Genetic basis of pod borer (*Helicoverpa armigera*) resistance and grain yield in *desi* and *Kabuli* Chickpea (*Cicer arietinum* L.) under unprotected conditions

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Summary

A series of half-diallel crosses involving early, medium and late maturity *desi* and *kabuli* type chickpea (*Cicer arietinum* L.) genotypes with stable resistance to *Helicoverpa* pod borer, along with the parents, were evaluated at two locations in India to understand the inheritance of pod borer resistance and grain yield. Inheritance of resistance to pod borer and grain yield was different in *desi* and *kabuli* types. In *desi* type chickpea, the additive component of genetic variance was important in early maturity and dominance component was predominant in medium maturity group, while in the late maturity group, additive as well as dominance components were equally important in the inheritance of pod borer resistance. Both dominant and recessive genes conferring pod borer resistance seemed equally frequent in the *desi* type parental lines of medium maturity group. However, dominant genes were in overall excess in the parents of early and late maturity groups. In the *kabuli* medium maturity group, parents appeared to be genetically similar, possibly due to dispersion of genes conferring pod borer resistance and susceptibility, while their F_1s were significantly different for pod borer damage. The association of genes conferring pod borer resistance and susceptibility in the parents could be attributed to the similarity of parents as well as their F_1s for pod borer damage in *kabuli* early and late maturity groups. Grain yield was predominantly under the control of dominant gene action irrespective of the maturity groups in *desi* chickpea. In all the maturity groups, dominant and recessive genes were in equal frequency among the *desi* parental lines. Dominant genes, which tend to increase or decrease grain yield are more or less present in equal frequency in parents of the early maturity group, while in medium and late maturity groups, they were comparatively in unequal frequency in *desi* type. Unlike in *desi* chickpea, differential patterns of genetic components were observed in *kabuli* chickpea. While the dominant genetic component was important in early and late maturity group, additive gene action was involved in the inheritance of grain yield in medium duration group in *kabuli* chickpea. The dominant and recessive genes controlling grain yield are asymmetrically distributed in early and medium maturity groups in *kabuli* chickpea. The implications of the inheritance pattern of pod borer resistance and grain yield are discussed in the context of strategies to enhance pod borer resistance and grain yield in *desi* and *kabuli* chickpea cultivars.

Introduction

Chickpea (*Cicer arietinum* L.) is the third most important grain legume in the world grown in an area of about 10 million ha with a production of 7.8 million tons (FAO, 2003). India contributes a large proportion to the total world area (62%) and production (75%). There are two types of chickpea: *desi* and *kabuli*. Although *desi* types are small seeded (and have colored seed coat) and are traditionally grown in warmer climates in South Asia and East Africa, *kabuli* types are large-seeded (usually with beige or cream colored seeds)

suited to the more temperate climates of West Asia. In India, both types of chickpeas are grown in diverse agro-ecological niches normally in the postrainy winter season, exploiting residual moisture. The current productivity level of chickpea in India is $872 \, \text{kg ha}^{-1}$, which is far lower than its potential (up to $4 \, \text{t ha}^{-1}$) realized at research stations, demonstration plots, and farmer managed on-farm trials. Of the several biotic stresses, *Helicoverpa* pod borer damage is one of the major causes for low productivity of chickpea.

Gram pod borer, *Helicoverpa armigera* (Hübner), is the most important pest on chickpea, which causes substantial yield losses estimated at over $328 million in the semi-arid tropics (ICRISAT, 1992). The resource-poor farmers in developing countries are unable to use chemical pesticides (which are also associated with huge environmental costs) to manage pod borer. Host plant resistance (HPR) can play a major role in *Helicoverpa* management. Development of crop cultivars with resistance to pod borer is the most cost-effective and eco-friendly option and holds great promise for *Helicoverpa* management, particularly under subsistence farming conditions in the developing countries (Sharma et al., 1999). Availability of stable resistance sources is a prerequisite for HPR breeding. The ICRISAT genebank at Patancheru, India, holds a world collection of more than 17,000 accessions of chickpea. Screening of more than 14,000 germplasm accessions and breeding lines at ICRISAT, Patancheru and the All India Coordinated Pulses Improvement Project (AICPIP) centers, have resulted in the identification of several genotypes with low to moderate levels of resistance to *Helicoverpa* pod borer, and their use in breeding programs. Some of these have also been found to be resistant in different agro-climatic zones under natural infestation conditions at test locations. Germplasm accessions of wild relatives of chickpea (*Cicer bijugum*, *C. judaicum*, and *C. pinnatifidum*) with high-level resistance to pod borer have also been identified (Sharma et al., 2003).

An understanding of the inheritance of resistance is essential for systematic and efficient genetic enhancement of pod borer resistance. The limited information available in the literature indicated the importance of additive (Singh et al., 1991) and both additive and dominance (Salimath et al., 2003) genetic variance in *desi* types, while dominance genetic variance was important in the inheritance of pod borer resistance in *kabuli* type chickpea (Singh et al., 1991). All these studies, besides involving genotypes with variable maturity durations,

are from various groups of scientists across different locations, using different resistant genotypes. Further, the results and conclusions drawn from these studies are inconsistent and tend to contradict each other. Comprehensive studies on genetics of resistance to *Helicoverpa* in different maturity groups in both *desi* and *kabuli* chickpeas are limited. Maturity duration of cultivars is one of the important criteria for their farm level adoption to fit into varied cropping patterns and environmental conditions in chickpea production areas. We therefore, analyzed earlier datasets from studies conducted at ICRISAT during early 1980s on several half-diallel crosses of different maturity groups (made to study genetic control of pod borer resistance) in both *desi* and *kabuli* chickpeas to draw meaningful conclusions on the nature of genetic control of pod borer resistance in chickpea. Although the datasets are old, we felt that the joint consideration of the results from studies on a larger set of half-diallel crosses would provide a meaningful interpretation of the inheritance of resistance to pod borer in chickpea.

The objectives of this study were to estimate and interpret the components of genetic variance for *Helicoverpa* resistance and grain yield under unprotected conditions using a series of half-diallel crosses involving resistant and susceptible *desi* and *kabuli* chickpea genotypes of early, medium and late maturity groups.

Material and methods

Nine different half-diallel crosses were made involving varying number of *desi and kabuli* chickpea genotypes (with different levels of pod borer resistance) during 1980 to 1984. The F_1's along with their parents were evaluated during the succeeding year of F_1 synthesis i.e. from 1981 to 1985 by using a randomized compete block design (RCBD) with three replications. Each entry was raised as a single row plot of 4 m length with a spacing of 60 cm between the rows and 20 cm within a row. All the recommended agronomic practices, except pest control measures, were followed to raise a good and healthy crop. The details of the number of parents, their maturity group and the location of evaluation are presented in Table 1. Observations were recorded on five randomly selected plants in each plot for *Helicoverpa* pod borer damage (%) and grain yield (g plant^{-1}). Pod borer damage was estimated as percentage of pods damaged under natural infestation conditions.

Table 1. Details on the size of the diallel crosses in *desi* and *kabuli* chickpea, parents used, their maturity group and location and year of evaluation

Trial no.	Size of dialell crosses	Parents used	Maturity group	Location of evaluation	Year of evaluation
1	6 × 6 *Desi*	ICC 12475, ICC 12479, ICC 10667, ICCL 78190, ICC 4918, ICCL 78194	Early maturity	ICRISAT, Patancheru, India	1982–83
2	5 × 5 *Desi*	ICC 12475, ICC 12479, ICC 12478, ICC 4918, ICCL 78194	Early maturity	ICRISAT, Patancheru, India	1983–84
3	6 × 6 *Desi*	ICCL 78190, ICC 12480, ICC 12476, ICCL 78188, ICC 4918, ICCL 78194	Early maturity	ICRISAT, Patancheru, India	1983–84
4	6 × 6 *Desi*	ICC 12476, ICCL 78192, ICC 3137, ICCL 78186, ICC 5003, ICC 11525	Medium maturity	ICRISAT, Patancheru, India	1981–82
5	6 × 6 *Desi*	ICC 3474, ICC 5800, ICC 10614, ICCV 7, ICCL 78187, ICCL 78192	Medium maturity	ICRISAT, Patancheru, India	1982–83
6	6 × 6 *Desi*	ICCL 78187, ICCL 79048, ICCL 80101, ICC 3137, ICCL 78191, ICC 4954	Late maturity	Hisar, India	1984–85
7	5 × 5 *Kabuli*	ICC 7510, ICC 12491, ICC 12495, ICC 10761, ICC 8835	Early maturity	ICRISAT, Patancheru, India	1983–84
8	4 × 4 *Kabuli*	ICC 12496, ICC 12492, ICC 12494, ICCL 78189	Medium maturity	ICRISAT, Patancheru, India	1984–85
9	4 × 4 *Kabuli*	ICC 12492, ICC 4856, ICCL 78183, ICC 12494	Late maturity	Hisar, India	1984–85

Biometric and genetic analyses

Each set of diallel crosses was analyzed separately following analysis of variance (ANOVA) of RCBD model to test the significance of differences among the parents and their F_1's for pod borer damage and grain yield. The assumptions of ANOVA were satisfied for these two traits in all the diallel sets. The test of homogeneity of error variances (Bartlett, 1937) in different diallel set trials was carried out to examine the statistical validity to compare the results of diallel set trials, which were conducted in different years. Genetic analyses were conducted according to the diallel model of Hayman (1954a, 1954b) and its modification for half-diallel by Jones (1965). The adequacy of additive–dominance genetic model was tested using the consistency of differences between Wr and Vr across the parental arrays.

Under an additive–dominance genetic model, the components of genetic variance (D: additive; H_1 and H_2: dominance; and F: average covariance of additive and dominance effects over all the parental arrays) were estimated following Hayman (1954b). The average degree of dominance was estimated as $(H_1/D)^{1/2}$. The relative distribution of increasing (positive) and decreasing (negative) genes among common parents of arrays was assessed using the ratio $H_2/(4H_1)$. Deviation of this ratio from its expected value of 0.25, within the limits of sampling variance, was taken as evidence of lack of symmetrical distribution of increasing and decreasing genes. The relative distribution of dominant and recessive genes among the parents as a whole was inferred from F statistic as well as from the ratio $[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$. While the significance of F statistic in positive direction indicates an overall excess of dominant genes, significance in the negative direction indicates an overall excess of recessive genes among the parents. On the other hand, non-significance of F statistic was indicative of symmetric distribution of dominant and recessive genes. Within the limits of sampling variance, the ratio $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$ should be equal to unity if the dominant and recessive genes are symmetrically distributed among the parents. The narrow-sense and broad-sense heritabilities were estimated following Hayman (1954b).

The significant negative or positive correlation between the parental order of dominance (Wr + Vr) and the mean of the common parent of the array (Yr) (after standardization to zero mean and unit variance) was used to infer whether the genes which confer resis-

tance to pod borer damage or enhance yielding ability are predominantly dominant or recessive, respectively among the common parent of the arrays. Further, whenever correlation coefficient between (Wr + Vr) and Yr was significant, standardized values of Wr + Vr were plotted against corresponding standardized values of Yr to identify the parental array, which possess predominantly either dominant or recessive genes with increasing or decreasing effects for the traits.

Results and discussion

Hayman's (1954a, 1954b) approach of diallel analysis was chosen for the present study for resolving the genetic architecture of *Helicoverpa* pod borer resistance and grain yield in chickpea because it provides more genetical information than any other biometrical genetic method available to date (Christie & Shattuck, 1992), within the framework of assumptions of diallel analysis.

Before discussing and interpreting the results on the estimates of genetic components of variation and derived genetic ratios, it is necessary to examine the fulfillment of assumptions of diallel analysis. Since chickpea is a self-pollinated diploid species and parents used in the present study are homozygous lines, two of the six assumptions, i.e., requirement of diploid segregation and homozygous parents are met. The assumption of no epistasis is also met as indicated from consistency of (Wr − Vr) over the parental arrays in all the diallel sets ($P > 0.05$) considered for genetic analysis. Non-significance of the variance due to the item 'b$_2$', barring a few exceptions (Table 2) indicated the fulfillment of independence of gene distribution among the parents (Morley Jones, 1965; Mather & Jinks, 1982; Roy, 2000) in all the diallel sets. The assumptions of multiple alleles are not considered seriously and there has been little discussion of the results from a failure of this assumption (Christie & Shattuck, 1992). Further, multiple allelism of genes in parents does not invalidate the estimate of average degree of dominance (Al-Rawi & Kohel, 1969). In the present study, differences between the reciprocal crosses are ignored because, the general requirements of any analysis of variance of diallel set of crosses are that it provides appropriate tests of significance of principal genetic components, namely additive and dominance components, irrespective of whether there are reciprocal differences (Mather & Jinks, 1982). Therefore, only half diallel cross sets are analyzed. Thus, by and large, the

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Table 2. ANOVA (Morley Jones, 1965) showing the mean squares and their corresponding degrees of freedom in 9 diallel crosses in chickpea

Source	Trial 1 *Desi* early	Trial 2 *Desi* early	Trial 3 *Desi* early	Trial 4 *Desi* medium	Trial 5 *Desi* medium	Trial 6 *Desi* late	Trial 7 *Kabuli* early	Trial 8 *Kabuli* medium	Trial 9 *Kabuli* late
Grain yield (g plant^{-1})									
Rep	40.66 (2)[1]	38.6 (2)	37.34 (2)	28.27 (2)	18.23 (2)	132.98 (2)	41.59 (2)	70.23 (4)	934.76 (2)
a	125.76 (4)**	38.93 (5)^{ns}	81.19 (5)**	79.68 (5)**	24.29 (5)**	650.62 (5)**	189.83 (4)***	99.78 (3)**	78.83 (3)^{ns}
b	58.07 (10)^{ns}	30.67 (15)^{ns}	30.06 (15)^{ns}	40.61 (15)*	7.87 (15)^{ns}	261.81 (15)*	338.65 (10)***	7.25 (6)^{ns}	448.82 (6)^{ns}
b_1	212.06 (1)*	139.73 (1)*	95.59 (1)*	195.11 (1)**	3.23 (1)^{ns}	1900.09 (1)**	18.86 (1)^{ns}	0.43 (1)^{ns}	765.5 (1)^{ns}
b_2	61.23 (4)^{ns}	18.16 (5)^{ns}	38.85 (5)^{ns}	40.48 (5)^{ns}	2.91 (5)^{ns}	120.66 (5)^{ns}	481.16 (4)***	9.91 (3)^{ns}	203.74 (3)^{ns}
b_3	24.74 (5)^{ns}	25.51 (9)^{ns}	17.89 (9)^{ns}	23.52 (9)^{ns}	11.15 (9)^{ns}	158.21 (9)^{ns}	288.6 (5)***	6.68 (2)^{ns}	658.1 (2)^{ns}
Error	29.07 (28)	20.46 (40)	17.43 (40)	19.62 (40)	6.410	135.73 (40)	40.78 (28)	14.39 (36)	298.47 (18)
Pod borer damage (%)									
Rep	1.88 (2)	20.88 (2)	3.71 (2)	40.78 (2)	7.31 (2)	38.27 (2)	1.1 (2)	45.15 (4)	8.3 (2)
a	347.04 (4)**	367.77 (5)**	450.65 (5)**	156.13 (5)**	171.84 (5)**	242.78 (5)**	25.36 (4)^{ns}	40.97 (3)^{ns}	6.79 (3)^{ns}
b	22.71 (10)^{ns}	34.26 (15)^{ns}	38.66 (15)^{ns}	51.96 (15)*	11.92 (15)^{ns}	92.56 (15)**	54.88 (10)^{ns}	56.73 (6)^{ns}	12.96 (6)^{ns}
b_1	62.33 (1)*	83.02 (1)^{ns}	79.36 (1)^{ns}	14.97 (1)^{ns}	0.23 (1)^{ns}	889.05 (1)**	30.39 (1)^{ns}	3.00 (1)^{ns}	0.32 (1)^{ns}
b_2	17.92 (4)^{ns}	12.03 (5)^{ns}	70.76 (5)*	84.87 (5)*	16.92 (5)^{ns}	69.97 (5)^{ns}	60.84 (4)^{ns}	106.22 (3)*	21.49 (3)^{ns}
b_3	18.62 (5)^{ns}	41.19 (9)^{ns}	16.31 (9)^{ns}	37.8 (9)^{ns}	10.45 (9)^{ns}	16.61 (9)^{ns}	55.00 (5)^{ns}	9.37 (2)^{ns}	6.49 (2)^{ns}
Error	13.1 (28)	23.38 (40)	23.44 (40)	26.04 (40)	19.71 (40)	32.15 (40)	28.92 (28)	26.34 (36)	11.3 (18)

[1]Figures in parenthesis are degrees of freedom.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ^{ns}non significant at $P < 0.05$ level of significance.

Table 3. Estimates of pod borer damage (%), range and mean among *desi* and *kabuli* chickpea parents and their F_1's in different diallel trials

Trial no.	Size of the diallel crosses	Parents		F_1's		
		Range	Mean	Range	Mean	$\pm$SE
Desi						
Trial 1	6 × 6 Early maturity	8.6–32.0	19.7	11.0–26.8	17.2	2.80
Trial 2	5 × 5 Early maturity	11.0–28.9	18.4	6.1–27.1	15.5	3.12
Trial 3	6 × 6 Early maturity	11.5–34.1	20.8	12.1–27.0	18.2	2.79
Trial 4	6 × 6 Medium maturity	6.4–24.7	12.4	3.3–19.2	11.3	2.79
Trial 5	6 × 6 Medium maturity	4.7–20.7	9.8	5.0–17.9	9.0	2.77
Trial 6	6 × 6 Late maturity	13.1–37.0	20.0	8.8–17.2	11.6	3.27
Kabuli						
Trial 7	5 × 5 Early maturity	10.3–19.0	14.2	5.0–19.9	12.4	3.10
Trial 8	4 × 4 Medium maturity	9.0–14.0	12.3	8.5–17.8	12.1	2.60
Trial 9	4 × 4 Late maturity	5.5–6.8	6.0	3.4–8.6	5.4	1.71

assumptions of diallel analysis have been met and the interpretation of the results on genetic components was made based on their qualitative rather than quantitative assessment. Further, homogeneity of error variances as indicated from non-significance of Bartlett's test provided sufficient statistical validity to compare the results, which were obtained in different years. Although the diallel crosses and their parents were evaluated in different years, the more or less similar pod borer damage under natural infestation in all the *desi* and *kabuli* chickpea diallel trials, irrespective of their maturity groups, provided further support to compare the results (Table 3). In general, the mean pod borer damage was lower in F_1's than their parents in both *desi* and *kabuli* chickpeas. However, variability in pod borer damage between the F_1's was higher than their parents (Table 3).

Pod borer resistance

Desi type chickpea

Although only additive and dominance genetic variances were predominant in all the three early and one of the two medium maturity diallel trials, respectively, additive as well as dominance components of genetic variances were equally important in the inheritance of pod borer resistance in late maturity group in *desi* chickpea (Table 4). Such differential nature of gene action governing pod borer resistance in different maturity groups has been earlier reported by Gowda et al. (1983), Singh et al. (1991), and ICRISAT (1981, 1982, 1983, 1984,

1985). Recently, Salimath et al. (2003) reported the involvement of both additive and non-additive gene action in the inheritance of pod borer resistance, although their results were maturity non-specific. The predominance of dominance genetic variation in one of the medium maturity diallel trial appeared to be the result of lower pod borer damage in many of the F_1's, compared to their parents as reflected from the mean pod borer damage (Table 4). Both dominant and recessive genes seemed to be equally frequent in the parental lines of medium maturity group as indicated by non-significant *F* statistic.

However, dominant genes are in overall excess in the parents of early and late maturity groups as implied from significant positive estimates of *F* statistic. This is adequately supported from Wr − Vr graphs, wherein most of the parental array points were nearer to the origin (graphs not presented). The significance of the variance due to the item 'b$_1$' (Table 2) provided the evidence that these genes exhibited directional dominance. The unequal distribution of dominant and recessive genes is also adequately supported by the ratio $[(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F]$, which deviates from unity. Further, the genes which tend to reduce pod borer damage i.e., confer resistance are dominant in medium and late maturity groups as suggested from positive and significant correlation between parental order of dominance (Wr + Vr) of each array and the mean of the common parent of the array (Yr). On the other hand, non-significant correlation between (Wr + Vr) and (Yr) implied that equal number of dominant genes contained in the parents of early maturity group

Table 4. Estimates of components of genetic variance and ratios for pod borer damage (%) in 9 diallel crosses in chickpea

Statistic/Source	Trial 1 Desi early	Trial 2 Desi early	Trial 3 Desi early	Trial 4 Desi medium	Trial 5 Desi medium	Trial 6 Desi late	Trial 7 Kabuli early	Trial 8 Kabuli medium	Trial 9 Kabuli late
D	53.71***	81.58***	88.60***	28.26***	24.32*	100.91***	8.26	4.07	−1.45
H_1	22.11	49.40**	75.01***	25.51	98.16***	92.60**	80.10*	77.48***	5.32
H_2	23.09	44.16**	41.03*	25.40	80.11***	68.23*	70.73*	60.62**	3.74
F	−20.82	31.97	46.73*	2.41	18.68	90.36**	13.66	12.46	−7.81
h^2	10.12	23.74*	16.11	−7.76	−10.13	174.51***	6.88	−15.32	5.82*
$(H_1/D)^{1/2}$	0.64	0.78	0.92	0.95	2.01	0.958	3.11	4.36	€
$H_2/(4H_1)$	0.26	0.22	0.14	0.25	0.20	0.184	0.22	0.20	0.18
$[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$	0.54	1.67	1.80	1.09	1.47	2.755	1.72	2.08	€
h_b^2	76.42	62.26	67.20	49.52	55.04	51.747	40.51	42.40	30.34
h_n^2	66.05	44.39	52.89	33.26	20.45	26.178	4.11	9.27	24.55
F-Prob. (parents and F$_1$s)	<0.001	<0.001	<0.001	0.005	0.002	<0.001	0.139	0.075	0.501
F-Prob. (Parents *vs* F$_1$s)	0.039	0.067	0.074	0.910	0.453	<0.001	0.312	0.732	0.875
F-Prob. (parents)	<0.001	<0.001	<0.001	<.001	0.002	<0.001	0.235	0.307	0.946
F-Prob. (F$_1$)	<0.001	<0.001	<0.001	0.056	0.010	0.678	0.130	0.034	0.197
F-Prob. (Wr − Vr)	0.351	0.303	0.074	0.600	0.515	0.727	0.083	0.986	0.475
b_{WrVr} [Ho: $b = 1$]	0.784	1.117	0.712	0.825	0.678	0.785*	−0.564**	0.952	0.687
r (Yp, Wr + Vr)	0.677	0.727	0.161	0.792	0.835*	0.974*	0.567	−0.381	−0.510
T prob [Ho: $r = 0$]	0.209	0.102	0.760	0.061	0.038	0.001	0.319	0.619	0.490

D: Additive genetic variance; $(H_1/D)^{1/2}$: Average degree of dominance; H_1: Dominance genetic variance; H_2: Dominance genetic variance; F: Product of add. By dom. Effects; h^2: Overall dominance effects of heterozygous loci; $H_2/(4H_1)$: distribution of genes with increasing & decreasing effects; $[(4DH_1)^{1/2} + F]/[(4DH_1)^{1/2} - F]$: distribution of dominant & recessive genes; h_b^2: broad sense heritability; h_n^2: narrow sense heritability; F Prob.(Wr − Vr): F prob. from the Wr − Vr graph; b_{WrVr}: slope from regression of Wr − Vr graph.
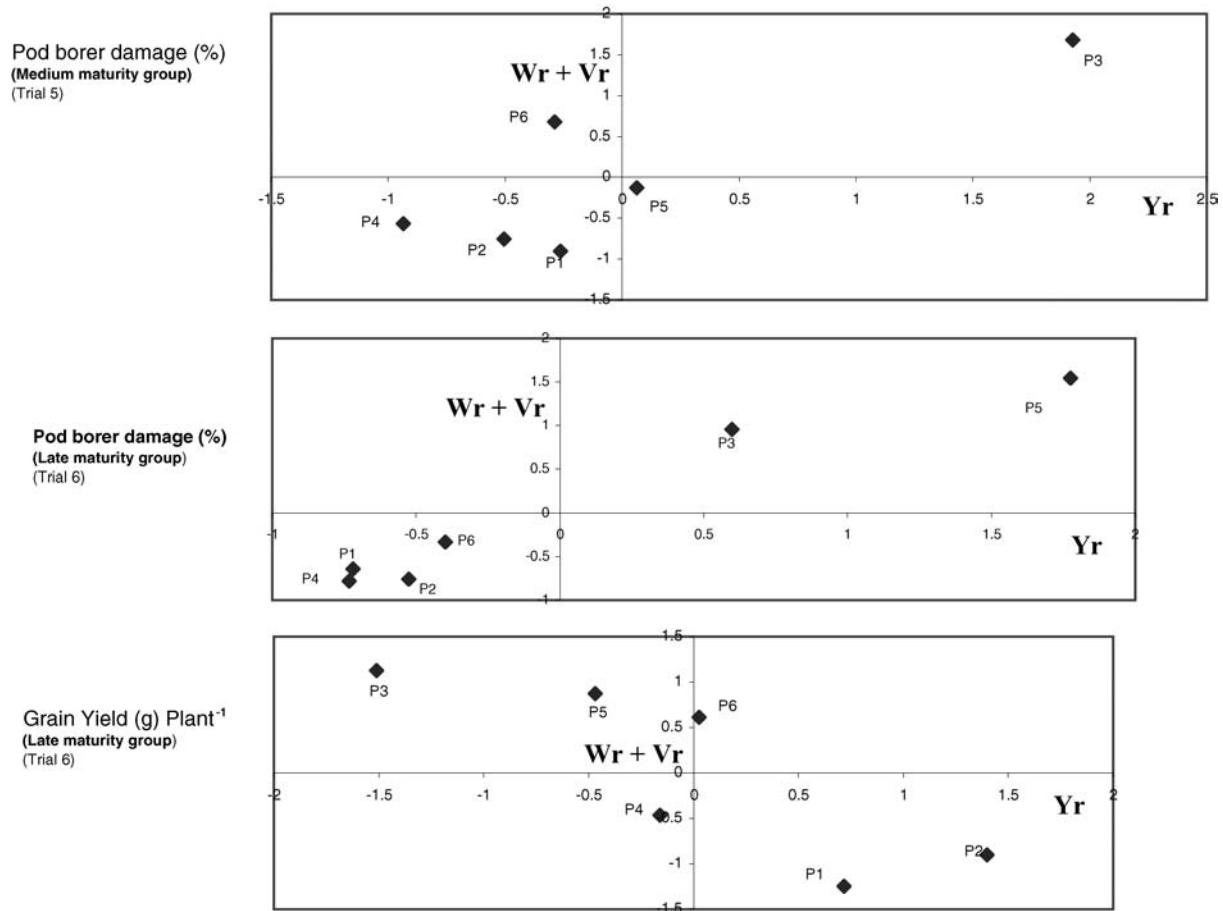* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$;€ Negative estimates.

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Figure 1. Standardised deviation graph of (Wr + Vr) versus Yr for pod borer damage and grain yield in *Desi chickpea*.

tend to confer resistance and susceptibility to pod borer damage that is also represented by the derived genetic ratio $H_2/4H_1$ which is nearly equal to 0.25. However, parents of medium and late maturity groups had unequal frequency of dominant genes that confer resistance and susceptibility to pod borer damage ($H_2/4H_1$ deviated from 0.25). For instance, while four of the six parents involved in late duration group had an excess of dominant genes, three of the six parents in the medium maturity group had an excess of dominant genes conferring pod borer resistance (Figure 1).

Kabuli type chickpea

Although parents appeared to be genetically similar, in the *kabuli* medium maturity group, F_1s significantly differed for pod borer damage (Table 4). The dispersion of genes conferring resistance and susceptibility to pod borer in the parents could have resulted in non-

significant differences for pod borer damage. From the results it could be observed that only dominance genetic variation played a major role in the inheritance of pod borer resistance, unlike in the *desi* medium maturity group, wherein, either only additive (in one diallel set) or both additive as well as dominance genetic variation (in other diallel set) were important. The non-significance of additive genetic variation is obvious, as the parents did not differ significantly. However, the observed dominance genetic variation is surprising because, the parents of medium maturity *kabuli* type chickpea possess an excess of recessive genes as could be inferred from the Wr − Vr graph (Figure 2), wherein all the parental array points are away from the origin and the gene action is not only the property of genes *per se*, but also their frequencies (Falconer, 1989). It follows therefore, that a few of the dominant genes present in the parents have larger effects and contributed to a greater extent towards the variation in pod
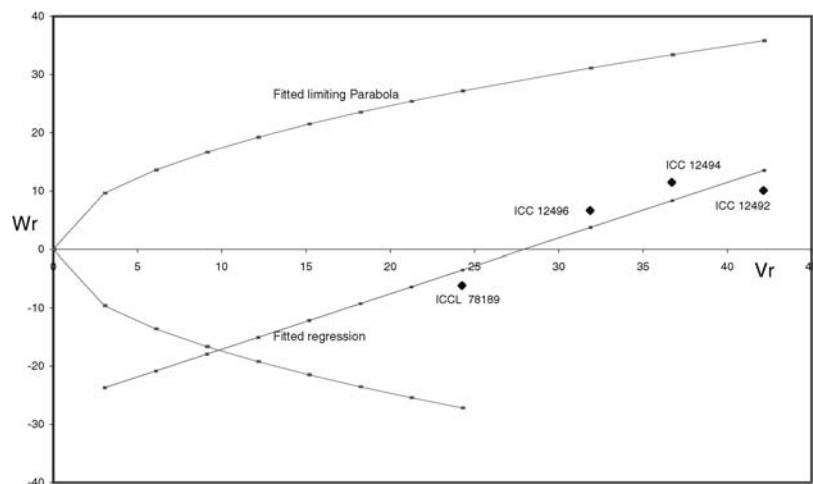
Figure 2. Wr − Vr graph for pod borer damage (%) in Kabuli-medium maturity (Trial 8).

borer damage. The unequal frequency of dominant and recessive genes in the parents is also adequately supported by the ratio $[(4DH_1)^{1/2} + F/(4DH_1)^{\frac{1}{2}} - F]$, which deviated from unity. Even among these few dominant genes, equal numbers of them have decreasing and increasing effects on pod borer damage as evident from non-significant correlation between (Wr + Vr) and (Yr) suggesting that only a fraction of dominant genes present in the parents confer resistance to pod borer. Therefore, attempts to develop pod borer resistant lines from the derivatives of the crosses among these parents may not be fruitful.

In early and late maturity groups of *kabuli* type chickpea, both parents and their F_1s were genetically similar for pod borer damage. Contrary to medium maturity group, association of genes conferring pod borer resistance and susceptibility in the parents could be the reason for the similarity of parents as well as their F_1s. It

may not be appropriate therefore, to discuss the results on the estimates of components of genotypic variation for pod borer damage in early and late maturity groups of *kabuli* chickpea. Nevertheless, critical examination of pattern of parental array points in Wr − Vr graphs (Figures 3 and 4), offers significant implications. The parents ICC 12495 in the early maturity group (Figure 3) and ICC 12492 (Figure 4) in the late maturity group (near the origin) and ICC 7510 in early maturity group and ICC 12494 in late maturity group (away from the origin) have occupied extreme positions in the Wr − Vr graph, implying that while ICC 12495 and ICC 12492 possess an excess of dominant genes, ICC 7510 and ICC 12494 possess an excess of recessive genes for pod borer damage. The positions of these parental array points also suggests that a few recessive genes in ICC 12495 and ICC 12492 and a few dominant genes in ICC 7510 and ICC 12494 confer pod borer resistance. It
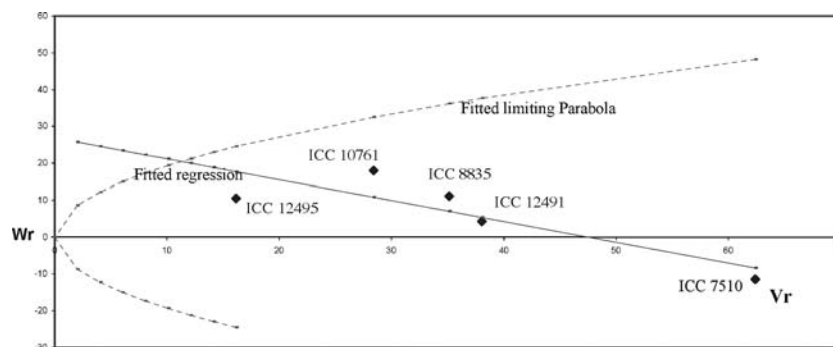

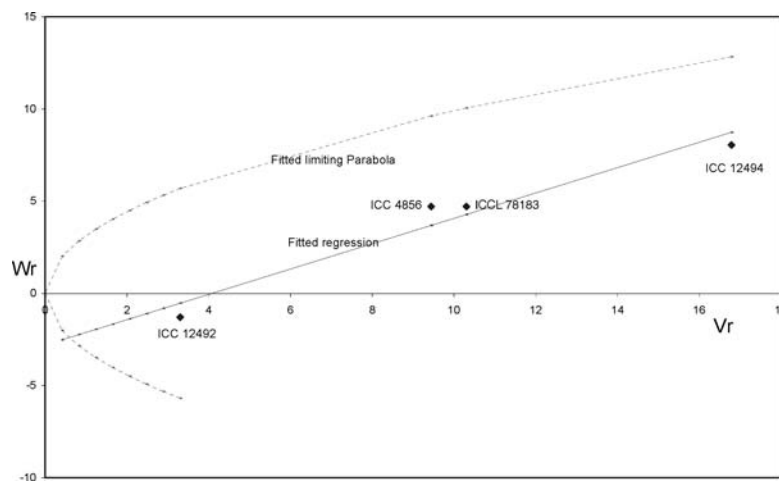*Figure 3.* Wr − Vr graph for pod borer damage (%) in Kabuli-early maturity (Trial 7).

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Figure 4. Wr − Vr graph for pod borer damage (%) in Kabuli-late maturity (Trial 9).

follows therefore, that these parents are extreme as far as pod borer resistance is concerned. When these parents are crossed, the frequency of genes conferring resistance to pod borer is increased in the progeny. Hence, chances of recovering lines with enhanced levels of pod borer resistance from the segregating generations derived from the crosses involving these diverse parents are higher. The chances of realizing productive F_1s are higher and the frequency of superior inbred progenies is also higher from such F_1s, when diverse parents are crossed. Hence, it is worthwhile to involve these parents in crossing programs to derive higher frequency of lines with enhanced pod borer resistance in early and late maturity *kabuli* chickpea.

It is important to note that the differential gene action observed in different maturity groups of *desi* and *kabuli* chickpeas in the present study is not due to differences in the extent of pod borer damage in different maturity groups, but due to different genetic architecture of the pod borer resistance in the parents. This is because pod borer damage in both *desi* and *kabuli* diallel crosses and their parents was by and large similar and hence, comparable irrespective of their maturity groups (Table 3), contrary to normal expectation that late maturity groups experience higher pod borer damage than medium and early maturing counterparts in that order.

Implications for breeding for pod borer resistance

Predominance of fixable i.e., additive genetic variance coupled with comparatively higher narrow sense her-

itability with equal frequency of genes exhibiting increasing and decreasing effects on pod borer resistance suggested the effectiveness of pedigree selection in enhancing the pod borer resistance levels in two of the three early-maturity diallel trials (Trial 1 & Trial 2) in *desi* chickpea.

In contrast, as the genes, which confer resistance to pod borer damage, are dominant in medium maturity *desi* chickpeas, selection during early segregating generations may not be effective and hence selection should be deferred till F_5 (in *kabuli* type, parents may not contribute significantly to pod borer resistance in crosses involving them as they possessed fewer genes for resistance). Salimath et al. (2003) also suggested delaying selection for pod borer resistance till F_5 in such situations. Alternatively, selection should be preceded by intermating in F_2 for one or two cycles to break the conserved linkage blocks, which are considered to be one of the reasons for non-additive gene action (Salimath et al., 2003).

Equal importance of additive and dominant genetic variance coupled with an excess of dominant genes conferring pod borer resistance in a majority of the parents of late maturity group indicated the usefulness of pedigree selection in advanced segregating generations derived either from a cross between a pod borer resistant donor parent and an agronomically superior parent (to exploit additive genetic variation) or from a population developed through recurrent selection (to exploit both additive and dominance genetic variance) for upgrading pod borer resistance and simultaneously maintaining higher grain yielding ability. Recurrent selection in the population developed by random mating

of the pod borer resistant parents in high yielding background used in diallel matings would facilitate accumulation of favorable gene combinations in homozygous and heterozygous state. The pure lines developed from such populations would be expected to exhibit enhanced levels of pod borer resistance. Effectiveness of pedigree selection for pod borer resistance has also been reported by Sharma et al. (2003) and Dua et al. (2001). However, an optimistic caution is necessary while using pedigree selection for pod borer resistance, considering the existence of tight linkage between susceptibility to *Fusarium* wilt (*F. oxysporum* f.sp. *ciceri*) and resistance to pod borer in chickpea. Biparental matings in early segregating generations of a multiple cross involving a few *Helicoverpa* and *Fusarium* wilt resistant genotypes in high yielding background would provide increased opportunity for recombination, which facilitates disruption of tight linkage between gene(s) for these two resistant traits. The utility of biparental mating in breaking the unfavourable associations between traits has been reported in bread wheat (Yunus & Paroda, 1983; Nanda et al., 1990), safflower (Parameshwarappa et al., 1997) and chickpea (Kampli et al., 2002a, 2002b).

Several researchers (Singh et al., 1990; Lateef, 1990; Lateef and Sachan, 1990; van Rheenen, 1991; Chaturvedi et al., 1998; Sharma et al., 2003) were able to identify breeding lines that have dual resistance to pod borer and *Fusarium* wilt. However, the levels of resistance in germplasm accessions are low (Dua et al., 2001; Sharma et al., 2003) and the genes conferring the resistance to pod borer and *Fusarium* wilt are different in different resistance sources (Dua et al., 2001) and presumably these sources have lower stability (Dua et al., 2003). Perhaps improving the population derived from multiple crosses between dual resistant parents through S_1 recurrent selection before embarking on pedigree selection would be a better strategy to increase the frequency of genotypes possessing dual resistance. Focused efforts were made at ICRISAT to pyramid the resistance genes to increase the level of resistance in breeding lines. Eight resistant lines were involved in a multiple crossing scheme (four single crosses and two double crosses leading to one eight way cross). Screening F_2 to F_5 generations led to the identification of promising line such as ICCV 95992 (<1% pod damage compared to 7% pod damage in resistant check, ICC 12475) (Dua et al., 2001; Sharma et al., 2003). The identification of several breeding lines *viz.*, ICCL 87316, ICCL 87317 and ICCV 95992 possessing stable resistance to *Helicoverpa* and high grain yield poten-

tial and germplasm lines ICC 12478, ICC 12479, and ICC 14876, having stable resistance to *Helicoverpa* and moderate yield potential (Sree Latha et al., 2003), could be used in enhancement of pod borer resistance in elite agronomic background.

Grain yield

Desi type chickpea

Irrespective of the maturity group, only dominance components of genetic variance appeared to be involved in the inheritance of grain yield and obviously, narrow sense heritability was very low in all the six diallel sets (Table 5). These findings are in conformity with those of Bhatt and Singh (1980), Ugale (1980), Katiyar and Solanki (1983), Singh and Sidhu (1983), Kunadia et al. (1986), Shinde (1988), Mian and Bahl (1989), and Deshmukh and Patil (1995). However, the reports of Gowda (1975), Asawa and Tiwari (1976), Sandhu et al. (1977), Gowda and Bahl (1978) contradict present findings, which indicated the involvement of additive genetic variance. Singh et al. (1992), Singh et al. (1993), Annigeri et al. (1996), Sarode (1997) and Girase (1999) reported the importance of additive as well as non-additive genetic variance. Very few of these studies have focussed on revealing gene action in the inheritance of grain yield in delineated maturity groups such as in the present study.

In all the maturity groups, dominant and recessive genes occur in equal frequency among the parental lines (non-significant '*F*' statistic), which is adequately represented by near-unit value of the ratio $[(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F]$. Also, the dominance displayed by the genes present in the parents is mono-directional as implied from the significance of 'b_1', (Table 2) in all the maturity groups. Dominant genes which tend to increase or decrease grain yield occur more or less in equal frequency in parents of early maturity group ($H_2/4H_1$ ratio is nearly 0.25); while those present in parents of medium and late maturity groups are comparatively in unequal frequency ($H_2/4H_1$ deviated from 0.25). The significant negative correlation of parental order dominance of each array (Wr + Vr) with the mean of the common parent of the array (Yr) suggested that the genes, which tend to increase the grain yield are dominant in parents of late maturity group. For example, three of the six parents in late maturity group had genes, which enhance grain-yielding ability irrespective of whether they were dominant or

Table 5. Estimates of components of genetic variance and ratios for grain yield in 9 diallel crosses in chickpea

Statistic/source	Trial 1 *Desi* early	Trial 2 *Desi* early	Trial 3 *Desi* early	Trial 4 *Desi* medium	Trial 5 *Desi* medium	Trial 6 *Desi* late	Trial 7 *Kabuli* early	Trial 8 *Kabuli* medium	Trial 9 *Kabuli* late
D	−12.89	−9.52*	9.06	1.53	2.70	63.70	39.69	13.30*	14.47
H_1	97.07***	48.12***	45.67**	8.51*	62.88***	438.01**	500.88***	4.87	497.51*
H_2	81.16**	48.20***	39.09**	7.96*	51.76***	338.59**	369.76***	3.72	469.44*
F	−27.67	−15.99	1.08	−4.66	−2.03	61.00	96.09	−3.04	8.63
h^2	57.88***	36.26***	23.84*	−2.29	38.89***	412.12***	7.61	11.12	151.14
$(H_1/D)^{1/2}$	€	€	2.27	2.36	4.83	2.62	3.55	0.61	5.87
$H_2/(4H_1)$	0.21	0.25	0.21	0.23	0.21	0.19	0.19	0.19	0.24
$[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$	€	€	1.06	0.22	0.855	1.45	2.03	0.68	1.11
h_b^2	55.03	42.73	49.42	45.36	51.48	50.02	76.07	41.18	31.05
h_n^2	23.70	8.97	21.09	28.48	19.55	18.82	21.90	37.22	3.92
F-Prob. (Parents & F$_1$s)	0.013	0.102	0.008	0.048	0.006	0.004	<0.001	0.015	0.416
F-Prob. (Parents *vs.* F$_1$s)	0.012	0.013	0.024	0.480	0.003	<0.001	0.503	0.867	0.127
F-Prob. (Parents)	0.538	0.723	0.025	0.107	0.034	0.031	0.044	0.008	0.859
F-Prob. (F$_1$)	0.013	0.124	0.037	0.055	0.045	0.074	<0.001	0.078	0.308
F-Prob. (Wr − Vr)	0.743	0.936	0.973	0.592	0.267	0.617	0.018	0.585	0.575
b_{WrVr} [Ho: $b = 1$]	0.189*	0.510	0.505**	0.368**	0.265	0.314**	−0.105**	0.795	0.354
r (Yr, Wr + Vr)	0.826	0.484	0.805	0.726	−0.367	−0.835*	0.562	−0.015	−0.999
Tprob [Ho: $r = 0$]	0.084	0.331	0.054	0.102	0.475	0.038	0.324	0.985	<0.001

D: Additive genetic variance; $(H_1/D)^{1/2}$: Average degree of dominance; H_1: Dominance genetic variance; H_2: Dominance genetic variance; F: Product of add. By dom. Effects; h^2: Overall dominance effects of heterozygous loci; $H_2/(4H_1)$: distribution of genes with increasing & decreasing effects; $[(4DH_1)^{1/2}+F]/[(4DH_1)^{1/2}-F]$: distribution of dominant and recessive genes; h_b^2: broad sense heritability; h_n^2: narrow sense heritability; F-Prob. (Wr − Vr): F Prob. from the Wr − Vr graph; b_{WrVr}: slope from regression of Wr − Vr graph.
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; €Negative estimates.

recessive (Figure 1). Contrastingly, the dominant genes present in the parents of early and medium maturity groups showed a tendency to either decrease or increase grain yield in equal frequency as implied from non-significant correlation between (Wr + Vr) and (Yr).

Kabuli type chickpea

Unlike in *desi* chickpeas, differential patterns of genetic components were observed in *kabuli* chickpeas. For example, while only dominance genetic component was important in early and late maturity groups, only additive gene action was involved in the inheritance of grain yield in medium maturity group (Table 5). The dominant and recessive genes controlling grain yield are asymmetrically distributed in early and medium maturity groups as indicated from large deviation of the ratio $[(4DH_1)^{1/2} + F/(4DH_1)^{1/2} - F]$ from unity. The asymmetrical distribution of dominant and recessive genes was adequately supported by Wr − Vr graphs (not presented). For example, in the early maturity group, out of five parents, one had an excess of recessive genes while another had an excess of dominant genes for grain yield. The remaining three parents had a more or less equal number of dominant and recessive genes. It appeared that all those genes that displayed dominance had a major effect on the expression of grain yield and hence contributed to significance of dominance genetic variation in the early maturity group. In the medium maturity group, out of four parents, two had an excess of dominant genes and the other two had an excess of recessive genes. It appeared that most of these acted in additive fashion with larger ef-

fects on grain yield, contributing significantly towards additive genetic variation in medium maturity group. The non-significant correlation between (Wr + Vr) and (Yr) indicated that while half of the dominant genes present in the parents tend to decrease grain yield, the other half tend to increase grain yield in both the maturity groups. It is interesting to note that all those genes which either enhance or decrease grain yield seems to be asymmetrically distributed in the parental lines irrespective of whether they are dominant or recessive as suggested from the ratio $H_2/4H_1$, which deviated from 0.25 in both the maturity groups. These suggest that genes that enhance grain yield are dispersed among the parents.

In the late maturity group, the observed variation in grain yield did not have any genetic basis as neither parents nor their F_1s were significantly different (Table 5). However, from Wr − Vr graph (Figure 5) it is clear that the parents ICC 4856 and ICCL 78183 (with an excess of dominant genes) and ICC 12492 and ICC 12494 (with an excess of recessive genes) appeared to be genetically diverse for the expression of grain yield. Crosses among these extreme parents could probably produce superior segregants with enhanced grain yield.

Implications for breeding for higher productivity

It is clear from present as well as past findings that grain yield is predominantly under the control of non-additive gene action irrespective of the maturity groups in *desi* type and in early maturity *kabuli* type chickpea. Probably due to this predominance of non-fixable genetic variation coupled with low heritability,
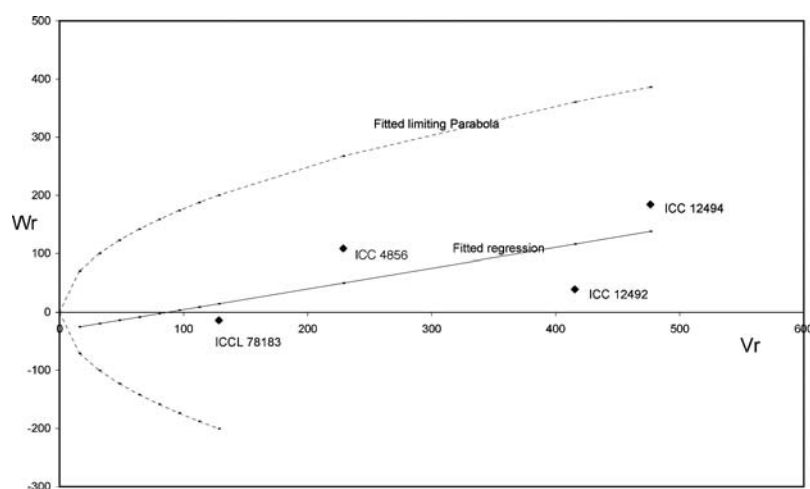

Figure 5. Wr − Vr graph for grain yield in Kabuli-late maturity (Trial 9).

it has not been possible to achieve a breakthrough in productivity of chickpea. Also, it has been argued that the lack of sufficient variability (due to its strictly inbreeding behavior) is one of the reasons for the failure of enhancing the chickpea productivity to a desired level (Kampli et al., 2002a). The use of conventional breeding methods such as pedigree, single seed descent and bulk methods are associated with the weakness of causing rapid homozygosity and low genetic variability especially in the presence of linkage blocks and inverse relationships among the desirable traits (Clegg et al., 1972). To circumvent these problems, a suitable procedure needs to be adopted, which exploits both additive and non-additive gene effects besides disrupting undesirable associations and uncovering concealed variability. Perhaps one or two cycles of recurrent selection in a population derived from a multiple cross, which not only exploits both additive and non-additive gene effects and pyramid desirable traits from different sources, but also disrupt undesirable linkages to a certain extent; followed by pedigree or single seed descent or bulk-pedigree methods would have better prospects to improve grain yield. Biparental mating of segregants in recurrent selected population would further augment in disrupting the undesirable linkages in addition to releasing a considerable spectrum of variability (Girase et al., 2002; Kampli et al., 2002a, 2002b).

The impact of biparental mating (in an F_2 population) in enhancing genetic variability, heritability and expected genetic advance for grain yield besides substantially improving the correlation of grain yield with components traits such as plant height, number of secondary branches, pods per plant and 100 seed weight has been reported by Kampli et al. (2002a, 2002b) in chickpea. Such increased correlation between grain yield and its component traits would be valuable in indirect selection for grain yield, as it is more efficient than direct selection for grain yield *per se*. Effectiveness of indirect selection for grain yield via pod number and seed weight has been earlier reported by Bisen et al. (1985), Salimath and Bahl (1985) and Kumar and Bahl (1992) in chickpea. It should be relatively easy to enhance productivity of medium duration *kabuli* type chickpea, as only additive genetic variation is important.

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