Theoretical and Applied Genetics 45, 294–299 (1975)

Heterosis, Combining Ability and Reciprocal Effects for Agronomic and Chemical Characters in Sesame

D. S. MURTY

Department of Botany, Osmania University, Hyderabad (India)

Summary. The extent of heterosis was examined for six agronomic and two chemical characters in a complete diallel cross experiment involving a set of ten self-pollinated varieties of sesame (*Sesamum indicum* L.) of diverse ecogeographic origin. The magnitude of general and specific combining ability variances and differences in reciprocal F_1 hybrids were also investigated.

Heterosis was, on average, highest for seed yield (33%), followed by number of capsules per plant (16%). Mean percent heterosis was small for earliness, plant height and number of primary branches, while it was insignificant for number of secondary branches and percentage of oil. Significant negative heterosis was observed for percentage of protein.

Percent heterosis was generally higher in Indian × exotic crosses than in Indian × Indian and exotic × exotic crosses. The exotic lines appeared to be useful in Indian sesame breeding programmes, particularly in the improvement of earliness, number of secondary branches, seed yield and protein content.

Additive as well as non-additive gene action seemed to govern the expression of the various characters studied. General combining ability variances were predominant for days to flowering, plant height, number of primary branches and number of secondary branches, while specific combining ability variances were in moderate to high proportions for seed yield, percentage of oil and percentage of protein. T.M.V.-2 and S. I. 770 were the best general combiners for many of the characters while S. I. 1783 and Sel-R were found to be the best for earliness and oil content respectively. Significant variances due to reciprocal effects were also detected for some of the characters.

Isolation of pure lines was preferred to production of hybrids in sesame, and crossing selected sibs in the early segregating generations followed by inbreeding seemed to be a desirable breeding procedure.

Introduction

Sesame (*Sesamum indicum* L.) is generally considered to be a self-pollinated crop. However, varying degrees of natural cross-fertilization have been reported in this species (Joshi, 1961; Khidir, 1972). A considerable amount of heterosis has also been reported (Pal, 1945). Riccelli and Mazzani (1964) noted that heterosis in sesame was more conspicuous in the hybrids of cultivars from distant localities or their derivatives but the information on this aspect is limited and the few estimates of heterosis available have not been related to any particular type of gene action. Moreover, the concept of combining ability which has been instrumental to the genetic improvement of several self- and cross-pollinated crops does not seem to have found application in sesame breeding. It was felt that an appraisal of the extent of heterosis and the nature of gene action in sesame would be valuable to breeders, since ultimately it is the nature and magnitude of the genetic variance in the base population that indicate the appropriate breeding procedures to be adopted and the nature of the commercial variety (pure line, hybrid, synthetic or blend) to be produced. Diallel experiments involving diverse germplasm were initiated in sesame in order to obtain information on (i) the extent of heterosis in intervarietal crosses, (ii) magnitude of the general and specific combining ability variances, and (iii) reciprocal effects in F_1 hybrids. The results of these investigations form the subject of this paper.

Materials and Methods

The material selected for this study comprised ten self-pollinated varieties of sesame and all the possible crosses among them. The parents, both of Indian and exotic origin, exhibited a wide range of variability for the various agronomic and chemical characters examined (Table 1). The material was raised in the kharif, 1970, in a randomized complete block design with three replications. The plot size was a row of 3.5 m. The inter-plant distance was 25 cm and the inter-plot distance was 50 cm. Thus there were 14 plants per plot. Days to flowering, plant height (cm), number of primary and secondary branches, and number of capsules per plant were recorded on the middle ten plants leaving two plants on either end of the plot, while seed yield was bulked over all the ten plants. Percentage of oil and protein were determined for a single random seed sample from the plot yield. Percentage of oil was determined by extracting ground seed material in Soxhlet's apparatus for $5^1/_2$ hours with petroleum ether (40–60 °C). Percentage of crude protein was estimated by determining the total percent nitrogen of the seed by the semi-micro-Kjeldahl's procedure and multiplying it by the factor 6.25. Statistical analyses of the data were based on individual plant observations for all the characters except seed yield, oil and protein percentages. Angular transformation was used for oil and protein percentages. Analyses of combining ability were carried out according to the procedures outlined by Griffing (1956) for method I, model I, assuming fixed effects. The general combining ability variances associated with

Table 1. *Mean performance of ten sesame parents for various agronomic and chemical characters*

S. No.	Parents	Days to flowering	Plant height	No. of pri. branches	No. of sec. branches	No. of capsules per plant	Plot yield	% of oil	% of protein
1	T.M.V.-2	58.4	156.2	7.3	3.3	201.3	120.6	45.72	21.83
2	Sel-R	48.7	138.3	6.0	2.6	160.0	98.0	44.16	18.50
3	Sel-M	47.6	140.8	5.5	2.8	146.5	101.6	48.11	16.83
4	Chanda-3	48.1	146.7	6.2	3.8	174.7	116.0	46.07	21.00
5	T-85	50.2	143.0	5.9	4.2	171.3	106.6	45.14	23.56
6	Entry No. 8 (Russia)	45.8	133.9	5.5	2.2	164.3	104.3	45.04	21.09
7	S.I. 770 (Nigeria)	42.5	113.3	6.0	4.7	166.6	113.3	40.53	20.00
8	T.S. 25-12	41.6	116.2	4.5	2.2	132.3	86.2	44.36	21.27
9	N.S. 20768 (N.Sudan)	39.7	109.1	4.5	3.3	127.2	85.3	45.06	20.10
10	S. I. 1783 (U.S.A.)	36.6	85.5	4.2	2.7	106.3	57.0	45.78	24.48
	S.Em ±	0.69	2.69	0.24	0.47	8.78	13.3	0.82	0.51

Table 2. *Analysis of variance of parents and hybrids — Mean squares*

Source	d. f.	Days to flowering	Plant height	No. of pri. branches	No. of sec. branches	No. of capsules per plant	Plot yield	% of oil	% of protein
Replications	2	18.0	787.1*	6.10	3.33	5132.8	2763.7**	11.86**	2.67**
Treatments	99	564.0**	6099.2**	29.20**	70.11**	42462.8**	2090.3**	12.04**	5.30**
Indian parents	5	887.8**	5322.2**	24.26**	16.73**	17282.1**	459.2	6.22**	9.12**
Exotic parents	3	464.4**	11792.2**	20.47**	35.52**	25898.0**	1860.6**	17.34**	6.33**
Indian × Indian hybrids	29	312.33**	3224.9**	40.11**	84.79**	631237.7**	1362.5**	14.40**	4.63**
Indian × exotic hybrids	47	470.9**	3972.6**	21.81**	67.28**	32321.4**	2166.2**	10.69**	5.42**
Exotic × exotic hybrids	11	427.3**	6940.7**	22.60**	84.63**	32497.3**	2161.0**	7.96**	2.29**
Parents *vs.* hybrids	1	13.9**	9914.1**	7.54**	2.79	176261.7**	29113.3**	7.06	5.57**
Indian parents *vs.* Indian × Indian hybrids	1	263.5**	0.3	24.94**	0.00	77497.9**	13142.4**	0.93	2.20
Indian parents *vs.* Indian × exotic hybrids	1	2209.3**	5363.0**	4.97**	27.31**	40460.2**	4082.3*	0.05	2.75
Indian parents *vs.* Exotic × exotic hybrids	1	6438.6**	51805.9**	13.55**	1.30	236.1	11881.0**	0.03	0.59
Replications × Treatments	198	14.2	218.2	1.86	6.84	2314.2	531.7	2.02	0.80
Sampling error	2700	1.8	30.9	0.72	1.61	457.0	—	—	—

each common parent were also computed following Griffing (1956) as:

$$\hat{\sigma}^2_{g_i} = (\hat{g}_i)^2 - \frac{p-i}{2p^2}\hat{\sigma}^2 \quad \text{and}$$

$$\hat{\sigma}^2_{s_i} = \frac{1}{p-2}\sum_{j\neq i}\hat{s}^2_{ij} - \frac{1}{2p^2}(p^2 - 2p + 2)\,\hat{\sigma}^2$$

$$\text{where} \quad \hat{\sigma}^2 = \frac{\hat{\sigma}^2 e}{bc}.$$

Results

The analysis of variance revealed significant differences among the treatments, Indian and exotic parents and all the three classes of hybrids for all the characters (Table 2). The mean squares due to Indian × exotic hybrids were large for days to flowering, plant height, seed yield and percentage of protein. Significant heterosis was observed for all the characters except number of secondary branches and percentage of oil. The F_1 hybrids, on average, yielded significantly more seed, were earlier, taller and had more primary branches, more capsules and less seed protein (Table 3). Many hybrids had more secondary branches and yielded more oil than their mid-parents, but this was not evident in the overall percent heterosis, which was insignificant due to the cancellation of positive and negative heterosis in individual hybrids. Only one hybrid was earlier than the earliest parent. None of the hybrids exceeded the tallest parent and in no case did the hybrids yield more oil and protein than the best parent. For seed yield, as many as thirteen hybrids outyielded the best parent, the range of their percentage heterosis being 6.3 to 63.5.

An examination of the percentage heterosis for seed yield in the three groups of hybrids (Table 4) showed that the origin of the parents had considerable influence on the degree of heterosis expressed. The range of yield performance and heterosis percent were higher in the Indian × exotic crosses, although the mean performance of Indian × exotic and Indian × Indian hybrids were comparable. In fact, many of the high-yielding hybrids were Indian × exotic crosses. For number of capsules per plant also, the mean percent heterosis in Indian × exotic hybrids was 18.6 while that of Indian × Indian and exotic × exotic hybrids was 13.8 and 16.5, respectively.

Combining ability analyses revealed (Table 5) that general combining ability variance was larger than specific combining ability variance for all the characters except percentage of oil, indicating the predominance of additive gene action. The sca variance was considerable for seed yield and percentage of protein. The variances due to reciprocal effects were also significant for all characters except seed yield, percentage oil and protein. However, the reciprocal effects were generally small: crosses showing large reciprocal effects were mostly Indian × exotic combinations.

Estimates of general combining ability and average specific combining ability variances associated with each parent are given in Table 6. Parents which showed significant general combining ability effects in the desired direction are distinguished by an asterisk on their corresponding general combining ability variances. The environmental variances com-

Table 3. *Heterosis in a ten parent diallel cross of sesame*

Character	Generation mean		Range of % heterosis over mid-parent	Overall % heterosis	Number of hybrids showing significant heterosis in the desired direction		
	P	F_1			over mid-parent	over better parent	over best parent
Days to flowering	45.92	45.56	−11.56 to 12.50	−0.78**	18	4	1
Plant height in cm	128.30	134.32	− 6.75 to 22.06	4.69**	26	6	0
No. of primary branches	5.56	6.05	−10.52 to 33.89	8.81**	32	11	4
No. of secondary branches	3.18	3.46	−55.50 to 86.20	8.80	20	10	6
No. of capsules per plant	155.05	180.57	−11.50 to 45.20	16.45**	32	20	8
Seed yield in gms per plot	98.89	131.75	− 7.50 to 73.70	33.22**	30	16	13
Percentage of oil	45.00	45.46	− 7.46 to 11.11	1.02	13	5	0
Percentage of protein	20.86	20.28	−32.34 to 11.77	−2.78**	5	2	0

** Significant at 1% level

Table 4. *Yield (in gms) performance and heterosis in different groups of parents and hybrids*

Group	Performance		% Heterosis	
	Range	Mean	Range	Mean
Indian parents	86.2 to 120.6	104.9	—	—
Exotic parents	57.0 to 113.3	90.0	—	—
Indian × Indian hybrids	102.3 to 171.1	134.5	2.5 to 56.5	28.20
Indian × exotic hybrids	95.5 to 197.3	132.2	−7.5 to 73.7	35.62
Exotic × exotic hybrids	99.4 to 161.8	122.4	15.6 to 53.4	37.08

Table 5. *Analysis of variance for combining ability and reciprocal effects — Mean squares*

Source	d. f.	Days to flowering	Plant height	No. of pri. branches	No. of sec. branches	No. of capsules per plant	Plot yield	% of oil	% of protein
G.c.a.	9	171.02**	1791.82**	7.21**	15.03**	10300.24**	3019.48**	18.99**	6.57**
S.c.a.	45	5.69**	74.81**	0.51**	1.79**	901.84**	832.46**	43.59**	2.17**
Reciprocal effects	45	1.41**	15.78**	0.16**	0.38**	225.92**	97.18	0.73	0.32
Error	+2700	0.06	1.03	0.02	0.05	15.23	177.25	0.67	0.26

* Error degrees of freedom for the characters yield, % of oil and % of protein are 198
** Significant at 1% level, G. c. a. General combining ability, S. c. a. specific combining ability

Table 6. *Estimates of general combining ability and specific combining ability variances associated with each parent*

Parent		Days to flowering	Plant height	No. of pri. branches	No. of sec. branches	No. of capsules	Plot yield	% of oil	% of protein
T.M.V.-2	A	18.31	146.12*	1.25*	0.84*	1790.29*	384.86*	1.81	0.43*
	B	2.54	29.86	0.45	1.55	837.97	365.45	0.90	0.16
Sel-R	A	0.00	13.72*	0.00	0.51	33.06	42.01	3.21*	1.20
	B	2.57	21.97	0.26	0.95	489.92	406.73	1.44	2.21
Sel-M	A	0.18	10.26*	0.01	0.33	50.71	−7.88	0.11*	0.64
	B	1.47	15.00	0.18	0.43	193.04	340.08	1.53	0.83
Chanda-3	A	4.66	63.00*	0.05*	0.10*	108.30*	68.06*	0.06	0.12
	B	1.95	14.11	0.14	0.92	452.79	158.88	1.72	1.40
T-85	A	9.36	79.34*	0.16*	0.10*	245.17*	3.11	−0.05	0.21*
	B	0.70	38.47	0.22	0.53	337.00	153.13	1.02	1.29
Entry No. 8 (Russia)	A	1.05	10.00*	0.00	0.25	2.44	4.07	0.00	0.02
	B	1.67	10.53	0.15	0.33	103.02	115.73	0.77	0.27
S.I. 770 (Nigeria)	A	7.29*	147.82*	0.14*	3.31*	452.57*	304.25*	1.71	0.03*
	B	3.10	30.63	0.37	0.92	364.46	689.68	0.58	0.55
T.S. 25-12	A	6.60*	120.96	0.72	0.92	947.95	130.79	0.05	0.04*
	B	2.06	14.06	0.13	0.77	307.80	218.41	2.17	0.51
N.S. 20768 (N.Sudan)	A	0.07*	1.65	0.17	0.39	344.52	138.92	0.30	0.00
	B	2.43	39.58	0.18	1.39	360.03	94.21	0.55	0.42
S.I. 1783 (U.S.A.)	A	29.37*	213.12	0.70	0.00	653.13	210.77	0.70*	0.14*
	B	1.91	74.43	0.11	0.51	344.52	113.67	2.39	2.26
	$\sigma^2 e$	0.06	1.03	0.02	0.05	15.23	177.25	0.67	0.26

A = $\hat{\sigma}^2 gi$ = General combining ability variance of ith parent
B = $\hat{\sigma}^2 si$ = Specific combining ability variance of ith parent
$\hat{\sigma}^2 e$ = Error variance

puted on an individual plant basis are also given at the end of the table. The negligible specific combining ability variance associated with S.I.1783 for days to flowering indicates that it uniformly transmitted its earliness to all its hybrids, whereas the high specific combining ability variance associated with S.I.770 indicates that there were specific combinations of S.I.770 with certain parents which flowered earlier than expected. For this reason S.I.1783 is probably superior to S.I.770 as a general combiner for earliness. Similar reasoning indicated that the relative magnitudes of general combining ability and specific combining ability variances associated with the parents showed that T.M.V.-2 and S.I.770 were better general combiners for plant height, number of primary and secondary branches, number of capsules per plant and seed yield. For percentage of oil, Sel-R was found to be a better general combiner, while T.M.V.-2 was better for protein content.

Discussion

The extent of heterosis has often been measured in three ways, namely, heterosis over mid-parent, better parent and the best parent. All three methods were followed in the present investigation and it was observed that heterosis over mid-parent was conspicuous for all the characters. While yield and its component characters, namely, number of primary and secondary branches and number of capsules per plant, exhibited heterosis over the best parent, the developmental traits showed heterosis over the better parent only. In future sesame breeding programmes, therefore heterosis over the better parent could be a better measure of heterosis. The overall yield heterosis in the present studies was 33.2% in contrast to the 66.2% observed by Riccelli and Mazzani (1964). This difference in percent heterosis might be due to several reasons. Firstly, the genetic diversity of the parents used in the present investigation could be less than that of the parents used by Riccelli and Mazzani (1964), since they used varieties from many countries. Differing agroclimatic conditions in the experiments, with particular reference to soil type and plant spacing, might be another reason. Thirdly, non-allelic interactions, which can either increase or decrease the expression of heterosis (Hayman, 1957, 1958), might bear some responsibility.

Heterosis has frequently been related to the degree of genetic diversity of the parents crossed and corn breeders have frequently stressed the importance of the diverse origin of parents entering the hybrid in obtaining increased yields (Griffing and Lindstrom, 1954; Timothy, 1963; Paterniani and Lonnquist, 1963). The present investigations involving sesame germ plasm from diverse sources have given similar results. Matzinger and Wernsman (1968) and Vandenberg and Matzinger (1970) obtained a similar relationship between genetic diversity and heterosis in their extensive investigations on *Nicotiana*. In the present study too, the levels of percentage heterosis for seed yield were higher in Indian × exotic and exotic × exotic hybrids than in Indian × Indian hybrids. Many of the hybrids with higher yield and number of capsules were from crosses between Indian and exotic parents. However, the mean percentage heterosis of Indian × exotic hybrids was slightly less than that of exotic × exotic hybrids, indicating that heterosis increases with increased divergence only to a certain extent; extremely divergent crosses may result in decreased heterosis (Moll *et al.*, 1965) which can only result from epistasis (Eberhart and Gardner, 1966). Although the range of percentage heterosis and yield *per se* were higher in Indian × exotic crosses, they did not differ in their mean performance from Indian × Indian crosses. This may not be surprising if it is noted that the Indian parents are late, tall and high yielding whereas the exotic parents are early, short and low yielding. It might also be pointed out that the grouping of the parents and hybrids is quite arbitrary and geographical distribution need not always be directly related to genetic diversity (Murty and Arunachalam, 1966).

The present study has also brought out the importance of significant reciprocal effects, however small, for the characters, days to flowering, plant height, number of primary and secondary branches and number of capsules per plant, in F_1 hybrids of sesame. Pal (1945) observed several instances of reciprocal differences in sesame crosses but he felt that they were, on the whole, unimportant. In view of reports on the inconsistency of reciprocal effects over generations in other crops (Smith and Fitzsimmons, 1965; Muehlbauer *et al.*, 1971; Emara, 1970), it may be necessary to carry out further studies involving advanced generations for reciprocal hybrids and discover whether they are consistent over further generations.

Gca variances were larger than *sca* variances for days to flowering, plant height, number of primary and secondary branches and number of capsules per plant, indicating the predominance of additive gene action. However, the magnitudes of *sca* variances were double those of *gca* variances for percentage of oil, and were in moderate proportions for plot yield and percentage of protein. In the presence of significant *sca* variances the *gca* variances reflect not only additive variances but also non-additive variances (Griffing, 1956). Hence, addi'ive as well as non-additive gene action might be controlling the inheritance of the various characters studied. The occurrence of significant heterosis for many of the characters also corroborates this conclusion. However, in the present study, the experimental population arose from crossing chosen homozygous lines derived after long selection and did not represent a random sample of the sesame population as a whole. The experimental material was the sole population about which inferences were made and the extent of possible bias due to genotype-environmental interactions is also not known.

In the light of reports on heterosis and considerable natural cross pollination in sesame, Rajan (1967) suggested that it should be possible to apply to this crop, methods intended for cross pollinating species and that a hybrid breeding programme could be one of them. Since both additive and non-additive gene actions are governing the expression of all the characters, hybridization followed by inbreeding also seems to be a profitable procedure in the improvement of this crop. *Inter se* crossing among the inbred generations may further help to break tight linkages and capitalize on the predominant additive gene action.

Acknowledgements

The material formed a part of thesis submitted by the author to the Osmania University, Hyderabad, for the degree of Ph. D. He wishes to thank Dr. M. Hashim for guidance and Prof. M. R. Suxena for encouragement. He is also indebted to Dr. G. V. Ramana Murty, Director, Indian Central Oilseeds Committee, Hyderabad, and Dr. N. Ganga Prasad Rao, Coordinator, All India Coordinated Sorghum Improvement Project, Hyderabad, for their valuable advice. Thanks are also due to Dr. G. Harinarayana for going through the manuscript. The award of a Senior Research Fellowship by the Indian Council of Agricultural Research is gratefully acknowledged.

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Received February 28, 1974
Communicated by B. R. Murty

Dr. D. S. Murty
International Crops Research Institute
for the Semi-Arid Tropics
1-11-256, Begumpet
Hyderabad – 500016 (India)