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ORIGINAL PAPER

Mechanisms of resistance to *Helicoverpa armigera* and introgression of resistance genes into F_1 hybrids in chickpea

V. Lakshmi Narayanamma · H. C. Sharma · C. L. L. Gowda · M. Sriramulu

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Abstract The noctuid pod borer, *Helicoverpa armigera* is a major pest of chickpea, and host plant resistance is an important component for managing this pest. We evaluated a set of diverse chickpea genotypes with different levels of resistance to *H. armigera*, and their F_1 hybrids for oviposition non-preference, antibiosis, and tolerance components of resistance under uniform insect infestation under greenhouse/laboratory conditions. The genotypes ICC 12476, ICC 12477, ICC 12478, ICC 12479, and ICC 506EB were non-preferred for oviposition under no-choice, dual-choice, and multi-choice conditions, and also suffered lower leaf damage in no-choice tests as compared to the susceptible check, ICCC 37. Antibiosis expressed in terms of low larval weights was observed in insects reared on ICC 12476, ICC 12478, and ICC 506EB. Weight gain by the third-instars was also low on ICC 12476, ICC 12477, ICC 12478, ICC 12479, and ICC 506EB at the podding stage. Non-preference for oviposition and antibiosis (poor larval growth) were also expressed in hybrids based on ICC 12477, ICC 12476, ICC 12478, ICC 12479, and ICC 506EB as compared to the hybrids based on the susceptible check, ICCC 37, indicating that oviposition non-preference and antibiosis in the F_1 hybrids is influenced by the parent genotype. Loss in grain yield was lower in ICC 12477, ICC 12478, ICC 12479, and ICC 506EB compared to that on ICCC 37. The genotypes ICC 12477, ICC 12478, ICC 12479, and ICC 506EB showing antixenosis, antibiosis, and tolerance mechanism of resistance to *H. armigera* can be used for developing chickpea cultivars for resistance to this pest.

Keywords *Helicoverpa armigera* · Chickpea · Host plant resistance · Oviposition non-preference · Antibiosis · Tolerance

Introduction

Chickpea, *Cicer arietinum* (L.) is the third most important grain legume in the world, after dry beans and peas. It is cultivated in over 42 countries in South Asia, East Africa, North and Central America, Mediterranean Europe, and Australia. Globally, chickpea is grown in 10.2 million ha with an average production of 7.9 million tons, and an average productivity of 770 kg ha^{-1} (FAO 2005). Chickpea yields have remained almost static over the past two decades largely because of heavy losses due to insect pests and diseases, of which the noctuid pod borer, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) is the most important pest worldwide. It causes yield loss of over US $2 billion in the semi-arid tropics, despite application of insecticides costing >$500 million annually (sharma 2005). It has also developed high levels of resistance to several insecticides. In addition to the huge direct economic losses, there are serious deleterious effects of pesticides on the environment. It is in this context that host plant resistance assumes a central role for minimizing the losses due to *H. armigera*.

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V. L. Narayanamma · H. C. Sharma (✉) · C. L. L. Gowda
International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Hyderabad, Andhra Pradesh 502 324, India
e-mail: h.sharma@cgiar.org

V. L. Narayanamma · M. Sriramulu
Acharya NG Ranga Agricultural University (ANGRAU), Rajendranagar, Hyderabad 500 030, India

Resistance to *H. armigera* in chickpea is expressed in terms of oviposition non-preference, antibiosis, and tolerance or recovery resistance (Lateef 1985; Cowgill and Lateef 1996; Sharma et al. 2005a). Because of staggered flowering of chickpea genotypes and variation in *H. armigera* populations over space and time, it has not been possible to obtain a precise estimate of the contribution of different components of resistance under field conditions. Therefore, we evaluated a set of diverse chickpea genotypes and their F_1 hybrids under uniform infestation using cage techniques under greenhouse conditions, and detached leaf assay under laboratory conditions to quantify the contribution of oviposition non-preference, antibiosis, and tolerance components of resistance to *H. armigera* in chickpea. We also studied the introgression of resistance genes into the F_1 hybrids to devise appropriate strategies for developing chickpea cultivars with resistance to this pest.

Materials and methods

Plants

The plants were grown under greenhouse and field conditions at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India, during the 2003–2005 post-rainy seasons (October–March). Nine chickpea genotypes (eight *Desi* and one *Kabuli* type) were selected for these studies based on earlier reaction of these genotypes under field conditions (Lateef 1985; Sharma et al. 2005a). The test material included ICC 506EB—resistant; ICC 12476, ICC 12477, ICC 12478, and ICC 12479—moderately resistant; and ICCC 37 (ICC 12426), ICC 3137, ICCV 2 (ICC 12968), and ICC 4918—susceptible. These lines were mated in all possible combinations. Each of the nine genotypes was used as a female parent, and pollen from the remaining eight lines was used to produce F_1 hybrids on different plants of the same genotype. To achieve this objective, the anthers were removed before pollen production. The stigmas were dusted with pollen from the male parents after 3 days. The F_1 hybrids and their parents were tested for oviposition non-preference and antibiosis components of resistance to *H. armigera* at the flowering stage using cage technique and detached leaf bioassay.

The test genotypes were raised on a sterilized mixture of black soil (Vertisols), sand, and farmyard manure (2:1:1). The soil was filled into medium sized pots (30 cm in diameter and 30 cm in depth). The seeds were sown 5 cm below the soil surface and watered as and when required. Ten seeds were sown in each pot, and five plants with uniform growth were retained in each pot at 10 days after seedling emergence (DAE). The plants were fertilized with 20 g di-ammonium phosphate per pot at 15 DAE. There were five pots for each genotype. The plants were raised in the greenhouse, which was cooled by desert coolers (27 ± 5°C and 65–90% RH). The parents and their F_1 hybrids were also grown under field conditions on four row plots of 2 m length (4×2 m), at a plant–plant spacing of 60 cm $\times$ 10 cm during the post-rainy season (Oct–March). Terminal branches (20 cm long) from the plants at the flowering stage (45–50 DAE) were used for studies on oviposition non-preference under laboratory conditions. The plants raised under greenhouse conditions were tested using the no-choice cage technique, and detached leaf assay under laboratory conditions at 30 and 45 days after seedling emergence.

Insects

Field-collected larvae of *H. armigera* were reared in the laboratory on the natural host for one generation before being mixed with the laboratory culture to avoid contamination with the nuclear polyhedrosis virus, bacteria, or fungi. The *H. armigera* culture was maintained on chickpea flour based artificial diet (Armes et al. 1992). The neonates were reared in groups of 200–250 in 200 ml plastic cups having a 2–3 mm layer of artificial diet on the bottom and sides of the cup for 5 days. After 5 days, the larvae were transferred individually to six-cell well plates (each cell well 3.5 cm in diameter, 2.0 cm in depth) to avoid cannibalism. Adults were released inside a cage (30 cm $\times$ 30 cm $\times$ 30 cm) for oviposition. The eggs were removed daily and sterilized in 2% sodium hypochlorite solution. Neonates or third-instar larvae were used for infesting the test plants under greenhouse and laboratory conditions as described below.

Oviposition by the *Helicoverpa armigera* females on different chickpea genotypes under no-choice, dual-choice, and multi-choice conditions

Oviposition by the females on different genotypes was studied under no-choice, dual-choice, and multi-choice conditions for the nine parent genotypes, while only dual-choice test was used to study oviposition non-preference on F_1 hybrids. Fresh flowering branches (20 cm long) brought from the field, were placed in a conical flask (150 ml) with 100 ml water, and plugged with cotton wool. Three branches of each genotype were kept in a conical flask and exposed to *H. armigera* females for oviposition inside the cage (30 cm $\times$ 30 cm $\times$ 30 cm). For no-choice tests, chickpea branches from a single genotype were placed in

the center of the cage. For dual-choice tests, branches from the test genotype and the susceptible check, ICCC 37 were placed at the opposite corners of the wooden cage. A cotton swab soaked with 10% sucrose solution was placed in the center of each cage in a Petri dish as food for adults. The chickpea branches offered as oviposition substrate were replaced on alternate days, while the sucrose solution was changed every day. Three pairs of moths were released inside each cage for no-choice and dual-choice tests. There were five replications in no-choice tests, 10 replications for dual-choice tests. The eggs laid on chickpea branches were counted daily, removed with the help of camel hairbrush, placed in a Petri dish. The oviposition studies were continued till the females survived and laid eggs.

Non-preference for oviposition under multi-choice conditions was studied by keeping all the nine test genotypes (ICC 506EB, ICC 12476, ICC 12477, ICC 12478, ICC 12479, ICC 4918, ICCC 37, ICC 3137, and ICCV 2) inside a large wooden cage (80 cm × 70 cm × 60 cm). Conical flasks containing chickpea branches were placed inside the wooden cage equidistant from each other inside the cage. Ten pairs of adult moths were released inside the cage and provided with sucrose solution in a cotton swab. To avoid predation by the ants, Tanglefoot® glue was applied to all the four legs of the wooden cage. The experiment was repeated three times.

Detached leaf assay to assess antibiosis to *Helicoverpa armigera*

Plastic cups of 250 ml capacity (4.5 cm × 11.5 cm) were used for detached leaf assay (Sharma et al. 2005b). Solidified agar-agar (3.5%) was used as a substratum for holding chickpea terminal branches (with 3–4 fully expanded leaves) in a slanting manner inside the cup. Ten neonate *H. armigera* larvae were released on the chickpea leaves with a camel hair brush. The material was tested for resistance to *H. armigera* at the vegetative (30 DAE), flowering (45–50 DAE), and podding stages of the crop. At the podding stage, plastic containers of 9 cm × 6.5 cm were used to evaluate the test material for resistance to pod damage. Chickpea branches with 8–10 pods were collected from the field and immediately placed into agar–agar substratum as described before. A single third-instar pre-weighed larva was released in each plastic container and then covered with a lid. The experiments were terminated when >80% of leaf area and/or pods were damaged in the susceptible control, or when there were maximum differences between the resistant and susceptible checks, which normally occurs at 4–5 days after releasing the larvae on the leaves/pods. Data were recorded on leaf and/or pod damage (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged), larval survival, and larval weights.

No-choice cage screening for resistance to *Helicoverpa armigera* under greenhouse conditions

The smaller larvae (1–5 days old) of *H. armigera* usually feed on the leaves and flowers, while the third-instar onwards feed on the pods. Therefore, genotypic resistance to *H. armigera* was evaluated at the vegetative and flowering stages. At 15 days after seedling emergence (DAE), the test genotypes were infested with 20 neonates of *H. armigera* per five plants (Sharma et al. 2005c). At the flowering stage, only three plants were retained in each pot, and infested with 20 neonate larvae, while at the podding stage, three plants were infested with six pre-weighed third-instar larvae. Five plants at vegetative stage and three plants at the flowering and podding stages were also kept as un-infested controls for each genotype to compute the yield loss due to damage by *H. armigera*.

The test genotypes were evaluated for leaf feeding visually on 1–9 scale (1 = <10% leaf area damaged, and 9 = >80% leaf area damaged) (Sharma et al. 2005c). The number of larvae surviving after the feeding period were recorded in each replication, and placed in 25 ml plastic cups. The weights of the larvae were recorded at 4 h after separating them from the food. The data were expressed as percent larval survival and mean weight of the surviving larvae. In plants infested at the podding stage, data were recorded on leaf/pod damage, and weight gain by the larvae as follows:

$$\text{Weight gain}(\%) = \frac{\text{Final weight of the larva} - \text{Initial weight of the larva}}{\text{Initial weight of the larva}} \times 100$$

Recovery resistance (tolerance)

The test genotypes were evaluated for their ability to recover (tolerance component of resistance) from damage by *H. armigera* in plants infested at the vegetative stage under no-choice conditions in the greenhouse on a 1–9 scale (1 = plants with good recovery and looking similar in vegetative growth and pod setting to un-infested control plants, and 9 = plants with poor recovery and <80% vegetative growth as compared to the uninfested control plants). Tolerance component of resistance was also measured in terms of number of pods damaged and grain yield plant^{-1} in the plants infested at the vegetative and podding stages. The yield loss, taken as a measure of tolerance component of resistance, was calculated as follows:

$$\text{Yield loss}\,(\%) = \frac{\text{Yield of un-infested plant} - \text{Yield of infested plant}}{\text{Yield of un-infested plant}} \times 100$$

Statistical analysis

Data were subjected to analysis of variance by using GENSTAT release 5.2. Numbers of eggs laid were transformed to square root values ($\sqrt{x} + 0.05$), and the data was subjected to analysis of variance. Paired "*t*" test was used to test the significance of differences between the genotypes under dual-choice conditions. In no-choice and multi-choice tests, the significance of differences between the treatments was measured by *F*-test, while the treatment means were compared using the least significant difference (LSD) at $P = 0.05$.

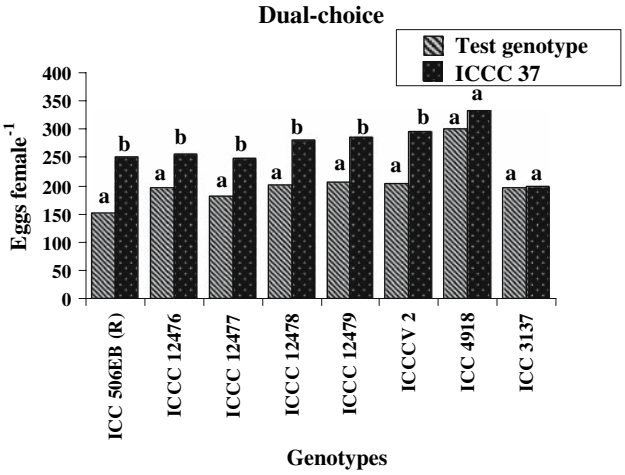

Fig. 2 Oviposition by the females of *Helicoverpa armigera* on nine chickpea genotypes under dual-choice conditions (ICRISAT, Patancheru, 2004/2005 post-rainy seasons)

Results

Oviposition by the *Helicoverpa armigera* females on different chickpea genotypes under multi-choice, dual-choice, and no-choice conditions

Under multi-choice conditions, lowest numbers of eggs were laid on the resistant check, ICC 506EB, followed by ICC 12476, ICC 12477, ICC 12479, and ICC 3137 (Fig. 1); while ICC 506EB, ICC 12476, ICC 12477, ICC 12478, ICC 12479, and ICCV 2 were less preferred for oviposition as compared to the susceptible check, ICCC 37 under dual-choice conditions (Fig. 2). Under no-choice conditions, lower numbers of eggs were recorded on ICC 506EB, ICC 12476, ICC 12477, ICC 12478, and ICC 12479 than on the susceptible check, ICCC 37 (Fig. 3). The genotypes ICC 506EB, ICC 12476, ICC 12477, and ICC 12479 were less preferred for oviposition under no-choice, dual-choice, and multi-choice conditions as compared to the susceptible check, ICCC 37.

Significantly lower numbers of eggs were laid on the F_1 hybrids than on the susceptible check, ICCC 37, except on hybrids based on ICC 12479 (Fig. 4). The numbers of eggs ranged from 132 eggs per female on the hybrid ICC 506EB × ICC 12476 (resistant × resistant cross) to 284 eggs per female on the hybrid ICCC 37 × ICC 4918 (susceptible × susceptible cross). The number of eggs laid on hybrids based on resistant parent, ICC 506EB as a female parent varied from 172 to 189 compared to 249 to 291 eggs on the hybrids based on the susceptible parent, ICCC 37,

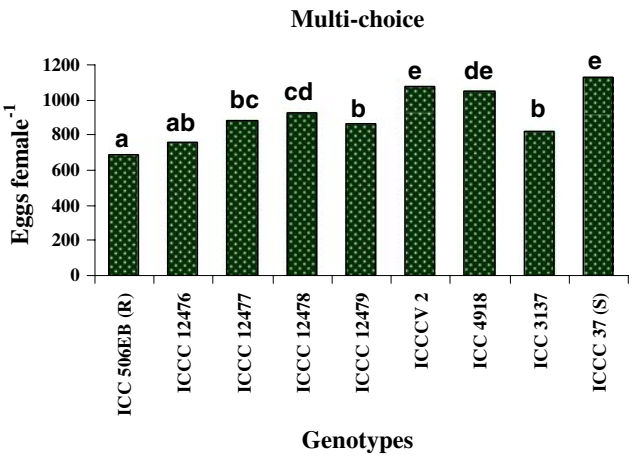

Fig. 1 Oviposition by the females of *Helicoverpa armigera* on nine chickpea genotypes under multi-choice conditions (ICRISAT, Patancheru, 2004/2005 post-rainy seasons)

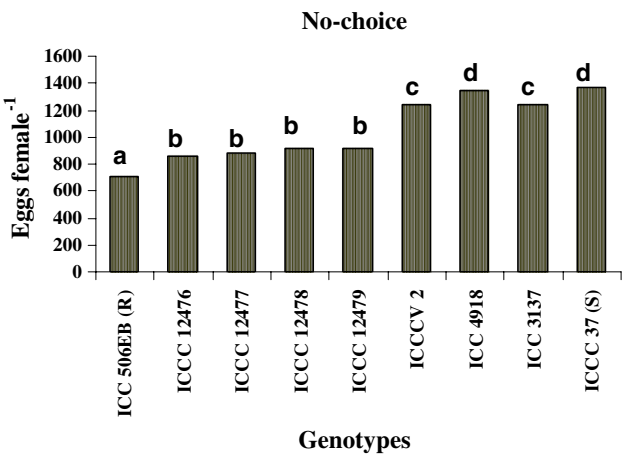

Fig. 3 Oviposition by the females of *Helicoverpa armigera* on nine chickpea genotypes under no-choice conditions (ICRISAT, Patancheru, 2004/2005 post-rainy seasons)

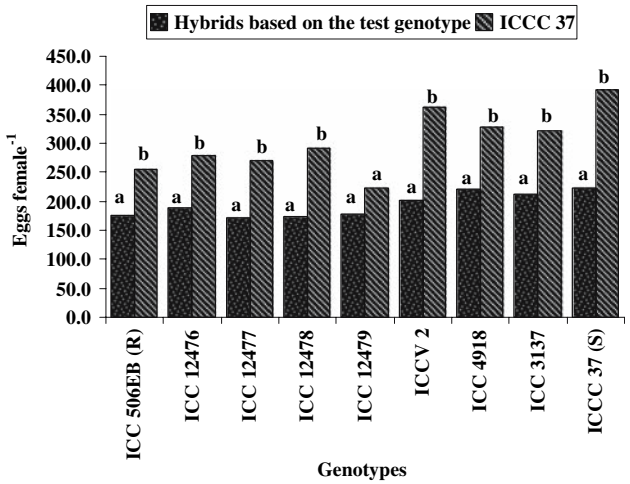

Fig. 4 Oviposition by the females of *Helicoverpa armigera* on 72 hybrids based on nine chickpea genotypes under dual-choice conditions (ICRISAT, Patancheru, 2004/2005 post-rainy seasons)

suggesting that the resistance/susceptibility of the female parent influenced the oviposition on the F_1 hybrids.

Expression of resistance to neonate larvae of *Helicoverpa armiger*a under no-choice cage tests in the greenhouse

During the vegetative stage, minimum leaf feeding (damage rating, DR 3.9) was observed in the resistant check, ICC 506EB as compared to a DR of 8.8 on the susceptible check, ICCC 37 (Table 1). Larval survival was significantly lower on ICC 506EB, ICC 12477, and ICC 12478 as compared to that on the susceptible check, ICCC 37; while the larval weights were lower (45.1–47.8 mg) in larvae fed on ICC 506EB and ICC 12476 as compared to those fed on ICCC 37 (55.3 mg). During the flowering stage, larval feeding was lower (DR 4.9–6.1), on ICC 506EB, ICC 12476, ICC 12477, and ICC 12478 as compared to that on the susceptible check, ICCC 37 (DR 8.7) (Table 2). Larval survival was lower on ICC 506EB, ICC 12476, ICC 12477, and ICC 12478 as compared to the susceptible check, ICCC 37. Larvae gained lower weights (55.8–58.0 mg) when reared on ICC 506EB, ICC 12476, ICC 12477, and ICC 12478 as compared to those reared on ICCC 37 (72.5 mg). However, the differences between the genotypes were non-significant.

Reaction of chickpea genotypes to pod damage by third-instar larvae of *Helicoverpa armigera*

During the podding stage, when the plants were infested with third-instar larvae, leaf/pod feeding was lowest on the resistant check, ICC 506EB (DR 3.9), and highest in the susceptible check, ICCC 37 (DR 8.1) (Table 3). Larval survival was lower on ICC 506EB, ICC 12478, ICC 12479, ICC 3137, and ICCV 2 as compared to that on the susceptible check, ICCC 37. Weight gain by the larvae was lower in larvae fed on ICC 12476, ICC 12477, and ICC 506EB as compared to those fed on ICCC 37.

Recovery resistance (tolerance)

Recovery of the plants infested at the vegetative stage was better in ICC 506EB, but poor in ICCC 37 (Table 1). The grain yield in the infested plants was 5.5–10 g compared to 10.1–13.6 g in the un-infested control plants. The loss in grain yield was greater (>50%) in case of ICCC 37, ICC 3137, ICC 12476, and ICC 12477 as compared to that on ICC 506EB and ICCV 2 (5.7–10.2%). Recovery of plants infested at the flowering stage was better in case of ICC 506EB and ICC 12479 as compared to the susceptible check, ICCC 37 (Table 2). At the flowering stage, the grain yield in the infested plants was 2.6–5.0 g compared to 3.3–6.3 g in the un-infested plants, while the loss in grain yield was greater (>23.1 to 58.3%) in case of ICCC 37, ICC 12476, ICC 3137, and ICC 4918 as compared to that on ICC 12477, ICC 12478, ICC 12479, and ICC 506EB (+4.9 to 10.5% loss). The recovery in the plants infested at the podding stage was poor in case of ICC 3137, ICC 4918 and ICCC 37 as compared to the resistant check, ICC 506EB (Table 3). In the plants infested with the third-instar larvae at the podding stage, the grain yield was 2.9–5.2 g compared to 4.7–6.5 g in the un-infested plants. The genotypes ICC 12477, ICC 12478, ICC 12479, and ICC 506EB recorded lower loss (8.6–15.4%) in grain yield as compared to ICCC 37 (55.3%).

Relative resistance/susceptibility of parents and their F_1 hybrids to neonate larvae of *Helicoverpa armigera*—detached leaf assay

The genotypes ICC 3137, ICC 4918, and ICCC 37 suffered significantly more leaf damage as compared to the resistant check, ICC 506EB (Table 4). Larval survival was significantly lower on ICC 12476, ICC 12477, ICCV 2, and ICC 506EB as compared to that on the susceptible check, ICCC 37. Weight gain by the larvae was significantly lower on ICC 506EB, ICCV 2, ICC 12479, ICC 12476, ICC 12477, and ICC 12478 (5.36–6.29 mg per larva) as compared to 11.36 mg on the susceptible check, ICCC 37. Leaf damage rating in the F_1 hybrids based on different genotypes ranged from 5.1 in hybrids based on ICC 12479 to 6.3 in hybrids based on ICC 3137 (Table 4). Larval survival was 51 and 66% in hybrids based on ICC 12477 and ICC

Table 1 Expression of resistance to neonate larvae of *Helicoverpa armigera* in nine chickpea genotypes during the vegetative stage under no-choice cage tests in the greenhouse (ICRISAT, Patancheru, 2003–2005, post-rainy season)

Genotype	Damage rating*	Larval survival (%)	Larval weight (mg)	Recovery resistance**	Grain yield plant^{-1} (g)		Yield loss (%)
					Infested	Uninfested	
ICC 12476	6.1^{b}	71.0^{c}	47.8	2.5^{b}	6.2^{b}	12.5^{c}	50.6^{c}
ICC 12477	6.3^{bc}	65.0^{ab}	59.5	2.8^{cd}	6.3^{b}	12.7^{c}	50.8^{c}
ICC 12478	6.1^{b}	66.7^{a}	54.1	2.5^{b}	7.4^{c}	13.3^{c}	44.7^{b}
ICC 12479	6.1^{b}	70.0^{bc}	55.3	3.0^{cd}	7.3^{c}	12.1^{c}	39.7^{b}
ICCV 2	5.9^{b}	71.0^{c}	55.9	2.4^{bc}	10.7^{e}	11.4^{b}	5.7^{a}
ICC 4918	8.2^{d}	83.3^{d}	59.3	2.0^{b}	6.6^{b}	12.9^{cd}	49.2^{c}
ICC 3137	7.2^{cd}	79.0^{d}	49.8	2.6^{b}	5.3^{a}	10.7^{a}	51.5^{c}
ICC 506EB (R)	3.9^{a}	63.3^{a}	45.1	3.3^{d}	9.0^{d}	10.1^{a}	10.2^{a}
ICCC 37 (S)	8.8^{d}	84.5^{d}	55.3	1.6^{a}	5.5^{a}	13.6^{d}	59.4^{d}
F-probability	<0.001	<0.001	0.81	<0.001	<0.001	<0.001	<0.001
LSD (*P* 005)	0.96	5.27	NS	0.60	0.50	0.80	5.50

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

** Recovery resistance score (1 = Plants showing <10% recovery following insect damage, and 5 = plants showing >80% recovery following insect damage). R = Resistant check S = Susceptible check. Five plants were infested with 20 neonate larvae at 15 days after seedling emergence. NS = Non-significant. The figures followed by the same letter in a column are not significantly different at $P < 0.05$

Table 2 Expression of resistance to neonate larvae of *Helicoverpa armigera* in nine chickpea genotypes during the flowering stage under no-choice cage tests in the greenhouse (ICRISAT, Patancheru, 2003–2005, post rainy season)

Genotype	Damage rating*	Larval survival (%)	Larval weight (mg)	Recovery resistance**	Grain yield plant^{-1} (g)		Yield loss (%)
					Infested	Un-infested	
ICC 12476	6.1^{abc}	63.3^{a}	58.0	2.2^{abcd}	4.2^{b}	6.0^{b}	29.8^{f}
ICC 12477	5.8^{ab}	66.7^{a}	55.5	2.4^{cd}	5.0^{bc}	5.4^{a}	6.7^{bc}
ICC 12478	6.1^{abc}	66.7^{a}	55.8	2.1^{ab}	4.8^{bc}	5.4^{a}	10.5^{c}
ICC 12479	6.3^{bc}	70.0^{ab}	61.1	2.5^{d}	3.9^{b}	3.7^{a}	+4.9^{a}
ICCV 2	6.5^{bc}	71.0^{ab}	71.0	2.3^{b}	2.7^{a}	3.3^{a}	17.2^{d}
ICC 4918	8.8^{d}	83.3^{b}	73.5	1.9^{ab}	2.8^{a}	3.6^{a}	23.1^{e}
ICC 3137	7.4^{cd}	75.5^{ab}	72.5	2.0^{abc}	3.9^{b}	5.1^{ab}	24.5^{e}
ICC 506EB (R)	4.9^{a}	60.1^{a}	57.5	3.3^{e}	5.9^{c}	6.1^{b}	2.0^{b}
ICCC 37 (S)	8.7^{d}	85.0^{b}	72.5	1.8^{a}	2.6^{a}	6.3^{b}	58.3^{g}
F-probability	<0.001	<0.001	0.21	<0.001	<0.001	<0.001	<0.001
LSD (*P* 0.05)	1.35	15.97	NS	0.44	1.09	2.32	5.47

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

** Recovery resistance score (1 = Plants showing <10% recovery following insect damage, and 5 = plants showing >80% recovery following insect damage). R = Resistant check

S = Susceptible check. Three plants were infested with 20 neonate larvae at 45 days after seedling emergence. NS = Non-significant. + = Increase in yield in the infested plants. The figures followed by the same letter in a column are not significantly different at $P < 0.05$

506EB, respectively, and the larvae gained lower weights when fed on hybrids based on ICC 506EB and ICC 12476 compared to the larvae fed on hybrids based on ICCC 37.

Discussion

The genotypes ICC 12476, ICC 12477, ICC 12478, ICC 12479, and ICC 506EB were less preferred for oviposition under dual- and multi-choice conditions, suggesting that oviposition non-preference is an important component of resistance to *H. armigera* in chickpea. Cowgill and Lateef (1996) and Sison et al. (1996) recorded fewer eggs on the resistant genotype, ICC 506EB than on ICC 4918 and ICCC 37. There is a positive correlation between numbers of eggs laid under laboratory and field conditions (Srivastava and Srivastava 1989), and therefore, dual-choice, no-choice, or multi-choice assays under greenhouse/

Table 3 Expression of resistance to third-instar larvae of *Helicoverpa armigera* in nine chickpea genotypes under no-choice cage tests in the greenhouse during the podding stage (ICRISAT, Patancheru, 2003–2005 post rainy season)

Genotype	Damage rating*	Larval survival (%)	Weight gain (%)	Recovery resistance**	Grain yield (g)		Yield loss (%)
					Infested	Un-infested	
ICC 12476	6.4^{b}	73.3^{bc}	871.1^{a}	1.8^{b}	3.9^{b}	5.4^{abc}	27.9^{b}
ICC 12477	6.8^{b}	73.3^{bc}	987.2^{b}	1.7^{b}	4.4^{bc}	5.3^{abc}	15.4^{a}
ICC 12478	6.7^{b}	66.7^{ab}	1104.7^{cde}	1.5^{b}	4.6^{c}	5.1^{ab}	8.6^{a}
ICC 12479	6.8^{b}	66.7^{ab}	1148.9^{e}	1.8^{b}	4.5^{c}	5.0^{a}	10.8^{a}
ICCV 2	6.5^{b}	65.0^{ab}	1072.4^{d}	1.6^{b}	3.1^{a}	4.7^{a}	33.8^{b}
ICC 4918	8.1^{c}	76.7^{bc}	1242.3^{f}	0.9^{a}	2.9^{a}	5.9^{bcd}	50.5^{c}
ICC 3137	6.9^{b}	68.5^{a}	1063.0^{c}	0.8^{a}	3.1^{a}	4.9^{a}	35.8^{b}
ICC 506 EB (R)	3.9^{a}	56.7^{a}	927.0^{ab}	2.1^{b}	5.2^{d}	6.1^{cd}	15.0^{a}
ICCC 37 (S)	8.1^{c}	80.7^{c}	1332.5^{g}	0.7^{a}	2.9^{a}	6.5^{d}	55.3^{c}
F-probability	<0.001	0.004	0.019	<0.001	<0.001	<0.001	<0.001
LSD (*P* 0.05)	0.52	12.58	75.00	0.55	0.45	0.81	8.3

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

** Recovery resistance score (1 = Plants showing <10% recovery following insect damage, and 5 = plants showing >80% recovery following insect damage). R = Resistant check S = Susceptible check. The figures followed by the same letter in a column are not significantly different at *P* <0.05

Table 4 Reaction of nine chickpea genotypes and their F_1 hybrids to neonate larvae of *Helicoverpa armigera* during the flowering stage in detached leaf assay (ICRISAT, Patancheru, 2004–2005, post-rainy season)

Parents/hybrids	Damage rating*	Larval survival (%)	Larval weight (mg)
Parents			
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 506EB (R)	3.6^{a}	54.0^{a}	5.36^{a}
ICCC 37 (S)	7.8^{d}	72.0^{bc}	11.36^{d}
F_1 hybrids based on different parents			
F_1s based on ICC 506EB	5.2^{b}	66.0^{abc}	5.58^{a}
F_1s based on ICC 12476	5.3^{bc}	53.0^{a}	6.63^{abc}
F_1s based on ICC 12477	5.0^{b}	51.0^{a}	7.27^{abc}
F_1s based on ICC 12478	5.2^{b}	55.0^{a}	7.20^{abc}
F_1s based on ICC 12479	5.1^{b}	60.8^{abc}	8.08^{abc}
F_1s based on ICCV 2	5.8^{b}	53.5^{a}	8.06^{abc}
F_1s based on ICC 4918	6.0^{bcd}	53.0^{a}	9.10^{bc}
F_1s based on ICC 3137	6.3^{bcd}	64.0^{abc}	8.88^{bc}
F_1s based on ICCC 37	6.1^{bcd}	64.8^{abc}	8.61^{abc}
F-probability	<0.001	<0.001	<0.001
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. S = Susceptible check. The figures followed by the same letter in a column are not significantly different at *P* <0.05

laboratory conditions provide a good measure of genotypic performance for oviposition non-preference under field conditions. Comparatively lower oviposition was recorded in hybrids based on ICC 12477, ICC 12478, ICC 12479, and ICC 506EB, as compared to the hybrids based on the susceptible check, ICCC 37, indicating that oviposition on F_1 hybrids is influenced by the parents, and is inherited in the progeny.

Antibiosis to *H. armigera* in chickpea is expressed in terms of larval mortality, decreased larval and pupal weights, prolonged larval and pupal development, failure to pupate, and reduced fecundity (Srivastava and Srivastava

1990; Yoshida et al. 1995; Cowgill and Lateef 1996). Larval survival and weight gain by the larvae were lower on ICC 506EB, ICC 12476, ICC 12477, and ICC 12478 as compared to that on the susceptible check, ICCC 37. Reduced leaf feeding, larval survival, and weight gain were also observed in the hybrids based on resistant × resistant crosses than on hybrids based on susceptible × susceptible crosses, suggesting that antibiosis to *H. armigera* in chickpea is inherited in the progeny.

Recovery of the plants following insect damage and loss of grain yield provided a good measure of the genotypic ability to withstand and/or recover from insect damage. Reduction in grain yield also provides a good measure of agronomic performance of a genotype under insect infestation. Plant recovery from damage by *H. armigera* was better in case of ICC 506EB, ICC 12476, and ICC 12479 as compared to the susceptible check, ICCC 37; while loss in grain yield was lower in case of ICCV 2, ICC 12478, ICC 12479, and ICC 506EB across crop stages and infestation procedures as compared to that on the susceptible check, ICCC 37.

Conclusion

Oviposition non-preference, antibiosis, and tolerance are the major components of resistance to *H. armigera* in chickpea. The genotypes ICC 506EB, ICC 12476, ICC 12477, ICC 12478, and ICC 12479 showed reduced oviposition and suffered low leaf damage and loss in grain yield, while low larval survival and low weight gain was observed on ICC 506 EB, ICC 12476, and ICC 12477. These genotypes can be used in breeding for resistance to *H. armigera*. Oviposition, leaf feeding, and weight gain by the *H. armigera* larvae on the F_1 hybrids were influenced by the parents, indicating the potential for introgression of these components of resistance into the progenies to develop varieties with resistance to this pest.

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