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Combining Ability Studies in Pearl Millet (*Pennisetum typhoides* (Burm.) S. & H.)

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Summary. A line × tester analysis of combining ability involved five male-sterile lines from different sources and 10 inbreds of Pearl millet developed at Hissar (India). Additive × additive and additive × dominance types of gene interaction were found to predominate in the material under study. A high degree of association was found between general combining effects and the mean performance of lines and testers over crosses but no association was observed between *per se* performance of the crosses and their specific combining ability effects. Among the male sterile lines, L-110 proved to be the best general combiner, whereas H-297, followed by H-198, was the best of the inbreds. The crosses L-110 × H-440, L-110 × H-406, $18D_2A$ × H-297, 18 A × H-198 and L-110 × H-297, were superior to the released variety, Hybrid-1, used as control.

Pearl millet (*Pennisetum typhoides* (Burm.) S. & H.) is an important grain and fodder crop of India and many African countries. Considerable attention has been paid to its improvement in recent years. Rapid advances have been made in developing hybrids by using cytoplasmic male sterile lines. Because the nature of gene action is known to vary with the genetic architecture of the populations involved in hybridization and the degree of divergence between the parents concerned, it is necessary to pre-evaluate the parents for their combining ability. Such evaluation facilitates the selection of promising parents for heterosis breeding and producing high class hybrids. The present study gives the results of a line × tester analysis carried out on fifty hybrids between five male sterile lines and ten testers.

Material and Methods

The material consisted of 10 inbreds of the H-series, i.e. H-198, H-224 and H-240, H-297, H-319, H-323, H-403, H-406, H-414 and H-440, used as testers, and five male-sterile lines, $23D_2A$, $18D_2A$, 18A, L-110 and L-111, used as females. Fifty hybrids, ten pollinators and Hybrid-1 as control were grown at Haryana Agricultural University Farm, Hissar, in a randomized block design with three replications. The distance between rows and between plants within rows was 60 and 23 cm., respectively.

Observations on 14 randomly chosen plants from each plot were made for seven quantitative characters, days to flowering, total tillers, ears per plant, plant height, ear length, 1000-seed weight and grain yield per plant.

Combining ability analysis was based on a procedure developed by Kempthorne (1957) which is also related to design II of Comstock and Robinson (1952). A detailed outline of the procedure has been given by Rao et al. (1968).

Results

In the analysis of variance for combining ability (Table 1), the variances due to females, males and females × males were significant for most of the characters. Variances due to females for plant height, due to males for days to flower and 1000-grain weight, and due to females × males for days to flower were, however, not significant. The variance

Table 1. *Analysis of variance for combining ability*

Source of variation	D.F.	Mean sum of squares						
		Days to flower	Plant height	Total tillers	Ear per plant	Ear length	1000 seed weight	Grain yield per plant
Females	4	271.429*	654.75	9.541	18.332*	700.089*	20.249*	2535.03*
Males	9	50.530	1989.78*	10.921*	18.337*	208.86*	3.084	2257.98*
Females × males	36	28.859	735.75*	3.986*	4.790*	41.731*	2.805*	931.45*
Error	100	35.951	172.71	2.094	1.091	9.001	1.159	126.12
σ^2_f		8.086	−2.700	0.185	0.451	21.945	0.581	53.453
σ^2_m		1.445	83.602	0.462	0.903	11.150	0.091	88.453
σ^2_{fm}		−2.364	187.680	0.631	1.223	10.883	0.549	268.443
σ^2_{gca} [1]		4.766	40.451	0.324	0.677	16.548	0.300	70.944
$\sigma^2_{sca}/\sigma^2_{gca}$		−0.4960	4.6396	1.9475	1.8212	0.6577	1.8300	3.7838

* Significant at 5% level
[1] Averaged over males and females

Table 2. *Mean values of the hybrids and the overall mean performances of male-sterile lines and testers*

Characters	Lines	Testers H-198	H-224	H-240	H-297	H-323	H-319	H-414	H-406	H-403	H-440	Mean
1. Days to flower	$23D_2A$	61.60	56.00	64.30	55.90	63.80	64.90	62.60	61.20	52.70	55.60	59.90
	$18D_2A$	90.00	60.30	60.40	62.30	64.20	62.10	61.70	59.20	62.30	51.10	60.40
	18A	53.30	55.20	60.80	59.20	54.70	55.90	58.40	50.60	61.50	50.80	56.00
	L-110	57.40	50.70	53.20	55.70	51.20	51.20	53.60	49.40	53.40	55.50	53.10
	L-111	56.60	54.80	57.10	57.50	57.20	58.60	55.10	54.20	55.20	54.80	56.10
	Mean	57.80	55.40	59.20	58.10	58.20	58.50	58.30	54.90	57.00	53.60	
2. Plant height (cm)	$23D_2A$	173.00	162.60	157.00	178.90	171.10	159.60	172.10	176.40	145.20	177.90	167.40
	$18D_2A$	173.00	190.10	156.60	178.90	161.70	160.40	199.40	205.80	144.90	176.30	174.70
	18A	179.50	178.20	140.90	163.40	182.40	182.40	217.30	145.30	175.30	172.90	173.80
	L-110	161.60	144.30	175.20	185.00	188.20	177.30	181.00	172.40	143.80	156.70	168.50
	L-111	181.80	134.10	172.90	185.10	202.20	170.20	193.10	158.30	143.70	154.40	169.60
	Mean	173.80	161.90	160.50	178.30	181.10	170.00	192.60	171.60	150.60	167.60	
3. Total tillers per plant	$28D_2A$	6.50	4.50	7.50	5.00	5.20	6.20	7.40	6.00	5.90	3.20	5.70
	$18D_2A$	5.90	4.00	5.00	6.20	5.10	3.50	6.70	6.90	6.00	4.30	5.40
	18A	4.60	3.40	3.20	5.00	4.60	3.20	4.80	3.70	5.40	4.30	4.20
	L-110	4.90	4.80	3.00	8.50	3.50	3.10	4.50	8.50	4.90	4.00	5.00
	L-111	5.20	3.80	2.90	6.70	5.90	3.40	4.40	5.70	4.50	5.40	4.80
	Mean	5.40	4.10	4.30	6.30	4.90	3.90	5.60	6.20	5.30	4.20	
4. Ears per plant	$23D_2A$	8.50	5.30	5.70	6.00	5.50	6.10	6.20	5.60	6.60	3.70	5.90
	$18D_2A$	8.40	8.70	3.70	8.90	4.70	5.40	6.00	6.40	5.90	5.90	6.40
	18A	4.40	4.30	4.50	5.40	6.40	5.10	4.20	4.50	6.50	5.00	5.00
	L-110	3.50	5.60	5.00	7.80	5.70	4.50	5.00	3.60	4.80	3.50	4.90
	L-111	5.30	3.70	2.70	5.00	4.60	3.30	7.20	4.80	4.20	6.70	4.70
	Mean	6.00	5.50	4.30	6.60	5.40	4.90	5.70	5.00	5.60	5.00	
5. Ear length (cm)	$23D_2A$	25.20	26.90	26.90	23.70	35.90	29.30	22.40	19.70	23.70	27.00	26.00
	$18D_2A$	33.30	38.80	32.50	34.00	41.00	36.30	30.40	28.30	32.20	38.10	34.50
	18A	38.20	39.00	35.40	28.30	41.30	39.40	31.40	29.70	33.00	37.00	35.30
	L-110	27.90	26.10	27.60	41.10	28.50	35.10	30.20	25.60	20.30	27.50	29.00
	L-111	36.70	37.80	30.80	43.20	45.20	45.20	40.40	30.20	28.10	39.40	37.70
	Mean	32.30	33.70	30.50	34.10	38.40	37.10	31.00	26.70	27.50	33.80	
6. 1000-seed weight (gm)	$23D_2A$	6.52	7.57	5.60	8.03	6.79	7.62	7.20	6.45	7.58	8.60	7.10
	$18D_2A$	9.67	17.36	8.65	8.57	9.92	6.60	8.88	9.99	9.52	9.22	9.14
	18A	8.36	6.38	7.41	8.21	5.69	8.49	6.16	7.48	8.23	8.28	7.47
	L-110	9.08	7.35	6.23	7.19	8.07	8.39	7.79	6.53	7.56	7.67	7.59
	L-111	7.26	8.62	7.02	7.60	8.90	5.66	6.85	6.20	8.35	6.02	7.25
	Mean	8.18	8.06	6.98	7.92	7.87	7.35	7.18	7.33	8.25	7.96	
7. Grain yield per plant (gm)	$23D_2A$	53.00	39.50	40.33	88.60	35.10	47.45	29.52	41.51	85.18	46.89	50.71
	$18D_2A$	49.10	56.35	52.41	95.03	48.31	55.66	27.13	64.00	52.67	53.33	55.40
	18A	94.58	62.87	38.47	72.10	43.00	53.50	50.03	42.71	27.36	37.36	52.20
	L-110	87.98	48.33	81.33	90.27	33.58	45.17	75.88	104.25	63.29	106.37	73.69
	L-111	58.16	29.09	38.02	80.12	59.58	56.47	79.95	68.97	54.50	70.63	59.55
	Mean	68.56	47.23	50.21	85.22	43.91	51.65	52.50	64.29	56.60	62.92	
Male sterile lines:		$23D_2A$	$18D_2A$	18A	L-110	L-111						
Index values and ranks*:		23(IV)	20(II)	23(IV)	17(I)	22(III)						
Testers:		H-198	H-224	H-240	H-297	H-323	H-319	H-414	H-406	H-403	H-440	
Index values and ranks*:		28(II)	37(V)	55(X)	25(I)	44(VII)	49(IX)	46(VIII)	38.5(VI)	30(III)	32.5(IV)	

* Ranks in brackets based on overall mean performance of males/females considering all the characters, simultaneously.

components due to females (σ_f^2) were higher than those due to males (σ_m^2) for all the characters except ear length and 1000-seed weight. The variance components of specific combining ability (σ_{fm}^2) were considerably higher than those of σ_m^2 and σ_f^2 for plant height, total tillers, number of ears and grain yield per plant, but lower for days to flower and ear length. The preponderance of non-additive gene action in the inheritance of most of the characters is also shown by high values of the $\sigma_{sca}^2/\sigma_{gca}^2$ ratio*. There was evidence of overdominance in grain yield, 1000-seed weight, total tillers and ears per plant. Plant height and ear length showed partial dominance whereas negative heterosis was observed for days to flower.

* σ_{sca}^2 and σ_{gca}^2 are the variance components due to specific combining ability (σ_{fm}^2) and general combining ability $(\sigma_f^2 + \sigma_m^2)/2$, respectively.

To compare the general combining ability of the parents involved in the crosses, the mean performance of the parents over all cross combinations (Table 2) and the general combining ability effects were used (Table 3). The lines and testers were ranked on the basis of their mean performance over all the crosses with regard to all the characters, and these rankings are presented in Table 2. Among the male sterile lines, L-110 was found to be the best with an index value of 17. This line obtained first

Table 3. *General combining ability effects of the male-sterile lines and their testers*

	Days to flower	Plant height	Total tillers	Ears per plant	Ear length	1000-seed weight	Grain yield per plant	Index values & ranks *
Male sterile lines								
1. $23D_2A$	2.76	−5.16	0.71	0.49	−6.49	−0.61	−7.66	23(IV)
2. $18D_2A$	3.27	5.54	0.34	0.99	1.99	1.43	−2.97	20(II)
3. 18A	−1.07	4.34	−0.77	−0.36	2.78	−0.24	−5.87	23(IV)
4. L-110	−3.97	−2.29	−0.06	−0.51	−3.50	−0.12	15.33	18(I)
5. L-111	−0.99	−2.43	−0.23	−0.64	5.23	−0.46	1.16	21(III)
Standard error	1.09	2.40	0.26	0.19	0.55	0.20	2.05	
Testers								
1. H-198	0.68	7.94	0.38	0.63	−0.24	0.47	10.20	28(II)
2. H-224	−1.69	−10.19	−0.92	0.14	1.21	0.35	−11.14	36(V)
3. H-240	2.06	5.99	0.72	−1.09	−1.94	−0.73	−8.16	56(X)
4. H-297	1.04	6.14	1.26	1.22	1.55	0.21	26.85	24(I)
5. H-323	1.12	8.41	−0.13	−0.02	5.90	0.17	−14.45	45(VII)
6. H-319	1.42	−1.79	−1.11	−0.53	4.53	−0.35	−6.12	49(IX)
7. H-414	1.16	20.01	0.54	0.30	−1.53	−0.53	−5.87	46(VIII)
8. H-406	−2.16	−0.86	1.12	−0.45	−5.79	−0.38	5.89	38(VI)
9. H-403	−0.08	−21.79	0.30	0.20	−1.55	0.54	−1.77	29(II)
10. H-440	−3.53	−1.86	−0.76	−0.45	1.32	0.25	4.55	33(IV)
Standard error	1.55	3.39	0.37	0.27	0.77	0.28	2.90	

* Ranks based on overall sca effects.

Table 4. *Specific combining ability effects of the fifty hybrids with regard to different characters*

Characters	Lines	Tester H-198	H-224	H-240	H-297	H-323	H-319	H-414	H-406	H-403	H-440
1. Days to flower	$23D_2A$	1.05	−2.18	2.37	−5.01	2.81	3.61	1.57	3.49	−7.09	−0.74
	$18D_2A$	−1.06	1.61	−2.04	0.88	2.70	0.30	0.16	0.98	2.00	−5.75
	18A	−3.42	0.85	2.70	2.12	−2.46	−1.56	1.20	−3.28	5.54	−1.71
	L-110	3.58	−0.75	−2.00	0.52	−3.06	−3.36	−0.70	−1.58	0.34	5.89
	L-111	−0.20	0.37	−1.08	0.34	−0.04	1.06	−2.18	0.24	−0.84	2.21
2. Plant height (cm)	$23D_2A$	−2.24	5.49	−4.31	5.46	−4.51	−5.91	−15.21	9.96	−0.31	12.46
	$18D_2A$	−12.94	22.29	−15.41	−5.24	−24.71	−15.81	1.39	28.66	−11.31	0.16
	18A	−5.24	11.59	−29.91	−19.54	−2.81	6.19	20.49	−30.64	20.29	−2.04
	L-110	−16.51	−15.68	11.02	8.69	9.62	8.92	−9.18	3.09	−4.58	−11.61
	L-111	3.83	−25.74	8.86	8.93	23.76	1.96	3.06	−10.87	−4.54	−13.77
3. Total tillers per plant	$23D_2A$	0.38	−0.32	2.48	−2.00	−0.41	1.47	1.12	−0.87	−0.14	−1.78
	$18D_2A$	0.15	−0.42	0.35	−0.43	−0.14	−0.76	0.79	0.41	0.33	−0.31
	18A	−0.04	0.06	−0.34	−0.52	0.47	0.05	0.00	−1.68	0.84	0.80
	L-110	−0.45	0.75	−1.25	2.27	−1.34	−0.67	−1.01	2.41	−0.37	−0.21
	L-111	0.02	−0.08	−1.18	0.64	1.23	−0.29	−0.94	−0.22	−0.60	1.36
4. Ears per plant	$23D_2A$	1.97	−0.74	0.89	−1.12	−0.38	0.73	0.00	0.15	0.50	−1.75
	$18D_2A$	1.37	2.16	−1.61	1.28	−1.68	−0.47	−0.70	0.45	−0.70	−0.05
	18A	−1.28	−0.89	0.54	−0.87	1.37	0.58	−1.15	−0.10	1.25	0.40
	L-110	−2.03	0.56	1.19	1.68	0.82	0.13	−0.20	−0.85	−0.30	−0.95
	L-111	−1.10	−1.21	−0.98	−0.99	−0.15	−0.94	2.13	0.48	−0.77	2.38
5. Ear length (cm)	$23D_2A$	−0.57	−0.32	2.23	−3.86	3.99	−1.24	−2.08	−0.52	2.67	−0.33
	$18D_2A$	−0.95	3.10	−0.05	−2.04	0.61	−2.72	−2.56	−0.40	2.69	2.29
	18A	3.16	2.51	2.06	−8.53	0.12	−0.41	−2.35	0.21	2.70	0.40
	L-110	−0.86	−4.11	0.54	10.55	−6.40	1.57	2.73	2.39	−3.72	−2.82
	L-111	−0.79	−1.14	−4.99	3.92	1.57	2.94	4.20	−1.74	−4.65	0.35
6. 1000-seed weight (gm)	$23D_2A$	−1.05	0.12	−0.77	0.72	−0.48	0.88	−0.37	−0.27	−0.06	1.25
	$18D_2A$	0.06	0.87	0.24	−0.78	0.61	−2.22	0.27	1.23	−0.16	−0.17
	18A	0.42	−1.44	0.67	0.53	−1.95	1.37	−0.78	0.39	0.22	0.56
	L-110	1.02	−0.59	−0.63	−0.61	0.31	1.15	0.73	−0.68	−0.57	−0.17
	L-111	−0.46	1.02	0.50	0.14	1.48	−1.25	0.13	−0.67	0.56	−1.48
7. Grain yield per plant (gm)	$23D_2A$	−7.91	−0.07	−2.22	11.04	−1.16	2.86	−15.32	−15.09	36.24	−8.37
	$18D_2A$	−16.50	12.09	5.17	12.78	7.36	6.38	−22.40	2.71	−0.96	−6.62
	18A	31.88	21.51	−5.87	−7.25	4.95	7.12	3.40	−15.65	−23.37	−19.69
	L-110	4.08	−14.23	16.29	−10.28	−25.67	−22.41	8.05	24.66	−8.64	28.12
	L-111	−11.57	−19.30	−13.35	−6.26	14.50	3.06	26.29	3.55	−3.26	6.55

Standard errors: (1) 0.49; (2) 1.08; (3) 0.12; (4) 0.09; (5) 0.25; (6) 0.09; (7) 0.92

rank for grain yield and days to flower, second place for 1000-seed weight and plant height and third for total tillers. With index values of 20 and 22, respectively, the lines 18 D$_2$A and L-111 occupied second and third positions, although there was little difference between them in yielding ability. 23 D$_2$A and 18 A were the poorest general combiners.

It is interesting to note that the rankings of the male sterile lines based on gca-effects (Table 3) were the same as those obtained on the basis of mean performance (Table 2). The two lines, 18 A and 23 D$_2$A, were again the poorest general combiners with an index value of 23.

Comparison of the testers (Table 2 and 3) following the same procedure as for lines indicated that: (i) all the testers occupied the same rank by both methods of comparison; (ii) H-297 was the best parent, followed by H-198, H-403 and H-440, in that order. H-297 and H-198 showed high general combining ability for yield. Both these testers were tall type and medium-late.

In general, it was found that all those lines and testers which showed high general combining ability effects for grain yield proved to be high general combiners for other characters too (Table 2).

The performance of lines and testers in their specific cross combinations could be studied by comparing the actual mean performance of the crosses and the specific combining ability effects. For this purpose, the 5 best combinations with respect to each trait were selected, firstly on the basis of their *per se* performance (Table 2), and secondly, on the basis of their specific combining ability effects (Table 4). These were:

Characters	Per se performance	Sca-effects
Days to flower	L-110×H-406; 18A×H-406; L-110×H-224; 18A×H-440; **18D$_2$A×H-440**	23D$_2$A×H-403; **18D$_2$A×H-440**; 23D$_2$A×H-297; 18A×H-198; L-110×H-319
Plant height	**L-111×H-224**; *18A×H-240*; L-111×H-403; 18D$_2$×H-403	18A×H-406; *18A×H-240*; **L-111×H-224**; 18D$_2$A×H-323; 18A×H-297
Total tillers	*L-110×H-297*; *L-110×H-406*; 23D$_2$A×H-240; 23D$_2$A×H-414; 18D$_2$A×H-406	*L-110×H-297*; *L-110×H-406*; 23D$_2$A×H-319; L-111×H-440; L-111×H-323
Ears per plant	**18D$_2$A×H-297**; **23D$_2$A×H-198**; **18D$_2$A×H-198**; L-110×H-297; **L-111×H-414**	L-111×H-440; 18D$_2$A×H-224; **L-111×H-414**; **23D$_2$A×H-189**; **18D$_2$A×H-198**
Ear length	L-111×H-319; L-111×H-323; **L-111×H-297**; 18A×H-323; L-110×H-297	L-110×H-297; L-111×H-414; 23D$_2$A×H-323; **L-111×H-297**; 18A×H-198
1000 seed weight	18D$_2$A×H-224; **18D$_2$A×H-406**; 18D$_2$A×H-198; 18D$_2$A×H-403; 18D$_2$A×H-440	L-111×H-323; 18A×H-319; 23D$_2$A×H-440; **18D$_2$A×H-406**; L-110×H-319
Grain yield	**L-110×H-440**; **L-110×H-406**; 18D$_2$A×H-297; **18A×H-198**; L-110×H-297	23D$_2$A×H-403; **18A×H-198**; **L-110×H-440**; L-111×H-414; **L-110×H-406**

From the above list the following points were evident:

i) It was only in the yield and ears per plant where three crosses were common (the bold letters) to both comparisons, though the rankings occupied by them were different. For plant height and total tillers, there were only two common crosses; one of them in the case of plant height and both in the case of tillers occupied the same position (in italics). In most of the other cases, only one cross was common and that too occupied different positions.

ii) It seems that ranking on the basis of *per se* performance is not reflected by the ranking based on sca-effects.

iii) The crosses showing high mean performance for grain yield did not show high sca-effects or high mean performance for other characters also including yield components.

iv) In comparison with the mean grain yield (83.7 gm) per plant of the control, Hybrid-1, the means of the five crosses selected on the basis of their *per se* performance were found to be superior.

On the other hand, only three out of five crosses selected on the basis of sca-effects were found to be better than the control, while the crosses, 23 D$_2$A × × H-403 and L-111 × H-414, did exceptionally poorly (Table 2).

Discussion

The full exploitation of heterosis in pearl millet or in any other crop where crossing is tedious, depends upon (i) the availability of male sterile lines and (ii) the selection of inbreds with higher general combining ability against the available male sterile parents. Tests on the suitability of only a few male sterile lines, such as 23 A, 18 A and L-103 (Murty *et al.*, 1967) and 23 A and L-101A (Gupta *et al.* 1971), have been reported. The present investigation has revealed that, of the five male sterile lines, L-110 was the best general combiner, followed by 18 D$_2$A and L-111. 23 D$_2$A and 18 A were found to be the poorest, although their relative performance was the same as reported by Murty *et al.* (1967). Of the ten inbreds used as testers, H-297 proved to be the best general combiner, followed by H-198, H-403 and H-440.

The order of suitability of males and females as general combiners, remained the same whether it was based on *per se* performance or on gca-effects, indicating that suitable general combiners may be selected on the basis of mean performance itself. It does not seem to be necessary to estimate the gca-effects as is general in a line × tester analysis (Murty *et al.* 1967, Rao *et al.* 1968, Singh *et al.* 1971 and Gupta *et al.* 1971). Such comparison between *per se* performance and the gca-effects will also be useful in other designs, such as diallel.

In contrast to the high association between *per se* performance and gca-effects, there was no correlation between the mean performances of the crosses and their sca-effects. A comparison of mean performance on yield suggested that L-110 × H-440 was the best combination, followed by L-110 × × H-406, whereas in a similar comparison on the basis of sca-effects, the cross 23 D_2A × H-403 was found to be the best, followed by 18 A × H-198.

Keeping in view the objectives of heterosis breeding, the selection of cross combinations on the basis of *per se* performance would be more realistic. High sca-effects denote, undoubtedly, a high heterotic response, but this may be due to the very poor performance of the parents in comparison with their hybrids. Indeed, even with the same amount of heterotic effect, the sca-effects may be lower where the mean performances of the parents are higher. This suggests that estimates of sca-effects may not always lead to the correct choice of hybrid combination. These estimates may also be biased because of non-fulfilment of any of the assumptions involved in the models. Although the relative amounts of gca and sca-effects play a vital role in planning the most appropriate breeding programme, this objective could be fulfilled by the analysis of variance for combining ability itself. It is, therefore, advisable to give more emphasis to the *per se* performance than to the estimates of specific combining ability.

Although in the best hybrid combinations it was not always both parents which were the best general combiners, in all the good combinations at least one good general combiner was involved. This was particularly so when the *per se* performance was considered. The high performance of such combinations as high × high and high × medium general combiners indicates more additive × additive types of gene-interaction, whereas a few crosses with low × × low general combiners show non-additive types of epistatic interaction. In general, it seems that high gene-interaction in the present material is accountable mostly to additive × additive and additive × dominance types of gene action.

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