

Genetic analysis of agronomic characters in chickpea

I. Estimates of genetic variances from diallel mating designs*

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Summary. Twenty-eight diallel trials over 8 years and two locations were analysed to estimate genetic variances for agronomic characters of chickpea (Cicer arietinum L.). The data were analysed according to Method 4 and Model I of Griffing (1956). Days to flowering, plant height, and seed size were found to be predominantly under additive inheritance and were highly predictable. Both additive and non-additive genetic components were important for seed yield, number of branches, pods per plant, and seeds per pod. Although both general combining ability (gca) and specific combining ability (sca) varied significantly with generation, components of gca mean squares were invariably much larger than gca × generation interaction components, indicating that either the F_1 or the F_2 generation can be used to estimate the gca components effectively. Combined diallel analysis of F₂s over locations revealed the importance of combining ability × location interactions and emphasized the need for testing over more than one location for the precise estimation of combining ability. The implications of these findings and those reported earlier in the literature on the breeding strategies/methods for the genetic improvement of agronomic characters in chickpea are discussed.

Key words: Chickpea – Diallel analysis – Yield and yield components – Gene effects – Genotype × environment interaction

Introduction

The objectives of diallel analysis are (1) to identify the best combining parents and crosses for the trait under study and (2) to provide estimates of the combining ability variances for the characters to be improved. Diallel mating requires the systematic recombination within a set of parental genotypes and, normally, provides considerable variability among the resulting crosses. The chief disadvantage of the design is that the number of parents must be restricted (between five and ten in most cases), and crosses have to be made which, at the outset, are predictably of little value for crop improvement.

The utility of the diallel mating design for providing valid estimates of genetic parameters remains in question, mainly because of the failure of the parental sets to satisfy the assumptions on which most of the methods of analysis are based. Two of these, the independent distribution of the genes involved and the absence of epistasis are rarely, if ever, satisfied, as pointed out by Baker (1978). The failure of the former assumption probably leads to overestimation of the average level of dominance. Whether it also biases estimates of general (gca) and specific combining ability variances (sca) is not clear.

One of the main advantages of diallel analysis lies in determining the genetic nature of important quantitative traits. If the parents used were a random sample from a broad-based population and if the testing has been conducted over a sufficient number of environments, the results will quickly enable the breeders to choose the most appropriate breeding methods and selection procedures for the genetic improvement of a crop species. This has been rarely achieved in chickpea (*Cicer arietinum* L.) because of the limitations in obtaining adequate quantities of F₁ seeds by hand-pollination. Another point which has been rarely addressed in this crop is the effect of testing generations and genotype × environment $(G \times E)$ interactions on the estimates of genetic variances from diallel trials. At one extreme, the effects of these interactions may be so great that the estimates are unique

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Trial ^a no.	Number of parents	Generation	Number of replications	Year	Location ^b	Nature of parents
D1	18	F ₁	2	1975-1976	PA	Various Desi and Kabuli
D2	16	F ₁	3	1978-1979	PA	Various Desi and Kabuli
D3	8	$\overline{F_1}$	3	1978-1979	PA	Tall plant types
D4	10	F_1	3	1979-1980	PA	Various Desi and Kabuli
D5	16	$\overline{F_2}$	3	1979-1980	PA	Same as D3
D6	16	$\overline{F_2}$	3	1979-1980	HI	Same as D3
D7 A/B	9	$\overline{F_1}/\overline{F_2}$	4	1980-1981	PA	Short, medium duration (Desi)
D8	10	F_2	3	1980-1981	PA	Same as D7
D9	4	$\overline{F_1}$	3	1980-1981	PA	Helicoverpa resistant (Desi)
D10	6	F_1	2	1981-1982	PA	Tall plant types
D11	6	F_1	3	1981-1982	PA	Helicoverpa resistant (Desi)
D12	4	F_1	5	1981-1982	PA	Helicoverpa resistant (Kabuli)
D13	8	$\overline{F_1}$	3	1982-1983	PA	Short duration (Desi)
D14	6	F_1	3	1982-1983	HI	Long duration (Desi)
D15	5	F_1	3	1982-1983	PA	Multiseeded
D16	7	F ₁	3	1982-1983	PA	Early sown
D17	6	F_1	3	1982-1983	PA	Helicoverpa resistant (Desi)
D18	6	F1	3	1982-1983	PA	Helicoverpa resistant (Desi)
D19	11	F_1	3	1983–1984	PA	Short duration (Desi)
D20	8	F ₂	3	1983-1984	PA	Same as D13
D21	5	F_1	3	1983-1984	PA	Helicoverpa resistant (Desi)
D22	6	F ₁	3	1983-1984	PA	Helicoverpa resistant (Desi)
D23	5	F_1	3	1983-1984	PA	Helicoverpa resistant (Kabuli)
D24	12	F_1	3	1984-1985	PA	Short duration (Desi)
D25	12	F_1	3	1984-1985	HI	Long duration (Desi)
D26	6	F_1	3	1984-1985	HI	Helicoverpa resistant (Desi)
D27	4	F ₁	3	1984-1985	HI	Helicoverpa resistant (Kabuli)

Table 1. Description of chickpea diallel trials conducted between 1975 and 1985

^a D, Diallel set

^b PA, Patancheru, India; HI, HIsar, India

in each test. At the other extreme, consistent estimates may be obtained for highly heritable characters that will be extremely valuable for predicting the breeding value of the parents and their crosses.

Some of these aspects, particularly the general nature of the genetic control of important agronomic traits of chickpea, are examined in this paper using data from 28 trials with F_1 and F_2 generations of diallel crosses. The interpretation of the results from these diallel trials are restricted to the specific materials used in the experiments as the parents were deliberately chosen and cannot be regarded as a random sample from any population. We have examined the consistency of the estimates of genetic parameters obtained across parental sets and environments. The results have been discussed in view of the most appropriate and suitable breeding strategies for the genetic improvement of agronomic characters in chickpea.

Materials and methods

The F_1 and/or F_2 generations in 28 experiments of diallel crosses (D1-D28) without reciprocals were tested along with their

parental lines in either randomized complete block (RCB) or lattice designs at the research farms managed by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) at Patancheru (17°N 78°E) near Hyderabad and Hisar (29°N 75°E) in India between 1975 and 1985 (Table 1). The trials were conducted at each location in two to five replications.

The parents and F_1s were planted in plots of single rows, and the F_2s in plots of two or four 4-m-long rows. The distance between plants was 20 cm within and 60 cm between rows.

The parents were extremely diverse for seed type (desi or kabuli), duration (short or long), habit (tall to prostrate), and resistance to the pod borer (*Helicoverpa armigera*). They had one or two pods per node and a single or many seeds per pod.

Most of the trials were conducted at the ICRISAT Center at Patancheru, but a few were also grown at the ICRISAT Sub-Center, Hisar. Husbandry practices were relatively uniform. Sowing dates were usually during the last half of October, except for D16 (crosses of parents adapted to early sowing), which was shown in mid-September. Fertilizer and irrigation water were either not applied or were minimal. Protection against the pod borer was provided except to trials of crosses involving pod borer-resistant parents (D9, D11, D12, D17, D18, D21, D22, D23, D26, and D27).

Characters were measured on a single plant or on a plot basis. Records on single plants were taken from either five random plants (F_{1s}) or from ten random plants (F_{2s}) per plot and averaged for analysis. Data included the number of days from sowing to 50% flowering and to maturity; plant height (cm); the numbers of primary and secondary branches, pods per plant,

Trial no.	Days to flowering	Days to maturity	Plant height (cm)	Number of branches		Pods	Seeds	100-seed	Seed yield
				Primary	Secondary	per plant	per pod	mass (g)	per plant (g)
D1	1.35**	1.97**	5.31 **	0.240**	0.27 **	377.0**	0.004 **	15.15**	3.06**
D2	18.55**	8.14 **	3.81 **	0.035**	0.155 **	46.2**	0.002**	7.86**	2.48**
D3	67.08 **	31.01 **	71.82**	0.075*	3.315**	320.0**	0.003 **	1.69**	3.64**
D4	21.32**	4.13**	4.13 **	0.011 *	0.076*	151.45**	0.003 **	10.13**	7.32**
D5	24.57**	38.70**	ND	ND	ND	ND	ND	7.95**	1.77**
D6	34.28 **	0.77 **	ND	ND	ND	ND	ND	7.57**	2.85**
D7A	6.61 **	3.37 **	9.52**	0.025**	0.29 **	481.7**	0.003**	2.25**	14.03 **
D7B	6.03 **	3.47 **	6.85**	0.025**	0.19**	223.85**	0.002**	2.94 **	1.93
D8	24.69 **	18.55 **	ND	ND	ND	ND	ND	8.96**	5.87**
D9	ND	ND	ND	ND	ND	88.80	ND	ND	9.19
D10	50.51 **	25.01 **	2.53	0.035	0.145	86.70	0.0112 **	ND	2.91
D11	32.65**	28.17**	2.58**	0.085**	0.01	ND	ND	ND	0.61
D12	9.59*	6.90 **	0.98	0.000	0.13	ND	ND	ND	3.69 **
D13	7.74**	1.40*	0.00	0.025**	0.685**	416.15**	0.006 **	21.36**	4.27
D14	7.49 **	0.05	4.44*	0.000	3.30	355.5*	0.003*	1.41 **	8.70
D15	26.18**	9.92*	8.17**	0.030 **	0.585**	103.15**	0.002 **	0.05	3.98 **
D16	4.38 **	9.60 **	0.67**	0.005	0.48 **	325.25**	0.004 **	5.87**	1.27
D17	14.51 **	21.38**	0.23	0.019	0.05	102.50*	ND	ND	4.27**
D18	61.13**	21.83 **	1.90*	0.000	0.03	0.00	ND	ND	3.54 *
D19	0.66**	1.38 **	1.41 **	0.005	0.145**	117.3**	0.001 **	6.84**	2.25 **
D20	5.24 **	3.72**	ND	ND	ND	ND	ND	11.55**	7.655**
D21	14.59 **	0.28	1.07	0.035	0.18**	ND	ND	ND	14.37 **
D22	21.44**	4.92**	0.94*	0.000	0.11 *	ND	ND	ND	1.89
D23	61.40**	10.55 **	0.00	0.015	0.94 **	ND	ND	ND	5.85**
D24	15.77 **	6.70**	ND	ND	ND	ND	ND	2.96**	15.00**
D25	9.80**	ND	3.09**	0.000	0.00	287.3**	0.006**	1.48**	11.14**
D26	2.82 **	0.00	31.10**	0.000	0.33	ND	ND	ND	21.17*
D27	0.49	0.00	7.71	0.044 **	0.75	ND	ND	ND	41.72
Mean	20.40	10.07	7.65	0.03	0.55	217.7	0.004	6.83	7.377
SE	± 3.742	± 2.172	±3.359	± 0.011	± 0.198	± 37.18	± 0.001	± 1.36	± 1.586

Table 2. Estimates of components of general combining ability mean squares from diallel trials

ND, No data

**** Significant at 0.05 and 0.01 levels of probability, respectively

and seeds per pod; the mass of 100 seeds (g); and seed yield (g) per plant.

Analyses of variance were conducted for RCB designs in all cases. The diallel structure was analysed according to Method 4, Model I of Griffing (1956). Since parents are excluded in this analysis, it leads to unbiased estimates of gca and sca parameters. The estimates of gca and sca variance components, which are equivalent components of gca and sca mean squares [1/p-1) Σ gca²] and [2/p(p-3) Σ sca²] in this model, were calculated using the expectation of mean squares given for the Model I. Predictability ratios (additive genetic variance) were calculated according to Baker (1978).

The importance of the interaction effects of gca and sca with environments and the generations tested were examined in combined analyses of those sets of crosses that were either repeated in different environments or had F_1 and F_2 generations evaluated in the same season. The analyses were performed using the expectation of mean squares provided for fixed effects model by Singh (1973).

Results

The components of gca and sca mean squares were significant for all characters except the sca component for days to flowering for D1 (analysis not shown). The relative importance of additive and non-additive genetic effects for various characters was reflected by the predictability ratios, which were close to unity in the cases of days to flowering and to maturity, plant height, and 100-seed mass, indicating the predominance of additive gene effects for these traits. Both additive and non-additive effects were important for the remaining characters.

The pattern for gca and sca varied among diallels as demonstrated by the estimates of relevant components of gca and sca mean squares from the other diallel trials (Tables 2 and 3). In virtually every trial gca components were significant for days to flowering, seeds per pod, and seed mass. They were significant in most trials for days to maturity and pods per plant; in 60-75% of the trials they were significant for plant height and seed yield per plant; and in about 50% of the trials they were significant for primary and secondary branches. The components of sca mean squares were significant in more than 50% of the trials for days to flowering and to maturity and for 100seed mass, in about 30% to 40% of the trials for pods per

Trial no.	Days to flowering	Days to maturity	Plant height (cm)	Number of branches		Pods	Seeds	100-seed	Seed yield
				Primary	Secondary	per plant	per pou	шазэ (Е)	(g)
D1	0.60	0.90*	4.10**	0.078 **	0.61 **	427.0**	0.006 **	2.82 **	13.00**
D2	8.07**	4.43 **	2.58**	0.029	0.09	10.6	0.005 **	0.90 **	0.00
D3	19.11 **	23.95 **	1.85	0.00	0.00	264.5**	0.006 **	0.23*	22.33 **
D4	5.45**	4.56**	0.62	0.001	0.00	0.0	0.000	2.25**	0.00
D5	15.90**	12.35 **	ND	ND	ND	ND	ND	0.90 **	0.30
D6	4.17*	0.00	ND	ND	ND	ND	ND	0.65 **	0.00
D7A	7.26**	2.56	4.27**	0.039	0.80**	396.6**	0.002	1.14**	20.38 **
D7B	4.29**	4.09*	0.93	0.017	0.08	0.0	0.00	1.05 **	5.49
D8	3.37**	4.53 **	ND	ND	ND	ND	ND	1.37 **	0.00
D9	ND	ND	ND	ND	ND ·	798.3**	ND	ND	36.78 **
D10	8.61	2.80	0.00	0.029	0.73	388.5	0.003	ND	13.89
D11	7.47	15.27**	1.46	0.054*	0.00	ND	ND	ND	1.36
D12	2.29	2.13	0.00	0.039	0.22	ND	ND	ND	0.02
D13	2.91*	0.55	0.50	0.021	0.26	504.9	0.00	1.24 *	25.43
D14	3.42*	0.71	0.00	0.000	0.00	5.7	0.003	0.66	0.00
D15	10.49 **	3.92*	0.00	0.000	0.35*	129.5*	0.002*	0.03	8.63 **
D16	0.93	4.55**	0.00	0.000	0.09	0.0	0.001 *	0.80 **	0.00
D17	8.73*	18.95**	1.20	0.000	0.03	93.4	ND	ND	0.03
D18	5.05	3.67*	0.66	0.000	0.07	0,0	ND	ND	0.00
D19	1.10**	2.63 **	1.22*	0.000	0.20*	149.0	0.00	1.18 **	5.19*
D20	1.96* [*]	5.97**	ND	ND	ND	ND	ND	0.91 **	1.34
D21	5.04	13.73	0.30	0.000	0.00	ND	ND	ND	0.00
D22	13.17**	4.74	1.02	0.000	0.00	ND	ND	ND	0.97
D23	71.76**	37.10**	5.62	0.000	1.07*	ND	ND	ND	8.66 **
D24	4.38 **	0.00	ND	ND	ND	ND	ND	0.40*	30.26*
D25	0.52	ND	0.00	0.000	0.00	0.0	0.00	0.18*	0.00
D26	1.15	0.00	4.07	0.010	1.22	ND	ND	ND	5.57
D27	2.71	0.34	0.00	0.025*	0.94	ND	ND	ND	21.52
Mean	8.14	6.71	1.38	0.015	0.37	198.0	0.002	0.98	7.90
SE	±2.608	<u>+</u> 1.721	±0.361	± 0.005	±0.111	±60.32	±0.001	± 0.171	±2.041

Table 3. Estimates of components of specific combining ability mean squares from diallel trials

ND, No data

**** Significant at 0.05 and 0.01 levels of probability, respectively

plant and seeds per pod, and in less than 25% of the trials for plant height, primary and secondary branches, and seed yield. The magnitude and frequency of the significance of gca mean square components were much greater than those of the sca components in the majority of cases. The variation in the estimates of components of gca and sca mean squares was highest for plant height and seeds per pod, respectively.

The relative magnitude and importance of additive and non-additive variances in the genetic control of various agronomic characters were further revealed by the predictability ratios (Table 4). These reflected the preponderance of additive genetic effects for 100-seed mass, days to flowering and plant height. For other characters both additive and non-additive effects were important as the average predictability ratios over trials were less than 0.8.

The combined analysis of F_{2S} (D5 and D6) grown at two places in the same season (analysis not shown) indicated that the location and interaction of crosses with locations had large and highly significant effects on all the characters. Location did not interact with sca for 100-seed mass and seed yield but significantly interacted with gca for all characters and with the sca for days to flowering and to maturity. For seed yield the interactions of genetic effects with locations were much more important than the genetic effects alone.

Combined analysis of D7A and D7B diallel trials over the F_1 and F_2 generations (analysis not shown) revealed that generation significantly affected the estimates for all characters except primary branches per plant, seeds per pod, and 100-seed mass. The interactions between crosses and generations were significant for all characters except the number of primary branches. Generation did not interact with either gca or sca effects for primary branches per plant and seeds per pod, but interacted significantly with both gca and sca for days to flowering, plant height, secondary branches per plant, and seed yield. Generation interacted significantly with gca for days to maturity and pods per plant, and with sca for 100-seed mass. The components of mean squares for gca were much larger than those for gca × generation

Table 4. Predictability ratio $(2 - gca^2/2 - gca^2 + -sca^2)$ in chickpea diallel trials

Trial	Days to flowering	Days to maturity	Plant height (cm)	Number of branches		Pods per plant	Seeds	100-seed	Seed yield
				Primary	Secondary	per prant	per pou	mass (g)	(g)
D1	0.69	0.69	0.56	0.75	0.31	0.47	0.40	0.84	0.19
D2	0.82	0.79	0.75	0.71	0.76	0.90	0.64	0.95	1.00
D3	0.88	0.72	0.98	0.57	1.00	0.71	0.50	0.94	0.25
D4	0.89	0.64	0.93	0.96	1.00	0.85	1.00	0.90	1.00
D5	0.76	0.87	ND	ND	ND	ND	ND	0.95	0.92
D6	0.94	1.00	ND	ND	ND	ND	ND	0.96	1.00
D7A	0.65	0.73	0.82	0.58	0.42	0.71	0.71	0.82	0.58
D7B	0.74	0.63	0.94	0.75	0.83	1.00	1.00	0.85	NS
D8	0.94	0.89	ND	ND	ND	ND	ND	0.93	1.00
D9	ND	ND	ND	ND	ND	0.18	ND	ND	0.33
D10	0.92	0.95	NS	NS	NS	NS	0.90	ND	NS
D11	0.90	0.79	0.78	0.76	NS	ND	ND	ND	NS
D12	0.89	0.87	NS	NS	NS	ND	ND	ND	0.97
D13	0.84	0.83	NS	0.71	0.84	0.62	1.00	0.98	NS
D14	0.81	NS	1.00	NS	NS	0.98	0.65	0.82	NS
D15	0.83	0.84	1.00	1.00	0.77	0.61	0.69	NS	0.48
D16	0.90	0.81	1.00	NS	0.92	1.00	0.94	0.94	NS
D17	0.77	0.69	NS	NS	NS	0.69	ND	ND	0.98
D18	0.96	0.92	0.85	NS	NS	NS	ND	ND	1.00
D19	0.55	0.51	0.70	NS	0.59	0.61	0.89	0.92	0.46
D20	0.84	0.56	ND	ND	ND	ND	ND	0.96	0.92
D21	0.85	NS	NS	NS	1.00	ND	ND	ND	0.90
D22	0.77	0.68	0.65	NS	1.00	ND	ND	ND	NS
D23	0.63	0.36	NS	NS	0.64	ND	ND	ND	0.57
D24	0.88	1.00	ND	ND	ND	ND	ND	0.94	0.50
D25	0.97	ND	1.00	NS	NS	1.00	0.94	0.95	0.62
D26	0.83	NS	0.94	NS	NS	ND	ND	ND	0.87
D27	NS	NS	NS	0.78	NS	ND	ND	ND	NS
Mean	0.83	0.76	0.86	0.76	0.79	0.74	0.79	0.92	0.73
SE	±0.021	±0.034	±0.037	± 0.044	±0.063	± 0.064	± 0.056	± 0.013	±0.064

ND, No data; NS, nonsignificant (for gca and sca variances)

interactions. The relative importance of interaction with generations was much higher for sca than for gca effects for all traits.

Discussion

A general trend of the genetic control of characters can be ascertained from estimates of components of gea and sca mean squares from a large number of diallel trials. In diallel analysis the gea is a function of additive genetic effects, but may partially include some dominance effects when gene frequencies are not equal to one-half and/or parents are included in the analysis to estimate the variances (Singh and Paroda 1984). Griffings analysis, Method 4, which excludes the parents, provides accurate estimates of general combining ability. This study demonstrates that additive genetic effects $(2\Sigma \text{ gca}^2)$ were greater than non-additive effects $(\Sigma \text{ sca}^2)$ for plant height, days to flowering, and 100-seed mass. Earlier reports support these results (Gupta and Ramanujam 1974; Asawa and Tiwari 1976; Gowda and Bahl 1978; Singh and Mehra 1980; Malhotra et al. 1983; Dhaliwal and Gill 1973). Thus, days to flowering, plant height, and 100-seed mass in chickpea can be improved by a simple selection scheme, such as the pedigree method, since both additive and additive \times additive genetic effects, which are prominent for these characters, are easily fixable in the early generations. Seed mass, which is a highly heritable and important yield component in chickpea, can be used effectively as an indirect selection criterion for improving seed yield (Singh and Paroda 1986).

The results, which indicate the importance of both gca and sca effects for days to maturity, branches per plant, pods per plant, seeds per pod, and seed yield, are in close agreement with those reported by Lal (1972), Singh and Mehra (1980); Singh et al. (1982); Malhotra et al. (1983), and Singh and Paroda (1989). However, Gupta and Ramanujam (1974), Asawa and Tiwari (1976), Sikka (1978), Gowda and Bahl (1978), and Yadavendra and Kumar (1987) reported non-additive genetic effects to be of major importance for the above characters. Such disparities may arise from differences in the genetic constitution of the parental materials studied, variation in the environment, the techniques used in analysing the data, and the precision of the experiment.

Exploitation of the non-additive genetic effects in the form of using F_1 hybrids in chickpea is not feasible because of the problem of crossing. Nevertheless, homozygous lines equal to or better than the F_1 have been reported to have been developed from highly heterotic crosses in self-pollinated crops. Such examples of transgression have been given by Smith (1952) in tobacco (Nicotiana tabaccum), Williams (1959) in tomato (Lycopersicon esculentum), Aestaviet (1964) in barley (Hordeum vulgare), and Singh (1980) in mungbean (Vigna radiata). Singh (1974) also suggested the possibility of deriving pure lines performing better than or as well as F_1 hybrids in chickpea. These examples suggest that a larger proportion of non-additive effects in self-pollinated crops seems to be due to additive x additive effects and that selection be deferred to later generations. Linkage is another factor that complicates the problem in selection. If linkages are predominantly of the repulsion type, a generation of intercrossing to increase the opportunity of recombination may become important.

In the combined analysis of F_1s and F_2s , the testing generation significantly interacted with gca for all characters except primary branches, seeds per pod, and 100seed mass. However, since the magnitude of the gca component was much larger than those of the interaction components, as is evident from the $\Sigma \operatorname{gca}^2 / \Sigma \operatorname{gca}^2 \times \operatorname{gener-}$ ation ratio, either of the generations can be considered equally effective in providing reasonable estimates of gca for most characters. The interactions between sca and generation were also significant for days to flowering, plant height, secondary branches, seed mass, and seed yield. But unlike gca, the magnitudes of the sca components were smaller than those of the interaction components, as indicated by the $\Sigma \operatorname{sca}^2 / \Sigma \operatorname{sca}^2 \times \operatorname{generation}$ ratios. The major cause of these interactions must have been the variation in inbreeding depression among the crosses, which is not so uncommon in this crop (Deshmukh and Bhapkar 1982; Tewari and Pandey 1987). The possible biases in the estimates of gca and sca that may be caused by inbreeding have been discussed by Stuber (1970). The implications of the present study, involving only one trial to determine the unbiased estimates of sca components, are obviously limited, and more studies are required over generations for confirmation.

The combined analysis of two similar F_2 diallel trials over two contrasting locations showed that location interacted significantly with gca for all of the characters studied and with sca for days to flowering and to maturity. The $\Sigma \operatorname{gca}^2/\Sigma \operatorname{gca}^2 \times \operatorname{location}$ ratio, which was less than 1 for days to maturity and seed yield and greater than 1 for days to flowering and seed mass, suggested that the additive genetic effects of the latter two characters were relatively more stable over locations. The $\Sigma \sec^2/\Sigma \sec^2 \times \text{location ratios}$, which were less than 1 in all four cases, suggested large interactions of sca with location. It is difficult to find any published report in the literature on the above aspects in chickpea, but large combining ability × location/environment interactions have been reported in several other self-pollinated crops (Malhotra et al. 1980, Singh et al. 1983; Kumar et al. 1983; Gupta et al. 1986). The results of the present study indicate the importance of such interactions and suggest the inclusion of more locations in the analysis of combining ability.

References

- Aestaviet K (1964) Heterosis and selection in barley. Genetics 49:159-164
- Asawa BM, Tiwari AS (1976) Analysis of genetic architecture in segregating populations of gram (*Cicer arietinum* L.). Z Pflanzenzucht 77:251-256
- Baker RJ (1978) Issues in diallel analysis. Crop Sci 18: 533-536
- Deshmukh RB, Bhapkar DG (1982) Heterosis and inbreeding depression in chickpea. Indian J Genet 42:208-212
- Dhaliwal HS, Gill AS (1973) Studies of heterosis, combining ability and inheritance of yield components in a diallel cross of Bengal gram. Theor Appl Genet 43: 381-386
- Gowda CLL, Bahl PN (1978) Combining ability in chickpea. Indian J Genet 38:245-251
- Griffing B (1956) Concept of general and specific combining ability in relation to diallel crossing system. Aust J Biol Sci 9:463-493
- Gupta KR, Dahiya BS, Singh KP (1986) Combining ability studies over environments in pea. Crop Improv 13:134-137
- Gupta VP, Ramanujam S (1974) Genetic architecture of yield and its components in Bengal gram. Indian J Genet 34A:793-799
- Kumar H, Sharma GS, Singh RB (1983) Genotype × environment interaction in relation to combining ability in spring wheat. Indian J Genet 43:232-238
- Lal B (1972) Diallel analysis of grain yield and some other quantitative traits in bengal gram (*Cicer arietinum* L.). M.Sc. thesis, Punjab Agricultural University, Ludhiana, India
- Malhotra RS, Gupta PK, Arora ND (1980) Diallel analysis over environments in mungbean. Indian J Genet 40:64-66
- Malhotra RS, Singh KB, Lal B (1983) Combining ability for yield and its components in chickpea. Indian J Genet 43:149-151
- Sikka G (1978) Heterosis and combining ability studies in *Cicer* arietinum L. M.Sc. thesis, Haryana Agricultural University, Hisar, India
- Singh D (1973) Diallel analysis for combining ability over several environments – II. Indian J Genet 33:469–481
- Singh KB (1974) Exploitation of heterosis in pulse crops. Indian J Genet 34A: 731-808
- Singh KB, Malhotra RS, Respana BL (1982) Inheritance studies for yield and its components in chickpea. Genet Agrar 36:231-245
- Singh M (1980) Genetic and immunochemical analysis of heterosis in green gram [Vigna radiata (L.) Wilczek]. Ph.D. thesis, Haryana Agricultural University, Hisar, India
- Singh O, Paroda RS (1984) A comparison of different diallel analysis. Theor Appl Genet 67:541-545

- Singh O, Paroda RS (1986) Association analysis of grain yield and its components in chickpea following hybridization and a combination of hybridization and mutagenesis. Indian J Agric Sci 56: 139–141
- Singh O, Paroda RS (1989) A comparative analysis of combining ability and heterosis in irradiated and non-irradiated diallel populations of chickpea. Indian J Pulses Res 2:1-9
- Singh R, Bhullar GS, Gill KS (1983) Combining ability over environments in durum wheat. Indian J Genet 43:152-155
- Singh SP, Mehra RB (1980) Genetic analysis of yield and yield components in Bengal gram. Indian J Genet 40:482-489
- Smith HH (1952) Fixing transgressive vigor in Nicotiana rustica. In: Gower JW (ed) Heterosis. The Iowa State College Press, Ames, pp 161–174
- Stuber CW (1970) Estimation of genetic variances using inbred relatives. Crop Sci 10:129–135
- Tewari SK, Pandey MP (1987) Heterosis and inbreeding depression in chickpea. Indian J Genet 47:261-264
- Williams W (1959) The isolation of 'pure lines' from F₁ hybrids of tomato, and the problem of heterosis in inbreeding crop species. J Agric Sci 53: 347-353
- Yadavendra JP, Kumar S (1987) Combining ability in chickpea. Indian J Genet 47:67-70