Population Improvement of Pearl Millet and Sorghum: Current Research, Impact and Issues for Implementation

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Abstract

Populations of pearl millet and sorghum are being developed and improved for a variety of purposes. In this paper, we present a global review of current populations, their composition, and methods for improvement. The potential impact of these programs is indicated by recent results regarding responses to recurrent selection and the linkages of population improvement with development of lines and varieties in these two crops. Recent research on generating interpool populations and modeling responses to alternative recurrent selection methods are presented for population improvement of pearl millet.

Population improvement involves the generation of broad-based gene pools and their improvement through recurrent selection. Favorable genes should be concentrated through recurrent selection, resulting in increased mean of the population and superior performance of the best families (Hallauer, 1981). Population improvement provides ample opportunities for recombination after each cycle of selection.

The tandem cycling of selection and recombination is particularly important for improvement of polygenic traits and for simultaneous improvement of several traits (Doggett, 1982). This method could increase the effective use of non-elite source materials, where the greater opportunities for recombination could break linkages between genes for the desired trait and unfavorable agronomic characteristics.

A wide range of methods have been developed for population improvement. Several reviews of these methods (Hallauer, 1981; Hallauer and Miranda, 1988; Simmonds, 1979; Witcombe, in press) are available in the literature. In this paper we will focus specifically on current activities and research pertaining to population improvement in pearl millet and sorghum. This review covers the period from 1986 to 1996.

Pearl Millet and Sorghum Populations and Their Improvement

The diversity of pearl millet and sorghum random-mating populations and the approaches taken for their improvement

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and utilization correspond to the range of economic and adaptive requirements being addressed. A recent review provides a list of pearl millet populations developed by ICRISAT and cooperating National Agricultural Research Systems (NARS) in India and Africa (Rai and Kumar, 1994). We document here the genetic composition and selection history of pearl millet (Appendix 1) and sorghum (Appendix 2) populations currently receiving the greatest efforts world wide or representing the most important populations for a particular region.

Pearl Millet Populations

Population Groups

Pearl millet population development in both the Sahelian and Sudanian Zones of Western Africa has focused on intervarietal crosses, primarily between local landraces and elite varieties. Populations for the Sahelian Zone are earlier maturing (less than 100 days), whereas those for the Sudanian Zone mature in 100-150 days (Appendix 1). Populations for both zones are subjected to selection for grain yield, downy mildew resistance, and resistance to insect pests.

Populations being improved in the Asian region can be classified into three groups (Appendix 1). For the drier areas with less than 400 mm rainfall, early-maturing populations (60-75 days in non-stressed environments) are developed from stress-tolerant local germplasm and inter-population crosses between local germplasm and early-maturing elite germplasm. Selection is for adaptation to northern Indian growing conditions and increased productivity of grain and stover, improved seed set, higher tillering (as a determinant of stover quality and yield stability), and downy mildew resistance. A high proportion of germplasm in these populations originates from India and Pakistan, particularly from the driest millet-growing regions.

Populations for the higher rainfall (greater than 400mm) millet-growing regions in Asia contain larger proportions of African germplasm, ranging from half to primarily African-based, and are later-maturing (75-90 days). Selection pressure is predominantly for increased grain yield, panicle size, and downy mildew resistance. These populations vary in the prevalence of Togo germplasm (Andrews and Kumar, 1996) and in expression of stem, grain, and panicle characteristics of the Bold Seeded Early Composite.

A third group of populations in the Asian region includes those that have broader geographic domains or target environments outside of Asia (Appendix 1). These populations should serve new or emerging demands for early-maturing grain hybrids, population hybrids, and industrial uses.

Populations developed in Nebraska likewise provide source material for developing parents for pearl millet grain-hybrids (Appendix 1).

Selection Methods

The recurrent selection methods used most often to improve the populations in the first two Asian groups are full sib progeny (FSP), S_1 progeny, and S_2 progeny methods (Table 1). The full-sib method offers two advantages: 1) FSPs, being non-inbreds, are less affected by environmental stresses and commonly have lower error variances than inbred progenies (Schipprack, 1993); and 2)

FSPs are generated in the random mating phase in the off-season, enabling completion of one cycle of selection per year in the target environment. This method is particularly useful for populations being improved for adaptation to the heat, moisture deficits, and long photoperiods of northwestern India. However, skilled hand crossing is required to produce adequate numbers of full-sib progenies with sufficient seed quantities for multilocation testing, especially for populations with small panicle size. Multiple pollinations of the same two plants and bulking seed from reciprocal crosses between them has proven useful in producing new full sibs.

The three-stage S_2 progeny-testcross procedure is relatively new, but its advantages may lead to increased use in the future. This method begins with full-sib progeny (FSP_{S2}) selection with intensity of 30% (Table 1). Three hundred to four hundred S_1 progenies (S_1P) generated from selected FSP_{S2}s are initially tested for resistance to downy mildew (20-40% selection intensity) in the greenhouse, and the more resistant progenies are then tested for productivity. Single plants from selected S_1P are selfed and test crossed to one elite male-sterile tester; the resulting S_2 test crosses are evaluated primarily for selfed seed set and pollen fertility restoration in the target environment. This procedure, through greater inbreeding, aims to improve seed set, possibly via elimination of translocations that have poor chromosomal pairing with elite material, and to increase the frequency of restorer alleles in the population for use in development of pollen parents for topcross and single-cross hybrids.

The S_1P selection procedure is occasionally used, primarily where increased resistance to downy mildew is required. A large number (500-800) of S_1P are tested for downy mildew resistance using a modified greenhouse testing procedure (Weltzien and King, 1995). The most resistant progenies are then tested in mul-

Table 1. Most commonly used recurrent selection procedures for pearl millet improvement at ICRISAT Asia Center in collaboration with Indian NARS.

Season	Full-sib procedure	S_1 procedure	S_2 testcross procedure
Rainy season 1	Full-sib progenies (FSP_{S0}) tested in the target environment (TE)	Selfing within half-sib or full-sib progenies in the TE	Full-sib progenies (FSP_{S2}) tested in TE
Off season 1	Random mate selected full-sibs by plant to plant crossing to create new full-sib progenies (FSP_{S0})	S_1 progenies tested in a) downy mildew, and b) off-season drought evaluations	Selfing in selected full-sib progenies, S_1 progenies tested for downy mildew resistance
Rainy season 2		Selected S_1 progenies evaluated for yield in TE	More resistant S_1 progenies evaluated for yield in TE
Off season 2		Random mate selected S_1 progenies by forming half-sib or full-sib progenies	Testcross and self within selected S_1 progenies
Rainy season 3			S_2 progeny testcrosses evaluated in TE
Off season 3			Random mate selected S_2 progenies by forming full-sib progenies (FSP_{S2})

tilocation yield trials in collaboration with breeders from the target environments. This procedure is widely used in populations targeting environments with higher, more reliable rainfall, where S_1P testing is more feasible due to less abiotic stress. More populations can be handled with the two-stage S_1P procedure, as yield evaluations occur only every other year.

Selected populations at ICRISAT (IAC) also are improved by backcrossing to enhance specific traits such as bristles (long awns), yellow or white grain color, photoperiod insensitivity, or male sterility. The advantages of this procedure are outlined in a later section on sorghum.

Sorghum Populations

Diverse breeding objectives and studies on selection methodology are being pursued at several universities in the U.S., focused primarily on grain sorghum populations with temperate adaptation.

Purdue University

An array of populations have been developed at Purdue University (Appendix 2). Also, populations containing 0%, 50%, 75%, or 100% of an elite base population based on 20 elite R-lines were developed to study the relationship between the level of eliteness of the initial populations and the performance of their derivatives (G. Ejeta, 1996, personal communication).

University of Nebraska-Lincoln

At the University of Nebraska-Lincoln (UNL), populations based on earlier B- and R-lines and newly utilized germplasm accessions are being generated for various feed grain quality parameters (high and low rate of *in vitro* starch digestibility, total starch content, and pepsin insoluble nitrogen) (J. Pedersen, 1996, personal communication). Two B populations (D.J. Andrews, 1996, personal communication) and a restorer population (J.D. Eastin, 1996, personal communication) have been recently developed (Appendix 2).

Fort Hays Experiment Station

A series of methodology studies is underway at the Fort Hays Experiment Station of Kansas State University (K. Kofoid, 1996, personal communication). A study of alternative family-based selection procedures is being conducted, continuing selection started in Nebraska in the early 1970s in NP3R and NP5R populations. No differences were found among procedures in NP3R based on predicted gains (Table 2). A study testing the feasibility of gametophytic selection for stress tolerance is underway, with selection pressure induced by holding pollen in pollinating bags for either 45 or 90 minutes prior to pollination. No significant response to selection was observed after two years of evaluation. The feasibility of mass selection for drought tolerance is being tested using plants grown in 5 cm diameter cones in the greenhouse. Water is withheld from 30 days after sowing until a visual assessment of plant death reaches 75-80%. Surviving plants are intermated, and recombined seed is sown in the field at high density (530,000 plants ha^{-1}). Also, the effectiveness of single location, single replicate evaluations of S_1 progeny with augmented designs is being compared with a replicated procedure.

Kansas State University

The major research thrusts in population improvement of sorghum at Kansas State University (KSU) include improvement of grain yield and adaptation to drought stress, animal feed value of grain, and *Fusarium* and charcoal rot resistance (Bramel-Cox, 1996, personal communication). Each of these are summarized below.

Divergent S_1 family selection in the population KP9B is being conducted collaboratively between KSU and UNL with selection under optimal [KP9B(MD)] or drought-stress conditions (KP9B(GC)). The fourth cycle of each selection scheme is underway. Predicted gains (Zavala-Garcia et al., 1992) and realized gains (Maciel, 1995) are reported. Also, the same base population, KP9BC$_0$, was improved for three cycles using a modified full-sib method with multi-location evaluation; selection was based on a rank summation index across locations. Predicted gains from this method have been reported by Chisi et al. (1996).

The improvement of feed value of the grain was pursued in the KP7BC$_0$ population with two separate S_1 selection schemes. One scheme uses protein digestibility via the pepsin digestion technique as the sole criterion [KP7B(DG)], whereas the rank summation for grain yield and protein digestibility was used in the other [KP7B(RS)]. Bramel-Cox et al. (1990) describe these criteria and predicted gains from selection.

Selection for resistance to *Fusarium* and charcoal rot (*Macrophomina phaseolina*) in the KP8BC$_0$ population was conducted for two cycles, using toothpick inoculation, on half-sib families at two locations in Kansas (Bramel-Cox and Claflin, 1989).

ICRISAT Asia Center

An array of populations for long-term improvement of key agronomic traits or trait combinations and resistances to major insect pests are being developed and improved at the ICRISAT Asia Center (IAC), India (Appendix 2).

The Shoot Pest population, for shootfly (*Atherigona soccata*) and stem borer (*Chilo partellus*) resistance, and the Head Pest population, for midge (*Contarinia sorghicola*) and earhead bug (*Calocoris angustatus*) resistance, trace their origins to populations begun in the early 1970s at ICRISAT, India. The earlier shoot pest population was mass selected for shootfly and stem borer resistance for approximately one decade, followed by progeny-based selection in the late 1980s (Agrawal and Taneja, 1989; ICRISAT, 1988). By the beginning of this decade, the Head Pest and Shoot Pest populations had relatively high means but low variances. Thus in 1991 introgression of large numbers of diverse sources of resistance was con-

Table 2. Predicted gains from one cycle of alternative family selection methods, using direct selection with 20% selection intensity in two sorghum populations in Kansas, U.S.

Population	Family	Days to anthesis days	Plant height cm	Grain yield kg ha^{-1}	Test weight kg m^3
NP5R	S1	4.8	11.9	270	19.8
NP3R	S1	3.3	11.6	404	23.5
NP3R	HS	2.0	9.0	150	26.0
NP3R	FS	3.6	10.0	361	24.8

Kofoid, unpublished data

ducted into both populations (Wehmann et al., 1992; Appendix 2). These new populations are heavily based on landrace material of tall stature (greater than 2m), with considerable photoperiod sensitivity and segregation for grain characteristics.

Mass selection has been used extensively at IAC for improvement of the Large Grain, High Tillering (Reddy and Prasada Rao, 1993), Early Dual Purpose, and Guinea Grain Mold populations. The Large Grain and High-Tillering populations are being managed as open populations (Reddy, 1994). These populations have predominantly white grain color, except for the Early Dual-Purpose population which is segregating for grain color and testa.

Progeny-based selection methods have been used to improve the US/R and RS/R populations. Two cycles of S_1 progeny selection for increased grain and stover yield within restricted growth duration were recently completed in the US/R(DP) population (Rattunde, 1994). A modified base index with standardized values for grain, stover yield, early maturity and lodging resistance, weighted by the relative economic weights and estimated heritabilities of each trait, was used for selection. The genetic variation for seedling vigor observed in the US/R(C1) and RS/R(C1) populations (Rattunde, 1992) has been exploited through three cycles of full-sib selection for seedling vigor in each population (Rattunde, 1993).

ICRISAT Southern and Western African Programs

The populations developed by ICRISAT and NARS collaborators in the Southern African region (Appendix 2) target contrasting agro-ecological zones (A.B. Obilana, 1996, personal communication; ICRISAT, 1989). Guinea and Caudatum (J. Chantereau, 1996, personal communication) and Guinea × Caudatum (D.S. Murty, 1996, personal communication) populations are currently being developed in Mali (Appendix 2).

Genetic Gains from Population Improvement

Pearl Millet Response to Selection

Substantial increases for grain yield per se have been obtained through progeny-based recurrent selection in an array of populations in India. Gains of 1.9 to 5.0% per cycle in six populations (Super Serere, New Elite, Inter Varietal, Medium, Early and D2 Composites) selected for two to five cycles were exhibited in 1982 in a multi-location evaluation in India (Pheru Singh et al., 1988). A similar range of gains (0.9 to 4.9%) was exhibited by four composites, selected for three to six cycles, when their cycle bulks were evaluated in India from 11°N to 29°N over three years (Rattunde and Witcombe, 1993). The highly significant gains in grain yield were most closely related to increases in the number of seeds per panicle (Table 3). Ten cycles of *per sé* selection in the Medium Composite resulted in increases in combining ability of 1.2 to 1.8% per cycle, depending on the tester used, as well as a 4.3% per cycle gain in grain yield in the population per se (Witcombe, in press).

Mass selection is expected to be more effective for plant traits that have relatively high heritabilities on a single plant basis such as plant height (h^2=0.58), panicle length (h^2=0.64) and seed mass (h^2=0.52), and less effective for less heritable traits like grain yield (h^2=0.29) (Rattunde et al., 1989). Mass selection for grain yield, when conducted in a single location, can also result in location-specific responses (Rattunde, 1988; Table 4).

Recurrent selection for resistance to downy mildew has proven very effective. Two cycles of progeny selection with a modified glasshouse screening procedure in a highly susceptible population, WRajPop88, significantly reduced downy mildew incidence from 13.4% in Cycle 0 to 1.8% in Cycle 2 bulk (Weltzien R. and King, 1995).

Sorghum Response to Selection

Responses to two cycles of S_1 selection for early-maturing, dual-purpose sorghum in the US/R(DP) population were recently evaluated in India, the country of selection, and under rainfed conditions in the Sudan, an important target environment for short-duration sorghums. Large responses of both grain (13.2%) and stover (16.4%) yields were observed in India while maturity was held constant (Table 5, Rattunde, unpublished data). The yield gains were primarily achieved in the first cycle of selection and were associated with a 1.4 day increase in time to flower in that cycle. Time to flower was reduced to near that of the original population in the second cycle. Estimates of genetic variability remained unchanged over the two cycles of selection for grain yield, but were reduced for stover yield and time to flower (Table 6). The pattern of response observed in Sudan was similar to that observed in India (Table 5, Rattunde and Ibrahim, unpublished data). The results from India and Sudan are noteworthy as both grain and stover yields were increased; total biomass was increased within a constant growth duration; and these gains were expressed over a wide range of soil fertility and climatic conditions.

Responses to two cycles of S_1 family selection in KP9B under drought-stress

Table 3. Means of base (C_0) and most advanced selected population (C_t) from five pearl millet composites evaluated at three locations in India in the 1987 rainy season for six agronomic traits.

Composite and cycle	Grain (kg ha^{-1})	Bloom (days)	Height (cm)	Individual seed mass (mg)	Seeds panicle^{-1}	Panicles m^{-2}
MC C_0	2300	50.3	226	8.86	2160	12.5
MC C_8	3160**	50.9	222	9.41	2590*	12.3
IVC C_0	2550	53.0	242	9.61	2730	9.9
IVC C_6	2660	53.5	225*	8.52*	2540	11.1*
NELC C_0	2140	54.2	210	8.33	2440	11.4
NELC C_5	2880**	54.5	224	8.95	3030**	11.0
SRC C_0	1860	55.3	219	8.50	2190	9.3
SRC C_3	2880**	52.3*	235*	8.79	2640**	11.8**
D2C C_0	2110	51.0	153	8.37	2170	12.2
D2C C_5	2490	50.4	160	8.63	2500	11.3
LSD 0.05	390	2.4	16	0.91	394	1.1

*, ** Significant difference between base and advanced cycle population at $P<0.05$ and $P<0.01$, respectively.
(Rattunde and Witcombe, 1993).

Table 4. Grain yield responses (kg ha^{-1} deviations from unselected bulk) to one cycle of mass selection for grain yield per se and for an index of physiological determinants of grain yield[a] in the pearl millet Early Composite at the location of selection (PAT) in central India (17°N), Northern India (HSR, 29°N), and Southern India (BSR, 11°N).

Selection criteria	Locations		
	PAT	HSR	BSR
Grain yield per se	351*	133	252
Physiol-index	649**	72	-264

[a] Index based on growth rate, growth duration and harvest index.

*, ** denotes significant differences between base and selected population at $P<0.05$ and $P<0.01$, respectively.

(Rattunde, 1988)

Table 5. Progress from S_1 progeny index selection for early dual-purpose sorghum in the US/R (DP) population.

Cycle	Grain (t ha^{-1}) India[a]	Grain (t ha^{-1}) Sudan[b]	Stover (t ha^{-1}) India	Stover (t ha^{-1}) Sudan	Flowering (d) India	Flowering (d) Sudan
Cycle 0	2.77	1.12	4.16	2.04	56.7	65.6
Cycle 1	3.04 (10.0)[c]	1.30 (16.1)	4.96 (19.3)	2.22 (8.8)	58.1 (2.5)	65.2 (-0.6)
Cycle 2	3.13 (13.2)	1.26 (13.0)	4.84 (16.4)	2.06 (1.0)	57.0 (0.6)	63.7 (-2.8)
LSD (P=0.05)	0.05	0.11	0.09	0.18	0.02	0.70

[a] 60 FS per cycle, three fertility environments at Patancheru, India 1994.

[b] 20 FS per cycle in rainfed environment, Wad Medani, Sudan, 1995.

[c] % change from C0.

(Rattunde, Ibrahim, unpublished)

Table 6. Genetic components of variance and their standard errors of US/R (DP) Sorghum Population Cycle 0 and Cycle 2 full-sibs in India.

Cycle	Grain	Stover	Flowering
Cycle 0	9.2±2.36	78.2±15.58	1.2±1.14
Cycle 2	8.8±2.28	48.6±10.82	0.7±1.37

(Rattunde, unpublished data)

[KP9B(GC)] and optimal conditions [KP9B(MD)] in the midwest U.S. have been evaluated in both low- and high-productivity environments. Grain yield gains of 20% from selection under stress were exhibited at both the high- and low-productivity test sites (Table 7, Maciel, 1995). These gains were larger than those obtained by two cycles of selection under more optimal conditions. Also, the grain yields of the ten best families from both selection schemes were distinctly superior to those from the original $KP9BC_0$ (Table 8). The best families from selection under optimal conditions were slightly later flowering and distinctly taller than those selected under stress. Estimates of genetic variance were smaller among the stress-selected $KP9B(GC)C_2$ families as compared to non-stress-selected $KP9B(MD)C_2$ families (Table 7).

Gridded mass selection for individual panicle grain weight in IAP4R in Iowa was shown to have effectively increased grain yield by 2.06% cycle^{-1} over three cycles in this broad-based population (Secrist, 1989; Secrist and Atkins, 1991). Mass selection included initial culling of late flowering plants and resulted in decreased time to flower in the Cycle 3 population, relative to Cycle 0. Four cycles of mass selection for cold tolerance in Purdue Population 9, through natural selection with early spring sowings, increased cold emergence by 2.8% cycle^{-1} (Bacon et al., 1986). Four cycles of gridded mass selection for threshed panicle weight significantly increased grain yield 250 kg ha^{-1} (1.2% of C_0 mean), but resulted in highly significant indirect responses for days to flower (1.6 days) and plant height (9 cm) (Maves and Atkins, 1991). Four cycles of mass selection for increased seed size in IAP3BR(M) significantly increased seed size but decreased grain yield (Kwolek et al., 1986). Six cycles of mass selection for shootfly resistance in the original Shoot Pest population had reduced shootfly deadheart frequency from 71.2% to 58.5% (ICRISAT, 1988). Mass selection was not effective for resistance to stem borer (*Chilo partellus*) (ICRISAT, 1988). Seven cycles of mass selection for white grain color and guinea glume and grain type, initially with mild selection intensity, achieved high frequencies of both in the Guinea × Caudatum Grain Mold population.

Table 7. Grain yield (kg ha^{-1}) and genetic variance (σ^2_g) of the sorghum base-population KP9BC$_0$ and the stress-selected KP9B (GC) C$_2$ and non-stress-selected KP9B (MD) C$_2$ at three high- and three low-productivity test sites in the midwest U.S. in 1993 and 1994.

Test sites	KP9BC$_0$	KP9B (GC) C$_2$	KP9B (MD) C$_2$
Mean grain yield			
High	4763	5699 (20%)	**5446 (14%)**
Low	2742	**3284 (20%)**	3155 (15%)
σ^2_g grain yield			
High	360767	109889	**222218**
Low	305681	**306388**	446478

Bold = "direct" selection
(Maciel, 1995)

Table 8. Means of the top 10 families from the base sorghum population KP9BC$_0$ and the stress-selected KP9B (GC) C$_2$ and non-stress selected KP9B (MD) C$_2$ at three high- and three low-productivity test sites in the midwest U.S. in 1993 and 1994.

	Grain kg ha^{-1}	Flower d	Height cm	Seed number/m^2
High-sites				
KP9BC0	6277	68	110	28607
KP9B (GC) C$_2$	7102	69	109	31729
KP9B (MD) C$_2$	6765	71	117	31398
Low-sites				
KP9BC0	3843	65	113	15699
KP9B (GC) C$_2$	4433	67	112	17684
KP9B (MD) C$_2$	4393	68	120	18407

Bold = "direct" selection
(Maciel, 1995)

Issues in Implementation of Population Improvement

Linking Population Improvement with End-Product Development

The economic benefits of population improvement are ultimately realized when genetic material from these populations is used to develop lines and varieties for cultivation by farmers. The interface between population improvement and end product development has rarely received attention in the literature. In this section we review the methods used in sorghum and pearl millet for exploiting improved populations for end-product development. Also, the conflict between maximizing long-term genetic gains through population improvement and developing agronomically elite finished products will be addressed.

Sorghum

Superior families developed and identified through recurrent selection provide a starting point for line development in sorghum. Traditional pedigree selection methods used during the inbreeding process produce pure lines for direct use as varieties or hybrid parental lines or, more frequently, as improved parental material for advancing pedigree breeding activities. Selection against the male-sterile gene would also be required, but is easily handled by identifying sterile plants at flowering. This approach has been used in the development of lines from S_1 families originating in several populations at Purdue (Ejeta, 1996, personal communication), and in the ongoing derivation of restorer lines and dual-purpose varieties out of the US/R(DP) population at ICRISAT (IAC).

In broad-based populations, genetic variation and potential long-term genetic gains are maximized. However, because these populations tend to have low means for critical agronomic traits, frequencies of elite segregates are low. Thus, lines derived from these populations rarely, if ever, possess the full complement of required agronomic characteristics. These lines would represent improved source material useful in crossing with elite lines.

Elite populations, in contrast, would restrict introduction of undesirable alleles for such traits as height, maturity, fertility reaction, and grain and panicle characteristics during population development. These restrictions would be imposed through limiting introduction into the population as well as culling undesirable agronomic types during random mating. A much higher frequency of elite lines would be derived from such populations. However, the narrow genetic base would limit genetic variation and potential long-term genetic gains if it is used as a closed population.

Additive genetic variation σ^2_A is a function of the number of loci segregating (n), the frequency of favorable (p) and unfavorable alleles (q), and the breeding value α (Falconer, 1981); it can be expressed with the following formula:

$$\sigma^2_A = \Sigma^n 2pq\alpha^2$$

σ^2_A can be increased by increasing either n for the trait of interest or the frequency of p if it is less than 0.5 for the desirable allele. The introduction of new alleles or increasing the frequency of desirable alleles can be achieved by introgression of exotic source materials.

Researchers at KSU are pursuing introgression into elite populations, using population backcrossing, to accommodate the contradictory goals of deriving elite lines and making long-term gains in the source population (Bramel-Cox and Cox, 1989; Menkir et al., 1994a,b). Introgression of the exotic sources at less than 50% of the nuclear genome by backcrossing to the elite population would maintain the eliteness of the population.

Effective introgression using a population backcross approach would require sampling enough plants during backcrossing to retain a maximum diversity of alleles from the exotic source. Also, when new source material is introgressed into a population already improved for that trait, screening at each level of backcrossing would insure retention of more genes for that trait when handling small population sizes. For example, when introducing new greenbug resistance alleles into an existing greenbug-resistant population, the resulting BC_2F_2 can be put directly into a pedigree program. Alternatively, additional random mating can be done to break undesirable linkages prior to line derivation, as is being done for chinchbug resistance at KSU.

This open-population approach with population backcrossing has been applied in the KP9B and KP7B populations at KSU for such diverse objectives as greenbug resistance, grain-nutritional quality, drought tolerance, chinchbug resistance, heterosis, and cold tolerance. Ten R lines from population introgression of a stress tolerant line (IS22253 from Zimbabwe), a Chinese line (258), and a biotype e greenbug-resistant source (IS2388) are expected to be released from Kansas State University this year.

Pearl Millet

Because pearl millet is a cross-pollinated crop, an array of economically viable variety types can be derived from populations. Descriptions of the different end-products and the methods used to derive them from populations are outlined below:

- Use a population directly as an open-pollinated variety (OPV)

Mass selection within a population for more restricted plant type and phenology is a common method of developing OPVs in pearl millet. This approach is exemplified by the development of ICMV155 through a single cycle of mass selection for grain yield and similar plant height, panicle type, and maturity in the NELC population after four cycles of progeny-based selection (Pheru Sing et al., 1994). A modified mass selection method is quite important in India. In this method, Indian program scientists do single plant selection of selfed plants for agronomic type and adaptation in the target environment, and the resulting S_1 progenies are tested at ICRISAT for resistance to downy mildew. The more resistant progenies are recombined to form the experimental variety (Weltzien R. and Hash, 1995).

- Form an OPV from families selected from a population

Varieties can be produced by recombining families selected on performance information obtained during the testing phase of a progeny-based population improvement program. Generally a small number (10 to 15) of full-sib or S_1 families are selected to produce a variety. A series of experimental varieties can be produced by imposing different selection criteria or different weightings for individual selection criteria. The use of selection indices based on standardized trait values has proved useful for this method of variety development. Because these varieties are narrow-based populations, further selection can be done for enhancing critical traits, such as resistance to downy mildew, or for increasing uniformity for a specific plant type. The variety ICTP 8203, developed from five S2 progenies from the Iniadi landrace population is currently being grown on more than 600,000 hectares in the Indian state of Maharashtra (ICRISAT, 1996).

- Develop topcross hybrids

Populations can be used as the pollen parent to produce topcross hybrids. The first topcross hybrid JBH1 was released in India in 1996. Its pollinator was developed from the Bold Seeded Early Composite via test crossing to select for fertility restoration; progeny testing for agronomic type and resistance to downy mildew; and mass selection for uniform maturity. Initial seed production of this hybrid by a public agency in India is already under way. Diverse topcross pollinators (TCPs) are being developed at ICRISAT (IAC) from an elite, medium-maturity population (MC C_{10}) and from earlier-maturing, Indian landrace-based populations (WRajPop, ERajPop, EHiTiP, CZ-IC 416, and LRE 118). The labor and resources required to produce effective TCPs are relatively modest for populations like MC C_{10}, having high frequency of restorer alleles. However, much greater effort is required to develop TCPs from the more landrace-based populations for use in stress-prone environments, due to their low restoration frequency with current male-sterile lines and more frequent fertility restoration problems under heat and drought conditions in the areas of cultivation. TCPs also are narrow-based populations and would be amenable to continued selection for traits such as resistance to ever-evolving downy mildew pathogen populations and time to flower to nick with male-sterile lines.

- Derive inbreds for use as hybrid parents

Pedigree breeding methods can be used to develop inbred pollen and seed parents from population-derived progenies. Several pearl millet populations have been developed specifically as source material for deriving either pollen or seed parental lines (Appendix 1). The Extra Early R and Extra Early B Composites were constituted by selecting for the non-Togo phenotype in the former and the Togo phenotype in the latter, to develop genetically distinct and heterotic gene pools. The S_2 test cross procedure (Table 1) is well-suited for identification of potential restorer lines.

Open-pollinated varieties (OPVs) play a very important role in Indian farming systems. The cultivation of hybrids is increasing in some areas (ICRISAT, 1996), yet OPVs will continue to play an important role because their broader genetic base contributes to more durable downy mildew resistance; their longer period of pollen shedding reduces risks of ergot and smut; and the grain yields of the best released OPVs usually are on par with the best released single-cross hybrids [the All-India Coordinated Pearl Millet Improvement Project (AICPMIP) advanced variety and hybrid trial results, 1993-1996].

Collaboration between national program scientists operating in the target environment and scientists with more regional or international focus, such as those at ICRISAT, can be very effective for developing finished products from populations (Weltzien R. and Hash, 1995). Opportunities for collaboration include such activities as identification of population bulks for use as source material; formation of test units; evaluation / selection of test units; and recombination and production of seed (Weltzien R. and Hash, 1995). The effectiveness and growing importance of these efforts is indicated by the predominance of collaboratively bred varieties submitted for testing in the All India Coordinated Pearl Millet Improvement Program since 1994.

Reciprocal Recurrent Selection of Sorghum and Pearl Millet

Comstock et al. (1949) first suggested the use of population improvement to enhance heterosis between two populations. Reciprocal recurrent selection (RRS) maximizes the genetic divergence between the populations for loci with dominance effects, by basing selection on crosses generated with one parent from each population. This method would be useful for crop species where hybrids are commercially viable and large inter-population heterosis is expected or observed. These conditions are met for both pearl millet and sorghum, but especially for pearl millet. Furthermore, this approach allows integration of long-term and short-term breeding objectives (Eyherabide and Hallauer, 1991).

The use of RRS in sorghum, especially full-sib reciprocal recurrent selection, is hampered by the sterility system used to enable random mating. All crosses (test and selection units) would be generated using a male-sterile as the female for which no selfed seed can be produced. Thus from the selected full-sibs, only the male parents from each cross can be used as recombination units, effectively reducing selection intensity and failing to capture genes from those female parents producing superior crosses.

Reciprocal full-sib selection has been used to improve the sorghum populations KP9BC$_0$ and GTPP7R, a derivative of TP24. 100 to 200 reciprocal full sibs from each population (with that population as male parent) were tested collaboratively by KSU at Garden City and the University of Nuevo Leon in Monterrey, Mexico. The top 15% full sibs were selected from the best stress site, and remnant S$_1$ seed of the male parents was used for recombination. Estimates of genetic variances, heritabilities, and intra-population predicted gains were reported by Chisi (1993). Estimates for the genetic variability and mean were found to be consistently higher in the TP24 × KP9B (TP24 as female) than the KP9B × TP24 reciprocal crosses, suggesting that significant cytoplasmic effects may exist (P. Bramel-Cox, 1996, personal communication).

Generating Inter-Pool Populations of Pearl Millet

Population Diallel Analyses

Crossing populations representing contrasting genetic sources may exploit heterosis, increasing the mean productivity and the genetic variation of the resulting interpool populations. Such population crosses are frequently used in pearl millet population improvement to combine groups of traits and thus increase variability for productivity and adaptation. The choice of parents often is based on knowledge of the performance and specific characteristics of potential parental populations. Knowledge about heterotic patterns among populations could be helpful in choosing parents for making population crosses. Population diallel analyses are designed to allow description of the nature and amount of heterosis generated by population crosses, and should help to identify specific crosses or types of crosses to exploit.

A series of pearl millet population diallels with primary focus on grain yield have been recently conducted in Asia [11 longer duration (Ali, 1996) and ten early-maturing populations (Presterl and Weltzien R., unpublished)], and in Africa [five widely grown improved landraces (Ouendeba et al., 1993) and 11 improved varieties and landraces (ICRISAT, 1992)]. A diallel of five diverse populations also was conducted to study inheritance patterns and methods for improvement of vegetative growth index (Lynch et al., 1995). The early population diallel (Presterl and Weltzien R., unpublished) will be described as an example of this approach using the analysis of Gardner and Eberhart (1966).

Ten early-maturing populations were identified; they varied for yield potential under favorable conditions, adaptation to moisture and heat stress, and yield components such as panicle and grain size and tillering. These populations represented a continuum from local landrace, basically unimproved populations, to highly bred exotic materials, with each having certain merits for the targeted hot, dry millet growing region of northwestern India.

The population cross F_1s and parents were evaluated for three years in multilocation trials in the target region. The results indicated that the F_1 grain yield was determined by both the per se performance of the parental populations and the level of heterosis (Table 9). Heterosis was attributable primarily to specific heterosis of the individual F1 combinations, indicating that the pattern of heterosis was complex. Of the four F1s having the highest grain yields and mid-parent heterosis greater than 20%, two were elite × elite crosses, one an elite × high-tillering landrace cross, and one an elite × high-tillering exotic.

This analysis was useful for describing the level and pattern of heterosis obtainable through formation of interpool populations and for identifying superior populations for further use or improvement. The complex pattern of heterotic expression and the way it was dramatically influenced by the sample of test environments make it difficult, however, to predict more generally which type of populations would combine best.

Farmers' Involvement in Generating Interpool Populations

It is generally assumed that breeders have the full responsibility and comparative advantages over farmers in the choice of germplasm and the breeding activities associated with development of interpool populations (Sperling and Scheidegger, 1996; Ceccarelli et al., 1996). However, experiences in Namibia (Ipinge and Bidinger, 1996, personal communication) and on-farm varietal evaluations in western Rajasthan from 1992 to 1995 (Weltzien R. et al., 1996a) suggest that for a cross-pollinated crop like pearl millet, some farmers are involved in these activities.

Farmers involved in on-farm pearl millet varietal evaluations saved seed of the experimental varieties that possessed specific traits of interest. This seed was most often sown in mixture with their own variety to reduce risk of failure in the event of severe stress. The mixed sowing and cross pollination between the newly selected genetic material and the local material resulted in interpool populations, which farmers have continued to sow in subsequent seasons.

The potential benefits of farmers' involvement in interpool population formation include:

- ample recombination over several seasons
- larger population sizes than are feasible on experiment stations, with greater possible intensity of selection
- reduction in frequency of unadapted genotypes, because both natural selection and farmers' selection operate under the target, albeit variable, environmental conditions (Weltzien R. et al., 1996b)
- breeders' ability to focus more on improvement of traits difficult to select for on a single plant basis (Weltzien R. et al., 1996b; Weltzien R. et al., 1996c).

Table 9. Percent sums of squares among entries and significance of mean squares from a diallel of early-maturing pearl millet populations for grain yield and stover yield in three Rajasthan environments.

Source of variance	Grain yield	Stover yield
Varieties	44 **	45 **
Heterosis	56 **	55
Average	5 **	4 *
Variety	9	6
Specific	42 **	45

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
(Presterl and Weltzien R., unpublished data)

There is ongoing experimentation at ICRISAT (IAC) to quantify the feasibility of involving farmers in developing population crosses and of managing genetic diversity through evaluation of farmer-generated seed stocks.

Modeling Selection Gains from Alternative Recurrent Selection Methods

Completely and rigorously comparing the effectiveness of the many alternative recurrent selection methods and variants for each through field experimentation is extremely difficult, if not impossible. Computer modeling enables comparisons of alternative methods, without the risk of confounding different genetic materials, selection and test sites, selection intensity, and resources used, as would be the case across independently conducted recurrent selection programs. Furthermore, progress with a given method depends on the effectiveness with which resources are allocated.

A rigorous modeling effort was conducted to compare the effectiveness of a series of selection methods that have been or could be expected to be used for population improvement of pearl millet (Schipprack, 1993). The methods include mass selection, half-sib, full-sib, S_1 and S_2 family evaluations, as well as two combined methods, S_1 followed by S_2 family, and full-sib followed by S_1 family selection. All methods were compared at common levels of total labor capacity and rates of inbreeding in the population. The ratios of genotypic, genotypic × environmental and error variances used in modeling were based on estimates of these parameters from population progeny trial data from ICRISAT (IAC). The expected response to selection was estimated as gain in General Combining Ability per year (G(y)) by applying the formula

$$G(y) = i_{(\alpha)}\, p_{xy}\, \sigma_y / Y$$

where $i_{(\alpha)}$ is the intensity of selection, p_{xy} the coefficient of the correlation between the selection and the response criterion (GCA), σ_y the standard deviation of the response criterion, and Y the number of years per cycle.

Modeling was first used to optimize resource allocation within each method for the numbers of progenies, locations, and replications tested, to maximize expected gains from that method under the limitations of resources and maintenance of genetic diversity. The optimal configurations of each method were then compared over a range of available labor capacity.

Major differences were found among the alternative methods for estimated selection gains for head yield per year (Table 10). Compared to the estimated gains from the highest ranked full-sib method, the second to fifth ranked methods achieved only 90%, 75%, 71%, and 50% as much progress. The assumed levels of correlation between per se performance and GCA did influence the relative gains. Under a tighter correlation (0.8), the gains from the selfed progeny methods increased, but these were still only 84% of the gains achieved by the full-sib method. The highest ranking method, when assuming a correlation of 0.8, was the combined full-sib/S_1 family method, whose estimated gains were 6% higher than the full-sib method.

The ranking of methods showed no change over a broad range of labor availability (Figure 1). Only at the lowest labor levels and highest correlation between per se performance and GCA were predicted gains from S_1 line selection greater than for full-sib selection (Figure 2). Also the

Table 10. Selection response per year for pearl millet head yield from alternative recurrent selection procedures optimized for allocation of labor modeled under high (P=0.8) and intermediate (P=0.5) correlations of per se performance with GCA.

	Selection response	
Recurrent selection procedure	P=0.5	P=0.8
Mass selection*	0.22	0.22
Half-sib family*	0.34	0.34
Full-sib family	0.51	0.51
S1 line (one stage)	0.27	0.43
S2 line (one stage)	0.23	0.43
S1 line (two stage)	0.26	0.42
S1 line/S2 line	0.26	0.46
Full-sib/S1 line	0.46	0.55

*S1 lines from S_0 single plants used for recombination.
(W. Schipprack, 1993)

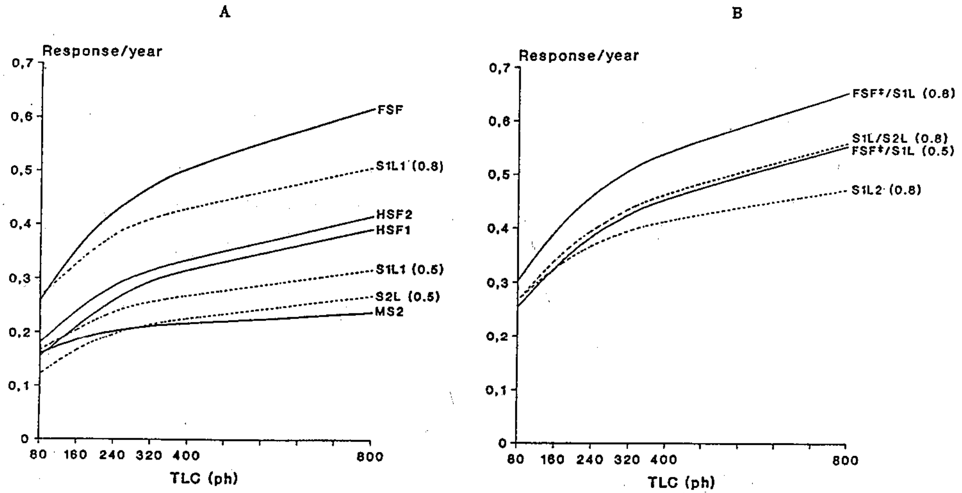

Figure 1. Standardized selection response per year for head yield (HY) expected from alternative RS procedures without preselection as a function of the total labor capacity (TLC) using the standard optimization conditions. Figures in parentheses indicate the coefficient assumed for the correlation between performance per se and GCA of S_1L.
A: one-stage RS procedures. B: two-stage RS procedures. (Schipprack, 1993)

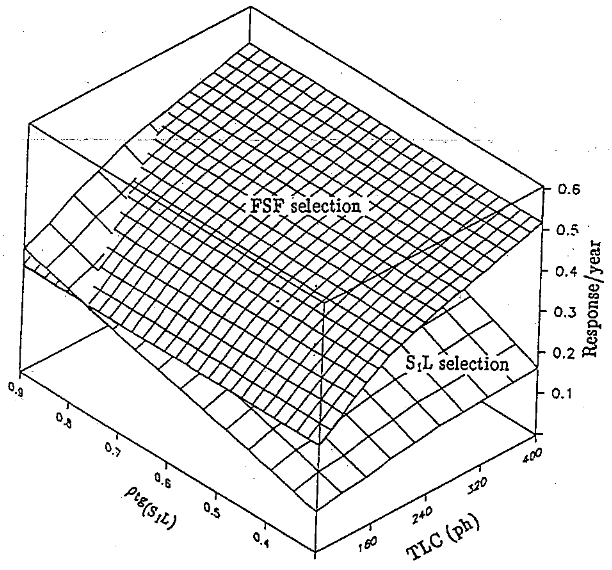

Figure 2. Standardized selection response per year for head yield (HY) expected from FSF and S_1L selection as a function of the total labor capacity per year (TLC) and the correlation between performance per se and GCA of S_1L [$ptg_{(S1L)}$]. (Schipprack, 1993)

ranking of methods was similar across a range of assumed levels of dominance (σ^2_D/σ^2_A ratios of 0.25 to 0.75).

In the past, full-sib selection methods were rarely used at IAC for pearl millet (Pheru Singh et al., 1988; Rattunde and Witcombe, 1993). Schipprack's (1993) results have led to extensive use of full-sib evaluation for yield and agronomic traits in India. His results are based on restricting the rate of inbreeding to 1% per year, which would be appropriate when pursuing long-term population improvement. However, when shorter term goals are pursued, a higher rate of inbreeding would be acceptable and the ranking of the recurrent selection methods may change.

Conclusions

Population improvement of pearl millet and sorghum is currently being conducted with diverse materials and objectives. In the future, population improvement will be an essential breeding tool.

Effective utilization of the tremendous genetic diversity available in these species will be vital for genetic enhancement of productivity and stability of these crops. Population improvement allows more recombination and a larger number of favorable alleles than is possible with the same number of plants handled via pedigree methods. The documented gains in population means and superior families achieved through recurrent selection show the effectiveness of this general approach. In pearl millet, the increased use of populations for development of pollinators, especially top cross pollinators, would contribute greatly to the diversification of hybrids available for cultivation.

The choice of specific methods for population improvement will have important consequences for the gains achieved. Modeling the efficiency of alternative evaluation methods for improvement of pearl millet populations showed more than two-fold differences. The open-population approach with introgression via population backcrossing should improve the source populations within the context of an applied program, especially for sorghum. This method would provide both source material for immediate development of finished products as well as longer-term genetic enhancement required for future gains.

The open-pollinated pearl millet varieties and pure-line sorghum varieties derived from populations can be readily propagated by local seed systems. The impact of population improvement could be greatly enhanced if new ways for interfacing research institutions with local seed systems could be explored and developed. This is especially true for regions and conditions where seed enterprises are currently not providing improved products to farmers.

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Appendix 1. Pearl Millet populations currently being developed, improved or representing the most important populations in a region.

Population	Genetic composition/origin	Selection history/use
Institutions: ICRISAT Sahelian Center, Niger, West African NARS. Target Environments: Sahelian Zone, 300-600 mm rain, 60-100 d maturity.		
Gueriniari Intervarietal Composite (GRGB)	Population cross between Guerguera (Niger) and Iniadi (GB 8735 large seeded Togo type), cross combination identified in population diallel (1989-90), five F_1s, selected from original 36 F_1s between 14 selected full-sibs random mated [1994][a]	2 stage S_1, multilocation
ISC Intervarietal Composite (ISC-851)	Approximately 180 F_1s from intervarietal crosses involving 40 West African improved varieties and prominent landraces [1985]	Random mated (3), 2 stage S_1, multilocation
Long Head Gene Pool (LGHP)	Accessions from Western Niger [1989-90]	Random mated (3), 2 stage S_1, multilocation
Medium Maturing Composite (MMC)	Accessions from Northern Nigeria [1989-90]	Random mated (3), 2 stage S_1, multilocation
Institutions: West African NARS, ICRISAT-Mali Target Environments: Sudanian Zone, 600-900 mm rain, 100-150 d maturity		
ICMC-IS 101	Intervarietal cross between Kapelga, photoperiod-sensitive late cultivar from central Burkina Faso, and GT 79, nearly day-neutral cultivar Iniadi from Togo [1992]	One cycle of recurrent selection completed and derivation of elite lines; currently no active breeding
RP 1004	Intervarietal cross between Kapelga, photoperiod-sensitive late cultivar from central Burkina Faso, and GT 85, nearly day-neutral cultivar Iniadi from Togo [1992]	One cycle of recurrent selection completed and derivation of elite lines; currently no active breeding
Institutions: ICRISAT Asia Center, India, Asian NARS Target Environments: Asia, primarily northwestern India, <400 mm rainfall, very early maturity (60 to 70d under favorable conditions).		
Western Rajasthan population (WRajPop 88)	14 landrace accessions from NW India selected from 155 accessions tested in Rajasthan and Patancheru. [1989]	Random mated (3), selection on differing progeny types (C4)
Early Rajasthan population (ERajPop 91)	30 S_1 lines from 4 selected Western Rajasthan landraces IP 3188 (n=3), IP 3228 (12), IP 3464 (10), IP 3246 (5) [1991]	Random mated (3), full-sib selection (C3), multilocation
Early High Tillering Population (EHiTiP 92)	600 full-sibs, 30 from each of 20 population crosses among 9 populations, ERajPop 91, Early Pakistan Pop, LRE 49 x EC C6, HiTiP 88, HiTiP 89, PakLR74 x EC 89, PakLR74, HiTiP TCP, EC C6 [1992]	Random mated (3), full-sib selection (C2), multilocation
CZP-IC 416	Two interpopulation crosses from the early population diallel; EPDT-5 (EC C6 x LRE 128) (58S), EPDT-41 (Pak LR 74 x EC 89) (41 FS) and EPDT-5 x EPDT-41 (82 FS) [1994]	Random mating (3), C1 of testcross (S_2 lines on 841A for seed setting and fertility restoration
RCB-IC 956 (EC 89)	Population cross of EC C6 with BSEC. [1989]	Random mated (2), two cycles, modified mass selection; mild mass selection for earliness, panicle type in Rajasthan, S_1 selection for DM resistance at IRC
RCB-IC 948	Interpopulation cross of EC II with WRajPop 89, selected from an early-population diallel [1990]	Random mated (3), first cycle of S_1 progeny selection initiated,multilocation
Barmer population	5 Western Rajasthan landrace accessions, collected by NBPGR and ICRISAT in 1992, selected on-station by farmers in a drought year at Jodhpur [1994]	Third random mating being completed
Jakharana	Tall, long panicled, late maturing landrace accession from Sikar district, Rajasthan crossed with ICMV 155, a variety derived from the NELC population [1996]	Third random mating being completed
Target Environments: Asia > 400 mm rainfall, particularly more productive pearl millet growing environments throughout the Indian sub-continent and Pakistan		
New Elite Composite II (NELC II)	Crosses of NELC with progenies from a late-population diallel, predominantly African, non-Togo [1994]	Random mated (3), initiate progeny selection, multilocation, augmented design in 1996

Population	Genetic Composition/Origin	Selection History/Use
Smut Resistant Composite III (SRC III)	Crosses of SRC II with progenies from a late-population diallel, predominantly African, non Togo [1994]	Random mated (3), initiate progeny selection, multilocation, augmented design in 1996
Smut Resistant Composite II (SRC II)	Interpool crossing of Smut Resistant Composite and Intervarietal Composites [1987]	Random mated (3), progeny selection, multilocation, augmented design (C3), propose one more cycle of selection and then terminate
Early Smut Resistant Composite II (ESRC II)	One cycle of MSL in SRC II for earliness, largely African, non-Togo (1988)	Progeny selection, multilocation, augmented design (C3)
Medium Composite 94 (MC 94)	Crosses of elite materials from Medium Composite (C10) with elite Bold Seeded Early Composite materials (ICMV 88908 = Okashana 1), 3/4 African, 1/4 Indian, 50% Togo [1990]	Random mated (3), progeny selection, multilocation, augmented design (C1) emphasize reduced height, large grain size
High Head Volume B Composite (HHVBC)	West African Landraces crossed with elite lines (1990)	Progeny selection at IAC (C4), agronomic type, seed setting under selfing

Target Environments: Broad range of existing or potential production systems

Population	Genetic Composition/Origin	Selection History/Use
Extra Early R Composite (EERC)	Early progenies under extended day-length from broadest range of composite bulks & lines, non-Togo phenotype [1995]	Random mated (4), initiate mass selection in target environment, progeny downy mildew screening, testcross to determine fertility restoration at IAC
Extra Early B Composite (EEBC)	Early progenies under extended day-length from broadest range of composite bulks & lines, Togo phenotype [1992]	Random mated (4), use as source material to derive B lines
SADC White Grain Composite (SADC WGC)	Developed in Zimbabwe from white grained germplasm accessions [1994]	Propose progeny selection, multilocation, augmented design, for grain yield, potential for industrial & food uses
Early Composite II (EC II)	Early Gene Pool, predominantly Indian [1984]	Progeny selection, multilocation, augmented design [C6] for grain yield, medium duration
Dwarf Nigerian Composite (NCD_2)	Nigerian Composite	Test cross selection (C3) for sterility maintenance on A_4 cytoplasm; backcrossing (BC_2) to convert to A_4 cytoplasm; potential female parent for population hybrids, especially for Western Africa

Institution: University of Nebraska-Lincoln, U.S.
Target Environments: Dwarf grain pearl millet growing areas

Population	Genetic Composition/Origin	Selection History/Use
NPM-1 (PI 574382)	14 selfed plants from Nebraska Dwarf Pearl Millet Population progenies selected for large heads, good self fertility, medium maturity (55-65 d to flower) and height (<80 cm) [1985]. Andrews, et al. 1995. Crop Sci. 35:598.	Random mating (1) with mild selection, unreplicated S_1 (1 cycle), gridded mass selection (2 cycles), use as pollinator or source of restorer lines on A_1 cytoplasm.
NPM-2 (PI 574383)	7 selfed plants from Nebraska Dwarf Pearl Millet Population selected for early maturity (<55 d to flower) dwarf (<60 cm) high-tillering plant type with 4 or more erect tillers and good self fertility [1985]. Andrews et al. 1995. Crop Sci. 35:598.	Random mated (1) with mild selection, unreplicated S_1 (1 cycle), gridded mass selection (2 cycles), use as pollinator or source of restorer lines on A_1 cytoplasm
NPM-3 (PI 574544)	9 dwarf inbred lines of diverse origin (from A_1 maintainer breeding program) identified as restorers on A_4 cytoplasm [1992]. D.J. Andrews and J.F. Rajewski. 1995. Crop Sci. 35:1229.	Random mated (2), use as source of pollinators for A_4 cytoplasm

[a] Year of origin

Appendix 2. Sorghum populations currently being developed, improved or representing the most important populations in a region.

Population	Genetic Composition/Origin	Selection methods/ Recombination
Institution: Purdue University, Indiana, U.S. **Target Environments: Temperate grain sorghum areas and areas requiring *Striga* or grain mold resistance.**		
Purdue Population 34		
Purdue Population 35	Early B population developed from 30 B lines	Used for line derivation
Purdue Population 37	*Striga* Resistant population from 20 internationally tested *Striga* resistant lines	Used for line derivation
Purdue Population 40	Mold resistant population from elite mold resistant lines	Used for line derivation
Institution: University of Nebraska - Lincoln, U.S. **Target Environments: Temperate grain sorghum growing areas**		
Nebraska Stress Tolerant Food Quality Population (NP37)	Derived from 2 cycles of S1 progeny selection for drought tolerance in Nebraska/Kansas from Texas Population TP24 [1966][2]	Source of drought tolerant food quality tan plant B lines
Nebraska Early Duration B-Line Population	13 diverse very early maturing B lines from US x tropical food quality introgression program crossed onto sterile F$_2$ plants from cross CK60Bms$_7$ x N122B, and backcrossing B-lines to resulting sterile F$_2$s [1996]	Source for derivation of very early B-lines
Nebraska Medium Duration B-Line Population	26 diverse medium maturing B lines from US x tropical food quality introgression program crossed onto sterile F$_2$ plants from cross CK60Bms$_7$ x N122B, and backcrossing B-lines to resulting sterile F$_2$s [1996]	Source for derivation of medium duration B-lines
Nebraska Population 39 (NP39)	S$_2$ families (n=100) from TP24R selected out of 900 for grain yield and maturity under severe preanthesis drought stress at Garden City, KS [1988]	Random mated (3), use as tan-plant population for US Great Plains

Institution: Kansas State University, Manhattan, Kansas
Target Environments: Temperate dry land grain sorghum areas with unpredictable drought and requirement for early maturity

Population	Genetic Composition/Origin	Selection History/Use
KP7B	First stage: IAP2Bms$_3$ sterile plants crossed with BOK 11, BKS 9, BKS 45, BKS 46, BKS 52, BKS 56, BTx 623 and BTx 625, resulting F$_2$ sample random mated in isolation. Second stage: One sub-population generated by random mating the F$_2$ sample under extreme drought and heat and selecting agronomically desirable male steriles. A second subpopulation generated by crossing unselected F$_2$ and Yellow Endosperm Kafir ms$_3$ steriles as females with BKS 9, BKS 45, BKS 56, BKS 67, BOK 11, BSC 599, B1778, B1887, B4R, BTx 625, BSC 35-6 and BTx 2803, and advancing these F$_1$s to F$_2$. The two subpopulations were bulked in equal quantities and random mated in isolation under moderate drought and heat stress. [1984]	Random mated (>3), 2 cycles S$_1$ selection for protein digestibility or protein digestibility and grain yield. A elite B population
KP8B	Steriles of Yellow Endosperm Kafir ms$_3$ and the first stage F$_2$ population of KP7B were crossed with drought tolerant B lines including BKS 9, BKS 18 BKS 67, BSC 35-6, B1887, BSC 599, BTx 2803, B4R and BTx 625. The F$_1$s were selected for agronomic desirability under drought and heat stress. [1985]	Random mated, 2 cycles half-sib selection for resistance to charcoal rot and *Fusarium*
KP9B	IAP2Bms$_3$ steriles crossed with all B lines used in first stage of developing KP7B as well as BKS 66, BTx 2749, BTx 2752, D. Redlan, 81H2-138, 81H2-242, 81H5-62, 81H5-112, 81H5-218, 81H6-63, 81H6-69, BKS 67, BKS 68 and B7904. The F$_2$ was bulked as the major component, with YE Kafir F$_2$ms$_3$, and random mated under severe drought and heat in 1983, with selection of agronomically desirable sterile and fertile plants. All selections were grown head-to-row under moderate heat and drought and agronomically desirable sterile plants selected in 1984.	Selection using S$_1$, full-sib, reciprocal recurrent selection emphasizing adaptation to dryland conditions. An elite B population that is broader based than KP7B

Institution: ICRISAT Asia Center, Patancheru, India

Target Environments: Dual-purpose sorghums for Asian Post-Rainy Season under declining temperature, stored soil moisture and short day conditions

Population	Genetic Composition/Origin	Selection Methods and Criteria/Use
Large Grain Population (ICSP LGP)	9 large grained landraces were crossed to US/B (C6) and resulting F_1s were crossed to alternative accessions from the same set [1990]	Multiple cycles of single-location mass selection for grain size
Shoot Pest Population	F_2s from crosses among 98 landraces and 17 breeding lines representing diverse sources for shoot fly and/or stem borer resistance were introgressed into the original shoot pest population [1992]	Random mating (3), mass selection for shootfly resistance and adaptation to the post-rainy season (C4)

Target Environments: Grain or dual-purpose sorghum areas in Asian Rainy-Season with 90-120 d growth durations

Population	Genetic Composition/Origin	Selection History/Use
B Population (ICSP B)	10 bold-grain lines, 47 progenies of QL3 x 296B with downy mildew resistance, 5 midge resistant lines, approximately 18 high-yielding B-lines, crossed to male steriles (ms3) of US/B-C6 [1989]	Additional introgression of PS 19349, 296B, M 35-1 with continued mass selection for large, round, lustrous grain, grain number and shootfly resistance
US/R Dual Purpose Population (ICSP US/R (DP))	US/R population composed of converted African materials selected from Purdue Populations PP1, PP3 and PP5 and Nebraska Populations NP4BR, NP5R and NP8, contains ms3 [1975]	Random mation (0), S_1 progeny selection for grain and stover yield, early maturity and lodging resistance. Selection initiated in 1991 with S_1 progenies from the US/R C1 and C2 bulks. Two cycles completed.
Early Dual-Purpose Population (ICSP EDP)	Steriles of 22 S_1 progenies selected in the first cycle of improvement of ICSP US/R (DP) were crossed with landraces (IS 869, IS 8101, IS 19159, IS 20545, IS 22500, IS 23897, IS 24335, IS 24436), breeding lines (IS 18758c-591T, IS 18758c-618), and forage variety HC 260. All materials were chosen based on multi-environment data with selection indices containing grain-, stover-yield and early flowering. [1992]	Random mating (3), mass selection for grain and head characteristics
Head Pest Population (ICSP HP)	F_2s from crosses among 27 landraces and 6 breeding lines representing diverse sources of resistance to head bug and midge were introgressed into a bulk of approximately 100 steriles of the previous Head Pest Population [1992]	Random Mating (3), initiated multi-location (India and Kenya) two-stage (S_1/S_2) progeny testing for midge resistance
High Tillering Population (ICSP HT)	21 early-maturing fast-growth lines and 4 uniculm lines tillering under stress from diverse countries, 2 grain grass lines, 3 sudan grass lines, 2 high-tillering forage lines from SADC/ICRISAT, 7 sweet stalk lines, 3 brown midrib lines, 1 anthracnose and 1 downy mildew resistant line were crossed to male steriles of US/B C6 [1990]	Random mating (3), mass selection for tillering (2 to 3 plant^{-1}) at 35 DAE, large leaves with brown midrib and mild pressure for anthracnose resistance (C3)

Target Environment: Higher rainfall areas (>800mm) in Western and Central Africa

Population	Genetic Composition/Origin	Selection History/Use
(Guinea) Grain Mold Population	A Guinea-Caudatum population was formed by crosses of 35 mold-resistant and 4 susceptible lines to 5 US/R and 12 US/B population derivatives in 1984, and resulting progenies of these crossed with 23 mold resistant, 27 high-yielding and 14 dwarf & early lines in 1987. Introgression of 12 conspicuum types initiated 1996 in parallel to mass selection	Random mating (4), mass selection for white-grain and guinea glume (1990-1993) as well as reduced plant height (1993-1996) and against nodal tillers (1996)

Institutions: SADC/ICRISAT SMIP

Target Environments: Contrasting agro-ecological zones prevalent in Southern Africa

SDSP-Hot/Dry	Based on 4 populations (TP24R04/TP15R05, TP21RB03, 84PP-19M, PP-19) with highest grain yields at Sebele, Botswana and Makaholi, Zimbabwe [1992?]	Random mating (4) with selection; populations made available to regional NARS
SDSP-Cool/Dry	Based on 4 populations (TP24R04/TP15R05, TP8, WAEC3PC82R, KP8B) with highest grain yields at Matopos and Lucydale, Zimbabwe [1992?]	Random mating (4) with selection; populations made available to regional NARS

Population	Genetic Composition/Origin	Selection History/Use
SDSP-Drought Conditions	Based on 4 populations (TP24R04/TP15R05, TP15, TP21RB03, KP9BSO) with highest grain yields at Muzarabani, Zimbabwe and Golden Valley, Zambia [1992?]	Random mating (4) with selection; populations made available to regional NARS
SDSP-Broad Adaptation	Based on 4 populations (TP24R04/TP15R05, TP1RB03, ?, ?) with highest grain yields across all zones	Random mating (4) with selection; populations made available to regional NARS
Institutions: CIRAD/ICRISAT		
Target Environments: Sudanian Zone of Western Africa		
Guinea Population	13 Guinea accessions from West Africa (54-14, 54-36, 64-17, 87-86, Nazongala, Oueni, CSM 282, CSM 335, CSM 382, CSM 485, 87-45, 87-46, 50-8) crossed to ms3 source. One (10 accessions) or two-backcrosses (3 accessions) made to the accessions, with accessions as female in last backcross. BC$_1$F$_2$ (n=10) and BC$_2$F$_2$ (n=3) were bulked. [1994]	Random mating (2) completed in 1996
Caudatum Population	12 Caudatum accessions (IS 2333, IS 2867, IS 3413, IS 3547, IS 8219, IS 8848, IS 23516, CSM 309, CSM 315, Gadiabani, S 8136 from Mali, mostly colored grain and chosen for grain mold resistance) crossed to ms3 source and backcrossed once, using the caudatum accessions as female parents. BC$_1$F$_2$ entries bulked. [1994]	Random mating (2) to be completed in 1996. Intended selection for grain mold resistance
Guinea-Caudatum Population	Selected landraces, improved and adapted high yielding lines and a few resistant sources. [1996]	Random mating with selection to be initiated in 1997

[1] Selection cycles completed.

[2] Year the population was generated.