is obtained from the increase in leaf dry matter accumulation and specific leaf weight. Calculation of net daily growth rate combines the dry

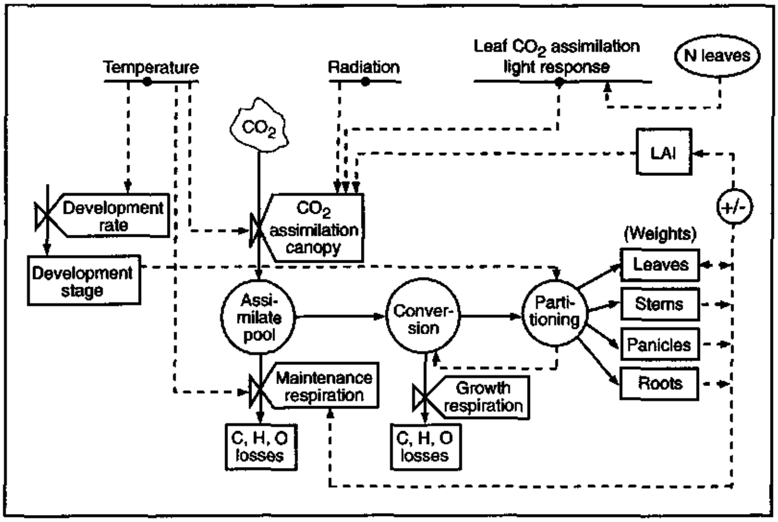

Figure 2. A schematic representation of the model ORYZA1. Boxes are state variables, valves are rate variables, circles are intermediate variables. Solid lines are flows of material, dotted lines are flows of information. Source: Kropff et al., 1994a.

weight increase of leaves, stems, and grain using partitioning coefficients that depend on the stage of phenological development. The number of spikelets per unit area is determined by the crop growth rate between panicle initiation and flowering. Adverse temperature at the time of meiosis/pollination may result in spikelet sterility. Grains accumulate dry matter if available and until maximum grain weight (input in the model) is reached or when the crop reaches physiological maturity.

Input requirements of the model are: geographical latitude, daily maximum and minimum temperatures, solar radiation, and dates of seeding and transplanting. Varietal characterization is required in the form of phenological development rates, relative leaf area growth rate, specific leaf area, spikelet formation factor, 1000 grain weight, leaf N content and fraction of stem reserves.

Other tools

To extract crop parameters from experimental data sets, tools have been developed in the SARP project. DRATES (Kropff et al., 1994a) provides the rates of crop development in different stages. EXTRACT (Matthews, unpublished) using DSSAT input files (Tsjui et al., 1994) extracts the complete range of input parameters from an experiment and creates input data files for ORYZA1. To create random variation in input parameters such as those required for plant type design studies, RIGAUS (Bouman & Jansen, 1993) is very useful. By specifying, the lower and upper limits of parameter values and some information on distribution properties of these values, one can obtain a wide array of 'hypothetical varieties' with different combinations of parameters.

Validation and parameterization experiments

The crop model is first validated with the experimental data in the target environment, in particular, for the capability to simulate varietal differences. ORYZA1 has been validated using a number of experiments conducted in several environments varying in climate, fertility, genotype and management (Kropff et al., 1994a). The relative contribution of environmental variables, varietal characteristics, and crop N status to the accuracy of model simulations was evaluated by comparing predicted to observed rice yields when different parameter inputs were used to explain yield variation due to N treatment × variety × year effects (Kropff et al., 1994a). Reasonable simulation results were obtained when the variety-specific coefficients for development rate in the vegetative stage (DVRJ) and grain filling phase (DVRR), the effect of N status on the relative growth rate of the leaf area (RGRL), and the measured specific leaf N were input in the model. This indicates that the large differences in yield due to season, variety, year, and N supply can be explained by the ecophysiological ORYZA1 model with a relatively small number of variables as input. It also emphasises the importance of N on leaf area development and photosynthesis for explaining yield differences.

For using crop models for design of plant types it is important to know the range of variation available in germplasm in critical plant parameters. Often, additional experiments need to be done for this. Similarly, for using models in genotype by environment interaction studies, plant input parameters need to be determined for the breeding lines.

Often the results of validation and parameterization may show linkages between parameters and insensitivity of some parameters and/or over-sensitivity of some others. In such cases, there is a feedback possibility for the improvement of crop models and other tools.

Simulation

If model performance is satisfactory in the target environment, it can be used to predict crop growth and development in different situations. These situations can be differences in plant parameters (genetic variance) or variation in temperature and radiation (environmental variation), or management (date of planting, population, N content) or a combination of all. By varying the plant input parameters within the range determined from parameterization experiments and using weather data of target environments, and the desired management, one can determine the effect of various traits on the performance of rice. Of course, this assumes that there is no correlation between input parameters. Any such correlation should be built in the models as feedback. The whole process can be repeated a number of times depending upon the availability of weather data. Thus, a number of options can be evaluated in a short time and the 'optimal' solution identified.

SARP Application Workshop

A workshop was organized at IRRI in April 1994, in which plant breeders, physiologists, agronomists, meteorologists, statisticians and crop modellers participated. The purpose of this meeting was to discuss this framework. Expectations of plant breeders from modelling were highlighted, feasible opportunities were summarized, hands-on training was given on the model ORYZA1 and other tools, and case studies were presented to illustrate different parts of this framework. Based upon the discussions, the SARP collaborators formulated their case studies for future work. The subsequent papers present expectations, opportunities and case studies for using crop models in plant breeding.

References

Aggarwal, P.K., M.J. Kropff, R.B. Matthews & C.G. McLaren, 1995. Using simulation models to design new plant types and to analyse genotype and environment interactions. In: M. Cooper & G. Hammer (Eds), The analysis and exploitation of plant adaptation in agricultural crop improvement programs. CAB, Wallingford (in press).

Berge, H.F.M. ten, M.J. Kropff & M.C.S. Wopereis (Eds), 1994. The SARP project phase III (1992-1995) Overview, Goals, Plans. SARP Research Proceedings, IRRI, AB-DLO, TPE-WAU, Wageningen, 124 pp.

Bouman, B.A.M. & M.J.W. Jansen, 1993. RIGAUS: Random input generator for the analysis of uncertainty in simulation. CABO-TPE Simulation Reports no 34, 26 pp.

Dingkuhn, M., F.W.T. Penning de Vries, S.K. De Datta & H.H. van Laar, 1991. Concept for a new plant type for direct seeded flooded tropical rice. In: Direct seeded flooded rice in the tropics. Selected papers from the International Rice Research Conference, 27-31 August 1990, Seoul, Korea. IRRI, Los Baños, Philippines, pp. 17-38.

Donald, C.M., 1962. In search of yield. J. Aust. Inst. Agric. Sci. 28: 171-178.

Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.

Hunt, L.A., 1993. Designing improved plant types: a breeder's viewpoint. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 3-17.

Kropff, M.J. & H.H. van Laar (Eds), 1993. Modelling crop-weed interactions. CAB, Wallingford and IRRI, Los Baños, 269 pp.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994a. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, AB-DLO and TPE-WAU, Wageningen and IRRI, Los Baños, 110 pp.

Kropff, M.J., K.G. Cassman, S. Peng, R.B. Matthews & T.L. Setter, 1994b. Quantitative understanding of yield potential. In: K.G. Cassman (Ed.), Breaking the yield barrier. IRRI, Los Baños, pp. 21-38.

Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: F.W.T. Penning de Vries, M.J. Kropff, P.S. Teng & G.J.D. Kirk (Eds), Systems simulation at IRRI. IRRI Research Paper Series, November 1991, Number 151, pp. 13-19.

Penning de Vries, F.W.T., D.M. Jansen, H.F.M. ten Berge & A. Bakema, 1989. Simulation of ecophysiological processes of growth of several annual crops. Simulation Monographs 29. Pudoc, Wageningen and IRRI, Los Baños, 271 pp.

Penning de Vries, F.W.T., P.S. Teng & K. Metselaar (Eds), 1993. Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht/Boston/London and IRRI, Los Baños, 542 pp.

Spitters, C.J.T., H. van Keulen & D.W.G. van Kraalingen, 1989. A simple and universal crop growth simulator: SUCROS87. In: R. Rabbinge, S.A. Ward & H.H. van Laar (Eds), Simulation and systems management in crop protection. Simulation Monographs, Pudoc, Wageningen, pp. 147-181.

Tsjui, G.Y, G. Uehara & S. Balas (Eds), 1994. DSSAT version 3: A decision Support System for Agrotechnology Transfer (Vols 1, 2 & 3). International Benchmark Sites Network for Agrotechnology Transfer (IBSNAT), University of Hawaii, Honolulu, Hawaii, ISSN 0883-8631.

Expectations of plant breeders from crop physiology and modelling

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Abstract
The coming decades pose a tremendous challenge to agricultural scientists to develop technology for higher food production. From the plant breeding perspective, the principal challenges are attaining higher yield potential in favourable environments, increasing stability and yield potential in unfavourable environments, incorporation of durable disease and pest resistance in new varieties, improvement in grain quality, and development of more efficient breeding methods and selection procedures. In this paper, we have identified areas where we look forward to contributions from crop physiology and simulation modelling in meeting these challenges.

Introduction

Plant breeding has been practised since the domestication of crop plants 10,000 years ago. The application of science to plant breeding, however, did not begin until the rediscovery of Mendel's law in 1901. Nevertheless, even by practising the policy of 'crossing the best with the best and hoping for the best' (Marshall, 1991), plant breeding was able to develop better varieties in many crops. A typical example is the development of so-called modern varieties of major cereals, particularly rice and wheat, which resulted in the 'green revolution' of the sixties. This enabled many countries, particularly in the developing world having a rapid population growth, to meet their food demands. However, 30 years later, we are again faced with a similar crisis. The world population is still growing rapidly and may reach 8 billion by the year 2020. Most of these people will be in developing countries where rice is the major staple food. It is estimated that the world's annual rough rice production must grow from today's 520 Mt to 880 Mt in 2025 - an increase of 70%. In many parts of the world there is still considerable yield gap, which should be able to meet, at least partially, the increased food needs. But in other parts, in particular, in the favourable environments of China, Korea, and south and south-east Asian countries, rice yields are reaching close to potential yields. Eighty percent of the current rice production of the world comes from such favourable areas. The world will continue to be dependent on these areas for greater rice production.

At the same time, we are faced with stagnating or declining yield potential (Kropff et al.,

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1994a). The yield potential of rice has not increased above 10 t ha^{-1} ever since the release of IR8, 30 years ago, although significant achievements have been made in attaining yield stability, increasing per day productivity and improving grain quality. There is an urgent need to secure the past yield gains and further increase the yield potential of rice and other major food crops in favourable areas.

Rainfed lowlands, uplands and deep water environments constitute a large proportion of rice cultivation in Asia. In these unfavourable environments, crops can suffer from drought, salinity, floods, weeds and other soil constraints. Few varieties and/or production technologies have been developed for such environments. Strong genotype × environment × management interactions demand that varieties tailored to specific agro-ecosystems be developed.

Thus, there is a tremendous challenge facing agricultural scientists to develop technologies for greater food production in the coming decades. This increase has to be achieved on less land with less inputs such as labour, water, nitrogen and pesticides in such a way that the scarce natural resources remain conserved. From the plant breeding perspective, the principal challenges can be summarized as follows:

- Attaining higher yield potential in favourable environments,
- Increasing stability and yield potential in variable environments,
- Incorporating durable disease and insect resistance,
- Improving grain quality, and
- Improving efficiency of breeding methods and selection procedures.

In facing these challenges, plant breeders expect scientific support from disciplines such as genetics, pathology, entomology, physiology and more recently tissue culture and molecular biology. So far, there has been limited direct use of the physiological knowledge in plant breeding (Rasmusson, 1987; Marshall, 1991) although Donald (1968) with his concept of plant ideotype laid the foundation for collaborative research between breeders and plant physiologists. Availability of process-based crop models and other systems approaches has provided yet another opportunity to accelerate the use of plant physiological knowledge in agricultural planning and development. There have been rapid developments in the fields of crop physiology and modelling in the last two decades (Penning de Vries et al., 1993; Goldsworthy & Penning de Vries, 1994). Most of this research was focused on developing better understanding of crop-weather interactions and for developing improved agronomic production technology. Use of crop modelling may also be helpful in increasing the efficiency of plant breeding. In this paper, we present our view point of where breeders would like to have the physiological and modelling inputs for the above mentioned challenges in rice.

Higher yield potential in favourable environments

Increasing yield potential is one of the principal objective of rice breeding programmes. A major activity in this is to conceptualize plant type designs and identification of genetic donors for the important traits. Exploitation of heterosis is another avenue to increase rice yield potential. In the current scenario, there is also increasing recognition for sustainability issues. Thus, the resource use efficiency in a rice production system is as important as increasing the yield potential. Nitrogen is the most used fertilizer in rice fields. Direct seeding is catching up in many parts of Asia because of labour shortages. We have, therefore, to develop rice varieties with greater nitrogen use efficiency and competitiveness to weeds, common in a direct seeding environment.

New plant type designs

The challenge in ideotype breeding is the identification of critical traits, which on combination will result in higher yield potential. Donald (1968) sparked off physiological research on ideotypes, today several of them have been proposed by different scientific groups for major crops. However, not many breeders practised ideotype breeding because of lack of convincing demonstration of the importance of a specific trait, large number of traits (as against one trait-yield), limited genetic variability in suitable donors and pleiotropic effects. The problem is confounded with the difficulty in screening methods for some of these traits. Molecular approaches may gradually become available for marker-aided selection for yield components and other quantitative traits (Bennett et al., 1994). Crop models need to identify critical traits and define breeding goals for different ecosystems. For this, crop models should be robust, based on sound physiological understanding and tested in targeted environments. Recently, simulation models have been used to design new plant types in rice (Dingkuhn et al., 1991; Penning de Vries, 1991; Kropff et al., 1994b; Aggarwal et al., 1995). These studies have identified several traits relating to source size and sink capacity that need to be changed to obtain a quantum increase in yield potential. However, many of the proposed traits are not easy to measure in screening large number of breeding lines. It would be better if traits are identified based on a teams' decision comprising of breeders, physiologists, agronomists, and modellers to enable the use of interdisciplinary knowledge.

At IRRI, one of our major goals is to develop rice varieties with 30 - 50% higher yield potential than the existing semi-dwarf varieties for tropical environments (Khush, 1990). Based on earlier conceptual physiological and simulation modelling research, we have identified the following characteristics that are desirable in new plant type (IRRI, 1989; Khush, 1990; Fig. 1):

- Low tillering capacity with 3 - 4 panicles per plant when direct seeded,
- No unproductive tillers,
- 200 - 250 grain per panicle,
- 90 - 100 cm tall,
- Sturdy stems,
- Vigorous root system,
- Multiple disease and insect resistance,
- 110 - 130 days growth duration,
- Harvest index of 0.6, and
- 13 - 15 t ha^{-1} yield potential.

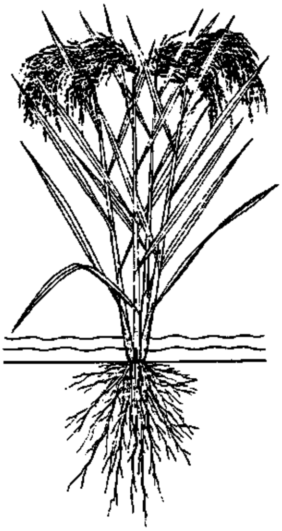

Figure 1. The new plant type in direct-seeded irrigated rice. Source: IRRI, 1989.

We now have breeding lines with characteristics similar to this new plant type, based on tropical *japonicas*. These lines have semi-dwarf stature, sturdy stems, dark green and thick leaves, 8 - 10 productive tillers when grown at low densities, no unproductive tillers and 150 - 200 grains per panicle. Insect and disease resistance, and suitable grain quality still needs to be incorporated into these lines. At present, these lines are being tested in the field. Crop modelling can assist in evaluating the suitability of this plant type and in suggesting alternate ones. Lack of genetic variability in *indica* rices, which earlier limited the choice of donors to the primary gene pool, is no more a major constraint. The availability of tissue culture techniques such as embryo rescue, protoplast fusion which alone or in combination with genetic transformation techniques now allows breeders to exploit genetic variability even from secondary and tertiary gene pools. Crop models can also assist in extrapolating the performance of these lines in different regions and rice growing seasons of Asia and in determining suitable agronomic management for them. We also need to know if different traits would be required in some specific ecosystems.

Exploitation of heterosis

Hybrid rices, by exploiting the phenomenon of hybrid vigour, have shown a 20 - 30% increase in yield potential in several crops. In China, hybrid rices helped increase rice production by nearly 200 Mt from 1976 to 1991 (Yuan, 1994). However, these hybrids perform poorly in tropical environments. Nevertheless, recent research has indicated the superiority of *indica* rice hybrids over *indica* rice inbreds in tropical environments as well (Virmani et al., 1991; Virmani et al., 1994). Increased yield of tropical rice hybrids was due to heterosis in total biomass, early vegetative growth, spikelet number and to some extent heterosis for individual grain size (Ponnuthurai et al., 1984). Hybrids between *indica* and tropical *japonica* rices may show even greater heterosis due to the genetic diversity of the parents (Bharaj et al., 1994).

A major constraint in utilizing hybrid rice technology is the need to obtain fresh hybrid rice seeds for every planting season and the high cost of hybrid rice seed production. Using the available technology of hybrid rice seed production (Virmani & Sharma, 1993), yields of 1 - 2 t ha^{-1} of hybrid seed and 1.5 - 2.0 t ha^{-1} of pollen parent seed have been obtained. This limited seed production is largely due to poor outcrossing and asynchronous flowering of male and female parents (Table 1). Environmental factors such as temperature, humidity and wind speed at the time of pollination and fertilisation play a great role in regulating outcrossing percentage. It is a challenge to crop modellers to develop suitable simulation models to mimic the various processes and their environmental regulation that affect the magnitude of outcrossing and thus seed setting. Such models, if available, would be of great value to plant breeders in guiding development of strategies for increasing hybrid rice seed production, such as determining the optimum time of sowing of the two parents. National Agricultural Research Systems and private seed companies are making efforts to identify suitable areas and seasons for hybrid rice production. Can crop models provide this information in a relatively shorter time frame?

Efficiency of resource use

An eco-regional approach is one of the new paradigms in agricultural research. The main guiding principles of this approach for developing countries is increasing crop productivity with efficient use of external inputs such as fertilizers, irrigation, labour and pesticides while maintaining or increasing the natural resource base. Nitrogen is one of the key nutrients that limit crop growth and production in many production situations. In many such systems, it should be possible to optimize N use efficiency by changing crop management practices. For example, recent studies conducted at IRRI have shown that the 'yield decline' in rice observed in experimental fields could be corrected by suitable nutrient management (Cassman et al., 1993). Nevertheless, there are significant varietal differences in nitrogen use efficiency. Can crop physiology and models indicate the key traits for increased N use efficiency?

The practise of direct-seeding is spreading in many parts of Asia because of the ready

Table 1. Hybrid seed production in tropics and subtropics obtained on CMS IR62829 A, 1990 - 1991.

Location	Seed yield ($t\ ha^{-1}$)	Outcrossing rate (%)
IRRI	0.8 - 1.3	27 - 37
Philippines	0.8 - 1.2	23 - 43
India		
Northwestern	0.9 - 1.7	34
Southern	0.6 - 1.9	-
Vietnam, Southern	0.7 - 2.2	19 - 33

availability of herbicides and unavailability of labour. However, the greater use of pesticides may not be environment friendly. We, therefore, need to develop varieties with greater competitive ability against weeds. Competitive ability differs between crops and between cultivars of the same species. Often there is a negative correlation between competitive ability and yield potential (Moody & De Datta, 1982). Is it possible for crop models to suggest with confidence the plant traits that will provide the rice plant greater competitive ability against weeds and yet not compromise on yield potential?

Increased productivity and stability in unfavourable environments

Unfavourable environments are characterized by variable water regimes (drought as well as submergence) and by soil toxicities and deficiencies. Grain yields in these environments are low and unstable. Progress in developing improved varieties for these environments has been extremely slow. However, some of the most disadvantaged farmers live in such environments. We have redoubled our efforts to develop improved varieties for these variable environments. First, we have attempted to characterize and classify the major unfavourable rice growing environments into five major categories. Representative sites have been identified for each of these categories for selection and evaluation of breeding materials. We have also refined our breeding methodologies with a goal to select for traits for drought resistance, submergence tolerance, yield stability, and wide adaptability in areas of unfavourable and erratic rainfall (Khush & Virmani, 1991). Strategic research is needed to determine the impact of different traits on adaptability and yield potential.

Crop physiology and models have a greater role to play in unfavourable environments. Together with Geographical Information Systems, they should help in biological characterization of the physical environment (geography, soil, climate, etc.), and thus define key environmental domains for which improved varieties are to be developed. A modelling approach can also provide estimates of yield probability based on our understanding of genotype by environment interactions. In addition, crop simulation should assist in fine tuning variety design and selection procedures. A large number of traits have been proposed earlier for drought prone environments, but we need to know their real worth before spending our limited resources in breeding for them.

Greater resistance to pests and diseases

The plant breeding efforts to incorporate insect and disease resistance into crops have been very successful. Availability of molecular techniques has further enhanced our ability to incorporate genes for insect and disease resistance in rice. We are now attempting to incorporate durable resistance to pests.

Systems approaches have been used in recent times to investigate the dynamics of pest population, frequency and intensity of disease pressures and to determine opportunities for reducing indiscriminate use of pesticides. This has found applications in estimating yield losses due to disease or insect damage and for determining the sensitivities of crops to timing and intensities of damage in specific environments. The development and use of pest-crop models will provide a better understanding of the epidemiological effects that various resistance components may have on reducing the rate of pest infection/epidemics. Such information will help in developing better screening methods for evaluating pest resistant varieties. Through a greater holistic understanding of crop-pest interactions, it should be possible for systems scientists to suggest traits required in a variety under different agronomic and pest environments.

Improvement in grain quality

Cereals including rice, wheat, maize, sorghum and millets provide a large proportion of the food intake of people in developing countries. However, they have poor amino acid profiles. Improving the level of such limiting amino acids as lysine will greatly help in solving malnutrition problem. Nutritional quality is therefore always an important objective of plant breeding programmes. Quality varies between crops and between varieties of the same species. Breeding for higher yield does not necessarily mean lowering grain quality. Several high yielding rice varieties with acceptable grain quality have been bred by plant breeders around the world.

Protein content is an important trait that conventional plant breeding has not significantly improved. We hope that biotechnology tools such as induction and selection of amino acid overproducing mutants at cellular level will help improve the lysine content of rice. There is considerable influence of soil nutrient management on grain nitrogen content and hence protein content. Crop physiology and models may be able to identify agronomic and breeding opportunities for increasing grain N content without sacrificing yield potential.

Scented rice is preferred in many parts of the world and fetches a higher price in the market. The aroma content of these varieties changes with location indicating significant genotype by environment interactions for this characteristic. However, the specific agro-climatic requirements of these rices are not clear. Perhaps crop physiology/biochemistry and modelling can identify the specific cultural requirements for combining desired aroma quality with high yield potential.

Improving efficiency of breeding programmes

Development and release of a variety is a complex process that may extend over a period of 10 - 15 years. Assistance from other research disciplines to increase the efficiency of this process would be very welcome. We have great expectations from tissue culture and molecular biology in reducing the breeding cycle of varieties and in exercising marker-based selection. There are a number of opportunities for plant physiologists and modellers as well, to develop methods and tools for increasing the efficiency of plant breeding processes.

The entire process of variety development can be divided into several steps (Fig. 2). The first task of the plant breeder is to conceptualize a plant type design and then to identify the appropriate donors for the desired traits. As discussed earlier, crop modelling can assist in defining critical traits. Once parents have been identified, hybridization is done, and F_1 and F_2 offspring are grown in spaced populations. Decisions are needed at this stage to reject relatively unsuitable plants (or select few suitable plants) from a large number of segregating populations. The breeder uses his judgement to predict the behaviour of these spaced plants when grown in a community. This is not an easy task. Is it possible for models to predict the expected plot yield of such spaced plants, as in F_2 generation, considering all inter-plant competition aspects? Or, can physiologists and modellers suggest suitable criteria to identify best plants? Needless to say, these criteria should be easy to measure and available to a large number of breeders and their technicians. At present, we generally screen for easy to measure/score/observe criteria such as early seedling vigour, canopy architecture, days to 50% flowering, crop duration, plant height, numbers of tillers, panicles and spikelets per panicle, and grain type. Fortunately, RFLP maps are now becoming available that can be used to tag genes governing various agronomic traits, including quantitative trait loci. This would help plant breeders in marker-based selection for complex traits which have been difficult to select through conventional approaches. In F_3 to F_7/F_8 pedigree nurseries are grown, where lines that fit the conceptual plant type and have desirable agronomic characters are selected. We need sound advise on optimal spacing that should be maintained in these nurseries for obtaining the best expression of breeding lines.

Once the breeding lines have become homozygous, they are bulked and then tested in observational, replicated and multi-location yield trials. These multi-site trials are expensive to conduct and need several crop seasons to understand genotype by environment (G × E) interac-

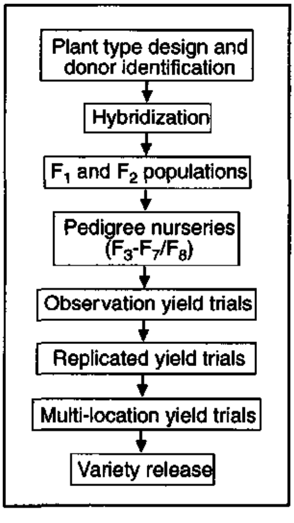

Figure 2. The plant breeding process for variety development.

tions. If crop models can simulate this G × E interaction, it would be possible to reduce the number of sites/seasons and thus increase the efficiency of the whole plant breeding process of variety development. The expectations from crop models in analysing, interpreting and extrapolating G × E interactions are discussed in detail elsewhere in these proceedings (Chaudhary, 1995; McLaren, 1995).

Conclusions

Plant breeding is a complex, laborious and time consuming process. Our current physiological knowledge has not yet been used directly in plant breeding. There are a number of opportunities for crop physiology and modelling to assist in increasing the efficiency of plant breeding programmes. However, for these applications, crop models should be robust in their scientific quality, sensitive to a breeders requirements and easy to use. Case studies are needed to demonstrate the usefulness of the systems approach in crop improvement programmes.

References

Aggarwal, P.K., M.J. Kropff, R.B. Matthews & C.G. McLaren, 1995. Using simulation models to design new plant types and to analyse genotype and environment interactions. In: M. Cooper & G. Hammer, (Eds), The analysis and exploitation of plant adaptation in agricultural crop improvement programs. CAB, Wallingford (in press).

Bennett, J., D.S. Brar, G.S. Khush, N. Huang & T.L. Setter, 1994. Molecular approaches. In: K.G. Cassman (Ed.), Breaking the yield barrier. IRRI, Los Baños, pp. 63-76.

Bharaj, J.S., S.S. Virmani & G.S. Khush, 1994. Yield heterosis in Indica/Tropical japonica and Indica/Indica crosses of rice. Agron. Abst., Amer. Soc. Agron. Meeting, Seattle, Washington, Nov 13-18, 1994, pp. 104.

Cassman, K.G., M.J. Kropff, J. Gaunt & S. Peng, 1993. Nitrogen use efficiency of rice reconsidered: What are the key constraints? Plant and Soil, 155/156: 359-362.

Chaudhary, R.C., 1995. Global evaluation of rice genotypes through INGER - expectations from crop modelling. This volume.

Dingkuhn, M., F.W.T. Penning de Vries, S.K. De Datta & H.H. van Laar, 1991. Concept for a new plant type for direct seeded flooded tropical rice. In: Direct seeded flooded rice in the tropics. Selected papers from the International Rice Research Conference, 27-31 August 1990, Seoul, Korea. IRRI, Los Baños, Philippines, pp. 17-38.

Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.

Goldsworthy, P. & F.W.T. Penning de Vries, 1994. Opportunities, use, and transfer of systems research methods in agriculture to developing countries. Kluwer Academic Publishers, Netherlands, 366 pp.

IRRI, 1989. IRRI towards 2000 and beyond. International Rice Research Institute, P.O. Box

933, 1099 Manila, Philippines, 66 pp.

Khush, G.S., 1990. Varietal needs for environments and breeding strategies, In: K. Murlidharan & E.A. Siddiq (Eds), New frontiers in rice research. Directorate of Rice Research, Hyderabad, India, pp. 68-75.

Khush, G.S. & S.S. Virmani, 1991. Rice breeding strategies for the nineties. In: P. Deturck & F.N. Ponnamperuma (Eds), Rice production on acid soils of the tropics. Institute of fundamental studies, Kandy, Sri Lanka, pp. 227-233.

Kropff, M.J., K.G. Cassman & H.H. van Laar, 1994a. Quantitative understanding of the irrigated rice ecosystem and yield potential. In: S.S. Virmani (Ed.), Hybrid rice technology, new developments and future prospects. International Rice Research Institute, Los Baños, pp. 97-113.

Kropff, M.J., K.G. Cassman, S. Peng, R.B. Matthews & T.L. Setter, 1994b. Quantitative understanding of yield potential. In: K.G. Cassman (Ed.), Breaking the yield barrier. IRRI, Los Baños, pp. 21-38.

Marshall, D.R., 1991. Alternative approaches and perspectives in breeding for higher yields. Field Crops Res. 26: 171-190.

McLaren, C.G., 1995. Combining statistics and crop models for improved plant breeding strategies. This volume.

Moody, K. & S.K. De Datta, 1982. Integration of weed control practices for rice in tropical Asia. In: M. Soerjani, D.E. Barnes & T.O. Robertson (Eds), Weed control in small farms. Asian-Pacific Weed Science Society, Biotrop Special Publication no. 15, Bogor, pp. 37-47.

Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: F.W.T. Penning de Vries, M.J. Kropff, P.S. Teng & G.J.D. Kirk (Eds), Systems simulation at IRRI. IRRI Research Paper Series, November 1991, Number 151, pp. 13-19.

Penning de Vries, F.W.T., P.S. Teng & K. Metselaar (Eds), 1993. Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht/Boston/London and IRRI, Los Baños, 542 pp.

Ponnuthurai, S., S.S. Virmani & B.S. Vergara, 1984. Comparative studies on the growth and grain yield of some F1 rice hybrids. Philip. J. Crop Sci. 93: 183-193.

Rasmusson, D.C., 1987. An evaluation of ideotype breeding. Crop Sci. 27: 1140-1146.

Virmani, S.S. & H.L. Sharma, 1993. Manual for hybrid rice seed production. IRRI, Los Baños, Philippines.

Virmani, S.S., J.B. Young, H.P. Moon, I. Kumar & J.C. Flinn, 1991. Increasing rice yield through exploitation of heterosis. IRRI, Los Baños, Philippines.

Virmani, S.S., G.S. Khush & P.L. Pingali, 1994. Hybrid rice for tropics: potentials, research priorities and policy issues. In: R.S. Paroda & Mangla Rai (Eds), Hybrid research and development needs in major cereals in Asia-Pacific regions. FAO Regional Office, Bangkok, Thailand, pp. 61-86.

Yuan, L.P., 1994. Increasing yield potential in rice by exploitation of heterosis. In: S.S. Virmani (Ed.), Hybrid rice technology: new developments and future prospects. IRRI, P.O. Box 933, Manila 1099, Philippines, pp. 1-6.

Global evaluation of rice genotypes through INGER - expectations from crop modelling

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Abstract

This paper summarizes the current status of INGER and the mechanism of global testing of elite rice germplasm. The future focus of the programme is illustrated. A number of issues where crop modelling could help plant breeders and INGER have been raised. These collaborative studies and model applications may increase the efficiency of global germplasm testing. A work plan needs to be charted and implemented.

Introduction

Several networks have been established at international, national and regional level to test crop germplasm over a broad range of environments, to provide opportunities for scientists to form structured working partnerships that boost research efficiency by saving on time and reducing costs and duplication and shorten time for varietal development and thus rapid transfer of new genetic technology to the farmers. The benefits of such networking are tremendous, especially in the countries with limited funds and scientific manpower.

The international network for genetic evaluation of rice

The International Network for Genetic Evaluation of Rice (INGER) has been conducting global evaluation of rice germplasm since 1975 (it was known as International Rice Testing Program (IRTP) until 1988) with the following main objectives:

- To make the worlds elite rice germplasm available to all rice scientists for direct use or in crosses within breeding programmes,
- To provide rice scientists with an opportunity to assess the performance of their own advanced breeding lines over a wide range of climatic, cultural, soil, disease and insect-pest conditions,
- To identify genetic sources of resistance to major biotic stresses and tolerance for abiotic stresses,

Eds P.K. Aggarwal, R.B. Matthews, M.J. Kropff & H.H. van Laar
Applications of systems approaches in plant breeding. SARP Research Proceedings, AB-DLO, TPE-WAU, Wageningen and IRRI, Los Baños (1995), pp. 23-30.

- To monitor and evaluate the genetic variation of pathogens and insect-pests,
- To serve as the centre for information exchange on how varietal characteristics interact with diverse rice growing environments, and
- To promote cooperation and interaction among rice improvement scientists.

The networking in INGER is unique with a multi-lateral flow of breeding material and information, and a commitment of resources from participating nations. Almost 1000 rice scientists from National Agricultural Research Systems (NARS) in about 95 countries in Asia, Africa, and Latin America have been participating in this global network coordinated by International Rice Research Institute (IRRI, Philippines) (Table 1). Other international centres (IARC) such as Centro Internacional de Agricultural Tropical (CIAT, Columbia), International Institute of Tropical Agriculture (IITA, Nigeria), and West Africa Rice Development Association (WARDA) work together with IRRI. Agronomists, physiologists, plant pathologists, entomologists, soil scientists of IARCs and NARS join plant breeders in germplasm evaluation. At IRRI all divisions, centres, programmes and consortia are involved in the network.

INGER has two types of nurseries - ecosystem-oriented nurseries and stress-oriented nurseries (Table 2). Ecosystem-oriented nurseries are focused towards the rainfed upland, rainfed lowland, irrigated and submergence prone environments. There are observational nurseries where a large number of breeding lines are evaluated and yield nurseries where a limited number of genotypes is evaluated in replicated trials. In the stress-oriented nurseries the effect of major biotic (pests, diseases) and abiotic (temperature, moisture, soil) stresses is determined.

Impact of INGER

INGER has been one of the most effective programmes of IRRI. It has made visible impact on the varietal improvement programme of NARS and IARC by allowing genetic flow of rice between countries and making available diverse germplasm (according to extensive evaluation reports). The following are more specific facts about the impact of INGER:

1. *Genetic flow within and between countries:*
   Since its inception in 1975 more than 38,000 breeding lines and varieties have been provided by INGER for evaluation. Out of these, 290 breeding lines originating from 31 countries have been released as 454 varieties in 57 countries in Asia, Africa, Latin America and Caribbean countries. More than 1790 varieties developed by NARS have used INGER provided lines as one of the parents.
2. *Increased genetic diversity and enhanced sustainability:*
   Several thousand lines have been used to generate breeding lines in various countries. Over 38,000 breeding lines and varieties shared through INGER have helped diversify the genetic base of farmers' varieties in various countries. These varieties with diverse genetic background for pest, disease and abiotic stress resistance result in reduced crop loss and assure sustainability (Alluri et al., 1993).

Table 1. Number of active INGER test locations and cooperators.

Region/country	Number of locations	Number of cooperators
East Asia		
China	12	73
Japan	2	2
Korea	8	31
Taiwan	4	4
Southeast Asia		
Cambodia	7	8
Indonesia	16	23
Laos	1	1
Malaysia	4	5
Myanmar	13	32
Philippines	7	10
Thailand	21	80
Vietnam	18	36
South Asia		
Bangladesh	12	37
Bhutan	3	1
India	65	136
Nepal	4	12
Pakistan	7	16
Sri Lanka	4	14
West Asia & North Africa		
Afghanistan	1	2
Egypt	3	8
Iran	5	17
Iraq	1	1
West Asia & North Africa (cont.)		
Morocco	1	1
Saudi Arabia	1	1
Sudan	1	1
Turkey	1	2
Sub-Sahara Africa		
Ivory Coast	2	3
Mozambique	3	2
Nigeria	2	3
Senegal	2	4
South Africa	1	2
Tanzania	2	4
Zaire	1	1
Zambia	1	1
Latin America		
Argentina	2	2
Brazil	3	6
Colombia	3	5
Costa Rica	1	1
Guyana	1	1
Nicaragua	1	1
Europe		
Italy	1	1
Oceania		
Papua N. Guinea	3	1

3 *Economic impact:*

A critical analysis of the economic impact of world-wide germplasm exchange indicated that each variety contributes US$ 2.5 million to the world economy (Evenson & Gollin, 1992). Countries such as Vietnam and Indonesia became rice exporters by making use of these varieties, while relatively poor countries, such as Cambodia, which had no research infrastructure, have depended solely on INGER provided material for their varietal improvement programme through which recently rice production was re-established. Out of 14 varieties released and used in Cambodia, 11 came through INGER (Chaudhary & Mishra, 1993).

Table 2. Global INGER nurseries during 1994, 1995 and 1996.

Name of Nursery	Entries	Countries	1994	1995	1996
Ecosystem oriented					
A. Irrigated:					
IIRON	197	30	90	90	90
IIRYN-E	30	19	80	80	80
IIRYN-M	30	12	50	50	50
IRHON	100	8	20	30	30
IRBON	77	10	8	20	20
IRTON	100	-	-	-	20
IRFAON	100	-	-	-	20
B. Rainfed Lowland:					
IRLON (M, L)	50	14	60	60	60
IRLYN -M	24	8	35	30	30
IRLYN-L	20	-	-	-	30
C. Deepwater/Tidal:					
IDRON	37	10	40	30	30
D. Upland:					
IURON	79	19	60	60	60
IURYN	30	9	40	-	-
Stress oriented					
A. Diseases:					
IRBN	306	23	100	90	80
IRBBN	80	14	-	50	-
IRTN	92	7	35	-	30
B. Insect-pests:					
IRWBPHN	41	10	35	-	?
IRBPHN	75	14	-	40	40
IRSBN	50	14	-	50	-
IRGMN	50	6	-	40	-
C. Soil problems:					
IRSSTN	106	16	50	-	50
IRDTN	44	12	40	-	?
IRCTN	75	26	-	50	50?
Total	-	-	15	15	16

IIRON: Intl Irrigated Rice Observational Nursery;
IIRYN-E,M: Intl Irrigated Rice Yield Nursery;
IRHON: Intl Rice Hybrid Observational Nursery;
IRBON: Intl Rice Boro Observational Nursery;
IRTON: Intl Rice Temperate Observtnl. Nursery;
IRFAON: Intl Rice Finegrain Aromatic Obsv. Nsery;
IRLON: Intl Rnfd Lowland Rice Observtnl. Nursery;
IRLYN: Intl Rnfd. Lowland Rice Yield Nursery;
IDRON: Intl Deepwater Observtnl. Nursery;
IURON: Intl Upland Rice Observational Nursery;
IURYN: Intl Upland Rice Yield Nursery;
IRBN: Intl Rice Blast Nursery;
IRBBN: Intl Rice Bacterial Blight Nursery;
IRBPHN: Intl Rice Brown Planthopper Nursery;
IRCTN: Intl Rice Cold Tolerance Nursery
IRTN: Intl Rice Tungro Nursery;
IRSBN: Intl Rice Stem Borer Nursery;
IRGMN: Intl Rice Gall Midge Nursery;
IRSSTN: Intl Rice Soil Stress Nursery;
IRDTN: Intl Rice Drought Tolerance Nursery;
IRWBPHN: Intl Rice Whitebacked Planthopper Nursery;

Emerging issues in global evaluation of germplasm

Plant breeders are interested in the identification of the most promising breeding lines for a specific environment within a short time, with precision and with minimum manpower and funds. The key issues can be summarized as follows:

- Can testing sites be stratified (G × E studies, biological probe modelling)?
- Can key sites be identified through 'biological mapping'?
- Can key sites be characterized for germplasm evaluation and G × E extrapolation?
- Can the number of testing locations be reduced?
- Can the testing period of the genotypes be reduced?
- Can genotypes suited to a given agro-ecological paradigm be defined?
- Can modelling help in matching genetic diversity to ecosystem needs (targeted evaluation)?
- Are there models to match genetic diversity to pathosystems?
- What are the avenues for SARP - plant breeders - INGER interaction on above issues?

The above questions are a few major ones, answers of which may provide a basis for an INGER - modelling workplan. It would give INGER and its cooperating NARS located in 95 countries tremendous benefit, and the modellers a tremendous opportunity of using hundreds of test sites in these countries. As one of the oldest networks, INGER, through its cooperators, can provide quality data and excellent support for multi-location evaluation of crop models.

INGER 2000

A new phase of INGER, 'INGER 2000', has been prepared recently to address these emerging issues. The core objective of this programme is international exchange and evaluation of rice germplasm to increase sustainable yields and broaden the genetic base of farmers' varieties. The major components of this project will be:

- Global germplasm exchange, evaluation and use of rice genetic diversity,
- Genotype by Environment studies (G × E),
- Pre-breeding activities and technical support,
- Training and monitoring, and
- Improved linkages and management.

The second component (i.e. G × E) should provide a platform for interaction between INGER objectives and modelling groups.

G × E interaction studies

The interaction of plant genotype with variable environments has been used for several purposes. The type of interaction may classify the variety for its responsiveness or stability or unstability across a range of growing environments. The reactions of the genotypes may also help in classifying mega-environments into sub-sub-environments. Such information helps in identifying the suitability of a variety or group of varieties for specific sub-environments irrespective of their location. Thus, varieties, breeding lines and segregating populations can be developed and moved rapidly across the globe. There are a number of approaches for such studies, and methodological developments in this area are rapid.

Evaluation of traditional germplasm and promising breeding materials in different environments is especially important for the less favourable rice ecosystems because of the strong G × E interactions. Such G × E interactions in the less favourable ecosystems makes extrapolation of multi-location testing programmes extremely difficult with the existing statistical tools. Process-driven simulation models could be used to understand these G × E interactions as additional tools to evaluate the performance of promising breeding materials, and to extrapolate results using long-term weather records.

Multi-site testing of parental lines will reveal genetic differences in different environments, including environments differing in pest biotypes and disease pathotypes. Models for the characterization of rice pathosystems would be very useful. Mapping pathosystem diversity is an important component for deployment strategies that minimize chemical use for the management of rice pests. That involves careful targeting of rice diversity to the diversity of the pathosystems. While much can be achieved in the laboratory, or under controlled conditions in the glasshouse, for instance, targeted field evaluation of germplasm is one of the essential elements in crop improvement.

In the past, INGER activities were weak in this respect, and only limited genotype × environment studies were conducted in crop-weather relations and modelling. Other than the lack of interest in that area, difficulties of the collaborators from NARS in conducting the unsupported trials were the main limitations. Moreover, most methods to analyse and interpret data for G × E were then in the developmental stage. Data for multi-location and multi-year testing may be analysed using linear-regression analysis, classical cluster analysis, shifted multiplicative model cluster analysis, pattern analysis, principal coordinate analysis and crossover interaction analysis etc. to study the behaviour of genotypes, and to classify and to group environments. Systems tools can assist in global evaluation of rice germplasm by addressing the following issues:

- Identification of key sites through 'biological mapping',
- Characterization of key sites as a basis for the testing and extrapolation,
- Use of modelling tools to match genetic diversity to ecosystem needs,
- Developing more efficient field designs, methods for G × E studies, and environment characterization techniques.

The process-driven simulation models may help in the understanding of these G × E interactions, evaluate the performance of promising breeding materials, and extrapolate results using long-term weather records.

Biological mapping and modelling

A major challenge of this activity is to match genetic diversity to the needs of farmers in the heterogeneous and variable rice ecosystems. To date, our work has focused on the favourable, and less variable, irrigated ecosystem. The challenge today is for the less favourable ones.

For the favourable environments, crop improvement has relied to a considerable extent on major gene complexes that were identifiable by testing large numbers of different genotypes through the activities of INGER. Today, our understanding of the processes involved in enhancing productivity and sustainability highlight the importance of quantitative genetic systems, which are more difficult to identify in conventional testing programmes. This understanding has led to the concept of the use of 'probe' genotypes that are selected for their ability to discriminate the environment. The differential response of the probe genotypes is used to 'biologically' characterize the diverse environments. Thus the plant, not the geographer, is the sensor of the environment. With multi-variate analysis and GIS, maps for rice adaptation as sensed by the rice plant can be drawn. Then traditional germplasm and promising breeding materials can be pre-tested in targeted key sites. This biological characterization by carefully designed sets of genotype probe entries is especially important for the less favourable rice ecosystems. The development of this research will facilitate the selection of parental types for breeding, and the incorporation of suitable genetic materials into INGER nurseries. Expected outputs of this research are:

- Biological characterization of variable environments,
- Analysis of genotype × environment interaction to identify key sites and 'domains' for targeted testing and extrapolation, and
- Characterization of land races in different environments and identification of more stable or widely adapted genotypes.

Characterization of key sites

The sites selected for representation of 'domains of adaptation' require careful characterization of their physical and biological components, since this information is needed to calibrate the crop simulation models now available for further assessment and extrapolation of genotype performance. We envisage that in most cases, these key sites will be congruent with many of the sites at which IRRI and the NARS are currently collaborating, such as the Rainfed Lowland and the Upland Rice Research Consortium sites, and we expect to strengthen these linkages significantly through INGER 2000. Expected outputs of this collaborative activity are:

- Uniform and reliable weather data base,
- Gene mapping of the pathosystems, and identification and verification of resistance to diseases of rice,
- Minimum data sets on crop growth and yield,
- Genetic coefficients for the rice simulation models, and
- Defined domains of adaptation.

Models to match diversity to ecosystem needs

Process-driven crop models are now available for rice and its pest ecosystem environments. They provide an opportunity to 'grow' the plant on the computer. Their application can greatly increase the efficiency and efficacy of germplasm evaluation. Instead of testing a wide range of germplasm at many sites, the new approach would be based on more rigorous targeted evaluation at a few selected key sites only. This limited calibration will be used to predict the performance of diverse germplasm for adaptation to the different environments. This will help IRRI and the NARS to focus their breeding and germplasm evaluation efforts, and to provide timely feedback to drive these efforts.

Through INGER, this activity will build upon the on-going Simulation and Systems Analysis for Rice Production (SARP) network that involves 16 interdisciplinary teams from 9 countries. Expected outputs of INGER-SARP collaboration are:

- Improved rice growth model to predict performance under variable-resource environments,
- Pre-testing of unimproved and improved varieties for specific environments, and
- Prediction of genotypic adaptation to the different environments.

References

Alluri, K., R.C. Chaudhary & E.A. Akinsola, 1993. Building bridges for rice improvement in Africa through international collaboration. American Soc. Agron. meeting, 7 - 12 November 1993, Cincinnati, Ohio, U.S.A.

Chaudhary, R.C. & D.P. Mishra, 1993. INGER, germplasm and Cambodian rice farmer: A fruitful encounter. American Soc. Agron meeting, 7 - 12 November 1993, Cincinnati, Ohio, U.S.A.

Evenson, R. & D. Gollin, 1992. The economic impact of the International Rice Germplasm Center (IRGC) and the International Network for Genetic Evaluation of Rice (INGER). Yale University, U.S.A, Unpublished Report, 50 pp.

Genotype by environment interaction and selection - experiences in sorghum, and expectations for rainfed lowland rice

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Abstract

Crop performance in rainfed environments is unpredictable, due to seasonal variability, spatial heterogeneity, and interaction between genotype and environment. This paper examines how field experimentation and crop simulation may be used together to enhance the likelihood of success in a crop improvement programme in such environments. Experience with sorghum in semi-arid environments of North-Eastern Australia is used as a case study, before outlining the approach to be adopted in understanding the adaptation of rice to the rainfed lowlands of South and South-East Asia. The paper concludes by considering the strengths and weaknesses of the approach.

Introduction

In rainfed agriculture, crop performance is highly variable and unpredictable. Yields are strongly influenced by seasonal characteristics, and by spatial heterogeneity over soil types, topographic sequences and agrohydrologic conditions. These variables, in turn, interact with the cultivar chosen and the cultural practices employed. As a result, the interaction between genotype and environment is highly significant, complicating the task of identifying an improved cultivar or a better cultural practice. In order to have a higher average yield, the desired cultivar or practice should be more stable over a range of environments, with a reduced probability of crop failure. This is especially important in subsistence agriculture, where the survival of the farmer and the family is largely dependent on the season's harvest.

In order to evaluate the performance of a cultivar or practice, the researcher must replicate the experiment over a set of sites and years, which reasonably represent the range of environments likely to be encountered in the long-term. Careful selection of sites, judicious design of experiments, balanced collection of data and appropriate use of statistical tools will enhance the chances of success. Nevertheless, the number of environments which may be experimentally tested is limited, due to financial and practical constraints. A suitably validated crop model could be used to simulate the performance of a cultivar or practice over long-term weather data, thus permitting a probability distribution of crop yield to be obtained. Likewise, the benefit of

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incorporating a particular trait may be evaluated, by changing the values of parameters in the model, and examining the impact on yield and risk of crop failure.

This paper examines the use of field experiments and crop simulation together in crop improvement programmes. Previous research on adaptation of grain sorghum to the semi-arid environments of North-Eastern Australia is used as a case study. The research approach being used to examine adaptation of rice to the rainfed lowlands of South and South-East Asia is then outlined. Finally, the strengths and weaknesses of the approach are discussed.

Adaptation of grain sorghum to semi-arid environments

Sorghum is grown on heavy-textured soils in semi-arid environments of North-Eastern Australia. Successful production is dependent on antecedent soil water, and on the highly variable within-season rainfall (Wade & Hammer, 1986; Hammer & Wade, 1986). As a basis for understanding adaptation of sorghum, ten experimental hybrids differing in maturity and genetic background were selected and grown under irrigated and rainfed conditions in environments ranging from temperate to tropical (Wade, 1986). Relevant cultural practices were also examined, in order to understand interactions between genotype and management. The approach involved the use of crop models to simulate crop response over a wider range of sites and years than could be examined experimentally (Hammer & Wade, 1985).

Over locations, mean site yields ranged from 1 to 10 t ha^{-1}, with the lowest yields obtained for rainfed crops on the shallow cracking clays of Central Queensland (Wade et al., 1989). Genotype by environment (G × E) interaction was significant, and hybrids were identified which were preferentially adapted either to low- or to high-yielding environments (Wade, 1993). Experimental results indicated that crop phenology was a crucial factor for yield stability, and phenology also influenced the interaction with cultural practices (Wade & Douglas 1990; Wade et al., 1993a). Analysis of variance, regression and covariate analyses were effective in examining these multi-location data. When pattern analysis was employed in 1988, there was no further improvement in data interpretation.

Grain yield of sorghum had been reported to decline from temperate to tropical environments (Miller, 1982), with preferential adaptation to tropical conditions being associated with a lower base temperature (Thomas & Miller, 1979). When temperature response was examined for the ten experimental hybrids, no evidence was obtained to support this assertion (Wade et al., 1993b). Preferential adaptation either to low- or to high-yielding environments was most strongly associated with response to water stress. Differences in phenology (Wade et al., 1994), in transpiration efficiency (Hubick et al., 1990; Hammer & Muchow 1991; Donatelli et al., 1992; Wade, 1993; Henderson et al., 1994), and to a lesser extent, in radiation use efficiency (Hammer & Vanderlip, 1989) were the dominant factors.

These relationships for light and water use efficiency were used to develop QSORG, a dynamic grain sorghum crop simulation model, in which conversion efficiency for the more limiting resource (radiation or water) was used to obtain the daily increment in dry matter production, which in turn, was partitioned to leaf, stem, root and grain, depending on growth stage (Hammer & Muchow, 1991). SORKAM (Rosenthal et al., 1989) and CERES (Jones & Kiniry, 1986) are other sorghum models similar in complexity to QSORG. Carberry & Abrecht (1991) have examined the differences between these models. Briefly, the models use similar strategies to simulate the primary processes of crop development, assimilate accumulation and yield in response to climate and soil parameters, but they differ for some traits and the interactions between them. For example, while crop duration is determined by temperature, photoperiod and genotype in all three models, SORKAM uses leaf number to define crop duration, CERES calculates a number of growth stages, and QSORG simulates panicle initiation and anthesis directly. Important differences arise in relation to interactions. Only SORKAM permits water stress to alter crop duration, and none of the models have a capacity for nutrition to alter crop duration. Further details are provided by Carberry & Abrecht (1991).

SORKAM was used to examine yield probabilities for alternative crop durations and cultural practices. The model was first tested against experimental data for the genotypes and environments considered, to check the validity of the simulations (Wade et al., 1991). Fig. 1 illustrates that the model was satisfactory in most instances. Exceptions were when extremely long duration cultivars were used, when rainfall intensity was sufficiently high to increase runoff and reduce soil water storage, and when row spacing was outside the range considered in the model. Simulations were only conducted for valid combinations of input parameters (Table 1). As a consequence, the simulated results were in good agreement with experimental data. The output was presented as cumulative distribution functions, which were used to assess the impact of alternative crop durations or cultural practices on risk (Gerik et al., 1992; Wade et al., 1992).

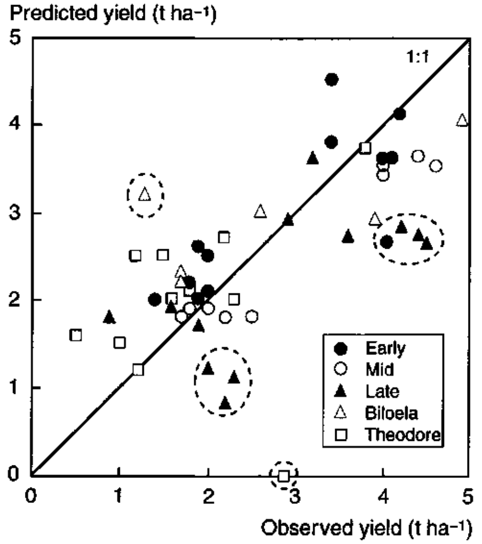

Figure 1. Comparison of predicted yield from the SORKAM grain sorghum model with observed yield for a range of row spacings and plant densities at two sites, and a range of plant densities and crop durations in two seasons. Circled values are outliners mentioned in the text. Source: Wade et al., 1991.

Table 1. Default settings chosen for SORKAM simulations at each site. Source: Wade et al., 1991.

		Katherine	Emerald	Dalby
Simulated years		59 - 88	40 - 69	35 - 64
Planting date	- first	15 Dec.	21 Dec.	28 Sept.
	- last	30 Jan.	23 Feb.	1 Jan.
Available soil water$_{max}$ (cm)		12.8	11.2	22.4
Available soil water at planting (cm)		6.0	10.0	10.0
ET correction factor		1.1	1.3	1.2
Solar radiation	- dry	24	21	20
(MJ)	- wet	22	12	15
	- amplitude	5	11	7
Hydrologic curve number		78	80	91
Field slope (%)		0.5	0.5	1.0

An example of the use of the cumulative distribution function is provided in Fig. 2, for response of sorghum to plant density and row spacing at Katherine, Emerald and Dalby in Australia (Wade et al., 1991). Strategies are compared for three possible farmer attitudes to risk. The 'risk taker' who owns his property may be willing to lose a crop in a poor season, if yield and profit can be maximised in a favourable season. High density in narrow rows would be the strategy employed in this instance. In contrast, a 'risk avoider' may wish to minimise the risk of crop failure so he can pay his debts, even if it means sacrificing yield and profit in a good season. This farmer would grow the crop in wide rows at low density, in order to provide a store of soil water as a buffer against dry periods. Standard practice is a compromise between these extremes. The yield probabilities shown in Fig. 2 quantify these concepts, so that number of crop failures, likely yields and economic returns may all be evaluated (Wade et al., 1991).

Using SORKAM, the optimum crop duration for Central Queensland was shorter than was reported using the QSORG model (Muchow et al., 1991). Comparison with experimental evidence revealed that the difference in simulated output was mainly due to two factors (Wade et al., 1994). At these low-yielding sites, crop duration was extended under extreme water stress. If the model failed to adjust phenology for water stress, the resulting simulations favoured cultivars of longer duration. Starting conditions also greatly influenced the results from simulation. If a full profile of soil water at planting was assumed, rather than setting the model to run continuously through the fallow period in order to calculate soil water at planting, fewer crop failures were predicted. Thus, the adequacy with which the trait is modelled, and the assumptions used in conducting the simulation, are critical to success (Wade et al., 1994).

Testing the SORKAM model also indicated that further improvement was possible, by upgrading the subroutines for several traits (Rosenthal et al., 1989; Wade et al., 1991).

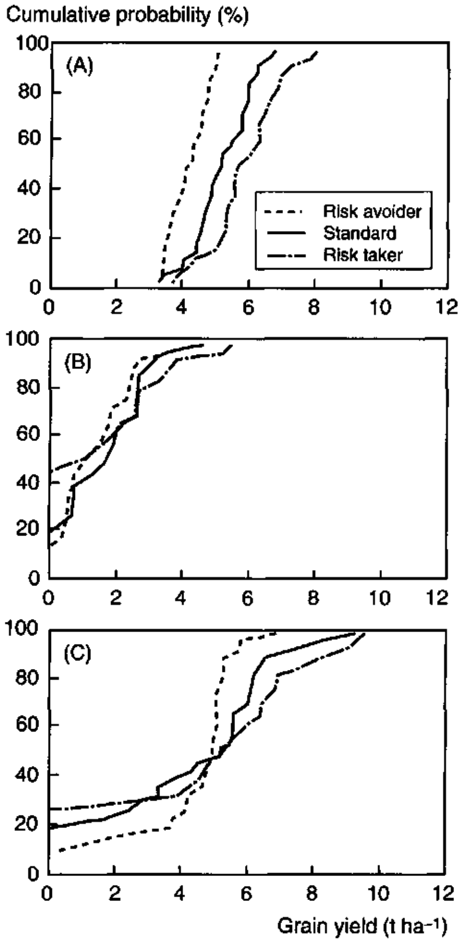

Figure 2. Cumulative distribution functions for sorghum yield based on simulation analysis for three production strategies at (A) Katherine, (B) Emerald and (C) Dalby. Source: Wade et al., 1991.

Experiments were conducted to obtain suitable data, and improved subroutines were developed for crop phenology (Hammer et al., 1989) and seed number (Wade et al., 1992). The light extinction coefficient used in the model was confirmed (Rosenthal et al., 1993).

Thus in the sorghum programme, experimental and simulation approaches were successfully combined to indicate optimum crop durations and cultural practices for the water-limited environments of North-Eastern Australia. At the same time, valuable lessons were learned about the need to carefully consider the adequacy of the model for the stated purpose, and the relevance of the simulation to the target environment. This is especially important when examining the potential benefit of incorporating a particular trait into an improved genotype. Not only the trait itself, but its interactions with other traits and with the relevant environmental parameters must be considered.

Adaptation of rice to rainfed lowland environments

Rainfed lowland rice encounters an environment more complex than for any other rainfed crop. Because rainfed lowland rice is grown in bunded fields without water control, hydrologic conditions may fluctuate from submergence to drought, with major consequences for root growth, nutrient availability and weed competition (Garrity et al., 1986). Various systems of crop establishment are employed, from direct dry-seeding to transplanting, and seedling vigour, weed competitiveness and capacity to withstand stress are influenced by the choice. Surveys of constraints to rainfed lowland rice production indicate that drought, weeds, submergence, soil fertility, crop establishment, soil physical characteristics and socio-economics are the major problems (Widawsky & O'Toole, 1990). In farmers' fields, the ultimate challenge is the combination of seasonal variability, spatial heterogeneity, agrohydrologic complexity, and their interactions with genotype and management.

A new research project will seek to identify traits and germplasm better adapted to the constraints of the rainfed lowlands. Research on genotype × environment interaction will be used to assist the development of selection procedures and their use in breeding better cultivars. Crop simulation modelling will be used as an integral component of these activities, because the target environment is complex and unpredictable, and the traits of interest are strongly interactive with environment. Experiments will be conducted at selected locations of the Rainfed Lowland Rice Research Consortium. At each location in each season, one hundred advanced breeding lines will be grown, together with five probe lines. The probe lines, chosen to differ in crop duration, drought resistance and weed competitiveness, will occur more frequently in the trial design. This will permit more detailed measurements to be taken on the probe lines, which should assist interpretation of the simpler observations taken on the breeding lines.

For each plot, recordings will be taken on the full array of observations normally obtained in breeding trials, including crop phenology, drought score, disease reaction, plant height, phenotypic acceptability and grain yield. On designated plots of the probe lines, leaf area, dry weight, root growth, water extraction, leaf water potential, leaf relative water content and plant nutrient uptake will also be measured. When these data are combined with daily meteorological data (maximum and minimum temperature, radiation, rainfall and evaporation), and soil physical and chemical characterisation (soil description, textural classes, pF, conductivity, and nutrient status by layer) for each site, genotypic coefficients may be developed for the five probe lines. The development, growth and yield of the probe lines may then be simulated over sites and years, using an appropriate rice simulation model (e.g. CERES Rice, Ritchie et al., 1987; ORYZA1, Kropff et al., 1994; ORYZA_W, Wopereis, 1993).

The models can then be used for a number of purposes. Firstly, sites may be characterized for the expected timing and duration of water deficit. This would permit consideration of how representative conditions are at each site in each season, relative to long-term expectations. Selection pressure may need to be adjusted for seasonal conditions. Alternatively, effort may be necessary to ensure suitable conditions are provided for screening purposes, for example, by installing rainout shelters. Secondly, performance of the probe lines may be simulated over a wider range of sites and years than the main experimental programme would allow. This would indicate the performance and stability of the probe lines in the full array of environments likely to be encountered in the rainfed lowlands. Breeding lines with traits similar to a probe line may be expected to perform similarly to it over environments. Finally, the effect of alternative traits may be more thoroughly evaluated, by adjusting genotypic coefficients in the model, and examining their impact over long-term meteorological data.

Conclusions and prospects for future research

To be effective, the use of simulation models cannot be divorced from the experimental process. Rather, crop models should be used as one of the tools at the disposal of the crop scientist. Quality data are needed to use the model effectively, and as a result of conducting the simulations, it may be necessary to conduct further experiments, either to test the predictions or to further improve the model. In conducting the simulations, care must be taken to ensure that the genotypes and traits examined are robustly modelled and suitably validated, and that the starting conditions for the simulations are representative of the target environment. Such a multi-faceted approach should enhance the chances of success in trying to identify ways of selecting better genotypes or identifying improved cultural practices.

References

Carberry, P.S. & D.G. Abrecht, 1991. Tailoring crop models to the semiarid tropics. In: R.C. Muchow & J.A. Bellamy (Eds), Climatic risk in crop production: models and management for the semiarid tropics and subtropics. CAB Int., Wallingford, pp. 157-182.

Donatelli, M., G.L. Hammer & R.L. Vanderlip, 1992. Genotype and water limitation effects on phenology, growth, and transpiration efficiency in grain sorghum. Crop Science 32: 781-786.

Garrity, D.P., L.R. Oldeman, R.A. Morris & D. Lenka, 1986. Rainfed lowland rice ecosystems: characterisation and distribution. In: Progress in rainfed lowland rice. IRRI, Philippines, pp. 3-24.

Gerik, T.J., L.J. Wade, W.D. Rosenthal & R.L. Vanderlip, 1992. Optimising cultural practices for grain sorghum in relation to climatic risk at three locations in the United States, using the SORKAM model. Mathematics and Computers in Simulation 33: 415-419.

Hammer, G.L. & L.J. Wade, 1985. Crop adaptation of grain sorghum in semi-arid environments - a modelling approach. In: D.A. Charles-Edwards, J.R. Childs, J.G. Dingle, M.A. Foale, R.J. Hampson & S.J. Mill (Eds), The application of computer models to farm management, extension and research. The Australian Institute of Agricultural Science, (Queensland Branch). pp. 4.5.1- 4.5.17.

Hammer, G.L. & L.J. Wade, 1986. Agroclimatic analysis for grain sorghum in Australia, 2.

Water limitation. In: M.A. Foale & R.G. Henzell (Eds), Proc. First Australian Sorghum Conference, Gatton, Feb. 86, pp. 4.23-4.32.

Hammer, G.L. & R.C. Muchow, 1991. Quantifying climatic risk to sorghum in Australia's semiarid tropics and subtropics: model development and simulation. In: R.C. Muchow & J.A. Bellamy (Eds), Climatic risk in crop production: models and management for the semiarid tropics and subtropics. CAB International, Wallingford, pp. 205-232.

Hammer, G.L. & R.L. Vanderlip, 1989. Genotype by environment interaction in grain sorghum, 1. Effects of temperature on radiation use efficiency. Crop Science 29: 370-376.

Hammer, G.L., R.L. Vanderlip, G. Gibson, L.J. Wade, R.G. Henzell, D.R. Younger, J. Warren & A.B. Dale, 1989. Genotype by environment interaction in grain sorghum. 2. Effects of temperature and photoperiod on ontogeny. Crop Science 29: 376-384.

Henderson, S., S. von Caemmerer, G.D. Farquhar, L.J. Wade & G.L. Hammer, 1994. Correlation of carbon isotope discrimination and transpiration efficiency in lines of the C_4 species *Sorghum bicolor* in the glasshouse and the field. Australian Journal of Plant Physiology (in press).

Hubick, K.T., G.L. Hammer, G.D. Farquhar, L.J. Wade, S. von Caemmerer & S. Henderson, 1990. Carbon isotope discrimination varies genetically in C_4 species. Plant Physiology 91: 534-537.

Jones, C.A. & J.R. Kiniry, 1986. CERES-Maize. A simulation model of maize growth and development. Texas A&M University Press, College Station.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, International Rice Research Institute, Philippines, 110 pp.

Miller, F.R., 1982. Genetic and environmental response characteristics of sorghum. In: L.R. House, L.K. Mughogho & J.M. Peacock (Eds), Sorghum in the eighties: Proceedings of the international symposium on sorghum, 2-7 November 1981. ICRISAT, Patancheru A.P., India, pp. 393-402.

Muchow, R.C., G.L. Hammer & P.S. Carberry, 1991. Optimising crop and cultivar selection in response to climatic risk. In: R.C. Muchow & J.A. Bellamy (Eds), Climatic risk in crop production: models and management for the semiarid tropics and subtropics. CAB International, Wallingford UK, pp. 235-262.

Ritchie, J.T., E.C. Alocilja, U. Singh & G. Uehara, 1987. IBSNAT and the CERES-RICE model. In: Weather and rice. International Rice Research Institute, Philippines, pp. 271-283.

Rosenthal, W.D., R.L. Vanderlip, B.S. Jackson & G.F. Arkin, 1989. SORKAM: A grain sorghum crop growth model. TAES Computer Software Documentation Series MP1669, Texas Agric. Exp. Stn., College Station, Texas, USA.

Rosenthal, W.D., T.J. Gerik & L.J. Wade, 1993. Radiation use efficiency among grain sorghum cultivars and plant densities. Agronomy Journal 85: 703-705.

Thomas, G.L. & F.R. Miller, 1979. Base temperatures for germination for temperate and tropically adapted sorghums. In: Proc. Eleventh biennial grain sorghum research and utilisation conference, 28 Feb - 2 Mar, 1979. Texas Grain Sorghum Producers Association, Lubbock Tx, pp. 24.

Wade, L.J., 1986. Adaptation of grain sorghum in semi-arid environments, a direct testing approach. In: M.A. Foale & R.G. Henzell (Eds), Proc. First Australian sorghum conference, Gatton, Feb. 86, pp. 4.1-4.11.

Wade, L.J., 1993. Adaptation of grain sorghum in the semi-arid tropics. Project Report QO93004, Queensland Department of Primary Industries, Brisbane, 34 pp.

Wade, L.J. & G.L. Hammer, 1986. Agroclimatic analysis for grain sorghum in Australia, 1. Temperature and solar radiation. In: M.A. Foale & R.G. Henzell (Eds), Proc. First Australian sorghum conference, Gatton, Feb. 86, pp. 4.12-4.22.

Wade, L.J. & A.C.L. Douglas, 1990. Effect of plant density on grain yield and yield stability of sorghum hybrids differing in maturity. Australian Journal of Experimental Agriculture 30: 257-264.

Wade, L.J., A.C.L. Douglas, D.G. Mayer, R.G. Henzell, G. Gibson, J. Warren, G.L. Hammer & A.B. Dale, 1989. The performance of diverse sorghum hybrids in a range of different environments. In: M.A. Foale, B.W. Hare & R.G. Henzell (Eds), Proc. Australian sorghum workshop, Toowoomba, Feb. 28 - Mar. 1, 1989. Occasional Publication 43, Australian Institute of Agricultural Science (Queensland Branch), Brisbane, pp. 238-247.

Wade, L.J., R.J.K. Myers & M.A. Foale, 1991. Optimising plant stand in response to climatic risk. In: R.C. Muchow & J.A. Bellamy (Eds), Climatic risk in crop production: models and management for the semiarid tropics and subtropics. CAB International, Wallingford UK, pp. 263-282.

Wade, L.J., T.J. Gerik, W.D. Rosenthal & R.L. Vanderlip, 1992. Identifying strategies to minimise climatic risk for grain sorghum, using the SORKAM model. In: K.J. Hutchinson & P.J. Vickery (Eds), Proc. Sixth Australian agronomy conference, 10 - 14 February 1992, Armidale, pp. 210-214.

Wade, L.J., A.C.L. Douglas & K.L. Bell, 1993a. Variation amongst sorghum hybrids in the plant density required to maximise grain yield over environments. Australian Journal of Experimental Agriculture 33: 185-191.

Wade, L.J., G.L. Hammer & M.A. Davey, 1993b. Response of germination to temperature amongst diverse sorghum hybrids. Field Crops Research 31: 295-308.

Wade, L.J., A.C.L. Douglas & D.G. Mayer, 1994. Defining traits for selection using isopopulations of sorghum. Euphytica 72: 73-85.

Widawsky, D.A. & J.C. O'Toole, 1990. Prioritising the rice biotechnology research agenda for eastern India. The Rockefeller Foundation, New York, 86 pp.

Wopereis, M.C.S., 1993. Quantifying the impact of soil and climate variability on rainfed rice production. PhD Thesis, Wageningen Agricultural University, the Netherlands, 188 pp.

Combining statistics and crop models for improved plant breeding strategies

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Abstract
The scope for the involvement of statistical analysis of genotype by environment (G × E) interaction with crop simulation modelling in plant breeding is investigated. Three principle methods of statistical analysis of G × E interactions are reviewed: traditional stability regression models, additive main effects and multiplicative (AMMI) models and pattern analysis involving a combination of cluster analysis and ordination.
The main challenge for the use of crop models in breeding is identified as a need for models of sufficient sensitivity to be able to distinguish between relatively similar breeding lines. The main constraint to their use is the need to have detailed genetic parameters for breeding lines to be modelled. Statistical analysis interacting with crop modelling of specific varieties could be used to provide a site index in stability regressions. Pattern analysis could be used to identify representative varieties for genotype groups. These could be simulated over climatic and geographic variation to indicate risk assessment and adaptation of the groups. Finally, simulation of probe genotypes, sensitive to specific stresses could be used to aid interpretation of observed G × E interaction.

Introduction

Genotype by environment (G × E) interaction can be defined as the way in which individual genotypes respond to differences in environment. In the statistical sense, it can be measured as a vector of residuals from the main effects of genotype (G) and environment (E) in a two-way classification of response measurements. Hence, the interaction is essentially a multivariate quantity depending critically on both the set of genotypes evaluated and the set of environments. The potential for utilization of G × E interaction in breeding programmes relies on the extent to which these interaction deviations are heritable so that positive deviations, which represent adaptation, can be utilized. G × E can be used to identify breeding domains or mega environments more precisely than average assessment of site quality or analysis of environmental factors. Since G × E interactions are properties of the genotypes and environments studied, domains defined through them will also depend on the current pool of breeding material.

The difficulties of utilizing G × E interaction in plant breeding lie in its dependence on the

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specific genotypes and environments examined, and on the expense of covering sufficient range of environments to effectively classify the interactions. Crop modelling can play a role in the utilization of G × E interaction by lessening the effects of both these limitations, provided model parameters can be efficiently estimated for breeding material and provided crop models are sufficiently sensitive and environmental data are readily available so that G × E interactions can be reliably predicted.

This in essence represents the principal challenge to the utilization of crop models in breeding programmes: are they sufficiently sensitive to distinguish between relatively similar breeding lines and is it possible to obtain genetic parameters for a sufficiently wide range of breeding lines to make their simulation feasible?

Modern statistical models can help by identifying principal factors influencing interaction, by classifying environments and genotypes into groups with similar interactive responses and by establishing the reliability of model predictions of G × E interactions.

Statistical models for G × E interaction

Traditional statistical analysis of G × E interaction involved the development of stability parameters based on the regression of variety yields on an index of site quality (Fig. 1) and on deviations from this regression (Finlay & Wilkinson, 1963; Eberhart & Russel, 1966).

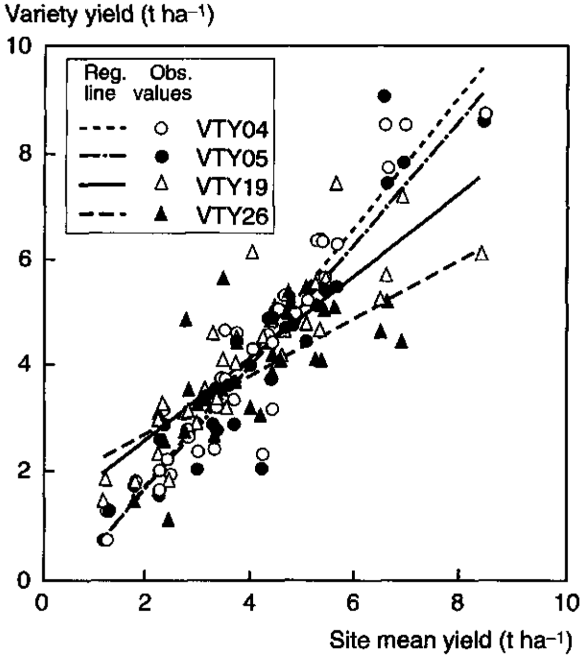

Figure 1. Stability regressions for four extreme varieties from International Irrigated Rice Yield Nursery - Early (IIRYN-E (92)).

Problems with this analysis were the choice of site index, which was usually taken to be the mean response of all varieties tested at a site, and the difficulty in interpreting the stability parameters. In fact, the analysis is also limited by the fact that site quality, as measured by average yield, is very often not the main force driving interaction, and hence, the model is frequently inadequate.

A more recent approach involves the use of AMMI models which propose multiplicative terms for the G × E interaction. These form a much richer class of models than linear or even polynomial models. Hence, much better fits can be achieved greatly improving precision and predicted values (Kempton, 1984; Zobel et al., 1988).

Interaction between genotypes and environments can be graphically presented using biplots (Bradu & Gabriel, 1978) such as in Fig. 2, where adaptation of the varieties (numbered points) to environments, (lettered spokes) is indicated by the distance from the origin of the perpendicular projection of the variety part onto the site spike.

These models have good precision in estimating variety responses, they are very flexible in accounting for factors driving interaction effects and they provide a useful definition of breeding domains in terms of best adapted varieties (McLaren & Chaudhary, 1994). Problems with the AMMI models are that they have no clear theoretical relationship with breeding strategies, and interpretation relies on the clustering ability of interaction ordination, and on the availability of good site or genotype characterization.

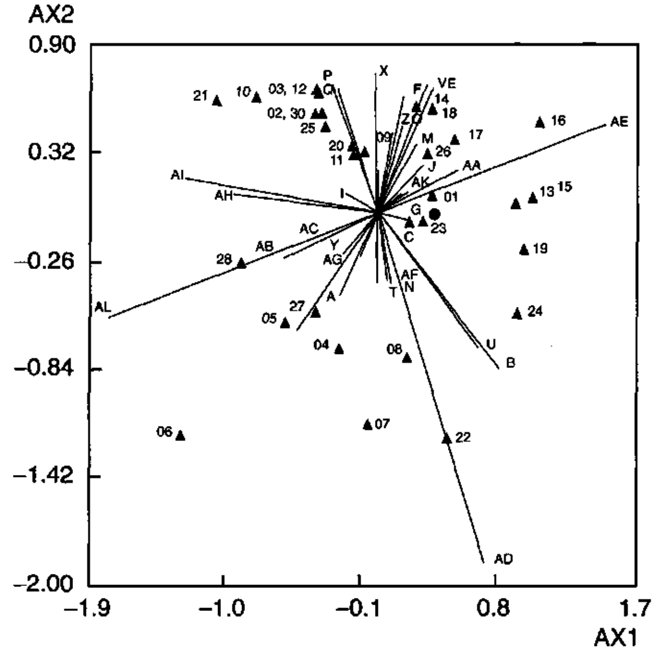

Figure 2. Interaction biplot for the AMMI2 model for data from IIRYN (92) (model fit: 38.6% of G × E SS).

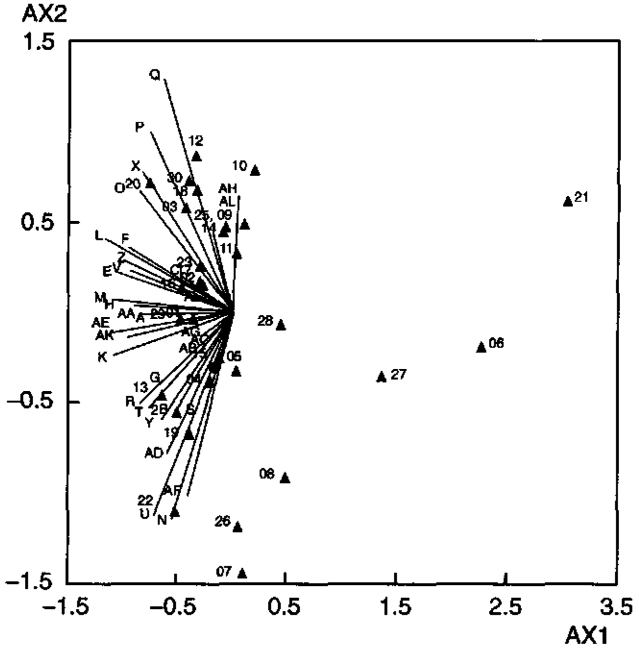

Figure 3. Biplot of the first two ordination scores for environment standardized data from IIRYN-E (92) (the model with two axes accounts for 73% of G × E SS).

A second, but related approach to G × E analysis is Pattern Analysis, which is a combination of hierarchical classification and principal components analysis (PCA, DeLacy & Cooper, 1990). Pattern analysis uses hierarchical classification on environment standardized data to define clusters of environments and genotypes which have the same pattern of interaction. This is followed with a PCA ordination of the same standardized data leading to ordination scores which are plotted to aid interpretation (Fig. 3). Cluster groups can be superimposed on the biplot to stress similar interaction patterns.

Pattern analysis explicitly exploits classification for reducing the dimensionality of the interaction problem. The cluster groupings of genotypes and environments can be used to define distinct response patterns indicating interaction between the two sets of clusters (Fig. 4). Pattern analysis has a direct relationship to indirect selection strategies when specified data standardizations are used in certain experimental settings (Cooper & DeLacy, 1994).

Major problems with Pattern Analysis are the choice of data standardization and the distance matrix to be used for cluster analysis. The classical problem of cluster definition found in all cluster analysis applications is also present. The ordination component (PCA) of Pattern Analysis is equivalent to AMMI analysis when the data are standardized by removing main effects and applying PCA to the raw residuals.

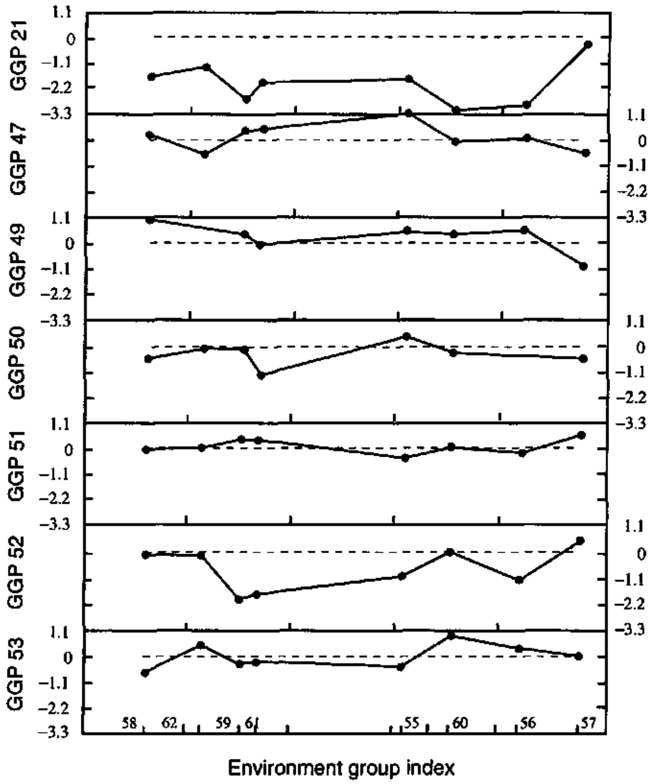

Figure 4. Response plots for genotype groups from IIRYN-E(92).

Crop modelling and plant breeding

The principal challenge to crop modelling for its effectiveness in plant breeding is one of sensitivity of the models. For it to be an effective tool in any breeding programme, it must accurately simulate differences in performance of genotypes of interest. This is somewhat different to the traditional role of crop models which simulate crop production of distinct varieties over different management levels.

Physiological parameters of the breeding lines need to be distinguishable in the crop model. Since elite breeding lines are presumably close in physiological behaviour, this requires a very high degree of model sensitivity and detailed measurement of the parameters on a wide range of breeding material.

For crop modelling to be effective in breeding strategies which aim to use G × E interaction, the situation is even more complicated because the relevant range of environmental parameters need to be sensitively measured in addition to the genotypic parameters.

A very simple role for crop modelling would be the provision of an index of site quality for use in traditional G × E analysis. This could be achieved by simulating performance of number of check varieties over a wide range of weather conditions at each site. Regression of observed test variety lines on the simulated index would give an idea of stability. Regression of the same check variety yields on the simulated index would give an idea of the effect of specific weather conditions.

Definition of breeding environments could also be achieved by crop models by modelling a set of probe genotypes known to discriminate between breeding environments. A target region could be divided into breeding domains in which different sets of germplasm could be tested.

By modelling a range of probe genotypes and selected environments known to discriminate between the genotypes, it is possible that the crop parameters determining the specific interaction could be identified. Hypothetical varieties could then be modelled combining the crop parameters conferring most advantage as an indication of suitable traits and breeding targets.

The impossible task of accurately modelling a rapidly changing set of breeding lines implies a limited role for modelling in selection strategies. However, an interesting combination of modelling, pattern analysis and AMMI prediction could be used to extend the geographical range of selection programmes. If pattern analysis is used to define principal groups of genotypes with similar patterns of interaction, one member from each group could be simulated at a wide range of environments. Then, the AMMI model could be used to impute the yields of the other entries at these environments and the resulting prediction used to limit the number of entries tried at all sites.

Conclusions

The role of crop modelling in plant breeding strategies depends critically on the ability of the models to distinguish between breeding lines and their interactions with environments.

Because of the large task of calibrating models for specific genotypes and because of the rapidly changing genotypes in breeding programmes, it would appear that the best approach is to identify probe genotypes and place a concerted effort on modelling these varieties and their interaction. Outputs from such an exercise could include:

- Better identification of breeding domains,
- Understanding of the physiological basis of G × E,
- Identification of important traits for utilization of G × E interaction, and
- Extrapolation of variety testing to a wider range of environments than is possible by direct trials.

References

Bradu, D. & K.R. Gabriel, 1978. The biplot as a diagnostic tool for models of two-way tables. Technometrics 20(1): 47-68.

Cooper, M. & I.H. DeLacy, 1994. Relationships among analytical methods used to study genotypic variation and genotype by environment interaction in plant breeding multi-environment experiments. Theoretical and Applied Genetics (in press).

DeLacy, I.H. & M. Cooper, 1990. Pattern analysis for the analysis of regional variety trials. In: M.S. Kang (Ed.), Genotype by environment interaction and plant breeding. Louisiana State University, Baton Rouge, pp. 301-334.

Eberhart, S.A. & W.L. Russel, 1966. Stability parameters for comparing varieties. Crop Sci. 6: 36-40.

Finlay, K.W. & G.N. Wilkinson, 1963. The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res. 14: 42-754.

Kempton, R.A., 1984. The use of biplots in interpreting variety by environment interactions. J. Agric. Sci. 103: 123-135.

McLaren, C.G. & R.C. Chaudhary, 1994. Use of additive main effects and multiplicative interaction models to analyse multilocation rice variety trials (in press).

Zobel, R.W., M.J. Wright & H.G. Gauch, 1988. Statistical analysis of yield data. Agron. J. 80: 388-393.

The application of crop growth simulation in evaluation of large plant germplasm collections

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Abstract
Extensive multi-locational and multi-seasonal evaluation is traditionally needed to assess plant characteristics. However, because of limited resources, this procedure can not be applied to large germplasm collections, and therefore, an efficient method is required that allows assessment of plant characteristics of large numbers of accessions under various environmental conditions, utilizing a limited number of evaluation results. Among the many techniques that have been developed to analyse genotype × environmental interaction, explanatory crop growth models can account for part of the genotype × environment interaction on the basis of quantitative knowledge on the relations between plant genotypic and environmental characteristics. Current crop growth simulation models are generally better suited for explanation of the effects of environmental variation than for analysis of small genetic differences between crops. They can, therefore, best be applied to analyse the consequences of pronounced variation in genetic characters, with well-established relations with environmental characters, and which have a relatively high heritability. If applied to early generations in the selection process, this may increase selection efficiency.

Introduction

The key role of germplasm collections in plant breeding, and their frequent use, puts high demands on their evaluation. This generally comprises two steps: a preliminary evaluation by the gene bank's crop curator, in which a limited number of traits of interest to the majority of users is recorded, followed by a more specific evaluation of promising material on the basis of specifications employed by breeders.

Plant germplasm collections typically consist of large numbers of accessions. For example, the gene bank of the International Rice Research Institute (IRRI) comprises about 75,700 rice accessions (IRRI, 1993), and the gene bank of the International Center for Agricultural Research in the Dry Areas (ICARDA) comprises about 51,000, 20,000 and 22,000 accessions of cereals, food legumes and forages, respectively (ICARDA, 1993). As the institutes' mandate regions include many distinct environments, extensive multi-locational or multi-seasonal

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evaluation would be needed to assess plant characteristics. However, this expensive procedure cannot be applied to such large collections, and, therefore, preliminary evaluations are generally restricted to one replication in time and space. Considerable genotype × environment (G × E) interaction makes extrapolation of single-evaluation results impossible, if location × year interaction is significant (Lin & Binns, 1988). Therefore, evaluation results have often limited applicability. Moreover, extensive evaluations may still not lead to unequivocal results. Consequently, if germplasm centres are forced to limit their evaluation programmes because of financial constraints (Giles, 1990), assessment of the potentials of germplasm for cultivation under different climatic conditions comes under pressure, so that initial selections have to be made on the basis of preliminary characterization and evaluation covering only one or very few seasons, often at a single location. This involves the risk that part of the useful germplasm may not be recognized as such, and thus not be utilized.

Therefore, an efficient method is required that allows assessment of plant characteristics of large numbers of accessions under various environmental conditions, utilizing a limited number of evaluation results.

Genotype × environment interactions

The complexity of G × E interactions during the processes of collection, evaluation, breeding and cultivation is illustrated in Table 1. Evolution, domestication and cultivation have resulted in a certain genotype A, which is adapted to environment 1 and manifests itself as phenotype A1. The plant germplasm collector is for some reason interested in phenotype A1, and deposits a sample of genotype A in the gene bank. Genotype A is evaluated in environment 2, which generally differs from that at the collection site, with the result that phenotype A2 is described. If the original germplasm is distributed, then genotype A is grown as phenotype A2 or A3, dependent upon the environment of cultivation, which may be similar to or different from the environment of evaluation. If the germplasm is subjected to selection pressure during breeding, then genotype B is selected on the basis of its phenotype B2. If selection takes place in the future environment of cultivation, then the result will be genotype C, grown as phenotype C3. Many other forms of breeding exist, which only adds more genotypes and phenotypes. As opinions vary on the best selection environment for a given environment of cultivation (Ceccarelli et al., 1993; Ceccarelli & Grando, 1991; Zavala-García et al., 1992), genotypes B and C may even be cultivated in a fourth environment. Plant genetic resources and plant breeding therefore have to deal with at least three environments: the environment of origin, of evaluation and selection, and one or more of cultivation.

In all cases it remains difficult to determine a plant genotype, as there is always a surrounding environment, and observations are generally phenotypic. Plant characteristics, that are the result of many underlying processes (e.g. grain yield), are particularly difficult to determine genotypically. Unequivocal quantification of more fundamental plant characteristics (e.g. temperature sum to anthesis and characteristics of the light response curve) is usually easier.

Table 1. Plant genotypes and phenotypes evolution and domestication, via collection and breeding, to modern cultivation.

Activity	Plant genotype	Environment	Plant phenotype
Evolution, Domestication, Cultivation	A	1	A1
Collection	A	1	A1
Characterization, Evaluation	A	2	A2
Breeding	A ® B	2	A2 ® B2
		or	or
	A ® C	3	A3 ® C3
Cultivation	A	2	A2 or A3
	B	or	B2 or B4
	C	3	C3 or C4

Resolving G × E interactions

Various techniques have been developed to address G × E interaction, and to analyse the effects of environmental factors on plant characteristics.

Environmental characterization of the collection region may be used in assessing plant genotypic characteristics and forecasting growth under different climatic conditions. Provided that the germplasm originates from the collection region (i.e. has not been recently introduced), agronomic practices and ecological characteristics during domestication and cultivation have influenced its genotypic constitution. Hence, a relation exists between the agro-ecological conditions of the region of provenance and the morpho-physiological make-up of the plant. It may be expected also, that the former can be related to phenotypic plant characteristics at locations with different environmental conditions, although the relation with the genotype is stronger. Such relations are used, for instance, when a breeder requests seeds from 'a dry region' in search for drought tolerance. An other example is tolerance to late season frosts in Syrian durum wheat landraces (Elings & Nachit, 1993). Elucidation of such relations may contribute to understanding of plant performance in different environments, which otherwise can only be obtained through evaluations that are relatively expensive. However, establishment of unequivocal relations is likely to be hampered by G × E interactions, and by the lack of information on the environment of origin.

Analysis of variance (ANOVA) tests the significance of the effects of factors and their interactions, and establishes experimental error (Bowman, 1989; Sokal & Rohlf, 1981). This technique analyses effects of population, year, location, fertilizer application and other environmental factors. An ANOVA provides a qualitative indication of the relative importance of factors, and is therewith a first step in analysis of experiments. However, it does not provide insight in the mechanisms underlying variation, and therefore, it offers little scope for understanding and predicting crop growth under different environmental conditions.

Westcott (1986) distinguishes six additional techniques: linear regression and related stability parameters, cluster analysis, principal component analysis, use of environmental variables, geometrical methods, and stochastic dominance procedure. All techniques appear to fail with respect to using environmental variables, as was already noted by Eberhart & Russell (1966): 'Until we can measure such (environmental) factors in order to formulate a mathematical relation with yield, the average yield of the varieties in a particular environment must suffice'. Recently, Eskridge (1990) advocated the use of a decision-theory concept known as safety-first. This is a decision-making tool which explicitly quantifies how a plant breeder weighs the importance of yield relative to stability.

Regression models are used particularly frequently by breeders. However, the technique was developed to provide stability parameters (Eberhart & Russell, 1966; Finlay & Wilkinson, 1963) that can be used in germplasm selection, not to offer a tool for yield prediction in specific environments. It is a data-based descriptive model, and not a predictive model based on external variables (Lin et al., 1986). Analyses using stability statistics provide some insight in G × E interaction, but remain descriptive, and do not explain plant growth and development. Therefore, their predictive capacity is limited.

The additive main effects and multiplicative interaction (AMMI) model (Zobel et al., 1988) has gained popularity in recent years (e.g. van Eeuwijk & Elgersma, 1992). This technique combines analysis of additive main effects (genotype, environment) with analysis of multiplicative interaction effects (see also McLaren, 1995).

Crop growth simulation

Crop growth simulation models dynamically describe dry matter production and phenological development, incorporating plant genetic and environmental characteristics. Explanatory crop growth models allow the understanding of larger systems on the basis of the knowledge gained by experimentation on smaller systems (de Wit, 1982), and can account for part of G × E interaction on the basis of quantitative knowledge on the relations between plant genotypic and environmental characteristics. They allow extrapolation of effects at the level of single plant organs to the growth of a complete canopy in a continuously changing field environment (Spitters & Schapendonk, 1990) and, therefore, G × E interactions and the consequences for yield are reproduced on a daily basis.

Integration of crop growth simulation in evaluation

Fig. 1 presents a possible selection and evaluation scenario in which simulation of crop growth is used to acquire knowledge with respect to agronomic performance of the germplasm in different environments. Especially if a large collection is evaluated, division of this collection in relatively homogeneous sub-collections can be considered. Such classification could be based on, for instance, regions of origin, morphological or physiological characteristics, or colloquial naming (Elings & Nachit, 1991), as in the case of Syrian durum wheat landraces. However, in case of other crops and other regions, a different classification system may be required. Dividing a large collection in smaller ones has the advantage that it is easier to select a limited number of genotypes which are representative for the larger group of genotypes they are selected from (which is, in this case, the sub-sample, instead of the much larger entire collection). This limited number of genotypes is evaluated multi-locationally and/or multi-seasonally, and the evaluation results are used in simulation studies that explore crop growth and production in different environments. In case of the example given in Fig. 1, four sets of genotypes, each representing one sub-sample of the large germplasm collection, are studied through evaluation and simulation. The simulation studies can be extended to other genotypes, which are to a limited extent characterized in the separate characterization experiments. This can provide a broader assessment of the collection. Only if the evaluation and simulation results are promising, the particular sub-sample of genotypes is considered for further detailed evaluation. In the example in Fig. 1, sub-samples 1, 3 and 4 are discarded. Evaluation or simulation performance of the genotypes of

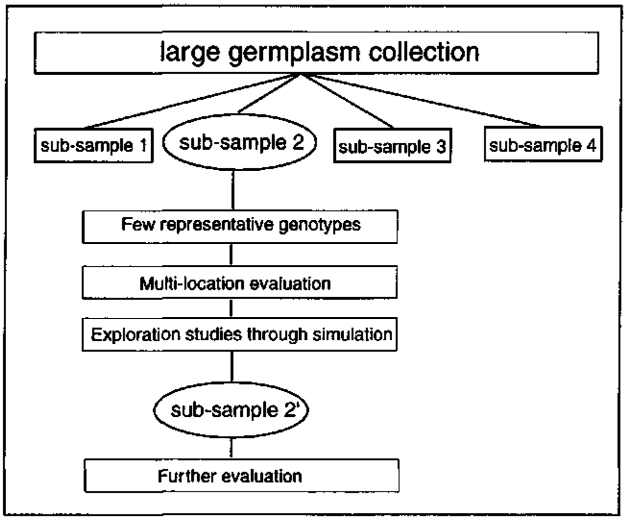

Figure 1. An example of a selection and evaluation programme that makes use of crop growth simulation to explore crop growth and production in different environments.

of sub-sample 2 justify its further evaluation. This further evaluation may follow any desirable design, including further application of simulation techniques. Alternatively, it may be preferable to proceed with only part of sub-sample 2, and incorporate some genotypes of the other sub-samples as well.

Evaluation efficiency is increased, as resources are focused on crop growth and production of a few genotypes that are considered representative for a larger group of genotypes. The other genotypes are considered for evaluation only if their representatives provide reason for this. Evaluation efficiency is further increased through a substantial reduction of the number of evaluation environments and/or seasons, and replacement with exploration studies with simulation models.

Integration of crop growth simulation in selection

It is difficult to apply a simulation model to an F1 population, as crop growth and development of the selected Fn may be very different, due to change in genetic constitution of the plant material. While moving from an F1 to an Fn generation, yield increases, and other plant characteristics, such as disease resistance, change as well. Most crop growth models assume a constant morpho-physiological make-up of the plant, and do not allow a change as a consequence of selection pressure. Models that simulate change in allele frequency incorporate as yet a limited set of alleles, and are, therefore, not suitable to simulate the drift in the entire genetic constitution of a complete plant.

Evaluation of large germplasm collections

As a consequence of the large amounts of accessions they contain, plant germplasm collections cannot be evaluated multi-locationally and -seasonally, which restricts the quantity and quality of information on plant characteristics (see Introduction). To increase the efficiency of use of scarce resources, alternative selection methods should be followed. Also Kresovich & McFerson (1992) argue that filling every cell in a data base matrix may not be the wisest use of limited resources, and that some resolution may be sacrificed if an initial analysis of fragmentary data sets provides the curator with guidelines for more detailed evaluation.

In addition to the information supplied by traditional analytical techniques, crop growth simulation accounts for the effects of environmental factors on plant characteristics, so that G × E interactions and the consequences for yields are reproduced on a daily basis. Such an explanatory approach stands in contrast with descriptive techniques as regression analysis. Also, regression models may be difficult to parameterize for other genotypes, which is easier in case of simulation models.

A breeding programme must efficiently select genotypes that are suitable for cultivation in certain environments. As long as a sufficient number of genotypes is selected, it is acceptable, from a breeder's point of view, that other good germplasm is discarded during selection. There is a delicate balance between available genetic diversity, selection pressure, selection efficiency, and number of selected genotypes. In addition, preliminary evaluations of plant genetic resources are primarily aimed at establishing a general overview of the properties of an entire collection, and the relative values of individual accessions, which relaxes the demands on absolute accuracy in evaluation results, if it provides broad knowledge over diverse environments (Elings & van Keulen, 1993). In this preliminary phase of evaluation and selection, it is not necessary to determine accurately all potentially important plant characteristics. Generally, full accuracy is not obtained with crop growth simulation, and it is unlikely that estimates obtained with crop growth simulation are similar to actual yields that would have been obtained in field evaluations. However, for the above-mentioned reasons, this does not necessarily result in reduced selection efficiency.

Data on plant characters for which model performance is sensitive are required. Partly, these can easily be recorded in customary routine evaluations, such as date of anthesis and the related temperature sum. In these routine evaluations with one replication, all genotypes are sown anyway to obtain morphological descriptions, and therefore few additional plant characteristics can be obtained with little extra input (these characterization experiments are separate from the agronomic evaluation experiments). The plant characters that are selected for genotype description must, first of all, be easy to observe, such as flowering date, grain yield and particular morphological characters. A high heritability, or high stability over generations and environments, gives observations a wider value than only to the observed genotype in the particular environment of evaluation. Also, for food crops, a stable relation with dry matter production and grain yield is important. Additionally, basic information on, for instance, physiological characters is required. These may be determined experimentally on a limited number of selected genotypes, and then be applied more broadly. Environmental input may be long-term weather characteristics and preferably specific soil characteristics, if necessary complemented by specific weather or soil data representing more favourable or adverse growing conditions.

The evaluation of G × E interactions may be complicated by intra-population genetic heterogeneity, as in the case of landraces. Assessment of diversity forms an essential part of plant germplasm evaluation, since it indicates the breeding value of observed plant characteristics. The complex interplant relations within a landrace population are balanced towards long-term yield stability in the environment of origin. Intra-population variation can be quantified with ANOVA, however, this is of little predictive value for different environmental conditions. Also, regression analyses and crop growth simulation models at the population level, do not incorporate intra-population variation and do not explain, therefore, the consequences of heterogeneity in different environments. Possibly, application of competition models (e.g. Kropff & van Laar, 1993), which simulate growth and production of competing plants in a mixed stand, offer a solution.

Crop growth simulation has so far concentrated on explanation of environmental variation, and has been applied to only a few genotypes, which were in most cases genetically closely related, such as rice varieties IR64 and IR72. This has allowed extensive genotypic characterization of these genotypes. Comprehensive analysis of G × E interaction requires more attention for the genetic component of the variation in grain yield. As not all genotypes of a large collection can be characterized extensively, a balance has to be found between the number of genotypes and the number of relevant characters, such, that the analysis of genetic variation is not jeopardized. Simulation models can best be used to simulate the consequences of large genetic differences, such as the consequences of variation in date of anthesis for grain yield, in an early phase of the evaluation programme. The consequences of small genetic differences for crop growth can be evaluated by model studies, provided that the relevant plant characteristics are included in the model. However, it may appear difficult to explain small differences that are observed in a field experiment, if the model's own errors are relatively large. This may partly be solved by increasing the number of plant characteristics observed in the experiments, which supply data that reduce model error. For example, small variation in harvest index (dry matter partitioning) may fall in this category.

Conclusions

Simulation models for crop growth are generally better suited for explanation of the effects of environmental variation than for analysis of small genetic differences between crops. Current models can, therefore, best be applied to analyse the consequences of pronounced variation in genetic characters, with well-established relations with environmental characters, and which have a relatively high heritability. If applied to early generations in the selection process, this may increase selection efficiency.

References

Bowman, D.T., 1989. Statistical procedures to measure population variation. In: H.T. Stalker & C. Chapman (Eds), Scientific management of germplasm: characterization, evaluation and enhancement. IBPGR Training Courses: Lecture Series 2. International Board for Plant Genetic Resources (IBPGR), Rome, pp. 65-73.

Ceccarelli, S., S. Grando & J. Hamblin, 1993. Relationship between barley grain yield measured in low- and high-yielding environments. Euphytica 64: 49-58.

Ceccarelli, S. & S. Grando, 1991. Environment of selection and type of germplasm in barley breeding for low-yielding conditions. Euphytica 57: 207-219.

Eeuwijk, F.A. van & A. Elgersma, 1992. Incorporating environmental information in an analysis of genotype by environment interaction for seed yield in perennial ryegrass. Heredity 70: 447-457.

Eberhart, S.A. & W.A. Russell, 1966. Stability parameters for comparing varieties. Crop Sci. 6: 36-40.

Elings, A. & H. van Keulen, 1993. Durum wheat landraces from Syria. IV. Simulation of growth and development. Eur. J. Agron. 3: 71-83.

Elings, A. & M.M. Nachit, 1991. Durum wheat landraces from Syria. I. Agro-ecological and morphological characterization. Euphytica 53: 211-224.

Elings, A. & M.M. Nachit, 1993. Field evaluation and simulation of frost tolerance in Syrian durum wheat landraces. Neth. J. Agric. Sci. 41:1-11.

Eskridge, K.M., 1990. Selection of stable cultivars using a safety-first rule. Crop Sci. 30: 369-374.

Finlay, K.W. & G.N. Wilkinson, 1963. The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. 14: 742-754.

Giles, R.J., 1990. Utilization of unreplicated observations of agronomic characters in a wheat germplasm collection. In: J.P. Srivastava & A.B. Damania (Eds), Wheat genetic resources: meeting diverse needs. John Wiley & Sons Ltd., Chichester, pp. 113-130.

ICARDA, 1993. Genetic Resources Unit, Annual Report for 1992. The International Center for Agricultural Research in the Dry Areas, Aleppo, Publication ICARDA-053, 170 pp.

IRRI, 1993. Program Report for 1992. The International Rice Research Institute, Los Baños, 316 pp.

Kresovich, S. & J.R. McFerson, 1992. Assessment and management of plant genetic diversity: considerations of intra- and interspecific variation. Field Crops Res. 29: 185-204.

Kropff, M.J. & H.H. van Laar (Eds), 1993. Modelling crop - weed interactions. CAB International, Wallingford and International Rice Research Institute, Los Baños, 274 pp.

Lin, C.S. & M.R. Binns, 1988. A method of analyzing cultivar × location × year experiments: a new stability parameter. TAG 76: 425-430.

Lin, C.S., M.R. Binns & L.P. Lefkovitch, 1986. Stability analysis: Where do we stand? Crop Sci. 26: 894-899.

McLaren, C.G., 1995. Combining ststistics and crop models for improved plant breeding strategies. This volume.

Sokal, R.R. & F.J. Rohlf, 1981. Biometry. The principles and practice of statistics in biological research. W.H. Freeman and Co., New York. 2nd edition, 859 pp.

Spitters, C.J.T. & A.H.C.M. Schapendonk, 1990. Evaluation of breeding strategies for drought tolerance in potato by means of crop growth simulation. Plant and Soil 123: 193-203.

Westcott, B., 1986. Some methods of analysing genotype-environment interaction. Heredity 56: 243-253.

Wit, C.T. de, 1982. Simulation of living systems. In: F.W.T. Penning de Vries & H.H. van Laar (Eds), Simulation of plant growth and crop production. Simulation Monographs, Pudoc, Wageningen, pp. 3-8.

Zavala-García, F., P.J. Bramel-Cox, J.D. Eastin, M.D. Witt & D.J. Andrews, 1992. Increasing the efficiency of crop selection for unpredictable environments. Crop Sci. 32: 51-57.

Zobel, R.W., M.J. Wright & H.G. Gauch, 1988. Statistical analysis of a yield trial. Agron. J. 80: 388-393.

Plant type designs for increased yield potential of irrigated rice - a simulation analysis

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Abstract
A methodological framework is presented for the applications of crop models in the design and evaluation of plant types for higher yield potential in specific environments. The framework is illustrated with a case study on irrigated rice in northern India. The results showed that for a large increase in yield potential, it is important that leaf area, above ground growth, spikelet number, potential grain weight and grainfilling duration are increased simultaneously. More work is needed to determine the genetic variation available in the germplasm for critical inputs for crop traits in the simulation models.

Introduction

Due to increasing food demand in the future, rice yield in the irrigated ecosystems must double by the year 2025 (Hossain, 1995). In order to achieve such a target, it is necessary to increase our effort to design new plant types for higher yield potential. Physiologists have earlier proposed several such designs for different crops (Donald, 1968; Hunt 1993) but they have generally not been used directly in breeding programmes. Major limitations for their use is the inconclusive evidence of the importance of a trait in increasing yield potential in different environments. Crop simulation models are tools that integrate the physiological knowledge and the effect of the edaphic, climatic and management environment on these traits. They are, therefore, suitable for determining critical traits for a desired yield potential in a specific environment. They have been recently used for such applications in wheat (Aggarwal, 1991), sorghum (Muchow et al., 1993), rice (Dingkuhn et al., 1989; Penning de Vries, 1991; Kropff et al., 1994b) and some other crops. In this paper, a framework is presented to use crop models in designing and evaluating new plant types for specific environments.

Material and methods

The various steps involved in the methodology are illustrated in Fig. 1. ORYZA1 (Kropff et al.,

Eds P.K. Aggarwal, R.B. Matthews, M.J. Kropff & H.H. van Laar
Applications of systems approaches in plant breeding. SARP Research Proceedings, AB-DLO, TPE-WAU, Wageningen and IRRI, Los Baños (1995), pp. 59-66.

1994a) was the crop model used for this case study.

Input requirements of the model are: geographical latitude, daily maximum and minimum temperatures, solar radiation, and dates of seeding and transplanting. Varietal characterization is required in the form of phenological development rates, relative leaf area growth rate, specific leaf area, spikelet formation factor, 1000 grain weight, leaf N content and fraction of stem reserves.

The performance of the model has been evaluated for several experiments varying in N input, variety, time and season of planting (Kropff et al., 1994a). The model predicted potential yields ranging from 6 to 15 t ha^{-1} in a range of contrasting environments reasonably accurately.

The critical inputs relating to leaf area, growth and development and sink size were varied in steps of 10% in the range of +50% to -50% to determine the major sensitive parameters of rice in a well irrigated and fertilized, disease-free environment of New Delhi. The later has a subtropical climate with rainfall during the rice growing season varying from 400 to 700 mm. The basic crop inputs were those determined for IR72 by Kropff et al. (1994a). Because only one parameter was varied at a time, this exercise is analogous to the field study of importance of different traits using near-isogenic lines.

To further examine the opportunities for increased yield potential, hypothetical plant types were generated in which several input parameters were varied simultaneously. This was achieved by using a random number generator programme - RIGAUS (Bouman & Jansen,

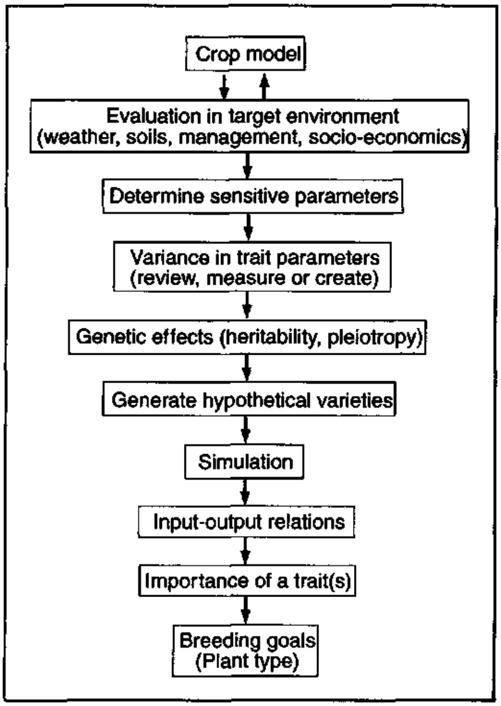

Figure 1. The flow chart of steps used for the application of crop models in the design and evaluation of plant types for specific environments.

Table 1. Model input parameters that were varied to create hypothetical plant types. Also shown is the range in which these parameters were varied. SLA, NFLV, FSH and FLV are development stage dependent functions. These were multiplied by the values shown in this table.

Name	Explanation	Standard value	Lower limit	Upper limit
DVRJ	Duration of basic vegetative period	.000773	.000550	.000900
DVRR	Duration of grainfilling period	.001783	.001600	.001800
RGRL	Relative leaf area growth during early periods	.008	.006	.012
SLA	Specific leaf area	1.	.8	1.2
NFLV	Leaf N content	1.	.8	1.2
FSH	Root:shoot ratio	1.	.8	1.2
FLV	Leaf:shoot ratio	1.	.8	1.2
SPGF	Spikelet formation factor	64900	50000	90000
WGRMX	1000 grain weight	24.9	20	30

1993) for the sensitive input parameters (Table 1). It was assumed that all inputs are uniform in distribution and vary within the limits shown in Table 1. The variation in some of the parameters is not very well known and therefore was assumed to be ±20% of the IR72 value. Inputs such as FSH, FLV, NFLV and SLA vary in the model as a function of the crop development stage (Kropff et al., 1994a). It was assumed that in hypothetical plant types this pattern of change with crop development remains the same. The value at any given development stage was obtained by multiplying with a constant (between 0.8 and 1.2) to get the appropriate value for the hypothetical variety. In practice, however, this range may be different.

One hundred hypothetical varieties were created with a random mix of different parameters within the specified range. The grain yield obtained by these varieties was determined using 1991 weather data of New Delhi. The plant types yielding at least 25% more than IR72 were identified from this analysis. Their performance was further tested for another 20 years by using the daily weather data of New Delhi from 1971 to 1991.

Results and discussion

Effect of variation in individual plant traits

The control crop (IR72) had a yield potential of 6.25 t ha^{-1} in the 1991 season. A 40 - 50% reduction in DVRJ (rate of development during vegetative stage) caused a 19 - 30 days increase in the duration of basic vegetative period. The grain yield of these plant types was 8 - 30% higher than IR72. These plant types had more dry matter production as well as higher number of spikelets and grains compared to IR72. By comparison, a 20 - 30% decrease in DVRJ resulted in 7 to 12 days increase in vegetative duration but yield of these plant types was lower

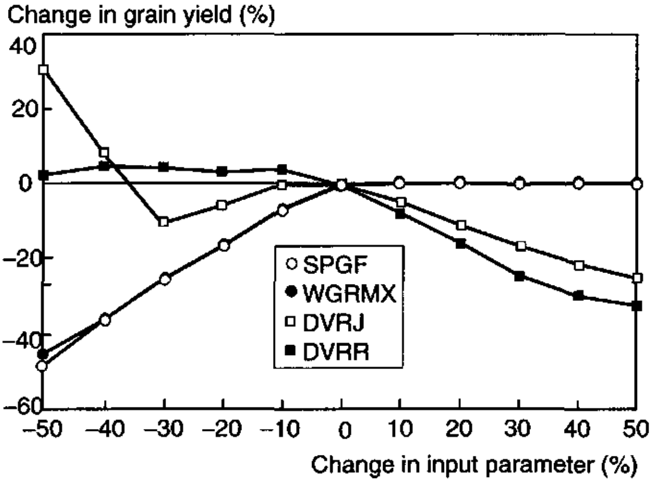

Figure 2. The effect of variation in model input parameters relating to crop duration (DVRJ and DVRR) and sink size (SPGF and WGRMX) on grain yield of irrigated rice in New Delhi.

than IR72 (Fig. 2). These crops had less number of grains than the control crop because the duration of grain formation period was reduced. Reduction in the vegetative period shifted grainfilling period to the days with relatively lower radiation and higher temperature. This reduced the grainfilling period and dry matter production. Simultaneously, these crops became sink limited. Increase in DVRJ reduced basic vegetative period in all cases and all such plant types had yields lower than IR72.

A reduction in post - anthesis development rate (DVRR) increased grainfilling duration by one or two days only since grains reached their pre-set potential weight by that time. Thus, in all these plant types the yields increased by less than 5% only. In the model, crop growth is terminated when all the available grains reach their maximum or when the crop reaches phenological maturity. Any decrease in grainfilling period resulted in reduced grain yields (Fig. 2).

Increase in sink size due to either an increase in number of spikelets or 1000 grain weight did not result in any increase in grain yield (Fig. 2). Increased spikelet numbers resulted in a compensation by a reduction in the weight of grains. Similarly, when maximum grain weight was set to a high level, the grain yield did not increase because there was not enough time available to fill those grains. In the model, there is a temperature dependent control of the grainfilling duration which terminates grain growth even if there are assimilates available for grainfilling.

Increase in LAI early in the season (caused by increased RGRL) or later (caused by increased SLA) had only a small effect on grain yield (Fig. 3). This increase was due to greater light interception resulting in more growth and hence more spikelets to be filled. But any reduction in either RGRL or SLA, in particular RGRL, resulted in a significant reduction in grain yield. A 50% increase in leaf N content resulted in 10% increase in grain yield. Increase in root:shoot ratio (decrease in FSH) greatly reduced yields but a 50% decrease in this ratio resulted in a

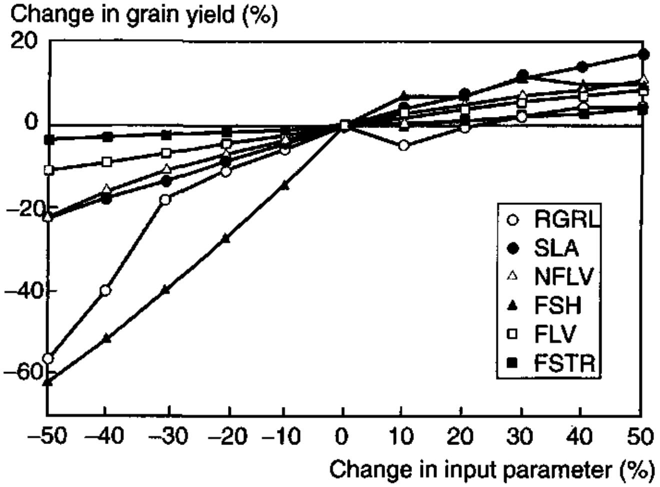

Figure 3. The effect of variation in model inputs relating to leaf area (SLA and RGRL), leaf N content (NFLV) and partitioning (FSH, FLV, FSTR) on grain yield of irrigated rice at New Delhi.

maximum increase of 12% in grain yield. Crops with relatively greater investment in leaves (greater FLV) had slightly increased yields (Fig. 3). Distribution of leaf N in the canopy, particularly during vegetative stage, had only a small effect on yield. Similarly, increased extinction coefficient for solar radiation interception had a very small positive effect but reduction in this during reproductive stages caused significant reduction in grain yield in both seasons (data not shown). The fraction of stem reserves (FSTR) had only a small effect on grain yield, irrespective of the magnitude of change in its value (Fig. 3).

These results indicate that the relative importance of different traits may change with season and a 50% change in individual traits can provide a maximum of 15 - 20% increase in yield potential. Adjustment of basic vegetative period may increase yields further than this limit but such crops may not fit in the cropping calendar. The magnitude of response to input change may, however, be different depending on cropping year, location and level of management.

Effect of variation in several traits

The performance of 100 hypothetical plant types with random combination of parameter input values was evaluated for the New Delhi environment of 1991 crop season. These plant types had random combination of nine input parameters relating to leaf area development (RGRL and SLA), phenology (DVRJ and DVRR), partitioning (FSH and FLV), leaf nitrogen content (NFLV), spikelet growth factor (SPGF) and 1000 grain weight (WGRMX). Nine plant types were identified that showed more than 25% increase in yield potential over IR72. The input parameter values for these plant types are shown in Table 2. These high yielding plant types had different combinations of various parameters. Similar increase in yield could be achieved

Table 2. Input parameter values of plant types yielding 25% more than IR72 at New Delhi.

PT	NFLV	SPGF	FLV	DVRJ	DVRR	RGRL	SLA	FSH	WGRMX
1	3	31.4	13	−8	0	20.8	−10.6	18	1.6
2	13	16.5	16	−19.9	-5.6	−6.5	−5.5	14	8.8
3	7	24	18.9	−12.3	-6.7	−9.9	14	19	1.6
4	−1.4	21.3	9	−27.8	-3.4	31.3	19	13	13.3
5	17	21.7	−1.8	−7.2	-7.3	−0.3	−12.9	19	2.8
6	−7.6	22.2	3	16	-8.4	24.6	1	15	0.8
7	18	29.6	2	−15.3	-10.1	45	2	11	13.7
8	13	28	7	8.7	-7.9	43.8	−10.5	12	11.2
9	−18.4	20.2	6	4.7	-4.5	21.5	10	13	16.5

through several mechanisms. For example, plant types 2, 3, 4, 5 and 6 had a similar increase in yield potential (25 - 30%) but only some of them had increased leaf N content or RGRL. In fact, in others (4 and 6 for leaf N and 2 and 3 for RGRL) there was a decrease. However, all plant types had increased shoot:root partitioning, greater SPGF (thus greater number of spikelets) and higher WGRMX (thus higher potential grain weight). It can be concluded from the above that for a large increase in yield potential there is a need for simultaneous increase in leaf area, above ground growth, sink capacity (number of spikelets and potential grain weight), and grainfilling duration.

The performance of four of these plant types (1, 4, 7 and 8) and IR72 was further examined for different cropping seasons by simulating potential growth of rice crops using actual weather data obtained from 1971 to 1991. The results showed that there were important differences in yield depending upon the plant type and the year of planting (Fig. 4). The control yields (IR72) varied between 4.1 and 9.3 t ha^{-1}. Fifty percent of yields exceeded 7.0 t ha^{-1}. Irrespective of the cropping season, the selected plant types had always a yield potential higher than IR72. Plant types 4 and 7 generally yielded more than the rest and between them the differences were small. There was a 50% probability that the yields of plant types 1 and 8 were greater than 8.5 t ha^{-1}.

Conclusions

The methodology used in this paper can be used for designing and evaluating plant type designs for specific environments. Crop models can be used for setting exact breeding goals for individual traits for any specific environment provided the effect of specific environment (soil type, climate, inputs and other management) is appropriately incorporated in the model. There is a limited data availability on the variation in the critical crop traits in diverse germplasm. Greater work is needed to quantify this variability as well as to testing the consequences of these variations in field and simulation environments. The pleiotropic efflects among the traits are also not well documented. Collaboration between physiologists, modellers and plant breeders needs to be encouraged.

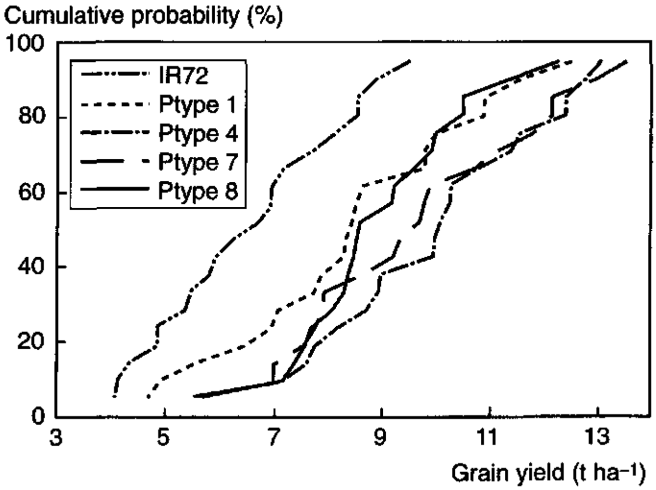

Figure 4. Cumulative probabilities of grain yield of irrigated IR72 and few selected plant types (PT) at New Delhi. See Table 2 for the details of plant types.

References

Aggarwal, P.K. 1991. Estimation of the optimal duration of wheat crops in rice-wheat cropping systems by crop growth simulation. In: F.W.T. Penning de Vries, H.H. van Laar & M.J. Kropff (Eds), Simulation and systems analysis for rice production. Pudoc, Wageningen, Netherlands, pp. 3-10.

Bouman, B.A.M. & M.J.W. Jansen, 1993. RIGAUS: Random input generator for the analysis of uncertainty in simulation. CABO-TPE Simulation Reports no 34, 26 pp.

Dingkuhn, M., F.W.T. Penning de Vries, S.K. De Datta & H.H. van Laar, 1991. Concept for a new plant type for direct seeded flooded tropical rice. In: Direct seeded flooded rice in the tropics. Selected papers from the International Rice Research Conference, 27-31 August 1990, Seoul, Korea. Intl Rice Res. Inst., Los Baños, Philippines, pp. 17-38.

Donald, C.M., 1968. The breeding of crop ideotypes. Euphytica 17: 385-403.

Hunt, L.A., 1993. Designing improved plant types: a breeder's viewpoint. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, The Netherlands, pp. 3-17.

Hossain, M., 1995. Sustaining food security for fragile environments in Asia: Achievements, challenges and implications for rice research. In: International rice research conference on fragile lives in fragile ecosystems, IRRI, Los Baños, Feb. 1995.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994a. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, IRRI, Wageningen, 110 pp.

Kropff, M.J., S. Peng, T.L. Setter, R.B. Matthews & K.G. Cassman, 1994b. Quantitative understanding of rice yield potential. In: K.G. Cassman (Ed.), Breaking the yield barrier. International Rice Research Institute, Philippines, pp. 5-20.

Muchow, R.C. & P.S. Carberry, 1993. Designing plant types for the semiarid tropics: agronomists' viewpoint. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, The Netherlands, pp. 37-61.

Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: Systems simulation at IRRI. IRRI Research Paper Series, November 1991, Number 151, pp. 13-19.

Applications of the INTERCOM model in plant breeding - model validation and effect of early leaf area growth on crop-weed competition in direct-seeded irrigated rice

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Abstract

Application of simulation models to identify and analyse parameters that significantly influence competitive ability of species could provide useful information to rice breeders in their search for more efficient plant types. In this paper, we use INTERCOM, a crop model developed to understand eco-physiological mechanisms of interplant competition. Results show satisfactory performance of the model in simulating growth and yield of rice and *Echinocloa crus-galli* in monoculture and in competitive environments. Simulated rice yield losses due to weed competition was similar to observed losses. It is also indicated that significant yield increases in direct-seeded irrigated rice could be realized by breeding for improved relative leaf area growth rate.

Introduction

Direct-seeding of irrigated rice is increasing due to non-availability of labour in many parts of Asia including Malaysia. Yield losses due to weeds are also generally much higher in direct-seeded rice compared to transplanted rice. The current trend in the demand for pest management strategies with reduced pesticides input places greater emphasis on the need to develop more competitive cultivars for efficient weed management (Khush, 1990).

Crop-weed competition in the real world is complex because a large number of interactions determine the competition process. Competitive ability of crops/cultivars is known to vary depending upon plant traits such as early growth, photosynthesis rate, plant height, seed weight, leaf angle and water and nitrogen use efficiency (Kropff et al., 1993). Crop models can be used as a quantitative tools in the understanding of competitive mechanisms between species, both under homogeneous as well as under patchy weed distribution often encountered in the field. Application of simulation models to identify and analyse parameters that significantly influence competitive ability of species could provide useful information to rice breeders in their search for more efficient plant types.

INTERCOM (Kropff & van Laar, 1993) is a recently developed crop model to understand ecophysiological mechanisms of interplant competition on the basis of the distribution of

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resources such as light, water and nutrients over species, and the way the species utilize these resources for their growth. Once validated, this model can be used for applications such as crop breeding for greater competitiveness against weeds, predicting crop yield losses as well as for designing better crop management practices. In this paper, we present some results of our case study where the long-term objectives are to use crop models for designing plant types for better weed competitiveness in direct-seeded irrigated rice environments. The specific objectives of this study are to validate the INTERCOM model for the analysis of weed competition effects in direct-seeded irrigated rice using our own experiments done in Malaysia to study competition effects and to use the validated model to evaluate the influence of relative growth rate of early leaf area development (seedling vigour) on competitiveness of rice cultivars.

Material and methods

The results of experiments previously reported (Rajan, 1991) were used in this analysis and validation study. Two experiments were conducted to study density effects. Pre-germinated rice (cv. MR84) and weed seeds were sown, with the rice at densities of 50, 100, 150 kg ha^{-1} in monocultures and in mixtures with the weed (*Echinocloa. crus-galli* (L.) Beauv. var. *crus-galli*) which was sown at a density of 130 plants m^{-2}. The first experiment was conducted in 1.0 × 1.0 × 0.8 m tanks (Rajan, 1991), while the second experiment was conducted in the field. The emergence dates for weed and crop were the same. The parameters measured for the crop in monoculture at the lowest density of 50 kg ha^{-1} and the weed in monoculture were used to calibrate the model. All other data were used to validate the model.

In another study, sowing dates, and hence emergence dates, of the crop were delayed relative to the weed. This experiment had the following treatments: 0, 7 and 14 days delay in sowing of pre-germinated crop seeds with respect to the sowing of pre-germinated weed seeds (Rajan, 1991). The results of this study were also used to validate the model.

Changes in plant parameters and validation

The plant parameter inputs that were changed to adapt the original INTERCOM model parameters for the local rice cultivar (MR84) and ecotype characteristics of the weed are shown in Table 1. The initial leaf areas (LA0, cm^2 $plant^{-1}$) for each species were y-axis intercept values derived from the plots of ln(LAI) versus temperature sum, and the relative growth rate of leaves (RGRL) were derived from the same relationships (i.e. slopes of the respective regression equations). Leaf area data from the rice (50 kg ha^{-1}) and weed (130 plants m^{-2}) in monocultures were used to derive these parameters.

The vegetative and reproductive development rates and partitioning parameters were derived employing the DRATES program (see Kropff et al., 1994) using data from monocultures in the first density experiment conducted in tanks. The used values for maximum plant height (HMAX) were values observed in monocultures.

Preliminary simulation runs made with the above parameter inputs showed that the model

Table 1. Input parameters changed in the INTERCOM model for this case study. LA0- initial leaf area (cm^2 plant^{-1}), DVRV- crop development rate before flowering (°Cd)$^{-1}$, DVRR- crop development rate after flowering (°Cd)$^{-1}$, FAGTB, FRTTB, FLVTB, FSTTB and FSOATB are fractions of total dry matter allocated to above-ground parts, roots, leaves, stems and reproductive parts, respectively, RGRL- relative leaf area growth rate (°Cd)$^{-1}$, HMAX- potential plant height (cm).

(A) CROP: Rice (cv. MR84)

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LA0  = 0.7743
DVRV = 0.00058
DVRR = 0.00175

FAGTB  = 0.,.55, .268,.75, .701,.95, .976,1., 2.7,1.
FRTTB  = 0.,.45, .268,.25, .701,.05, .976,0., 2.7,0.

FLVTB  = 0.,.68, .268,.57, .701,.41, .98,.08, 1.,0.,         2.7,0.
FSTTB  = 0.,.32, .268,.43, .701,.59, .98,.05, 1.,.03,2.,0., 2.7,0.
FSOATB = 0.,0.,            .701,0.,  .98,.87, 1.,.97,2.,1., 2.7,1.

RGRL = 0.01
HMAX = 110.
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(B) WEED: *E. crus-galli* var. *crus-galli*

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LA0  = 0.4513
DVRV = 0.000795
DVRR = 0.00207

FAGTB  = 0.,.55, .353,.78, .921,1., 1.76,1., 2.,1., 2.7,1., 3.5,1.
FRTTB  = 0.,.45, .353,.22, .921,0., 1.76,0., 2.,0., 2.7,0., 3.5,0.

FLVTB  = 0.,.6,  .353,.48, .921,.03, 1.76,.001, 2.,.001, 2.7,0., 3.5,0.
FSTTB  = 0.,.4,  .353,.52, .921,.96, 1.76,.05,  2.,.004, 2.7,0., 3.5,0.
FSOATB = 0.,0.,  .353,0.,  .921,.01, 1.76,.949, 2.,.995, 2.7,1., 3.5,1.

RGRL  = 0.0129
HMAX  = 160.
HS    = 0.00372
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underestimated growth of the weed, in particular plant height, both in monoculture and in mixtures, and yield loss in mixtures was, therefore, underestimated compared to observed values. Changes to the logistic height parameter (HS) for the weed was found to be necessary. Calibration runs with the weed in mixture with rice at the lowest density showed the need for a 20%

increase (from 0.0031 to 0.00372 (°Cd)$^{-1}$) in the HS parameter for the weed.

All other parameter inputs were based on competition experiments between rice (cv. IR64) and barnyard grass at IRRI (Kropff et al., 1992, unpublished; Kropff & van Laar, 1993).

Effect of early leaf area growth

Early leaf area growth is described in the model by the relative leaf area growth rate (RGRL). The potential influence of RGRL on the competitive ability of the rice cultivar was simulated by varying the rice RGRL value from 0.01 (°Cd)$^{-1}$ (the current observed value) to a maximum of a 20% increase.

Results and discussion

Model validation

Following the changes to the above parameters the simulated total above ground dry matter (TAGDM), leaf area index (LAI), and plant height showed close agreement to observed values in the rice monoculture and in the weed monoculture (Figs 1 and 2). Simulated TAGDM and LAI values were comparable to observed values in both species in monocultures and in mixtures for all rice densities (Figs 3 - 5).

The panicle weights (WSO) simulated for the three crop densities in monoculture and in mixtures were comparable to the observed values where the yield decline was significant when the crop and the weed emerged at the same time (Fig. 6A). The simulated competition effect and the resulting yield loss were more marked when there was delay in sowing of the crop (Fig. 6B).

A much lower yield predicted for a seven day delay in sowing of the crop compared to the observed value (Fig. 6B) and the corresponding yield loss showing extreme deviation (Fig. 6C), may be attributed to small differences in plant height during initial establishment. Pre-germinated crop seeds used in this study may have offered a comparative advantage in early development. This is also reflected in the common practice of sowing pre-germinated seeds adopted by farmers to achieve earlier crop establishment. Kropff et al. (1993) have also emphasized that in mixtures small differences in plant height or leaf area development may cause dramatic changes in the competitive relationships. In general, simulated yield losses were comparable to yield losses recorded in several experiments (Fig. 6D).

Effect of early leaf area growth

Increasing RGRL value for the rice cultivar by 5, 10, 15 and 20% of the current observed value resulted in a predicted grain yield increase of 0.52 to 1.40% only for rice in monocultures; however, in the mixtures with the weed (130 plants m^{-2}), when crop emergence coincides with weed emergence, the corresponding predicted yield increases were 9.3, 18.2, 24.5 and 30.9% of current values (Fig. 7). The results of this analysis indicate significant yield increases could be realized where weeds are present by breeding for traits giving improved RGRL.

Conclusions

The results of this study indicate that the INTERCOM model can be used for studying crop-weed interference in direct-seeded rice, and can be easily adapted for studying competition effects of other weed species where minimum data sets for the critical variables were available (Table 1).

The simulated outputs also indicate the potential for increasing yields by enhancing the competitive ability of crop cultivars. A more competitive cultivar would require less inputs for weed management. The usefulness of the model in identifying traits for breeders to consider in the selection of competitive cultivars is also indicated.

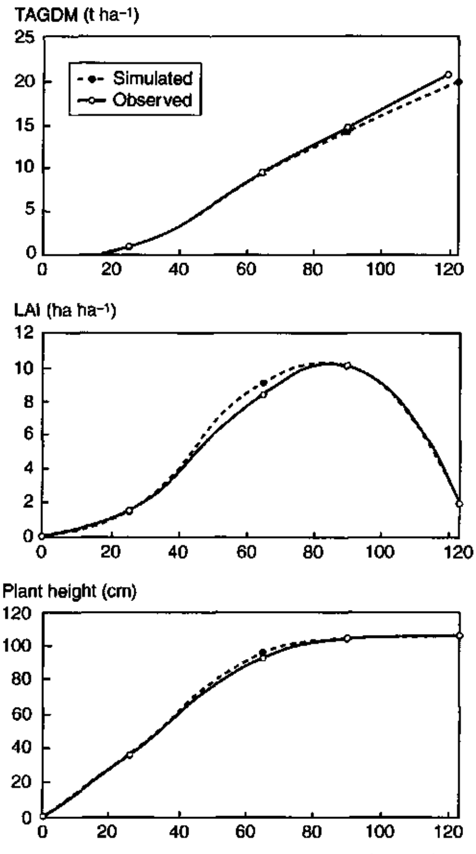

Figure 1. Observed and simulated values for total above-ground dry matter (TAGDM), leaf area index (LAI) and plant height (HGHT) for rice in monoculture.

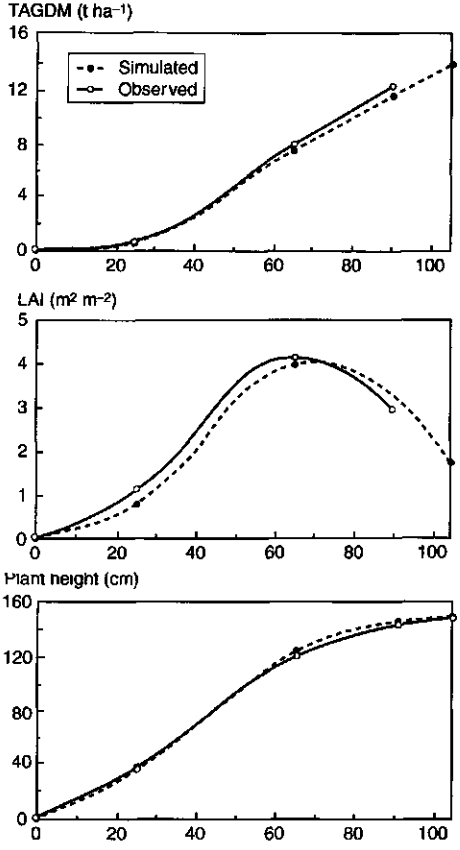

Figure 2. Observed and simulated values for total above-ground dry matter (TAGDM), leaf area index (LAI) and plant height (HGHT) for the weed in monoculture.

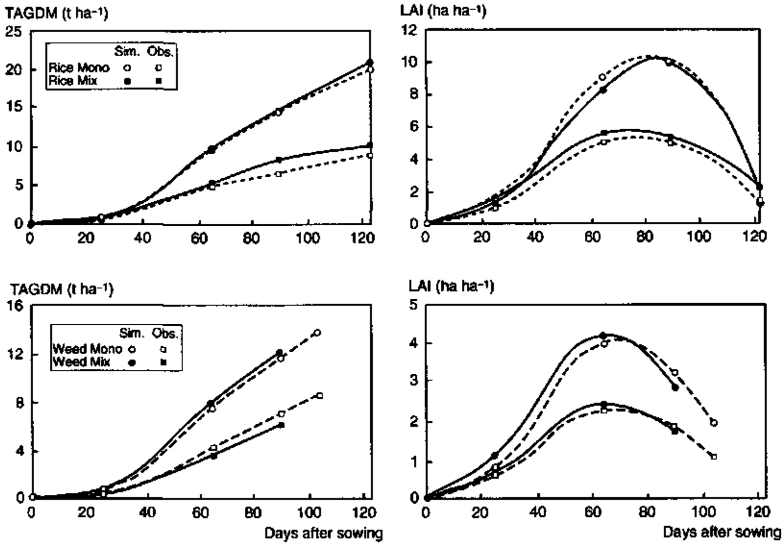

Figure 3. Observed and simulated values for total above-ground dry matter (TAGDM) and leaf area index (LAI) for rice sown at 50 kg ha^{-1} and the weed (130 plants m^{-2}) in monoculture and mixtures.

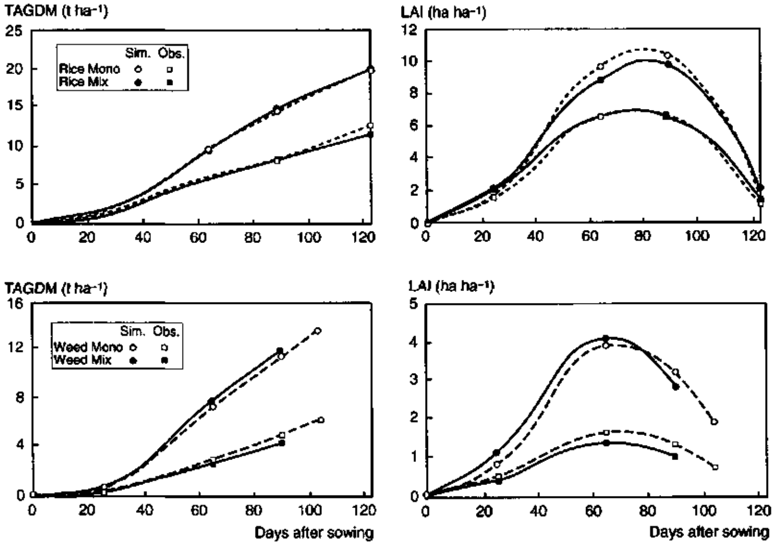

Figure 4. Observed and simulated values for total above-ground dry matter (TAGDM) and leaf area index (LAI) for rice sown at 100 kg ha^{-1} and the weed (130 plants m^{-2}) in monoculture and mixtures.

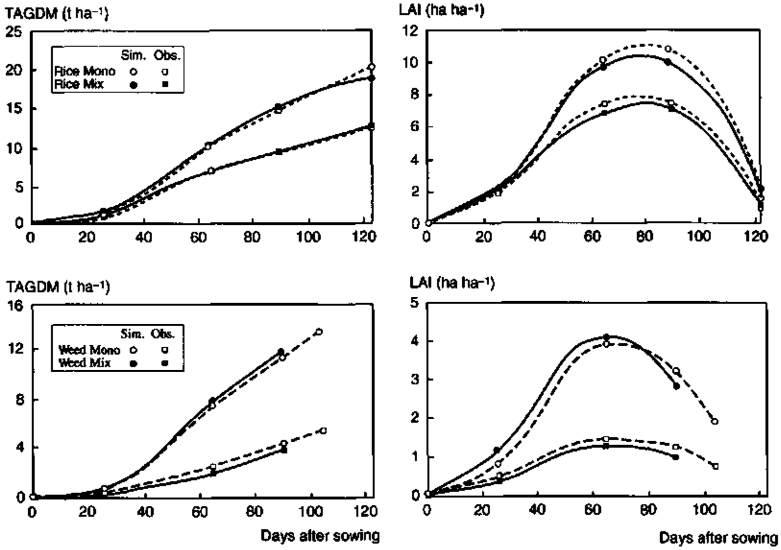

Figure 5. Observed and simulated values for total above-ground dry matter (TAGDM) and leaf area index (LAI) for rice sown at 150 kg ha^{-1} and the weed (130 plants m^{-2}) in monoculture and mixtures.

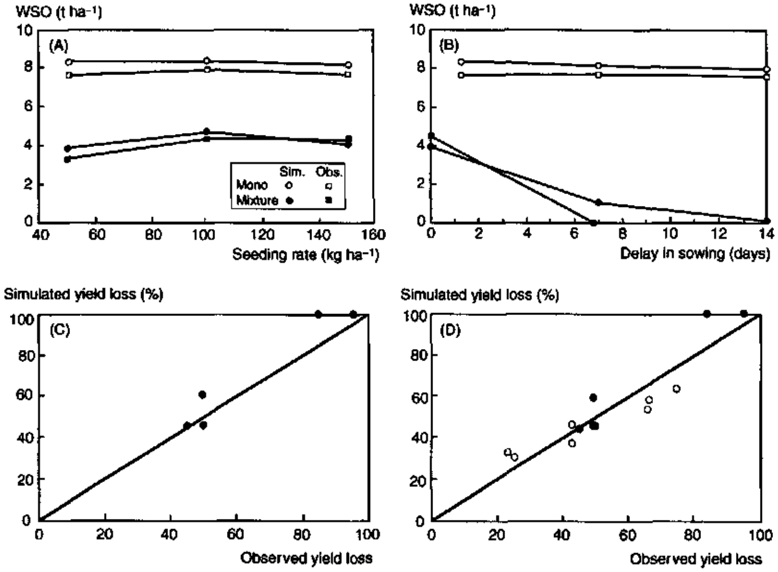

Figure 6. Observed and simulated yields (panicle weights, WSO) and yield loss for rice in monocultures and mixtures.

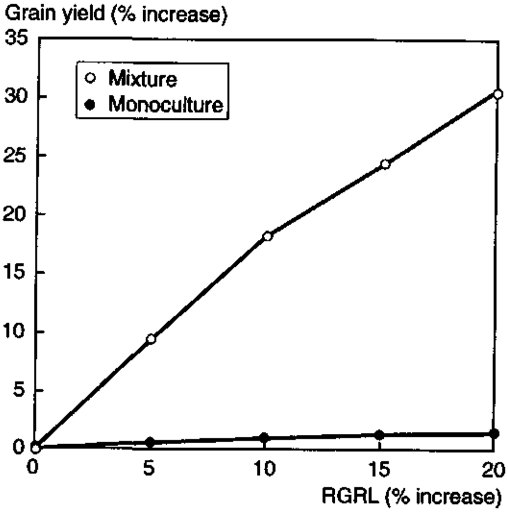

Figure 7. Yield response in rice to increase in RGRL.

References

Khush, G.S., 1990. Varietal needs for different environments and breeding strategies. In: K. Muralidharan & E.A. Siddiq (Eds), New frontiers in rice research. Directorate of Rice Research, Hyderabad, India, pp. 68-75.

Kropff, M.J. & H.H. van Laar (Eds), 1993. Modelling crop-weed interactions. CAB International, Wallingford and International Rice Research Institute, Manila, 274 pp.

Kropff, M.J., S.E. Weaver, L.A.P. Lotz, J.L. Lindquist, W. Joenje, B.J. Schnieders, N.C. van Keulen, T.R. Migo & F.F. Fajardo, 1993. Understanding crop-weed interactions in field situations. In: M.J.Kropff & H.H. van Laar (Eds), Modelling crop-weed interactions. CAB International, Wallingford and International Rice Research Institute, Manila, pp. 105-136.

Kropff, M.J., H.H. van Laar & R.B. Mathews (Eds), 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, IRRI, AB-DLO and TPE-WAU, 110 pp.

Rajan, A., 1991. Simulation of weed interference and yield loss in direct seeded irrigated rice. In: H.H. van Laar et al. (Eds), Case studies in crop growth simulation, 1990-1991. IRRI (Philippines), CABO and TPE, Wageningen (The Netherlands), pp. 147-152.

Quantification of the interference between *Echinochloa crus-galli* and transplanted rice - validation and sensitivity analysis of the model INTERCOM

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Abstract

The model INTERCOM was used to quantify competition between *Echinochloa crus-galli* and rice. The model was tested with data from field experiments conducted during the Thaladi season (1992 - 1993) at the Tamil Nadu Rice Research Institute, Aduthurai, India. The effect of weed density and the critical period for weed competition in transplanted rice (ADT38) was analysed. In general there was good agreement between simulated and observed values of growth parameters and grain yield. The effect of different densities of crop and weed, different aged seedlings, the period between crop and weed emergence and crop season, and the relative growth rate of the leaves were simulated. The results indicated that an increased crop density and younger seedlings would benefit the competitive ability of the rice crop. In this study, the critical period for crop weed competition was from 15 to 60 days after planting.

Introduction

The impact of weeds on rice has been studied for decades. Research indicated that world-wide over 10% of agricultural production is lost as a result of crop weed competition for light, water and nutrients (Parker & Fryer, 1975). Moody (1991) reported that weeds are a severe and widespread biological constraint to rice production, which results in an estimated yield loss of 10% which is equivalent to 46 Mt per year. The competitive interactions between rice and weeds are influenced by several morphological and physiological characteristics of the rice varieties and weed species, related to height growth, leaf area development and light absorption capacity of the leaves. Besides these physiological characteristics of the species, weed and crop density, spatial arrangement, the date of crop and weed emergence and the dynamic influence of environmental variables on growth processes determine the competitive processes. Recently, Kropff

Eds P.K. Aggarwal, R.B. Matthews, M.J. Kropff & H.H. van Laar
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AB-DLO, TPE-WAU, Wageningen and IRRI, Los Baños (1995), pp. 75-85.

& van Laar (1993) developed the crop simulation model INTERCOM to improve insight into the mechanism of competition between crops and weeds in agricultural systems, and as a guide in weed management decision-making. The model provides a tool to analyse the complex interaction between plants that compete for light, water and nitrogen in different ecological environments. It also facilitates the study of plant attributes determining the competitive ability of weeds, and the evaluation of weed-control strategies like quantification of non-lethal weed control measures such as bio-herbicides in terms of yield loss and low dosages of herbicides if their effects on physiological and morphological characteristics is known (Kropff & van Laar, 1993).

In this paper, the INTERCOM model was tested with field experimental data on the effects of weed density and the period of competition with transplanted lowland irrigated rice. The model was used to simulate the effect of weeds on rice yield under different weed and rice densities, different seedling ages, different times of weed emergence and for different seasons.

Material and methods

Model structure

The INTERCOM model simulates the following aspects of growth in competition:

- Phenological development,
- Morphological development (height and leaf area),
- Dry matter accumulation based on light capture in competition-situations, and
- Allocation of dry matter to the plant organs.

Input requirements of the model are: standard daily weather data (daily solar radiation, temperature, rainfall, average wind speed, vapour pressure), and parameter values that describe the morphological and physiological characteristics of the plant species.

Under favourable growth conditions, light is the main factor determining the growth rate of the crop and its associated weeds. From the leaf area indices (LAI) of the species and the vertical distribution of their leaf area, the light profile within the canopy is calculated. Based on photosynthesis characteristics of single leaves, the photosynthesis profile of each species in the mixed canopy is obtained. Integration over the height of the canopy and over the day gives the daily CO_2 assimilation rate for each species. The dry matter produced is partitioned among the various plant organs, using partitioning coefficients depending on the phenological development stage of the species. Phenological development is a function of the ambient daily average temperature. When the canopy closes, the increase in leaf area is obtained from the increase in leaf weight using the specific leaf area (SLA, m^{-2} leaf kg^{-1} leaf).

Data used to test the model

Data on the effects of *Echinochloa crus-galli* on rice cultivar ADT38 (a medium duration variety of 135 days) was collected from two field experiments conducted during the Thaladi season, 1992 - 1993 (i.e. wet season, October to February) on a clay-loam soil at the Tamil Nadu Rice Research Institute, Aduthurai.

Experiment I: Effect of herbicides on competitive ability of different weed species against rice

A randomized block design with four replicates was used. The effect of three herbicides was evaluated: Butachlor (1.5 kg ha^{-1}), Anilofos (0.45 kg ha^{-1}), and Anilofos and 2,4 D (0.3 and 0.4 kg ha^{-1}, resp.). Weedy checks with grasses, sedges, and broadleaved weeds and a weed-free check were included as well. For this study, the weedy check with grass weeds (mainly *E. crus-galli*, 12 m^{-2}) and the treatment with Butachlor applied at 1.5 kg per plot (2 m^{-2}) were taken. Rice was transplanted at 33 DAS (days after sowing).

Experiment II: Effect of different periods of competition of E. crus-galli on rice

A randomized block design with four replications was used. Different periods of weed infestation and weed-free conditions (15, 30, 45, 60, 75 days until harvest) after transplanting were studied.

The rice plant spacing was kept at 15 × 10 cm (66 hills m^{-2}) with 1 plant per hill. The weeds were seeded by hand uniformly by mixing them with sand on the day of rice transplanting. The sown weed seeds emerged after three days. The weed plants were thinned on the fifth day after sowing. Nitrogen was applied at the dosage of 30 kg ha^{-1} at each application, i.e. just before transplanting, mid-tillering, panicle initiation, between panicle initiation and flowering and at flowering. The crop was irrigated and the water depth was maintained between 2.5 - 5 cm. Five hills per plot of both the rice and weed plants per replication were sampled at panicle initiation, flowering and at physiological maturity. From these samples plant height, tillers, leaf area, dry weight and nitrogen content of leaves, stem, panicle and roots were measured. Grain yield and yield components were taken at harvest.

Application of the model

The INTERCOM model was used to analyse competition between ADT38 and *E. crus-galli*. Values for relative growth rate, leaf area, leaf nitrogen status, and specific leaf weight were estimated from the experimental data in the monoculture treatments. All other parameters for both rice and weed plants were adopted from Kropff & van Laar (1993). The model inputs obtained from the field experiments are given in Table 1.

Results and discussion

Validation of INTERCOM

The observed and simulated dry matter production of rice and *E. crus-galli* in monoculture and in mixture is given in Table 2. Total dry matter production was simulated using the measured specific leaf nitrogen as input (NLVTB, g N m^{-2} leaf).

Simulated total dry matter matched the measured weight in the rice monoculture at all growth stages except at physiological maturity. The lower observed values at this stage may be due to the slight incidence of bacterial leaf blight, which infested the crop at about 15 days after flowering. Simulated weed biomass in monoculture showed good agreement with the observed

Table 1. Input parameters used in the model, for acronyms see Kropff & van Laar (1993).

Parameters for rice cultivar ADT38:

```
LA0    = 0.75; HGHTI = 1.
WLVGI = 0.000005; WSTGI = 0.000003; WRTI = 0.000005
DVRV   = 0.000637
DVRR   = 0.001932
RGRL   = 0.01228

*Dry matter partitioning parameters
FAGTB   =  0.0,0.50, 0.50,0.75, 0.65,0.80, 1.0,1.0 , 2.00,1.00, 4.  ,1.0
FRTTB   =  0.0,0.50, 0.50,0.25, 0.65,0.20, 1.0,0.0 , 2.00,0.  , 4.  ,0.0
FLVTB   =  0.0,0.7 , 0.50,0.70, 0.65,0.50, 1.0,0.05, 2.00,0.0 , 4.  ,0.0
FSTTB   =  0.0,0.3 , 0.50,0.30, 0.65,0.50, 1.0,0.45, 2.00,0.0 , 4.  ,0.0
FSOATB =  0.0,0.0 , 0.50,0.00, 0.65,0.00, 1.0,0.50, 2.00,1.0 , 4.,  1.0

LAITB   = 0.0,0.04, 0.50,0.20, 0.65,2.25, 1.0,4.97, 2.0,0.90, 4.0,0.90
SAITB   = 0.0,0.0 , 0.50,0.03, 0.65,0.4 , 1.0,1.3 , 2.0,0.5 , 4.0,0.5
NLVTB   = 0.0,1.35, 0.50,1.17, 0.65,1.02, 1.0,0.59, 2.0,0.40, 4.,0.40
SLWTB   = 0.0,300., 0.50,352., 0.65,370., 1.0,524., 2.0,524., 4.0,524.
NPROFT = 0.,1., 1.,1.6, 1.8,1.5, 2.1,1.2, 4.,1.2
```

Parameters for *Echinochloa crus-galli*:

```
LA0    = 0.75; HGHTI=1.
WLVGI = 0.000005; WSTGI = 0.000003; WRTI = 0.000005;
DVRV   = 0.000984
DVRR   = 0.002056
RGRL   = 0.0156

* Dry matter partitioning parameters
FAGTB   =  0.0,0.60, 0.33,0.75, 0.53,0.80,
           1.0,1.0 , 2.00,1.0,  4.00,1.0 , 7.0,1.0
FRTTB   =  0.0,0.40, 0.33,0.25, 0.53,0.20,
           1.0,0.0 , 2.00,0.0,  4.00,0.0 , 7.0,0.0
FLVTB   =  0.0,0.7 , 0.33,0.65, 0.53,0.40,
           1.0,0.05, 2.00,0.0 , 4.00,0.0 , 7.0,0.0
FSTTB   =  0.0,0.3 , 0.33,0.35, 0.53,0.60,
           1.0,0.95, 2.00,0.0 , 4.00,0.0 , 7.0,0.0
FSOATB =  0.0,0.00, 0.33,0.0 , 0.53,0.00,
           1.0,0.00, 2.00,1.0 , 4.00,1.0 , 7.0,1.0
RTD     = 0.3

LAITB   = 0.0,0.01 , 0.33,0.10, 0.53,1.20, 1.0,2.67, 2.00,1.05,
          4.0,0.58 , 7.00,0.58
SAITB   = 0.0,0.002, 0.33,0.01, 0.53,0.15, 1.0,0.2 , 2.00,0.3,
          4.0,0.3  , 7.00,0.3
NLVTB   = 0.0,1.02 , 0.33,1.15, 0.53,1.54, 1.00,0.99, 2.00,0.76,
          4.0,0.76 , 7.00,0.76
SLWTB   = 0.0,210. , 0.33,320., 0.53,550., 1.00,600., 2.00,600.,
          4.0,600. , 7.00,600.
NPROFT = 0.,1., 1.,1., 1.8,1.3, 7.,1.3
```

Table 2. Observed and simulated growth components of rice and *E. crus-galli* in monoculture and in mixture.

		Rice		*E. crus-galli*	
Growth stages	DAS	Total DM (t ha^{-1})	Height (cm)	Total DM (t ha^{-1})	Height (cm)
Mono - Observed					
	50	0.094	40	0.050	14
PI	72	1.195	53	0.945	28
FL	105	7.570	81	6.710	73
PM	135	12.510	88	11.950	104
Mono - Simulated					
	50	0.100	49	0.071	17
PI	72	1.408	65	1.294	33
FL	105	8.478	87	7.701	81
PM	135	13.816	94	13.003	108
(Rice + *E. crus-galli* 2) - Observed					
	50	0.094	40	0.007	15
PI	72	1.180	52	0.098	26
FL	105	7.390	80	0.225	75
PM	135	11.780	87	0.530	102
(Rice + *E. crus-galli* 2) - Simulated					
	50	0.100	49	0.009	17
PI	72	1.400	65	0.129	33
FL	105	8.195	87	0.307	79
PM	135	13.217	94	0.687	108
(Rice + *E. crus-galli* 12) - Observed					
	50	0.092	33	0.042	10
PI	72	1.155	49	0.475	26
FL	105	6.550	75	1.150	65
PM	135	10.210	77	2.480	100
(Rice + *E. crus-galli* 12) - Simulated					
	50	0.100	49	0.054	17
PI	72	1.317	65	0.642	33
FL	105	7.508	87	1.420	79
PM	135	11.678	94	3.006	108

PI = Panicle Initiation; FL = Flowering; PM = Physiological Maturity;
Weed number = Plants m^{-2}; DAS = Days After Sowing.

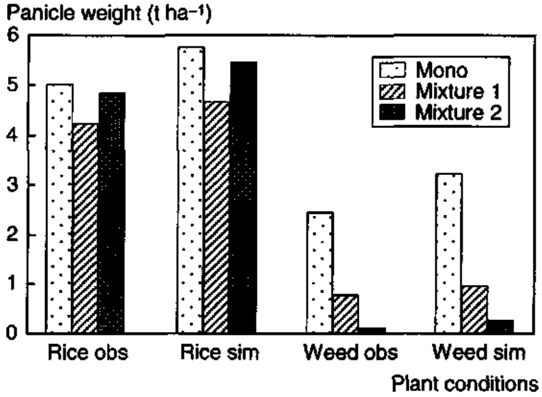

Figure 1. Simulated and observed panicle weights of rice and *E. crus-galli.*

values at all stages. Using the same set of parameters, good simulations were obtained for the mixture treatments with 12 and 2 plants of *E. crus-galli* m^{-2}. Simulated plant height also showed fair agreement with the observed values in monoculture in both rice and *E. crus-galli.* In mixture, simulated rice plant height was higher than the observed value. This is due to the lack of feedback of competition effects on height growth. Rao & Moody (1992) showed that competition between rice and *E. glabrescens* resulted in the reduction of plant height by 11.9 and 9.6%, respectively under transplanted situations and by 12.8 and 8.4% under wet seeded condition.

Simulated and observed yields due to competition between rice and *E. crus-galli* is given in Fig. 1. The INTERCOM model predicted a yield loss of 19.6 and 5.2% at weed densities of 12 (mixture 1) and 2 plants m^{-2} (mixture 2), respectively, which is close to the observed yield loss of 15.7 and 3.4%. Similar results were obtained by Kropff et al. (1993b) who used a wide range of data set from Kyushu (Japan), Arkansas (USA), California (USA) and Los Baños (Philippines). The relation between observed and simulated loss from the above experiments explained 93% of the variation and the regression of simulated versus observed was close to the 1:1 relationship ($y = -0.6 + 0.99x$). It can be concluded that the rice yield loss due to weeds can be explained by the INTERCOM model from differences in crop density, weed density, the period between crop and weed emergence and establishment method of rice.

Application of the INTERCOM model

Factors determining competition effects

Since the model performed well, it was used for further interpretation of competition effects. The effect of different densities of crop and weeds, seedling age, the period between crop and weed emergence, season, and the relative growth rate of the leaves (RGRL) were determined. During the Thaladi rice season, Cauvery Delta Zone farmers are using two crop densities, i.e.

Table 3. Simulated percentages of rice yield losses due to competition with *E. crus-galli*.

Sensitivity analysis		Rice population (hill m^{-2})	
		66	50
1. Rice + *E. crus-galli* densities			
E. crus-galli (plants m^{-2})	= 2	5.2	6.1
"	= 4	8.7	11.2
"	= 6	12.1	15.3
"	= 8	14.8	19.1
"	=10	17.3	22.1
"	=12	19.6	24.9
2. Effect of aged seedlings*			
Seedling age (days)	=24	16.1	17.7
"	=27	18.0	20.8
"	=30	19.0	22.1
"	=33	19.6	24.9
3. Weed emergence period*			
Days after planting	= 0	27.8	32.6
"	= 3	17.0	22.8
"	= 6	10.0	12.7
"	= 9	6.0	7.1
"	=12	2.5	3.3
"	=15	1.2	1.8
4. Seasonal influence*			
Kuruvai (135 days)		33.0	38.5
Thaladi (135 days)		19.6	24.2
Samba (135 days)		29.4	32.1
5. RGRL of rice*			
Measured (0.01228)		19.6	24.9
5% increase (0.01289)		15.5	20.0
10% increase (0.01350)		12.5	16.8

*Weed density of 12 m^{-2}

66 hills m^{-2} (15 × 10 cm spacing) and 50 hills m^{-2} (20 × 10 cm spacing) depending on the factors as variety, time of planting. The results of this analysis are summarized in Table 3.

Rice-weed densities Sensitivity analysis was done to determine the impact of the two rice crop densities (50 and 66 hills m^{-2}) in mixtures with six different weed densities (2, 4, 6, 8, 10 and 12 plants m^{-2}). The results show that by adopting a higher rice population of 66 hills m^{-2}, yield loss due to weed competition can be reduced. At a weed density of 12 plants m^{-2}, simulated yield reduction was 19.6 and 24.9% at 66 and 50 rice plants m^{-2}, respectively. This is mainly because of the higher population of rice which caused higher leaf area and early ground coverage by the foliage, thereby suppressing the weed growth.

Seedling age To investigate the changes in the competitive ability of rice as a result of transplanting shock, a sensitivity analysis was done with different seedling ages. The results showed that (Fig. 2), the yield reduction increased from 16.1 to 19.6%, when planting age of the seedlings are increased from 24 to 33 days.

Weed emergence period The relative emergence time of the weed and the crop affects competition. O'Donovan et al. (1985) reported that one day difference in emergence time of wild oats in barley or wheat changed the crop yield by about 3%. In a theoretical analysis, Fischer & Miles (1973) reported that weeds that emerge one day earlier than the crop were approximately twice as competitive as weeds that emerge simultaneously with the crop. Kropff et al. (1993a) also reported that yield loss is extremely sensitive to small changes in the period between crop and weed emergence. The sensitivity analysis done in this aspect using the INTERCOM model showed that the yield reduction was 27.8% when weed emerged at transplanting of rice. There was a drastic reduction in yield loss when weed emergence was delayed (Fig. 3).

Seasonal influence Environmental differences may affect the competitiveness of weeds. For example, Chu et al. (1978) reported that redroot pig weed (C_4 plant) grew about four times as rapidly as common lambsquarters (C_3) at high temperatures (29/24 °C day/night regime), but at the same rate at lower temperature of 24/18 °C. We found similar results (Table 3, section 4). Yield reduction was higher (33%) in the Kuruvai (June - September) than in the Samba season (29.4%; August - January). Yield loss was only 19.6% in the Thaladi season (October - February). The comparison of the weather conditions during these seasons is given in Fig. 4.

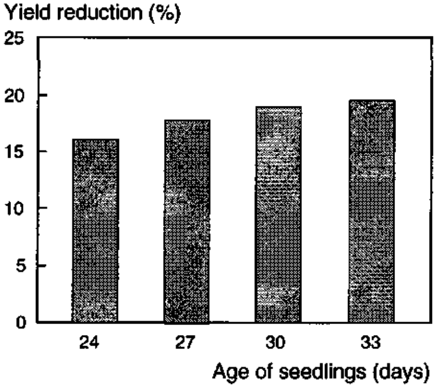

Figure 2. Yield reduction in rice due to weed competition at different aged seedlings.

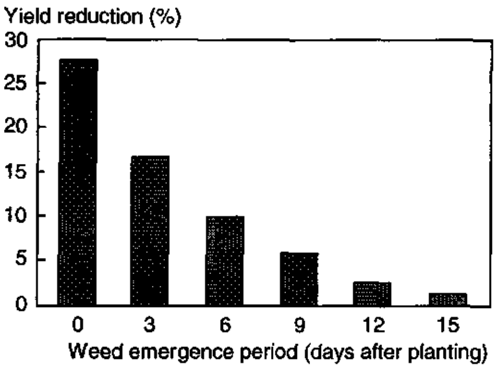

Figure 3. Yield reduction in rice at different weed emergence periods.

This shows that the solar radiation and temperature sum are highest in the Kuruvai season followed by the Samba season. Due to this, *E. crus-galli* being a C_4 plant, became more competitive than rice (C_3) during the Kuruvai season than in the Samba or Thaladi.

Relative Growth Rate of rice Leaves (RGRL) The most important trait determining competitive ability of rice was the RGRL (°Cd^{-1}) in the early part of season. The sensitivity analysis showed that yield loss was reduced by 4.1 and 4.9% with 5% increase in RGRL and 7.1 and 8.1% with 10% increase in RGRL at the rice plant densities of 66 and 50 hills m^{-2}, respectively (Table 3).

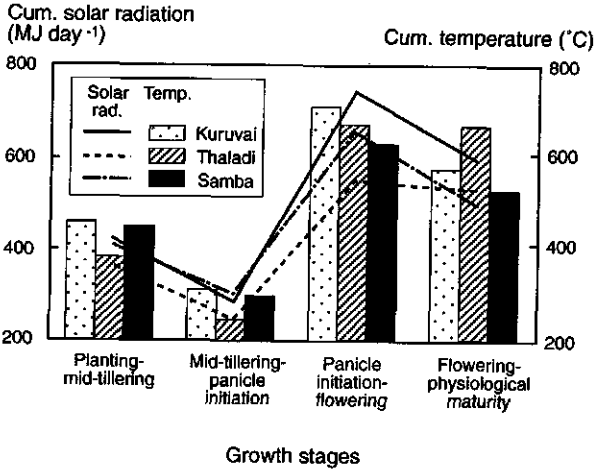

Figure 4. Weather conditions at different growth stages of rice (1992-1993).

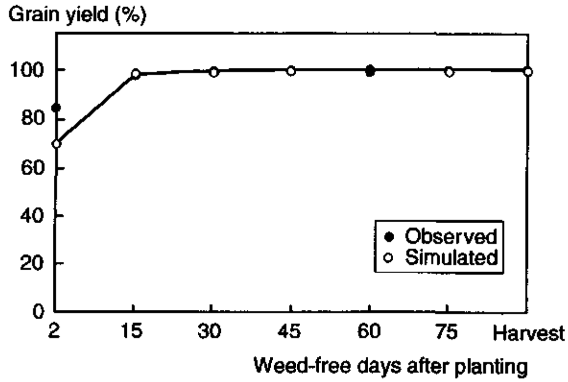

Figure 5. Effect of weed-free period on grain yield of rice.

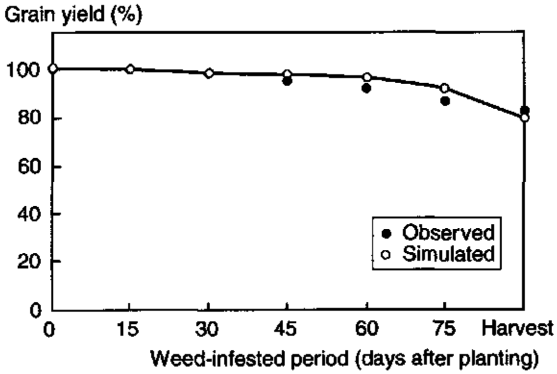

Figure 6. Effect of weed-infested period on grain yield of rice.

Critical period of rice - Echinochloa crus-galli competition

The results of the simulation runs for various durations of *E. crus-galli* competition are shown in Figs 5 and 6. From the observed values, it appears that at the natural weed density population of 12 plants m^{-2}, the weed free period required for the Thaladi season at Aduthurai ranged from 0 to 30 days after planting. The model simulated yield loss quite accurately in this experiment (linear regression of observed versus simulated yield percentage: intercept = 6.23, slope = 0.95; $P < 0.001$).

Acknowledgements

The authors thank Dr R.B. Matthews for his help to modify the INTERCOM model and to International Rice Research Institute, Philippines, and Tamil Nadu Agricultural University, Coimbatore, India for providing facilities.

Chu, C.C., P.M. Ludford, J.L. Ozbun & E.D. Sweet, 1978. Effects of temperature and competition on the establishment and growth of redroot pigweed and common lambsquarters. Crop Science 18: 308-310.

Fischer, R.A. & R.E. Miles, 1973. The role of spatial pattern in the competition between crop plants and weeds. A theoretical analysis. Mathematical Bioscience 18: 335-350.

Kropff, M.J. & H.H. van Laar (Eds), 1993. Modelling crop-weed interactions. CAB International, Wallingford, and International Rice Research Institute, Los Baños, 274 pp.

Kropff, M.J., N.C. van Keulen, H.H. van Laar & B.J. Schnieders, 1993a. The impact of environmental and genetic factors. In: M.J. Kropff & H.H. van Laar (Eds), Modelling crop-weed interactions. CAB International, Wallingford, and International Rice Research Institute, Los Baños, pp. 137-148.

Kropff, M.J., S.E. Weaver, L.A.P. Lotz, J.L. Lindquist, W. Joenje, B.J. Schnieders, N.C. van Keulen, T.R. Migo & F.F. Fajardo, 1993b. Understanding crop-weed interaction in field situations. In: M.J. Kropff & H.H. van Laar (Eds), Modelling crop-weed interactions. CAB International, Wallingford, and International Rice Research Institute, Los Baños, pp. 105-136.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, International Rice Research Institute, Philippines, 110 pp.

Moody, K., 1991. Weed management in rice. In: D. Pimentel (Ed.), Handbook of pest management in agriculture. 2nd edition, CRC Press Inc., Boca Raton, Florida, pp. 301-328.

O'Donovan, J.T., E. Ann de St. Remy, P.A. O'Sullivan, D.A. Dew & A.K. Sharma, 1985. Influence of the relative time of emergence of wild oat (*Avena fatua*) on yield loss of barley (*Hordeum vulgare*) and wheat (*Triticum vulgare*). Weed Science 33: 498-503.

Parker, C. & J.D. Fryer, 1975. Weed control problems causing major reductions in world food supply. FAO Plant Protection Bulletin 23: 83-95.

Rao, A.N. & K. Moody, 1992. Competition between *Echinochloa glabrescens* and rice (*Oryza sativa*). Tropical Pest Management 38: 25-29.

Simulating the effect of varietal adaptation to climate change

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Abstract
A crop model was used to study the effect of hypothetical varieties with greater tolerance to climatic change on rice production. Reduced spikelet sterility and increased crop duration were useful features for mitigating the detrimental effects of climate change.

Introduction

Climate change is likely to have a significant impact on agricultural production depending upon the magnitude of temperature and CO_2 increase. Matthews et al. (1995) estimated that in general rice production may be adversely effected by climate change. In this simulation analysis it was assumed that future cultivar would have the same characteristics as at present. However, plant breeding programmes are likely to develop newer varieties adapted to climatic conditions. It is important to determine plant characteristics that may be desirable in such adapted varieties.

Increased temperature significantly reduces spikelet sterility and crop duration in rice (Kropff et al., 1994; Matthews et al., 1995). This results in considerable yield reduction. In this paper, we have used the simulation model ORYZA1 (Kropff et al., 1994) to evaluate the possibility of using varieties with greater tolerance to higher temperatures to mitigate climate change effects.

Material and methods

The rice crop growth model, ORYZA1 (Kropff et al., 1994) was used in the present study to evaluate the effect of climate change on rice production in a few parts of India. It simulates the potential yield of rice in which the production is determined by crop characteristics and current temperature and radiation only, without any stresses resulting from water or nutrient shortage. The model was calibrated using data from an experiment conducted at the Tamil Nadu Rice Research Institute at Aduthurai in 1993. The observed and simulated yields for six cultivars showed good agreement (Mohandass et al., 1995).

The rice cultivar IR36 was used as the standard variety in the present study. Its parameters were determined from a trial conducted at Tamil Nadu Rice Research Institute, Aduthurai, Tamil

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Table 1. Percent increase in grain yield due to greater tolerance of spikelet sterility to climate change.

Location	Increase in grain yield (%)	
	Main season	Second season
Aduthurai	9.6	0
Bijapur	15.6	5.6
Coimbatore	1.3	0
Cuttack	5.1	19.0
Hyderabad	0.1	-
Kapurthala	0	-
Pattambi	0	0
Madurai	16.0	0
Patencheru	0	0

Nadu, India during the dry season (June-September) of 1993. Simulation analyses were done for Aduthurai, Coimbatore, Bijapur, Coimbatore, Hyderabad, Pattambi, Madurai, Patencheru (all in southern India), Cuttack in eastern India and Kapurthala in northern India. These sites were selected because of the availability of the weather data. Dates of sowing and transplanting for a site were based on the local standard practice.

The climate change scenario for various locations was provided by the Goddard Institute of Space Studies (GISS) based on a doubled CO_2 concentration.

Results and discussion

Spikelet sterility

High temperatures, particularly above 33 °C, reduce spikelet fertility (Uchijima, 1976). Considerable variation among varieties is known for this threshold level (Satake & Yoshida, 1978). The effect of a shift in the sensitivity of spikelet sterility by 2 °C was simulated for both main and second planting season based on the simulated future climate. The results indicated that there was an increase in grain yield for several locations, particularly in the main planting season (Table 1). Grain yield increased by 5.6 and 19% for Bijapur and Cuttack only in the second season.

Crop duration

Often, lengthening the growing season results in a yield increase. Significant differences in crop duration result because of variation in the length of the vegetative period before panicle initiation (Vergara & Chang, 1985). Change in grain yield was simulated by assuming that vegetative duration of IR36 can be increased. The results showed that except for Aduthurai, the grain yield increased with increase in the duration of the vegetative phase. Thus, it is concluded that the plant type with a vegetative duration of 52, 66, 60 and 70 days would be optimal for future climate scenarios at Aduthurai, Bijapur, Coimbatore and Cuttack, respectively.

References

Kropff, M.J., H.H. van Laar & R.B. Matthews, 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, International Rice Research Institute, Los Baños, Philippines and AB-DLO, TPE-WAU, Wageningen, The Netherlands, 110 pp.

Matthews, R.B., M.J. Kropff, D. Bachelet & H.H. van Laar (Eds), 1995. The impact of global climate change on rice production in Asia: a simulation study. CAB, Wallingford, in press.

Mohandass, S., A.A. Kareem, T.B. Ranganathan & S. Jeyaraman, 1995. Rice production in India under current and future climates. In: R.B. Matthews et al. (Eds), The impact of global climate change on rice production in Asia: a simulation study. CAB, Wallingford, in press.

Satake, T. & S. Yoshida, 1978. High temperature-induced sterility in indica rices at flowering. Jap. J. Crop Sci. 47: 6-17.

Uchijima, T., 1976. Some aspects of the relation between low air temperature and sterile spikelets in rice plants. J. Agric. Meteorol. (Tokyo) 31: 199-202.

Vergara, B. & T.T. Chang, 1985. The flowering response of the rice plant to photoperiod. A review of the literature. International Rice Research Institute, Los Baños, Philippines, 61 pp.

Simulating yields and ranking of rice genotypes in multi-location trials

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Abstract

Improved varieties are traditionally identified through a series of multi-location trials (MLT) where a number of competing genotypes are compared. Relative superiority of a genotype is assessed by its ranking, disease and pest scoring and grain type. The crop simulation model ORYZA1 was used to simulate the ranking obtained by genotypes in such a MLT conducted at five sites in Tamil Nadu, India in 1991. A more detailed field experiment was conducted at one of the sites to determine model input parameters.

Results showed that the mean observed and simulated ranking based on grain yield were generally close to each other for most genotypes. The top three genotypes identified by MLT were also identified by simulation. Potential is indicated for application of crop models in increasing the efficiency of MLT.

Introduction

In the state of Tamil Nadu, India, higher yielding genotypes are identified through a series of yield tests, including progeny row trials (PRT), preliminary yield trials (PYT), and comparative yield trials (CYT) at different rice research stations of the Tamil Nadu Agricultural University (TNAU). Selected genotypes from CYT are then pooled in various duration groups and tested simultaneously at all locations in Multi-Location Trials (MLTs) for a few years. The promising genotypes in MLT are finally tested in farmers fields at more than 80 locations throughout the state under Adaptive Research Trials (ART). The best genotypes are then released as new varieties for general cultivation by farmers. This process takes a minimum of 8 to 10 years. The MLTs alone involve a three-year period with more than 30 field experiments at 10 - 11 rice stations. Thus, it is evident that this multi-location evaluation involves a major share of resources of plant breeders and technicians.

Crop growth simulation models are increasingly being used to support agricultural research,

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training and extension programmes. Recently, greater attention has been paid to their use in plant breeding programmes (e.g. Shorter et al., 1988; Penning de Vries, 1991; Hunt 1993; Palanisamy et al., 1993; Aggarwal et al., 1995). The major applications of crop models are in the fields of plant-type design and understanding of genotype by environment interactions.

The results of crop simulation are generally sensitive to the values of the parameters used in the model. Often there is some uncertainty in these parameters, which affects the reliability of simulated absolute yields. However, crop models adequately describe the relative trends caused by environmental variations. This is of considerable use in the process of cultivar selection where *ranking* of grain yields is the method used to determine the relative superiority of a genotype rather than the *absolute* yield values. Palanisamy et al. (1993) examined the use of the MACROS rice model (Penning de Vries et al., 1989) in assessing the performance (indicated by ranking) of pre-release long duration rice genotypes in several locations of Tamil Nadu. It was found that the model was able to correctly identify two out of the three best genotypes determined in trials. In this paper, we explore the possibility of using a similar model, ORYZA1 (Kropff et al., 1994), for a related study with short duration genotypes. The specific objective was to simulate the ranking of pre-release rice genotypes in an irrigated MLT at several locations in Tamil Nadu.

Material and methods

The Multi-Location Trial (MLT)

An irrigated MLT using transplanted rice conducted in 1991 at five rice research stations in Tamil Nadu was selected for the analysis. These sites were - Aduthurai (11° N, 79.5° E, 19.5 m), Coimbatore (11° N, 77° E, 431 m), Madurai (8.5° N, 79° E, 147 m), Tirur (13.7° N, 78.6° E, 39.5 m) and Ambasamudram (8.5° N, 77.4° E, 40 m). Daily weather data at these sites are routinely collected and for 1991 the data were free from obvious instrument errors and other inconsistencies. The trial consisted of eight rice genotypes - three released varieties as checks (CO37, ASD18 and IR64), and five pre-release genotypes (ACM60, IET9976, TNAU851979, TNAU841434, AS90043).

Parameterization of genotypes

Another more detailed field experiment was conducted at the Tamil Nadu Rice Research Institute (TNRRI, Aduthurai) in the same dry season of 1991 (June to September). The above mentioned eight genotypes were planted in a replicated randomized design. The sowing and transplanting dates were 19 June and 19 July, respectively. Fertilizer (150 kg N, 60 kg P_2O_5 and 60 kg K_2O ha^{-1}) was applied according to recommended practice. In addition, 12.5 t ha^{-1} green manure was incorporated in the experimental plot. Plant samples were collected at transplanting and subsequently at ten days interval. Roots, stems, leaves and panicles were separated, dried and weighed to determine the partitioning tables for the crop model. Grain yield and yield components were determined at maturity. Dates of 50% flowering and maturity were recorded.

The crop model ORYZA1 (Kropff et al., 1994) validated for its performance in several tropical environments was used for this case study. The model requires inputs of crop development rates, dry matter partitioning coefficients, leaf N content, relative growth rate of leaves, specific leaf area, stem reserves and spikelet growth factor for characterizing a genotype. The recorded dates of sowing, transplanting, flowering and maturity for each genotype in the experiment were used to determine the specific pre- and post-flowering development rates using the program DRATES (Kropff et al., 1994). These rates, dry matter partitioning tables, actual dates and daily weather data were used to simulate the growth, development and yield of different genotypes at all five locations. Possible genotypic differences in other plant characteristics were not measured, so for these, default values of the variety IR72 (Kropff et al., 1994) were used for all genotypes. The performance of each genotype at each site was ranked using simulated yields.

Results and Discussion

Crop yields

Observed yields varied between 5.6 and 6.8 t ha^{-1} at Coimbatore, between 4.5 and 6.6 t ha^{-1} at Aduthurai, 3.3 to 5.5 t ha^{-1} at Madurai, 4.9 to 6.5 t ha^{-1} at Ambasamudram and 2.5 to 5.1 t ha^{-1} at Tirur. Relatively low yields at Tirur and Ambasamudram were recorded due to occasional water stress in the experimental plots. The mean difference between lowest and highest yielding genotypes was rather small - only 0.78 t ha^{-1} (Table 1). Simulated yields at all locations were much higher than observed yields. In general, they ranged between 7.0 and 9.0 t ha^{-1} for all genotypes at different locations (data not shown). The mean simulated yield of different genotypes varied from 7.3 to 8.7 t ha^{-1} (Table 1). Perhaps, the standard leaf N content of IR72

Table 1. Measured and simulated grain yields and ranks of different genotypes. All values are averages of the five locations (see text).

Genotype	Grain yield t ha^{-1}		Rank	
	Measured	Simulated	Measured	Simulated
AS90043	5.46	8.67	1	2
TNAU851979	5.22	8.46	2	3
ACM60	5.18	8.72	3	1
IET9976	5.12	7.28	4	8
ASD18	5.08	8.20	5	6
CO37	4.94	7.90	6	7
TNAU841434	4.82	8.36	7	5
IR64	4.68	8.42	8	4

used in the present study, which was determined from well-fertilized experiments at IRRI, Philippines, was too high for our experimental conditions.

Ranking of genotypes

The mean observed and simulated ranking based on grain yield were generally close to each other for most genotypes (Table 1). AS90043 was first in observed ranking and simulation indicated this to be second. Similarly, TNAU851979 obtained second rank in MLT and third in simulation. IET9976 was fourth in MLT and IR64 eighth but in simulation results they interchanged their positions. Some variability in ranking is possible because the measured grain yields of different genotypes were rather close. For example, the difference in grain yield between first and the third genotype was only 0.28 t ha^{-1} and 0.78 t ha^{-1} between first and last genotype. It appears that it is difficult to simulate such small differences between genotypes. Moreover, several genotypic characteristics required as input in ORYZA1 were assumed to be same for all genotypes. This could be another reason for the discrepancies in the results. In addition, the trials were not completely free from biotic and abiotic stresses as was assumed in the simulations. More efforts need to be made for more accurate physiological characterization of the genotypes.

Despite limited genotypic calibration and other problems mentioned earlier, the first three genotypes identified by MLT were also identified by simulation. Based on grain yield ranking, diseases and pest scorings, and grain type, determined in this MLT conducted at 11 locations, three genotypes - AS90043, TNAU841434 and TNAU851979 were advanced to 1992 MLT testing. Subsequently, AS90043 alone was promoted to MLT in 1993 and 1994. Our simulation studies of 1991 MLT also identified AS90043 and TNAU851979 as the promising genotypes (second and third ranks). Simulations of subsequent MLTs was not possible due to inclusion of genotypes for which parameters had not been obtained. Nevertheless, our results suggest that simulation is capable of identifying the best genotypes based on their relative yield potential. More work with well parameterized MLTs in contrasting environments is needed.

Conclusions

Multi-location evaluation of genotypes for identification of new varieties is a resource demanding process. Our preliminary studies indicate the potential of simulation models in identifying the best genotypes. More work is needed with MLTs conducted in different agro-environments.

References

Aggarwal, P.K., M.J. Kropff, R.B. Matthews & C.G. McLaren, 1995. Using simulation models to design new plant types and to analyse genotype and environment interactions. In: M. Cooper & G. Hammer (Eds), The analysis and exploitation of plant adaptation in agricultural crop improvement programs. CAB, Wallingford (in press).

Hunt, L.A., 1993. Designing improved plant types: a breeder's viewpoint. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 3-17.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, IRRI, Wageningen, 110 pp.

Palanisamy, S., F.W.T. Penning de Vries, S. Mohandass, T.M. Thiyagarajan & A.A. Kareem, 1993. Simulation in pre-testing of rice genotypes in Tamil Nadu. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 63-75.

Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: Systems Simulation at IRRI. IRRI Research Paper Series, November 1991, Number 151, pp. 13-19.

Penning de Vries, F.W.T., D.M. Jansen, H.F.M. ten Berge & A. Bakema, 1989. Simulation of ecophysiological processes of growth in several annual crops. Simulation Monographs, Pudoc, Wageningen and IRRI, Los Baños, 271 pp.

Shorter, R., R.J. Lawn & G.L. Hammer, 1988. Improving genotypic adaptation in crops - a role for breeders, physiologists and modellers. Exp. Agric. 27: 155-175.

A model for simulation of hybrid rice seed production

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Abstract

A simulation model for hybrid rice seed production is presented. The model was calibrated and validated using multi-location experiments conducted in southern China, and showed that the phenological development of parent plants of hybrid rice could be predicted and described with acceptable precision.

The model was divided into three components: data management, simulation and result output. The control over each component is menu-driven. The system provides a basis for decision-making before sowing and for predicting behaviour after sowing. With suitable estimates of model input parameters, it is possible to simulate and predict phenological development of various parent plants at different sites and years in potential production environments, and to determine optimal sowing dates of different cultivars.

Introduction

Hybrid rice cultivation is gaining in popularity in Asia. In China, the first country to produce hybrid rice in the world, the area under hybrid rice is over 12 Mha, or 36% of the total rice planted.

Hybrid rice seed is produced by mixed cropping of different varieties (parents) of rice. The seed parent (A line) is generally long-duration, whereas the pollinator parent (R line) is mostly short-duration. Synchronizing flowering dates of the parents is important because pollen from the R line must be available to the A line throughout its flowering period. Simultaneously, it is important to consider environmental regulation of growth and development of parental lines to ensure flowering in optimal light, temperature, water and nutrient conditions, and to avoid the influence of unfavourable weather (light, temperature, drought). Therefore, synchronizing flowering by optimizing sowing dates and regulation of phenological development of seed and pollinator parents are essential aspects of cultivation technology of hybrid rice seed production.

To synchronize flowering of parents two methods are used: (*i*) selection of appropriate seeding dates of the parents in the seedbed, and (*ii*) manipulation of the flowering date in the field. The difference in time required for flowering was used to adjust the seeding dates of the parents in the early period. However, this criterion is unstable because it changes with location,

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year and growth stage. Later, several other methods such as temperature sums, young-ear length and several statistical approaches were used to improve the prediction of flowering dates. Since these approaches were empirical and placed less emphasis on plant development and the effect of environmental factors the predictions and decisions were still not precise. This paper describes a new approach using computer simulation, introduced to the areas of hybrid rice production for the first time, in which the seed production of hybrid rice is quantified, optimized and eventually put into user-friendly software. It is of great significance for the modernization of prediction and regulation, cultivation and management of the seed production of hybrid rice.

Description of the model

The model consists of three submodels:

- A submodel for the development calendar of parental lines,
- A submodel for determining optimal sowing dates of the parental lines, and
- A prediction and decision-making model for hybrid rice seed production.

The model assumes that the hybrid rice seed production is for potential production environments, i.e. with optimal availability of irrigation and nutrients and with no pest and disease infestation.

Development calendar of the parental lines

Phenological development of parental lines

In favourable growth conditions, temperature, daylength and varietal characteristics are the main factors determining the development rates of the crop. The degree-days approach (sum of average temperature above a lower threshold) assumes that the rate of development is linearly related to the daily mean temperature above a base temperature. Although simple, it neglects the influence of maximum and optimum temperature on development. Gao et al. (1992) presented a flexible non-linear equation to predict the rate of phenological development based on temperature, daylength and the varietal characteristics. However, the equation presented by Gao et al. (1992) for describing the effect of temperature does not ensure that the maximum development rate occurs at the pre-determined optimum temperature. Therefore, an improved equation, presented by Yin et al. (1995), was used in this study for simulating the temperature effect on the development. This equation, incorporated with the daylength effect described by Gao et al. (1992), is expressed as:

$$\frac{dM}{dt} = 1/N = e^{K}\left[\left(\frac{T - T_{base}}{T_{opt} - T_{base}}\right)\left(\frac{T_{high} - T}{T_{high} - T_{opt}}\right)^{\frac{T_{high} - T_{opt}}{T_{opt} - T_{base}}}\right]^{P} e^{G(DL-DL^*)} \qquad (1)$$

with $T < T_{base}$, $T = T_{base}$; $T > T_{high}$, $T = T_{high}$; and $DL < DL^*$, $DL = DL^*$;

where N is days for a certain phenological development phase; M is the developmental stage; dM/dt is the development rate of the period, which is expressed with the inverse of the days required for completing a developmental stage (d^{-1}); T is the mean temperature of the developmental stage; T_{opt}, T_{high}, T_{base} are the optimum, maximum and base temperatures, respectively; DL is the average daylength for the developmental stage; DL* is the critical photoperiod; K is a coefficient of the varietal basic vegetation period; P is the temperature-sensitivity coefficient of the variety; G is the photoperiod-sensitivity coefficient of the variety.

In optimal growth conditions (where $T=T_{opt}$, $DL \leq DL^*$), the above equation simplifies to:

$$1/N_0 = e^{K}\text{, or } N_0 = e^{-K} \tag{2}$$

where N_0 is the varietal basic vegetative period for the variety.

Leaf number development of parental lines

Leaf number is a measure of the plant's physiological age but can also be used to indicate synchrony in organogenesis. Dynamic simulation of leaf number development of parental lines may help in developing criteria for hybrid rice seed production.

Leaf number development is based on the leaf appearance rate. Temperature is the main driving force for leaf appearance, but it has been observed in many field experiments that the rate of leaf appearance declines in time. The number of days required for a given variety to develop for a specific leaf under constant optimal conditions is constant (Gao et al., 1992). The number of days up to a certain leaf development stage is calculated as a function of the leaf number by the following exponential equation:

$$L_j = e^{-Kl}\left(\frac{T}{T_{opt}}\right)^{a} N_j^{b} \quad \text{with } T < T_{base}, T=0;\ T > T_{opt}, T=T_{opt}, \tag{3}$$

where L_j is the j-th leaf on the main stem; N_j is the actual number of days from seedling emergence to the j-th leaf appearance; T is the average temperature from seedling emergence to the j-th leaf appearance; T_{opt}, T_{base} are the optimum and base temperatures for leaf development, respectively; Kl, a and b are parameters of the model.

In optimal growth conditions ($T \geq T_{opt}$), the above equation simplifies into:

$$L_j = e^{-Kl} \times N_{j0}^{\ b} \tag{4}$$

where N_{j0} is the required number of days from emergence to the j-th leaf appearance at optimum temperature.

Eqn 3 can be rearranged as:

$$N_j = \left(L_j\, e^{Kl}\right)^{1/b}\left(\frac{T_{opt}}{T}\right)^{a/b} \tag{5}$$

and substituting Eqn 4,

$$N_j = N_{j0}\left(\frac{T_{opt}}{T}\right)^{a/b} \tag{6}$$

Substituting the daily mean temperature (T_i) for the value of T in Eqn 6, the actual cumulative value in day units from emergence to the j-th leaf appearance is determined by the following equation:

$$\sum_{i=1}^{N}\frac{N_{j0}}{N_j}=\sum_{i=1}^{N}\left(\frac{T_i}{T_{opt}}\right)^{a/b}=N_{j0} \qquad (7)$$

Integration over the day gives the daily temperature, the physical days for the cumulative leaf number since emergence N_{j0} is obtained. Then, the leaf numbers of the j-th leaf can be calculated by the simulation model.

Sub-model for determining the optimum sowing date

It has been observed in many experiments that the flowering pattern differs between rice parental lines. The seed parent flowers concentrically and its flowering period is short while the pollinator parent flowers dispersedly and its flowering period is long. In general, for hybrid seed production of the 'Xieyou' combination, the seed and the pollinator parents must begin heading simultaneously but for the 'Shanyou' combination, the pollinator parent must flower one to two days before the seed parent. In order to determine the optimum sowing date for the parents, it is necessary to consider the corresponding days for the parents from sowing to flowering. In a potential production environment, the days from sowing to flowering depends only on the varietal characteristics of the parent lines and the weather conditions. Therefore, the model to determine the optimum sowing date is based on the reverse calculation of the phenology model described previously. The calculation is done in the following steps:

1. The optimum flowering date (D_{flower}) is selected in different locations according to the standard weather criteria for the ideal flowering conditions for hybrid rice seed production, namely-the temperature is between 25 and 35 °C for three continuous days, the air humidity in the field is between 70 and 80%, and there are three or more consecutive non-rainy days.
2. The optimum flowering date for the parents is converted to its daynumber - $JD(D_{flower})$.
3. $JD(D_{flower})$ is assumed to be the beginning daynumber and the development stage for the j-th day expressed as DVS(i).
4. It is assumed that the development stage at flowering is DVS(f)=1 and the development stage at sowing is DVS(s)=0. The Julian sowing date JD_{sow} is determined as follows:

$$DVS(s)=DVS(f)-\sum_{JD(D_{flower})}^{JD(D_{sow})}DVS(i) \qquad (8)$$

   where DVS(s) = 0., $JD(D_{sow})$ is the daynumber after the required number of iterations to bring the DVS to zero. The value of $JD(D_{sow})$ is then reconverted to the calendar date D_{sow}.

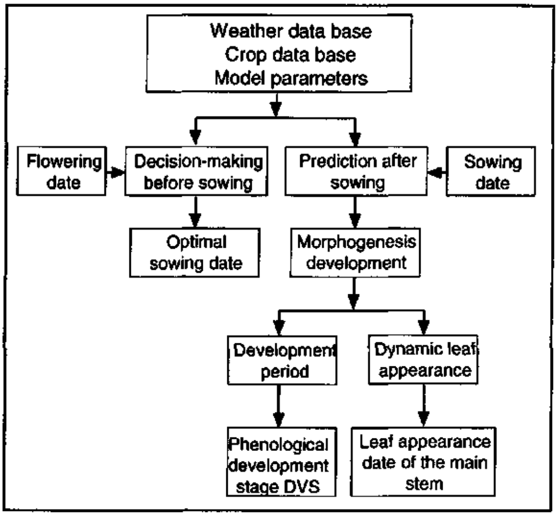

Figure 1. The general structure of the system.

The prediction and decision-making submodel

Based on the above submodels, a prediction and decision-making system for hybrid rice seed production was developed for use on microcomputers. Quick Basic with pull-down menu facilities, was used for programming and Foxbase Plus was used for database management.

The general structure

The system was divided into three components: data management, simulation, and output of results. The simulation section consists of two parts (*i*) the decision-making model before sowing (to determine the optimum sowing dates of the parents), and (*ii*) the prediction model after sowing (to predict the phenology of the parents). The action and the relationship between the component parts of the system is indicated schematically in Fig. 1. The structure of constituent modules for the overall system is shown in Fig. 2.

Operation of the system

The input data for the system includes daily weather data and crop data. The crop data for this paper includes three kinds of typical hybrids and their parents in southern China (Table 1).

Crop data are stored in four files. File 1 stores varietal growth stages dates in different years, sites and sowing dates. File 2 stores the varietal leaf appearance dates, File 3 stores the varietal parameters for parents growth stages (K, P, G, T_{high}, T_{base}, T_{opt}, DL*') and File 4 contains the varietal parameters for the parents' leaf development model (K1, a, b, T_{opt}, T_{base}).

To operate the package, a computer with 640K memory and a hard disk is needed. The control over the input and output files, and main program is facilitated with pull-down menus. The flow diagram for the system is illustrated in Fig. 3.

Table 1. Source of the crop data.

Hybrid	Combination	Parent	Year	Site
Shane 6	A line	ZS97A	1979-1980	More than ten provinces and
	R line	IR26	1979-1980	cities in southern China
Shanyou 64	A line	ZS97A	1992	Fulian (Jiangxi Province)
	R line	CE64-7	1992	Fulian (Jiangxi Province)
Xieyou 46	A line	XQ-A	1992	Fulian (Jiangxi Province)
	R line	MY46	1992	Fulian (Jiangxi Province)

The user can select crop data, model parameters and weather data in different locations and years as well as modify the original data. The system can simulate and predict varietal development course, daily leaf development, total leaf numbers on the main stem etc. for hybrid parents in different years, sites and growing seasons. The user can compare the growth and development of parents with actual data.

The following outputs can be selected for display on the screen or for printing:
- Tables for the optimum sowing date of the parents,
- Tables for the leaf appearance on the main stem of the parents, and
- Tables for the growth and development of the parents.

In addition, the time course of daily leaf number and development stage can be displayed on the screen.

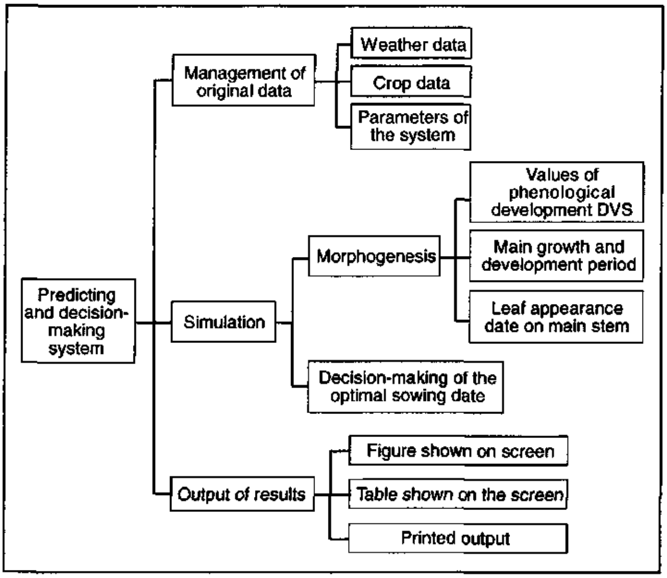

Figure 2. Structure of the module system.

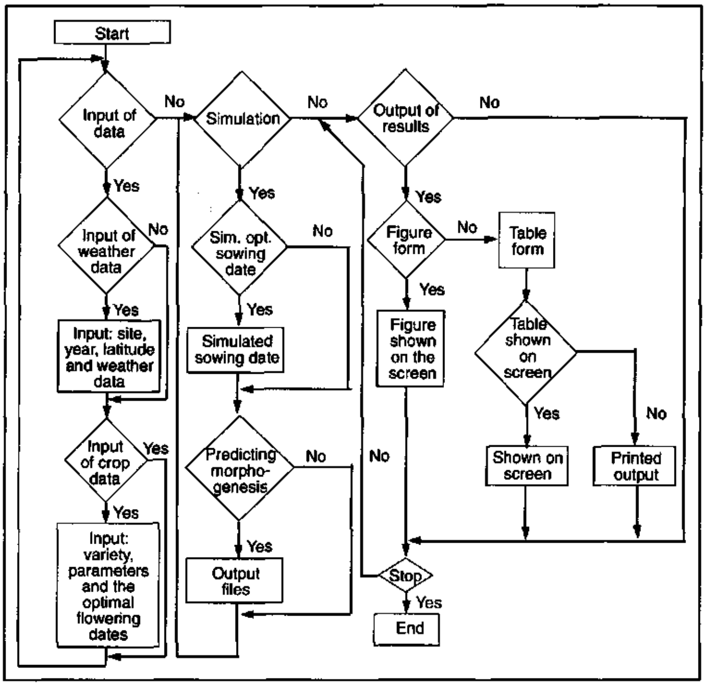

Figure 3. Flow chart of the system.

Determination of the model parameters

Accuracy in the prediction and decision-making for hybrid seed production depends on accurate determination of the model parameters. In principle, these parameter values are variety specific and do not change with environment. Therefore, once a set of crop parameters has been determined at a certain location, it can be used for extrapolation to other places.

Parameters for the phenology model In this paper, the three 'cardinal' temperatures and the critical photoperiod daylength were derived from literature. For rice, these values are typically 10, 30 and 40 °C and 13 h, respectively (Gao et al., 1992). For obtaining development rate parameters for the period from sowing to flowering, the model of the development rate was converted to the linearized average basic model. The daily mean temperature and daylength are replaced with the mean temperature and mean daylength for the phase. The values of parameters are obtained with acceptable precision with multi-variable regression approach. The average basic model (Eqn 1) can be expressed as:

$$\ln\left(\frac{1}{N}\right) = K + P\left[\ln\left(\frac{T - T_{base}}{T_{opt} - T_{base}}\right) + \left(\frac{T_{high} - T_{opt}}{T_{opt} - T_{base}}\right)\ln\left(\frac{T_{high} - T}{T_{high} - T_{opt}}\right)\right] + G\,(DL - DL^{*}) \qquad (9)$$

The model parameters (K, P, G) for the period from sowing to flowering were estimated by using this approach and the data from the research reports of National Research Cooperative Groups on the meteorological conditions of hybrid rice production in 1979. The results are shown in Table 2.

Parameters for the leaf development model The above method and the same data set were also used for determining the leaf development parameters (Kl, a, b). The results are shown in Table 3.

Validation of the system

The system was evaluated using 45 data sets, which are partly from field experiments conducted at Fulian, Jiangxi, China in 1992 and partly from experiments of National Research Cooperative Group on the meteorological conditions of hybrid rice production in 1980. The simulated crop development was compared with the observed dates (Tables 4 and 5). The results indicate that the difference between simulated and observed values was less than five days. As there is always some uncertainties in observed values of flowering date, this difference is within acceptable limits. Similarly, the observed and simulated values of leaf appearance also fitted well (Figs 4a and 4b). This close agreement gives some confidence in the use of the system in a practical way.

Table 2. Estimated parameter values for the development model (sowing-flowering, see Eqn 1).

Variety	K	P	G	Correlation coefficient
IR26	−4.4329	1.4632	−0.0135	0.9362
ZS97A	−4.1517	1.1925	0.0022	0.8657
MY46	−4.4878	1.3401	0.0461	0.9443
CE64-7	−4.7442	1.0955	0.3379	0.9173
XQ-A	−4.1728	1.2395	0.0349	0.9417

Table 3. Estimated parameter values for the leaf appearance model (sowing-flowering, Eqn 5).

Variety	Kl	a	b	Correlation coefficient
IR26	0.0751	0.4517	0.7078	0.9244
ZS97A	0.0901	0.4211	0.6906	0.9536
MY46	0.0825	0.4645	0.6487	0.8967
CE64-7	0.0856	0.4581	0.6059	0.9142
XQ-A	0.0872	0.3877	0.6473	0.9335

Table 4. Observed and simulated development stage of parents.

Variety	Site		Sowing date	Panicle differ.	Flowering date
ZS97A	Xuzhou	Obv.	Apr 30	June 24	Jul 25
		Sim.	Apr 30	June 20	Jul 20
ZS97A	Xuzhou	Obv.	May 30	July 15	Aug 9
		Sim.	May 30	July 10	Aug 7
ZS97A	Xuzhou	Obv.	June 10	July 21	Aug 16
		Sim.	June 10	July 20	Aug 17
IR26	Xuzhou	Obv.	May 30	Aug 5	Sep 1
		Sim.	May 30	Aug 4	Sep 2
IR26	Changsa	Obv.	June 30	Aug 16	Sep 28
		Sim.	June 30	Aug 15	Sep 30
MY46	Jindezeng	Obv.	May 16	July 12	Aug 15
		Sim.	May 16	July 10	Aug 12
CE64-7	Jindezeng	Obv.	May 25	July 16	Aug 15
		Sim.	May 25	July 14	Aug 16
XQ-A	Jindezeng	Obv.	June 5	July 13	Aug 10
		Sim.	June 5	July 9	Aug 7

Table 5. Observed and simulated values of the optimal sowing dates.

Variety	IR26	ZS97A	MY46	XQ-A	CE64-7
Simulated	May 19	June 14	May 2	May 4	May 24
Obverated	May 16	May 10	May 5	May 5	May 25

Application of the system

The system outputs have several applications. It simulates and predicts the development process of a variety or parental lines used in hybrid rice seed production in a particular environment, defined by its daylength and temperature. This information can be used to develop different cropping patterns suitable for various agro-climatic zones with the help of medium-term and long-term weather forecasts. It also provides the theoretical basis for expanding the area of hybrid rice seed production to new places. The deviation in flowering dates of the parents estimated by using the real-time weather observations and long-term forecasts can be used to take appropriate regulatory measures in time. Finally, the effect of climatic change on the growth and development process of different hybrid parents in a particular environment can also be evaluated using the present system.

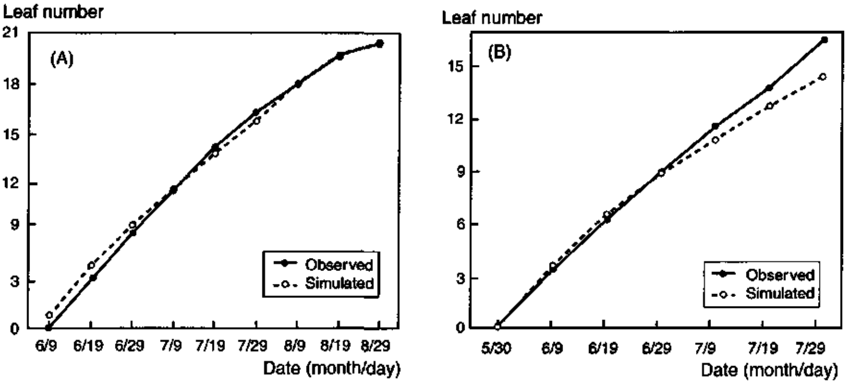

Figure 4. Comparison between observed and simulated leaf appearance of parents: (A) Xuzhou 1979, cv. IR26; (B) Xuzhou 1979, cv. ZS97A.

Conclusions

A prediction and simulation system of hybrid rice seed production has been developed. A non-linear model describes the effect of temperature and photoperiod on the phenological development. Used in reverse, the model could determine optimal sowing dates from optimal flowering dates of the parental lines. Validation studies indicate satisfactory performance of the development model and decision support system.

Future work

The photoperiod change may influence the relation between crop development and the temperature. Similarly, temperature change may influence the photoperiod response of the crop. The three 'cardinal' temperatures and critical daylength in the model are approximate values from literature. The total number of leaves on the main-stem for the parents change with the latitude and the sowing date indicating photoperiodic interaction. Quantitative information needs to be developed to improve these relationships.

The value of the system is also restricted by the assumption of potential production environment, i.e. no biotic and abiotic stresses. If the model is improved to account for the effect of stresses, it will be able to play a more important role in hybrid rice seed production.

References

Gao L., Z. Jin, Y. Huang & L. Zhang, 1992. Rice clock model - a computer model to simulate rice development. Agric. For. Meteorol. 60: 1-16.

Yin, X., M.J. Kropff, C.G. McLaren & R.M. Visperas, 1995. A nonlinear model for crop development as a function of temperature. Agric. For . Meteor. (in press).

Variability in crop physiological inputs used in simulation models of rice

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Abstract

A field experiment was conducted in the dry season of 1993 in Muara, Indonesia to determine the extent of variation present in several physiological parameters used in the crop simulation model ORYZA1 relating to crop development, leaf area, leaf N, growth and yield in 17 rice varieties. There was considerable varietal difference in the relative leaf area growth rate, specific leaf area, development rate of the basic vegetative period, leaf nitrogen content, spikelet growth factor and 1000 grain weight. In general, there were no significant correlations among the crop inputs used in the model.

Introduction

Crop models are increasingly being used for applications in agricultural research and development. Recently, in the SARP project their use has been suggested for increasing the efficiency of plant breeding programmes (ten Berge et al., 1994). A major area where information is lacking in this application programme is the magnitude of variability in model input parameters relating to crop growth, development and yield. This information is desired both for the design and evaluation of plant types as well as for understanding and interpreting genotype by environment interactions. In this paper, our objective is to document the variability in crop input parameters and functions used in the model ORYZA1 (Kropff et al., 1994).

Material and methods

A field experiment with 17 varieties was conducted in the 1993 dry season at Muara, Indonesia. The crop was sown on 28 May 1993 and transplanted on 17 June 1993. Three seedlings per hill were planted at a 25 x 25 cm spacing. The field was maintained well irrigated and free from pests throughout the crop growth. Fertilizer was applied at the rate of 120-50-50 kg NPK ha^{-1}. Phenological observations were recorded for all varieties. Plants were sampled at regular intervals to determine the weights of the crop components, leaf area and leaf N content. Grain yield

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and yield components were determined at maturity. Crop parameters were estimated from this data to be used as input parameters in the model ORYZA1.

Results and discussion

Leaf area

ORYZA1 simulates leaf area in two different ways. During initial stages it uses the concept of relative leaf area growth till LAI becomes 1. Later the increase in leaf weight is multiplied by the specific leaf area (SLA) to determine the net change in leaf area.

Relative leaf area growth rate (RGRL) varied from a low value of 0.00496 (IR46) to a high value of 0.0095 (°Cd)$^{-1}$ (IR48). Varieties IR64, Cipunegara, Cisokan, Ciliwung, Cisadane and Barumun had relatively higher RGRL than other varieties (Table 1). IR72 had a RGRL value of 0.00653 as compared to 0.008 (°Cd)$^{-1}$ reported by Kropff et al. (1994). This indicates that this parameter may have some other environmental influence than temperature alone.

Specific leaf area (SLA) varied just after transplanting from 0.0017 ha leaf kg^{-1} leaf (IR70) to 0.0038 ha leaf kg^{-1} leaf (IR46). But after that stage, the variation among varieties was less, as is evident from small standard deviations particularly between panicle initiation stage and flowering (Fig. 1). The mean value continued to decline indicating increase in leaf thickness with crop age.

Dry matter partitioning

Fraction of shoot dry matter allocated to leaves (FLV) varied from 35 to 44% of the total shoot weight up to much later than panicle initiation (up to crop development stage, DVS = 0.78). Subsequently, there was a sharp fall and the allocation became almost nil at the flowering stage (Fig. 2). During early stages of crop growth (before DVS = 0.4), there was considerable difference among varieties in the allocation as was clear from the large standard deviation values (Fig. 2). This allocation fraction varied from 0.31 (IR46) to 0.51 (B. solo).

Fraction of shoot dry matter allocated to stems (FST) was fairly constant up to much later than panicle initiation, the mean value varied between 0.56 and 0.61 only up to that stage. During later stages, the allocation to stems was reduced but there was some (0.15) allocation for some time even after anthesis (DVS=1., Fig. 3). At this stage, varietal differences were prominent; there was no allocation to stems in IR36 whereas it was 0.41 in IR64 and IR70. This variation can significantly affect allocation to panicles and hence grain yield.

Fraction of stem reserves (FSTR) The fraction of dry matter allocated to the stems, that is stored as reserves (FSTR) and mobilized for grain growth, can provide considerable buffering against environmental stresses. In our study, FSTR varied a lot among varieties (Table 1). The mean value was 10.8% whereas the minimum and maximum values were 4% (IR42) and 31% (IR36). Most IRRI varieties except IR36 had values lower than 10%.

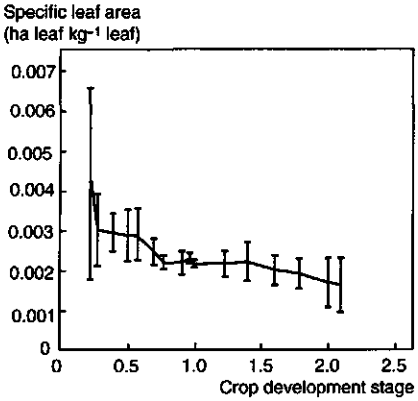

Figure 1. Specific leaf area as a function of crop development stage (DVS). Vertical lines indicate ±1 standard deviation.

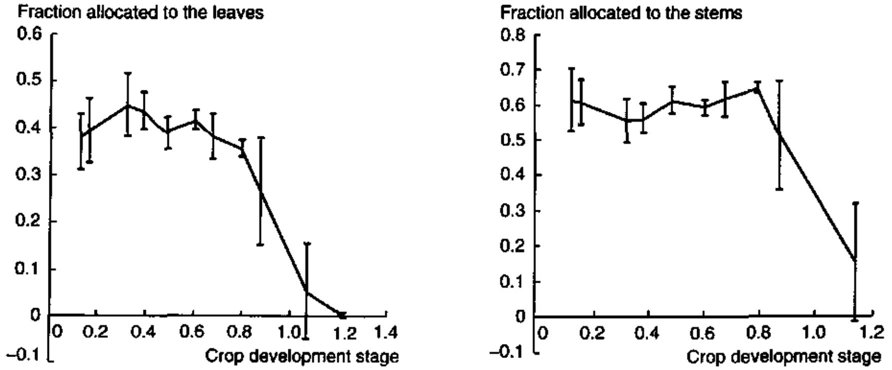

Figure 2. Fraction of dry matter allocated to the leaves as a function of crop development stage (DVS).

Figure 3. Fraction of dry matter allocated to the stems as a function of crop development stage (DVS). Vertical lines indicate ±1 standard deviation.

Leaf nitrogen content

ORYZA1 uses leaf N content (NFLV) as an input. There was significant variation in this input variable among rice varieties although they were grown with the same management. The mean NFLV was 1.3 g N m^{-2} up to panicle initiation, later it decreased almost linearly up to mid-grainfilling (Fig. 4). In the initial stages (shortly after transplanting) varieties such as IR42 and IR70 had a NFLV value of more than 2 g N m^{-2} whereas some others such as IR46, IR72 and IR74 had values lower than 1 g N m^{-2}. The differences became smaller at about panicle initiation. During grainfilling, IR46 maintained a very high leaf nitrogen content (1.6 g N m^{-2}) as compared to other varieties where NFLV dropped to below 0.75 g N m^{-2}.

Crop development rate

Juvenile phase Crop development rate during the juvenile phase (DVRJ, (°Cd)$^{-1}$) is the main parameter that results in variation in crop duration. In our study, most varieties were similar in duration and thus this parameter varied little. Generally the value of DVRJ was close to the mean value (Table 1) except for varieties IR66, B. solo and Cisokan where the rate was higher. These varieties thus were shorter in duration.

Grainfilling period Crop duration during grainfilling is determined by the temperature dependent development rate (DVRR, (°Cd)$^{-1}$). There was a very small variation in this among rice varieties (Table 1). The values for all varieties were within a range of 0.00144 to 0.00215 (°Cd)$^{-1}$.

Table 1. Variation among rice varieties in some parameters used in ORYZA1, for acronyms see text.

Variety	RGRL (°Cd)$^{-1}$	FSTR (-)	DVRJ (°Cd)$^{-1}$	DVRR (°Cd)$^{-1}$	SPGF (no kg^{-1})	WGRMX (mg grain^{-1})
IR36	0.007095	0.310	0.000564	0.002157	54277	22.6
IR42	0.007467	0.040	0.000537	0.001476	47624	21.9
IR46	0.004962	0.070	0.000549	0.001438	41578	22.1
IR48	0.009540	0.060	0.000549	0.001438	71020	29.2
IR64	0.008897	0.100	0.000680	0.001702	34913	26.2
IR66	0.008293	0.040	0.000722	0.001604	75482	21.5
IR70	0.008236	0.080	0.000537	0.001476	65413	21.2
IR72	0.006531	0.110	0.000525	0.001869	74666	22.5
IR74	0.007656	0.090	0.000564	0.001699	52600	25.0
Cipunegara	0.008330	0.132	0.000537	0.001809	42257	29.8
Krueng aceh	0.006686	0.070	0.000594	0.001603	51427	26.7
Cisokan	0.008710	0.063	0.000661	0.001755	47231	22.0
Ciliwung	0.009326	0.159	0.000549	0.001438	42670	25.6
Cisadane	0.009462	0.018	0.000594	0.001603	40604	27.8
Way seputih	0.007468	0.110	0.000594	0.001603	59890	26.6
Barumun	0.008901	0.190	0.000513	0.001559	78288	26.9
B. solo	0.006451	0.200	0.000680	0.001702	37510	20.7
Mean	0.007883	0.108	0.000585	0.001643	53968	24.6
Stand. deviation	0.001260	0.072	0.000063	0.000187	14284	2.9

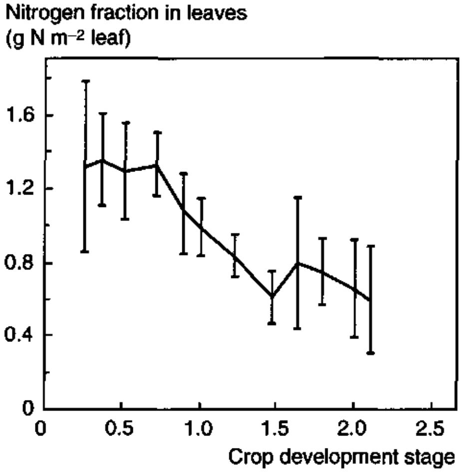

Figure 4. Leaf nitrogen content as a function of crop development stage (DVS). Vertical lines indicate ±1 standard deviation.

Sink size

Spikelet formation factor In ORYZA1, the number of spikelets formed per unit area is dependent upon the growth between panicle initiation and flowering. Higher growth in this period translates in to higher number of spikelets. There was a significant variation among rice varieties in this factor. The number of spikelets per unit dry matter growth (SPGF, number kg^{-1}) was very large (>65000) for varieties IR48, IR66, IR72 and Barumun (Table 1). By comparison, varieties - IR64 and B. solo had SPGF values lower than 40000. The SPGF values for IR36, IR64 and IR72 are different from those reported by Kropff et al. (1994) indicating that there is a need to consider the effect of other environmental factors on SPGF.

Grain weight ORYZA1 uses individual grain weight (WGRMX) as the upper limit of dry matter that grains can accumulate. Once that level is reached grain growth terminates even if assimilates are available for grainfilling. The WGRMX varied depending upon the variety from a low value of 20.7 to 29.8 mg $grain^{-1}$ (Table 1).

Correlation among model inputs

For studying the effect of different plant traits on grain yield, it is important that there are no significant correlations among the parameters. Alternatively, the model should account for such correlations. To examine the relation among parameter values, a simple linear correlations matrix was determined. For development stage dependent functions, values at critical stages were used. Thus, for NFLV, SLA, FST, and FLV values at DVS = 0.72 (between panicle initiation and flowering) were used for determining correlations.

The results showed that there were only very few significant correlations among plant parameters (Table 2). Even the significant ones had a very low value of coefficient. There was a slight relation between RGRL and WGRMX. The physiological cause of this relation is not

Table 2. Correlation matrix among crop inputs of the model ORYZA1, for acronyms see text.

	RGRL	FSTR	DVRJ	DVRP	DVRR	SPGF	WGRMX	NFLV	FST	FLV	SLA
RGRL	1.000	-0.164	0.066	0.054	-0.187	0.116	0.514*	-0.475	-0.028	-0.028	0.274
FSTR		1.000	-0.151	-0.104	0.600*	-0.012	-0.088	-0.014	-0.311	0.360	0.412
DVRJ			1.000	0.894**	0.128	-0.239	-0.284	-0.082	-0.158	0.149	0.339
DVRP				1.000	0.010	-0.196	-0.364	-0.036	-0.215	0.237	0.321
DVRR					1.000	-0.047	-0.115	0.175	-0.205	0.210	0.015
SPGF						1.000	-0.037	0.187	-0.074	0.114	-0.015
WGRMX							1.000	-0.007	0.014	-0.061	-0.195
NFLV								1.000	-0.086	0.138	-0.712**
FST									1.000	-0.985**	-0.035
FLV										1.000	0.057
SLA											1.000

clear. The small relation between FSTR and DVRR can also not be explained physiologically. Perhaps such relations may simply be coincidental. There was a very significant relation between DVRJ and DVRP, the two rates controlling crop duration before anthesis. The very significant negative relation between FST and FLV is easily understood and built in the model. The negative relation between SLA and NFLV indicates that thin leaves have less nitrogen per unit area. Thus, these input should not be varied independently in applications of ORYZA1 for plant type design.

Conclusions

There are considerable varietal differences in rice varieties in the crop physiological inputs used in the model ORYZA1. In particular, there are large variations in the initial development stages. Several parameters are likely to have more environmental effect than proposed earlier by Kropff et al. (1994). It is important to quantify these effects in order to use ORYZA1 for understanding genotype by environment interactions.

References

Berge, H.F.M. ten, M.J. Kropff & M.C.S. Wopereis, 1994. The SARP Project, Phase III (1992 - 1995). Overview, goals, plans. SARP Research Proceedings, IRRI, Los Baños and AB-DLO, TPE-WAU, Wageningen, 124 pp.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, IRRI, Los Baños and AB-DLO, TPE-WAU, Wageningen, 110 pp.

Photothermal response of flowering in rice cultivars

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Abstract

Temperature and photoperiod are the two major environmental determinants of development to flowering in rice (*Oryza sativa* L.). Two experiments were conducted to provide a basis for accurately quantifying the temperature effect and to estimate durations of photoperiod sensitive and insensitive phases of pre-flowering development in rice. Separate effects of day and night temperatures on the rate of development from sowing to flowering were detected, indicating an apparent thermoperiodic phenomenon in floral development of rice. In most cases, day temperature exerted a greater influence than night temperature, in contrast with the relative importance of night temperature previously reported for rice. The results also indicated that it is necessary to partition the period from sowing to flowering into photoperiod-insensitive and sensitive phases for a model to accurately predict photoperiodic effects.

Introduction

An accurate prediction of the time to flowering is a major requirement for crop growth simulation models. In rice (*Oryza sativa* L.), the interval between sowing and flowering varies strongly between cultivars and largely depends on the growing environment. Since the ripening phase from flowering to maturity is relatively constant (Yoshida, 1981), the period from sowing to flowering largely determines the total growth duration of a rice cultivar (Vergara & Chang, 1985).

Temperature and photoperiod are the major environmental variables that determine the time to flowering in rice (Yoshida, 1981). The effect of temperature in a crop is often described by various thermal time methods that accumulate daily temperatures above a crop- or cultivar-specific base value at which the crop stops its development. These methods generally assume that the relation between development rate and temperature is linear (Hodges, 1991), whereas, the actual relationship may be non-linear over a wide range of conditions (Loomis & Connor, 1992). The thermal time approach also ignores the often substantial effect of photoperiod on development.

As a short-day plant, almost all rice cultivars flower earlier when exposed to shorter

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photoperiods, but the degree of sensitivity varies greatly among cultivars (Vergara & Chang, 1985). However, the rice plant is photoperiod-insensitive for some time after sowing; thereafter, the plant is responsive to photoperiodic stimulus until the panicle has started to develop (Vergara & Chang, 1985; Collinson et al., 1992).

Many quantitative models have been developed to describe phenological events of annual crops in relation to temperature and photoperiod (e.g. Horie et al., 1986; Roberts & Summerfield, 1987; Alocilja & Ritchie, 1991; Gao et al., 1992). These models vary in form from the simple linear additive to variously non-linear multiplicative functions of temperature and photoperiod. However, our initial studies with these models indicate that they only perform well when the environmental parameters vary in a small range. These results have indicated two key issues which need to be studied to improve the existing models.

First, existing models are based on the daily mean temperature and assume that effects of day and night temperatures on the development are essentially the same. However, some studies (e.g. Went, 1944) indicated different effects of day and night temperatures on plant growth and development. Many studies (e.g. IRRI, 1977) have shown that the temperature at night is more important than the day value for controlling crop development.

Secondly, most existing models ignore the fact that the photoperiod-sensitive phase (PSP) of the development to flowering is sandwiched by the pre-photoperiod-sensitive phase or basic vegetative phase (BVP) and the post-photoperiod-sensitive phase (POP).

The objectives of the present paper are to demonstrate whether there are separate effects of day and night temperature on the development to flowering in rice, and to quantify the durations of the BVP, PSP and POP of pre-flowering development in diverse cultivars of rice.

Material and methods

Two experiments were conducted at the International Rice Research Institute (IRRI), Los Baños, Philippines.

Experiment 1

Twenty-four rice cultivars (Table 1) were chosen based on their origin, year of release, and previous experience of their relative responses to photoperiod in our study and elsewhere (e.g. Vergara & Chang, 1985).

In this experiment, a set of temperatures was carefully chosen, to compare the development of diverse rice cultivars under different diurnal temperature regimes with comparable mean values. The experiment was conducted in five naturally-lighted growth chambers. Treatments included one diurnally constant (22 °C) and four diurnally alternating temperatures (day/night: 26/22, 30/22, 22/26 and 22/30 °C. Treatments 22/22, 26/22 and 30/22 °C were expected to give the response of the development rate to day temperatures between 22 and 30 °C with a constant night temperature of 22 °C, whereas treatments 22/22, 22/26 and 22/30 °C were chosen to vary night temperatures between 22 and 30 °C with a constant day temperature of 22 °C.

Table 1. Rice cultivars investigated in the presented study.

Cultivars	IRGC* accession no.	Origin	Sensitivity to photoperiod
Indica			
IR5[2]	10321	IRRI	medium
IR8[1,2]	10320	IRRI	weak
IR36[1,2]	30416	IRRI	weak
IR42[1,2]	36959	IRRI	medium
IR64[1,2]	66970	IRRI	weak
IR72[1,2]	76330	IRRI	weak
Azucena[1]	00328	Philippines	medium
CO36[1,2]	28556	India	strong
MR84[1,2]	73077	Malaysia	medium
Guang Lu Ai 4[1]	28480	China	weak
ADT36[1,2]	64818	India	weak
Carreon[1,2]	05993	Philippines	strong
TN1[1]	38845	China (Taiwan)	weak
Peta[1]	00035	Indonesia	medium
Shan You 63[+1,2]	-	China	weak
IR64616H[+1,2]	-	IRRI	weak
Japonica			
Nipponbare[1,2]	12731	Japan	medium
Koshihikari[1,2]	08305	Japan	medium
Akihikari[2]	76300	Japan	weak
Eiko[1]	09417	Japan	weak
Fujisaka 5[1]	00244	Japan	weak
Lao Lai Qing[1,2]	53396	China	strong
Xiu Shui 11[1,2]	-	China	medium
Stejaree 45[1]	46980	Korea	weak
Hwasong[1,2]	-	Korea	medium
Illpoom[1,2]	-	Korea	medium
Odea[2]	-	Korea	weak

[*] International Rice Germplasm Centre at IRRI, Los Baños

[+] *Indica* hybrid cultivar

- Not on IRGC listing

[1] Tested in Experiment 1 (24 cvs)

[2] Tested in Experiment 2 (20 cvs)

Temperature settings were maintained at ± 1 °C. The day and night temperatures were imposed for 12 h d^{-1} in each of alternating diurnal cycle by setting 'square wave' temperature regimes. The photoperiod was maintained throughout the experiment as 12 h d^{-1} from 6.00 h to 18.00 h, coinciding with the period of the day temperature. CO_2 concentration and relative humidity in the chambers were maintained at 340 ± 10 ppm and 70 ± 5%, respectively. There were three replicate pots for each treatment, each containing one plant. Records were made on individual tillers of the times of flowering for each plant.

Experiment 2

This experiment was conducted to estimate the durations of the BVP, PSP and POP of pre-flowering development in rice. This was done by mutually moving plants between short-day (SD) and long-day (LD) photoperiods at regular intervals after sowing. The experiment was undertaken at the greenhouse-darkroom facilities of IRRI. A total of 20 cultivars with contrasting origins were tested (Table 1).

All plants were grown in one-litre pots arranged in a randomized complete block design on mobile trolleys which were moved daily into an open-sided greenhouse between 08.00 h and 17.00 h, after which they were distributed among the darkrooms. The darkrooms were provided with different hours of 450 lux supplementary light by incandescent and fluorescent lamps to obtain the required photoperiods. The temperature in the darkrooms was maintained at 24 ± 2 °C. The photoperiods used for SD and LD regimes were 10 and 14 h d^{-1}, respectively. However, due to the reported differences in photoperiod sensitivity (e.g. Collinson et al., 1992), the LD regime for cvs CO36 and Carreon was 12.5 h d^{-1}. The mutual transfer between SD and LD started at 5 - 12 days after sowing (DAS) and ended at 84 - 107 DAS, depending on the cultivar. After a plant was transferred, it was grown in the new photoperiod until flowering. There were two replicate pots for each treatment, each containing one plant.

Plants were observed daily to determine the flowering time of individual tillers. In these control treatments (i.e. the treatments where plants were grown continuously at SD or LD), more pots were added so that there were enough plants to be dissected to determine time of panicle initiation (PI) at the control regimes. PI was taken to be equivalent to stage 2, as described by Yoshida (1981), i.e. apex appears to the naked eye as a fuzzed tip of 0.2 - 0.5 mm.

Results and discussion

Experiment 1

The mean rate of development to flowering, i.e. inverse of days from sowing to flowering, was strongly affected by both day and night temperatures in each of the 24 cultivars tested in Exp. 1. Three typical response patterns were obtained from the results of these cultivars (Fig. 1). In most cultivars, the responses to day temperature were different from those to night temperature.

Only one exception was cv. Azucena in which responses were essentially the same for day and night (Fig. 1A). In three *indica* cvs IR8, Guang Lu Ai 4, and Shan You 63, plants under

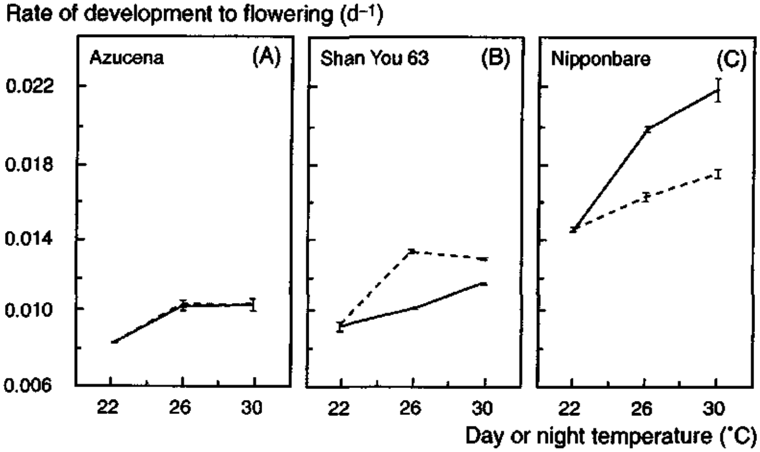

Figure 1. Effects of day temperatures between 22 and 30 °C with a constant night temperature of 22 °C (solid lines) and effects of night temperatures between 22 and 30 °C with a constant day temperature of 22 °C (broken lines) on the rate of development from sowing to flowering in three representative rice cultivars. Vertical bars indicate means ± standard errors.

the regimes of cool days following warm nights developed rapidly when compared to those with warm days following cool nights (Fig. 1B). This resulted in the response curve to night temperature higher than to the day. It would appear from these three cultivars that the effect of night temperature is more important than day temperature. However, a different trend was obtained in most other cultivars where plants under the regime of cool days following warm nights developed slowly when compared to those with warm days following cool nights (Fig. 1C). This difference was more evident between 30/22 and 22/30 °C regimes than between 26/22 and 22/26 °C. Thus, these cultivars responded more to day temperature than to night temperature. The warm nights with cool days often had an effect similar to the constant cool environment of delaying flowering.

The data from this experiment for rice support the view that there are separate effects of day and night temperatures on the development process. This was referred as 'thermoperiodicity' by Went (1944). Several workers have explained thermoperiodicity due to non-linearity in the relationship between temperature and rate of development (e.g. Loomis & Connor, 1992). In most phytotron experiments, night temperatures are set lower than the day temperatures (e.g. IRRI, 1977). These night temperatures were in the range where rate of development increases proportionally with increasing temperatures. If the nonlinearity was the only reason to account for the thermoperiodicity, plants would always flower simultaneously in the 26/22 and 22/26 °C treatments, and in the 30/22 and 22/30 °C treatments.

Went (1944) and IRRI (1977) concluded that the night temperature was more important in controlling crop development than the day temperature. However, the relative importance of the night temperature for development was detected in the present study for only three out of the 24 tested cultivars. In most other cultivars, the day temperature exerted a greater influence than the night temperature. Therefore, the relative importance of day and night temperatures varies among cultivars. The consistent importance of night temperature found by IRRI (1977) can be attributed to the longer duration of night regimes (16 h d^{-1}) than the day regimes (8 h d^{-1}) and the lower temperatures for the night (18 - 24 °C) than the day (20 - 36 °C) temperatures in that experiment.

Experiment 2

Days from sowing to flowering for each treatment in Exp. 2 were plotted as a function of the time of transfer for each cultivar. Fig. 2 illustrates this for cultivar MR84. A similar trend was also obtained for other cultivars. The change in the response line indicates the start or end of the PSP. The duration of the BVP was shorter in *japonica* than *indica* cultivars. Fig. 2 also indicates that once plants become sensitive, the sensitivity remains the same during the whole PSP, since the delay in days to flowering as affected by the time of SD-to-LD transfer during the PSP is strongly linear.

A model has been developed to enable the complete data set to be analysed simultaneously in order to estimate the durations of the BVP, the PSP both in SD and LD, and the POP of each cultivar (Yin et al., in preparation). Estimated values of the four variables varied greatly among cultivars (Table 2). However, the POP varied relatively less; it typically ranged from 20 to 30 d. The duration of the BVP varied from 16.7 to 45.4 d. The duration of the PSP at SD varied from 6.1 to 24.1 d, and the PSP at LD varied from 10.5 to 76.5 d, depending on the sensitivity of a cultivar. Hence, the PSP spanned only a part of the duration of the whole pre-flowering period.

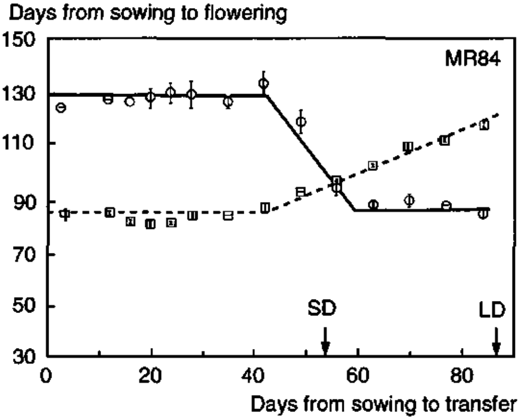

Figure 2. The duration from sowing to flowering of cultivar MR84 transferred from short-day to long-day (circle) or from long-day to short-day (square) at various times after sowing. Vertical bars indicate means ± standard errors. The arrows indicate the time of panicle initiation for plants continuously grown at short-days (SD) or long-days (LD), respectively.

Table 2. Durations (d) of the basic vegetative phase (BVP), the photoperiod-sensitive phase at the short-day (PSP$_S$) and long-day (PSP$_L$), and the post-photoperiod-sensitive phase (POP) of development to flowering in 20 rice cultivars.

Cultivar	BVP	PSP$_S$	PSP$_L$	POP	R^2	n*
Indica						
IR5	40.7	23.3	66.9	23.2	0.959	31
IR8	40.3	24.1	39.8	28.0	0.916	32
IR36	27.9	16.5	29.0	23.8	0.933	32
IR42	42.0	17.2	59.8	25.6	0.988	28
IR64	40.2	13.9	34.8	20.5	0.949	28
IR72	42.0	15.6	27.8	23.4	0.865	28
CO36	23.6	17.6	52.2	35.8	0.981	26
MR84	44.6	14.1	57.4	27.1	0.983	28
ADT36	35.7	6.1	19.1	23.9	0.923	32
Carreon	20.0	9.6	43.6	23.3	0.978	32
Shan You 63	30.0	14.2	38.0	28.3	0.928	32
IR64616H	45.4	15.3	26.5	20.2	0.885	28
Japonica						
Koshihikari	18.4	12.5	30.0	22.6	0.971	28
Nipponbare	16.7	13.8	42.8	20.6	0.989	28
Akihikari	32.2	11.8	18.4	18.0	0.728	32
Xiu Shui 11	22.3	8.1	59.0	33.6	0.994	30
Lao Lai Qing	25.5	9.7	76.5	37.2	0.996	27
Hwasong	23.0	7.4	31.5	24.1	0.966	30
Illpoom	19.6	15.7	32.6	27.9	0.981	28
Odea	34.1	3.6	10.5	23.6	0.776	32

* number of environments fitted

The dissection of control plants showed that PI had occurred typically before or at the end of the PSP, depending on the cultivar or photoperiod treatment. Comparison between days from sowing to PI and days from sowing to the end of the PSP (Fig. 3) indicates that, by average, photoperiod sensitivity ends at about 4 - 5 d after PI.

It was assumed in most of the existing models (e.g. Gao et al., 1992) that sensitivity of the plants to photoperiod remains the same throughout the whole period from sowing to flowering. In contrast, the results in Exp. 2 confirm that the rice crop model CERES-Rice (Alocilja & Ritchie, 1991) is correct to partition the period from sowing to flowering into photoperiod-insensitive and photoperiod-sensitive phases. However, the model of CERES-Rice assumes that the end of PSP coincides with PI. The results of our work would suggest that the PSP ends on average, at 4 - 5 d after PI (Fig. 3). This result is compatible with the observation that PI occurred after only about 80% of the PSP has elapsed (Collinson et al., 1992).

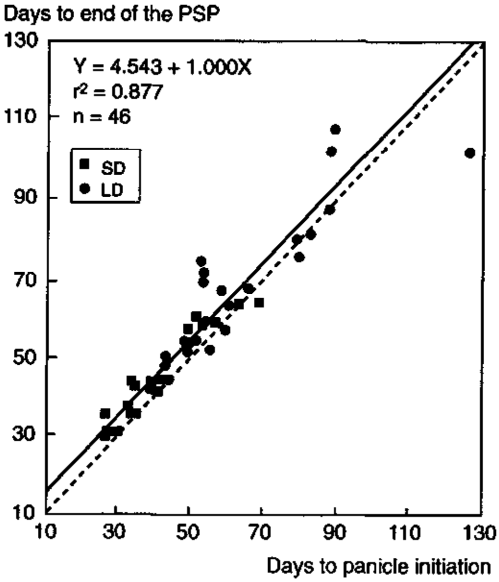

Figure 3. Comparison between days from sowing to the end of the photoperiod-sensitive phase (PSP) (quantified in Table 2) and days from sowing to panicle initiation (PI) at both short-day (SD) and long-day (LD) photoperiods from results of the 20 rice cultivars tested in Exp. 2. The dashed line represents the 1:1 relationship and the solid line is the regression line.

Conclusions

Our studies show the different effects of day and night temperatures on flowering in rice. In most cases, day temperature exerted a greater influence than night temperature. The relative importance of the night temperature reported in previous studies (e.g. IRRI, 1977) was due to the fact that the night temperatures were in the range where the rate of development increases proportionally with increasing temperatures whereas the day temperatures were in the range which probably limited crop development.

For modelling purposes, the interval between sowing and flowering can be divided into three phases, i.e. BVP, PSP and POP. The PSP did not necessarily end at PI as is assumed in some models. Further studies would be needed to determine temperature sensitivity during each of these three phases.

We now have a reasonable database for rice from which the development from sowing to flowering can be modelled with confidence. A new model for predicting rice phenology based on the above experiments is in development. This data base also documents the extent of genetic variation available in phenology parameters used in crop models for several *indica* and *japonica* cultivars. This information would be of considerable use in applications of crop models for designing new plant types.

References

Alocilja, E.C. & R.T. Ritchie, 1991. A model for the phenology of rice. In: T. Hodges (Ed.), Predicting crop phenology. CRC Press, Boca Raton, Florida, pp. 181-190.

Collinson, S.T., R.H. Ellis, R.J. Summerfield & E.H. Roberts, 1992. Durations of the photoperiod-sensitive and photoperiod-insensitive phases of development to flowering in four cultivars of rice (*Oryza sativa* L.). Annals of Botany 70: 339-346.

Gao, L., Z. Jin, Y. Huang & L. Zhang, 1992. Rice clock model - a computer simulation model of rice development. Agric. and For. Meteorol. 60: 1-16.

Hodges, T., 1991. Temperature and water stress effects on phenology. In: T. Hodges (Ed.), Predicting crop phenology. CRC Press, Boca Raton, Florida, pp. 7-13.

Horie, T., H. Nakagawa & T. Kira, 1986. Modelling and prediction of the developmental processes of rice. I. Dynamic model for predicting the flowering date. Japan. J. Crop Sci. 55: 214-215.

International Rice Research Institute (IRRI), 1977. Annual report for 1976. IRRI, Los Baños, Philippines, pp. 113-120.

Loomis, R.S. & D.J. Connor, 1992. Crop ecology: productivity and management in agricultural systems. Cambridge University Press, Cambridge, pp. 104-128.

Roberts, E.H. & R.J. Summerfield, 1987. Measurement and prediction of flowering in annual crops. In: J.G. Atherton (Ed.), Manipulation of flowering. Butterworths, London, pp. 17-50.

Vergara, B.S. & T.T. Chang, 1985. The flowering response of the rice plant to photoperiod. IRRI, Los Baños, Philippines, 61 pp.

Went, F.W., 1944. Plant growth under controlled conditions. II. Thermoperiodicity in growth and fruiting of the tomato. Am. J. of Botany 31: 135-149.

Yoshida, S., 1981. Fundamentals of rice crop science. IRRI, Los Baños, Philippines, 269 pp.

Variation in the rate and duration of grainfilling in rice genotypes

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Abstract
Field experiments were conducted in the wet and dry season of 1992 and 1993 at IRRI to determine the variability in effective grainfilling (EGF) duration in six *indica* varieties. Effective grainfilling duration varied from 24 to 32 days in the dry and 18 to 26 days in the wet season but these differences were statistically non-significant. Mean growth rates of the panicle within the EGF varied from 229 to 298 kg ha^{-1} d^{-1} in the dry season, and from 162 to 228 kg ha^{-1} d^{-1} in the wet season.

Introduction

The key to ideotype breeding is the identification of the critical traits that are associated with yield increase. Crop simulation models have recently been used for this purpose in rice (Dingkuhn et al., 1991; Penning de Vries, 1991; Kropff et al., 1994b; Aggarwal et al., 1995). These studies identified increased sink size, a longer period of effective grainfilling, longer green leaf area duration and sustained canopy photosynthesis within the grainfilling period as the main characteristics required to obtain a large increase in grain yield. Initial simulation studies using ORYZA1 showed that panicle dry matter of 9.3 t ha^{-1} can be expected in the dry season with a grainfilling duration of 24 days (Kropff et al., 1994a). Yields were further increased to 11.7 t ha^{-1} with a grainfilling period of 31 days. A yield of 14.7 t ha^{-1} was reached when grainfilling duration was set to 40 days. Thus, a very critical component for increase in grain yield is related to grainfilling duration.

Genetic variability in critical traits including grainfilling duration must be known to realistically show that considerable gains in yield can be achieved with the manipulation of these traits. Senadhira & Li (1989) found significant variation in the grainfilling duration in 21 cultivars in the dry season. Grainfilling period ranged from 16 to 40 days. In this study, however, the agronomic practices were not suitable for achieving maximum yields because N application was low and spacing was very wide resulting in inadequate radiation interception. This may have effected the expression of full genetic variation in grainfilling duration. This paper describes the results of our recent experimental studies to determine the level of genetic variation available in effective grainfilling duration in six *indica* cultivars grown under optimal management.

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Material and methods

Six *indica* varieties were used in this study. These were - Bg276-5, Bg90-2, IR72, IR54, IR64616H (a hybrid rice variety) and IR62398-AC201-2. The first four varieties were selected from the earlier studies of Senadhira & Li (1989) for their contrasting grainfilling periods. The other two varieties were recently developed high yielding lines.

Experiments were conducted in the wet (WS, 1992) and the dry season (DS, 1993) at the IRRI experimental farm. All varieties were used in both seasons except IR64616H, which was used only in the dry season. The experiments were laid out in a randomized complete block design with four replicates. Seedlings were prepared using the seedling tray method to ensure uniformity at transplanting and minimize the transplanting shock. Transplanted seedlings were 12 days old. Urea was applied in 4 splits: 60-60-60-40 kg N ha^{-1} in the dry season and 26.7-26.7-26.7-30 kg N ha^{-1} in the wet season at transplanting, mid-tillering, panicle initiation and at first flowering. Solophos was basally applied at 15.5 kg P ha^{-1}. Intensive pest management was applied throughout the whole growing season.

Dates of panicle initiation (PI) and 90% flowering (90% of the hills have at least one flowering panicle) were recorded. Dry weight of panicles was monitored at 0, 4, 8, 12, 15, 18, 24, 30, 37 and 40 days after flowering (DAF) in the dry season and at weekly intervals in the wet season. In each replicate, 12 hills were harvested per sampling date and a subsample of six hills were processed further for growth analysis. The panicles were oven dried for three days at 80 °C.

Effective grainfilling (EGF) period

In this paper, we have determined effective grainfilling period (EGF) defined by Yoshida (1981) as the period where most of the grain dry weight is accumulated. The Weibull function was fitted using least squares to the mean panicle dry weights over time, expressed as days after panicle initiation. The function is defined as:

$$Y = A - b \times e^{-c\,d\,x}$$

where Y is panicle weight, A is maximum panicle weight, b, c and d are constants and x is the number of days after panicle initiation.

Fig. 1 illustrates the procedure of determining the EGF period. A smooth sigmoid curve was fitted to the growth of the panicle from PI to flowering (Fig. 1A). The rate of panicle growth increases from PI to a maximum and then decreases to maturity, with inflection points on both sides of the maximum (Fig. 1B). The EGF period is defined as the time between the two inflection points of this rate. It corresponds to the approximately linear phase of the dry matter accumulation curve where rapid accumulation occurs. Mathematically, the points of inflection are the points at which the second derivative has a slope equal to 0. Since the third derivative is

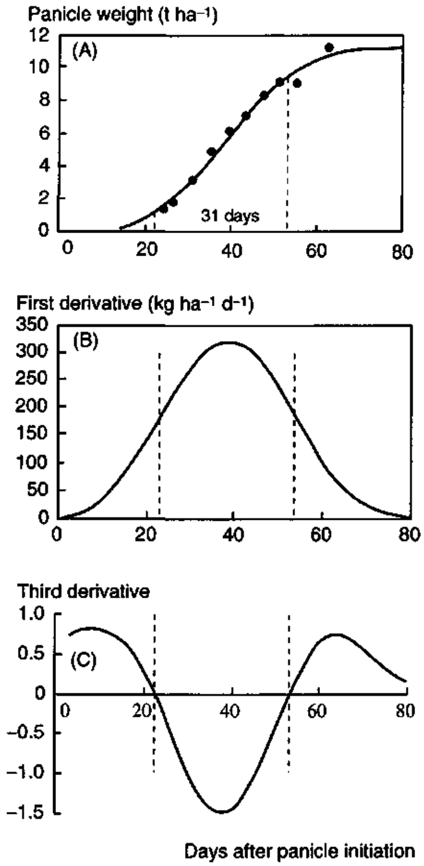

Figure 1. Determination of the inflection points for the boundaries of effective grainfilling duration.

Table 1. Effective grainfilling period (EGF, d) and mean panicle growth rate (PGR, kg ha^{-1} d^{-1}) of different varieties in the dry (DS) and the wet seasons (WS). Means with the same letter in a column are not significantly different at 0.05 probability levels.

Variety	EGF		PGR	
	DS	WS	DS	WS
IR64616H	26 a	-	292 a	-
IR62398-	32 a	25 a	292 a	202 a
Bg90-2	31 a	26 a	271 ab	162 a
IR54	24 a	18 a	298 a	178 a
IR72	25 a	19 a	275 ab	228 a
Bg276-5	28 a	22 a	229 b	162 a
c.v.	13.1	19.2	13.1	14.1

the slope of the second, the third derivative shows exactly where the points of inflection are (Fig. 1C). Hence, the EGF period excludes the lag phase where the curve slowly accumulates before the first inflection point and where the curve starts to level off after the second inflection point. Mean filling rate at any point in the EGF phase was calculated as the slope of the straight line between inflection points:

$$PGR = (w_2 - w_1) / (t_2 - t_1)$$

where PGR is the panicle growth rate or filling rate, w_1 and w_2 are the panicle dry weights at the inflection points, and t_1 and t_2 are the dates of the two inflection points.

Results and discussion

Effective grainfilling duration

In the dry season, effective grainfilling period ranged from 24 to 32 days, and 18 to 26 days in the wet season (Table 1). IR62398-AC201-2 and Bg90-2 had the longest grainfilling duration both in the dry and wet seasons. By comparison, IR72 and IR54 had the shortest EGF. However, these differences were statistically non-significant. In fact, there was no significant difference across seasons as well in different genotypes. Senadhira & Li (1989) earlier found significant differences in grainfilling duration of rice varieties. One reason for this disagreement could be the measurement procedure employed in the two studies. We sampled all panicles in several hills to determine mean EGF for the whole canopy as compared to Senadhira & Li (1989) studies who determined grainfilling duration for main shoots alone. Yoshida (1981) also did not find differences in grainfilling duration. Lack of variation in grainfilling duration is also documented in other cereals as well (IRRI, 1982).

Panicle (grain) growth rates

There was no variation in panicle growth rates (PGR) among varieties in the wet season (Table 1). In the dry season, IR64616H and IR62398-AC201-2 and IR54 had a very high PGR as compared to Bg276-5.

Conclusions

This study was done with a limited number of varieties which indicated absence of significant variation in effective grainfilling duration. And yet there were differences in grain yield among varieties. Thus, it is evident that the grainfilling process is a complex interplay of several physiological factors and no single trait can explain all the variation in grain yield. There is a need to do more studies to elucidate the role of sink and source size and grainfilling duration in regulating grainfilling in a larger number of genotypes.

References

Aggarwal, P.K., M.J. Kropff, R.B. Matthews & C.G. McLaren, 1995. Using simulation models to design new plant types and to analyse genotype and environment interactions. In: M. Cooper & G. Hammer (Eds), The analysis and exploitation of plant adaptation in agricultural crop improvement programs. CAB, Wallingford (in press).

Dingkuhn, M., F.W.T. Penning de Vries, S.K. De Datta & H.H. van Laar, 1991. Concept for a new plant type for direct seeded flooded tropical rice. In: Direct seeded flooded rice in the tropics. Selected papers from the International Rice Research Conference, 27-31 August 1990, Seoul, Korea. IRRI, Los Baños, Philippines, pp. 17-38.

IRRI, 1982. Production potential of crop plants. IRRI, Los Baños, Philippines.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994a. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, IRRI, Wageningen, 110 pp.

Kropff, M.J., K.G. Cassman, S. Peng, R.B. Matthews & T.L. Setter, 1994b. Quantitative understanding of yield potential. In: K.G. Cassman (Ed.), Breaking the yield barrier. IRRI, Los Banos, pp. 21-38.

Senadhira, D. & G.F. Li, 1989. Variability in rice grain-filling duration. International Rice Research Newsletter 14(1): 8-9.

Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: F.W.T. Penning de Vries, M.J. Kropff, P.S. Teng & G.J.D. Kirk (Eds), Systems simulation at IRRI. IRRI Research Paper Series, November 1991, Number 151, pp. 13-19.

Yoshida, S., 1981. Fundamentals of rice crop science. International Rice Research Institute, Philippines, 269 pp.

Photosynthetic responses of rice hybrids and inbreds in field conditions

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Abstract

The photosynthetic rates of individual leaves of tropical and subtropical *indica* hybrids were compared with the best *indica* inbred cultivars for two different positions in the canopy under a wide range of light intensities. The objectives were to determine if there were any differences in photosynthetic capacity between hybrids and inbred cultivars and to establish the relationship between light intensity and rate of photosynthesis in field conditions. Two *indica* inbreds, IR72 and IR65598-112-2, and two hybrids, IR64616H and Shanyou 2070, were grown under optimum management conditions in the Philippines in the dry season of 1994. Results showed that there was a significant difference in the rate of maximum photosynthesis between the flag leaf (number one) and the third leaf. The photosynthetic rate of IR64616H was higher than Shanyou 2070 and the inbreds. These differences in the rate of photosynthesis could be explained by differences in leaf nitrogen concentration.

Introduction

Reports from China show that yield of commercial hybrid rices is about 20% higher than the best inbred varieties (Yuan & Virmani, 1988). Some authors have suggested that this 'heterotic' effect in rice is due to enhanced photosynthesis (e.g. Lin & Yuan, 1980; Murayama et al., 1984). However, the results are not consistent; other researchers have observed little heterosis in single-leaf photosynthetic rates (e.g. Kabaki et al., 1976; Yamauchi & Yoshida, 1985). Akita (1988) suggested that these inconsistent results were mainly due to differences in leaf nitrogen concentration in the various studies.

In many simulation models, canopy photosynthesis is estimated by integrating the rate of photosynthesis of individual leaves, where it is assumed that all leaves have the same photosynthesis-light response curve (PLRC) (e.g. ORYZA1, Kropff et al., 1994). However, it is likely that the PLRC varies with variety and leaf position. This study compares the PLRC of individual leaves of elite hybrids and the best inbred cultivars under optimum management environments, with the objectives of comparing the photosynthetic capacity of hybrid and inbred rice and establishing the PLRC of leaves in different positions in the canopy for use in a crop

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simulation model.

Material and methods

A field experiment was conducted during the dry season (January - May) of 1994 at the International Rice Research Institute (IRRI), Los Baños, Philippines. The experiment was laid out in a split-plot design with four replications. Main-plots were three nitrogen fertilizer rates (0, 80 and 210 kg N ha^{-1}) and the subplots were four genotypes: the inbreds IR72 and IR65598-112-2, the tropical hybrid IR64616H, and the subtropical hybrid Shanyou 2070 from China. For convenience, IR65598-112-2 and Shanyou 2070 are referred to hereafter as IR65598 and SY2070, respectively. Twelve-day-old seedlings were transplanted on 25 January 1994 at a hill spacing of 20 × 20 cm with three plants per hill. Crops were well-irrigated, and kept free from pests and diseases.

Leaf photosynthetic rates were measured with a portable photosynthesis system (LI-6200, LI-COR, USA). At flowering, five fully-expanded flag leaves (leaf one) and five third leaves from each plot were selected for measurement. The PLRCs of each leaf were determined by measuring photosynthetic rates repeatedly under varied light intensities obtained by shading from full sunlight by adding layers of mesh screen. For measuring photosynthetic rates in the third leaves, the crop canopy was held open using iron supporting brackets to allow greater penetration of solar radiation to these lower leaves. Photosynthesis in these leaves was measured after one hour to allow acclimatization to the new conditions. All measurements were made between 10 a.m. and 2 p.m. Since the dates of flowering were similar in the four varieties, measurements of photosynthesis for *all* genotypes were done on the same day, and only on mainstems, to ensure the same phenological stage in each case.

Results and discussion

The PLRC of single leaves follows a saturation type of function, characterized by the initial slope at low light intensities (the initial light use efficiency, ε) and the asymptote at high light intensities (maximum photosynthesis, A_m), which can be described by a negative exponential function (Goudriaan, 1982). The photosynthetic rates increased curvilinearly with the increase in photosynthetically active radiation (PAR) for both flag and third leaves in all genotypes, but there were significant differences in the asymptotes of the two types, with the flag leaves reaching maximum photosynthetic rates of more than 30 μmol CO_2 m^{-2} s^{-1} compared to the 12 μmol CO_2 m^{-2} s^{-1} of the third leaves (Fig. 1). There was little difference in the PLRCs of the hybrids and inbreds for leaves in the same position in the canopy, although the hybrid IR64616H showed a consistent tendency for higher photosynthetic rates than the other varieties (Figs 2 and 3). Photosynthesis reached saturation point between 1700 - 1800 μmol PAR m^{-2} s^{-1} for flag leaves, and between 500 - 800 μmol PAR m^{-2} s^{-1} for third leaves.

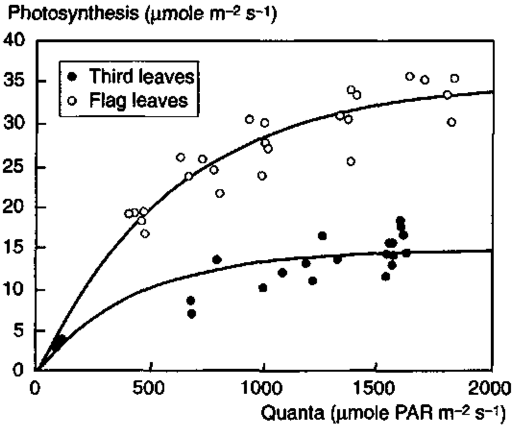

Figure 1. Comparison of the CO_2 assimilation-light response curve of single leaves of flag and third leaves at flowering in the hybrid IR64616H.

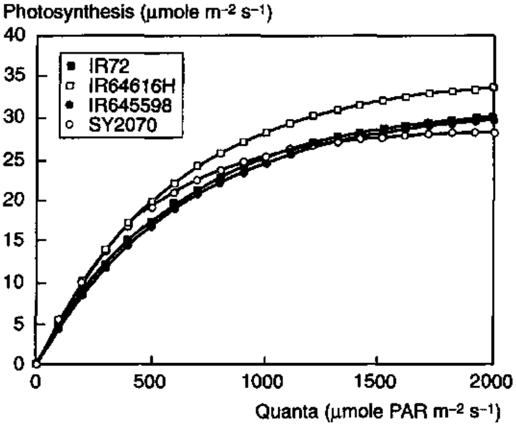

Figure 2. Comparison of the CO_2 assimilation-light response curve of flag leaves at flowering between hybrids and inbreds (fitted lines).

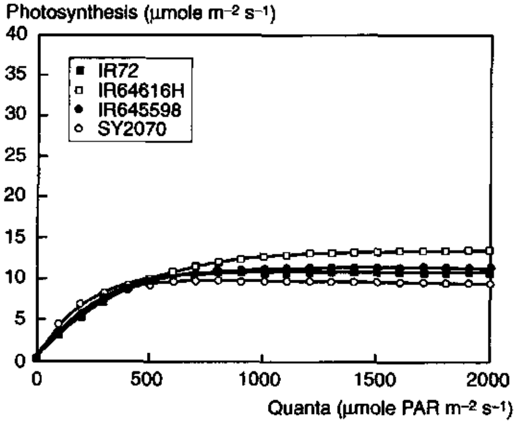

Figure 3. Comparison of the CO_2 assimilation-light response of third leaves at flowering stage between hybrids and inbred (fitted lines).

Table 1. The parameters of the CO_2 assimilation-light response ($A = A_m (1 - \exp(-\varepsilon\, I_a/A_m))$* for the genotypes used in the study.

Genotype	Leaf position	A_m µmol CO_2 m^{-2} s^{-1}	ε µmol CO_2 (µmol quanta)$^{-1}$	Leaf N content g N m^{-2}
IR72	flag	30.76	0.051	1.86
	third	11.41	0.075	0.99
IR64616H	flag	34.41	0.058	1.96
	third	14.06	0.035	1.05
IR65598-112-2	flag	30.85	0.048	1.75
	third	11.89	0.041	0.67
Shanyou 2070	flag	28.23	0.063	1.62
	third	10.08	0.082	0.75

* A refers to photosynthesis; A_m, maximum photosynthesis; ε, light use efficiency; I_a, light intensity.

Table 1 shows the parameters of the PLRC for each variety and leaf position obtained by curve-fitting to the measured data. Reflecting the data in Figs 2 and 3, the maximum rate of photosynthesis (A_m) varied with genotype - for both leaf positions, IR64616H had the highest values, followed by IR72 and IR65598, with Shanyou 2070 having the lowest values. These differences could largely be explained by leaf nitrogen concentration (Fig. 4), which varied from 0.67 to 1.05 g N m^{-2} depending upon the genotype and leaf position. Nitrogen concentration in the flag leaves was higher than in the third leaves, resulting in their higher A_m values (Table 1).

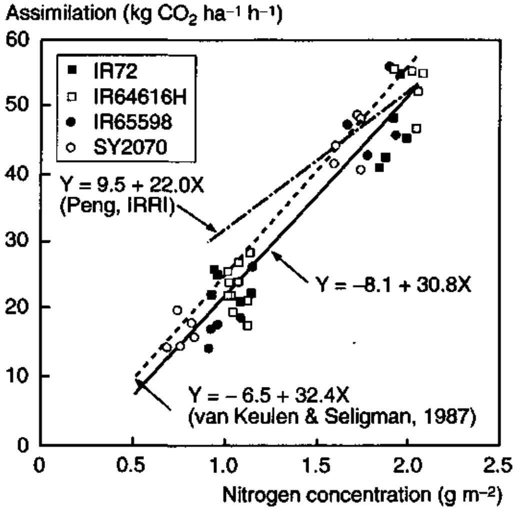

Figure 4. The relationship between the maximum rate of CO_2 assimilation of single leaves and the leaf nitrogen concentration on a per area basis. Also shown are the relationships estimated by Peng (pers. comm.) and van Keulen & Seligman (1987).

There was a slight difference in the initial light use efficiency (ε) among genotypes (Table 1), but this did not seem to be related to leaf nitrogen content. Average values of e across genotypes were 0.055 μmol CO_2 per mol quanta for the flag leaf and 0.047 for the third leaf. These values are similar to published figures for a C_3 crop (Boote & Loomis, 1991).

The third leaves had much lower maximum photosynthetic rates compared to the flag leaves partly due to their low nitrogen content. The relation between A_m and leaf nitrogen content was linear, confirming previous findings by van Keulen & Seligman (1987) and Peng (IRRI, pers. comm.), although our results are closer to the former relationship than the latter (Fig. 4).

Conclusions

The maximum photosynthetic rates of tropical hybrid rice (IR64616H) were higher than those of subtropical hybrid rice (Shanyou 2070) and inbred genotypes when all were grown in a tropical environment. There was a large difference in the rate of photosynthesis between flag leaf and lower leaves which apparently was related to leaf N content. Initial light use efficiency showed only limited variation.

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References

Akita, S., 1988. Physiological bases of heterosis in rice. In: Hybrid rice. International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines, pp. 67-77.

Boote K.J. & R.S. Loomis, 1991. The prediction of canopy assimilation. In: K.J. Boote & R.S. Loomis (Eds), Modeling crop photosynthesis - from biochemistry to canopy. Crop Society of America and America Society of Agronomy, Wisconsin, USA, pp. 109-140.

Goudriaan, J., 1982. Some techniques in dynamic simulation. In: F.W.T. Penning de Vries & H.H. van Laar (Eds), Simulation of plant growth and crop production. Simulation Monographs, Pudoc, Wageningen, pp. 66-84.

Kabaki, N., S. Akita, I. Tanaka & A. Amemiya, 1976. Photosynthesis and photo-respiration of cultivated rice and F1 hybrids. Japanese Journal of Crop Science 45 (extra issue) 2: 177-178.

Keulen, H. van & N.G. Seligman, 1987. Simulation of water use, nitrogen and growth of a spring wheat crop. Simulation Monographs, Pudoc, Wageningen, 310 pp.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, AB-DLO, TPE-WAU, Wageningen, and IRRI, Los Baños, 110 pp.

Lin, S. & L.P. Yuan, 1980. Hybrid rice in China. In: Innovative approaches to rice breeding. International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines, pp. 35-51.

Murayama, S., N. Ogasawara, S. Miyasato & A. Nose, 1984. Dry matter production of F1 rice hybrids. III. Heterosis in photosynthetic activity. Japanese Journal of Crop Science (extra issue) 2: 100-101.

Yamauchi, M. & S. Yoshida, 1985. Heterosis in net photosynthesis rate, leaf area, tillering and some physiological characters of 35 F1 rice hybrids. J. Exp. Bot. 36: 274-280.

Yuan, L.P. & S.S. Virmani, 1988. Status of hybrid rice research and development. In: Hybrid rice. International Rice Research Institute, P.O. Box 933, 1099 Manila, Philippines, pp. 7-24.

Opportunities for the application of systems approaches in plant breeding

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Abstract
Crop simulation models provide a number of opportunities for greater integration of inter-disciplinary knowledge, in particular, that of crop physiology in plant breeding programmes. This paper describes frameworks to use systems approaches in design and evaluation of plant types for targeted environments, increasing the efficiency of multi-location evaluation of genotypes and for determining suitable planting dates of parents for increasing hybrid seed production. In the project Simulation and Systems Analysis for Rice Production (SARP), case studies have been developed to illustrate the usefulness of these approaches in different rice producing environments of Asia.

Introduction

The techniques of systems approaches are increasingly being used in agricultural research, planning and development. Crop models and simulation - major systems tools have been effectively used for optimizing crop management practices, agro-ecological characterization, and for evaluating the impact of climatic variability and climatic change (Penning de Vries et al., 1993). There is considerable expectation for using these approaches in increasing the efficiency of plant breeding programmes as well (Shorter et al., 1989; Hunt, 1993; Chaudhary, 1995, Khush et al., 1995). These expectations can be summarized as follows:

- To design and evaluate plant types in various ecosystems,
- To increase the efficiency of the selection process,
- To develop methodologies for efficient multi-location evaluation of genotypes,
- To develop decision models for increasing the outcrossing percentage in the process of hybrid seed production,
- To assist in determining the critical factors limiting yield in resource constraint environments and opportunities to overcome these, and
- To evolve strategies for integrated pest management and varietal adaptations to pests and diseases.

In order to meet these challenges, a framework has been developed to apply systems knowledge

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to plant breeding programmes (Aggarwal et al., 1995a). In this paper, we summarize our views on how systems approaches could contribute in some areas of plant breeding programmes with specific examples for rice.

Design and evaluation of plant types

Breeders spend considerable time and effort in conceptualizing plant types (Hunt, 1993). The largest challenge in ideotype breeding is deciding which traits to combine. Conceptual physiological models of plant types for increased yield potential have been proposed, but progress with this approach has been limited due to the difficulty of identifying critical traits, feedbacks, evaluation in specific environments, and lack of genetic variability in such traits (Marshall, 1991). Simulation models may provide useful tools for examining hypotheses and for setting breeding goals for different traits using historical weather data and techniques of risk analysis. Sensitivity analysis of the model parameters is analogous to the creation of genetic isolines since only one parameter is changed while keeping the rest of the plant characteristics constant. They have been used for designing plant types in rice (Dingkuhn et al., 1991; Penning de Vries, 1991; Kropff et al., 1994b, Aggarwal et al., 1995b) and in other crops (Jordan et al., 1983; Hammer & Vanderlip, 1989; Aggarwal 1991; Muchow & Carberry, 1993).

A methodological framework for using crop models in the design and evaluation of plant types has been proposed by Aggarwal (1995). This approach requires a crop simulation model that has been well evaluated in the target environment (Fig. 1). The latter consists of climatic factors and their variability, soil factors, management factors such as date of sowing/transplanting, population, fertilizer and water availability and socio-economic conditions in the region. The critical crop parameters in the target environment are determined by means of a sensitivity analysis of traits. For these sensitive parameters, the level of genetic variation available in germplasm is determined from values reported in the literature or measured in available germplasm. Alternatively, options to increase variability by genetic means need to be assessed. It is important to determine the range and the boundaries of this variation, in particular in the parents used in the crossing programmes. Simultaneously, it must be assessed if such traits are heritable and if there are associated pleiotropic effects.

Having determined the extent of variation in critical and heritable traits, hypothetical varieties can be constructed with different combinations of traits. Programmes for random generation of input parameter values such as RIGAUS (Bouman & Jansen, 1993) can be very useful for creating a large number of independent combinations. The yield of such hypothetical varieties can then be determined for the target environment. The results can then indicate the importance of different traits in a specific environment as well as set the breeding goals for individual traits. The framework was recently illustrated with a case study for sub-tropical, irrigated rice in northern Indian environments (Aggarwal, 1995) and for tropical environments of Philippines (Aggarwal et al., 1995b).

Although this systems approach appears attractive, it also has some limitations. Key

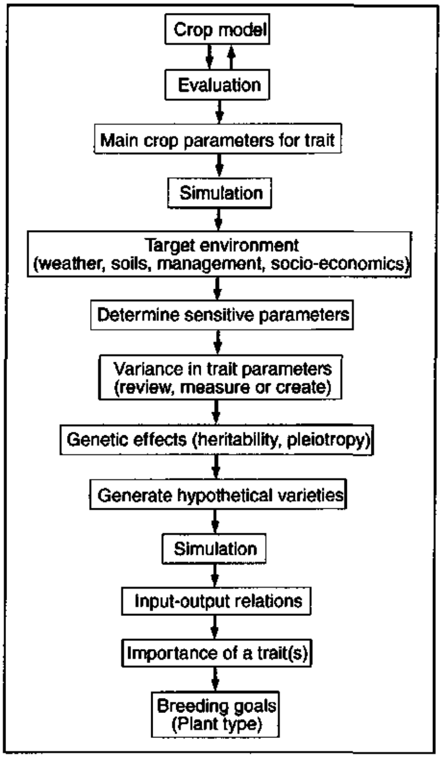

Figure 1. A framework for the use of crop models in design and evaluation of plant types for specific environments. Source: Aggarwal, 1995.

morphological parameters recorded by breeders. e.g. early vigour, panicle and tiller number, panicle and plant heights, grain size and quality, pest reaction are not yet incorporated in rice simulation models (e.g. ORYZA1). Information on major physiological trait compensation, heritability, genetic background, pleiotropy for the model inputs is generally lacking. Crop models may not be sensitive to all yield limiting factors in different environment. For example, in drought prone environments (particularly uplands) acidity, phosphorus and other nutrients and weeds can be major constraints. Models used for plant type design in such environments should be sensitive to these factors. Lodging has a high probability in tropical environments, particularly in the wet season and/or in high fertility situations. This is not considered in crop models. Nevertheless, provided the negative linkages among traits and physiological processes are adequately included in crop models, a systems approach to plant type design can give useful indications to which characteristics breeders may be able to select for higher yield potential. In the project Simulation and Systems Analysis for Rice Production (SARP) (ten Berge et al., 1994), efforts are being made to identify critical plant traits in regional agro-environments and on collecting information on genetic variability in these traits. Few preliminary examples of this can be found in these proceedings (Sutoro & Makarim, 1995; Zhu et al., 1995; Dionora & Kropff, 1995).

There have been significant developments in the field of systems approaches to link crop physiology based models to the damage caused by pests and diseases. Models are now available to simulate the effect of a wide variety of pests on yield loss in several crops. These models have allowed us to estimate loss profiles and damage thresholds to assist in decision making in integrated pest management. They can also be used to determine required strategies in the germplasm for minimizing damage caused by various pests in different climates, soil types and cultural practices. Alternatively, simulation models can also be used to assess the relative performance of proposed plant types in scenarios of various levels of pests in different agro-ecosystems.

Assisting multi-environment testing

Apart from conceptualizing plant types and selecting appropriate parents, line evaluation and release is another major activity consuming considerable resources of plant breeders (Hunt, 1993). Newly developed genotypes are evaluated over several seasons and across several locations to determine their adaptation or stability over environments. For example, rice evaluation trials are conducted in hundreds of locations by the International Network for Genetic Evaluation of Rice (INGER). Similarly, in the state of Tamil Nadu in India, multi-location evaluation of rice is done over a period of 10 years at 100 locations and a variety may be evaluated in as many as 288 experiments before it is released (Palanisamy et al., 1993). Despite such extensive testing it is impossible to cover the whole range of environments. It may often happen that a specific environmental challenge may not be available in natural environments to enable effective discrimination among breeding lines. Simulation models, well characterized in terms of critical physiological traits, together with historical weather data and techniques of risk analysis may be used for environmental characterization of sites and to assist in evaluating and extrapolating the performance of a genotype from one site to another (Elings, 1995; Palanisamy et al., 1995).

Identification of superior genotypes is generally done by ranking yields of breeding lines and their quality and pest resistance scores relative to control checks. Simulation models can be used to assess the relative performance of breeding lines in a relatively short time following the methodology shown in Fig. 2. The necessary crop inputs can be measured at a few carefully selected sites and the G × E interactions quantified over other sites. Optimization programmes such as GENCALC (Hunt et al., 1993) are also available to determine the model input parameters from experimental observations. The methodology can be used to assess the performance of various genotypes across a much wider range of management options than would be possible by experimentation. Palanisamy et al. (1995) used ORYZA1 to determine the relative performance of pre-release genotypes across the state of Tamil Nadu, India. The average simulated ranking of genotypes across locations showed a reasonable agreement with the measured values. The first two lines identified by experimentation were also selected by simulation. Although this experience is encouraging, small differences between lines (say less than 500 kg ha^{-1}), commonly observed in many well conducted advanced multi-environment trials are difficult to

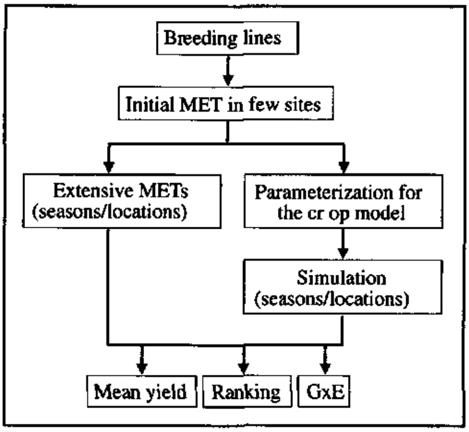

Figure 2. A framework for the use of crop growth models in multi-environment trials.

simulate with crop models largely because of inaccuracies in measurement of model inputs and the fact that it may be beyond models resolution. Such differences may not be statistically significant but nevertheless breeding lines get different rankings. Conventional field trials also encounter stresses such as pests and other management problems which may affect the expression of full yield potential. It is not clear if ranking of genotypes takes care of this problem. The decision to identify a variety is dependent upon pest resistance score as well as grain quality. These are not being simulated in the model at present.

New statistical tools such as additive main effects and multiplicative interaction models (AMMI) and pattern analysis are being used to discriminate among varieties and to explain G × E interaction (McLaren, 1995). Crop simulation models may be able to replicate G × E interactions as determined by statistical analysis of experimental data. The effectiveness of this approach in extending the range of experimentation in G × E research was recently evaluated by Aggarwal et al. (1995b). The sequence of steps used are shown in Fig. 3. The experimental data from a preliminary multi-location trial was subjected to pattern analysis. Six genotype groups with similar G × E interactions were identified. One variety from each group was chosen to be the reference genotype representing that group. Data for another multi-location trial was generated with ORYZA1 for the same varieties. These were used to obtain hypothetical G × E effects as residuals from the additive model applied to this new data. Also an AMMI analysis with two interaction axes was fitted to the newly generated data for the reference varieties only. This was used to estimate environment scores for the new sites. These were combined with the genotype scores from the original simulation to provide estimates of the interaction effects in the new sites.

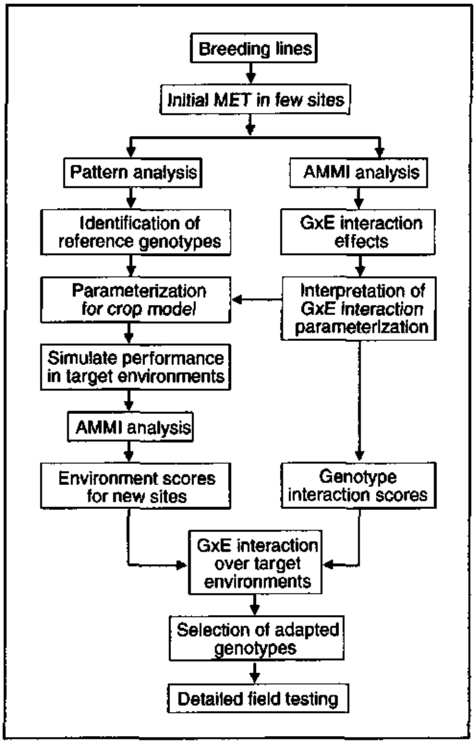

Figure 3. A framework for using together statistical models and crop growth simulation models for increasing the efficiency of multi-environment evaluation (MET). Source: Aggarwal et al., 1995.

The results showed that environmental and G × E effects were of similar magnitude to that of many INGER multi-environment trials. A highly significant positive correlation was observed between the estimated and actual simulated interaction effects indicating the potential for this type of combination of statistical analysis and crop modelling to extend insight by G × E interactions. Work is now in progress in the SARP project, in collaboration with regional, national and international germplasm evaluation networks, to evaluate the usefulness of this approach in analysing and interpreting G × E interaction. Based on the success of this approach, it may be possible to extrapolate performance of a crop population from one site to another, reduce the number of locations in varietal evaluation programmes, classify environments, and to describe why a particular variety does not perform well in all locations.

Hybrid seed production

Hybrid seed production of rice is limited largely due to poor outcrossing and asynchronous flowering of male and female parents (Virmani et al., 1994). Environmental factors such as temperature, humidity and wind speed at the time of pollination and fertilization play a great role in regulating outcrossing percentage. In order to synchronize flowering period of male and female parents to increase hybrid seed production, trials are conducted at several locations to determine the optimal planting dates. Crop simulation models are now available that can assist in decision making about planting calendar of parents in different environments (Xu, 1995). Applications of such models can greatly assist breeders to determine rapidly the suitable areas and seasons for hybrid seed production. However, it is critical for such applications that good quality daily weather data for few years is available for the target locations.

Simulating the entire process of outcrossing which involves flower opening, anthesis, pollen dispersal, pollination, fertilization and survival of the young seed (embryo) may not be easy to accomplish at this stage, in view of the limited knowledge available about many of the mechanisms involved.

Predicting crop's behaviour from single plant data

An important activity of a breeding programme is to reject/select plants from spaced segregating populations. Breeders use their own judgement to relate the performance of the spaced plants to that in a population. Crop models that are sensitive to crop geometry may be able to predict the performance of spaced plants when grown in a community. However, these models should be able to predict the effect of different spacings (competition) on the crop geometry. Several such models are now available. However, the major limitation in using them in the breeding context is that there is very limited plant material available for determining physiological model inputs. The later often requires destructive plant sampling (such as for estimating partitioning coefficients). Only morphological parameters such as early seedling vigour, canopy architecture, days to 50% flowering, crop duration, plant height, numbers of tillers, panicles and spikelets per panicle, and grain type are conventionally recorded in plant breeding trials. In addition, the number of segregating plants (or families of plants) may be just too many to parameterize and simulate. There is a need to develop methodology to cluster them into groups.

Breeding for non-optimal environments

Actual yields are often much lower than potential yields because of insufficient availability of growth-limiting resources to the crop (water and/or nutrients, mainly nitrogen) and growth reduction by insects, diseases and weeds. In these situations, the system is much more complex. Because different processes may be more important in various production situations, new plant type designs have to be developed for a specific production environment. In situations where there is a considerable yield gap, it might be more efficient to first identify the major constraints and management strategies to improve the resource-use efficiency for the limiting factors or to reduce pest effects before designing new crop ideotypes, so that the breeding effort, which is a long term investment, can be focused on the major problems that cannot be solved by improved management. Crop models can greatly facilitate the identification of critical yield limiting factors. Quantitative understanding of the impact of limiting resource on crop yield on the basis of the effects on the different processes through crop models can be instrumental in targeting genotypes to different environments. Breeding for traits in resource limiting environments may often have compensatory effects on yield potential. It should be possible to design better plant types for these environments as well following the framework shown in Fig. 1 and considering various feedbacks.

Muchow & Carberry (1993) conducted a detailed simulation study for evaluating the performance of several crops (sorghum, maize and kenaf) in the semi-arid tropics in Australia. They showed the great advantage of using models for the evaluation of plant types in extremely variable environments with respect to drought. They simulated yield probabilities for different plant types in different environments using many years of weather data. Their results indicated that the choice of plant type depends on the attitude to risk. For example, an earlier maturing variety improved yields in lower yielding years, and increased yield stability, but the variety performed less in higher yielding years. This analysis shows that well validated models can help fine tune variety design and selection based on long term yield assessments, whereas conventional agronomic evaluation would require enormous investments in time and money.

Another example is the design of genotypes that have a higher competitive ability versus weeds. An ecophysiological simulation model for interplant competition was used to identify traits that determine the competitive ability of a crop (Kropff & van Laar, 1993). The most important traits were: rapid early leaf area development, number of tillers and plant height, and more horizontally oriented leaves in early growth stages (vertical ones later on because of yield potential. In experiments, rice varieties that differed in these traits were evaluated with respect to their competitive ability versus a standard purple coloured variety. The variety with all required traits, Mahsuri, reduced the growth of the purple variety so much, that all purple rice plants died before the final harvest (Kropff, unpublished results).

Conclusions

A number of opportunities are available for greater integration of inter-disciplinary knowledge into plant breeding programmes. The key areas are - design and evaluation of plant types for specific environments, increasing the efficiency of multi-location testing and in hybrid seed production programmes. Preliminary examples of exploiting these opportunities are gradually becoming available. Crop models may need more development for application in other activities of plant breeding such as selection among segregating populations. There is a need to strengthen research programmes involving plant breeders, physiologists, and crop modellers for illustrating these possible applications. Simultaneously, user-friendly interface programmes should be developed for the use of breeders and other non-modellers to allow greater integration of systems approach in plant breeding.

References

Aggarwal, P.K., 1991. Estimation of the optimal duration of wheat crops in rice-wheat cropping systems by crop growth simulation. In: F.W.T. Penning de Vries, H.H. van Laar & M.J. Kropff (Eds), Simulation and systems analysis for rice production. Pudoc, Wageningen, The Netherlands, pp. 3-10.

Aggarwal, P.K., 1995. Plant type designs for increasing yield potential of irrigated rice - a simulation analysis. This volume.

Aggarwal, P.K., R.B. Matthews & M.J. Kropff, 1995a. A framework for applications of crop simulation models in plant breeding. This volume.

Aggarwal, P.K., M.J. Kropff, R.B. Matthews & C.G. McLaren, 1995b. Using simulation models to design new plant types and to analyse genotype and environment interactions. In: M. Cooper & G. Hammer (Eds), The analysis and exploitation of plant adaptation in agricultural crop improvement programs. CAB, Wallingford (in press).

Berge, H.F.M. ten, M.J. Kropff & M.C.S. Wopereis, 1994. The SARP Project, Phase III (1992 - 1995). Overview, goals, plans. SARP Research Proceedings, IRRI, Los Baños, AB-DLO, TPE-WAU, Wageningen, 124 pp.

Bouman, B.A.M. & M.J.W. Jansen, 1993. RIGAUS: Random input generator for the analysis of uncertainty in simulation. CABO-TPE Simulation Reports no 34, 26 pp.

Chaudhary, R.C., 1995. Global evaluation of rice germplasm through INGER - expectations from crop modelling. This volume.

Dingkuhn, M., F.W.T. Penning de Vries, S.K. De Datta & H.H. van Laar, 1991. Concept for a new plant type for direct seeded flooded tropical rice. In: Direct seeded flooded rice in the tropics. Selected papers from the International Rice Research Conference, 27-31 August 1990, Seoul, Korea. International Rice Res. Inst., Los Baños, Philippines, pp. 17-38.

Dionora, M.J.A. & M.J. Kropff, 1995. Variation in the rate and duration of grainfilling in rice varieties. This volume.

Elings, A., 1995. The application of crop growth simulation in evaluation of large plant germplasm collections. This volume.

Hunt, L.A., 1993. Designing improved plant types: a breeder's viewpoint. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 3-17.

Hunt, L.A., S. Pararajasingham, J.W. Jones, G. Hoogenboom, D.T. Inamura & R.M. Ogoshi, 1993. GENCALC: Software to facilitate the use of crop models for analyzing field experiments. Agron. Journ. 85: 1090-1094.

Jordan, W.R., W.A. Dugas & P.J. Shouse, 1983. Strategies for crop improvement for drought-prone regions. Agric. Water Manage. 7: 282-299.

Khush, G.S., S.S. Virmani & P.K. Aggarwal, 1995. Expectations of plant breeders from crop physiology and modelling. This volume.

Kropff, M.J., H.H. van Laar & R.B. Matthews (Eds), 1994a. ORYZA1, an ecophysiological model for irrigated rice production. SARP Research Proceedings, IRRI, Los Baños, and

AB-DLO and TPE-WAU, Wageningen, 110 pp.

Kropff, M.J., S. Peng, T.L. Setter, R.B. Matthews & K.G. Cassman, 1994b. Quantitative understanding of rice yield potential. In: K.G. Cassman (Ed.), Breaking the yield barrier: Proceedings of a workshop on rice yield potential in favorable environments, International Rice Research Institute, Philippines, pp. 5-20.

Kropff, M.J. & H.H. van Laar (Eds), 1993. Modelling crop-weed interactions. CAB, Wallingford and IRRI, Los Baños, 269 pp.

Marshall, D.R., 1991. Alternative approaches and perspectives in breeding for higher yields. Field Crops Res. 26: 171-190.

McLaren, C.G., 1995. Combining statistics and crop models for improved plant breeding strategies. This volume.

Muchow, R.C. & P.S. Carberry, 1993. Designing plant types for the semiarid tropics: agronomists' viewpoint. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 37-61.

Palanisamy, S., F.W.T. Penning de Vries, S. Mohandass, T.M. Thiyagarajan & A.A. Kareem, 1993. Simulation in pre-testing of rice genotypes in Tamil Nadu. In: F.W.T. Penning de Vries, P.S. Teng & K. Metselaar (Eds), Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 63-75.

Palanisamy, S., P.K. Aggarwal, T.M. Thiyagarajan & T.B. Ranganathan, 1995. Simulating yield and ranking of rice genotypes in multi-location trials. This volume.

Penning de Vries, F.W.T., 1991. Improving yields: designing and testing VHYVs. In: Systems simulation at IRRI. IRRI Research Paper Series, November 1991, Number 151, pp. 13-19.

Penning de Vries, F.W.T., P.S. Teng & K. Metselaar (Eds), 1993. Systems approaches for agricultural development. Kluwer Academic Publishers, Dordrecht, The Netherlands, 542 pp.

Shorter, R., R.J. Lawn & G.L. Hammer, 1988. Improving genotypic adaptation in crops - a role for breeders, physiologists and modellers. Exp. Agric. 27: 155-175.

Sutoro & A.K. Makarim, 1995. Variability in crop physiological inputs used in simulation models of rice. This volume.

Virmani, S.S., G.S. Khush & P.L. Pingali, 1994. Hybrid rice for tropics: potentials, research priorities and policy issues. In: R.S. Paroda & Mangla Rai (Eds), Hybrid research and development needs in major cereals in Asia-Pacific regions. FAO Regional Office, Bangkok, Thailand, pp. 61-86.

Xu, Q., 1995. A model for simulation of hybrid rice seed production. This volume.

Zhu, D., M.J. Kropff, R.B. Matthews & M.J.A. Dionora, 1995. Photosynthesis-light response of rice hybrids and inbreds in field conditions. This volume.