Genetic analysis of pod borer (Helicoverpa armigera) resistance and grain yield in desi and kabuli chickpeas (Cicer arietinum) under unprotected conditions

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Abstract

 $\textsf{Half-dial}$ le ross progenies of *desi* (45F₁s and 45F₂s) and $\boldsymbol{\mathsf{k}}$ abuli (28F₁s and 28F₂s) chickpeas (*Cicer arietinum*) along **with their parents (10 desi and 8 kabuli) with varying levels of pod borer resistance (PBR) were evaluated in replicated field trials under unprotected conditions during 2001-2002 post-rainy season at International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, India to study the inheritance of pod borer, Helicoverpa armigera (Hub.), and grain yield. Additive genetic variation was important for the inheritance of PBR in desi chickpea. However, both additive and dominance genetic variations were important in the inheritance of PBR in kabuli chickpea. However, dominance genetic variation was predominant in the inheritance of grain yield in both desi and kabuli chickpeas. The correlation coefficient between general combining ability (gca) effects estimated based** on data of F₁ and F₂ generations was fairly higher, while it **was lower for specific combining ability (sca) effects in desi chickpea for PBR. The correlation coefficient between gca effects and between sca effects estimated based on F1 and F2 generations' data for PBR in kabuli chickpea and for grain yield in desi and kabuli chickpeas were very low. Chickpea lines with significant gca effects for PBR and grain yield in desi and kabuli chickpeas were identified. The implications of study results are discussed in relation to strategies to enhance PBR and grain yield levels.**

Key words: Combining ability, desi chickpea, diallel, kabuli chickpea, inheritance, pod borer resistance

Introduction

Chickpea, Cicer arietinum L. is the third most important food legume globally grown in 11 million ha with 8.4 million ton production. India contributes a large proportion to the total world area (62%) and production

(65%). Pod borer, Helicoverpa armigera (Hub.) is the most important biotic constraint limiting chickpea production. The intensive use of the conventional insecticides to control H. armigera damage has led to the development of insecticide resistant populations in India. Therefore, the development of improved cultivars with pod borer resistance is a cost effective and environmentally benign technology to reduce yield losses, particularly under subsistence farming conditions.

Although several studies have been made to estimate combining ability and to unravel the genetics of pod borer resistance (PBR) and grain yield in desi and kabuli chickpeas, the results are inconsistent. Comprehensive studies involving large number of parents with varying levels of PBR and more than one filial generation derived from crosses between such parents would provide dependable estimates of genetic components of variance. The objectives of the present study were to assess the nature of the genetic control of PBR and grain yield in selected desi and kabuli chickpea genotypes using the relativity assumption-less diallel data analysis model [1].

Materials and methods

Field evaluation

Seven pod borer resistant and three susceptible desi genotypes; and eight kabuli genotypes (five pod borer resistant, one moderately resistant and two susceptible genotypes) diverse for the agronomic characters (Table 1) were selected for the study. These pod borer resistant and susceptible lines were identified based on the

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SI.No.	Genotype	Pedigree	Reaction to pod borer	Days to 50% flowering	Days to maturity	
	Kabuli chickpea					
1	ICC 12491	ICC 10870 HR (JM-2575)	Resistant	63	118	
2	ICC 12492	ICC 5264 HR (GL-645)	Resistant	64	123	
3	ICC 12493	ICC 5264 HR (GL-645)	Resistant	71	121	
4	ICC 12494	P-52-P1-359038 (NEC 2059)	Resistant	68	119	
5	ICC 12495	ICC 7559 HR (P-9625)	Resistant	72	121	
6	ICC 12968	ICCV ₂	Moderately resistant	34	94	
7	ICC 4962	K4	Susceptible	70	114	
8	ICC 4973	L 550	Susceptible	72	111	
	Desi chickpea					
1	ICC 12475	ICC 506 HR (P386)	Resistant	55	104	
2	ICC 12476	ICC 6663 HR (NEC-764)	Resistant	67	115	
3	ICC 12477	ICC 10460 HR (RPSP-194)	Resistant	54	110	
4	ICC12478	ICC 10667 HR (62-10-3)	Resistant	58	115	
5	ICC 12479	ICC 10619 HR (G 130)	Resistant	60	110	
6	ICC 12490	ICC 4935 HR (C-235)	Resistant	70	117	
7	ICC 14876	ICCV7	Resistant	60	105	
8	ICC 4918	Annegeri	Susceptible	51	107	
9	ICC 12426	ICCC 37	Susceptible	55	102	
10	ICC 3137	P-3659-2	Susceptible	64	119	

Table 1. Characteristics of the kabuli and desi chickpea genotypes used in the study

screening of over 14,800 germplasm accessions through open-field technique under natural and unprotected conditions at ICRISAT, Patancheru, India. Forty-five desi chickpea and twenty-eight kabuli chickpea crosses, excluding reciprocals, were made following half-diallel mating design. F_1 and F_2 generations of desi and kabuli chickpea crosses were evaluated along with their parental lines in two separate trials in randomized complete block design (RCBD) with three replications at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru (17°N 78°E) near Hyderabad, India during 2001-02 post-rainy season. While the F_1 s and their parents were planted in plots of single rows, F_{2} s were planted in 4 rows plots of 2 m length adopting row-torow spacing of 30 cm and 10 cm within a row. All crop husbandry practices were followed, except protection against pod borer, since the purpose was to screen for PBR. Data on number of pods damaged by H. armigera and grain yield per plant⁻¹ (g) were recorded on five randomly selected plants from each of the 45 F_1 s of desi and 28 $F₁$ s of kabuli chickpea and their parents

and on 30 randomly selected plants from each $F₂$ generation of 45 desi and 28 kabuli chickpea crosses. The pod borer damage (PBD) was estimated as percent of damaged pods in each plant under natural infestation conditions.

Biometric-genetic analyses

The mean values of data recorded on sample plants for PBD and grain yield were used for statistical analysis. Both desi and kabuli chickpea half-diallel crosses were analyzed separately following analysis of variance (ANOVA) of RCBD model to test the significance of differences among the parents and their F_{q} s and F_{2} s for PBD and grain yield. After confirming the significance of parents and their F_1 and F_2 s of *desi* and *kabuli* chickpeas, the general combining ability (gca) and specific combining ability (sca) effects and their variances for PBD and grain yield were estimated as per the method 2, and model I (fixed effects) of Griffing [1]. All the statistical analysis was carried out using GENSTAT statistical software.

Results and discussion

Griffing [1] model of half-diallel crosses data analysis was chosen for the present study for estimating the genetic potential of the selected desi and kabuli chickpea genotypes and assessing the genetic architecture of PBR and grain yield because the model is based on combining ability analysis. The main advantage of combining ability analysis is that it provides empirical summary of complex observations and reasonable basis for assessing breeding value of parental lines and for forecasting the performance of crosses but yet make no genetical assumptions. Being based on first-degree statistics, combining ability effects are statistically robust, and being genetically neutral they are equally applicable to both self and cross pollinated crops [2]. Therefore, Griffing [1] model was chosen for half-diallel data analysis, which requires relatively few assumptions necessary for an ANOVA [7]. Besides providing the estimates of *gca* effects of parents and *sca* effects of crosses, the analysis provides the method for diagnosis and estimation of $\sigma^2_{\ \rm A}$ and $\sigma^2_{\ {\rm D}}$ by translating covariance of HS and FS [11]. The consistency of (Wr-Vr) over parental arrays for PBD ['F' probability = 0.8 in F_1 and 0.6 in F_2 in *desi* chickpea (Table 2); 0.6 in F_1 and 0.7 in $F₂$ in *kabuli* chickpea (Table 3) and grain yield plant⁻¹ ('F' probability = 0.08 in F₁ and 0.07 in F₂ in *desi* chickpea (Table 2); 0.09 in F_1 and 0.07 in F_2 in *kabuli* chickpea (Table 3) indicated lack of evidence for the presence of epistasis and hence provided the unbiased estimates of σ^2 A and σ^2 _D.

Pod Borer Resistance

Desi type chickpea

Variance components: The ANOVA revealed significant variation among parents as well as their F_1 s and F_2 s for PBD (Table 2), justifying the selection of parents for the study. As expected, F_1 s and F_2 s showed higher variability to PBD compared to those of parents, as indicated from higher range of PBD in $\mathsf{F}_\mathtt{1}$ s and $\mathsf{F}_\mathtt{2}$ s than that in parents (Table 4). The substantial differences in gca effects of parents (as suggested from significant σ_{g}^{2}) for PBD must have resulted in progenies (F₁s and $F₂$ s) with differential abilities to resist PBD (Table 2). While both $\sigma^2_{\rm g}$ and $\sigma^2_{\rm s}$ for PBD were significant in F₁s, only $\sigma^2_{\;\;\;\beta}$ was significant in F_2 s, suggesting the importance of both $\sigma^2_{\ A}$ and $\sigma^2_{\ b}$. However, greater magnitude of $\sigma^2_{\ A}$ than $\sigma_{\vert_{\rm D}}^2$ clearly indicates preponderance of $\sigma_{\vert_{\rm A}}^2$ in the inheritance of PBR. The estimates of the predictability ratio, closer to unity in both F_1 s and F_2 s reinforce the importance of $\sigma^2_{\scriptscriptstyle{\text{A}}}$. Gowda *et al.* [3] have also reported

the importance of σ_A^2 in the inheritance of PBR in *desi* chickpea genotypes of early maturity group. It should be noted that most of *desi* chickpea genotypes used in the present study belong to early maturity group.

Combining ability effects

Though hybrids are not the immediate cultivar options in chickpea, the development of productive crosses which are likely to result in higher frequency of superior lines in advanced segregating generations assumes importance, considering the limited resources available. The significant and a fairly higher positive correlation between parental mean performance and their gca effects estimated based on both F_1 s and F_2 data (Table 5) indicated that mean PBD of parents is a good indicator of their *gca* effects and the selection of parents for crossing programs to generate useful variability based on their PBD, is effective. This has practical significance in reducing time required for data analysis and thus increases the efficiency of selecting parents just by visual observation for use in breeding for PBR. In the present study, three lines, ICC 12478, ICC 12479, and ICC 14876 (based on F_1 and F_2 data) and additional two lines, ICC 12475 and ICC 12477 (based on F_2 data alone) with significant negative gca effects (Table 5) are good parents for PBR breeding. Gowda et al. [3] have also reported that these lines manifest decreasing effects on pod borer damage. Parents ICC 12478, ICC 12479 and ICC 14876 with desirable gca effects are also known to have stable PBR with moderate grain yield potential [16]. These parents can be used to develop productive crosses to generate useful variability for selecting lines with enhanced PBR.

Significant and positive correlation coefficient $(r = 0.77)$ between *gca* effects estimated based on F₁ and F_2 data (Table 5) suggest that g ca effects of parents based on F_1 and F_2 data are comparable and parents selected based on either F_1 or F_2 data would be reliable. This is expected, since gca effects are the manifestation of additive properties of genes (as reflected from a very high magnitude of $\sigma^2_{\scriptscriptstyle\rm A}$ relative to $\sigma^2_{\scriptscriptstyle\rm D}$), the responses of F_1 and F_2 populations to PBD are similar. However, poor correlation coefficient ($r = 0.02$) between sca effects estimated based on $\mathsf{F}_\mathtt{1}$ and $\mathsf{F}_\mathtt{2}$ data suggested that the specific combinations selected based on $F₁$ data need not be the same as those based on $\mathsf{F}_2^{\vphantom{\dagger}}$ data. Such poor correlation between *sca* effects based on $\mathsf{F}_\mathtt{1}$ and $\mathsf{F}_\mathtt{2}$ data is not surprising considering differential segregation of different crosses in $F₂$ as a rule [4].

Predominance of fixable additive genetic variance

Table 2. Analysis of variance and estimates of general combining ability (gca) and specific combining ability (sca) variances in F₁ and F₂ generation of 10 x 10 half-diallel crosses in *desi* chickpea

*Significant at P < 0.05; **Significant at P< 0.01

*Significant at P < 0.05; **Significant at P < 0.01

i.e., σ^2 suggests the effectiveness of pedigree selection in advanced segregating generations for enhancing the PBR. Effectiveness of pedigree selection for PBR has also been reported by Sharma et al. [5], Dua et al. [6], and Singh et al. [7].

Kabuli type chickpea

Variance components: Significant variation among kabuli chickpea parents as well as their F_1 s and F_2 s was evident for PBD (Table 3). F_1 s and F_2 s showed variable responses to PBD compared to those of parents as indicated from higher range in PBD in F_\natural s and F_\natural s than that in parents (Table 4). The significance of both $\sigma^2_{\;\;\;\mathsf{g}}$ and $\sigma^2_{\;\;\mathsf{s}}$ in F₁s as well as F₂s (Table 3) indicated the importance of both additive and dominance gene action for PBR in kabuli chickpea. However, the greater magnitude of $\sigma_{_{\text{D}}}^{\text{2}}$ than $\sigma_{_{\text{A}}}^{\text{2}}$ estimates based on $\mathsf{F}_{_{\text{1}}}$ s data, and exactly reverse trend ($\sigma_{\scriptscriptstyle\mathsf{A}}^{\scriptscriptstyle 2}$ > $\sigma_{\scriptscriptstyle\mathsf{D}}^{\scriptscriptstyle 2}$) based on $\mathsf{F}_{\scriptscriptstyle 2}$ data suggests that the genetic control of PBR was different in kabuli chickpea. Recent studies of Gowda et al. [3], using separate half-diallel crosses (F,s) involving kabuli chickpea lines with different maturity groups have clearly showed that only dominance genetic variation is important in the inheritance of PBR irrespective of maturity duration. The differences in inheritance pattern of PBR in *desi* (predominance of $\sigma^2_{\ \mathsf{A}}$) and *kabuli* (predominance of σ_{D}^{2}) chickpeas could possibly due to differences in resistance mechanisms. While both antixenosis and antibiosis mechanisms appear to operate in conferring PBR in desi chickpea, only antibiosis appear to be the major mechanism for PBR in kabuli chickpea [8]. However, the relationship between mechanism and inheritance of PBR needs confirmation from the systematic studies using carefully chosen lines.

Combining ability effects

The positive, but not significant, correlation between parental mean PBD and their gca effects in kabuli chickpea (Table 6) indicated that mean PBD of parents provide moderate indications about their gca effects. In the present study, ICC 12492 (based on F_1 and F_2 data) and additional two lines, ICC 12493 and ICC 12495 (based on $F₂$ data alone) with significant negative gca effects appeared to be good combiners for low PBD. Gowda et al. [3] have also reported decreasing effects of these lines. These lines could be used as potential parents to develop productive crosses to generate variability for use in breeding for PBR. The correlation coefficient ($r = 0.32$) between gca effects estimated based on F_1 and F_2 data (Table 6) was moderate in kabuli chickpea, indicating little correspondence

between *gca* effects estimated from F_1 and F_2 data. Predominance of both $\sigma^2_{\ A}$ and $\sigma^2_{\ D}$ might be the cause for moderate correspondence between gca effects estimated from F_1 and F_2 data.

Given that both $\sigma^2_{\ A}$ and $\sigma^2_{\ D}$ are important in the present material with a slight edge in favor of $\sigma_{\scriptscriptstyle \mathrm{D}}^2,$ selection during early segregating generations may not be effective and hence selection should be deferred till F_{5} . Salimath *et al.* [9] have also suggested delaying selection for PBR in chickpea till F_5 in such situations. A combination of bulk and pedigree breeding methods (evolutionary breeding approach) [10] seems most appropriate. In this approach, the individuals are exposed to natural infestation by pod borer in hot-spots and those that survive will be bulked and carried forward till F_5 at which majority of the individuals attain near homozygosity. From F_5 onwards, the population will be handled using pedigree selection for PBR in elite agronomic background.

Grain yield

Desi chickpea

Variance components: The ANOVA indicated significant variability among the parents and F_1 crosses and their F_2 progenies (Table 2). The importance of both σ^2_{g} and $\sigma_{\rm s}^2$ (Table 2) were evident with predominance of the latter, which is amply reflected from much higher magnitudes of $\sigma_{\scriptscriptstyle\rm D}^2$ than $\sigma_{\scriptscriptstyle\rm A}^2$ in both ${\sf F}_{\scriptscriptstyle\rm 1}$ and ${\sf F}_{\scriptscriptstyle 2}$ generations. These findings are in agreement with those of Deshmukh and Patil [11] and Gowda et al. [3].

Combining ability effects

The good general combining parents such as ICC 4918 and ICC 12426 (identified based on both $\mathsf{F}_{_{1}}$ and $\mathsf{F}_{_{2}}$ data) and ICC 12475, ICC 12476 and ICC 12478 (identified based on F_1 data alone) (Table 5) could be used in producing productive crosses. Among these parents, ICC 12476 possess an excess of dominant genes; ICC 12426, ICC 12478 and ICC 4918 possess an excess of recessive genes; ICC 12475 possess equal frequency of dominant and recessive genes for grain yield under unprotected conditions [3]. Thus, it is clear that these parents with significant positive gca effects are diverse for nature of genes controlling grain yield. However, predominance of dominance gene action would make selection in the early generation ineffective. Therefore, selection should be preceded by bi-parental mating in $F₂$ for one or two cycles to disrupt the conserved linkage blocks, which are considered to be one of the reasons for non-additive gene action [9]. Effectiveness of indirect Table 4. The estimates of range and mean pod borer damage (%) and grain yield plant" in *desi* (10 x 10) and kabuli (8 x 8) chickpea half-diallel crosses progenies (F_{1} s and F_{2} s and their parents)

Size of the diallel crosses/trait	Parents		F.s		F_{2} s	
	Range	Mean	Range	Mean	Range	Mean
Desi Chickpea (10 x 10 half-diallel)						
Pod borer damage (%)	$6.4 - 12.7$	12.9	$7.1 - 24.0$	12.7	$6.7 - 23.7$	12.3
Grain yield plant ⁻¹ (g)	$7.9 - 13.0$	11.6	11.4-30.2	17.7	11.4-22.3	15.7
Kabuli Chickpea (8 x 8) half-diallel)						
Pod borer damage (%)	$10.1 - 19.0$	14.9	$8.0 - 19.3$	14.2	$6.7 - 24.2$	13.4
Grain yield plant ⁻¹ (g)	$4.2 - 12.7$	10.3	$10.2 - 25.7$	14.3	12.4-31.0	17.0

Table 5. Estimates of general combining ability effects of parents in F_1 and F_2 generations of 10 x 10 half-diallel crosses in desi chickpea

*Significant at P < 0.05; *Significant at P<0.01

selection for grain yield via pod number has been earlier reported by Bisen et al. [12], Salimath and Bahl [13] and Kumar and Bahl [14] in chickpea.

Kabuli chickpea

Variance components: The ANOVA revealed significant variation among parents as well as their F_1 s and F_2 s for grain yield plant⁻¹ (Table 3). The range in grain yield plant $^{-1}$ was comparable in F₁s and F₂s and was much larger than in parents (Table 4). The significance of both $σ²_g$ and $σ²_g$ indicated the importance of both $σ²_A$ than σ^2 _p. However, the higher magnitude of σ^2 _p than σ^2 _A is a

clear evidence for predominance of $\sigma_{_{\rm{D}}}^{\rm{2}}$ in the inheritance of grain yield. These results are in agreement with those reported by Gowda et al. [3].

Combining ability effects

The poor correlation between gca effects of parents and sca effects of crosses estimated based on F_1 and F_2 data could be attributed to predominance of non-fixable genetic variation (dominance) which renders lower prepotency of individuals between $\mathsf{F}_\mathtt{1}$ and $\mathsf{F}_\mathtt{2}'$ s, resulting in differential performance for grain yield. These factors together contribute to poor correspondence between

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Table 6. Estimates of general combining ability effects of parents in F_1 and F_2 generations of 8 x 8 half diallel crosses in kabuli chickpea

*Significant at P < 0.05; **Significant at P< 0.01

 F_1 and F_2 for *gca* and *sca* effects. Nevertheless, parents selected based on gca effects are useful for producing productive crosses and the crosses selected based on sca effects will be useful to select superior recombinant lines in advanced segregating generations. Parents such as ICC 12495 and ICC 12968 and ICC 12492, ICC 12495 and ICC 4962 were found to contribute genes with increasing effects to F_1 and F_2 progenies, respectively as suggested from their significant positive gca effects.

Predominance of dominance gene action (nonfixable genetic variation) retards progress in genetic improvement of grain yield, and selection in early generations would not be effective. The adoption of bulkpedigree selection, wherein segregating populations will be subjected to natural selection up to F_5 followed, by pedigree selection methods would have better prospects to improve grain yield. Such an approach not only helps retain sufficient variability but also allows populations to experience natural selection pressures for stresses prevalent in target locations. Selection for grain yield and other desirable traits from F_5 onwards would be effective for improving productivity. Such a strategy augurs well with that proposed by Toker and Cagirgan [15], who have advocated that the selection for major biotic and abiotic constraints in the target environment prior to selection for grain yield per se would be most effective strategy to enhance and stabilize the

productivity in kabuli chickpea. Several indirect selection criteria have been found be effective in improving grain yield. Biological yield, plant height, and number of branches and pods are proved to be effective indirect selection traits for enhancing yield potential in kabuli chickpea [15-17]. As number of branches and pods are easy to observe in the field level, they can assist in selecting for improved grain yield in kabuli chickpea.

ICC 12475 and ICC 12495 have shown desirable gca effects for both PBD (negative and significant) and grain yield (positive and significant). Hence, it is desirable to use these lines extensively while breeding chickpeas were observed for PBR. The differences between *desi* and kabuli chickpeas for the nature of inheritance of pod borer resistance (PBR). While additive genetic variation is predominant for the inheritance of PBR in *desi* chickpea, both additive and dominance genetic variations are important for PBR in kabuli chickpea. On the other hand, dominance genetic variation was predominant in governing the inheritance of grain yield in both desi and kabuli chickpeas. It is suggested that the use of diverse (for gca effects) parents is necessary for producing productive crosses from which to derive superior breeding lines for enhanced PBR and grain yield. As the parents used in the present investigation constitute a selected set of desi and kabuli chickpea genotypes, the interpretation of the results on the combining ability and genetics of

PBR and grain yield is applicable only to those parents used in the study.

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