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Gene action for cold tolerance in chickpea *

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Summary. Six crosses were investigated using combining ability and generation mean analyses for reaction to cold tolerance in chickpea (*Cicer arietinum* L.). The combining ability variances revealed the significance of both additive and nonadditive gene effects, with preponderance of additive gene effects. The generation mean analysis revealed the presence of genic interactions in addition to additive and dominance gene effects. Among the interactions, additive × additive and dominance × dominance with duplicate epistasis were present. Cold tolerance was dominant over susceptibility to cold. Selection for cold tolerance would be more effective if dominance and epistatic effects were reduced after a few generations of selfing.

Key words: Gene action – Cold tolerance – *Cicer arietinum* – Generation mean analysis

Introduction

In the Mediterranean basin, chickpea (*Cicer arietinum* L.) is traditionally a spring-sown crop. The research conducted at the International Center for Agricultural Research in the Dry Areas (ICARDA) has demonstrated that winter-sown chickpea has almost double the yield compared to the traditional spring-sown crop, provided cultivars possess tolerance to cold and *Ascochyta* blight [*Ascochyta rabiei* (Pass.) Lab.] Singh (1990). More than 3,200 germ plasm accessions have been evaluated at ICARDA for cold tolerance, and sources of tolerance have been identified (Singh et al. 1989). However, little information is available to date on the inheritance of cold tolerance in chickpea (Malhotra and Singh 1990). Therefore, the present study was undertaken to investigate the nature of gene action involved in the inheritance of cold tolerance and to detect genic interactions, if present.

Materials and methods

Six single crosses of chickpea involving four parents (ILC 3470, FLIP 82-64C, FLIP 81-16C, and FLIP 81-21C) that differed in reaction to cold tolerance were made during the 1985–86 season at Tel Hadya, Syria, the main experiment station of ICARDA. ILC 3470 was chosen because it possesses the best source of tolerance among the 5,000 landraces that ICARDA has evaluated. Likewise, FLIP 82-64C was found to have the highest level of cold tolerance to date among the 1,000 breeding lines subjected to evaluation. FLIP 81-16C and FLIP 18-21C represent the 90% susceptible material at the center. Seeds of F_1s and their parents were grown during the 1986–87 season to produce F_2 seeds and to make backcrosses. The materials, comprising four parents, six F_1s, six F_2s, and 12 backcrosses, were grown during 1987–88 in compact family blocks, following randomized block design with three replications. Each family block was represented by two parents, their F_1s, F_2s, and backcrosses (BC_1 and BC_2). Each of the parents, F_1, BC_1, and BC_2, were grown in a single-row plot and each F_2, in a six-row plot. Each row was 2 m long, and spacings between and within rows were maintained at 45 and 10 cm, respectively. The sowing was done on 28 September 1987 at the Tel Hadya farm. Nonexperimental susceptible-cum-indicator check rows were sown after every four test rows. The experimental area was fertilized at the rate of 50 kg P_2O_5 ha^{-1}. Three irrigations of 50 mm each were performed, the first on 28 September, the second on 16 October, and the third on 5 November prior to the onset of rains. The autumn sowing was timed so that the plants reached the late vegetative stage when the cold spell started during December. Pre-emergence application of 3.0 kg a.i. of terbutrine and 0.5 kg a.i. of pronamide ha^{-1} was carried out to control weeds.

The 1987–88 season had 21 days of freezing temperatures, with a low of −7.4 °C. The susceptible-cum-indicator rows were killed by early February 1988. Soon after the killing of indicator

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Table 1. Generation means averaged over replications for cold tolerance (on a 1–9 scale) in different crosses between chickpea lines

Cross	P_1	P_2	F_1	F_2	BC_1	BC_2
ILC 3470 × FLIP 81-16C	3.096±0.041	9.000±0.000	3.957±0.139	4.261±0.043	3.375±0.183	5.788±0.319
ILC 3470 × FLIP 81-21C	3.218±0.057	9.000±0.000	4.263±0.117	4.384±0.046	3.774±0.082	7.340±0.171
FLIP 82-64C × FLIP 81-16C	4.723±0.053	9.000±0.000	4.780±0.059	4.952±0.054	4.429±0.089	7.690±0.207
FLIP 82-64C × FLIP 81-21C	4.783±0.060	9.000±0.000	4.600±0.118	5.088±0.062	4.623±0.067	7.302±0.231
ILC 3470 × FLIP 82-64C	3.261±0.065	4.750±0.062	3.735±0.071	3.740±0.025	3.231±0.133	4.065±0.115
FLIP 81-16C × FLIP 81-21C	9.000±0.000	8.999±0.001	8.714±0.267	8.897±0.017	8.927±0.054	8.940±0.034

Scale: 1 = free from any damage; 5 = intermediate; 9 = plant killed

Table 2. General combining ability (GCA) and specific combining ability (SCA) analysis for reaction to cold tolerance using a 4 × 4 diallel cross

Source	*df*	Mean squares based on diallel involving	
		Parents and F_1s	Parents and F_2
GCA	3	13.353**	13.748**
SCA	6	1.513**	1.178**
Error	18	0.025	0.009
$\sigma^2 g/\sigma^2 s$		1.326	1.792

** = Significant at $P \leq 0.01$
$\sigma^2 g$ = Estimated variance for general combining ability
$\sigma^2 s$ = Estimated variance for specific combining ability

rows, the materials were evaluated for cold tolerance on a 1–9 scale, where 1 = no visible symptoms of damage; 2 = highly tolerant, up to 10% of leaflets show withering and drying; 3 = tolerant, 11–20% leaflets and up to 20% branches show withering and drying; 4 = moderately tolerant, 21–40% leaflets and up to 20% branches show withering and drying; 5 = intermediate, 41–60% leaflets and 21–40% branches show withering and drying; 6 = moderately susceptible, 61–80% leaflets and 41–60% branches show withering and drying; 7 = susceptible, 81–99% leaflets and 61–80% branches show withering and drying; 8 = highly susceptible, 100% leaflets and 81–99% branches show withering and drying; and 9 = plant killed. Data were recorded on all plants except the two border plants, one at each end of the row.

The mean data for parents, F_1s, and F_2s for each replication were also used for combining ability analysis using Griffing's (1956) method 2, model 1. The individual values for cold tolerance for six generations (P_1, P_2, F_1, F_2, BC_1, and BC_2) in each replication were used for generation mean analysis (Hayman 1958). The joint scaling test suggested by Cavalli (1952) was applied to test the adequacy of genetic models.

Results and discussion

Means of the parents, F_1s, F_2s, and backcrosses of six crosses for cold tolerance reaction are given in Table 1. Perusal of means of F_1s and parents exhibited no heterosis for cold tolerance.

Combining ability analysis

The analysis of variance for combining ability for parents and F_1s, and for parents and F_2s, revealed the significance of mean squares due to general combining ability and specific combining ability (Table 2). This illustrated that both additive and dominance effects were important in the inheritance of cold tolerance in chickpea. Furthermore, of the two effects, the additive effects were more important, because the ratio between the estimate of variance component due to general combining ability ($\sigma^2 g$) and specific combining ability ($\sigma^2 s$) was more than one.

Generation mean analysis

The results pertaining to the joint scaling tests and estimates of gene effects based on three or more parameter models are given in Table 3. The test of goodness-of-fit using a joint scaling test for the three-parameter model for different crosses revealed the significance of χ^2 for five out of six crosses. This showed that additive and dominance parameters alone were not adequate to explain the cold tolerance reaction in these crosses, and also that genic interactions may play a role in the expression of cold tolerance. The nature of gene effects in each of the six crosses is presented in Table 3 and is discussed below by cross.

Cross 1 (ILC 3470 × FLIP 81-16C). The χ^2 value using the five-parameter model involving m, d, h, i, and j parameters was close to zero, with 100% of the variation accounted for by these five parameters. This suggests there was nothing beyond these five parameters to explain the cold tolerance reaction in this cross. Furthermore, additive (d), dominance (h), and additive × additive (i) gene effects were significant.

Cross 2 (ILC 3470 × FLIP 81-21C). The χ^2 value was significant for all models involving different combinations. Thus, only the six-parameter model could explain the cold tolerance reaction in this cross. Perusal of χ^2 and

Table 3. Estimates of gene effects for cold tolerance in six crosses of chickpea

Cross	m	d	h	i	j	l	χ^2
ICL 3470 × FLIP 81-16C (Cross 1)	6.028** ±0.020	2.972** ±0.020	−3.103** ±0.080	–	–	–	86.14 (99.6)⁺⁺
	4.569** ±0.162	2.952** ±0.020	−0.619* ±0.288	1.479** ±0.164	−0.981 ±0.641	–	0.00 (100)
ILC 3470 × FLIP 81-21C (Cross 2)	6.078** ±0.027	2.922** ±0.027	−2.521** ±0.082	–	–	–	188.70 (98.8)
	2.230** ±0.355	2.906** ±0.028	6.584** ±0.989	3.864** ±0.351	–	−4.551** ±0.676	12.30 (99.8)
	1.417** ±0.424	2.891** ±0.029	9.020** ±1.210	4.692** ±0.423	1.350** ±0.384	−6.176** ±0.819	–
FLIP 82-64C × FLIP 81-16C (Cross 3)	6.777** ±0.025	2.223** ±0.025	−2.356** ±0.060	–	–	–	216.00 (98.2)
	3.941** ±0.395	2.154** ±0.026	3.200** ±1.090	2.905** ±0.392	–	−2.366** ±0.708	24.57 (99.4)
	2.432** ±0.499	2.139** ±0.027	7.730** ±1.420	4.430** ±0.498	2.245** ±0.453	−5.385** ±0.934	–
FLIP 82-64C × FLIP 81-21C (Cross 4)	6.874** ±0.029	2.126** ±0.029	−2.708** ±0.089	–	–	–	78.07 (99.1)
	4.332** ±0.367	2.117** ±0.030	2.756** ±0.960	2.551** ±0.362	–	−2.488** ±0.641	5.53 (99.8)
	3.393** ±0.542	2.109** ±0.030	5.570** ±1.530	3.498** ±0.542	1.141 ±0.485	−4.370** ±1.020	–
ILC 3470 × FLIP 82-64C (Cross 5)	3.945** ±0.040	0.751** ±0.044	−0.357** ±0.078	–	–	–	9.19 (95.4)
	4.005** ±0.045	0.749** ±0.044	−0.817** ±0.180	–	–	0.546** ±0.193	1.15 (99.1)
FLIP 81-16C × FLIP 81-21C (Cross 6)	8.999** ±0.000	0.000 ±0.000	−0.186** ±0.029	–	–	–	1.60 (94.2)

* Significant at $P \leq 0.05$
** Significant at $P \leq 0.01$
⁺⁺ Value in parenthesis is variance accounted for by the parameters in the model as proportion of total variance

variances accounted for by each model indicated that the model with m, d, h, i, and l parameters accounted for 99.4% of the variation in cold tolerance and exhibited the lowest, but significant, χ^2 value. Based on this model, the estimates of all five parameters were significant.

Cross 3 (FLIP 82-64C × FLIP 81-16C). The χ^2 values for different models based on various combinations of parameters revealed that none of the models had a good fit. The estimates of all the parameters were significant in the six-parameter model.

Cross 4 (FLIP 82-64C × FLIP 81-21C). The χ^2 value was significant for all models, but was minimum for the model involving m, d, h, i, and e. These parameters contributed 99.8% toward total variation for cold tolerance reaction for this cross. Furthermore, the estimates of all these parameters were significant.

Cross 5 (ILC 3470 × FLIP 82-64C). The χ^2 value was minimum and nonsignificant for the five-parameter model involving m, d, h, i, and l. Only the estimates of m and d were significant for this model.

Cross 6 (FLIP 81-16C × FLIP 81-21C). The χ^2 value based on the three-parameter model was nonsignificant. This indicated that the additive-dominance model was sufficient to explain the cold tolerance reaction in this cross and only that the h estimate was significant.

The joint scaling test generally revealed that the genic interactions were present and responsible for the expression of cold tolerance in chickpea. Examination of gene effects of all crosses revealed that both additive and dominance gene effects were significant for most of the crosses and were thus important. Previous cold tolerance studies using diallel cross analyses in chickpea (Malhotra and Singh 1990) and in pea (Markarian and Anderson 1966; Auld et al. 1983) reported the significance of both additive and nonadditive gene effects. Malhotra and Singh (1990), using the graphical analysis of Jinks (1954), suggested the absence of genic interaction for cold tolerance. The reasons for such variations could be attributed to differences in the parental lines used for these analyses or to the inability of diallel cross analysis to detect the interactions. Thus, this is the first study which indicated the presence of genic interactions in the expression of cold tolerance in chickpea. Furthermore, the fact that the coefficient of 'h' is negative in all the crosses indicates that tolerance to cold is dominant over susceptibility to cold in the present material. Also, the signs of h and l estimates, being opposite in almost all crosses, indicate the presence of duplicate epistasis. Although additive (d) and additive × additive (i) gene effects, which can be fixed, are present in almost all crosses, the presence of dominance (h) and duplicate epistasis would tend to retard the pace of progress through selection in early generations. Thus, selection for cold tolerance would be more effective if the dominance and epistatic effects were reduced after a few generations of selfing.

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