

Population Breeding Methods in Pearl Millet Improvement (*Pennisetum americanum*)*

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SUMMARY – The population improvement program in pearl millet at ICRISAT is described. The two major methods of selection employed are half-sib and S_1 . The half-sib method is used on less important composites as it is less resource consuming. The S_1 progeny method used employs two-stage progeny testing and is described in detail. Selection for resistance to downy mildew and smut is incorporated into the S_1 progeny testing method. A range of methods has been used at ICRISAT to improve composites. Significant progress for yield has been made in most of the composites. No method has proven to be superior to another, although a strict scientific comparison cannot be made as population size, selection intensity, etc., have not been kept constant across methods and composites. An experiment is described in which four methods of selection were compared in a single composite, with up to six cycles of selection. Response to selection was poor with all methods, and there were no significant differences between the methods. Two cycles of selection using reciprocal recurrent selection were carried out in two pairs of populations. Although the individual performances of the populations improved, there was no improvement in inter-population performance. Comparisons of composite bulks and varieties derived from them are described. The varieties are formed using a higher selection intensity than that used to produce the composite bulk. The varieties from later cycles of the composites were higher yielding than the varieties from the earlier cycles. When single progenies or a number of progenies were used to form varieties, as expected, the multi-progeny varieties outyielded the single progeny varieties as they had less inbreeding depression. The optimum strategy of producing varieties is discussed.

Key words : *Pennisetum americanum*, *Pennisetum glaucum*, pearl millet, recurrent selection, population improvement, progeny testing.

The ICRISAT breeding program for pearl millet has recently been reviewed by ANDREWS *et al.* (1985b) with emphasis on breeding for disease resistance. In this paper we review the use of several population breeding

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methods in pearl millet and report experimental results and the progress that has been made in this breeding program. The two methods of recurrent selection that are currently used at ICRISAT, modified half-sib and S_1 , are described in detail as an aid to any breeder who proposes to adopt recurrent selection methods in pearl millet.

The success of population breeding methods, particularly recurrent selection, in the improvement of maize populations has led to its application in the improvement of other cross-pollinated crops. Although these techniques have been little used in pearl millet, mass selection, and recurrent selection using S_1 testing, have been used in landrace populations in Africa to produce a large number of composites (PETERS *et al.*, 1972 ; LAMBERT, 1983). BURTON (1983) reported on the use of recurrent restricted phenotypic selection in pearl millet at Tifton, Georgia. At ICRISAT, we introduced in 1973 the use of recurrent selection on pearl millet on an extensive scale (ANDREWS *et al.*, 1982).

In recurrent selection, in contrast to classical pedigree breeding, large amounts of genetic variability can be readily created by hybridization between many parents. This variability can be maintained in a population, by the use of recurrent intermating, whilst the population is improved by selection. This allows repeated opportunities for selection and recombination, and transgressive segregation. The most important aspects of a successful recurrent selection program are the choice of parents, to form a base population with a large amount of desirable genetic variability, and the use of a suitable selection procedure.

Formation and selection of composites

Pearl millet composites at ICRISAT have been formed by random mating a large number of selected genotypes (37 to 230) originating from diverse sources in Africa and India. Three or four generations of random mating generated highly variable composites which were

subjected to different selection procedures (S_1 , S_2 , full-sib, and half-sib). All these methods involve the testing of progenies with the selection and recombination of those which prove superior. Currently we use two breeding methods: S_1 progeny selection (2 years or 3 seasons per cycle) and a modified half-sib method (1 year or 2 seasons per cycle).

Downy mildew (*Sclerospora graminicola* (Sacc.) Schroet.) is the major disease of pearl millet and it causes severe grain yield losses. Screening for downy mildew resistance is regularly done by growing the progenies in the downy mildew nursery under high disease pressure at both the progeny testing and recombination stages in each cycle in the S_1 method, and at the recombination stage in the half-sib. Screening for smut (*Tolyposporium penicillariae* Bref.) and recently for rust (*Puccinia penniseti* Zimm.) is also done, but only in a few selected composites. Higher-yielding, disease-resistant progenies, with acceptable agronomic characteristics, are random mated to produce the population for the next cycle of selection. A few of these very high-yielding, disease-resistant progenies are selected and random mated to produce disease-resistant, high-yielding varieties. In general, selection intensities of 20 to 25 % (about 50 progenies) are applied for advancing the composite to the next cycle, and intensities of 2-4 % (about 5 to 9 progenies) for selecting the parents of varieties.

The yield of the varieties depends on the genetic advance made in the composites during recurrent selection, and the efficiency with which the varieties are selected from the composites.

Initially, nineteen composites were advanced under recurrent selection during the course of the population breeding program, but this has been progressively reduced, as individual composites have either been dropped or merged. Eight composites are currently being improved; each composite is maintained with a specific region or characteristic in view. The varieties or inbred lines derived from them will, therefore, differ

markedly in their characteristics and will be suitable for different regions or purposes. For example, the Early Composite can be used as a source of pollinators for the breeding of hybrids for areas where earliness is an important trait. Composites which are late in maturity, such as the New Elite and Inter Varietal composites, are good sources of parental material for varieties adapted to the southern region of India.

Genetic gains from recurrent selection

Composite bulks resulting from different cycles of selection have been evaluated in trials to determine the progress made over cycles of selection. Different cycle bulks of six composites were tested in a trial conducted at three locations in the 1982 rainy season (Table I). The results of the comparison of the C_0 and advanced cycle bulks indicated gains per cycle for grain yield from 1.8 % in the Super Serere Composite to 5.0% in the D_2 Composite. SPRAGUE and EBERHART (1977) reported that in maize, gains of 2.0 to 4.6 % were obtained by different workers using various methods.

Resistance to downy mildew in all the six composites also improved, although the relative difference in the initial and advanced cycles were small due to the initially high level of resistance of the composites (Table I). Plant height and maturity did not change markedly because mild selection pressure was applied for these traits; only extremely late or tall progenies were discarded during the selection program.

Although no rigorous comparison between methods of selection can be made as e.g. selection intensities, population size, and genetic variances were not constant, no method proved to be superior in practice in gains per year (Figure 1).

The erratic performance of the Super Serere Composite was because selection was not only for yield but for bristledness, and bristled plants were often lower-yielding than the non-bristled. When the Super Serere Composite is excluded, in most cycles, in all

Table I Effect of recurrent selection on various characters in six pearl millet composites.

Composite	No. of cycles	Grain yield (1) (kg/ha)				Gain per cycle (2)		
		Cycle		SE of mean	Gain (2) (%)	Time to (1) 50 % bloom (d)	Plant (1) height (cm)	Downy (3) mildew (%)
		C_0	Latest					
Super Serere (SSC)	5	1930	2300	±109	1.9	-0.1	-0.2	-0.2
New Elite (NELC)	3	2360	2570	± 75	2.6	0.2	-0.1	-0.5
Inter Varietal (IVC)	4	2110	2390	± 77	1.9	-0.4	-2.0	-0.1
Medium (MC)	5	1880	2280	± 72	3.2	-0.5	-1.7	-0.2
Early (EC)	4	1890	2260	±109	4.1	0.6	1.0	-0.3
D_2 (D_2C)	2	1970	2270	± 93	5.0	0.3	0.8	-1.3
SE						±0.3	±0.5	±1.0

(1) Grain yield, time to 50% bloom and plant height from mean of three locations.

(2) Gains per cycle (%) for grain yield calculated from regression analysis.

(3) From downy mildew nursery, ICRISAT Center, Patancheru.

composites, a positive advance is made. Indeed, in only NELC and IVC, in one cycle, no advance was made.

Comparison of recurrent selection methods

There are many recurrent selection methods which may involve test crossing, progeny testing or phenotypic selection of individual plants. These are described by SPRAGUE (1966). We have compared two selection methods that use progeny testing (full-sib and S_2) and

two methods based on individual plant selection, gridded mass selection (GMS) and recurrent restricted phenotypic selection (RRPS). GMS was proposed by GARDNER (1961), and RRPS by BURTON (1974). S_2 progeny selection takes 2 years (4 crop seasons) per cycle while the other methods take one year per cycle (2 crop seasons for full-sib and one season for RRPS and GMS).

The selection methods were conducted for six years on the World Composite, which was constituted at Ahmadu Bello University in Nigeria. Three cycles of S_2 selections and 6 cycles of the other selection methods have been completed. S_2 and full-sib selection involved replicated yield trials using time to 50 % bloom, plant height and head weight as additional selection criteria but without the use of a formal selection index. RRPS and GMS involved visual phenotypic assessments of the above characters on a single, spaced-plant basis.

About 225 S_2 or full-sib progenies were tested in each cycle, and 10 % of the highest-yielding progenies, of desirable height and maturity, were recombined in each cycle. In RRPS and GMS, 2 000 hills were planted (20 cm \times 75 cm spacing) and divided into 20 equal grids. From each grid, the best 10 % of the plants (10 plants/grid) were selected; for RRPS, each plant was used as both the female and pollen parent and in GMS the population was grown in isolation and open-pollinated seeds were harvested.

The original composite bulk was compared with the various advanced-cycle bulks developed from these methods in the rainy season of 1982 at ICRISAT Center. No significant differences were observed among bulks for any of the characters which formed the selection criteria (Table II). Apart from RRPS, in which selection

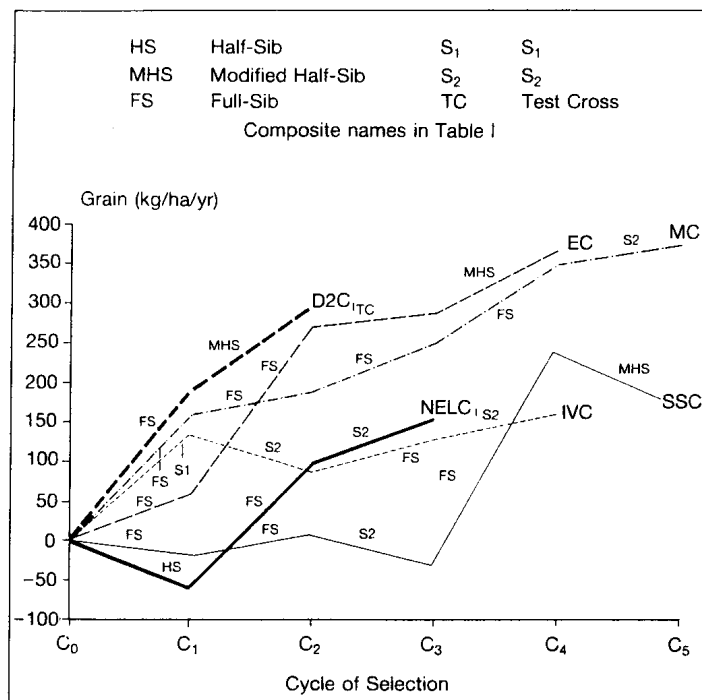


Figure 1 : Gain in six composites for grain yield over cycles of selection using six selection methods

Table II Changes in grain yield, plant height and time to 50% bloom in World Composite cycle bulks under various selection methods, compared at ICRISAT, 1982 rainy season.

Character	Breeding method	Cycle Bulk							Genetic advance per year (%)
		C ₀	C ₁	C ₂	C ₃	C ₄	C ₅	C ₆	
Grain yield (kg/ha) (1)	S_2	2300	2600	2400	2500	-	-	-	0.9
	FS	2300	2500	2400	2400	2300	2300	2600	0.6
	GMS	2300	2200	2400	2200	2400	2300	2400	0.8
	RRPS	2300	2200	2300	2300	2200	2300	2200	-0.3
Plant height (cm) (2)	S_2	200	203	199	203	-	-	-	0.1
	FS	200	200	196	198	191	185	193	-0.1
	GMS	200	198	198	191	197	195	205	0.1
	RRPS	200	192	197	194	194	196	193	-0.3
Time to 50% bloom (d) (3)	S_2	48	52	52	49	-	-	-	0.3
	FS	48	49	48	49	48	45	44	-1.5
	GMS	48	47	48	47	50	48	51	1.0
	RRPS	48	50	48	48	51	50	49	0.5

(1) $SE \pm 97$, CV 10.3%

(2) $SE \pm 3.4$, CV 4.2%

(3) $SE \pm 0.5$, CV 2.3%

for individual plants were made on preflowering characteristics, all the methods were equally effective in slightly increasing the grain yield at the rate of 0.6-0.9 % per year.

Plant height remained practically unchanged over the cycles, except for full-sib selection which was effective in reducing it. The full-sib method was also effective in selecting for earliness. For GMS selection, there was a change towards lateness which is expected, for visual selection was done at harvest and tended to favour late-maturing plants which look more promising at that time than the early ones.

These results need to be treated with caution as they are based on one year's data. Nevertheless, this study, and the results presented in Figure 1, lead to conclusions similar to those drawn from experiments on recurrent selection methods in maize, that it is difficult to determine if selection methods differ significantly in their efficiency (GENTER and EBERHART, 1974). In fact, it is the breeding objective and resources available which are more important in determining the application of a particular method.

Other Recurrent Selection Methods

Reciprocal full-sib recurrent selection, as described by HALLAUER (1973), was carried out on two pairs of populations. Results from two cycles of selection indicated that it was effective in improving the performance of the populations, *per se*, but ineffective in improving the level of inter-population performance. This is perhaps expected in a crop which has undergone little breeding work and in which there is preponderantly additive genetic variation. Recurrent selection for specific combining ability to an established male-sterile line, 81A (ICMA 1), is being tried and results, so far, are encouraging.

The modified half-sib and S_1 methods used at ICRISAT

On the basis of the above results, published experimental evidence on maize, and our own experience it was concluded that the choice of method was less important than the way in which the method is carried out. Consequently, considerable thought has gone into the modified half-sib and S_1 methods adopted, and these have been revised in the light of the results obtained. We use the half-sib method because it is faster per cycle and much less resource-consuming than the S_1 method. The S_1 selection system is used only on the highest yielding composites on which we place greater emphasis, and on those composites where disease resistance is particularly important (e.g. the Smut Resistant Composite).

Modified half-sib selection

The method first outlined in ANDREWS *et al.* (1982) has various important features which distinguish it from a normal half-sib system.

To improve selection efficiency, the method employs gridded mass selection of half-sib families. To reduce the amount of inbreeding in the second and subsequent cycles, an equal number of half-sib progenies are taken from each progeny that was selected for recombination.

Selection is carried out within the half-sib rows. To increase the efficiency of within-row selection, the plants are spaced 30 cm apart to give improved phenotypic expression, and selfed plants are selected to control both the female and male parent. About 5 of the best selfed plants are selected from each selected row; a smaller number than five was found to reduce the reliability of the selection response.

• Cycle 1 – First season: the generation of half-sibs

From a random-mated population, 540 visually-selected plants are harvested. The progenies of these plants are half-sib families and are grown in 27 grid blocks by randomly allotting twenty half-sib families per grid. The intra-row plant spacing is 30 cm and the row length is 9 m. In this way, at the rate of 30 plants per half-sib row, 16 200 plants are grown.

After eliminating poor rows, eight to ten selected plants are selfed in the remaining half-sib rows. At the time of harvest, on the basis of the yield of the half-sib rows and a visual assessment of the individual plants, four to five, superior, selfed plants from the best two half-sib rows in each of the 27 grids are selected.

– Second season: random-mating

The selfed seed of the selected plants from the 54 selected progenies, bulked on a progeny basis, are random mated in isolation or through manual pollination.

After random mating, ten half-sib plants are selected from each of the random mated progenies and grown in the same fashion to initiate the next cycle. In this manner, inbreeding is minimized as all 54 selected progenies are represented in the next generation.

– Formation of varieties

About 200 of the best selfed plants are selected from the better half-sib progenies. The S_1 progenies of these are evaluated in the following crop season in a replicated trial and the superior ones are recombined to make varieties. Some of the superior S_1 progenies are also introgressed into the population at the next random mating.

S_1 selection

Formation, evaluation and random mating of the selected progenies are the three essential steps of the S_1 selection scheme. A minimum of three crop seasons are required to complete one cycle. With a system of two crops per year, one cycle is completed in two years, but at ICRISAT we have adopted an extra season of S_1 testing and use four crop seasons in one cycle.

It could be argued that if four seasons per cycle are to be used, then, S_2 selection will be superior to S_1 selection. Theoretically, S_2 selection is advantageous as the genetic variance between S_2 lines is greater than that between S_1 lines. However, there are also disadvantages in that, in S_2 selection, there is almost no non-additive variation, so S_2 selection can improve populations as selfed bulks better than as random mating populations (HORNER *et al.*, 1969). In S_2 selection, a limited number of S_2 families can be tested in a replicated trial. Therefore, either a limited number of S_1 lines are selected and several plants are selected from each, or more S_1 lines are selected but only a single plant is selected from each. In our opinion, both strategies are unreliable. We are aware that, in the first case, data from a single season, single location trial in the off season is such a poor predictor of yield in the main season that it does not justify a very high selection intensity between the S_1 families. In the second case, selecting single plants from a progeny row is unreliable as again the selection of the progeny rows in the off season is unreliable and there is a high probability of selecting single plants which give poor S_2 progenies. For the above reasons, the more accurate selection that is possible between S_2 lines due to the greater genetic variance between them is less advantageous than theoretically supposed.

We have adopted an S_1 system with a two-stage selection procedure. The first season test is used to apply a relatively low selection intensity by discarding about half the S_1 lines, and in the next season the test on the remaining lines (planted from remnant seed) is replicated and multilocal. Selection takes into account the pedigree of the S_1 lines, that is, the performance of sister S_1 lines and the parental half-sibs. Moreover, the method still permits the selection of selfed, disease-resistant plants from the selected S_1 progenies in a downy mildew nursery.

- Cycle 1 – 1st season: the half-sib generation

From a population which has undergone three to four generations of random mating, about 700-900 open-pollinated plants are selected. The progenies of these plants, which are half-sib families, are grown head-to-row in an unreplicated fashion in the main crop season (the rainy season). After rejection of a small proportion of the half-sib rows, four to five good plants are selected and selfed in each row. At the time of harvesting, better selfed heads from the better half-sib rows are harvested.

- Cycle 1 – 2nd season: preliminary evaluation of S_1 progenies

In the following off season (summer season), 600-700 S_1 progenies are grown at one location, ICRISAT Center, in a replicated trial with single row plots. On the basis of grain yield, maturity and other characters, the 250-300 best S_1 progenies are selected, taking into account the performance of their sister S_1 lines.

- Cycle 1 – 3rd season: final evaluation of S_1 progenies

Using remnant S_1 seed, all the 250-300 selected S_1 progenies are evaluated in multilocal trials, with

three replications and one row-plots. Usually, three locations are used. The same set of progenies is screened for downy mildew, smut and rust resistance in disease nurseries under high disease pressure.

Finally, on the basis of yield and disease resistance, the 50-60 best performing progenies are identified and selected, taking into account the performance of the half-sib family from which they were derived. The selfed, bulk seed of downy mildew-resistant plants from the selected S_1 progenies, obtained from the downy mildew nursery, is used for recombination in the next cycle. Similarly, 10-15 very high-yielding, disease-resistant progenies are also selected as potential parents of varieties, again using pedigree data. Their bulk, selfed seed is also obtained from the downy mildew nursery.

- Cycle 1 - 4th season: random mating

The 50-60 high-yielding, disease-resistant progenies (which are now the S_2 bulks of the selected S_1 's) are random mated in a crossing block. In the crossing block, generally equal numbers of rows of each progeny are planted, and more or less equal amounts of pollen are collected from each progeny and crossed to equal numbers of plants in each progeny.

After random mating, 750-900 good plants are selected and grown as half-sib rows to initiate the next cycle. To reduce the level of inbreeding, equal numbers of plants (about 15) from each recombined S_1 line are selected.

- Formation of varieties :

In each cycle very high-yielding, disease-resistant S_1 progenies are identified and grouped on the basis of their performance in single locations and across locations. Five to nine selected progenies, selected on the basis of both specific and general adaptation, are crossed among themselves to generate multi-progeny varieties which are evaluated in multilocal trials. Some of the highest yielding progenies are sib-multiplied to produce single-progeny varieties.

Loss of genetic variation in recurrent selected population

SURESH BABU (1981) studied the effects of three cycles of full-sib recurrent selection on genetic variation for various characters in the Medium Composite. One hundred random S_1 progenies derived from the bulks of each of the four cycles of recurrent selection were evaluated at ICRISAT Center in 1980. The between progeny variance, which is the major proportion of variability in S_1 lines, was significant in each bulk for all the characters studied (Table III). Except for grain yield, where the magnitude of variation fluctuated over cycles, there was indication of a decline in genetic variance for height, ear-length and time to bloom.

Table III Estimates of genetic variance due to test entry ($\sigma^2 g$) and genotype coefficient of variation (gcv) for grain yield, plant height, time to 50 % bloom, ear length in various cycles of the Medium composite, compared at ICRISAT, 1980 rainy season (Suresh Babu, 1981).

Character	C_0		C_1		C_2		C_3	
	$\sigma^2 g$	gcv (%)	$\sigma^2 g$	gcv (%)	$\sigma^2 g$	gcv (%)	$\sigma^2 g$	gcv (%)
Grain yield (kg/ha)	45962	21.6	29903	17.5	67571	23.3	39890	18.4
Plant height (cm)	182	8.6	123	7.1	120	6.9	96	6.3
Time to 50 % bloom (d)	14.8	6.9	15.3	7.1	10.0	5.8	9.9	5.9
Ear length (cm)	7.6	12.6	5.6	11.0	5.8	11.1	2.9	8.0

Keeping in view the possibility of a decline in genetic variability, new variability is introduced into the composites at most or all of the recombination generations. Varieties which have performed well in advanced trials that were derived from the previous cycles are regularly included in the recombination generations in their respective composites. Genotypes from sources other than the composites are only included in the crossing block after being selected from a full cycle of progeny testing. In order to test them such genotypes are crossed with the composite by using the bulk pollen of the composite progenies planted for recombination. The progeny of these crosses are half-sibs and these are grown alongside the half-sib progeny rows derived from the random-mating generation of the cycle. If the half-sib of the cross is selected on the basis of its performance, then in the half-sib method selfed plants from it are used in the next recombination generation. In the S_1 method, several S_1 progenies from the selected half-sib row are advanced to the S_1 testing stage. Only S_1 progenies of the crosses that perform as well as the best S_1 progenies of the composite are selected for recombination in the commencement of the next cycle. This method of introgression is conservative, since only half the parentage of the S_1 of a cross chosen for introgression is from the genotype being introgressed, but it ensures that only genotypes that combine very well with the composite can be introgressed.

This introgression means that the elite products of other breeding programs can be safely utilised in the recurrent selection program. This appears to be a sound strategy as most successful pedigree breeding programs exploit crosses between the most elite material currently available.

Formation of varieties

Number of parents

Varieties are formed by recombining lines derived from single composites as described above. Two types of varieties are routinely made and tested; progeny

varieties are produced by sib-mating a single S_1 or S_2 progeny, whilst the majority of the varieties are derived by intermating five to ten S_1 or S_2 progenies. Varieties formed from several progenies are usually superior (Table IV). Thus, although progeny varieties offer the advantage of phenotypic uniformity, this is outweighed by their usually inferior yielding ability. Inbreeding depression in pearl millet is high (RAI *et al.*, 1985) and consequently the superiority of varieties which are less inbred is not surprising.

Selection of parents

The performance of progenies, *per se*, has been the chief criterion in the past for their selection as parents of varieties. A comparison of the selection differential of parental progenies and the actual performance of the resulting varieties suggests that the varieties formed by exerting a high selection differential of the parents may not necessarily be the highest-yielding. There is generally a weak but variable correlation between the selection differentials and the actual performances of the varieties. This may be because performance, *per se*, may not be a good estimation of the combining ability of the parent, or because the yields of the parental lines and the varieties are subject to too much experimental error, or because different numbers of parents give different amounts of inbreeding depression. In the future, it is intended to estimate combining abilities by evaluating the topcross performance of progenies using the parental population as a tester as recommended by LONNQUIST (1968), and to compare combining ability to performance, *per se*, as the selection criterion.

The progenies chosen as parents have been selected on the basis of their performance at single locations or on across-location performance. Varieties chosen on across location performance have in their names the year of selection prefixed by an A, whilst the location name (H for Hisar, P for Patancheru, B for Bhavanisagar) is used for varieties formed from progenies selected on single location performance (Table V). The varieties with parents chosen across location perform better than average, but they are not always the best varieties (Table V).

Table IV Grain yield of single-progeny and multi-progeny (1) varieties tested at four locations in the Advanced Population Variety Trial (APVT) in 1982 and 1983 rainy seasons.

Composite	Grain yield (kg/ha)							
	Single-progeny varieties				Multi-progeny varieties (1)			
	No.	Mean	Min.	Max.	No.	Mean	Min.	Max.
1982								
Inter Varietal	4	2600	2360	2750	2	2590	2550	2630
Medium	1	2490	-	-	1	2540	-	-
Super Serere	1	2470	-	-	1	2520	-	-
Serere Composite I	2	2500	2370	2620	3	2630	2570	2670
WC-C75 (check)		2430				2430		
SE		±90				±90		
1983								
New Elite	4	2590	2270	2740	4	2830	2800	2910
Smut Resistant	2	2510	2370	2630	2	2630	2520	2730
WC-C75 (check)		2530				2430		
SE		±100				±90		

(1) The multi-progeny varieties had a range of 2-7 progenies as parents mean of 5.5.

Table V Comparative performance of varieties derived from initial and advanced cycles of 3 composites, at various locations.

Source composite	Variety	Grain yield (kg/ha)	% of checks (1)	Variety	Grain Yield (kg/ha)	% of checks (1)
Inter Varietal Composite	Varieties from 3rd cycle (2)			Varieties from 5th cycle (4)		
	IVC-H78	1810	118	IVC-P8201	2880	125
	IVC-A78	1770	115	IVC-P8204	2870	123
	IVC-P78	1730	113	IVC-A82	2790	122
	IVC-S78	1700	111	IVC-B8201	2650	115
				IVC-P8206	2600	113
	Checks	1535		IVC-B8202	2560	112
	SE	±74		IVC-P8202	2470	108
				IVC-P8205	2470	108
				IVC-P8203	2460	107
				Checks	2295	
				SE	±100	
	Varieties from 4th cycle (2)			Varieties from 6th cycle (4)		
	MC-H78	1660	108	MC-A82	2780	121
Medium Composite	MC-A78	1530	100	MC-B82	2600	113
	MC-P78	1510	98	MC-P8205	2480	108
	Checks	1535		MC-P8204	2480	108
	SE	±74		MC-P8206	2410	105
				MC-P8202	2360	103
				MC-P8207	2350	102
				MC-P8201	2330	102
				MC-P8203	2280	99
				Checks	2295	
				SE	±100	
New Elite Composite	Varieties from 2nd cycle (3)			Varieties from 4th cycle (4)		
	NELC-A79	2600	109	NELC-P8204	2810	122
	NELC-P79	2490	104	NELC-P8202	2530	110
	NELC-H79	2450	103	NELC-P8201	2460	107
	Checks	2385		Checks	2295	
	SE	±87		SE	±100	

(1) WC-C75 and ICMS 7703. (2) Mean of 7 locations, 1979 rainy season. (3) Mean of 4 locations, 1980 rainy season. (4) Mean of 4 locations, 1983 rainy season.

Cycles of selection

Continuous improvement in the performance of populations should enhance the opportunities for the selection of superior genotypes in the subsequent cycles (HALLAUER and MIRANDA, 1981). These genotypes can be used either as parents of hybrids (after inbreeding) or of varieties, providing a continuous inflow of improved germplasm for those programs. GARDNER (1978) suggested that if population improvement can be achieved without a significant reduction in genetic variability, the best double and single cross hybrids from a series of random lines from the improved population will exceed the population mean by 20 to 30%. Although no comparative data are available, many high-yielding hybrids have been produced, at ICRISAT, using pollinators derived from composites.

HARRIS *et al.* (1972) reported that following nine cycles of mass selection on Hays Golden, an open-pollinated variety of maize, S_1 lines from the C_9 population were significantly superior to S_1 lines from C_0 , both for performance of the S_1 lines, *per se*, and their test crosses. A comparison of pearl millet varieties developed from C_1 and C_2 or C_3 cycles of five composites was made in 1979 in a replicated trial conducted at three locations (Table VI). Varieties from advanced cycle composites did not consistently out-yield the varieties formed from earlier cycles. These results are expected when the gains per cycle are comparatively small and the varieties compared are from one or two consecutive cycles. A more extensive investigation of yielding ability of different cycle varieties was made by comparing varieties from initial and advanced cycles of four composites against two common checks in two different trials (Table V). In each composite, better varieties from the later cycle showed improvement over the best varieties from the earlier cycle.

Table VI Comparative performance of varieties derived from 1st and advanced cycle of selection, tested at three locations in the 1979 rainy season.

Variety	Cycle	Grain Yield (kg/ha)	% of C_1	Time to 50% bloom (d)	Plant height (cm)
WC-C75	C_1	2230		51	190
WC-B77	C_3	2220	-0.4	50	180
IVC-A75	C_1	2230		50	182
IVC-P77	C_2	2380	+6.9	50	183
MC-C75	C_1	2160		48	182
MC-K77	C_3	2340	+8.4	49	178
SSC-C75	C_1	2290		50	185
SSC-P77	C_3	2170	-5.4	50	180
LC-P75	C_1	2220		50	187
LC-A77	C_2	2180	-1.9	52	188
SE		±106		±0.4	±3.2

Other strategies of forming varieties

A further possibility in the strategy of forming varieties from the composites is the intermating of parents from different composites, rather than, as has been done to date, recombining parental lines from the same composite. Earlier work at ICRISAT which examined a diallel cross of composites has shown that the composites differ in their combining abilities. Across-composite varieties may well outperform within-composite varieties, but the parental lines would need to have similar phenotypes if the variety is to be acceptably uniform.

In the seventh International Pearl Millet Adaptation Trial, IPMAT 7 (ICRISAT, 1984), an advanced composite bulk out-yielded all the varieties and synthetics on the basis of data from 25 locations. Though composite bulks are unacceptably variable as varieties, the results of this trial indicate that mass selection on a bulk may be a better method of forming a widely adapted variety than recombining a small number of parental lines. A high intensity of selection for good agronomic characteristics of high to moderate heritability (ear length, height, earliness, and exertion) is being carried out using spaced plants, on a high-yielding composite, the New Elite Composite, with a view to testing this hypothesis. Alternatively, it may be better to use a much larger number of progenies to form the varieties, say 20 or 30, compared to the five to ten presently used. As the cycles advance and the composites improve in both yield and uniformity for morphological characteristics, a larger number can be taken without markedly reducing the selection differential for grain yield.

Conclusions

The use of population breeding methods at ICRISAT has been successful in genetically improving the composites subjected to recurrent selection. One variety, WC-C75, released for general cultivation in India (ANDREWS *et al.*, 1985a) is widely grown. Other varieties are outperforming WC-C75 in advanced trials and are likely to be released.

Experience has shown that the method of selection is not a critical factor in determining progress, but what is important is the precise manner in which the chosen method is carried out. In the recurrent selection methods, at ICRISAT, experimental error is reduced either by replication over seasons and locations, or by the use of grids in selection as used by GARDNER (1961). Attempts are made to reduce inbreeding by taking into account the pedigree of selected lines, and by introgressing new genetic material having good combining ability with the composite at the recombination stage. An essential factor is also that the base populations of the composites are high-yielding and have a high genetic variance.

Evidence has shown that varieties do not markedly outperform the composite bulks from which they are derived. Since there is evidence that dominant genetic variation is important in pearl millet as displayed by substantial inbreeding depression (RAI *et al.*, 1985), methods which take into account the dominant genetic variation in the selection of parents for varieties may be superior. Work is being carried out, to test these assumptions, by using the parental population as the broad-based tester. The possibilities of producing varieties which are less inbred, by mass selecting bulks, by using a larger number of progenies, or by selecting parents across composites are being investigated.

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Bibliographical references

- ANDREWS D.J., GUPTA S.C., SINGH P., 1985a. Registration of WC-C75 pearl millet. *Crop Sci.*, 25 : 199-200.
- ANDREWS D.J., RAI K.N., SINGH P., 1982. Recurrent selection in pearl millet populations. All India Coordinated Millets Improvement Project Workshop, Coimbatore, 20 pp.
- ANDREWS D.J., KING S.B., WITCOMBE J.R., SINGH S.D., RAI K.N., THAKUR R.P., TALUKDAR B.S., CHAVAN S.B., SINGH P., 1985b. Breeding for disease resistance and yield in pearl millet at ICRI-SAT. *Field Crops Res.*, 11 : 241-258.
- BURTON G.W., 1974. Recurrent restricted phenotypic selection increases forage yields of Pensacola bahiagrass. *Crop Sci.*, 14 : 831-835.
- BURTON G.W., 1983. Breeding pearl millet. *Plant Breed Rev.*, 1: 162-182.
- GARDNER C.O., 1961. An evaluation of effects of mass selection and seed irradiation with thermal neutrons on yield of corn. *Crop Sci.*, 1 : 241-245.

GARDNER C.O., 1978. Population improvement. In : *Maize Breeding and Genetics*. (Ed. D.B. Waldan) John Wiley and Sons Inc., New York, pp. 207-228.

GENTER C.F., EBERHART S.A., 1974. Performance of original and advanced maize populations and their diallel crosses. *Crop Sci.*, 14 : 881-885.

HALLAUER A.R., 1973. Hybrid development and population breeding in maize by reciprocal full-sib selection. *Egypt. J. Genet. and Cytol.* 1 : 84-101.

HALLAUER A.R., MIRANDA J.B., 1981. *Quantitative Genetics in Maize Breeding*. Iowa State University, Ames, Iowa, 468 pp.

HARRIS R.E., GARDNER C.O., COMPTON W.A. 1972. Effect of mass selection and irradiation in corn measured by random S_1 lines and their test crosses. *Crop Sc.*, 12 : 594-598.

HORNER E.S., CHAPMAN W.H., LUTRICK M.C., LUNDY H.W., 1969. Comparison of selection based on yield of topcross progenies and of S_2 progenies in maize (*Zea mays* L.). *Crop Sci.*, 9 : 539-543.

ICRISAT, 1984. The Seventh International Pearl Millet Adaptation Trial (IPMAT 7)-1984. ICRISAT, Patancheru P.O., India, 49 pp.

LAMBERT C., 1983. L'IRAT et l'amélioration du mil, présentation des travaux. *L'Agron. Trop.* 38 (1) : 78-88.

LONNQUIST J.H., 1968. Further evidence on testcross versus line performance in maize. *Crop Sci.*, 4 : 580-584.

PETERS L.V., ODELE S., ATADA E., 1972. Bulrush Millet Breeding. In : *Annual Report 1972*. East African Agriculture and Forestry Research Organisation. East African Community, Nairobi, pp. 81-87.

RAI K.N., ANDREWS D.J., SURESH BABU, 1985. Inbreeding depression in pearl millet composites. *Zeitschrift für Pflanzenzüchtung*, 94 : 201-207.

SPRAGUE G.F., 1966. Quantitative genetics in plant improvement. In : *Plant Breeding* (Ed. K.J. Frey), Iowa State University Press, Ames, Iowa, pp. 315-354.

SPRAGUE G.F., EBERHART S.A., 1977. Corn breeding. In : *Corn and Corn Improvement*. (Ed. G.F. Sprague), American Society of Agronomy, Inc., Wisconsin, pp. 305-362.

SURESH BABU V.S., 1981. Genetic advance after 3 cycles of recurrent selection in a composite population of pearl millet (*Pennisetum americanum* (L.) Leeke). Thesis (M.Sc.) submitted to Andhra Pradesh Agricultural University. Hyderabad College of Agriculture, Hyderabad, India, 49 pp.

Resumen

SINGH P., RAI K.N., WITCOMBE J.R., ANDREWS D.J. - **Utilización de las técnicas de selección de poblaciones con vistas al mejoramiento del mijo (*Pennisetum americanum*).**

El presente artículo describe el programa de mejoramiento de las poblaciones de mijo realizado en el ICRI-SAT. Los dos principales métodos de selección utilizados son el método por hermanastros y el método S_1 . El primer método requiere menos compuestos y es menos costoso. El método por selección de descendientes S_1 utiliza un test de descendencia de dos niveles que los autores describen detalladamente. La selección por la resistencia al mildiú y al carbón forma parte del método. En el ICRI-SAT se elaboró una serie de métodos para mejorar los compuestos. Se obtuvo un notable aumento del rendimiento de casi todos los compuestos. Ninguno de los métodos experimentados resultó superior a los demás, aunque fué imposible hacer una comparación exacta por el hecho que los parámetros utilizados, tales como el tamaño de la población y la intensidad de selección, no se pudieron mantener constantes en todos los métodos y compuestos. Se efectuó un ensayo con vistas a comparar 4 métodos de selección de un solo compuesto durante un período máximo de 6 ciclos de selección. Todos los

métodos respondieron poco a la selección y no se obtuvieron diferencias notables entre un método y otro. En dos pares de poblaciones se probaron dos ciclos de selección basados en una selección recurrente recíproca. A pesar de que mejoraron los rendimientos individuales dentro de estas poblaciones, no se obtuvo ninguna mejora de rendimientos derivada de cruces entre poblaciones. Se describen comparaciones entre distintas mezclas de compuestos y entre distintas variedades descendientes de esas mezclas. La intensidad de selección aplicada a la producción de variedades es superior a la que se requiere para obtener mezclas de compuestos. El rendimiento de las variedades descendientes de ciclos adelantados de compuestos fué superior al de las variedades descendientes de ciclos iniciales. Cuando se utilizaron simples descendientes o un número determinado de descendientes para obtener variedades, el rendimiento de las variedades de descendencia múltiple fué, como se había previsto, mayor que el de las variedades de descendencia única, porque las pérdidas debidas a la consanguinidad eran inferiores en las primeras. Se está estudiando una estrategia óptima de producción de variedades.

Palabras-clave : *Pennisetum americanum*, *Pennisetum glaucum*, mijo, selección recurrente, mejoramiento de poblaciones, prueba de descendencia.