

Inheritance of seed size in chickpea

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ABSTRACT

Six lines with a range of seed size from 10.42 to 58.42 g per 100 seeds were used in a complete diallel cross set to study the inheritance of seed size in chickpea (*Cicer arietinum* L.). Six parents, 15 F₁s, 15 F₂s, 15 BC₁, and 15 BC₂s were grown in a randomized complete block design with two replications at Tel Hadya, Syria during 1988-89. Data on 100-seed weight were recorded after the harvest of the experiment. Combining ability and generation mean analyses showed that both additive and non-additive gene effects were important with the preponderance of additive gene action for seed size. The combining ability, graphical and generation means analyses revealed the partial dominance of small seed size over large seed size suggesting that seed size is governed by recessive genes. Therefore, it is suggested that one backcross with a large-seeded parent may enhance the chances of large-seeded segregants. The generation mean analysis helped in detection of epistasis in 11 out of 15 crosses. Among epistatic effects, additive X additive effects, were noticed in six crosses, additive X dominance in four crosses, and dominance X dominance in six crosses. The narrow-sense heritability of seed size was >95%. As dominance and genic interactions also played a significant role, it is suggested to delay the selection of large seed size to F₃ generations onward so that these effects are reduced. Bulk-pedigree method is suggested for the improvement of seed size in chickpea.

Key words: *Cicer arietinum*, Combining ability, Generation mean, Inheritance, Seed size.

INTRODUCTION

Recent efforts made by the International Center for Agricultural Research in the Dry Areas (ICARDA) to introduce chickpea (*Cicer arietinum* L.) as a winter-sown crop in the Mediterranean region has brought a yield increase of >70% over the traditional spring-sown crop (SINGH, 1990). This phenomenal increase in seed yield of winter sowing of chickpea is due to the development and use of cultivars with resistance to *Ascochyta* blight [*Ascochyta rabiei* (Pass.) Lab.] disease and tolerance to cold, the two most important limiting factors for winter sowing of chickpea in the region. To date, more than 50 cultivars have been released in 18 countries for winter sowing (ICARDA, 1994). However, these new cultivars have small to medium seed size, whereas the local markets demand large seeds. Small-seeded culti-

vars are a major hurdle in the large scale introduction of winter sowing of chickpea.

Information on genetics of seed size of chickpea is limited. ARGIKAR (1956) reported that this character was controlled by a single recessive gene, while PATIL and D'CRUZ (1964) found it to be under the control of two genes. Results obtained by ATHWAL and SANDHA (1967) showed that small-seed size was partially dominant over large-seed size. In contrast, NIKNEJAD *et al.* (1971) found that large-seed size was partially dominant over the small-seed size. MALHOTRA *et al.* (1983), and SALIMATH and BAHL (1989) reported that both additive and non-additive components were significant for seed size, although additive gene effects were predominant. On the contrary KATIYAR *et al.* (1988) found predominance of non-additive gene action. Thus the information on seed size is conflicting.

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Because of slow improvement in seed size by the ICARDA's breeding programme, lack of clear cut information on this topic and absence of information from Mediterranean countries on the kabuli type chickpea, the inheritance of seed size was re-examined in cultivars with a wide range of variation.

MATERIALS AND METHODS

Lines ILC 4, ILC 149, ILC 211, ILC 2378, ILC 2407 and ILC 6104 with a wide difference in seed size (100-seed weight) were used in diallel crosses at Tel Hadya, Syria (latitude 36.01°N, longitude 36.56°E, 284 m asl), the main research station ICARDA during the 1987-88 winter season. Part of the F₁s obtained during the season along with their parents were grown at the ICARDA's research station at Terbol, Lebanon (latitude of 33 49°N, longitude of 35.59°E, 890 m asl) during the 1988 off season to make backcrosses and to provide F₂ seeds. Six parents, 15 F₁s, 15 F₂s, 15 BC₁'s (F₁ crossed with parent 1) and 15 BC₂ (F₁ crossed with parent 2) were grown in a randomized complete block design with two replications at Tel Hadya during the 1988-89 season. All parents, F₁s, F₂s and backcrosses were grown in 2.5 m long rows with 45 cm spacing between rows and 7 cm within rows. Each parent, F₁ and backcross were grown in single row plots, whereas each F₂ was grown in seven row plots. Cultural practices recommended for chickpea were followed. Observations on seed size were collected after the harvest of the experiment on 10 plants in each replication for each parent and F₁ and all available backcrossed plants and from 200 F₂ plants per cross.

Combining ability analyses of the diallel crosses using F₁ and F₂ were done following the Method II Model I (GRIFFING, 1956). The Graphical analyses were done following JINKS (1954). The generation mean analyses were done for 15 crosses, following HAYMAN (1958) and all possible models ranging from three parameter to six parameter models were fitted. The best model from each cross with very high R², non-significant and least Chi square (X²) value, and with the all parameters exhibiting statistically significant estimates, was selected and used for further interpretations.

RESULTS

Combining Ability

The analysis of variance (ANOVA) for combining ability revealed the significance of mean squares (MS) due to general combining ability effects (GCA) and specific combining ability effects (SCA) both in F₁ and F₂ generations (Table 1). Further, the MS due to GCA were highly sig-

TABLE 1
Analysis of variance for combining ability from F₁ and F₂ diallel crosses

Source of variation	d.f.	M.S.	
		F ₁	F ₂
GCA	5	868.12**	830.50**
SCA	15	13.52	9.36**
Error	20	0.82	1.33

** Significant at P ≤ 0.01.

nificant in both the F₁ and F₂ generations when tested against MS due to SCA.

The mean seed size of the parents (Table 2) revealed three groups of seed size, large (L) (>50g), medium (M) (between 35 ad 44g), and small (S) (< 13g). The parents ILC 149, ILC 2407 and ILC 6104 had positive and significant GCA effects and were thus good general combiners for large seed size (Table 2). On the contrary, the parents ILC 211, and ILC 2378 had negative and significant GCA effects and were poor general combiners for large seed size. The heterosis over mid parent and inbreeding depression of F₂ over F₁ were calculated for 15 crosses. These results were not presented in the tabular form as the heterosis of F₁ over mid parent (-30.48% to 5.97%) and the inbreeding depression of F₂ over F₁ (-9.86% to 4.70%) in different crosses were very low and of least practical significance.

Graphical Analysis

In Vr-Wr graphs based on 6 x 6 diallel crosses in F₁ (Fig. 1) and F₂ (Fig. 2) generations, the

TABLE 2
General combining ability (GCA) effects of parents in F₁ and F₂ generations of 6 x 6 diallel crosses

Parent	Seed size (g)	GCA effects	
		F ₁	F ₂
ILC 4	35.9	1.65	1.27
ILC 211	10.4	-13.58**	-13.59**
ILC 149	58.4	10.70**	10.45**
ILC 2378	12.8	-11.95**	-11.26**
ILC 2407	44.0	4.24**	4.26**
ILC 6104	51.7	8.94**	8.86**

** Significant differences at P ≤ 0.01.

regression line cut the Y-axis above the point of origin, indicating the presence of partial dominance for the 100-seed weight. The perusal of array points in the Vr-Wr graphs revealed that the parent ILC 211 was the nearest to point of origin and had the maximum concentration of dominant genes, and the parent ILC 149 was the farthest from the point of origin and had the maximum concentration of recessive genes. The correlation of parental means with parental order of dominance was positive and significant at $P \leq 0.01$ in F_1 ($r = 0.987$) and in F_2 ($r = 0.979$) diallel crosses. This suggests that dominant genes for seed size had negative effects or in other words the small seed size is dominant over large seed size. Further the heritabilities of seed size in narrow sense in F_1 generation (MATHER and JINKS, 1987) and F_2 generation (VERHALEN and MURRAY, 1969) of diallel crosses were as high as 95.0% and 96.3% respectively.

Generation Mean Analysis

The variances due to different parameters in the model were measured by R^2 and goodness of fit of the model (based on different parameters) was tested by the Chi-square (χ^2) value. Various models based on different parameters including at least three or more out of the six (m, d, h, i, j and l) were tested for their R^2 , χ^2 and the significance of different components of the

model were tested. One best fit model from each cross with very high R^2 and non-significant and low χ^2 value, and with significant values of different parameters was selected (Table 3).

The results for generation mean analysis for each cross are discussed below:

Cross 1 (ILC 4 X ILC 149). This cross involved medium X large seeded parents. Four parameter model with m, d, h, and i was a good fit. The additive gene effects were preponderant. The interaction in the cross was additive X additive type.

Cross 2 (ILC 4 X ILC 211). This cross involved medium X small seeded parents. Four parameter model with m, d, i and j was a good fit. Dominance gene effects was not important in this cross. The interactions in the cross were additive X additive and additive X dominance type.

Cross 3 (ILC 4 X ILC 2378). This cross involved medium X small seeded parents. Three parameter model with m, d and l was good fit. Dominance gene effect was not important in this cross. The interactions in the cross was dominance X dominance type.

Cross 4 (ILC 4 X ILC 2407). This cross involved medium X medium seeded parents. Three parameter model with m, d and h was a good fit. The additive gene effects were negative and dominance gene effects were positive. The genic interactions were absent.

Cross 5 (ILC 4 X ILC 6104). This cross involved medium X large seeded parents. Three

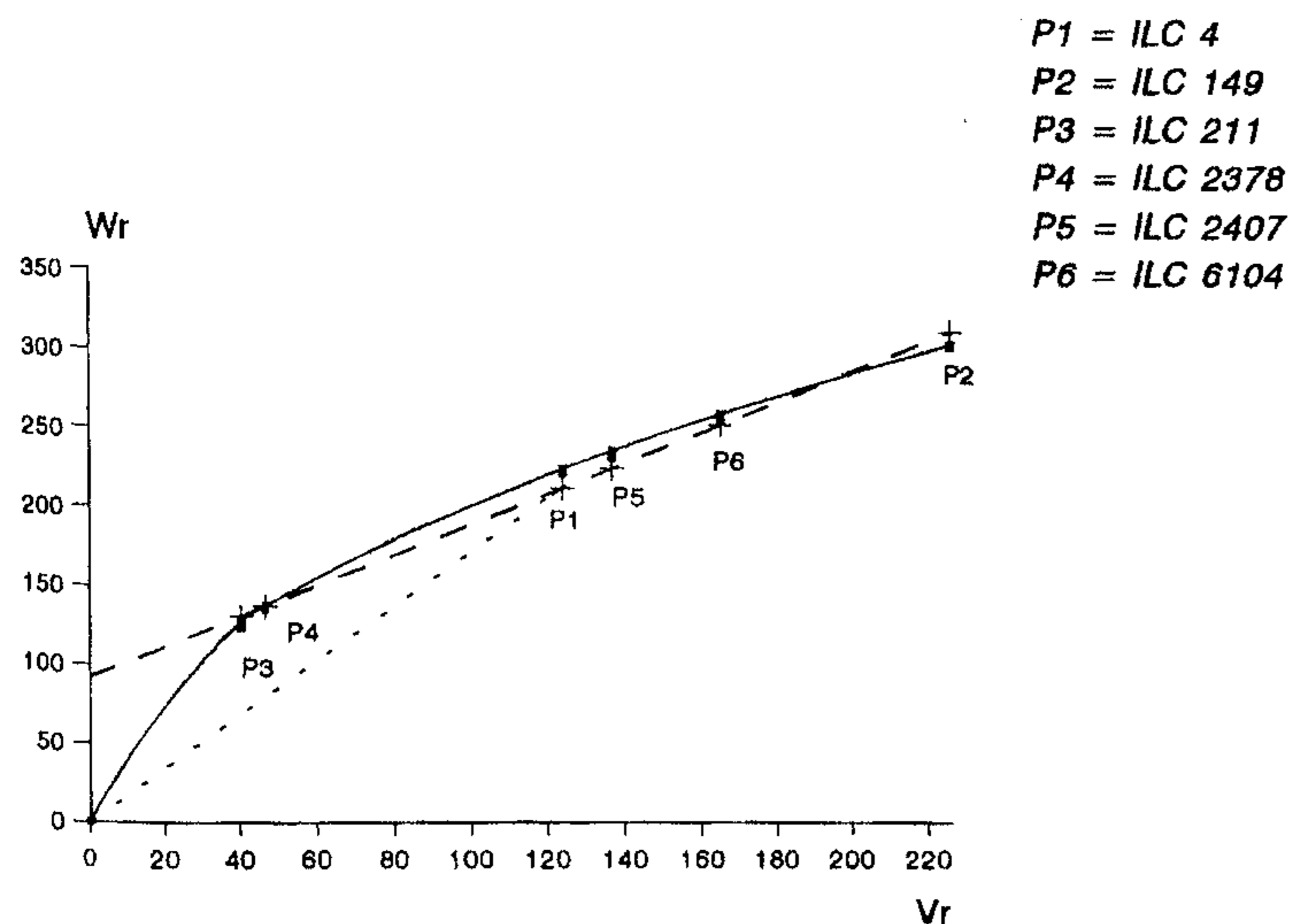


FIGURE 1 - Vr-Wr graph for seed size in a 6×6 diallel cross in F_1 .

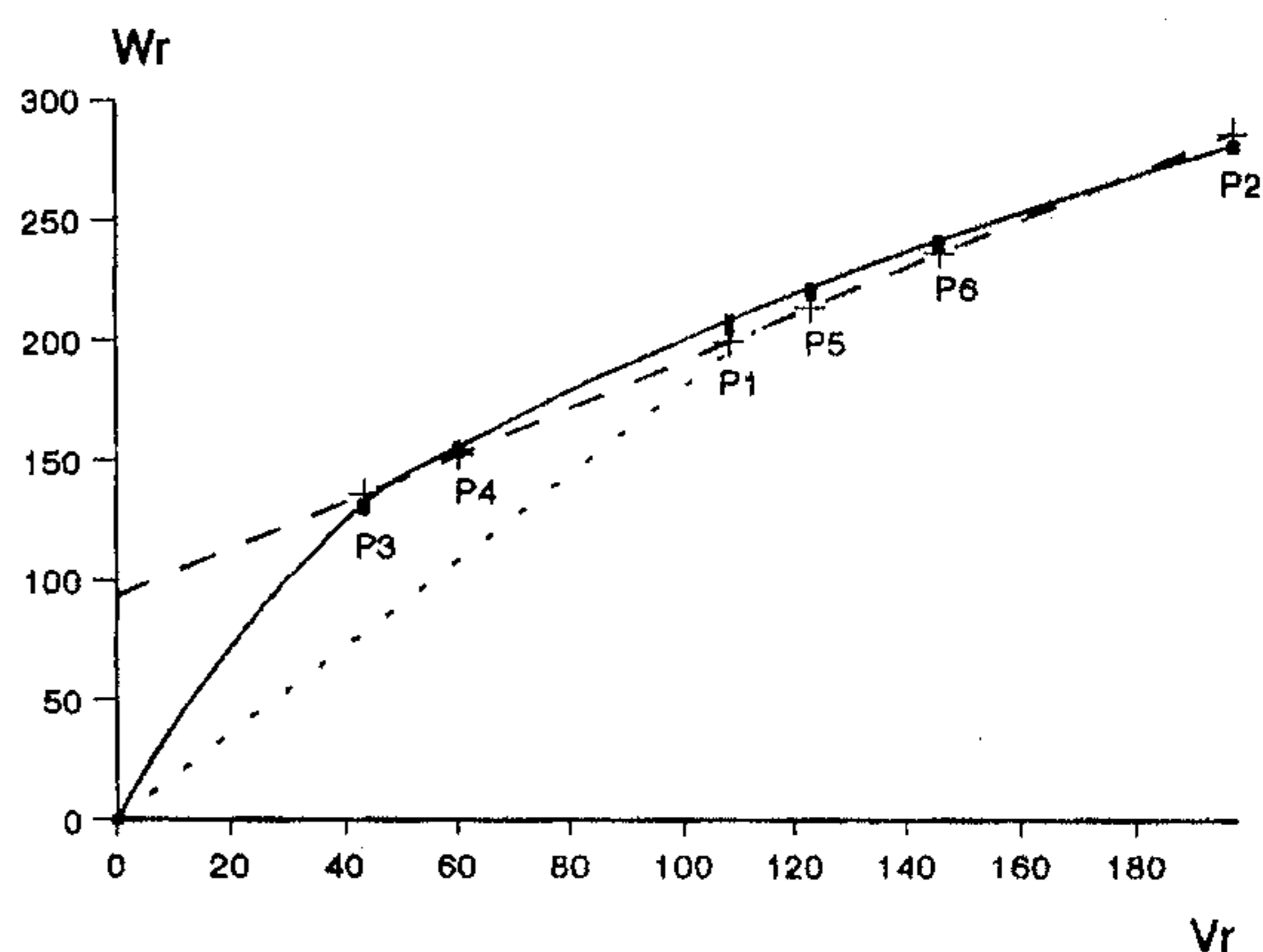


FIGURE 2 - Vr-Wr graph for seed size in a 6×6 diallel cross in F_2 .

TABLE 3

Estimates of gene effects, R^2 and Chi-square (χ^2) with probabilities (Prob) of significance for the best fit model in 15 crosses

Cross No.	Cross	m	d	h	i	j	l	R^2	χ^2	Prob
1	ILC 4 X ILC 149	40.92**	11.05**	4.23**	6.33**	-	-	98.8	5.705	0.058
2	ILC 4 X ILC 211	20.82**	12.78**	-	2.38**	16.76**	-	99.9	0.840	0.657
3	ILC 4 X ILC 2378	24.47**	11.59**	-	-	-	-2.17**	99.9	0.879	0.831
4	ILC 4 X ILC 2407	40.08**	-3.89**	1.38*	-	-	-	95.9	4.491	0.213
5	ILC 4 X ILC 6104	43.96**	7.79**	2.91**	-	-	-	99.3	2.674	0.445
6	ILC 149 X ILC 211	24.67**	23.95**	-	9.70**	-	-	99.9	4.410	0.221
7	ILC 149 X ILC 2378	35.62**	22.76**	-17.17**	-	-	8.12**	99.9	2.687	0.261
8	ILC 149 X ILC 2407	51.23**	7.20**	-10.00**	-	-	8.21*	99.7	0.700	0.705
9	ILC 149 X ILC 6104	55.06**	-3.38**	3.29**	-	-	-	99.6	0.342	0.952
10	ILC 211 X ILC 2378	16.20**	1.23**	-11.29**	-4.56**	-	7.35**	99.4	0.328	0.567
11	ILC 211 X ILC 2407	27.23**	16.81**	-13.47**	-	-6.77**	7.86**	100.0	0.642	0.423
12	ILC 211 X ILC 6104	26.03**	20.67**	-	5.06**	-	-	100.0	2.599	0.458
13	ILC 2378 X ILC 2407	52.90**	15.59**	-81.82**	-24.46**	-12.65**	52.35**	100.0	NA	NA
14	ILC 2378 X ILC 6104	32.23**	19.42**	-4.95**	-	-	-	99.9	5.845	0.119
15	ILC 2407 X ILC 6104	47.80**	-3.82**	-3.65**	-	-7.57*	-	98.2	1.530	0.465

NA = Not available as no degree of freedom was left for six parameter model for testing χ^2 values.

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

parameter model with m, d and h was a good fit. The additive gene effects were preponderant. Genic interactions were absent.

Cross 6 (ILC 149 X ILC 211). This cross involved the two extremes, large X small seeded parents. Three parameter model with m, d and i was a good fit. Dominance gene effect were absent. The interaction in the cross was additive X additive. All gene effects were fixable.

Cross 7 (ILC 149 X ILC 2378). This cross involved large X small seeded parents. Four parameter model with m, d, h and l was a good fit. Additive gene effects were preponderant. The interaction in the cross was dominance X dominance type. The signs of h and l were opposite.

Cross 8 (ILC 149 X ILC 2407). This cross involved large X medium seeded parents. Four parameter model with m, d, h and l was a good fit. Dominance gene effects were preponderant. The interaction in the cross was dominance X dominance type. The signs of h and l were opposite.

Cross 9 (ILC 149 X ILC 6104). This cross involved large X large seeded parents. Three parameter model with m, d, and h was a good fit. The additive gene effects were negative in this cross. Genic interactions were absent.

Cross 10 (ILC 211 X ILC 2378). This cross involved small X small seeded parents. Five pa-

parameter model with m, d, h, i and l was a good fit. Dominance gene effects were preponderant. The genic interactions were present and were of additive X additive and dominance X dominance type. The signs of h and l were opposite.

Cross 11 (ILC 211 X ILC 2407). This cross involved small X medium seeded parents. Five parameter model with m, d, h, j and l was a good fit. Additive gene effects were preponderant. The additive X dominance and dominance X dominance type of interactions were present in this cross. The signs of h and l were opposite.

Cross 12 (ILC 211 X ILC 6104). This cross involved small X large seeded parents. Three parameter model with m, d and i was a good fit. Only additive gene effects with additive X additive type of interaction were important.

Cross 13 (ILC 2378 X ILC 2407). This cross involved small X medium seeded parents. Only six parameter model was a good fit. Dominance gene effects were preponderant. The dominance and all the genic interactions were negative.

Cross 14 (ILC 2378 X ILC 6104). This cross involved small X large seeded parents. Three parameter model with m, d and h was a good fit. The additive gene effects were preponderant. The dominance gene effects were negative. The genic interactions were present.

Cross 15 (ILC 2407 X ILC 6104). This cross involved medium X large seeded parents. Four parameter model with m, d, h and j was a good fit. The additive X dominance type of interaction was present. Additive, dominance, and additive X dominance gene effects were negative.

DISCUSSION

The ANOVA for combining ability revealed the significance of both additive and non-additive gene effects for seed size. Further, the significance of MS due to GCA when tested against MS due to SCA in both the F_1 and F_2 generations revealed the preponderance of additive gene effects. The parents ILC 149, ILC 2407 and ILC 6104 had positive and significant GCA effects and were good general combiners for the large seed size. On the other hand, the parents ILC 211 and ILC 2378 had negative and significant GCA effects and were poor general combiners for the large seed size.

Graphical analyses in F_1 and F_2 generations indicated the presence of partial dominance for seed size. Correlations of parental means with parental order of dominance were positive. These suggested that dominant genes with negative effects controlled the inheritance of seed size. In other words, the small seed size was dominant over large seed size. ILC 211 and ILC 2378 had the concentration of dominant genes, whereas ILC 6104 and ILC 149 had the concentration of recessive genes.

High narrow sense heritabilities in F_1 and F_2 generations indicated that seed size is least influenced by environmental effects and can easily be transmitted through hybridization.

Out of the 15 crosses, the χ^2 value of goodness of fit for 3-parameter model (m, d, h) was non-significant in only four crosses (Cross numbers 4, 5, 9 and 14) (Table 3). This showed that the 3-parameter model (with m, d and h) explained a major portion of total genetic variation for seed size only in four crosses. The remaining 11 crosses with significant χ^2 values for three parameter models (with m, d and h parameters) showed the presence of genic interactions. Thus the models with more than three parameters were tried, and their goodness of fit were tested but details of these are

not presented to save the space. The χ^2 and R^2 values with probabilities of acceptance of goodness of fit of these models exhibited that some of models even had very high R^2 (> 99.5%) but Chi-square values were significant. This indicated that R^2 value alone was not sufficient to decide the best fit but χ^2 value along with R^2 gives better idea of the appropriate model. The estimates of the parameters based on 3, 4, 5 or 6 parametric models which had the high R^2 and minimum χ^2 values for 15 crosses are given in Table 3. Among these the best models included the ones with very high R^2 value, very low and non-significant χ^2 values and with all the parameters in the model being statistically significant at $P \leq 0.05$.

The estimates of parameters in 15 crosses revealed that additive gene effects were significant in all the crosses, and dominance gene effects were significant in 11 crosses (Table 3). The additive gene effects, in general, were higher as compared to the dominance gene effects except in Cross 8, Cross 10 and Cross 13, where dominance gene action was predominant. These three crosses also exhibited significant dominance X dominance type of genic interactions. All crosses, which exhibited dominance X dominance genic interactions, involved either ILC 2378 (a small-seeded line) or ILC 2407 (a medium-seeded line) or both as the parents.

The estimates of parameters in crosses involving large X large and medium X medium seed parents showed importance of both additive and dominance type of gene actions and did not exhibit any genic interactions. This suggests that selection for large seed size in such crosses was simple and most effective.

The small X small seeded crosses showed the significance of additive and dominance effects along with additive X additive (i), and dominance X dominance (l) type of genic interactions. The large X small-seeded crosses showed the significance of additive (d), dominance (h), additive X additive (i), or dominance X dominance (l) type of genic interactions. In the medium X large, and medium X small crosses all types of gene actions including additive (d), dominance (h), additive X additive (i), additive X dominance (j) or dominance X dominance (l) were observed. The selection in such cases should be delayed to later generations when

these genic interactions of j and l types are reduced.

The negative values of h in Cross numbers 7, 8, 10, 11, 13, 14 and 15 indicated that the alleles for smaller seed size were dominant over alleles controlling larger seed size. In five out of seven crosses, which exhibited negative h values, the signs of h and l estimates were different. This indicated that duplicate epistasis played a significant role in expression of seed size in these crosses.

From the present study, it is concluded that both additive and dominance gene action were important with preponderance of additive gene action for seed size than non-additive gene action. Furthermore, the small seed size seems to be partially dominant over the large seed size. The examination of data for parents, F₁s, F₂s and backcrosses revealed that seed size is governed by polygenes. Also gene actions in different crosses were different, especially in 11 crosses various types of genic interactions were present. The selection for the large seed size should be delayed to F₃ or later generations to reduce the effect of dominance and genic interactions considerably. In such a situation, it will be advantageous to follow the bulk-pedigree method. Since small seed size is at least partially dominant over large seed size, one backcross with the large-seeded parent may increase the possibility of large-seeded segregants.

The findings of this study are being implemented in the kabuli chickpea breeding programme at ICARDA. As a result, the new breeding lines have relatively larger seed size than the lines bred in the 1980s and also they are acceptable to consumers.

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