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# EVALUATION OF HETEROSIS THROUGH COMBINING ABILITY IN PEARL MILLET I. SINGLE CROSSES

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BREEDING new pearl millet strains received a set-back in India due to the high incidence of downy mildew and ergot. The early success recorded about a decade ago by high yielding hybrids is now offset by disease problems. Breeding of new hybrids is rightly based on diverse and disease-resistant cytoplasmic male-sterile lines; yet this alone cannot sustain a steady national yield level unless supplemented by other breeding approaches. Composite populations evolved on a wide disease-resistant genetic base should offer such necessary support. As observed in many cereals and cross-pollinated crops, multiple crosses can provide the requisite broad genetic base to produce composites, but repeatable procedures are needed first to evaluate single and multiple crosses, before outlining repeatable methods of producing composites. The work reported here, in two parts, is an attempt towards this.

## MATERIALS AND METHODS

A number of derived populations was obtained from a world collection of pearl millet germplasm through selfing (T-series), biparental matings (A-series) and irradiation (R-series). Four entries from each of these categories and from exotic collections (W-series) were diallel-mated and the 136 $F_1$ (without reciprocals) were evaluated in a randomised blocks design during 1973. The parents were partially inbred; the extent of inbreeding was unknown. Further, production of completely inbred lines, as a pre-requisite for diallel analysis, would take considerable time and cause heavy inbreeding depression. Hence one representative plant phenotype was chosen as female and the entire required number of crosses was made on it using its tillers also. When one female plant was inadequate, another phenotype similar in all respects was used; the choice of plants was so made as to keep this event rare. The same procedure was followed for pollen plants too. Though the procedure would restrict operational felxibility in the field, yet it ensured that the parent (male or female) was of one genotype—homozygous or heterozygous—uniformly throughout. The experiment was used for a relative assessment of parents or crosses only.

Observations were recorded on flowering time (FT), plant height (HT), number of effective tillers (NT), ear length (EL), seedling vigour (SV), 250-grain weight (GW) and yield per row (YD). SV was recorded as the dry weight of 5 random seventeen-day-old seedlings. GW and SV was recorded in 1973 and YD in 1974 only.

Every parent of the diallel ($F_1A$) was classified as High (H) or Low (L) general combiner. The mean of significant (from zero) general combining ability (GCA) effects was the norm and those parents with value above the norm were H and others L. By allotting a value of +1 for H, 0 for non-significant effects and −1 for L, a total score for each parent over characters was found. The mean of these total scores over parents provided the norm to classify finally a parent as H or L. Such a procedure was adopted to classify the specific combining ability (SCA) of crosses also. In addition, certain crosses received a total zero score due to cancellation of H and L effects over the component characters (denoted by C) or non-significant effects for each component character (denoted by N) (Arunachalam and Bandyopadhyay, 1979).

Five L parents were discarded and the remaining 11 parent diallel was grown in their $F_1$ and $F_2$ generation during 1974 providing $F_1B$ and $F_2$ for drawing conclusions. Plot sizes were a single row of

300 cm for $F_1$ and two rows for $F_2$. Heterosis was recorded over the superior parent only and the combining ability analysis was based on the fixed effects model (Griffing, 1956).

A cross was defined to be overall heterotic if it was heterotic for three or more component characters. Depending on the parental GCA, the crosses were grouped into the classes, HH, HL or LL. Following Arunachalam (1976), the co-variance of GCA and SCA between any two characters were worked out in $F_1B$.

## RESULTS

The ANOVA of combining ability showed significant differences among parents and hybrids for almost all component charactes in $F_1A$, $F_1B$ and F2. The GCA and SCA mean squares were significant showing, as expected, the importance of both additive and non-additive gene action. The estimates of SCA variance were higher than those of GCA. The covariance matrix of combining ability in $F_1B$ (Table 1) confirmed that this trend was upheld for every covariance too. GCA and SCA covariances were in the same direction except FT-HT and NT-YD. The GCA covariance between them was negative indicating that simultaneous utilisation of the additive gene action in respect of them was impractical. The negative association of GCA between FT-NT, NT-EL and NT-YD spelt out the non-feasibility of improvement in the major components of yield by direct selection. The positive association of GCA of YD with FT, HT and EL was offset by the negative association among the component characters. Further the large magnitude of SCA covariances would indicate the predominance of non-additive gene action controlling YD and any of its components (Table 1).

On an analysis of the GCA of parents (Table 2), 'AE5', 'AE 14', 'AE 33', 'TE 16', 'TE 19' and 'TE 22' were found to be H and others L in $F_1A$ with agreement in $F_1B$ (except for 4 cases). Since multiple crosses were made in $F_1A$,

TABLE 1

*Covariance matrix of combining ability components in $F_1B$*

| Estimate | | FT | HT | NT | EL | YD |
|---|---|---|---|---|---|---|
| FT | a | 1.3 | -4.0 | -4.9 | 0.8 | 6.1 |
| | b | 10.6 | 13.7 | -25.9 | 1.4 | 258.9 |
| HT | a | | 75.3 | 26.0 | 9.3 | 185.7 |
| | b | | 273.4 | 39.7 | 35.0 | 1768.3 |
| NT | a | | | 37.3 | -1.5 | -11.9 |
| | b | | | 125.2 | -4.0 | 295.1 |
| EL | a | | | | 3.2 | 29.3 |
| | b | | | | 8.2 | 209.0 |
| YD | a | | | | | + |
| | b | | | | | 26278.7 |

+ =Non-estimable; a=GCA; b=SCA

## TABLE 2

*The GCA of parents and distribution of heterotic single crosses*

| Parent | | | | $F_1A$ | | | | | | | $F_1B$ | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | g | | | HH | | HL | | LL | | Ov | HH | | HL | | LL | | Ov |
| | $F_1A$ | $F_1B$ | $F_2$ | a | b | a | b | a | b | a | a | b | a | b | a | b | a |
| AE 5 | H | H | H | 60 | 27 | 80 | 73 | — | — | 73 | 40 | 29 | 100 | 71 | — | — | 70 |
| AE 14 | H | L | L | 60 | 27 | 80 | 73 | — | — | 73 | 80 | 57 | 75 | 43 | — | — | 70 |
| AE 33 | H | H | H | 80 | 40 | 60 | 60 | — | — | 67 | 40 | 40 | 75 | 60 | — | — | 50 |
| AM 7 | L | L | L | — | — | 100 | 55 | 55 | 45 | 73 | — | — | 83 | 50 | 100 | 50 | 100 |
| TE 16 | H | H | H | 60 | 33 | 60 | 67 | — | — | 67 | 20 | 33 | 40 | 67 | — | — | 30 |
| TE 19 | H | H | L | 60 | 25 | 90 | 75 | — | — | 80 | 60 | 43 | 100 | 57 | — | — | 70 |
| TE 22 | H | H | H | 60 | 30 | 70 | 70 | — | — | 67 | 40 | 29 | 100 | 71 | — | — | 70 |
| TM 7 | L | H | L | — | — | 33 | 67 | 11 | 33 | 20 | — | — | 50 | 50 | 75 | 50 | 60 |
| RE 2 | L | H | L | — | — | 83 | 42 | 78 | 58 | 80 | — | — | 100 | 75 | 50 | 25 | 80 |
| RE 13 | L | — | — | — | — | 17 | 17 | 50 | 83 | 40 | — | — | — | — | — | — | — |
| RM 5 | L | L | L | — | — | 100 | 46 | 78 | 54 | 87 | — | — | 67 | 57 | 75 | 43 | 70 |
| RM 6 | L | — | — | — | — | 100 | 43 | 89 | 57 | 93 | — | — | — | — | — | — | — |
| WM 4 | L | H | L | — | — | 100 | 43 | 89 | 57 | 93 | — | — | 67 | 67 | 50 | 33 | 60 |
| WM 8 | L | — | — | — | — | 100 | 50 | 67 | 50 | 80 | — | — | — | — | — | — | — |
| WM 11 | L | — | — | — | — | 83 | 42 | 78 | 58 | 80 | — | — | — | — | — | — | — |
| WM 19 | L | — | — | — | — | 50 | 30 | 78 | 70 | 67 | — | — | — | — | — | — | — |

g=GCA; a=$P_a$; b=$P_b$; Ov=Overall

the GCA status observed in $F_1A$ will only be used in further discussion. It was observed that the parents derived from A- and T- series of the base material provided H general combiners while R- and W-series L counterparts.

Of the hybrids, 25 to 75% were heterotic for component characters in $F_1A$ (Table 3). The respective ranges were 22 to 65 and 20 to 58 in $F_1B$ and F2. Heterosis was prominent for FT and NT followed by GW and SV in $F_1A$ and YD in $F_1B$.

TABLE 3

*Percentage of crosses heterotic for component characters*

| | FT | HT | NT | EL | GW/YD | SV |
|---|---|---|---|---|---|---|
| $F_1A$ | 67 | 25 | 75 | 25 | 58 | 53 |
| $F_1B$ | 56 | 27 | 65 | 22 | 47 | — |
| $F_2$ | 58 | 47 | 42 | 20 | 24 | — |

Two percentages ($P_a$ and $P_b$) were computed to compare the frequency of heterotic crosses in HH, HL and LL formed on their parental GCA (Table 4). $P_a$ is the observed percentage of heterotic crosses. $P_b$ gives the conditional probability that a cross X falls in the group HH, HL or LL given that X is heterotic. It can be shown that, while $P_a$ is dependent on the number of crosses made in a group, $P_b$ is independent of the same. Thus, the precision of the relative comparisons based on $P_a$ is directly proportional to the degree of non-

TABLE 4

*Heterosis in relation to parental GCA*

| | | HH | HL | LL |
|---|---|---|---|---|
| $F_1A$ | n | 15 | 60 | 45 |
| | nh | 9 | 45 | 31 |
| | $P_a$ | 60 | 75 | 69 |
| | $P_b$ | 11 | 53 | 36 |
| $F_1B$ | n | 15 | 30 | 10 |
| | nh | 8 | 22 | 9 |
| | $P_a$ | 53 | 73 | 90 |
| | $P_b$ | 21 | 56 | 23 |

n=Number of crosses made; nh=Number of heterotic crosses.

discrepancy in the number of crosses made under HH, HL or LL (Arunachalam and Bandyopadhyay, 1979).

The number of crosses made in HH was lower than that in HL or LL in $F_1A$, HL group having the largest frequency of crosses both in $F_1A$ and $F_1B$ (Table 4). A comparison of $P_a$ clearly showed the superiority of HL crosses in $F_1A$ and failed to show it in $F_1B$. But a comparison of $P_b$ did emphasize HL superiority both in $F_1A$ and $F_1B$. More than genetic and geographic divergence, GCA divergence was needed for bringing about heterosis.

'AE 14', 'AE 5', 'TE 19' and 'TE 22' were the H parents consistent in producing heterotic crosses in $F_1A$ and $F_1B$ (Table 2) while 'RE2' and 'RM 5' were such L parents. It must be remembered that this result was based on 15 crosses per parent in $F_1A$ and on 10 in $F_1B$. Based on $P_b$, it was found that H parents produced more HL than HH heterotic crosses. But L parents produced less HL than LL heterotic ones. Such a clear picture could not be shown by $P_a$ for obvious reasons.

The observed heteroris was related to the combining ability components to examine whether it was brought about by epistatic forces like dominance and its interactions. It was observed that 25, 61 and 47% of heterotic crosses in HH, HL and LL groups showed high SCA effects (Table 5). Examining the $P_b$'s, it can be concluded that HL group contained not only high frequency of heterotic crosses but of high and low SCA effects as well. A choice would, therefore, be available to a breeder to choose a heterotic cross showing low or non-significant SCA. LL group contained large number of heterotic crosses with non-significant SCA and HH the lowest. Half of the 95 heterotic crosses expressed heterosis on the strength of high SCA only.

TABLE 5

*Distribution of heterotic single crosses in relation to combining ability components*

| SCA | HH | HL | LL | Total |
|---|---|---|---|---|
| H | 3 | 30 | 16 | 49 |
| L | 4 | 10 | 6 | 20 |
| C | 3 | 4 | 4 | 11 |
| N | 2 | 5 | 8 | 15 |
| Total | 12 | 49 | 34 | 95 |

H=High; L=Low; C=Zero by cancellation; N=Non-significant for all characters.

The hybrids between 'RE 2', 'RM 6', 'AM 7' and 'AE 5', 'AE 14', 'TE 19', 'RM 5' were found, in general, to be superior. Three of them, 'AM 7 × TE 19', 'RE 2 × RM 5' and 'AM 7 × AE 5' were used to evolve composite populations.

## DISCUSSION

A breeder is generally faced with the problem of evaluating a parent or a cross over a number of yield components; often conflicting results are produced by them. Usually his final decision is unduly influenced by the results on grain yield. This study concentrated, therefore, on an unbiased evaluation of parents and crosses in terms of genetic components like GCA and SCA. A repeatable method of designating a parent as H or L general combiner based on statistically tested GCA effects over a number of component characters was found very effective. The concepts also worked well to characterise the overall SCA of crosses.

Overall heterosis, as defined in this study, was related to the genetic status of a parent. HL crosses which ensured divergence in parental GCA held the top rank in heterosis followed by LL and HH in this study. The analysis of base material showed that A- and T- series, which represented the products of selected mating systems designed to improve yield, provided H parents. The relatively non-bred R- and W- series provided L counterparts. Crosses between them provided not only genetic and geographic but also combining ability divergence resulting in a high frequency of heterotic crosses. Observations made by Sriwatanapongse and Wilsie (1968) and Busbice and Rawlings (1974) that inter-group and inter-varietal crosses produced high heterosis in alfalfa are of relevance. Kang (1969) noted that high-yielding single crosses had low SCA and that dwarf × tall were superior in yield as compared to dwarf × dwarf combinations in sorghum. Our study has, for the first time, added a new criterion of parental GCA diversity for heterosis.

The high frequency of heterotic crosses found in HL was due to high SCA in 50% of cases (Table 5) and low or non-significant SCA in the rest. Similar was the trend in LL. But only 25% of heterotic crosses in HH had high SCA. It would seem therefore that the chances of sustaining the heterosis found in HH would be more than those in HL or LL. This superiority of HH was counterbalanced by the low frequency of heterotic crosses in it.

The modifications adopted in the mating process allowed only a relative assessment of parents. Three of the L parents of $F_1A$ were found to be H in $F_1B$ while only one of the H parents of $F_1A$ was L in $F_1B$. This would imply that the hybrids in $F_1B$ raised from a portion of seeds used for raising $F_1A$ was genetically more variable in the case of L than in that of H parents. Consequently, L parents were found to produce heterosis more frequently when crossed to other L parents (Table 2 and 'Results'). But, as expected, H parents produced heterosis more with L parents only. A feasible genetic basis provided by Langham (1961) for the success of HL was supported by this study.

Heterosis for characters governed by one gene is attributable to dominance. But for those governed by more than one gene, it is possible to realise heterosis on the basis of additive genetic effects and its interactions alone (Arunachalam 1977). The availability of heterotic crosses with non-significant SCA for every component character (Table 5) lends experimental support. High magnitude of heterosis realised without SCA in 'AE 14 × TE 19' (HH), 'AE 14 × RE 2' (HL), 'RM 6 × AE 5' (HL) and 'WM 19 × RE 2' (LL) for example, would allay the fear that heterosis in such crosses could not be high.

The observations based on comparing $P_b$ were more justifiable than those based on $P_a$ emphasizing the need for breeders to utilise $P_b$ in perference to $P_a$ in their studies.

However, the undesirable associations in respect of GCA among yield components and of YD with them, complicated by high SCA covariances, would reduce the chances of pure line breeding or direct utilisation of those crosses for high yield. Some of them were hence utilised in producing multiple crosses and composite populations, the results of which form the second part of this paper.

## SUMMARY

Genotypes belonging to four diverse groups, A-, T-, R- and W-series, of pearl millet were diallel-mated and evaluated in three generations, $F_1A$, $F_1B$ and $F_2$. Based on the information over a number of yield components, the parents were classified as High (H) or Low (L) general combiners. The method of classification was found stable. The frequency of occurrence of heterotic crosses was more in HL than in HH or LL. Experimental evidence for the presence of high heterosis without dominance or their interactions was obtained. Diversity in parental general combining ability was found necessary for realising heterosis in addition to genetic divergence. The possibilities of sustaining the heterosis observed in HH were counterbalanced by the low frequency of heterotic crosses occurring in it. A number of parents, crosses and concepts were identified for breeding for yield.

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