Arunachalam, V. and Reddy, B. B.
Evaluation of Heterosis Through Combining Ability in Pearl Millet. II. Multiple Crosses.
Indian Journal of Genetics and Plant Breeding, 41 (1981): 66-74.

[REPRINTED FROM THE *Indian Journal of Genetics & Plant Breeding*, Vol. 41, No. 1. March, 1981, pp. 66-74]

EVALUATION OF HETEROSIS THROUGH COMBINING ABILITY IN PEARL MILLET II. MULTIPLE CROSSES

V. ARUNACHALAM and B. B. REDDY

Indian Agricultural Research Institute, Regional Station, Rajendranagar, Hyderabad- 500 030 *India*

SINGLE crosses (SC) involving divese parental genotypes belonging to A-, T-, R- and W- series were evaluated in their F_1 and F_2 generations in pearl millet for yield and its attributes (Reddy and Arunachalam, 1981). Based on their overall general combining ability (GCA), the parents were characterised as high (H) or low (L). The realised heterosis in SC was related to GCA and specific combining ability (SCA) using repeatable methods. Some of the SC were used as female parents to produce 3- and 4-way crosses. The heterosis registered by those multiple crosses (MC) were examined in the light of parental and grand-parental components of combining ability to understand their utility in breeding productive composite populations. The results are evaluated in this paper.

MATERIALS AND METHODS

The SC, described in the first part of this paper, were grown during 1973 (F_1A). SC that had a mean seedling vigour (SV) (for details see I part) of 326 to 460 mgm/plant and at least one of whose parents had positive GCA were designated as H; those having an SV of 179 to 292 mgm/plant and one of whose parents negative GCA were L.

Six parents, three of which had positive GCA for SV (RM 6, WM 11 and TE 16) and three negative (AE 5, AE 33 and AE 14) were mated in a triallel design of Rawlings and Cockerham (1962) to produce 60 crosses—TLL. Three SC of F_1A, 'TM 7 × RM 5', 'WM 4 × RM 5' and 'WM 19 × RM 5', H for SV were mated in a line × tester design (LT) to five male parents selected for earhead characters resulting in 15 three-way crosses—3 LT.

Five SC high for SV, AM 7 × RM 6, RM 6 × WM 19, WM 8 × TM 7, TM 7 × TM 19 and AE 5 × RM 5 were involved in a full diallel mating giving 25 four-way crosses—4 DL. The same H parents were used as females and mated in an LT to five SC low for SV, AM 7 × WM 8, RM 6 × RE 2, WM 4 × RE 2, TE 16 × WM 19 and AE 14 × RE 13, producing 25 four-way crosses—4 LT. The MC were evaluated for FT, HT, NT, EL and YD described earlier.

RESULTS

Both GCA and SCA mean squares were significant for all the characters, as in SC. The GCA status of parents based on all characters (Table 1) differed from that of SV. The 6 entries used as parents in TLL retained the same GCA status as in F_1A except AE 14. For discussion, we shall keep the GCA status recorded in F_1A since the MC were made then. The observed frequency of H and L parents remained almost equal in TLL, 4 DL and 4 LT while that of L was more in 3 LT. A fair distribution of H and L grandparents was present in TLL while it was not so in 4 DL and 4 LT (Table 1). Most of the parents used in MC were heterotic as SC in F_1A and low in SCA. The GCA of parents of MC did

TABLE 1

The status of combining ability of parents and grandparents of multiple crosses

Parents	Grandparent			Heterosis in F_1A	Parent GCA	nh	
	GCA		SCA				
	F	M					
TLL							
RM 6	—	L	—	—	L	8	
WM 11	—	L	—	—	L	9	
TE 16	—	H	—	—	H	7	
AE 14	—	H	—	—	L	7	
AE 5	—	H	—	—	H	6	
AE 33	—	H	—	—	H	9	
RM 6 × WM 11	L	L	H	+	L	3	
RM 6 × TE 16	L	H	L	+	H	4	
RM 6 × AE 14	L	H	H	+	L	1	
RM 6 × AE 5	L	H	L	+	H	4	
RM 6 × AE 33	L	H	L	@	H	4	
WM 11 × TE16	L	H	H	+	L	3	
WM 11 × AE 14	L	H	L	+	L	4	
WM 11 × AE 5	L	H	L	+	L	3	
WM 11 × AE33	L	H	L	+	L	1	
TE16 × AE14	H	H	L	+	H	3	
TE16 × AE5	H	H	L	+	H	4	
TE16 × AE33	H	H	L	@	H	4	
AE14 × AE5	H	H	L	@	L	4	
AE14 × AE33	H	H	H	+	H	0	
AE5 × AE33	H	H	L	+	H	4	
3LT							
Sel 1	—	—	—	—	L	2	
Sel 2	—	—	—	—	L	1	
Sel 3	—	—	—	—	L	1	
Sel 4	—	—	—	—	L	1	
Sel 5	—	—	—	—	L	1	
TM7 × RM5	L	L	H	@	H	2	
WM4 × RM5	L	L	L	+	L	2	
WM19 × RM5	L	L	L	+	L	2	
*4*DL*							$
AM7 × RM6	L	L	L	+	L	1	1
RM6 × WM19	L	L	L	+	L	3	5
WM8 × TM7	L	L	H	+	H	3	5
TM7 × TE19	L	H	L	@	L	3	3
AE5 × RM5	H	L	L	+	H	3	4

TABLE 1—(*Contd.*)

Parents	Grandparent GCA F	Grandparent GCA M	Grandparent SCA	Heterosis in F_1A	Parent GCA	nh
**4*LT*						
AM7 × WM8	L	L	L	@	L	3
RM6 × RE2	L	L	L	+	L	4
WM4 × RE2	L	L	L	+	L	4
TE16 × WM19	H	L	L	@	H	4
AE14 × RE13	H	L	H	@	H	3

*Same status as female parents of 4LT; nh=Number of heterotic crosses produced; **As male parents; $ = As female parents in 4LT; + = Heterotic;-@ = Nonheterotic.

not bear obvious relationship to their GCA and SCA as SC in F_1A except that those SC, low in SCA with parents also low in GCA, were L as parents of MC (Table 1).

The probability, P_b (see I part) of recording heterosis was highest in (HL) ×H followed by (HH) ×L and (HH) ×H in TLL (Table 2). No heterosis was observed in (LL) × L, unlike 3 LT. (HL) × (LL) and (LL) × (HL) were the groups in 4 DL where heterosis was most frequent followed by (LL) × (LL). However, the trend was reverse in 4 LT. HL group of SC were the most successful as parents to produce heterotic MC in all the systems (Table 2).

All the 6 parental genotypes of TLL, SC parents of TLL except 'RM 6 × AE 14', 'WM 11 × AE 33' and 'AE 14 × AE 33', the female parents of 3 LT, all the parents of 4 DL and 4 LT except 'AM 7 × RM 6' were equally capable of producing heterotic crosses (Table 1). The efficiency of parents which were SC did not depend on their heterotic status in F_1A; however, the SC parents that had low overall SCA in F_1A produced higher frequency of heterotic MC than those that had high SCA. Such a clear distinction was not noticeable with regard to the GCA status of the grandparents of MC (Table 1).

A comparative evaluation of the genotypic potential to produce heterosis (Table 3) as parents in SC and grandparents in MC was made using the probability P_b. Since only a few of the 16 genotypes were involved as grandparents of MC, P_b was calculated afresh for those genotypes for SC and MC in each systems to provide an effective comparison. In general, the potential of genotypes as grandparents of MC was as high (or higher) as parents of SC. 'AM 7' and 'WM 4', both L, were the exceptions. Some of the L parents of SC were able to register higher heterotic potential as grandparents except those of W-series (Table 3).

TABLE 2

Distribution of heterotic multiple crosses

Male / Female		TLL H	TLL L	TLL T	3LT L	4DL HL	4DL LL	4DL T	4LT HL	4LT LL	4LT T
HH	n	12	12	24							
	nh	9	10	19							
	P_a	75	83	79							
	P_b	20	22	42							
HL	n	24	8	32		2	6	8	4	6	10
	nh	17	7	24		2	4	6	3	4	7
	P_a	71	88	75		100	67	75	75	67	70
	P_b	37	15	52		16	30	46	16	22	40
LL	n	4	0	4	15	6	6	12	6	9	15
	nh	3	0	3	6	4	3	7	4	7	11
	P_a	75	0	75	40	67	50	58	67	78	73
	P_b	6	0	6	40	30	24	54	22	40	60
T	n	40	20	60		8	12	20	10	15	25
	nh	29	17	46		6	7	13	7	11	18
	P_a	73	85	77		75	58	65	70	73	72
	P_b	63	37			46	54		39	61	

T=Total; n=Number of crosses made; nh=Number of heterotic crosses; P_a, P_b see text.

TABLE 3

A comparative evaluation of the potential of grandparents to produce heterosis

Parent	TLL		3LT		4DL		4LT	
	a	b	a	b	a	b	a	b
AE5	16	21			13	12	8	6
AE14	16	12					8	4
AE33	15	14						
AM7					13	2	8	6
TE16	15	20					7	6
TE19					14	12	9	4
TM7			5	14	4	22	3	12
RE2							9	12
RE13							4	4
RM5			33	48	16	12	9	6
RM6	19	18			14	14	9	12
WM4			36	14			10	6
WM8					14	14	9	9
WM19	19	15	26	14	12	12	7	13

a=Value of P_b in single crosses; b=Value of P_b in multiple crosses.

The range of heterosis recorded for various component characters (Table 4) clearly pointed out that MC involving more genotypes were superior than SC. This was especially true for NT and YD which were important for commercial propagation of populations.

TABLE 4

Range of heterosis recorded for component characters and produced by parents of multiple crosses

Character	SC		TLL		3LT		4DL		4LT	
	a	b	a	b	a	b	a	b	a	b
FT	0	7	0	20	2	5	0	7	0	6
HT	0	22	7	39	—	—	0	10	1	22
NT	0	134	0	181	11	58	0	226	6	150
EL	0	22	0	23	0	13	0	34	0	33
YD	0	50	0	67	45	93	0	122	8	42

SC=F_1A; a=Minimum %; b=Maximum %.

An examination of the SCA status was made to see whether the high magnitude of heterosis in MC was the direct result of epistatic interactions (Table 5). In general, MC with high SCA did not occur more frequently than those with low or non-significant SCA in any system Further, an appreciable frequency of

TABLE 5

Heterosis in multiple crosses in relation to combining ability

System	GCA	SCA H	L	C	N	Total
3LT	(LL) × L	2	4	—	—	6
*4DL	(HL) × (HL)	1	—	—	—	1
	(LL) × (HL)	2	2	—	—	4
	(LL) × (LL)	—	2	—	—	2
4LT	(HL) × (HL)	2	—	—	1	3
	(HL) × (LL)	—	—	1	3	4
	(LL) × (HL)	1	2	—	1	4
	(LL) × (LL)	2	2	—	3	7

*Excludes reciprocals.

heterotic crosses with non-significant SCA occurred in 4 LT for every yield component It was particularly high in (HL) × (LL) and (LL) × (LL) groups. The heterotic crosses in TLL were not examined from this angle, as this system based on a balanced genetic model admitting estimation of higher order interaction effects forms a separate paper. Arunachalam and Reddy, (1979).

A study of the covariance matrix of combining ability (Table 6) in 3 LT and 4 LT showed a larger magnitude of SCA than GCA , in general, for every componental pair. The negative association between FT and NT, the conflicting direction of GCA and SCA between HT, NT, EL and YD would emphasize that mere multiple crossing programme alone would not allow for direct selection for simultaneous improvement in yield and its components.

TABLE 6

Covariance matrix of combining ability in 3 LT and 4 LT

			FT	HT	NT	EL	YD
FT	3LT	g	-3.6	2.5	-0.6	-1.5	78.0
		s	11.4	4.9	-32.2	5.0	-726.7
	4LT	g	-0.2	3.2	-3.5	1.1	-7.0
		s	6.3	13.9	-23.0	-1.5	-138.3
HT	3LT	g		+	29.1	-33.9	428.6
		s		409.2	-303.4	119.0	-2740.7
	4LT	g		276.0	-55.5	13.7	-59.0
		s		165.2	107.7	3.9	2108.3
NT	3LT	g			+	20.0	-629.3
		s			368.7	-17.0	5246.8
	4LT	g			+	0.5	-271.1
		s			399.8	-11.6	2639.9
EL	3LT	g				+	296.3
		s				37.4	-441.5
	4LT	g				0.3	-37.7
		s				9.4	214.7
YD	3LT	g					+
		s					78100.6
	4LT	g					3386.1
		s					929.7

+ =Not estimable; g=GCA; s=SCA.

Discussion

The study on multiple crosses was mainly aimed at understanding whether they can produce stable heterosis of higher magnitude than single crosses that can be streamlined further into pure lines or populations. Clear evidence that crosses with high heterosis could be produced with low and non-significant SCA in 3 LT, 4 DL and especially in 4 LT was obtained (Tables 4 and 5). Most of the heterotic groups of crosses did involve a H × L single cross as one of its parents. The contention that H × L SC would be very useful in producing productive MC, made in the I part of this study, was upheld by the results on MC. In particular, HL female parents were consistent in producing high heterosis in all the systems (Table 2). It was also found that LL females produced good heterosis in 4 LT and 4 DL. The L parents, 'RM 5', 'RM 6', 'TM 7', 'WM 8' and 'WM 11', differed from their GCA status based on SV alone. One remedy would then be to raise a large F_1, include a number of diagnostic physiological and other stable components from seedling to maturity and record data at population level of each F_1 hybrid. This would counteract the problems caused by the small size of F_1 and the sub-sampling of 5 or 10 plants for data. In cross-pollinated crops like pearl millet where population improvement is relevant, this should not be difficult to practise. Intense studies are, therefore, needed to come to reliable conclusions in this regard.

Parental diversity in combining ability was again emphasized in heterotic MC. The heterotic groups of crosses invariably included parents and grandparents diverse in their GCA (Tables 1 and 2). A- and T- series parents provided H- and R- and W- series the L parents as seen in SC. Multiple crosses which held promise were invariably between A- or T- series and R- and W- series (Table 7). Thus we see that geographic diversity was coupled with combining ability diversity to produce heterosis, in every mating system. Some of the crosses had low or non-significant SCA. They were used to produce composite populations, someof which were high-yielding and are under All-India evaluation.

Having established that HL single crosses or MC involving it would ensure a higher probability of producing heterosis on a diverse genetical base, it would be necessary to chalk out means of identifying a H or L female parent. Since completely inbred parents are not used, one cannot identify a H or L genotype in F_1 and raise it again using remnant seeds to make MC. Thus the need is great to identify a plant as H or L before it comes to flowering so that the desired group of MC can be made. We used SV as a diagnostic character to serve such a purpose. This needs destructive sampling and thus the plants on which this trait is measured, are not available for hybridisation. This is evidently a reason why the GCA status based on it did not tally exactly with the overall status. Studies by Parker *et al.* (1970) in groundnut hold promise to identify other stable seedling characters and more studies are needed in this respect.

The undesirable associations with regard to GCA and SCA between pairs of important components (Table 6) would still make direct selection arduous.

TABLE 7

Mean and heterosis of some promising crosses used in breeding composites

	Cross		FT days	HT cm	*NT	EL cm	*YD gm	SCA
SC	AM7 × RE5	m	51	127	75	20	1222	H
		h	—	—	72	26	214	
	RE2 × RM5	m	51	157	56	26	1043	H
		h	—	—	44	—	176	
TLL	(RM6 × AE5) ×	m	42	140	139	24	1428	
	AE33	h	18	22	181	—	66	
	(RM6 × WM11) ×	m	55	148	63	20	1073	
	TE16	h	—	7	56	—	67	
	(TE16 × AE5) ×	m	49	126	84	22	1054	
	WM11	h	—	14	65	—	33	
4DL	(AM7 × RM6) ×	m	53	143	43	26	462	L
	(WM8 × TM7)	h	—	—	10	—	91	
4LT	(RM6 × WM19) ×	m	52	157	55	27	685	N
	(AE14 × RE13)	h	5	—	99	—	42	
	(WM8 × TM7) ×	m	53	136	60	24	626	N
	(TE16 × WM19)	h	4	—	118	—	25	

m=Mean; h=Heterosis %; *Over 3m row.

Evaluation of MC at population level in higher generations would give an idea of the direction and magnitude of changes in the covariance matrix of combining ability so that an appropriate stage in the discrete stochastic process can be selected for practising selection.

New and repeatable concepts of plant breeding value have become available through these studies and population breeding in pearl millet using them, we hope, will provide rich dividends in the near future in India.

SUMMARY

Using parents and single crosses classified as high or low general combiners, multiple crosses were made in triallel (TLL), 3-way line × tester (3 LT), 4- way diallel (4 DL) and 4-way line × tester (4 LT) designs in pearl millet. It was shown that H × L single crosses provided the best base to produce heterotic multiple crosses in all the systems. Several genotypes were found to provide more heterosis in multiple crosses when used as grandparents than in single crosses. A high frequency of heterotic crosses had non-significant SCA for all component characters and yield in 4 LT. Geographic diversity when coupled with combining ability diversity was found to produce high heterosis which was

much larger in multiple than in single crosses. The problems associated in producing desired multiple crosses to provide a broad genetic base for composite populations were discussed.

REFERENCES

Arunachalam, V. and B. B. Reddy. (1979). Basic studies on triallel crosses in pearl millet (***Pennisetum** typhoides* S. & H.) *Z. Planzenzucht.*, **83:** 368-74.

Parker, R. C., J. C. Wynne and D. A. Emery. (1970). Combining ability estimates in *Arachis hypogaea* L. I. Seedling response in a controlled environment. *Crop Sci.* **10:** 429–32.

Rawlings, C. O. and C. C. Cockerham. (1962). Triallel analysis. *Crop Sci.* **2:** 228–31.

Reddy, B. B. and V. Arunachalam. (1981). Evaluation of heterosis through combining ability in pearl millet. I. Single crosses. *Indian J. Genet.* **41:** 66-72.