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Genetic analysis of agronomic characters in chickpea. II. Estimates of genetic variances from line × tester mating designs

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Summary. Thirty line × tester experiments involving diverse chickpea (*Cicer arietinum* L.) germplasm were conducted over 8 years and three locations to determine the nature of the genetic variance for grain yield and related characters, and the effects of generation and environment on these genetic parameters. Days-to-flowering, 100-seed mass, and seeds per pod were predominantly under the control of additive genetic variance, while both additive and non-additive genetic components of variance were important for days-to-maturity, plant height, primary and secondary branches, pods per plant, and seed yield. The F_1 and F_2 generations were found equally useful in estimating the genetic variances for different characters because the generation did not significantly interact with genetic parameters in the majority of cases. Sites or seasons, on the other hand, showed significant interaction with genetic components of variances; additive variance showed a larger interaction with environments than non-additive variance. This indicated the importance of more than one site and/or season for unbiased estimation of the genetic components of variance. The results were compared with previous findings from diallel analyses.

Key words: Chickpea – Combining ability – Line × tester – Genetic variances – Yield and yield components

Introduction

The line × tester mating design is useful for the genetic analysis of various crop species. This design can be used to estimate components of genetic variance and to introduce specific characters into adapted backgrounds. In chickpea, relatively little information derived from this mating design is available on the genetic control of yield and related characters (Singh et al. 1977; Bhatt and Singh 1980; Salimath and Bahl 1988). The present study was undertaken to: (1) estimate the components of genetic variance in chickpea with the line × tester mating design, and (2) study the extent of the influence of environment (location/season) and testing generations on the gene effects. The data accumulated from a large number of trials were used to determine the genetic architecture of important agronomic characters so that the most effective breeding procedure can be suggested for the genetic improvement of this crop.

Materials and methods

Brief descriptions of the 30 line × tester trials conducted at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) between 1975 and 1985 are given in Table 1. Twenty nine of the trials were conducted at the ICRISAT Center, Patancheru, while 11 were conducted at the ICRISAT Sub-center, Hisar, and one at the ICRISAT Sub-center, Gwalior. We included 364 parental lines, representing diverse breeding materials [desi or kabuli types, short or long duration, tall to prostrate in habit, and susceptible or resistant to the pod borer (*Helicoverpa armigera*)], to make the series of 30 line × tester sets for experimentation. Twenty experiments included F_1 generation crosses, Seven included F_2 generation crosses, and three included both F_1 and F_2 generation crosses. Three experiments permitted direct comparisons of F_1 and F_2 generation crosses in the same season and location, while the F_1 and F_2 generation crosses in the other experiments were grown in different seasons.

The design of experiments, plot size, planting distance and management practices were the same as reported by Singh et al.

Table 1. List and description of chickpea line × tester trials conducted between 1975 and 1985

Trial[a] no.	No. of parents	Generation	No. of reps	Year	Location[b]	Nature of parents[c]	
						Lines	Testers
LT1	31 × 7	F₁	3	1975 76	PA	D K various;	D various
LT2	9 × 5	F₁	3	1978 79	PA	D various;	D cultivars
LT3	10 × 4	F₁	3	1978 79	PA	Tall types;	D cultivars
LT4	20 × 5	F₁	3	1979 80	PA	D cultivars;	D brdg. lines
LT5	20 × 5	F₁	3	1979 80	HI	D various;	D cultivars
LT6	9 × 5	F₂	3	1979 80	PA	Same parents as LT2	
LT7	9 × 5	F₂	3	1979 80	HI	-do-	
LT8	10 × 5	F₁	2	1979 80	HI	K cultivars;	D cultivars
LT9	10 × 5	F₁	3	1979 80	PA	Tall types;	K cultivars
LT10	6 × 4	F₁	3	1979 80	PA	Double podded;	Multiseeded
LT11	10 × 5	F₁, F₂	3	1980 81	PA	D brdg. lines;	D cultivars
LT12	20 × 5	F₂	3	1980 81	PA	Same parents as LT4	
LT13	15 × 5	F₂	3	1980 81	GW	Same parents as LT4	
LT14	10 × 4	F₁	3	1980 81	HI	K cultivars; resistant to *Helicoverpa*	K brdg. lines
LT15	10 × 4	F₂	3	1980 81	HI	Same parents as LT14	
LT16	10 × 5	F₂	3	1980 81	HI	Same parents as LT8	
LT17	7 × 6	F₁	3	1980 81	PA	Tall types;	D K cultivars
LT18	4 × 8	F₁	2	1980 81	HI	Double podded;	Multiseeded
LT19	15 × 4	F₁ F₂	2	1981 82	PA	D brdg. lines;	D cultivars
LT20	15 × 4	F₁ F₂	2	1981 82	PA	Same as LT19;	D cultivars
LT21	5 × 8	F₁	3	1981 82	PA	Tall types;	D cultivars
LT22	9 × 8	F₁	3	1982 83	PA	D short duration lines;	D short duration lines
LT23	8 × 9	F₁	3	1982 83	HI	D long duration lines;	D long duration lines
LT24	11 × 9	F₁	3	1983 84	PA	D cultivars;	D brdg. lines
LT25	9 × 8	F₂	4	1983 84	PA	Same parents as LT22	
LT26	4 × 4	F₁	3	1983 84	PA	D brdg lines;	D cultivars
LT27	6 × 9	F₁	3	1983 84	HI	D cultivars;	D brdg. lines
LT28	6 × 12	F₁	3	1984 85	PA	D short durn.;	D short duration
LT29	6 × 12	F₁	3	1984 85	HI	D long durn.;	D long durn.
LT30	3 × 6	F₁	3	1984 85	HI	K lines resis. to *Helicoverpa*	K cultivars

[a] LT indicates line × tester
[b] PA = Patancheru, India; HI = Hisar, India; GW = Gwalior, India
[c] D = Desi; K = Kabuli

(1992). Records were taken for days to 50% flowering and to maturity on a plot basis. Observations on plant height (cm), number of primary and secondary branches, pods per plant, and seeds per pod, 100-seed mass (g), and seed yield per plant (g) were recorded on a single plant basis. Data were taken on five (F₁) and ten (F₂) random plants per plot, and their mean values were used for statistical analysis. The analyses were conducted according to the methods of Kempthorne (1957). Variances due to general combining ability (σ^2 gca) and specific combining ability (σ^2 sca) were derived from expectations of mean squares. Additive genetic variances (σ_A^2) were expressed as proportions of the total genetic variances ($\sigma_A^2 + \sigma_D^2$)—the predictability ratio of Baker (1978). Correlation coefficients were computed between the experimental means and σ^2 gca and σ^2 sca over the experiments.

The importance of sites and generations, and their interactions with gca and sca variances, were examined in combined analyses of those sets of crosses that were either repeated in different environments or had both F₁ and F₂ generations evaluated in the same or different years.

Results

Estimates of components of variance due to gca were significantly greater than zero in nearly all trials for days-to-flowering, seeds per pod, and 100-seed mass (Table 2). They were significant in about 75% of the trials for days-to-maturity and plant height; in over 50% of the trials for pods and seed yields per plant; and in about 30% of the trials for primary and secondary branches per plant. With few exceptions, estimates of components of gca variance were greater than their corresponding sca variances (Table 3). The gca components of variance were also positively correlated with the experimental means for 100-seed mass and seed yield showing a tendency for scaling.

Estimates of components of sca variance were significant for days-to-flowering and for 100-seed mass

Table 2. Estimates of gca variance components from chickpea line × tester trials

Trial no.	Days-to-flowering	Days-to-maturity	Plant height (cm)	Number of branches		Pods per plant	Seeds per pod	100-seed mass (g)	Seed yield per plant (g)
				Primary	Secondary				
LT1	2.16*	ND^a	2.69**	0.000	0.14**	87.53**	ND	2.57'	7.27'
LT2	9.77*	5.16**	1.28**	0.002*	0.19**	55.53**	0.002*	4.44'	2.90'
LT3	10.10*	0.61	13.08**	0.006	0.19	0.00	0.006**	4.11'	1.84
LT4	5.68*	2.12**	2.54**	0.017**	0.09**	27.14**	0.002	3.77'	0.63'
LT5	6.52*	0.20**	2.08**	0.000	0.49	72.16	0.005**	0.39'	8.59'
LT6	16.71*	30.44**	ND	ND	ND	ND	ND	3.91'	150.94'
LT7	0.96*	0.55**	ND	ND	ND	ND	ND	1.42'	8.86
LT8	13.27*	0.44	1.82	ND	ND	ND	ND	1.99'	7.92'
LT9	2.51*	1.59**	3.42**	0.003	0.09	24.46**	0.003*	3.28'	2.59**
LT10	22.91	12.01**	3.64**	0.014*	0.01	0.00	0.005**	1.25'	0.00
LT11A	12.81*	3.51**	2.44**	0.011	0.14*	0.00	0.000	3.14'	1.24
LT11B	9.96*	3.88**	0.74*	0.008*	0.09	5.66	0.001**	3.27'	3.30*
LT12	9.41**	6.46**	ND	ND	ND	ND	ND	2.14'	53.64*
LT13	13.83**	0.21	1.35**	ND	ND	ND	ND	3.26'	20.08**
LT14	3.12*	ND	ND	ND	ND	ND	ND	1.86	23.71**
LT15	1.11**	0.18	1.47**	0.006	0.36	83.67	ND	0.75**	0.84
LT16	110.59**	0.21**	16.12**	0.021	0.29	93.88*	ND	1.14**	1.84
LT17	3.79**	6.04**	9.01**	0.006	0.05	127.42**	0.005**	10.50**	0.28
LT18	42.06**	0.00	3.05	0.000	3.72	130.53**	0.007	1.77	8.54
LT19A	1.99	1.57*	0.25	0.007	0.06	12.21	0.001'	3.70**	0.68
LT19B	5.79'	4.60*	0.08	0.002	0.10*	61.70**	0.002'	3.19**	0.80
LT20A	6.09'	6.48*	5.35*	0.026**	0.17**	20.66**	0.011'	4.38**	0.49*
LT20B	4.73'	7.18*	5.45*	0.002	0.12**	5.64	0.017'	3.20**	0.05
LT21	8.39'	3.62*	1.26	0.000	0.05*	28.03	0.007'	2.95**	0.68
LT22	7.42'	3.00*	1.01*	0.042**	0.26**	115.72**	0.009'	11.01**	1.53
LT23	2.03**	0.00	2.11*	0.000	0.01	1.99	0.005'	1.22**	8.10**
LT24	1.62*	0.52*	0.73*	0.007**	0.10**	65.66**	0.001'	8.11**	3.02**
LT25	6.46*	4.20*	ND	ND	ND	ND	ND	7.82**	5.96**
LT26	0.83*	2.61*	1.94**	0.018**	0.16**	7.88	0.012**	4.70**	1.38*
LT27	3.43*	ND	2.71**	0.160**	0.00	34.53	0.251	2.61**	0.93
LT28	9.44*	2.96**	ND	ND	ND	ND	ND	8.59**	0.58**
LT29	9.05*	ND	2.39*	ND	0.00	443.06*	0.003*	1.70**	11.13**
LT30	0.65	0.27	1.37	0.000	0.00	ND	ND	ND	4.82
Mean	11.07	3.81	3.31	0.015	0.275	62.71	0.017	3.69	10.46
SE	±3.405	±1.088	±0.725	±0.007	±0.145	±18.674	±0.012	±0.478	±4.733
r^b	0.003	−0.297	0.280	0.074	0.388	0.484	0.254	0.829**	0.477**

^a ND = no data
^b r = correlation coefficient between experimental mean and σ^2 gca
*, **, significant at 0.05 and 0.01 levels of probability, respectively

in about 50% of the trials, but for most other characters they were significant in only about 30% of the trials (Table 3). For primary branches per plant, sca variances were significant in only two out of 25 comparisons. The correlations between the sca variance and experimental mean were non-significant except for 100-seed mass.

The larger estimates of components of gca variance were reflected in predictability ratios (Table 4) that were close to one in more than 75% of the trials for days-to-flowering, 100-seed mass, and seeds per pod. For plant height, days-to-maturity, primary and secondary branches per plant, pods per plant and seed yield, the predictability ratios were less than 0.75 in about 30% to more than 50% of the trials.

The effects of generation on estimates of variance components were examined for trials where F_1 and F_2 crosses had been grown either in the same or in separate but adjacent trials (data not shown). The effects of generations were small and rarely significant and, with few exceptions (12 out of 112 comparisons), the interaction mean squares involving generations were not significantly greater than the error mean squares. Estimates of sca variance components were larger in the F_2 generation as compared with the F_1 generation in several trials.

Combined analyses of LT6 and LT7, and LT12 and LT13, were conducted to determine the effect of sites (Table 5). The estimates of gca and sca components of variances over two environments were significant

Table 3. Estimates of sca variance components from chickpea line × tester trials

Trial no.	Days-to-flowering	Days-to-maturity	Plant height (cm)	Number of branches		Pods per plant	Seeds per pod	100-seed mass (g)	Seed yield per plant (g)
				Primary	Secondary				
LT1	0.74**	ND[a]	1.71**	0.69	0.00	217.86**	ND	1.09**	9.54**
LT2	5.72**	3.96**	0.00	0.00	0.01	0.00	0.001	0.21	0.00
LT3	0.11	6.76**	2.06	0.00	0.59	102.38	0.002**	0.18*	7.14*
LT4	4.80**	15.02**	0.31	0.01	0.00	0.00	0.005	0.24*	0.00
LT5	5.17*	0.00	5.02**	0.01	2.54**	371.52*	0.010**	0.43**	27.94**
LT6	7.89**	1.30	ND	ND	ND	ND	ND	0.38*	50.10
LT7	0.00	0.42	ND	ND	ND	ND	ND	0.26	32.73
LT8	5.62**	0.04	0.00	ND	ND	ND	ND	0.00	0.00
LT9	3.73*	2.01	0.00	0.00	0.18	22.33*	0.007*	0.98**	3.15**
LT10	76.19**	14.14	1.53*	0.00	0.26*	125.09**	0.002	0.71**	3.97**
LT11A	1.14	1.09	1.10	0.00	0.01	422.91**	0.001	0.07	13.93*
LT11B	2.42**	0.25	1.31**	0.00	0.21*	82.73	0.000	0.92**	3.08
LT12	3.43**	0.60	ND	ND	ND	ND	ND	0.65	0.00
LT13	1.72	1.11	2.07	ND	ND	ND	ND	0.44**	3.62
LT14	0.00	ND	ND	ND	ND	ND	ND	0.53	21.02
LT15	0.44	0.00	0.00	0.00	0.68	287.10	ND	0.04	7.06
LT16	80.02**	0.00	10.41*	0.00	0.00	37.12	ND	0.42	0.00
LT17	0.42	2.01	0.02	0.01	0.18	0.00	0.001	1.78**	0.00
LT18	5.07	0.03	4.96	0.06**	2.60	242.59	0.010	0.41	14.18
LT19A	0.00	1.26	0.69	0.02	0.66**	131.83*	0.000	0.00	4.44*
LT19B	3.57*	2.12	0.00	0.02	0.00	0.00	0.000	2.34**	0.00
LT20A	0.85	0.00	0.00	0.00	0.11	2.14	0.000	0.58**	0.00
LT20B	0.00	0.41	0.25	0.03	0.07	61.53**	0.003**	0.39**	1.28*
LT21	0.37	3.45**	4.23**	0.07**	0.01	6.24	0.001	0.00	0.47
LT22	3.67**	1.89**	0.00	0.00	0.00	40.94	0.001	1.98**	0.51
LT23	0.95	0.00	1.13	0.02	0.00	72.74	0.004**	1.86**	0.00
LT24	0.31	0.00	0.86*	0.00	0.16**	13.80	0.000	0.58**	0.00
LT25	0.86**	0.93**	ND	ND	ND	ND	ND	0.60**	0.00
LT26	0.00	0.00	0.00	0.02	0.10	34.10	0.000	0.43	0.00
LT27	0.17**	ND	7.42**	0.33	0.45**	183.75**	0.130**	0.00	6.46**
LT28	1.75*	0.71*	ND	ND	ND	ND	ND	1.34**	0.47*
LT29	0.57	ND	0.00	ND	1.70*	269.01	0.002*	0.00	5.25
LT30	0.26	0.00	0.00	0.00	0.52	ND	ND	ND	0.00
Mean	6.60	2.05	1.67	0.05	0.44	113.7	0.009	0.620	6.56
SE	±3.233	±0.702	±0.500	±0.031	±0.148	±25.754	±0.006	±0.111	±1.975
r[b]	0.011	−0.087	0.063	0.218	0.299	−0.077	0.234	0.532*	0.273

[a] ND = no data
[b] r = correlation coefficient between experimental mean and σ^2 sca
*, **, significant at 0.05 and 0.01 levels of probability, respectively

for 100-seed mass but non-significant for days-to-flowering and days-to-maturity, and for seed yield. In the first set, genotype × site interactions were significant for all traits studied, while significant interactions occurred only for days-to-flowering and to maturity in the second set. The genetic variances were small when compared to the respective interaction variances.

Discussion

Additive gene effects were predominant for days-to-flowering, 100-seed mass, and seeds per pod. Both additive and non-additive gene effects were found to be important for days-to-maturity, plant height, primary and secondary branches per plant, pods per plant and seed yield. Singh et al. (1977), Bhatt and Singh (1980) and Salimath and Bahl (1988) reported predominantly additive genetic effects for 100-seed mass and an equal importance of additive and non-additive components of variances for days-to-maturity, plant height, primary and secondary branches per plant, pods per plant, and seed yield, but reports on the genetic control of seeds per pod are contradictory (Singh et al. 1977; Bhatt and Singh 1980). This ambiguity in results might be due to differences in materials and/or environments. The earlier studies on diallel analyses (Singh et al. 1992) provided parameters similar to those observed in the present study for days-to-flowering and maturity,

primary and secondary branches per plant, pods per plant, 100-seed mass, and seed yield. Differences in results between the diallel analyses and the present line x tester analyses appear mainly for plant height and seeds per pod. The diallel analyses indicated a predominantly additive genetic control for plant height, while for seeds per pod, both additive and non-additive genetic variance were found to be important. The amount of non-additive variance present in some of the experiments may be due to a bias in the estimation caused either by gamete-phase disequilibrium or by an error in sampling. It is an advantage of this series of trials that these biases disappear from the averages of such estimates.

The overall means of predictability ratios in the present study were > 0.5 for all the traits (Table 4), and > 0.7 for days-to-flowering and to maturity, plant height, seeds per pod, and 100-seed mass. The greater importance of σ_A^2 for the latter traits suggests the use of breeding systems that emphasize mainly σ_A^2. The amount of σ^2 AA contribution to the non-additive variance estimated for some characters is not known. However, if additive $\times$ additive epistatic variance was of importance, breeding systems would change very little because additive $\times$ additive epistatic variance can be exploited by pedigree breeding. Additive $\times$ additive variance increases during the selfing process so that selection in early generations should be handled accordingly.

The small quantities of hybrid seed produced by hand-pollination in chickpea prohibit an adequate testing of the F_1 generation. The effects of F_1 and F_2 generations and their interactions with the lines and testers were, therefore, examined in trials where F_1 and F_2 generations of same crosses were grown together. The non-significant effects of generations and its interactions with lines and testers clearly indicated that similar estimates of gca and sca variances were obtained from the F_1 and F_2 generations. Combining ability studies would, therefore, be much easier with increased seed quantities in the F_2 generation. In a few cases, however, the estimates of sca variance from the F_2 were larger than from the F_1 generation. This is unexpected since heterozygosity declines in the F_2 generation as compared to the F_1 generation. Similar results were reported by Jordaan and Laubscher (1968), Tandon et al. (1970), and Bhullar et al. (1979) in wheat and also for some characters in chickpea by Gowda and Bahl (1978). Linkage among the interacting genes and/or the effects of competition and heterogeneity might be responsible for such an increase in the estimates of sca variances.

Estimates of genotype $\times$ environment interaction variances provide measures of bias from estimating genetic parameters in one-environment experiments. Important interactions of genetic effects with sites and seasons have been reported in other self-pollinated crops (Paroda and Hayes 1971; Malhotra et al. 1980; Singh et al. 1983; Singh and Singh 1987). The combined analysis showed that environmental interactions involving gca were generally larger than those involving sca. This indicates that the gca component was more variable with the change in seasons or sites. In the breeding of pure-line varieties of self-pollinated crops such as chickpea, the gca component of variance is of greater importance because of its fixable nature. Consequently, adequate testing over sites and/or seasons is important to obtain unbiased estimates of gca variances. Singh et al. (1992) also observed the importance of multilocation trials in the estimation of genetic variances.

Days-to-flowering, seed size, and seeds per pod in chickpea were predominantly governed by additive genes, and selection in early generations will be effective in their improvement. On the other hand, selection for traits, such as days-to-maturity, primary and secondary branches, plant height, pods per plant, and seed yield, that are governed by both additive and non-additive genes, may be deferred to later generations to allow a decrease in dominance, additive $\times$ dominance, and dominance $\times$ dominance effects. An exact prediction of the selection response using estimates of genetic parameters, however, may be biased by scaling effects (Falconer 1980) which were observed for 100-seed mass and seed yield. The testing generations had very little effect on the estimates of the genetic parameters. However, environment (sites/seasons) showed larger interactions with the genetic effects emphasizing the need for testing in more than one environment.

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Table 4. Estimates of predictability ratio $(\sigma_A^2/\sigma_A^2 + \sigma_D^2)$ from chick pea line × tester trials

Trial no.	Days-to-flowering	Days-to-maturity	Plant height (cm)	Number of branches		Pods per plant	Seeds per pod	100-seed mass(g)	Seed yield per plant (g)
				Primary	Secondary				
LT1	0.74	ND[a]	0.61	NS[b]	1.00	0.28	ND	0.70	0.43
LT2	0.63	0.56	1.00	1.00	0.95	1.00	0.66	0.95	1.00
LT3	0.98	0.08	0.86	NS	0.24	NS	NS	0.96	0.20
LT4	0.54	0.12	0.89	0.63	1.00	1.00	0.28	0.94	1.00
LT5	0.56	1.00	0.29	NS	0.16	0.16	0.33	0.48	0.24
LT6	0.81	0.98	ND	ND	ND	ND	ND	0.95	0.86
LT7	1.00·	0.72	ND	ND	ND	ND	ND	0.91	NS
LT8	0.70	NS	NS	ND	ND	ND	ND	1.00	1.00
LT9	0.40	0.44	1.00	NS	NS	0.52	0.30	0.77	0.45
LT10	0.23	0.46	0.70	1.00	0.04	0.00	0.71	0.64	0.00
LT11A	0.92	0.76	0.69	NS	0.93	0.00	NS	0.98	0.08
LT11B	0.89	0.97	0.53	1.00	0.46	NS	1.00	0.88	0.68
LT12	0.85	0.96	ND	ND	ND	ND	ND	0.87	1.00
LT13	0.94	NS	0.57	ND	ND	ND	ND	0.94	0.92
LT14	1.00	ND	ND	ND	ND	ND	ND	0.78	0.45
LT15	0.83	NS	1.00	NS	NS	0.37	ND	0.97	NS
LT16	0.73	1.00	0.76	NS	NS	0.83	ND	0.84	NS
LT17	0.90	0.75	1.00	NS	NS	1.00	0.83	0.86	NS
LT18	0.89	NS	NS	0.00	NS	0.35	NS	NS	NS
LT19A	NS	0.55	NS	NS	0.08	0.08	1.00	1.00	0.13
LT19B	0.76	0.81	NS	NS	1.00	1.00	1.00	0.73	NS
LT20A	0.88	1.00	1.00	1.00	0.61	0.91	1.00	0.88	1.00
LT20B	1.00	0.97	0.98	NS	0.77	0.15	0.92	0.94	0.07
LT21	0.96	0.51	0.23	0.00	0.50	0.82	0.88	1.00	NS
LT22	0.67	0.61	1.00	1.00	1.00	0.74	0.90	0.85	NS
LT23	0.68	NS	0.65	NS	NS	NS	0.55	0.40	1.00
LT24	0.84	1.00	0.46	1.00	0.38	0.83	1.00	0.93	1.00
LT25	0.94	0.90	ND	ND	ND	ND	ND	0.96	1.00
LT26	1.00	1.00	1.00	0.47	0.62	NS	1.00	0.92	1.00
LT27	0.95	ND	0.27	0.37	0.00	0.50	0.66	1.00	0.14
LT28	0.84	0.81	ND	ND	ND	ND	ND	0.87	0.55
LT29	0.94	ND	1.00	ND	0.00	0.62	0.60	1.00	0.68
LT30	0.71	1.00	NS	NS	NS	ND	ND	ND	NS
Mean	0.80	0.74	0.75	0.68	0.59	0.56	0.75	0.87	0.62

[a] ND = no data
[b] NS = non-significant

Table 5. Components of variance from the combined analysis of variance of LT6 and LT7 (F$_2$, 1979/80, at Patancheru and Hisar), LT12 and LT13 (F$_2$, 1980/81, at Patancheru and Gwalior)

Item	LT6 and LT7				LT12 and LT13			
	Days-to-flowering	Days-to-maturity	100-seed mass (g)	Seed yield per plant (g)	Days-to-flowering	Days-to-maturity	100-seed mass (g)	Seed yield per plant (g)
Sites (S)	234.20**	401.90**	1.610*	2128.5*	310.87**	132.35**	0.50	40648.5**
Error	5.20	91.60	12.380	17173.0	116.70	103.40	14.11	76350.0
Testers (T)	4.30	10.20	1.059	217.3	21.53	6.19	5.19**	723.3
Lines (L)	10.25	8.38	4.916**	594.4	7.91	1.74	2.12**	94.6
S × T	3.50**	12.74**	0.465*	697.5**	−1.07	4.75**	0.02	425.1
S × L	9.91**	11.34*	0.713*	1579.4**	4.58**	1.11*	0.01	179.6
T × L	2.08	0.23	−0.017	302.7	3.03*	0.18	0.23	−423.0
S × T × L	2.67**	1.23	0.670**	223.0	−0.83	1.00	0.95**	−545.7
Error	5.60	23.30	2.150	3932.0	33.30	15.30	3.01	12610.0
σ^2 gca	7.60	6.50	5.500**	0.0	26.80	5.00	7.36	556.0
σ^2 sca	0.75	0.00	0.000	191.2	3.40*	0.00	0.00	0.0
σ^2 gca × S	12.59**	23.70**	0.970*	2207.6**	3.70**	6.00**	−0.22	750.0
σ^2 sca × S	2.67**	1.20	0.670**	223.0	−0.80	1.00	0.95**	−546.0

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

primary and secondary branches per plant, pods per plant, 100-seed mass, and seed yield. Differences in results between the diallel analyses and the present line x tester analyses appear mainly for plant height and seeds per pod. The diallel analyses indicated a predominantly additive genetic control for plant height, while for seeds per pod, both additive and non-additive genetic variance were found to be important. The amount of non-additive variance present in some of the experiments may be due to a bias in the estimation caused either by gamete-phase disequilibrium or by an error in sampling. It is an advantage of this series of trials that these biases disappear from the averages of such estimates.

The overall means of predictability ratios in the present study were > 0.5 for all the traits (Table 4), and > 0.7 for days-to-flowering and to maturity, plant height, seeds per pod, and 100-seed mass. The greater importance of σ_A^2 for the latter traits suggests the use of breeding systems that emphasize mainly σ_A^2. The amount of σ^2 AA contribution to the non-additive variance estimated for some characters is not known. However, if additive x additive epistatic variance was of importance, breeding systems would change very little because additive x additive epistatic variance can be exploited by pedigree breeding. Additive x additive variance increases during the selfing process so that selection in early generations should be handled accordingly.

The small quantities of hybrid seed produced by hand-pollination in chickpea prohibit an adequate testing of the F_1 generation. The effects of F_1 and F_2 generations and their interactions with the lines and testers were, therefore, examined in trials where F_1 and F_2 generations of same crosses were grown together. The non-significant effects of generations and its interactions with lines and testers clearly indicated that similar estimates of gca and sca variances were obtained from the F_1 and F_2 generations. Combining ability studies would, therefore, be much easier with increased seed quantities in the F_2 generation. In a few cases, however, the estimates of sca variance from the F_2 were larger than from the F_1 generation. This is unexpected since heterozygosity declines in the F_2 generation as compared to the F_1 generation. Similar results were reported by Jordaan and Laubscher (1968), Tandon et al. (1970), and Bhullar et al. (1979) in wheat and also for some characters in chickpea by Gowda and Bahl (1978). Linkage among the interacting genes and/or the effects of competition and heterogeneity might be responsible for such an increase in the estimates of sca variances.

Estimates of genotype x environment interaction variances provide measures of bias from estimating genetic parameters in one-environment experiments. Important interactions of genetic effects with sites and

seasons have been reported in other self-pollinated crops (Paroda and Hayes 1971; Malhotra et al. 1980; Singh et al. 1983; Singh and Singh 1987). The combined analysis showed that environmental interactions involving gca were generally larger than those involving sca. This indicates that the gca component was more variable with the change in seasons or sites. In the breeding of pure-line varieties of self-pollinated crops such as chickpea, the gca component of variance is of greater importance because of its fixable nature. Consequently, adequate testing over sites and/or seasons is important to obtain unbiased estimates of gca variances. Singh et al. (1992) also observed the importance of multilocation trials in the estimation of genetic variances.

Days-to-flowering, seed size, and seeds per pod in chickpea were predominantly governed by additive genes, and selection in early generations will be effective in their improvement. On the other hand, selection for traits, such as days-to-maturity, primary and secondary branches, plant height, pods per plant, and seed yield, that are governed by both additive and non-additive genes, may be deferred to later generations to allow a decrease in dominance, additive x dominance, and dominance x dominance effects. An exact prediction of the selection response using estimates of genetic parameters, however, may be biased by scaling effects (Falconer 1980) which were observed for 100-seed mass and seed yield. The testing generations had very little effect on the estimates of the genetic parameters. However, environment (sites/seasons) showed larger interactions with the genetic effects emphasizing the need for testing in more than one environment.

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