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Full-sib and Reciprocal Recurrent Selection in Relation to Pearl Millet Improvement

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Summary. During the years 1973 to 1976 two populations of Pearl millet with wide genetic base, namely, Delhi composite (DC) and Vijay composite (VC) were used to compare the response to selection by the full-sib family method from biparental material and reciprocal recurrent selection (RRS). The results indicated that it was possible to advance grain yield with one cycle of RRS by about 23 percent in the case of population DC and 21 percent in population VC, while for the full-sib selection method, the improvement in grain yield was not so rapid. The studies on the nature of gene action indicated that both additive and dominance gene actions were important for grain yield, ear length and ear girth. The coefficient of variation as a result of RRS was reduced in population DC, while it was comparable to base population in the other population. The correlation studies indicated that the magnitude of favourable correlation of different characters with grain yield were higher in case of RRS compared to the full-sib system. The presence of negative correlation of plant height with grain yield in both the improved populations indicated the possibility of breakage of unfavourable gene combinations through RRS and full-sibs developed from biparental mating.

Key words: Reciprocal recurrent selection – Full sibs – Pearl millet improvement – Breakage undesirable linkage

Introduction

In recent years some major advances have been made in India in the production of hybrids through use of male sterile lines (IARI 1977). Although there is a wealth of genetic variability present in this genus (Murty et al. 1967 a), systematic population improvement programmes have so far been limited, using only a narrow range of material. Population breeding can effectively utilize the enormous genetic variability present in this species, which holds better prospects for combining stable resistance with better yield using diverse germplasm (Kanwar and Ryan 1976). A comparison of methods of effectively improving these populations have not been made so far. The present study was, therefore, made to determine the relative efficacy of the two methods, full-sib and reciprocal recurrent selection in two populations, Delhi composite and Vijay composite, to develop an efficient method for use in population improvement. The estimates of genetic parameters in these two random mating populations were made by using biparental mating.

Materials and Methods

This study concerns two populations, Delhi composite (DC) and Vijay composite (VC). Delhi composite was obtained by taking a large number of open-pollinated bulks from the Indian collection. Vijay composite was developed by mass selection from a world collection of about 1,000 lines, crossed to Tift 23 A. Thus, both possess a wide genetic base for population studies. These two populations were grown at New Delhi (29° N) during 1973. For the full-sib system, 52 males from each of the populations were randomly selected and each of these was crossed to four randomly chosen plants, designated as females, in the same population. These 208 crosses from each population, designated as full-sibs, were grown during 1974 in a randomized incomplete block design with 3 metres row length, under two environments, one with irrigation and the other completely rainfed (both in Delhi), with two replications in each, as suggested by Comstock and Robinson (1948). In the case of reciprocal recurrent selection (RRS), 120 male plants were selected during 1973 from each of the above populations. These plants were selfed and each of these was crossed randomly to four plants, designated as females, of the other population as described by Comstock et al. (1949). All the seeds from the four crosses involving a single male parent were bulked and seed samples drawn to form progenies of that parent. These 120 topcross progenies from each population, along with a local check, were grown in

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two replications in a 11 × 11 partially balanced lattice design during the year 1974. From these progenies, the ten best lines produced by self-pollination from each of the populations were selected on the basis of mean grain yield per plant. These ten lines derived from each population were then intercrossed in all possible combinations during 1975. Equal numbers of seeds from the 45 single crosses were grouped together to constitute the synthetic-1 (cycle-1) populations of DC and VC. These two along with their respective base populations were grown in a randomized complete block design with eight replications during 1976. The plot unit consisted of four rows of 3 meters length, with spacing of 75 cm between the rows and 15 cm from plant to plant.

Data were recorded from five random plants of each experimental row. Seven agronomic characters, grain yield per plant (g), 1000-grain weight (g), ear length (cm), ear girth (cm), number of nodal tillers, days to 50 percent flowering and plant height (cm) were studied. The 208 full-sib treatments were statistically analysed by the method given by Comstock and Robinson (1948, 1952) for biparental progenies. The correlation coefficients and the coefficients of variation (C.V.) of the base and the synthetic-1 (cycle-1) were computed. Significance tests for C.V. were calculated (Lee and Yap 1975).

Results

Table 1 represents the mean of full-sib families and the estimates of genetic components of variance for seven characters in two populations (DC and VC). The relative mean performance of full-sib families showed a significant increase over the base population with regard to the characters grain yield, ear length, days to flower (towards earliness) and plant height (towards reduction) in population DC, while in the case of VC the increase was noted only in ear length and nodal tillers. For other characters the improvement was marginal and not significant. Amongst the selected families the highest yielding family in population DC showed an increase of 34 percent in grain yield and about 16 percent in ear length over the base population, besides being early in flowering and with reduced plant height (by about 30 cm). Similar improvement was also noted in the top yielding family of population VC, but the magnitude of improvement for all the characters was more in population DC.

Considering the estimates of genetic components of variance, it was observed that both additive and dominance components were equally important for grain yield and ear length in both the populations. Therefore, population breeding should maintain diversity and heterozygosity to sustain the yield increase. Since the additive and dominance components were equal in their contribution for grain yield, a narrow genetic base will reduce productivity. Similarly, inbreds, based on general combining ability alone, will not result in the desired constitution of the population. Therefore,

Table 1. Full-sib family means and estimates of genetic components of variance in the two populations Delhi (1) and Vijay composite (2) of pearl millet

Character	Population	Mean of full-sib families (X_1)	Mean of base population (X_2)	Difference ($X_1 - X_2$)	Mean of top most family (X_3)	Difference ($X_3 - X_2$)	Additive variance ($\hat{\sigma}^2$ A)	Dominance variance ($\hat{\sigma}^2$ D)	$\hat{\sigma}^2$ A × environment ($\hat{\sigma}^2$ AE)	$\hat{\sigma}^2$ D × environment ($\hat{\sigma}^2$ DE)	$\hat{\sigma}^2$ D/$\hat{\sigma}^2$ A
Grain yield per	1	60.2	51.6	8.6**	69.2	17.6**	98.57**	94.59**	84.52**	68.39*	0.96
plant (g)	2	45.0	40.8	4.2	54.0	13.2**	85.48**	78.36**	75.36*	73.45**	0.92
1000-grain	1	8.8	8.5	0.3	9.0	0.5	0.039*	0.028	0.031	0.026	0.72
weight (g)	2	8.3	8.4	– 0.1	8.8	0.4	0.034**	0.042*	0.029	0.034**	1.24
Ear length	1	23.4	22.2	1.2**	25.1	2.9**	1.41**	1.38**	1.52**	0.98**	0.98
	2	23.1	22.3	0.8**	24.8	2.5**	0.78**	0.80*	0.93**	0.72*	1.03
Ear girth	1	5.5	5.3	0.2	6.1	0.8**	0.019**	0.019	0.010*	0.007*	1.00
	2	5.2	5.1	0.1	5.9	0.8**	0.011*	0.009**	0.003	0.001	0.82
Number of nodal	1	6.3	5.9	0.4	7.1	1.2**	0.058**	0.041*	0.062*	0.046	0.71
tillers	2	5.8	5.2	0.6**	6.6	1.4**	0.069**	0.051*	0.048	0.054**	0.74
Days to flower	1	55.3	58.0	– 3.7**	52.8	5.8**	4.56**	0.92	5.23**	1.23	0.20
	2	53.8	55.2	– 1.4	52.5	– 2.7*	6.45**	0.78	4.63**	2.96	0.12
Plant height	1	167.7	175.0	– 7.3*	145.0	– 30.0**	76.23**	44.51*	69.43*	56.34	0.58
(cm)	2	188.0	191.5	– 3.5	180.0	– 11.5**	94.53**	81.54**	32.53**	70.43	0.86

* Significant at 5% level of probability
** Significant at 1% level of probability

monitoring for heterozygosity is necessary during inbreeding for line selection. The dominance component for ear girth in the population DC was not significant. This showed the greater role of additive variance in the control of this character. Similar observations were noted in population VC. With regards to other characters, such as number of nodal tillers and plant height, the magnitude of the additive component was larger than the dominance component. Additive variance was also predominant and significant in both the populations for number of days to flower. In the case of 1000-grain weight, additive variance was important in population DC and dominance variance for VC. The relative sizes of additive and dominance components were similar in both the populations for grain yield, ear length, number of nodal tillers and days to flower. However, there were differences between the populations for this proportion ($\hat{\sigma}^2 D/\hat{\sigma}^2 A$) for the other characters, but they were similar in trend. The estimates of relative magnitude of genotype × environmental variance indicated that both $\hat{\sigma}^2 AE$ and $\hat{\sigma}^2 DE$ were of similar magnitude, showing that both dominance and additive components were equally affected by environment, for grain yield and ear length in both the populations. Characters like 1000-grain weight, ear girth and number of nodal tillers appeared to show significant interaction, except for ear girth ($\hat{\sigma}^2 DE$) in population VC and 1000-grain weight ($\hat{\sigma}^2 AE$) in population DC. Plant height and days to flower ($\hat{\sigma}^2 AE$) showed significant interaction in both the populations. Therefore, the direct components of grain yield and characters like plant height and days to flower, which indirectly influence yield, have shown similar environmental interactions. It has not been possible to relate the nature of these interactions to specific characters.

The mean performance of topcross progenies, the mean of the best ten high yielding progenies, and the coefficient of variation (C.V.) along with the means of synthetic-1 (cycle-1) and base population for both the composites (DC and VC) are presented in Table 2. There were significant differences respecting grain yield, ear girth and days to flower (towards earliness), between the ten selected progenies and the mean of all the progenies (including the top ten) in both the populations, although selection was only for grain yield. No significant differences were observed for other characters. Considering the mean performance of improved populations after the first cycle of RRS, a significant increase in grain yield compared to base population in both the synthetics DC (23 percent) and VC (21 percent) were noted. A similar increase in all the yield components except for 1000-grain weight was observed in both the populations. Considerable reduction in days to flower and plant height was also visible

Table 2. Topcross progeny means and coefficient of variation of different characters along with means of synthetic-1 (cycle 1) and base population of composites Delhi (1) and Vijay (2)

Character	Population	Mean topcross progenies of ten best lines (X_1)	Mean topcross progenies of all lines (X_2)	Difference ($X_1 - X_2$)	Mean of synthetic-1 (cycle-1) (X_3)	Mean of the base population (X_4)	Difference ($X_3 - X_4$)	C. V. of synthetic-1 (cycle-1) (X_5)	C. V. of base population (X_6)	Difference ($X_5 - X_6$)
Grain yield per plant (g)	1	77.16	55.76	21.40**	64.60	52.40	12.20**	16.99	30.63	− 13.64**
	2	71.71	48.46	23.25**	50.80	42.00	8.80**	25.28	24.52	0.76
1000-grain weight (g)	1	8.80	8.69	0.11	8.88	8.50	0.38	3.00	3.68	− 0.68*
	2	8.30	8.30	0.00	8.20	8.40	− 0.20	4.00	3.24	0.76**
Ear length (cm)	1	24.6	23.9	0.7	25.50	21.80	3.70**	6.43	14.63	− 8.20**
	2	23.1	22.8	0.3	24.90	22.00	2.90**	12.86	12.36	0.50
Ear girth (cm)	1	5.42	5.28	0.14**	5.45	5.28	0.17*	5.88	8.84	− 2.96**
	2	5.36	5.25	0.11**	5.14	5.01	0.13*	6.06	5.39	0.67
Number of nodal tillers	1	6.4	6.2	0.2	7.40	5.80	1.60*	7.02	10.44	− 3.42**
	2	6.0	5.6	0.4	6.50	5.10	1.40*	16.00	16.15	− 0.15
Days to flower	1	54.2	56.0	− 1.8*	53.20	58.00	− 4.80**	5.15	13.21	− 8.06**
	2	53.1	55.2	− 2.1*	53.40	55.20	− 1.80*	10.97	11.49	− 0.52
Plant height (cm)	1	160.4	162.0	− 1.6	166.80	176.00	− 9.20**	12.99	12.49	0.50
	2	190.0	190.6	− 0.6	197.00	192.00	5.00	10.81	8.86	1.95*

* Significant at 0.05 level
** Significant at 0.01 level

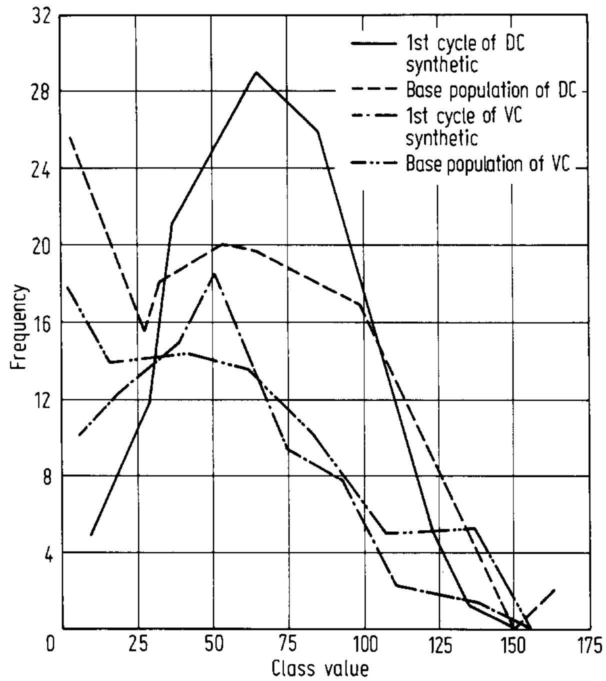

Fig. 1. Frequency distributions of grain yield per plant (g) of pearl millet for first cycles of RRS along with the base populations of DC and VC

in both the synthetic populations. However, the differences for plant height in VC were not significant compared to the base population. Therefore, any adverse associations between grain yield, plant height and days to flower could be overcome by breaking the linkages. The C.V. barring plant height and 1000-grain weight was comparable to base population in the case of synthetic VC. This was different from DC (synthetic), where significant reduction in C.V. was noted for all the characters. The frequency distribution of grain yield per plant for the first cycle of RRS and the base population of the composites (DC and VC) are presented in Fig. 1. The incidence of low yielding plants in the first cycle was considerably reduced in both the populations.

Correlation coefficients among seven pairs of characters of two populations in synthetic-1 (cycle-1) and full-sib families along with their differences (in magnitude) are presented in Table 3. The grain yield was positively and significantly correlated with all the yield contributing characters, in both composited synthetics and full-sib families. Days to flower and plant height were negatively correlated with grain yield in both the systems, but the magnitude of correlation for plant height with grain yield in the case of the

Table 3. Coefficients of correlation between different characters in synthetic-1 (cycle-1) of RRS (X_1) and full-sib families (X_2) along with their differences (X_1-X_2)

Characters		Grain yield per plant	1000-grain weight	Ear length	Ear girth	Number of nodal tillers	Days to flower	Plant height
Grain yield per plant	X_1	–	0.54**	0.46**	0.40**	0.47**	-0.53**	-0.58**
	X_2	–	0.26*	0.38**	0.34**	0.30**	-0.34**	-0.26*
	X_1-X_2	–	0.28**	0.08	0.06	0.17**	0.19**	0.32**
1000-grain weight	X_1	0.18	–	-0.03	0.48**	0.23*	0.05	-0.52**
	X_2	0.24*	–	-0.09	0.29**	-0.24*	0.03	-0.31**
	X_1-X_2	-0.06	–	-0.06	0.19**	-0.01	0.02	0.21**
Ear length	X_1	0.53**	-0.04	–	0.62**	0.09	-0.35**	-0.29*
	X_2	0.36**	0.01	–	0.32**	-0.02	-0.36**	-0.25*
	X_1-X_2	0.17**	-0.05	–	0.30**	0.11**	-0.01	0.04
Ear girth	X_1	0.39**	0.42**	0.52**	–	0.19	-0.32**	-0.38**
	X_2	0.29*	0.31**	0.28*	–	0.02	-0.31**	-0.33**
	X_1-X_2	0.10*	0.11**	0.24**	–	0.17**	0.01	0.05
Number of nodal tillers	X_1	0.41**	0.05	0.12	0.23*	–	-0.56**	-0.52**
	X_2	0.24*	0.06	0.10	0.16	–	-0.42**	-0.30**
	X_1-X_2	0.17**	-0.01	0.02	0.07	–	0.14**	-0.22**
Days to flower	X_1	-0.41**	0.03	-0.46**	-0.42**	-0.48**	–	-0.81**
	X_2	-0.38**	0.01	-0.40**	-0.31**	-0.37**	–	-0.69**
	X_1-X_2	0.03	0.02	0.06	0.11**	0.11**	–	0.12**
Plant height	X_1	-0.16	-0.47**	-0.49**	-0.38**	-0.38**	-0.67**	–
	X_2	-0.23*	-0.36**	-0.31**	-0.22	-0.39**	-0.34**	–
	X_1-X_2	-0.07	0.11**	0.18**	0.16**	-0.01	0.33**	–

– The lower half of matrix (indicated by –) corresponds to Vijay composite and the upper half to Delhi composite
*, ** Indicate significance at probability levels 0.05 and 0.01, respectively

synthetic was not significant. The yield components were also significantly and positively correlated among themselves. It was interesting to note, that as a result of RRS, the degree and nature of associations were altered significantly in the desired direction, especially in combinations of grain yield, with plant height, days to flower, 1000-grain weight and number of nodal tillers in case of synthetic DC, and for ear length, ear girth and number of nodal tillers in the synthetic population VC.

Discussion

Pearl millet is an important cereal crop of arid and semi-arid areas, mostly in India and Africa. The crop has a polyphyletic origin with a viscinism of more than 80 percent and due to its outbreeding nature has accumulated considerable genetic variability for vegetative, reproductive and physiological characters (loc. cit.). About 6,000 collections showing a wide spectrum of variation have been collected and maintained at Icrisat in India and a programme to develop high yielding varieties, utilizing this enormous variability, is already in progress. The present study was therefore undertaken to compare the reciprocal recurrent selection (RRS) and full-sib method to see if any substantial improvement could be achieved using any of these techniques.

The components of variance in the two populations of DC and VC were studied by analysing biparental progenies and showed that both dominance and additive variance were important for grain yield and ear length, while additive variance was more important for other agronomic characters. This substantiates the observations made by Sharma et al. (1979) and Singh (1974) that the additional variability generated through biparental mating was predominantly of an additive nature. Both the former reports do not indicate the actual gain under selection. In the present study the estimates could be related to the realized advance in grain yield and a change in the character association for the better. Most of the studies made on this crop refer to the presence of a high degree of non-additive variance for yield and other agronomic traits (Murty et al. 1967b; Gill et al. 1969; Badwal 1970; Singh et al. 1974). These, however, have been limited to a few inbreds, studied either through diallel mating or line × tester design. Thus, there was considerable scope for improvement of the local population, vis a vis biparental mating. With regard to interaction in relation to additive and dominance components, the additive component ($\hat{\sigma}^2$ AE) was more prone to environmental changes. This was expected, as both the populations were in the unimproved state and, therefore, the additive effects were likely to be more biased by interaction with the environment than the non-additive effects in the unselected group of material (Sprague and Cockerham 1959).

The impression that population programmes will provide greater stability due to limited genotype × environment interaction does not appear justified by the results of this study. The large size of $\hat{\sigma}^2$ AE/$\hat{\sigma}^2$ DE in both the populations for practically all the characters influencing grain yield, would suggest that the mechanism for stability over environment needs to be critically examined at the biochemical level, with simultaneous monitoring of the frequency alleles of some marker loci in populations under selection for yield.

Further improvement made on the material, generated through biparental mating using the full-sib method and following RRS in the base populations DC and VC, indicated that it was possible to advance grain yield with one cycle of RRS by about 23 percent in the case of population DC and 21 percent in population VC, while in the full-sib family selection method, the improvement was not so rapid, being limited to 16 percent in population DC and 10 percent in population VC over the base population. The RRS was very effective in improving the population per se in this study, although no further cycles of selection were carried out. Therefore, RRS appeared to be the best in the improvement of the present populations. In the present material, and also as reported by other workers (Pokhriyal 1977) dominance was the important type of gene action in this crop and the rapid gains obtained in RRS compared to full-sibs, may be due to exploitation of both additive and dominance types of gene action. The full-sib family system aims at exploitation of additive variance only, and is considered to be more efficient than mass or half-sib family selection in maize (William et al. 1965; Eberhart et al. 1966; Singh et al. 1976).

The RRS aims to increase the frequency of favourable genes in the population, as well as to maintain genetic variation and favourable gene combinations. Judging by the coefficient of variation value, it was found that variation was reduced in the improved population of DC, but not in synthetic VC. This was possibly due to release of cryptic variability in characters like plant height and 1000-grain weight and also owing to the unimproved state of population VC. As represented in Figure 1, the incidence of low yielding plants was greatly reduced by this method. Similar findings have been reported by Lee and Yap (1975) in maize.

The correlated response to selection of major agronomic characters with yield was similar in the two methods, but the magnitude of correlation of agronomic traits with yield was higher in RRS. The negative and significant correlation of grain yield with plant height in DC synthetic-1 (cycle-1) and non-significant but negative correlation in improved VC synthetic is of special significance in the present study. All the studies made so far and also in the present base populations (unpublished) indicate the presence of high positive correlation of grain yield with plant height (Burton 1952; Pokhriyal et al. 1967, 1976; Singh and Murty 1973) and consequently, it was difficult to breed high yielding varieties with moderate plant height. The possibility of breakage of such undesirable phase linkages in RRS have been pointed out by Comstock et al. (1949) and Rao and Krishnamurthy (1968). The presence of a similar negative correlation, though of lower magnitude, in the case of full-sibs also was not unexpected, since these families were derived from the biparental mating, which might have led to forced recombinations and breakdown of tight linkages, mostly in repulsion phase. As a consequence, rare recombinants which remained restricted due to linkage disequilibrium might have been exposed in the population (Comstock and Robinson 1952; Singh and Murty 1973). The breakage of this unfavourable linkage in the crop would overcome the plateau of limited response to selection imposed by plant height. Therefore, RRS is a useful system of mating for an accelerated generation of exploitable variability and brings substantial improvement in grain yield. The improvement in the full-sib system, though not so effective, involved a lesser degree of effort and time, and could be followed in the early stage of improvement of local populations to bring about quick results.

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