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HETEROSIS, INBREEDING DEPRESSION AND COMBINING ABILITY IN SORGHUM (*SORGHUM BICOLOR* (L.) MOENCH)

J. N. REDDY* AND P. JOSHI

Department of Genetics and Plant Breeding, Rajasthan College of Agriculture
Udaipur 313001

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ABSTRACT

Heterosis, inbreeding depression and combining ability were studied in a 6 x 6 diallel (excluding reciprocals) from F_1 to F_4 generations for grain yield and its five components in sorghum (*Sorghum bicolor* (L.) Moench). Among the different characters studied, highest heterosis in F_1 over better parent (87.5%) was recorded for grain yield/plant followed by number of grains/panicle (50.1%) and number of primaries/panicle (40.5%). All the hybrids which showed higher estimates of heterosis in F_1 in general also exhibited high inbreeding depression in F_2 and other segregating generations studied. The general (gca) as well as specific combining ability (sca) variances were found significant in all the four (F_1-F_4) generations for grain yield and its components studied except for number of primaries/panicle in F_3 and F_4 and for number of whorls/panicle in F_2 and F_3 generations. The magnitude of sca variance declined in F_2 and later generations. The predictability ratio showed preponderance of nonadditive genetic variance for grain yield and additive genetic variance for 1000-grain weight in sorghum. The study of F_1 and F_2 would be sufficient to assess repeatability of gca effects in advance generations. Four cross combinations, viz SPV 451 x SPV 474, SPV 474 x IS 508, CSV 10 x SPV 451 and CSV 10 x SPV 474 were identified as promising, which can be exploited to improve grain yield in sorghum.

Key words: *Sorghum bicolor*, heterosis, inbreeding depression, combining ability.

Most of the studies on heterosis [1, 2], inbreeding depression [3] and combining ability analysis [4, 5] in sorghum are based on F_1 and/or F_2 materials. Few studies have been done simultaneously on F_1 and F_2 generations [6, 7] highlighting the importance of obtaining combining ability estimates over generations. There is only one report on sorghum, where F_1, F_2 and F_3 in a 10 x 10 diallel mating system were studied simultaneously [8]. Studies on other autogamous crops have provided conflicting evidence on repeatability of combining ability estimates over generations. The present investigation has been, therefore, undertaken to study heterosis in F_1 over the better parent (BP), inbreeding depression over three (F_2, F_3

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[*] Present address: Central Rice Research Institute, Cuttack 753006.

and F_4) segregating generations and to estimate general and specific combining ability (gca, sca) from F_1 to F_4 generations for grain yield and its component characters in sorghum.

MATERIALS AND METHODS

The parental material involved five exotic x Indian derivatives (SU 104, CSV 10, CSV 11, SPV 451 and SPV 474) and a collection from World Germplasm (IS 508). Diallel crosses (excluding reciprocals) were effected with these six varieties. The parents and F_1–F_4 generations of the crosses were sown in a randomized block design with three replications at the research farm of the Rajasthan College of Agriculture, Udaipur. The plant- to-plant and row-to-row distances were 15 cm and 45 cm, respectively. Individual plots of parents and F_1s consisting of single 3 m long row, while F_2, F_3 and F_4 bulks of each cross in 3-row plots were planted. Data on ten random plants in parents and F_1s, and 30 plants in F_2, F_3 and F_4 bulks were recorded for grain yield/plant and its five component characters, viz. 1000-grain weight, grains/panicle, primaries/panicle, whorls/panicle, and panicle length. Plot means were used for statistical analysis. Heterosis over better parent (BP) and inbreeding depression in F_2, F_3 and F_4 generations over their preceding generations were calculated. The combining ability effects and variances were estimated separately for four (F_1–F_4) generations according to Model 1 and Method 2 of Griffing [9]. The general predictability ratio was calculated as suggested by Baker [10].

RESULTS AND DISCUSSION

HETEROSIS AND INBREEDING DEPRESSION

Among the different characters studied, the extent of positive heterosis over the better parent was highest for grain yield/plant. Heterosis for grain yield ranged from 7.7 to 87.5%, the mean being 43.9%. Maximum heterosis was recorded in the cross SPV 451 x SPV 474 (87.5%) closely followed by SPV 474 x IS 508 (66.2%) and CSV 10 x IS 508 (64.5%). These hybrids were also superior in per se performance. The findings of the present investigation on the magnitude of heterosis for grain yield are consistent with the earlier reports [11–13] in sorghum.

Grain yield is the final product, its expression depends on the contribution of component characters and the extent of their mutual cancellation. The present study revealed that hybrids which exhibited heterosis for grain yield were not heterotic for all the characters studied. Among the direct components, number of grains/panicle was important. The range of heterosis for this trait was from –5.7 to 50.1%, the mean being 25.8%. Second, twelve of the thirteen heterotic hybrids for grain yield also depicted heterosis for this trait. Nandanwankar et al. [2] and Vashi et al. [14] also reported that number of grains/panicle was the major contributor to heterosis for grain yield in sorghum. Among the remaining components, primaries/panicle exhibited maximum heterosis (40.5%), followed by whorls/panicle (30.4%), panicle length (25.4%) and 1000-grain weight (18.6%). Patel et al. [1] also observed significant heterosis for these attributes in sorghum.

One of the characteristics of heterosis is that the increased vigour is confined to F_1 generation. There is a considerable depression from F_1 to F_2 and later generations. It may be seen from the present results that hybrid combinations which showed higher estimates of heterosis, in general, also exhibited high inbreeding depression in one or other segregating generations studied. In the present study, nine out of thirteen heterotic hybrids for grain yield exhibited significant inbreeding depression in F_2 as well as in F_3 generations. The magnitude of inbreeding depression varied from 3.5 to 36.3% in F_2 and from 12.0 to 28.1% in F_3 generation. Similar variations in the magnitude of inbreeding depression for grain yield of sorghum has also been recorded by Kulkarni et al. [3] and Goyal and Joshi [4] in F_1 to F_2 and F_3 generations.

Variations in inbreeding depression in component characters from F_1 to F_2 and onwards revealed complexities in the inheritance of grain yield in sorghum. Among the different component traits, number of grains/panicle showed maximum inbreeding depression in F_2 (31.0%) as well as in F_3 (26.1%) generation. As regards 1000- grain weight, not only all the heterotic crosses showed significant depression, the test weight of the five nonheterotic crosses also declined significantly in F_2 or F_3 generations. Almost all the heterotic crosses for number of whorls/panicle and panicle length depicted significant inbreeding depression in F_2 or in one of the later segregating generations.

COMBINING ABILITY ANALYSIS

The general as well as specific combining ability (gca, sca) variances (Table 1) were significant in all the four (F_1–F_4) generations for grain yield and its component characters, except for number of primaries/panicle in F_3 and F_4 and for number of whorls/panicle in F_2 and F_3 generations. In self-fertilizing crops, heterozygosity is expected to decline in the advanced generations and ultimately specific combining ability variance should be nonsignificant. In the present study, though the magnitude of sca variance declined in F_2 and later generations for grain yield as well as other attributes, it still remained significant for most of the characters in all the generations. Significant contribution of sca variance in advance generations could be due to additive x additive interaction component. Another reason could be dissipation of linkages inflating the estimates and their likelihood of being in a more balanced phase. Bhullar et al. [15] explained significant contribution of sca variance in the advanced generations in wheat on the basis of evolutionary divergence among the progenies of the same parental arrey, each progeny bulk having different interaction system and on the presumption of high additive x additive interaction.

Table 1. Analysis of variance (mean squares) for combining ability in sorghum

Source	Generation	d.f.	Grain yield/ plant	1000-grain weight	No. of grains per panicle ($\times 10^3$)	No. of primaries per panicle	No. of whorls per panicle	Panicle length
Gca	F_1	5	305.2^{**}	67.1^{**}	322.6^{**}	110.2^{**}	2.2^{*}	9.3^{**}
	F_2	5	102.3^{**}	64.5^{**}	305.0^{**}	45.2^{**}	1.4^{*}	9.1^{**}
	F_3	5	59.7^{**}	53.0^{**}	228.0^{**}	23.6^{**}	1.0^{*}	7.1^{**}
	F_4	5	31.5^{**}	52.5^{**}	159.0^{**}	18.7^{**}	1.2^{*}	6.3^{**}
Sca	F_1	15	343.2^{**}	10.3^{**}	178.3^{**}	63.3^{**}	1.0^{**}	4.3^{**}
	F_2	15	107.6^{**}	5.2^{*}	86.0^{**}	20.7^{**}	0.2	1.0^{**}
	F_3	15	30.8^{**}	4.5^{*}	33.4^{**}	10.1	0.2	0.8^{**}
	F_4	15	18.6^{**}	3.6^{*}	30.1^{**}	7.0	0.3^{*}	1.5^{**}
Error	F_1	40	11.3	0.5	8.9	15.8	0.2	0.4
	F_2	40	9.3	0.3	10.8	7.7	0.1	0.3
	F_3	40	5.5	0.3	6.7	6.7	0.1	0.2
	F_4	40	4.0	0.3	4.6	4.1	0.1	0.2
Predictability ratio	F_1	—	0.2	0.6	0.3	0.3	0.4	0.4
	F_2	—	0.2	0.8	0.5	0.4	0.8	0.8
	F_3	—	0.3	0.8	0.7	0.6	0.7	0.7
	F_4	—	0.3	0.8	0.6	0.6	0.6	0.5

*,**Significant at 5% and 1% levels, respectively.

The predictability ratio indicated the importance of nonadditive genetic variance for grain yield and additive genetic variance for 1000-grain weight over generations. However, for the remaining characters preponderance of nonadditive genetic variance in F_1 and additive genetic variance in the segregating generations was observed. Similar results were reported by Goud et al. [16] and Singhania [17] for grain yield and Desai et al. [5] for 1000-grain weight from F_1 material. On the other hand, Niehaus and Pickett [6] and Govil and Murty [7] from F_1 and F_2 and Govil et al. [8] from simultaneous study of F_1, F_2 and F_3 generation material reported importance of both additive and nonadditive components of genetic variance in the inheritance of grain yield.

The magnitude and direction of combining ability effects provide guidelines for discriminating parents and their utilization. In the present study, significant gca effects have been recorded for all the characters studied (Table 2). However, none of the parents studied was a good combiner for all the attributes. In other words, the optimum level of different

Table 2. Estimates of general combining ability effects of different sorghum varieties

Character	Generation	SU 104	CSV 10	CSV 11	SPV 451	SPV 474	IS 508	SE (gi) ±
Grain yield/plant	F_1	-8.52**	3.98**	-6.01**	-0.20	5.57**	5.48**	1.09
	F_2	-4.51**	2.36**	-2.75**	-1.67	5.04**	1.53	0.99
	F_3	-3.53**	3.48**	-1.63*	-1.50*	2.76**	0.42	0.76
	F_4	-2.59**	2.63**	-1.03	-1.44*	1.28*	1.15	0.65
1000-grain wt.	F_1	-0.23	1.25**	-3.06**	-0.49*	-2.43**	4.97**	0.22
	F_2	0.24	1.29**	-2.62**	-1.16**	-2.61**	4.86**	0.16
	F_3	0.35*	1.09**	-2.37**	-0.93**	-2.51**	4.36**	0.18
	F_4	0.18	0.94**	-2.14**	-1.10**	-2.39**	4.51**	0.18
Grains/panicle	F_1	-260.01**	30.79	24.07	9.77	355.90**	-140.51**	30.50
	F_2	-161.97**	-13.38	67.21*	7.39	328.48**	-227.73**	33.54
	F_3	-145.55**	40.70	73.34**	-3.36	255.82**	-220.95**	26.43
	F_4	-108.20**	20.94	79.73**	10.79	199.27**	-202.53**	21.96
Primaries/panicle	F_1	-1.29	-3.76**	-3.09*	-0.19	2.06	6.27**	1.28
	F_2	0.15	-3.08**	-1.05	-1.52	2.42**	3.08**	0.90
	F_3	0.20	-1.98*	-0.17	-1.85*	1.74*	2.07**	0.84
	F_4	-0.24	-1.83*	0.44	-1.47	2.31**	0.78	0.65
Whorls/panicle	F_1	-0.09	-1.01**	0.46**	0.14	0.27*	0.23	0.13
	F_2	-0.07	-0.78**	0.37**	0.26*	0.01	0.21	0.12
	F_3	-0.07	-0.64**	0.37**	0.09	0.04	0.21	0.11
	F_4	-0.06	-0.72**	0.40**	0.13	-0.01	0.26**	0.11
Panicle length	F_1	0.33	-2.00**	0.19	1.14**	0.23	0.57**	0.19
	F_2	0.52**	-1.76**	0.62**	1.00**	-0.84**	0.47**	0.18
	F_3	0.45**	-1.56**	0.61**	0.91**	-0.72**	0.31*	0.14
	F_4	0.44**	-1.41*	0.78**	0.88**	-0.68*	0.04	0.15

*,**Significant at 5% and 1% levels, respectively.

attributes was not present in any of the parents used. The best parent identified was CSV 10, which was a good combiner for grain yield and 1000- grain weight. Nandanwankar et al. [12] also found CSV 10 (SPV 346) as a good combiner for grain yield.

Another parent, SPV 474, combined well for grain yield, number of grains and number of primaries, but it was a poor combiner for 1000-grain weight. Among the other parents, IS 508 was a good combiner for 1000-grain weight, number of primaries and panicle length, and CSV 11 for number of grains, number of whorls and panicle length. While parents, SU 104 and SPV 451 were poor combiners for most of the attributes. Looking to generally similar magnitude and direction of gca effects over generations, it could be concluded that the estimates from F_1 and F_2 generations would be sufficient to assess their repeatability in advance generations, reliability of F_2 estimates being marginally better. Similar observations were also made by Bhullar et al. [15] in wheat.

The magnitude of sca effects is of vital importance in selecting cross combinations with higher probability of generating desired transgressive segregates, particularly when the estimates are available over generations. The repeatability of sca effects of grain yield over generations was much less than for gca effects. This may be due to gradual reduction in the heterotic effects for grain yield from F_2 onwards. Out of the nine crosses, which exhibited significant and positive sca effects in F_1, only in three crosses (SU 104 x CSV 11, SU 104 x SPV 451 and SPV 451 x SPV 474) the effects were found to be significantly positive in all the generations studied. The dissipation of sca effects in the other crosses was variable. The inheritance of grain yield thus appears more complex in comparison to its direct components. The estimates of gca and sca effects in different crosses over generations indicated importance of additive, dominance as well as interaction effects in the inheritance of grain yield in sorghum.

Out of the eleven crosses with significantly positive sca effects for number of grains/panicle in the F_1, only two crosses (SU 104 x CSV 10 and SU 104 x SPV 451) exhibited similar magnitude of sca effects in all the segregating generations studied. Interestingly, in a good number of crosses, the sca effects were of similar magnitude over generations for test weight. Among the eight crosses, which depicted significant and positive sca effects in F_1 set, the crosses SU 104 x CSV 10, SU 104 x CSV 11, CSV 10 x IS 508, SPV 451 x SPV 474 and SPV 474 x IS 508 exhibited similar values over generations and in the cross SPV 451 x IS 508 in all generations except in F_1. Higher values of gca variance in comparison to sca variance and similar magnitude to sca effects over generations revealed the important role of additive and additive x additive type of interaction in the inheritance of test weight. As regards number of primaries/panicle, of the four crosses, viz SU 104 x IS 508, CSV 10 x SPV 451, CSV 10 x IS 508 and SPV 474 x IS 508 which depicted significant and positive sca effects in F_1, the same effects were also present in F_2 set in the first two crosses.

The ANOVA for combining ability (Table 1) revealed nonsignificant sca variance for number of whorls/panicle in the F_2 and F_3 diallel set. Out of the fifteen crosses studied, five crosses depicted significant and positive sca effects for number of whorls in F_1 diallel set and only one cross (CSV 10 x CSV 11) in F_4 generation. The nonsignificant estimates of sca effects in the segregating generations revealed preponderance of additive gene effects in the inheritance of this trait. As regards panicle length, out of the six crosses showing positive sca effects in F_1, significant positive sca effects in all other generations were recorded in only one cross, CSV 11 x SPV 474. The estimates of sca effects in the segregating generations revealed complexities in the inheritance of panicle length. In majority of crosses, for which sca effects were nonsignificant in the F_1 diallel set, the effects were significant in the segregating generations.

Table 3. Best specific combiners along with gca, per se performance and heterobeltiosis in sorghum

Character	Mean	Specific combination	Gca	BP heterosis (%)
Grain yield per plant (g)	101.3	SPV 451 x SPV 474	(L x H)	87.5**
	100.0	SPV 474 x IS 508	(H x H)	66.2**
	98.4	CSV 10 x SPV 451	(H x L)	64.5**
	92.9	CSV 10 x SPV 474	(H x H)	55.3**
1000-grain weight (g)	42.4	CSV 10 x IS 508	(H x H)	9.7**
	40.6	SPV 451 x IS 508	(L x H)	5.8*
	35.0	SPV 451 x SPV 474	(L x L)	18.6**
	39.0	SPV 474 x IS 508	(L x H)	0.6
Grains/panicle	2898.2	SPV 451 x SPV 474	(L x H)	28.1**
	2863.6	CSV 10 x SPV 474	(L x H)	26.6**
	2767.0	CVS 10 x SPV 451	(L x L)	50.1**
	2528.7	CSV 11 x SPV 451	(H x L)	48.2**
Primaries/panicle	71.2	SPV 474 x IS 508	(H x H)	36.4**
	68.4	SU 104 x IS 508	(L x H)	31.1**
	59.0	CSV 10 x SPV 451	(L x L)	40.5**
Whorls/panicle	14.9	CSV 11 x SPV 474	(H x H)	30.3**
	13.7	CSV 11 x SPV 451	(H x L)	19.7**
	13.0	SU 104 x IS 508	(L x L)	9.9*
	12.2	CSV 10 x IS 508	(L x L)	3.1
Panicle length (cm)	29.9	CSV 11 x SPV 474	(H x L)	25.4**
	28.7	SU 104 x SPV 451	(L x H)	11.3*
	28.2	SPV 451 x SPV 474	(H x L)	9.4**
	28.1	SPV 474 x IS 508	(L x H)	8.6**

*,**Significant at 5% and 1% levels, respectively.

H—high, L—low general combiner.

On the basis of present findings (Table 3), four cross combinations, viz. SPV 451 x SPV 474, SPV 474 x IS 508, CSV 10 x SPV 451 and CSV 10 x SPV 474, showed high BP heterosis, significant sca effects over generations, and also involved parents in the high gca for grain yield and some of its components. Such crosses should be exploited to develop strains with good grain yield in sorghum.

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