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Heterosis and Combining Ability in *Phaseolus aureus* Roxb.

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Summary. Heterosis and combining ability were estimated in F_1, F_2, F_3 and backcross generations of diallel cross in *Phaseolus aureus*. Hybrid vigour for yield compared with the mid-parent and better parent was noted in 21 and 20 F_1 hybrids, respectively. There was an appreciable amount of inbreeding depression in the F_2 and F_3 compared with the F_1 hybrids. Pod number seems to influence yield to a great extent. As expected, the high-yielding hybrids resulted from crosses between parents of diverse geographic origin. Combining ability analysis revealed that both g.c.a. and s.c.a. variances were important for yield, while g.c.a. variance was more important for seed size, pod number, cluster number and pods per cluster. The g.c.a. variance for yield appeared to be influenced by g. c. a. variances for yield components. In general, the crosses having high s.c.a. had one of the parents as high combiner for yield and other traits. The diallel study of different generations gave a comprehensive picture of combining ability.

Introduction

In *Phaseolus aureus*, heterosis for grain yield and other characters was observed by Bhatnagar and Singh (1964). Subsequently, Singh and Jain (1970) evaluated 20 crosses and observed heterosis in 75 per cent of hybrids when compared with the better parent. This study revealed that heterosis for yield was a reflection of heterosis in yield components, and genetic diversity among the parents played an important role in the manifestation of heterosis.

The approach of Griffing (1956) to the interpretation of combining ability in a diallel cross is engaging the attention of breeders working on self-pollinated crops. Singh and Jain (1971), using a diallel cross of five lines in *Phaseolus aureus*, reported the importance of both general and specific combining ability effects for grain yield, pods per plant and seeds per pod.

Although some preliminary information on heterosis and combining ability in the F_1 is available, detailed information on the segregating generations is still lacking. The purpose of this study was to estimate heterosis and combining ability for yield and its components in a diallel cross of the F_1, F_2, F_3 and back-cross generations in *Phaseolus aureus*.

Material and Methods

Seven promising and diverse lines, including Hyb. 4, Hyb. 45, L 24-2, No. 54, P 23-67, No. 305 and Jalgaon 781, hereafter referred to as P_1 to P_7, were used for this study. These parents are the improved varieties or lines from different areas of the country, namely, No. 54 and No. 305 (Punjab), Hyb. 45, Hyb. 4 (M.P.), Jalgaon 781 (Maharashtra), L 24-2 a line from Punjab and P 23-67 a single plant selection from I.A.R.I. The parents P 23-67 and Hyb. 45 are good yielders, having more pods per plant and pods per cluster, while No. 54 has more clusters per plant but the lowest number of pods per cluster and thus is a poor yielder. Hyb. 4 has the highest 100-seed weight and average yielding potential. A complete diallel set (excluding reciprocals), involving all seven parents in F_1 and F_2, and involving the first five parents in the F_3 and backcross generations, was studied. The F_2 seeds were obtained from the F_1 plants, while the F_3 seeds were obtained from the F_2 seeds, sown during July to Oktober 1968 and Spring 1969, respectively. The material was grown at Punjab Agricultural University, Ludhiana, from July to October, 1969, in a randomized block design with four repeats. Each replication had 192 experimental rows comprising 1 row each of 7 parents, 21 F_1's, 10 BC_1's and 10 BC_2's, and four and six rows of each F_2 and F_3 generation, respectively. The rows were 3 metres long and 60 cm apart and each contained 10 plants spaced 30 cm apart. Non-experimental rows were planted all round the plots to avoid border effect. Observations were recorded on 8, 32, 48 and 5 plants in each entry of F_1, F_2, F_3 and backcross generation per replication, respectively. Later, the data were converted to per plant basis for grain yield(g), 100-seed weight(g), pods per plant, clusters per plant and pods per cluster.

Analysis of variance to test the differences between parents and hybrids and between generations was conducted by simple randomized block and nested designs. Heterosis was calculated as the percentage increase or decrease over the mid-parent and better parent for yield and other traits. Statistical analysis of the data was carried out according to the two factors mating design of Kempthorne (1952) and the analysis of combining ability was made by the method II model I of Griffing (1956).

Results

Heterosis and Inbreeding Depression

Analysis of variance revealed that the variance due to parents vs hybrids was significantly high for all the characters except clusters per plant, while the variance for differences between generations within a cross was significant for yield, pods per plant and 100-seed weight (Table 1 a und b). Table 2 summarizes the results for heterosis and inbreeding depression. Generally, the F_1 means were higher than the mid-parent, F_2 and F_3 means for grain yield and other characters. F_2 and F_3 means were also higher than the mid-parent value. There was no significant depression in the mean yield of F_3 families compared

Table 1 a. *Analysis of variance for heterosis*

Source	d. f.	Mean square				
		Yield per plant	100-seed weight	Pods per plant	Clusters per plant	Pods per cluster
Progenies	27	129.39**	0.97**	2493.04**	184.94**	1.57**
Parents	6	22.77	1.59**	967.99*	100.98	0.81*
Hybrids	20	112.05	0.72**	2567.11**	205.46**	1.12**
Parents vs Hybrids	1	1093.08**	0.82**	9193.91**	177.20*	4.88**
Error	234	22.55	0.07	489.48	92.16	0.41

Table 1 b. *Analysis of variance of nested design*

Generation	Source	d. f.	Mean squares				
			Yield per plant	100-seed weight	Pods per plant	Clusters per plant	Pods per cluster
F_1 and F_2	Between crosses	20	117.74**	1.86**	3177.90**	268.36**	1.30**
	Between generations within a cross	21	73.89**	0.18**	1234.74**	138.43	0.43
	Between crosses	9	93.86**	1.52**	2797.23**	404.08**	1.73**
F_1 and F_3	Between generations within a cross	10	118.60**	0.17**	2367.31**	104.08	0.39
	Error	234	22.55	0.07	489.48	92.16	0.41

Table 2. *Mean performance of the parents, heterosis and inbreeding depression (in percent) for yield and its components in Phaseolus aureus*

Cross	Yield per plant		100-seed weight		Pods per plant		Clusters per plant		Pods per cluster		Inbreeding		Mean yield
	$\bar{P}$	BP	$\bar{P}$	BP	$\bar{P}$	BP	$\bar{P}$	BP	$\bar{P}$	BP	F_2	F_3	F_1
P_1	17.59		3.84		67.0		28.4		2.44		—		—
P_2	20.66		2.40		120.1		37.0		3.26		—		—
P_3	17.03		1.81		98.7		36.4		2.72		—		—
P_4	16.08		2.13		87.2		44.3		1.96		—		—
P_5	20.21		2.36		89.6		29.2		3.06		—		—
P_6	13.00		1.87		77.0		37.4		2.05		—		—
P_7	17.22		2.43		87.0		36.6		2.38		—		—
$P_1 \times P_2$	26.8	17.4	−5.1	−22.4	36.4	6.2	10.4	−2.4	23.5	7.8	14.7	10.3	24.26
$P_1 \times P_3$	81.7	78.8	−8.2	−32.6	66.8	39.9	54.3	37.4	6.6	1.1	40.4	38.6	31.45
$P_1 \times P_4$	18.5	13.5	15.1	−10.4	−14.0	−24.0	−27.2	−40.2	18.6	7.0	11.0	−11.5	19.96
$P_1 \times P_5$	34.4	25.7	10.0	−11.2	14.6	0.1	−9.4	−10.6	33.8	20.3	10.5	12.2	25.41
$P_1 \times P_6$	50.1	30.5	−5.9	−29.9	40.8	31.7	−5.8	−17.1	79.1	65.2	25.1	—	22.95
$P_1 \times P_7$	16.6	15.4	4.2	−15.1	9.1	−3.4	11.4	−1.1	4.6	3.3	10.8	—	20.29
$P_2 \times P_3$	52.2	38.8	15.2	0.8	13.0	2.9	6.8	5.9	11.4	2.2	31.5	27.4	28.67
$P_2 \times P_4$	72.6	53.4	11.5	5.4	40.5	21.2	25.3	15.1	11.5	−10.7	31.6	37.1	31.70
$P_2 \times P_5$	102.5	100.3	4.2	3.3	88.4	64.4	26.9	13.5	26.1	19.3	31.2	36.6	41.38
$P_2 \times P_6$	70.6	39.0	8.9	3.3	43.1	17.4	21.8	21.1	16.2	−5.2	25.8	—	28.72
$P_2 \times P_7$	1.3	−7.2	9.1	8.6	−3.8	−17.1	−4.9	−5.4	5.7	−8.6	6.6	—	19.18
$P_3 \times P_4$	19.8	16.4	1.0	−6.6	−7.6	−13.0	0.3	−8.6	−4.3	−17.7	9.9	−4.3	19.83
$P_3 \times P_5$	45.7	34.2	4.8	−7.6	47.0	−40.1	5.2	−5.2	34.9	27.5	14.7	31.0	27.12
$P_3 \times P_6$	26.8	11.8	6.5	4.8	23.7	10.1	12.2	10.7	12.6	−1.5	12.3	—	19.04
$P_3 \times P_7$	24.9	24.2	12.3	−2.1	−10.7	−15.9	8.2	7.9	−10.2	−15.8	18.0	—	21.39
$P_4 \times P_5$	41.3	26.8	9.8	4.7	18.2	16.6	−4.6	−20.8	18.3	−2.9	13.4	11.0	25.63
$P_4 \times P_6$	31.8	19.2	13.5	6.6	19.0	12.0	5.6	−2.5	21.0	18.1	−10.6	—	19.16
$P_4 \times P_7$	35.4	30.9	15.8	8.6	19.3	19.2	−7.9	−15.8	41.0	28.6	25.5	—	22.54
$P_5 \times P_6$	80.6	48.4	12.8	0.9	47.4	37.1	39.3	24.1	4.3	−12.7	32.5	—	29.99
$P_5 \times P_7$	8.2	0.2	33.5	31.3	−6.6	−7.9	17.3	−25.7	16.2	3.3	5.1	—	20.24
$P_6 \times P_7$	38.6	21.7	16.7	3.3	36.1	28.3	22.4	21.1	36.5	27.3	28.3	—	20.95
Average	41.9	30.4	8.8	−3.0	24.8	12.7	9.9	0.1	19.3	7.4	18.5	18.8	24.76

with the mean of F_2 plants. In all the crosses, the F_1 yielded significantly more than the mid-parent. The mean performance of F_2 and F_3 families was in general less than that of F_1 hybrids. The crosses, $P_2 \times P_5$, $P_1 \times P_3$, $P_5 \times P_6$, $P_2 \times P_4$ and $P_2 \times P_6$, showed high hybrid vigour for grain yield, pod number and clusters per plant, while the crosses, $P_5 \times P_7$ and $P_1 \times P_6$, were the best hybrids for bold seed and more pods per cluster, respectively (Table 2).

Combining Ability

Variance due to g.c.a. was highly significant for all the characters in all the generations except for grain yield in the F_3 generation (Table 3). The s.c.a. variance was significant for yield, pods and clusters per plant in the F_1 and backcross generations, and was significant for pods per cluster in the F_1 and F_3 generations. For 100-seed weight, s.c.a. variance was significant in all the generations. Variance due to g.c.a. was significantly greater than that due to s.c.a. in the F_2 generation for grain yield and in the F_2 and backcross generations for the rest of the characters.

Amongst the parents, P_2 and P_5 were good combiners for yield and pods per cluster, while all the others were average to low combiners for increased grain yield (Table 4). The parents, P_2 and P_4, were high combiners for pods and clusters per plant, respectively. For 100-seed weight, parents P_1 and P_7 were good combiners. The lines having high combining ability for grain yield showed average to high combining ability for other yield components.

The cross $P_2 \times P_5$ was the best combination for grain yield in the F_1 generation but in the backcross generation the cross $P_2 \times P_3$ was the best (Table 5). The crosses $P_1 \times P_3$ and $P_2 \times P_4$ also combined well for grain yield in the F_1 generation. The cross $P_2 \times P_5$ was the best combination for pods per plant and clusters per plant but it was an average

Table 3. *Analysis of variance for combining ability in different generations for yield and its components*

Generation	Source	d. f.	Mean square				
			Yield per plant	100-seed weight	Pods per plant	Clusters per plant	Pods per cluster
F_1	g.c.a.	6	72.51**	0.94**	1697.31**	81.23**	0.61**
	s.c.a.	21	31.78**	0.04**	556.30**	36.08	0.22*
F_2	g.c.a.	6	24.67**	1.17**	912.39**	78.13**	0.52**
	s.c.a.	21	4.62	0.13**	116.06	16.58	0.06
F_3	g.c.a.	4	9.26	0.95**	502.92**	68.49*	0.32*
	s.c.a.	10	5.08	0.05**	45.86	30.74	0.20*
$1/2\,(B_1 + B_2)$	g.c.a.	4	23.92**	1.77**	2087.48**	198.57**	0.56**
	s.c.a.	10	21.24**	0.14**	396.50**	77.97**	0.10
	Error	234	5.63	0.017	122.37	23.04	0.1032

* Significant at 5% level; ** Significant at 1% level

Table 4. *General combining ability estimates of parents for yield and its components*

Character	Generation	P_1	P_2	P_3	P_4	P_5	P_6	P_7
Yield per plant	F_1	− 0.42	3.54**	−0.20	−1.37	2.98**	1.83	− 2.70*
	F_2	− 0.14	1.93	−0.67	−0.23	2.52*	−1.78	− 1.63
	$1/2\,(B_1 + B_2)$	− 2.21	2.53*	−0.33	−1.23	1.24	—	—
100-seed weight	F_1	0.62**	−0.03	−0.37**	−0.09	0.04	−0.29	0.12*
	F_2	0.66**	−0.00	−0.41**	−0.11	0.02	−0.35**	0.19**
	F_3	0.62**	−0.02	−0.37**	−0.14*	−0.09	—	—
	$1/2\,(B_1 + B_2)$	0.62**	−0.07	−0.42**	−0.10	−0.03	—	—
Pods per plant	F_1	−12.26*	24.85**	2.62	−8.12	7.01	−1.56	−12.53*
	F_2	−14.33**	15.36**	4.59	1.32	4.98	−1.06	−10.86*
	F_3	−12.53*	11.25	1.51	−0.95	0.72	—	—
	$1/2\,(B_1 + B_2)$	−22.31**	17.42**	−2.19	0.90	6.18	—	—
Clusters per plant	F_1	− 4.40	2.25	1.73	2.21	−3.62	2.79	− 0.96
	F_2	− 4.67*	1.87	0.38	3.31	−2.14	2.90	− 1.65
	F_3	− 3.77	1.73	1.11	3.65	−2.72	—	—
	$1/2\,(B_1 + B_2)$	− 6.46*	3.03	1.70	2.64	−0.91	—	—
Pods per cluster	F_1	0.08	0.33*	−0.08	−0.35*	0.34*	−0.15	− 0.17
	F_2	− 0.03	0.31*	0.06	−0.22	0.33*	−0.28	− 0.17
	F_3	− 0.06	0.14	−0.06	−0.29	0.27	—	—
	$1/2\,(B_1 + B_2)$	− 0.14	0.29	−0.04	−0.32	0.21	—	—

* Significant at 5% level; ** Significant at 1% level

combiner for pods per cluster and seed size. The cross $P_1 \times P_3$ also showed significantly high s.c.a. effects for pods per plant. The cross $P_1 \times P_6$ was the best combination for pods per cluster in the F_1 generation. The crosses, $P_5 \times P_7$ and $P_1 \times P_4$ in the F_1, and $P_1 \times P_2$ and $P_1 \times P_7$ in the F_2, indicated high s.c.a. effects for bolder seed size.

Discussion

Analysis of variance for heterosis suggested that the hybrids performed significantly different from their parents for all the characters, while the F_2 and F_3 generations differed significantly from the hybrids for grain yield, pods per plant and 100-seed weight only.

In this study an appreciable amount of heterosis was present for yield and other characters as shown by the magnitude of variance ascribable to the differences between parents vs hybrids. It was evident that high-yielding parents tend to produce high-yielding hybrids. Another noteworthy point was that the parents from different geographical areas exhibited more heterosis than parents originating in the same region. Heterosis in yield appeared to be influenced by heterosis for the yield components, especially pod number. Generally the crosses between good or average performing parents showed more hybrid vigour for various characters.

This study indicated that both g.c.a. and s.c.a. variances were important for grain yield, which in turn suggests that the character is under the control of additive as well as non-additive gene effects. Similar results have been reported by Singh and Jain (1971) in mungbean, Singh and Dhaliwal (1972) in urid and Leffel and Weiss (1958) in soybean. For pod number, cluster number, pods per cluster and seed size, the g.c.a. variances were more pronounced indicating that for these characters additive gene action is more important; however, non-additive gene action also plays a role in their inheritance. Singh and Singh (1972) arrived at a similar conclusion for seed size and pods per cluster through graphical analysis.

It was noted that g.c.a. variance for yield appeared to be influenced by g.c.a. variance of its components, especially pod number and pods per cluster.

Wide divergence between the parents was evident from the highly significant differences in their combining ability estimates. The parents P_5 and P_2 (P 23−67 and Hyb. 45) were good combiners for seed yield as well as for pods and clusters per plant and pods per cluster, but average combiners for seed size. Furthermore, the parents which were good combiners for bold seed size were average combiners for yield. Thus it can be concluded that medium-seeded types have a tendency to yield high compared with bold-seeded types. The estimates of g.c.a. for various characters in the F_1 and subsequent genera-

Table 5. *Estimates of specific combining ability effects for yield and its components*

Cross	Yield per plant		100-seed weight				Pods/plant		Clusters/plant	Pods/cluster	
	F_1	1/2 ($B_1 + B_2$)	F_1	F_2	F_3	1/2 ($B_1 + B_2$)	F_1	1/2 ($B_1 + B_2$)	1/2 ($B_1 + B_2$)	F_1	F_3
$P_1 \times P_2$	−1.78	−2.90	−0.18	0.47**	0.32*	−0.04	8.49	−14.21	−4.44	0.21	0.42
$P_1 \times P_3$	9.16**	−0.40	−0.22	−0.77**	0.27	−0.47	41.33*	3.41	0.99	−0.16	−0.44
$P_1 \times P_4$	−1.16	0.27	0.36*	0.26	0.23	0.28	−19.73	−7.59	−4.55	−0.03	0.48
$P_1 \times P_5$	−0.07	2.57	0.19	0.29	−0.20	0.23	−11.46	1.74	−1.50	0.35	0.23
$P_1 \times P_6$	2.29	—	−0.20	−0.69**	—	—	8.80	—	—	1.18**	—
$P_1 \times P_7$	0.50	—	−0.03	0.60**	—	—	1.87	—	—	−0.30	—
$P_2 \times P_3$	2.41	8.75**	0.26	0.25	0.01	0.11	−10.29	10.58	2.30	0.17	−0.02
$P_2 \times P_4$	6.61*	2.62	0.10	−0.08	−0.06	0.03	22.46	11.58	−0.54	0.02	−0.04
$P_2 \times P_5$	11.93**	3.90	0.09	−0.02	0.17	0.00	59.13**	28.11*	13.92*	0.31	−0.52
$P_2 \times P_6$	4.09	—	0.08	−0.10	—	—	11.39	—	—	−0.01	—
$P_2 \times P_7$	−4.58	—	0.00	−0.13	—	—	19.64	—	—	−0.09	—
$P_3 \times P_4$	−1.52	0.91	−0.10	−0.02	0.27	0.16	−15.11	−1.91	2.69	−0.24	−0.08
$P_3 \times P_5$	1.42	−1.05	−0.05	−0.08	0.18	0.09	22.26	0.72	1.15	0.72	0.70
$P_3 \times P_6$	−1.84	—	0.06	0.28	—	—	1.23	—	—	−0.01	—
$P_3 \times P_7$	−1.37	—	0.08	0.24	—	—	−14.01	—	—	−0.38	—
$P_4 \times P_5$	1.10	2.70	−0.03	−0.01	0.06	0.04	0.80	21.32	−2.50	0.07	0.36
$P_4 \times P_6$	−0.55	—	0.09	0.30	—	—	0.97	—	—	0.00	—
$P_4 \times P_7$	3.70	—	0.06	0.00	—	—	17.64	—	—	0.67	—
$P_5 \times P_6$	5.92*	—	0.07	0.13	—	—	10.94	—	—	−0.44	—
$P_5 \times P_7$	−2.96	—	0.48**	0.27	—	—	−18.90	—	—	0.07	—
$P_6 \times P_7$	2.57	—	0.13	0.13	—	—	18.77	—	—	0.43	—

* Significant at 5% level; ** Significant at 1% level

tions reveal that the parents with high g.c.a. in the F_1 also showed superior combinations in subsequent generations, suggesting that their superiority was due to their having favourable genes with additive effects. This also suggests that the g.c.a. estimates obtained from the F_2 or subsequent generations are as reliable as those from the F_1 generation study. But this is not the case with s.c.a. estimates.

Among the crosses, the best combination was $P_2 \times P_5$ for yield as well as for pods and clusters per plant in the F_1 generation. Both the parents involved in this combination were high combiners for yield and were geographically diverse. Bond (1967), using winterbean, also observed that the highest yielding crosses had parents of high general combining ability. The consistently superior performance of the cross in the F_1 and subsequent generations indicates that dominant gene action was not predominant though present, which is also evident from the low magnitude of inbreeding depression (Table 2). Therefore, it appears that the high vigour shown by this cross is largely due to the concentration of favourable genes contributed by the two parents. In general, the crosses involving parents of diverse origin with high or average combining abilities were good combiners. Moreover, the crosses with high or average specific combining ability for yield components, especially pods and clusters per plant, showed high s.c.a. effects for yield.

It may be concluded that superior performance of hybrids for yield depends on the general combining ability of the parents for yield and its components, as well as on their genetic diversity. High performance for yield also appeared to be related to high specific combining ability for the yield components. Therefore, a plant breeder of self-pollinated crops should look for genetically diverse parents having high g.c.a. for yield and its component characters. From the segregating populations of crosses involving such parents, the isolation of high yielding lines is possible as a large part of the total genetic variance is a result of additive gene effects.

The study on combining ability has helped in selecting parents for the hybridization programme. It is suggested that the parents, Hyb. 45 and P 23–67 for grain yield and pods per cluster, Hyb. 4 for seed weight, Hyb. 45 for pods per plant, and No. 305 for clusters per plant, may be used in hybridization. This study has further helped in selecting three crosses, P 23–67 × Hyb. 45, Hyb. 45 × No. 54 and Hyb. 4 × L 24–2, which may be advanced for the isolation of high-yielding lines. In fact, the cross between P 23–67 and Hyb. 45 has already yielded a very high-yielding variety which has been named ML 1. This variety has a potential yield of over 2000 kg. per hectare and is currently being evaluated in the farmers' fields.

The study of combining ability in the F_1 and subsequent generations has given a much more comprehensive picture of this subject than would have been possible by studying the F_1 generation alone.

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Literature

1. Bhatnagar, P. S., Singh, B.: Heterosis in mungbean. Indian J. Genet. **24**, 89–91 (1964). — 2. Bond, D. A.: Combining ability of winter beans (*Vicia faba* L.) inbreds. J. Agric. Sci., Cambridge, **68**, 179–185 (1967). — 3. Griffing, B.: Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. **9**, 463–493 (1956). — 4. Kempthorne, O.: The design and analysis of experiments. New York: John Wiley and Sons 1952. — 5. Leffel, R. C., Weiss, M. G.: Analysis of diallel crosses among ten varieties of soybean. Crop Sci. **1**, 169–174 (1958). — 6. Singh, K. B., Jain, R. P.: Heterosis in mungbean. Indian J. Genet. **30**, 251–260 (1970). — 7. Singh, K. B., Jain, R. P.: Analysis of diallel cross in *Phaseolus aureus* Roxb. Theor. Appl. Genet. **42**, 279–281 (1971). — 8. Singh, K. B., Dhaliwal, H. S.: Combining ability for seed yield in black-gram. Indian J. Genet. **32** 99–102 (1972). — 9. Singh, T. P., Singh, K. B.: Mode of inheritance and gene action for yield and its components in *Phaseolus aureus*. Canad. J. Genet. Cytol. **14** 517–525 (1972).

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