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Studies of Heterosis, Combining Ability and Inheritance of Yield and Yield Components in a Diallel Cross of Bengal Gram (*Cicer arietinum* L.)

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Summary. A 5 × 5 diallel cross among well-adapted varieties of gram from different agroclimatic regions was studied for heterosis, combining ability and inheritance of days-to-flowering, primary branches, pods per plant, 100-seed weight and grain yield. A high degree of heterosis over mid-parent and better parent was observed for primary branches, no. of pods and grain yield, whereas very little heterosis was exhibited for days-to-flower and 100-seed weight. Crosses among lines of diverse origin generally gave higher heterosis and over-dominance than lines from the same region. Primary branch number, pod number, and grain yield exhibited positive over-dominance; days-to-flower showed negative over-dominance while 100-seed weight had no dominance. Both general and specific combining ability effects were significant for all the characters studied but g.c.a. effects appeared to be more important for days-to-flower, 100-seed weight and grain yield. Graphical analysis indicated additive effects for all the characters, with complete dominance for days-to-flower, no dominance for 100-seed weight and over-dominance for the other three characters. Dominant genes conditioned earliness, primary branch number and 100-seed weight. The role of various parents and crosses in planning a hybridization programme has been discussed.

Introduction

India is the main grower of Bengal gram in the world, having 76% of the world gram acreage and producing 80% of the total world output. In spite of the geographical and economic importance of gram in India, yield potential of the existing varieties is extremely low, so that the area under this crop is fast diminishing where irrigation facilities have been extended. Both the indigenous and exotic strains have been vigorously screened and exploited, which probably leaves little scope for further selection. A hybridization breeding programme has led to the evolution of a few promising strains but a systematic programme to understand the genetic constitution of the various complex quantitative traits has not been followed strictly. The success of a hybridization programme depends upon the judicious selection of parents and handling of the segregating generations. Allard (1960) reported that the ability of parents to combine well depends on complex interaction among genes which cannot be adjudged by mere yield and yield adaptation of the parents. The diallel cross technique developed by Griffing (1956) and Hayman (1954) facilitates the selection of promising parents and crosses, and the understanding of the genetic make-up of complex traits. Similar techniques have been employed in other crops with spectacular results. Weber *et al.* (1970), working with soybean, reported that both g.c.a. and s.c.a. effects were significant for seed yield and days -to-flowering but g.c.a. effects were more important for days-to-flowering and seed size. Bond (1966), using field beans, reported that most of the variance for seed yield, pods seed weight and days-to-flowering was associated with g.c.a. In gram, Abdul and Muhammad (1968) reported additive gene action with some genetic interaction for grain yield. In uridbean, Singh and Dhaliwal (1972) reported an additive type of gene action with partial dominance for grain yield. Information on the genetic make-up of quantitative traits in gram is greatly lacking. The present investigation was undertaken to select, among well-adapted parents, parents which combine well and to understand the genetic make-up of various quantitative traits in gram as an aid to handling the segregating generation.

Material and Methods

The material for the present investigation comprised five well-adapted varieties from different agroclimatic regions, viz., R.S. 11 (Rajasthan), G-130, Pb7 and C214 (Punjab) and T.3 (U.P.). A complete diallel set of 5 × 5 was made in the *rabi* 1970—71. Five parents and 10 crosses were sown in a randomised block design with four replications in *rabi* 1971—72 at Punjab Agric. University sub-station, Gurdaspur. Each plot consisted of a single row of 10′, accommodating 10 plants 1′ apart. Plot-to-plot distance was $1^1/_2$′. Non-experimental rows were raised on both sides of each replication to avoid any border effect. Data were recorded on 8 randomly selected plants from each plot for days-to-flowering, primary branches, number of pods, seed yield and 100-seed weight. Plot means were computed and the usual randomised block design analysis was carried out for all the characters studied. Means over replication were used for calculating heterosis and over-dominance. Combining-ability analysis was carried out using Method II and Model I of Griffing (1956). The diallel cross technique given by Jinks (1954) and Hayman (1954) was followed for graphical analysis.

Results

Analysis of variance of R.B.D. showed significant differences among progenies for all the characters under investigation (Table 2). The mean performance of parents and F_1's, for days-to-flowering, number of primary branches, no. of pods per plant, 100-seed weight and grain yield, are presented in Table 1. The highest expression for days to flowering, no. of primary branches, no. of pods, 100-seed weight and yield was recorded for parents C214, T.3, T.3, T.3 and T.3, respectively. The results of various aspects of analysis are discussed separately, as follows.

Table 1. *Mean performance of the parents and crosses*

Pedigree	Days to flowering	Primary branches per plant	Number of pods per plant	100-seed weight (gm.)	Grain yield per plant (gm.)
R.S. 11	147	5.50	186.3	13.76	26.25
G-130	131	8.88	237.8	12.59	38.67
C-214	152	7.88	257.8	12.30	38.07
PB-7	130	9.30	154.3	12.85	24.00
T-3	148	9.62	429.0	21.11	78.12
R.S. 11 × G-130	136	12.72	310.0	12.84	56.70
R.S. 11 × C-214	143	9.20	336.3	12.84	51.70
R.S. 11 × PB-7	144	12.02	322.5	13.32	48.10
R.S. 11 × T-3	143	11.32	286.5	17.81	56.22
G-130 × C-214	137	10.20	346.3	12.93	59.40
G-130 × PB-7	136	9.28	241.3	13.35	40.82
G-130 × T-3	137	11.38	250.5	16.98	50.92
C-214 × PB-7	148	10.30	274.5	13.64	44.48
C-214 × T-3	140	12.58	287.5	17.84	57.58
PB-7 × T-3	140	14.78	340.5	18.22	67.45
S. E. ±	1.860	3.075	32.2	0.257	4.65
C.D. at 5%	5.15	2.43	89.28	0.71	12.90

Table 2. *Analysis of variance of randomized block design*

Source of variation	Degrees of freedom	Mean Square				
		Earliness	Primary branches	Pod number	100-seed weight	Grain yield
Replication	3	19.66	11.940*	9788.3	1.4035**	372.58**
Progeny	14	162.35**	20.265**	18645.0**	30.6850**	844.57**
Error	42	13.81	3.075	4150.6	0.2646	86.58

* Significant at 5% level of significance.
** Significant at 1% level of significance.

Table 3. *Percentage increase over mid-parent (heterosis) and over better parent (over-dominance) of different crosses*

Cross	Earliness		Primary branches		Pod number		100-seed weight		Grain Yield	
	Heterosis	Over-dominance	Heterosis	Over-dominance	Heterosis	Over-dominance	Heterosis	Over-dominance	Heterosis	Over-dominance
R.S. 11 × G-130	−2	—	43	30	32	23	−3	—	43	32
R.S. 11 × C-214	−5	−3	27	14	34	23	−1	—	38	26
R.S. 11 × PB-7	4	—	40	23	47	42	—	—	48	45
R.S. 11 × T-3	−3	−3	33	15	−7	—	2	—	7	—
G-130 × C-214	−3	—	18	13	28	26	4	3	35	35
G-130 × PB-7	4	—	2	—	19	1	5	4	23	5
G-130 × T-3	−2	—	19	16	−33	—	1	—	−15	—
C-214 × PB-7	5	—	17	10	25	6	8	6	30	14
C-214 × T-3	−7	−6	30	24	−16	—	6	—	−1	—
PB-7 × T-3	1	—	36	35	14	—	7	—	24	—
C.D. at 5%	4.45	5.15	2.10	2.43	77.38	89.28	0.61	0.71	11.71	12.90

Heterosis and Over-dominance

Percentage increase or decrease of various F_1's over the mid-parent (heterosis) and better parent (over-dominance) is given in Table 3.

For days-to-flowering, maximum heterosis was exhibited by the cross C214 × Pb7, and only four crosses gave positive heterosis while no cross gave positive heterosis over better parent. The greatest negative heterosis and over-dominance was shown by C214 × T.3.

A high degree of heterosis and over-dominance was recorded for no. of primary branches. The cross R.S.11 × G130 gave 43% heterosis over mid-parent, followed by crosses R.S.11 × Pb7 (40%) and Pb7 × T.3 (36%). Considerable over-dominance was observed for Pb7 × T.3 with a value of 35%, followed by the

Table 4. *Analysis of variance for combining ability*

Source of variation	Degrees of freedom	Mean square				
		Earliness	Primary branches	Pod number	100-seed weight	Grain yield
g.c.a.	4	97.61 **	3.9726 **	5859.78 **	26.2370 **	423.575 **
s.c.a.	10	18.60 **	5.5021 **	4179.50 **	0.2446 **	125.249 **
Error	42	3.45	0.7687	1037.65	0.0661	21.645

** Significant at 1% level of significance.
* Significant at 5% level of significance.

cross R.S.11 × G130 with over-dominance 30%. All the crosses exhibited positive heterosis and over-dominance.

A maximum of 47% heterosis and 42% over-dominance was recorded for R.S.11 × Pb7. The cross G130 × T.3 gave the maximum negative heterosis of 33%. In general, 7 out of 10 crosses showed positive heterosis.

For 100-seed weight, seven crosses gave positive heterosis and three crosses over-dominance. In general, a high degree of heterosis was not observed for this character. The maximum of 8% heterosis and 6% over-dominance was recorded in cross C214 × Pb7.

Considerable heterosis over mid-parent and better parent was recorded for grain yield. Only two crosses showed negative heterosis. The cross R.S.11 × Pb7 gave 48% heterosis and 45% over-dominance, followed by the cross R.S.11 × G130. Over-dominance was recorded in six crosses.

Combining Ability Analysis

Analysis of variance for combining ability (Table 4) revealed that both g.c.a. and s.c.a. effects were highly significant for all the characters studied; g.c.a. effects were more important for days-to-flowering, 100-seed weight and grain yield. Both g.c.a. and s.c.a. effects are presented in Table 5 and discussed below.

For days-to-flowering, G130 gave the highest g.c.a. effects for earliness with a value of −5.257, whereas parent C214 gave the maximum g.c.a. effect of 3.886 for lateness, followed by R.S.11. Only two crosses gave s.c.a. effects for earliness, while others had high s.c.a. effects for lateness. The cross C214 × Pb7, involving a high × poor general combiner, gave the highest s.c.a. effects for lateness. Another cross C214 × T.3, involving best combiner × average combiner, gave the highest s.c.a. effects for earliness.

For primary branches, T.3 showed significant g.c.a. effects. R.S.11, G130, C214 gave negative g.c.a. effects . Pb7 was a poor combiner. Four out of ten crosses gave significant s.c.a. effects, while the others either gave negative s.c.a. effects or non-significant effects. The s.c.a. effects of R.S.11 × G130, R.S.11 × × Pb7, C214 × T.3 and Pb7 × T.3 did not differ significantly. Highest s.c.a. effects were recorded for the cross R.S.11 × G130 involving a poor × poor general combiner.

Table 5. *Estimates for general and specific combining ability effects*

Parent/Cross	Estimated combining ability effects				
	Earliness	Primary branches	Pod number	100 seed weight	Grain yield
R.S. 11	2.171 *	−0.818 *	−10.934	−0.660 *	− 4.423 *
G-130	−5.257 *	−0.092	−11.534	−1.096 *	− 1.451
C-214	3.886 *	−0.563	7.966	−1.015 *	− 0.851
PB-7	−2.400 *	0.428	−31.006 *	−0.675 *	− 6.651 *
T-3	1.600 *	1.045 *	45.508 *	3.446 *	13.276 *
S.E. ±	0.628	0.294	10.900	0.085	1.600
C.D. at 5%	1.996	0.940	34.440	0.274	4.960
R.S. 11 × G-130	−1.72	3.30 *	48.40	−0.23	13.25 *
R.S. 11 × C-214	−3.86 *	−0.15	55.20	−0.31	7.65
R.S. 11 × PB-7	3.43 *	2.08 *	80.37 *	−0.17	9.85 *
R.S. 11 × T-3	1.57	0.76	−32.09	0.20	− 1.98
G-130 × C-214	2.43	0.53	65.80 *	0.21	12.47 *
G-130 × PB-7	2.86	−1.39	− 0.23	0.30	− 0.33
G-130 × T-3	0.14	0.10	−67.55 *	−0.21	−10.15 *
C-214 × PB-7	5.71 *	0.11	13.47	0.79 *	2.77
C-214 × T-3	−6.29 *	1.77 *	−50.05	0.58 *	− 4.05
PB-7 × T-3	0.00	2.98 *	41.92	0.62 *	11.55 *
S.E. ±	1.62	0.72	28.12	0.23	4.06
C.D. at 5%	4.440	2.094	77.020	0.614	11.120

The highest no. of pods was recorded for parent T.3 which also gave the highest g.c.a. effects. Pb7 had significant g.c.a. effects for low pod number. All the other parents were poor combiners. Only three crosses exhibited significant s.c.a. effects. The highest s.c.a. effects were observed for cross R.S.11 × × Pb7, followed by G130 × C214, both involving poor general combiners. Most of the crosses involving T.3, the best general combiner, gave s.c.a. effects for low pod number.

T.3 gave maximum 100-seed weight and also maximum g.c.a. effects. All other parents gave significant g.c.a. effects for low 100-seed weight. The highest s.c.a. effects were recorded for the cross C214 × Pb7, a cross between poor general combiners. Two other crosses, C214 × T.3 and Pb7 × T.3, both involving poor × good general combiners, gave significant s.c.a. effects.

Highest seed yield was recorded for T.3, which also gave maximum g.c.a. effects for high yield, while the rest of the parents exhibited significant g.c.a. effects for low yield, Pb7 being the poorest combiner followed

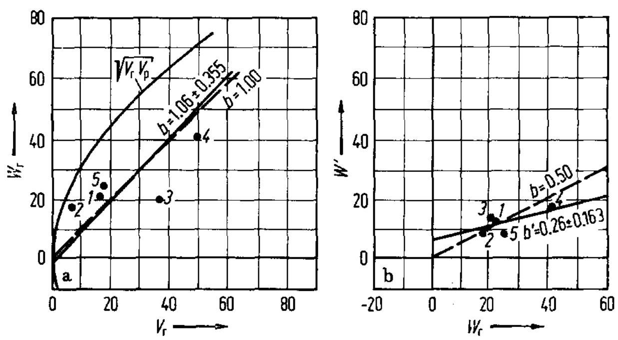

Fig. 1. a. VrWr graph and b. WrW' graph for days to flowering

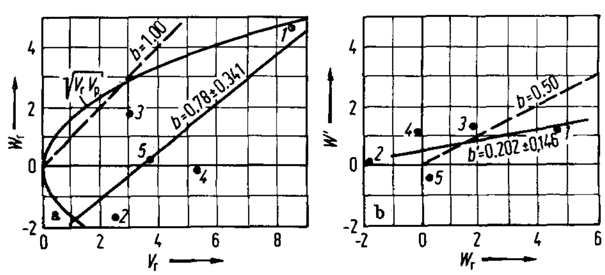

Fig. 2. a. VrWr graph and b. WrW' graph for primary branches

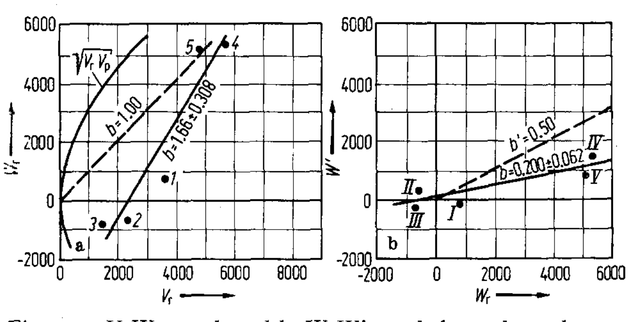

Fig. 3. a. VrWr graph and b. WrW' graph for pod number

by R.S.11 and G130. Significant s.c.a. effects for high yield were recorded for four crosses only, of which three crosses were between poor combiners. Only one cross, Pb7 × T.3 involving a poor × good general combiner, gave significant s.c.a. effects for high yield.

Graphical Analysis

VrWr (variance-covariance) and WrW' (covariance-covariance) graphs from Fig. 1–5 have been drawn for all the five characters; array points for the parents R.S.11, G130, C214, Pb7 and T.3 have been designated 1, 2, 3, 4 and 5, respectively.

The slope of the regression line ($b = 1.06 \pm 0.355$) in the VrWr graph (Fig. 1a) did not differ significantly from unit slope, indicating additive effects of genes for days-to-flowering. The regression line passed the parabola right on the point of origin indicating complete dominance. The parental array point for G130 was nearest to origin, showing that this parent possessed higher proportion of dominant genes, while Pb7 contained more recessive genes. Other parents were more or less balanced for dominant and recessive alleles. In the WrW' graph (Fig. 1b), the slope of regression line did not differ from 0.50, the expected slope, confirming the findings of the VrWr graph.

For primary branches, the slope of the regression line in the VrWr graph (Fig. 2a) did not deviate significantly from unit slope, indicating the absence of genic interaction. A high degree of over-dominance was obvious from this graph. The array point for R.S.11 was farthest from the origin and at the intersection of the parabola and regression line, showing that R.S.11 possessed a majority of recessive alleles for branch number. All the other parents had more dominant alleles. The array point 2 fell in the fourth quarter in the WrW' graph (Fig. 2b), confirming over-dominance.

The VrWr graph for pod number (Fig. 3a) indicated additive effects and over-dominance which were confirmed from the WrW' graph (Fig. 3b). Parents Pb7 and T.3 possessed most of the recessive alleles, while the other parents were symmetrical for negative and positive alleles for pod number. The wide spread of array points along the regression line indicated genetic variability among this group of parents.

For 100-seed weight, the VrWr graph (Fig. 4a) had $b = 1.02 \pm 0.05$, indicating absence of epistasis. There was no space between the parabola and the regression line, which was almost a tangent to the parabola, indicating absence of dominance. The WrW' graph (Fig. 4b) confirmed the previous findings.

The VrWr graph for grain yield (Fig. 5a) had a slope of regression $b = 1.36 \pm 0.32$, indicating additive effects of genes. The line of regression passed through the parabola below the origin, showing marked over-dominance. Array points for C214 and G130 were near the origin, showing that these parents possessed a majority of dominant alleles, compared with Pb7 which possessed more recessive alleles. The results of the VrWr graph were further confirmed from the WrW′ graph (Fig. 5b). The wide distribution of array points along the regression line indicated genetic variability among the parents.

Discussion

A maximum of 6% heterosis over better parent for early flowering was exhibited by the cross C214×T.3, and no other cross gave heterosis for lateness. There appeared to be over-dominance for earliness. In general, very little heterosis was observed for days-to-flowering. Both g.c.a. and s.c.a. effects were significant but g.c.a. effects were more important, indicating the additive effects of genes. Weber *et al.* (1970) in soybean, Singh and Dhaliwal (1971) in black gram and Bihari (1972) in gram also observed that g.c.a. effects were more important than s.c.a. effects. The cross C214×T.3 which gave the highest over-dominance and involved a high× ×average general combiner, also gave the highest s.c.a. effects with a value of −6.29. Parent G130, which took nearly the minimum days to flower, had the highest g.c.a. effects for earliness, while the reverse was also true. Graphical analysis indicated additive effects with complete to over-dominance. The position of the array point for G130 indicated that it possessed the maximum dominant alleles, indicating the dominance of earliness over lateness. These results agree with the findings of Singh and Dhaliwal (1971) in black gram and of Bihari (1972) in gram, where additive effects with dominance of earliness were observed for days to flowering.

For number of primary branches, a maximum of 43% and 35% heterosis over mid-parent and better parent respectively was observed. Ramanujam *et al.* (1964) and Bihari (1972) also observed a very high degree of heterosis for this character in gram. Two crosses, R.S.11×G130 and R.S.11×Pb7, gave 43% and 30%, and 40% and 23% heterosis over mid-parent and better parent, respectively. A very high degree of over-dominance was observed in all the crosses. High no. of primary branches appeared to be dominant over low no. of branches. Both g.c.a. and s.c.a. effects were equally important for no. of primary branches. The parent, T.3, which gave the highest no. of primary branches also showed the highest g.c.a. effects. Similarly, the cross with the highest heterosis, R.S.11×G130, gave the highest s.c.a. effects. Mostly, crosses between divergent parents gave high s.c.a. effects. Graphical analysis indicated the importance of additive effects and over-dominance. Parent T.3, which gave the maximum no. of primary branches, possessed the highest proportion of dominant alleles, while R.S.11 contained

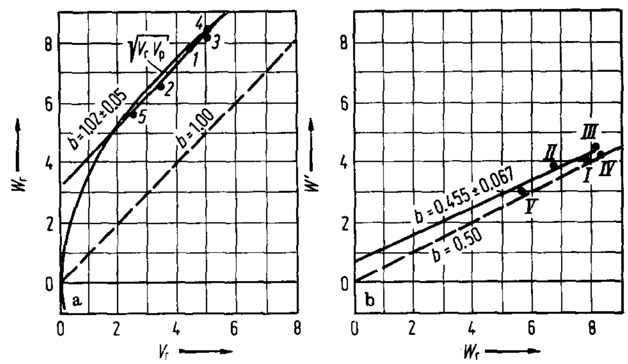

Fig. 4. a. VrWr graph and b. WrW′ graph for 100-seed weight

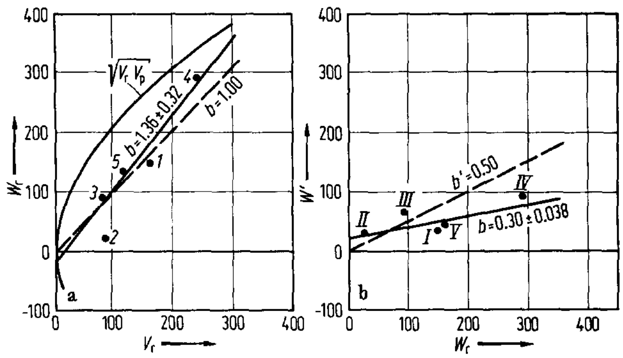

Fig. 5. a. VrWr graph and b. WrW′ graph for seed yield

most of the recessive alleles. High branch number appeared to be governed by dominant alleles. These findings confirm those of Bihari (1972) who reported additive gene effects in gram, with partial dominance.

For pod number, a very high degree of heterosis and over-dominance was observed. Pal (1945) reported that pod number was the only character in gram to exhibit heterosis and Ramanujam *et al.* (1964) also reported 37% heterosis for pod number. All the crosses except those involving parent T.3 gave over-dominance. The maximum heterotic effect over mid-parent and better parent was observed in the cross R.S.11×Pb7, the parents being of diverse origin. Both general and specific combining ability effects were equally important for this character. Parent T.3 gave the highest g.c.a. effects while Pb7 gave the lowest g.c.a. effects, in line with their *per se* performance. Two crosses, R.S.11×Pb7 and G130×C214, of low×low general combiners, gave the highest s.c.a. effects which might be due to additive×additive interaction of genes. Similar results were observed by Bond (1966) in field bean, Dhaliwal and Singh (1970) in black gram and Bihari (1972) in gram, who reported high g.c.a. effects for number of pods. Parents C214 and G130 appeared to have interacted for higher s.c.a. effects. Graphical analysis showed additive gene effects with over-dominance. Similar results were reported by Dhaliwal and Singh (1970) in black gram and Bihari (1972) in gram. T.3 and Pb7 seemed to possess most of the recessive alleles but a cross between them, T.3 × Pb7, gave a very high no. of pods, which might be caused by the additive × additive type of complementary gene interaction. Parents G130 and C214 possessed a majority of dominant alleles and a cross between them also gave a very high yield, and might be used to get segregation for high pod number.

For 100-seed weight, very low heterosis both over better and mid-parent was generally observed. The cross C214 × Pb7 gave 8% and 6% heterosis over mid- and better parent, respectively. Ramanujam *et al.* (1964) also reported 19% heterosis in gram. Little or no dominance was obviously in most of the crosses. Both general and specific combining ability effects were significant but g.c.a. effects were more important indicating the additive effects of genes to be more important. T.3 gave maximum g.c.a. effects with a value of 3.446. Two out of three crosses which gave high s.c.a. effects involved the best general combiners. Graphical analysis indicated additive effects of genes with no dominance. T.3, which had the greatest 100-seed weight, also possessed the highest proportion of dominant alleles. High 100-seed weight seemed to be dominant over low 100-seed weight. The cross C214 × Pb7, between parents containing higher proportions of recessive alleles, gave the highest s.c.a. effects, which might be due to combination of favourable alleles. The results of the present investigations are consistent with the findings of Bond (1966) in field beans, Abdul and Muhammad (1968) and Bihari (1972) in gram, who reported the importance of g.c.a. effects or additive effects with little dominance for 100-seed weight.

A very high degree of heterosis and over-dominance was observed for seed yield. A maximum of 48% and 45% heterosis over mid-parent and better parent, respectively, was observed in a cross involving parents of different origin (RS11 × Pb7). Ramanujam *et al.* (1964) and Bihari (1972) also reported a high degree of heterosis over better parent for grain yield in gram. Except for those involving T.3, all the crosses showed a high degree of over-dominance. General combining ability effects were more important, indicating the preponderance of additive gene effects. Parent T.3, which gave a high yield, also showed the highest g.c.a. effect. Three crosses involving parents with low general combining effects gave the highest specific combining ability effects; this might be due to combination in the hybrids of favourable alleles. Similar results were reported by Weber *et al.* (1970) in soybean, by Bond (1966) in field beans, Abdul and Muhammad (1968) in gram, and Singh and Dhaliwal (1972) in black gram where general combining ability effects were more important than s.c.a. effects. Graphic analysis showed the presence of additive effects with over-dominance. In general, parents with low yields had a majority of recessive alleles. These results agree with the findings of Singh and Dhaliwal (1972) in black gram where additive effects with negative over-dominance were observed.

Parent T.3 was a good general combiner for all other characters except days to flower where G130 had the highest g.c.a. effects for earliness. These two parents might be exploited in hybridization programme to effect improvement in these characters. The crosses C214 × T.3 for earliness, R.S.11 × G130 and Pb7 × T.3 for higher no. of branches, R.S.11 × × Pb7 and G130 × C214 for high pod number, C214 × Pb7, Pb7 × T.3 and C214 × T.3 for higher 100-seed weight, and R.S.11 × G130, R.S.11 × Pb7, G130 × C214 for high yield may be studied in further segregating generations, which are expected to throw up good segregates for the respective characters. Additive effects appear to predominate for all the characters so that the pedigree method of selection would be ideal for handling the segregating generations.

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Literature

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