

Nature of Gene Action and Maternal Effects for Pod Borer, *Helicoverpa armigera* Resistance and Grain Yield in Chickpea, *Cicer arietinum*

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Received October 12th, 2012; revised November 20th, 2012; accepted December 24th, 2012

ABSTRACT

Information on mechanisms and inheritance of resistance is critical to plan an effective strategy to breed for resistance to insect pests. Therefore, we evaluated a diverse array of chickpea genotypes (eight desi and one kabuli) with varying levels of resistance to the pod borer, *Helicoverpa armigera* to gain an understanding of the nature of gene action and possible maternal effects. The test genotypes were crossed in all possible combinations for a full diallel. The 72 F₁s (36 direct and 36 reciprocal crosses) along with the parents were evaluated for resistance to *H. armigera* under field conditions, and for antibiosis mechanism of resistance (larval survival and larval weight gain) by using detached leaf assay under laboratory conditions, and grain yield under un-protected conditions in the field. Additive gene action governed the inheritance of resistance to *H. armigera*, while non-additive type of gene action was predominant for inheritance of antibiosis component of resistance (larval survival and larval weight) and grain yield. Greater magnitude of $\sigma^2 A$ (17.39 and 1.42) than $\sigma^2 D$ (3.93 and 1.21) indicated the preponderance of $\sigma^2 A$ in inheritance of resistance to pod borer, *H. armigera* under laboratory and field conditions, respectively. There were no maternal effects for inheritance of resistance to pod borer and grain yield. Lines with significant *gca* effects for pod borer damage and grain yield were identified for further use in the resistance breeding program. 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 chickpea.

Keywords: Chickpea; Pod Borer; *Helicoverpa armigera*; Gene Action; Antibiosis; Maternal Effects; Combining Ability; Inheritance of Resistance

1. Introduction

Chickpea [*Cicer arietinum* Linn.], also known as Bengal gram or gram, is the second most important food legume in Asia, North Africa, and Mexico [1,2]. It is grown on 10.96 million ha worldwide with an average production of 8.79 million tons. Its productivity is 790 kg·ha⁻¹ [1-4]. India contributes a large proportion to total world area (62%) and production (75%) [1]. It is a source of high quality protein for people in many developing countries, including India. There are two types of chickpea: *desi* and *kabuli*. *Desi* type chickpeas accounts for 90% of world production, the remainder being *kabuli* type, but the area under *kabuli* chickpea is increasing worldwide [4]. In the recent past, chickpea, especially *kabuli* types, have witnessed export-driven expansion in the non-

traditional areas such as Australia and Canada. In India, both types of chickpeas are grown in diverse agro-ecological niches in the post-rainy season, mainly on residual moisture left over from the monsoon rains between July to October. The current productivity of chickpea in India is nearly 870 kg·ha⁻¹, which is far lower than its potential (up to 4 t/ha) realized in on-farm trials [4]. Over the past 50 years, the productivity of chickpea crop has not witnessed any significant increase as compared to the cereal crops, as biotic and abiotic constraints limit its production on the farmers' fields.

Gram pod borer, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) is the most important biotic constraint, which at times causes 90 to 95% damage [5]. The yield losses due to pod borer in chickpea have been estimated at over US\$328 million in the semi-arid tropics [6], and over \$200 million in India [7]. Intensive use of

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conventional insecticides to control *H. armigera* has led to the development of insecticide resistant populations [8], and the resource-poor farmers in developing countries are unable to use chemical pesticides to manage this pest. Therefore, there is need for development of improved cultivars with resistance to *H. armigera*, which is a cost effective and environmentally benign technology to reduce yield losses due to insect pests, particularly under subsistence farming conditions in the developing countries [9]. For each \$ invested in host plant resistance (HPR), farmers have realized a return of \$300 [10,11]. Several chickpea genotypes have been identified with exploitable levels of resistance to *H. armigera* [12-17]. Identification of sources of resistance and the knowledge of mechanisms and inheritance of resistance is essential for increasing the levels and diversifying the bases of resistance to insects, and to transfer the resistance genes into high-yielding cultivars. Chickpea has abundant genetic variation, in both qualitative and quantitative traits. The extensive variability available in *Cicer* germplasm is important to chickpea improvement.

An understanding of inheritance of resistance is essential for a systematic and efficient approach for genetic enhancement of pod borer resistance in chickpea. Although several studies have been made to estimate combining ability and to unravel the genetics of resistance to *H. armigera* and grain yield in *desi* and *kabuli* chickpeas, the results vary with the genetic material involved and across locations [14,18]. The past studies were largely based on a few F₁ crosses, as obtaining sufficient numbers of F₁ seeds in chickpea is a limiting factor, which might lead to inappropriate estimates of genotypic components of variation. Therefore, comprehensive studies involving a large number of parents with varying levels of pod borer resistance would provide dependable estimates of genetic components of variance. A successful breeding program requires selection of large number of parents with varying levels of resistance to pod borer for hybridization, followed by selection of desirable plants from the segregating generations for developing improved cultivars. This process involves an appropriate mating design [19], and diallel analysis is one of the biometrical techniques to evaluate and characterize genetic variability in a crop species, and for selecting the progenies with greatest promise for success [20].

The objectives of the present study therefore were to understand the nature of gene action, combining ability effects of the parents and their variances to understand the genetics of resistance to *H. armigera* in terms of pod borer damage under field conditions, antibiosis component of resistance (larval survival and larval weight) by using detached leaf assay under laboratory conditions, and grain yield under un-protected conditions using diallel analysis [21]. Efforts were also made to study the cy-

toplasmic effects (maternal effects) for resistance to *H. armigera* and the grain yield.

2. Materials and Methods

Nine diverse chickpea genotypes (involving eight *desi* and one *kabuli* genotypes, which included six pod borer-resistant and three -susceptible genotypes) were selected for the studies on nature of gene action for resistance to *H. armigera* (Table 1). These pod borer resistant and susceptible lines were identified based on the screening of over 14,800 germplasm accessions in the field under un-protected conditions at ICRISAT, Patancheru, India [13,22]. Full-diallel crosses (including reciprocals) were made during the 2003-04 post-rainy season. The F₁s along with their parents (81 entries) were evaluated during the following year, i.e. 2004-05 post-rainy season using a randomized complete block design (RCBD) with 3 replications at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India. Each entry was raised in a two rows, 2 m long with a spacing of 60 cm between the rows and 10 cm between the plants within a row. All the recommended agronomic practices were followed for raising the crop, except crop protection measures against *H. armigera*. Agronomic characteristics of the chickpea genotypes used for studying the nature of gene action are presented in Table 1. Observations were recorded on five randomly tagged plants in each plot for *H. armigera* damage and grain yield (g plant⁻¹). Pod borer damage was estimated as percentage of total number of pods under natural infestation. The F₁s and their parents were also evaluated by using detached leaf assay under laboratory conditions. Observations were recorded on leaf damage, larval survival and larval weights (Table 2) [23].

Biometric and Genetic Analyses

The mean values of the data recorded on sampled plants for *H. armigera* damage and grain yield were used for statistical analysis using GENSTAT 6.0. The data on diallel crosses were analyzed following analysis of variance (ANOVA) to test the significance of differences among the parents and their F₁s for pod borer damage and grain yield. Griffing [21] Method 1, model 1 was used to estimate the genetic potential of the chickpea genotypes and the genetic architecture of pod borer resistance and grain yield, as the model is based on combining ability analysis. It provided empirical summary of complex observations and a reasonable basis for assessing the breeding value of the parental lines, and predicting the performance of crosses. Being based on first degree statistics, the combining ability effects are statistically robust, but genetically neutral, as these are equally

Table 1. Characteristics of the chickpea genotypes evaluated for tolerance to pod borer, *Helicoverpa armigera* under natural infestation.

Genotype	Pedigree	Days to flowering	Days to maturity	Seeds pod ⁻¹	100 seed wt. (g)	Yield (kg ha ⁻¹)
DESI						
ICC 3137	P-3659-2	64.3	119.2	1.10	25.25	4196
ICC 4918	ICC 4918	50.9	107.0	1.19	19.93	3705
ICC 12426	ICCC 37	54.6	102.0	1.36	19.23	5552
ICC 506EB	BEG 78	55.4	104.4	1.21	16.07	2822
ICC 12476	ICC 6663 HR (NEC-764)	67.1	114.7	1.19	15.77	4486
ICC 12477	ICC 10460 HR (RPSP-194)	54.2	110.4	1.17	12.87	2370
ICC 12478	ICC 10667 HR (62-10-3)	58.1	114.9	1.09	15.04	3492
ICC 12479	ICC 10619 HR (G 130)	59.5	109.4	1.11	14.79	4674
KABULI						
ICC 12968	ICCL 82001	34.1	94.0	1.10	23.95	2965
LSD (P 0.05)		4.78	3.35	0.115	2.052	1287.5

Table 2. Reaction of nine chickpea genotypes to neonate larvae of *Helicoverpa armigera* in detached leaf assay during the flowering stage.

Parents	Damage rating*	Larval survival (%)	Larval weight (mg)
ICC 12476	5.8 ^{bc}	56.0 ^a	6.88 ^{abc}
ICC 12477	5.8 ^{bc}	56.0 ^a	6.48 ^{abc}
ICC 12478	5.2 ^b	76.0 ^c	5.84 ^{ab}
ICC 12479	6.2 ^b	58.0 ^{ab}	5.94 ^{ab}
ICCV 2	6.6 ^{cd}	56.0 ^a	5.06 ^a
ICC 4918	7.5 ^d	62.0 ^{abc}	9.88 ^c
ICC 3137	7.2 ^{cd}	72.0 ^b	7.08 ^{abc}
ICC 506 EB (R)	3.6 ^a	54.0 ^a	5.36 ^a
ICCC 37 (S)	7.8 ^d	72.0 ^{bc}	11.36 ^d
LSD (P 0.05)	1.35	14.56	3.39

*Damage rating (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged); R = Resistant check, and S = Susceptible check; The figures followed by the same letter within a column are not significantly different at $P \leq 0.05$.

applicable to in-breeders and out-breeders [24]. It requires no assumptions beyond those necessary for an ANOVA [20]. Besides providing the estimates of general combining ability (*gca*) effects of the parents and specific combining ability (*sca*) effects of the crosses, the analysis provided a method for diagnosis and estimation

of $\sigma^2 A$ (additive) and $\sigma^2 D$ (dominance) genetic components of the variance [25]. After confirming the significance of *gca* and *sca* effects and their variances, the additive and non-additive effects for pod borer damage and grain yield were estimated. The estimates of variances due to *gca* ($\sigma^2 g$) and *sca* ($\sigma^2 s$) effects provided the basis

for apt diagnosis and estimates of $\sigma^2 A$ and $\sigma^2 D$ genetic components of the variance.

3. Results and Discussion

3.1. Pod Borer Resistance

There were significant differences among the parents as well as their F_1 s for resistance to pod borer, *H. armigera*, both under field and laboratory conditions (Tables 3 and 4), justifying the selection of parents for this study. In general, the mean pod borer damage was lower in F_1 s than the parents, but the variability in pod borer damage between the F_1 s was greater than the parents. There were substantial differences in *gca* effects of the parents (as indicated by $\sigma^2 g$) for pod borer damage, which resulted in progenies (F_1 s) with differential abilities to resist pod borer damage (Tables 3 and 4). Both $\sigma^2 g$ and $\sigma^2 s$ were significant for pod borer damage in straight crosses. Only $\sigma^2 g$ was significant in reciprocal crosses, suggesting the importance of both additive and non-additive type of gene action. However, greater magnitude of $\sigma^2 A$ (17.39 and 1.42) than $\sigma^2 D$ (3.93 and 1.21) clearly indicated the preponderance of $\sigma^2 A$ in the inheritance of resistance to *H. armigera* (Tables 5 and 6). Gowda *et al.* [14,26] and Singh *et al.* [27] reported that additive and dominance genetic variances, respectively, were predominant for pod borer resistance in early- and medium-maturity genotypes. However, additive as well as dominance components of genetic variances were equally important

in the inheritance of pod borer resistance in the late-maturity genotypes. Salimath *et al.* [28] reported the involvement of both additive and non-additive type of gene action in the inheritance of pod borer resistance. The parental lines used in the current study mostly belonged to early- and medium-maturity groups, and the results suggested the predominance of additive type of gene action.

In the straight crosses, ICC 506EB, ICC 12477, ICC 12478, ICC 12479 and ICCV 2 were the best general combiners with significant negative *gca* effects and low pod borer damage (Table 7). Under laboratory conditions, ICC 506EB and ICC 12477 suffered low leaf damage rating with significant and negative *gca* in detached leaf assay (Table 8). Earlier studies have shown that ICC 12478, ICC 12479, ICC 14876, ICC 506EB and ICC 12477 have negative *gca* effects, and have a good ability to transmit additive genes to decrease pod borer damage [14,18]. These parents can be involved to generate useful variability for selecting lines with resistance to *H. armigera*. The hybrids ICC 506EB \times ICC 3137, ICC 12476 \times ICC 3137, ICC 12477 \times ICC 4918, ICC 12479 \times ICC 3137 and ICC 3137 \times ICCV 2 showed significant and negative *sca* effects, and were good specific combiners for resistance to pod damage by *H. armigera*. In detached leaf assay, the hybrids ICC 12477 \times ICC 37, ICC 3137 \times ICCV 2 and ICC 4918 \times ICCV 2 showed significant and negative *sca* effects for antibiosis resistance to *H. armigera* (Table 9). It is interesting to note that these crosses involve one parent with excess of

Table 3. Estimates of mean squares and variances due to general combining ability (GCA) and specific combining ability (SCA) effects for F_1 chickpea hybrids under natural conditions in the field (9×9 full diallel, Griffing 1956).

Trait	d.f	Pod borer damage (%)	Yield plant ⁻¹ (g)	Yield (kg ha ⁻¹)
Mean squares				
GCA	8	167.7**	26.97**	1969692.8**
SCA	36	11.25**	12.6**	585194.5**
Reciprocal effects	36	5.58	13.06**	247340.4
Error	160	4.16	6.38	212511.9
Variances				
$\sigma^2 g$		14.91**	2.14**	3.36**
$\sigma^2 s$		2.7**	1.98**	2.75**
$\sigma^2 r$		1.34	2.05**	1.16
$\sigma^2 A$		17.39	1.61	154400.4
$\sigma^2 D$		3.93	3.45	206762.3
A:D		2.21	0.23	0.37
PR		0.92	0.68	0.71

d.f. = Degrees of freedom; ** = Significant at P = 0.05 and 0.01 respectively; $\sigma^2 g$: Variance due to *gca*, $\sigma^2 s$: Variance due to *sca*, and $\sigma^2 r$: Variance due to reciprocal effects. $\sigma^2 A$: Additive variance, $\sigma^2 D$: Dominance variance, and PR: Predictability ratio.

Table 4. Estimates of mean squares and variances due to GCA and SCA for resistance to *Helicoverpa armigera* in chickpea (9 × 9 full diallel, Griffing 1956) (based on detached leaf assay).

Trait	d.f.	Damage rating ¹	Larval survival (%)	Larval weight (mg)
Mean squares				
GCA	8	8.48***	359.26**	22.77***
SCA	35	5.07***	297.25***	17.01
Reciprocal effects	35	5.58***	326.69***	21.43
Error	320	1.34	113.25	2.79
Variances				
σ^2_g		5.18	113.25	17.32
σ^2_s		0.81	44.23	2.38
σ^2_r		0.64	78.88	2.43
σ^2_e		0.27	22.65	0.56
σ^2_A		1.42	0.23	38.27
σ^2_D		1.21	0.50	50.21
PR		0.93	0.84	0.94

d.f. = Degrees of freedom; ¹Damage rating (1 = <10%, and 9 = >80% leaf/pod damage); **,*** = Significant at P = 0.01 and 0.001, respectively; σ^2_g : Variance due to gca, σ^2_s : Variance due to sca, σ^2_r : Variance due to reciprocal effects, and σ^2_e : Error variance; σ^2_A : Additive variance, σ^2_D : Dominance variance, and PR: Predictability ratio.

Table 5. Nature of gene action for pod damage by *Helicoverpa armigera* and grain yield in chickpea.

Trait	Genotypic variance		Nature of gene action	A:D	
	σ^2_A	σ^2_D			
Pod borer damage (%)	17.39	3.93	Additive	2.21	Over dominance
No. of pods plant ⁻¹	207.13	59.21	Additive	1.75	Over dominance
No. of seeds pod ⁻¹	0.005	0.001	Additive	1.63	Over dominance
Yield plant ⁻¹ (g)	1.61	3.45	Dominant	0.23	Partial dominance
Total plot yield (g)	2223.4	2977.4	Dominant	0.37	Partial dominance
Yield (kg ha ⁻¹)	154400.4	206762.3	Dominant	0.37	Partial dominance

Table 6. Nature of gene action for antibiosis component of resistance to *Helicoverpa armigera* (based on detached leaf assay).

Trait	Damage rating [*]	Larval survival (%)	Larval weight (mg)
Additive effect	1.42	0.23	38.37
Dominance effect	1.21	0.50	50.21
Heritability	1.13	0.29	56.26
Va—Additive gene effects	0.54	0.44	8.89
Vd—Dominance deviations	0.27	0.11	5.38
h ² /H ² (no. of gene groups)	1.06	-	2.62
h ² (heritability in narrow sense)	0.54	0.74	0.24

*Damage rating (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged).

Table 7. Estimates of general combining ability (GCA) effects of nine chickpea genotypes for pod damage by *Helicoverpa armigera* and grain yield under natural conditions.

Parents	Pod damage (%)	Yield plant ⁻¹ (kg)	Grain yield (kg ha ⁻¹)
ICC 506EB (R)	-3.02**	0.001	164.49
ICC 12476	0.36	-0.684	-261.138*
ICC 12477	-0.99*	-0.054	-389.303**
ICC 12478	-1.66**	-0.60	184.033
ICC 12479	-2.53**	-2.236**	92.137
Annigeri	1.11*	2.196**	512.479**
ICC 3137	7.02**	-0.227	-516.221**
ICCV 2	-1.68**	0.816	-24.272
ICCC 37(S)	1.39**	0.788	237.794*
S.E g (l)	0.454	0.561	102.44

Table 8. Estimates of general combining ability (GCA) effects of nine chickpea parents for resistance to *Helicoverpa armigera* (based on detached leaf assay).

Parents	Damage rating*	Larval survival (%)	Larval weight (mg)
ICC 506EB (R)	-0.81***	1.81	-1.59***
ICC 12476	-0.11	-2.82**	-0.69***
ICC 12477	-0.57***	-2.98**	-0.49**
ICC 12478	-0.22	-0.98	-0.36*
ICC 12479	-0.21	0.46	-0.03
Annigeri	0.90***	0.51	0.97***
ICC 3137	0.43***	2.90**	0.49**
ICCV 2	0.14	-2.61*	-0.06
ICCC 37 (S)	0.45***	3.70***	1.77***
S.E g(l)	0.27	5.05	0.93
GCA/SCA	0.50	0.23	0.51
PR	0.50	0.32	0.51

*Damage rating (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged). *, **, *** = Significant at P 0.05, 0.01 and 0.001, respectively. PR: Predictability ratio.

recessive genes, and the other with equal frequency of dominant and recessive genes [14], indicating that the parents involved in the crosses are diverse for nature of genes for pod borer resistance. It is desirable to exploit the crosses with significant *sca* effects, involving parents contrasting for *gca* effects, and for reaction to pod borer damage (resistant and susceptible). Recurrent selection in the population developed by random mating of the pod borer resistant parents in high-yielding background used

in a diallel would facilitate accumulation of favorable gene combinations in the homozygous and heterozygous state [14].

The *sca* effects for the reciprocal crosses were non-significant, indicating the importance of both additive and non-additive gene effects for pod borer resistance. The cross ICCV 2 × ICC 3137 showing significant and negative *sca* effects was good specific combiner for resistance to pod borer damage. Similar results have been

Table 9. Estimates of specific combining ability (SCA) effects of F₁s for antibiosis component of resistance to *Helicoverpa armigera* (based on detached leaf assay).

Cross	Damage rating ¹	Larval survival (%)	Larval weight (mg)
ICC 12476 × ICC 12477	0.26	-2.52	0.83
ICC 12476 × ICC 12478	-0.72	-9.52**	-0.32
ICC 12476 × ICC 12479	0.01	5.04	0.36
ICC 12476 × ICC 3137	0.31	-0.30	-1.29**
ICC 12476 × ICC 4918	-0.59	0.19	0.64
ICC 12476 × ICC 506EB	-0.04	4.69	-0.98*
ICC 12476 × ICC 37	-0.20	2.70	0.58
ICC 12476 × ICCV 2	0.61	-3.79	-0.42
ICC 12477 × ICC 12478	-0.26	-8.37**	-0.48
ICC 12477 × ICC 12479	-0.39	6.20*	-0.64
ICC 12477 × ICC 3137	-0.63	-4.25	-0.09
ICC 12477 × ICC 4918	1.24***	4.04	-0.53
ICC 12477 × ICC 506EB	0.20	-0.16	1.19*
ICC 12477 × ICC 37	-1.35***	2.95	-0.85
ICC 12477 × ICCV 2	-0.39	-1.73	0.77
ICC 12478 × ICC 12479	-0.29	-3.70	-0.29
ICC 12478 × ICC 3137	0.21	-2.15	0.35
ICC 12478 × ICC 4918	0.60	3.04	-0.18
ICC 12478 × ICC 506EB	-0.09	0.84	2.14***
ICC 12478 × ICC 37	-0.12	1.95	-1.38**
ICC 12478 × ICCV 2	0.65	-1.73	1.27*
ICC 12479 × ICC 3137	0.35	-1.68	2.41***
ICC 12479 × ICC 4918	-0.68	-0.39	0.54
ICC 12479 × ICC 506EB	-0.32	-1.69	-1.24*
ICC 12479 × ICC 37	-0.36	-3.48	-0.63
ICC 12479 × ICCV 2	0.69*	0.93	1.14*
ICC 3137 × ICC 4918	0.44	-4.83	-0.53
ICC 3137 × ICC 506EB	0.01	5.47	-1.28*
ICC 3137 × ICC 37	0.14	-1.52	0.80
ICC 3137 × ICCV 2	-1.56***	1.39	1.20*
ICC 4918 × ICC 506EB	-0.32	-3.75	-0.85
ICC 4918 × ICC 37	0.03	-2.53	1.90***
ICC 4918 × ICCV 2	-0.79*	1.78	-1.26*
ICC 506EB × ICC 37	0.73*	-1.93	-0.11
ICC 506EB × ICCV 2	0.25	4.48	0.24
ICC 37 × ICCV 2	-0.15	-4.41	-0.47
Sij (P = 0.05)	0.67	6.12	0.96

¹Damage rating (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged). *, **, *** = Significant at P 0.05, 0.01 and 0.001, respectively.

reported by Singh and Paroda [29]. Better progenies have been obtained from the crosses involving diverse parents for *gca* effects in groundnut [30]. Langham [31] has provided the evidence for the usefulness of divergent parents for maximizing potential transgressive lines in cross derivatives in rice. Effectiveness of pedigree selection for pod borer resistance in chickpea has also been reported by Sharma *et al.* [32] and Dua *et al.* [22]. Singh *et al.* [33] developed pod borer resistant chickpea line, ICCV 7 using pedigree selection of the lines derived from a cross between H 208 and BEG 482. However, caution is necessary while using pedigree selection for pod borer resistance, considering the existence of tight linkage between susceptibility to fusarium wilt (*Fusarium oxysporum* f. sp. *ciceri*) and resistance to pod borer in chickpea. Biparental matings in early segregating generations of a multiple cross involving a few pod borer and fusarium wilt resistant genotypes in high yielding background would provide increased opportunity for recombination, which will facilitate disruption of tight linkage between the genes for these traits [34,35]. Germplasm lines (ICC 12478, ICC 12479 and ICC 14876) having stable resistance to *H. armigera* and moderate yield potential [36] could be used in enhancement of pod borer resistance in elite agronomic background.

3.2. Larval Survival

There were significant differences among the parents as well as their F₁s for survival of *H. armigera* larvae (**Table 4**). In general, the mean larval survival was lower in F₁s than in parents. Greater magnitude of σ^2D (0.50) than σ^2A (0.23) clearly indicated the preponderance of σ^2D in the inheritance of antibiosis component of resistance (% larval survival) to *H. armigera* larvae (**Table 4**). In the straight crosses, ICC 12476, ICC 12477 and ICCV 2 were the best general combiners with significant negative *gca* effects for larval survival (**Table 8**). The hybrids ICC 12476 × ICC 12478 and ICC 12477 × ICC 12478 showed significant and negative *sca* effects and were good specific combiners for resistance to survival of *H. armigera* larvae (**Table 9**).

3.3. Larval Weight Gain

There were significant differences among the parents as well as their F₁s for weight of the *H. armigera* larvae. In general, the mean larval weights were lower in F₁s than in the parents. Greater the magnitude of σ^2D (50.21) than σ^2A (38.37) clearly indicated the preponderance of σ^2D in the inheritance of antibiosis to *H. armigera* in terms of weight gain by the *H. armigera* larvae in detached leaf assay (**Table 4**). In the straight crosses, ICC 506EB, ICC 12476, ICC 12477 and ICC 12478 were the best gen-

eral combiners with significant negative *gca* effects and low larval weights (**Table 8**). The hybrids ICC 12476 × ICC 3137, ICC 12476 × ICC 506EB, ICC 12478 × ICC 37, ICC 12479 × ICC 506EB, ICC 3137 × ICC 506EB and ICC 4918 × ICCV 2 showed significant and negative *sca* effects, and were good specific combiners for antibiosis resistance (weight gain) to *H. armigera* (**Table 9**).

In detached leaf assay, resistance to leaf feeding was governed by additive gene action. These results are in accordance with field observations by Gowda *et al.* [14,26] and Singh *et al.* [27]. Antibiosis component of resistance (based on larval survival and larval weight) was governed by non-additive type of gene action (**Table 6**).

3.4. Grain Yield

There were significant differences among the parents and the F₁ crosses (straight and reciprocal crosses) for grain yield (**Table 3**). The importance of both σ^2g and σ^2s was evident with predominance of the latter, which is amply reflected from a much higher magnitudes of σ^2D than σ^2A . Similar results have been reported by Deshmukh and Patil [37] and Gowda *et al.* [14]. The predominance of σ^2D indicated the importance of non-additive gene action. Since *gca* effects are the manifestation of additive properties of genes, parents selected based on *gca* effects will be useful for developing breeding lines with high grain yield. Parents with good general combining ability such as ICC 4918 could be used in breeding programs. Gowda *et al.* [14] reported that ICC 12476 possessed an excess of dominant genes, ICC 12426, ICC 12478 and ICC 4918 possessed an excess of recessive genes, while ICC 506EB possessed equal frequency of dominant and recessive genes for grain yield under un-protected conditions. Parents with significant and positive *gca* effects are diverse for the nature of gene action for grain yield. The combining ability variances were significant for both *gca* and *sca*. The predictability ratio of 0.23 showed that *gca* alone was not sufficient for predicting the performance of single cross progenies. Of the two genetic parameters, the magnitude of σ^2D was more than σ^2A , which emphasized that non-additive gene action, was involved in inheritance and expression of grain yield per plant (**Table 5**). These findings are in conformity with earlier reports [33-44]. However, the reports of Gowda [45], Asawa and Tewari [46], Sandhu *et al.* [47], and Gowda and Bahl [48] are contradictory to the present findings, which indicated the involvement of additive genetic variance. Singh *et al.* [49], Singh and Ocampo [50], Annigeri *et al.* [51], Sarode [52] and Girase [53] reported the importance of additive as well as non-additive genetic variances. The crosses ICC 12476 × ICC 37, ICC 12477 ×

Table 10. Maternal effects for seeds per pod in chickpea.

Pedigree	Seeds per pod	
	Straight crosses	Reciprocal crosses
ICC 506EB × ICC 12477	0.006	0.005
ICC 506EB × ICC 12478	-0.011	0.012
ICC 506EB × ICC 12479	-0.015	-0.015
ICC 506EB × ICC 4918	0.031	-0.003
ICC 506EB × ICC 3137	0.039	0.019
ICC 506EB × ICCV 2	0.057*	-0.043
ICC 506EB × ICC 37	-0.028	0.005
ICC 12476 × ICC 12477	-0.033	0.002
ICC 12476 × ICC 12478	0.057*	0.129
ICC 12476 × ICC 12479	-0.037	-0.006
ICC 12476 × ICC 4918	0.055*	0.004
ICC 12476 × ICC 3137	0.048	-0.037
ICC 12476 × ICCV 2	-0.01	-0.032
ICC 12476 × ICC 37	0.117**	-0.059*
ICC 12477 × ICC 12478	-0.01	0.024
ICC 12477 × ICC 12479	0.013	-0.03
ICC 12477 × ICC 4918	0.047	0.012
ICC 12477 × ICC 3137	-0.017	0.018
ICC 12477 × ICCV 2	0.008	0.04
ICC 12477 × ICC 37	-0.009	-0.01
ICC 12478 × ICC 12479	-0.023	-0.005
ICC 12478 × ICC 4918	-0.003	-0.033
ICC 12478 × ICC 3137	-0.003	-0.027
ICC 12478 × ICCV 2	-0.015	0.008
ICC 12478 × ICC 37	-0.006	-0.002
ICC 12479 × ICC 4918	-0.001	-0.041
ICC 12479 × ICC 3137	0.02	0.006
ICC 12479 × ICCV 2	-0.016	-0.001
ICC 12479 × ICC 37	0.083**	-0.002
ICC 4918 × ICC 3137	-0.03	-0.067*
ICC 4918 × ICCV 2	-0.042	-0.057
ICC 4918 × ICC 37	-0.044	0.042
ICC 3137 × ICCV 2	0.078**	0.026
ICC 3137 × ICC 37	-0.06*	0.056
ICCV 2 × ICC 37	-0.029	0.023

*,** = Maternal effects significant at P 0.05 and 0.01, respectively.

ICC 4918 and ICC 12478 × ICC 12479 with highly significant and positive *sca* effects were good specific combiners for grain yield. Interestingly, one of the parents of these crosses possessed an excess of dominant genes, while the other parent possessed an excess of recessive genes [14], suggesting the need to have genetic diversity for increased heterosis for grain yield. Theoretical investigations substantiating the necessity of parental diversity for better performance of crosses [54,55] lend adequate support to these practical considerations. Although there was a good correspondence between pod borer damage of crosses and their *sca* effects, the crosses (involving parents with contrasting *gca* effects) with significant *sca* effects need to be exploited for deriving superior lines for grain yield.

The significance of both $\sigma^2 g$ and $\sigma^2 s$ indicated the importance of both $\sigma^2 A$ and $\sigma^2 D$ in the reciprocal crosses. However, the higher magnitude of $\sigma^2 D$ than $\sigma^2 A$ is a clear evidence for predominance of $\sigma^2 D$ in the inheritance of grain yield. Crosses ICC 12477 × ICC 506EB, ICC 3137 × ICC 506EB, ICC 37 × ICC 506EB, ICCV 2 × ICC 12476 and ICC 37 × ICC 3137 with highly significant and positive *sca* effects were good specific combiners for increased grain yield. The grain yield is predominantly under the control of non-additive gene action, irrespective of the maturity groups in *desi* type chickpea. Due to predominance of non-fixable genetic variation coupled with low heritability, it has not been possible to achieve breakthrough in increasing the chickpea productivity. Lack of sufficient variability (due to its strictly inbreeding behavior) is one of the reasons for limited progress in increasing chickpea productivity to a desired level [36]. 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 [56]. Breeders need to exploit both additive and non-additive gene effects, besides disrupting undesirable associations and uncovering concealed variability. Biparental mating of segregants in a multiple crossing scheme might be useful in disrupting the undesirable linkages [34,35,57].

3.5. Maternal Effects

There was no maternal inheritance for pod borer damage and grain yield. The cross, ICC 12476 × ICC 37 showed positive and significant *sca* effects for seeds per pod, but ICC 37 × ICC 12476 showed negative and significant *sca* effects for number of seeds pod⁻¹, suggestive cytoplasmic inheritance for the number of seeds per pod (Table 10).

4. Conclusion

The present studies suggested that additive genetic variation was predominant for the inheritance of resistance to *H. armigera*, while dominance genetic variation was predominant in governing the inheritance of antibiosis component of resistance (larval survival and larval weight) and grain yield under un-protected conditions. The studies indicated the necessity of using diverse (for *gca* effects) parents for producing productive crosses, from which superior breeding lines could be derived for increasing the levels of resistance to pod borer, and for increasing the grain yield potential. There was no cytoplasmic inheritance for pod borer damage and grain yield, but the hybrid, ICC 37 × ICC 12476 showed cytoplasmic inheritance for number of seeds per pod. Studies on nature of gene action are useful in eliminating less productive crosses in F₁, and to concentrate on a few, but possibly more productive crosses [58]. Further studies on mechanisms and inheritance of resistance, and use of morphological, biochemical, and molecular markers will be useful for increasing the levels and diversifying the basis of resistance to *H. armigera* in chickpea [59,60].

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