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Antixenosis and antibiosis components of resistance to pod borer *Helicoverpa armigera* in wild relatives of pigeonpea

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Abstract. The legume pod borer (*Helicoverpa armigera* (Hubner)) is one of the most important pests of pigeonpea. The levels of resistance to *H. armigera* in the cultivated germplasm are quite low, and therefore there is a need to introgress resistance genes from wild relatives into the cultigen. We evaluated a diverse array of wild relatives of pigeonpea for oviposition non-preference and antibiosis components of resistance to *H. armigera*. The accessions ICPW 1 (*Cajanus acutifolius*), ICPW 13 and 14 (*C. albicans*), ICPW 159 and 160 (*C. sericeus*), ICPW 68 (*C. platycarpus),* ICPW 83, 90, 94, 125, 137, 141 and 280 (*C. scarabaeoides*), ICPW 207 (*Paracalyx scariosa)* and ICPW 210 (*Rhynchosia aurea*) showed high levels of antixenosis for oviposition under no-choice, dual-choice and multi-choice conditions. High levels of antibiosis were observed when the larvae were reared on leaves and/or pods of *C. acutifolius* (ICPW 1), *C. cajanifolius* (ICPW 29), *C. sericeus* (ICPW 160), *P. scariosa* (ICPW 207), *C. scarabaeoides* and *C. albicans*. Lyophilized leaf or pod powder incorporated into the artificial diet can be used to assess antibiosis to *H. armigera*, and high levels of antibiosis to *H. armigera* were observed in diets with leaf and/or pod powder of some of the accessions of *C. acutifolius*, *C. lineatus*, *C. sericeus*, *C. scarabaeoides*, *C. platycarpus*, *P. scariosa* and *R. aurea*. Post-embryonic development period was prolonged in insects reared on leaves and pods of wild relatives of pigeonpea. The accessions showing high levels of antixenosis and antibiosis can be used to increase the levels and diversify the bases of resistance to *H. armigera* in pigeonpea.

Key words: *Helicoverpa armigera*, pigeonpea, wild relatives, resistance mechanisms

Introduction

Pigeonpea (*Cajanus cajan* (L.) Mills. (Fabaceae)) is an important pulse crop in Asia and Africa. Though the potential yield of pigeonpea is 2.5–3.0 tonnes/ha, the average productivity is around 0.75 tonnes/ha. Much of the difference in potential yields and the actual harvest by farmers has been attributed to biotic and abiotic stress factors, of which the pod borer *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae) is the most damaging pest. Losses due to this pest in pigeonpea have been estimated to be US$ 317 million in the semi-arid tropics (SAT) (ICRISAT, 1992), and over US$ 2 billion on different crops worldwide (Sharma, 2005). To overcome these losses, farmers resort to excessive use of pesticides, resulting in the development of high levels of resistance to conventional insecticides (Kranthi *et al.*, 2002).

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Development of crop cultivars with resistance to *H. armigera* has a considerable potential in pest management (Fitt, 1989; Sharma *et al.*, 2005). Unfortunately, only low to moderate levels of resistance to *H. armigera* have been detected in more than 14,000 accessions of cultivated pigeonpea evaluated for resistance to this pest (Reed and Lateef, 1990). Wild relatives of crops have been exploited as a diverse pool of genetic resources for crop improvement, including insect and disease resistance (Brar and Khush, 1997; Hajjar and Hodgkin, 2007). Therefore, pigeonpea wild relatives might be a good source of genes for resistance to *H. armigera*. Indeed, high levels of resistance to *H. armigera* have been identified in wild relatives of pigeonpea such as *Cajanus scarabaeoides, Cajanus sericeus* and *Cajanus acutifolius* (Leguminoseae: Papilionoideae), which can be used as sources of resistance to *H. armigera* (Sharma *et al.*, 2001). Although oviposition non-reference and antibiosis have been associated with pod borer resistance in a few accessions of wild relatives of pigeonpea (Dodia *et al.*, 1996; Shanower *et al.*, 1997; Yoshida and Shanower, 2000; Sharma *et al.*, 2001; Green *et al.*, 2002, 2003, 2006), wild relatives of pigeonpea have not been fully characterized for different components (antixenosis and antibiosis) of resistance to *H. armigera.* Therefore, the present investigations were undertaken to identify species/accessions with high levels and different mechanisms of resistance to *H. armigera* for developing pigeonpea cultivars with resistance to this pest.

Materials and methods

Plant material

Twenty-nine accessions belonging to 13 species (*Cajanus scarabaeoides*, *C. cajanifolius*, *C. sericeus*, *C. albicans*, *C. acutifolius*, *C. lineatus*, *C. platycarpus*, *Rhynchosia bracteata*, *R. aurea*, *Dunbaria ferruginea*, *Flemingia bracteata*, *F. stricta* and *Paracalyx scariosa*) of wild relatives of pigeonpea (Leguminoseae: Papilionoideae) were evaluated for antixenosis for oviposition and antibiosis components of resistance to *H. armigera*, along with two genotypes of cultivated pigeonpea (*Cajanus cajan*), i.e. ICPL 87 as the susceptible check and ICPL 332 as the resistant check (Table 1). The test material was planted under field conditions at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Andhra Pradesh, India. The seeds were sown on ridges 75 cm apart, and thinned to a spacing of 30 cm between the plants at 15 days after seedling emergence. Each accession was planted in two-row plots, 2 m long. There were three replications in a complete randomized block design. The accessions belonging to annual species of the wild relatives (*C. scarabaeoides*, *C. cajanifolius*, *C. sericeus*, *C. acutifolius* and *C. platycarpus*) and the cultivated pigeonpea were planted twice at monthly intervals, while the perennial species (*C. albicans*, *C. lineatus*, *R. bracteata*, *R. aurea*, *D. ferruginea*, *F. bracteata*, *F. stricta* and *P. scariosa*) were planted only once to have leaves and pods of all the accessions for bioassay during the same period. Standard agronomic practices were followed (basal fertilizer – N:P:K: 100:60:40 kg/ha). A fungicide spray (metalaxyl 1.0 kg a.i./ha) was applied to control *Fusarium* wilt during the seedling stage. The crop was grown under rain-fed conditions between June and October (2005 and 2006), but irrigated at monthly intervals between November and February during the post-rainy period. Wooden pegs (1.5 m high) were used to provide support for *C. scarabaeoides* and *C. platycarpus* accessions, which have a creeping habit. Leaves, flowers and pods of similar age were collected from different accessions during December–January for studying antixenosis and antibiosis to *H. armigera*.

Insect culture

Larvae and adults of *H. armigera* for experiments were obtained from a colony maintained in the laboratory at ICRISAT. The laboratory colony of *H. armigera* was supplemented with natural population from the field to maintain heterogeneity. The larvae were reared on the chickpea-based artificial diet developed by Armes *et al.* (1992) at 27 ± 1 °C, 65 ± 5% relative humidity (RH) and 12 h photoperiod. The adults were released in 30 × 30 × 30 cm cages for oviposition. Nappy liners hung inside the cages were provided as a substrate for oviposition and adults were fed with 10% sucrose solution in absorbent cotton. Eggs laid on the nappy liners were sterilized with 1% sodium hypochlorite solution, and transferred into 200 ml plastic cups smeared with a 2 mm thick layer of artificial diet for rearing in groups of 250. After 5 days, the larvae were transferred to six cell-well plates (having 5–7 ml artificial diet in each cell well), and reared individually until pupation. Adults from this culture were used for studies on antixenosis for oviposition, while the larvae were used for assessing antibiosis to *H. armigera* in fresh leaves and pods, and by incorporating lyophilized plant parts into the artificial diet.

Antixenosis for oviposition to Helicoverpa armigera

Under no-choice conditions, *H. armigera* females were confined to five field-collected inflorescences of each accession inside a wooden cage

Table 1. Antixenosis for oviposition by *Helicoverpa armigera* females towards wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Species	Accession	No-choice conditions[1]	Multi-choice conditions[1]	Dual-choice conditions[1]	
				Susceptible control (ICPL 87)	Test genotype
Cajanus acutifolius	ICPW 1	151 (12.3)[2]	139 (11.7)[2]	98[a]	26[b]
C. acutifolius	ICPW 2	236 (15.4)	179 (13.3)	122[a]	54[b]
C. albicans	ICPW 13	65 (8.0)	84 (8.6)	115[a]	24[b]
C. albicans	ICPW 14	150 (12.2)	87 (9.0)	129[a]	41[b]
C. cajanifolius	ICPW 28	258 (15.9)	260 (16.1)	77[a]	37[b]
C. cajanifolius	ICPW 29	347 (18.6)	313 (17.7)	97[a]	55[b]
C. lineatus	ICPW 40	425 (20.4)	202 (14.2)	96[a]	79[b]
C. lineatus	ICPW 41	132 (11.4)	257 (16.0)	96[a]	64[b]
C. sericeus	ICPW 159	161 (12.7)	74 (8.5)	88[a]	59[b]
C. sericeus	ICPW 160	250 (15.6)	89 (9.4)	96[a]	61[b]
C. platycarpus	ICPW 68	141 (11.6)	141 (11.6)	96[a]	64[b]
C. scarabaeoides	ICPW 83	114 (10.6)	123 (11.0)	99[a]	27[b]
C. scarabaeoides	ICPW 90	56 (7.5)	93 (9.6)	87[a]	24[b]
C. scarabaeoides	ICPW 94	76 (8.7)	141 (11.6)	85[a]	32[b]
C. scarabaeoides	ICPW 116	89 (9.3)	168 (12.7)	104[a]	55[b]
C. scarabaeoides	ICPW 125	120 (10.9)	93 (9.5)	102[a]	40[b]
C. scarabaeoides	ICPW 130	125 (11.1)	155 (12.4)	85[a]	32[b]
C. scarabaeoides	ICPW 137	84 (9.2)	82 (8.8)	100[a]	33[b]
C. scarabaeoides	ICPW 141	167 (12.9)	121 (11.0)	81[a]	33[b]
C. scarabaeoides	ICPW 152	155 (12.4)	154 (12.2)	91[a]	26[b]
C. scarabaeoides	ICPW 278	179 (13.3)	175 (9.4)	75[a]	32[b]
C. scarabaeoides	ICPW 280	159 (12.6)	166 (13.2)	79[a]	26[b]
C. scarabaeoides	ICPW 281	245 (15.6)	88 (12.9)	77[a]	37[b]
Dunbaria ferruginea	ICPW 178	357 (18.8)	139 (11.8)	88[a]	67[b]
Flemingia bracteata	ICPW 192	307 (17.4)	77 (8.7)	73[a]	58[b]
F. stricta	ICPW 202	149 (12.1)	202 (14.2)	60[a]	50[a]
Paracalyx scariosa	ICPW 207	182 (13.5)	95 (9.7)	68[a]	38[b]
Rhynchosia aurea	ICPW 210	89 (9.3)	74 (8.5)	77[a]	57[b]
R. bracteata	ICPW 214	190 (13.8)	105 (9.9)	79[a]	49[b]
C. cajan (S)	ICPL 87	334 (18.2)	399 (20.0)	—	—
C. cajan (R)	ICPL 332	190 (13.7)	196 (20.0)	80[a]	41[b]
SE ±		(0.57)	(1.09)	—	—
LSD at $P = 0.05$		(1.59)	(3.03)	—	—

ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; S, susceptible check; R, resistant check; SE, standard error; LSD, least significant difference.
Under dual-choice conditions, the figures followed by the same letter in a row are not significantly different at $P \leq 0.05$.
[1] Number of eggs laid per female.
[2] Figures in parentheses are square root-transformed values.

(30 × 30 × 30 cm). The cut ends of the inflorescences were immersed in water in a 100 ml conical flask to keep them in a turgid condition. Five pairs of newly emerged moths were released inside the cage and provided with 10% sucrose solution in a cotton swab as food. The inflorescences were changed everyday. The moths were confined to the test material 2 days after emergence from the pupae (pre-oviposition period). Observations on egg laying were recorded for 3 days. There were five replications for each genotype in a completely randomized design.

Under dual-choice conditions, the female moths were offered a choice between the inflorescences of the susceptible check (ICPL 87) and the test genotype inside the cage as described above. Each test was repeated five times. Observations on oviposition were recorded as described above. Under multi-choice conditions, the inflorescences of all the 29 accessions, and the susceptible (ICPL 87) and resistant (ICPL 332) checks were kept inside a large cage (80 × 70 × 60 cm) in an environmental chamber (temperature day/night: 26/20 °C, RH 70% and photoperiod 12 h). Fifty pairs of newly

emerged moths were released inside the cage. The inflorescences were arranged in a completely randomized block design. The inflorescences were changed daily. Observations on egg laying were recorded as described above.

Antibiosis to *Helicoverpa armigera*

Larval survival and development on fresh leaves and pods. Survival and development of neonate larvae of *H. armigera* were studied on fresh leaves of different accessions. First fully expanded leaves were excised from the plants in the field and brought to the laboratory for bioassay. The leaves were kept fresh by wrapping the petiole in a wet cotton swab. The neonate larvae were released on the leaves in Petri dishes (7.5 cm diameter) with a camel hairbrush. The first and second instars were kept in groups of five per Petri dish, while the later instars were reared individually to avoid cannibalism. The leaves were changed on alternate days. The insects were kept at 27 ± 2 °C in the laboratory. There were five replications for each accession and 10 larvae per replication. Data on larval survival and larval weights were recorded on day 10 after initiating the experiment. Data on pupal weights were recorded 1 day after pupation. Data were also recorded on larval and pupal development periods.

Survival and development of neonate larvae were also studied on flowers and pods collected from the test genotypes in the field. The flowers/pods were placed on a moist filter paper in a Petri dish. First instars were transferred onto flowers with a camel hairbrush. The food was changed on alternate days. There were five replicates for each accession and 10 larvae per replication. Larvae were first reared on flowers for 5 days, and then on the pods of the same accession (following the feeding behaviour of the insect under natural conditions). The first instars were kept in groups of five per Petri dish, whereas the grown-up larvae (>5 days old) were reared individually. Data on larval survival and larval weights were recorded on day 10 after initiating the experiment. Data on pupal weights were recorded 1 day after pupation. Data were also recorded on larval and pupal development periods.

Larval development on artificial diets with lyophilized leaf or pod powder. Antibiosis to *H. armigera* was also assessed by rearing neonate *H. armigera* larvae by incorporating lyophilized leaf or pod powder of different accessions of wild relatives of pigeonpea into the artificial diet. Fully expanded leaves (collected from 50- to 55-day-old plants) and 10- to 15-day-old pods were freeze-dried in a lyophilizer for 36 h to avoid changes in biochemical composition of the leaves/pods. The leaves/pods were then powdered in a Willey mill and stored in a desiccator until used. To determine the optimum amount of leaf/pod powder needed in the artificial diet to assess antibiosis to *H. armigera*, different amounts of chickpea flour:leaf powder (75:0, 70:5, 65:10, 60:15 and 55:20 g) of the cultivated pigeonpea genotypes (ICPL 332 – resistant and ICPL 87 – susceptible) and the wild relative *C. scarabaeoides* (ICPW 83 – resistant) were incorporated into the before-mentioned artificial diet to prepare 300 ml diet. The lyophilized leaf/pod powder was soaked in 100 ml warm water and then blended for 2 min. Agar-agar (4.375 g) was boiled in 100 ml water, and then poured into the blender containing the leaf powder and other ingredients of the artificial diet. Finally, all the constituents were blended for 2 min, and 10 ml of this diet was poured into small plastic cups (25 ml capacity) and fed to the *H. armigera* larvae. Each treatment was replicated three times, and there were 10 larvae in each replication. Data on larval survival and larval weights were recorded on day 10 after initiating the experiment. Data on pupal weights were recorded 1 day after pupation. Data were also recorded on larval and pupal development periods.

Based on the above experiments, 10 g of leaf or pod powder of different accessions of wild relatives was incorporated into the artificial diet to assess antibiosis to *H. armigera* (which resulted in maximum differences in development of *H. armigera* on resistant and susceptible genotypes). There were three replications for each genotype, and 10 larvae in each replication. The rearing cups were kept at 27 ± 2 °C, 65 ± 5% RH and 12 h photoperiod. Data on larval survival and larval weights were recorded on day 10 after initiating the experiment. Data on pupal weights were recorded 1 day after pupation. Data were also recorded on larval and pupal development periods.

Statistical analysis

The data were subjected to analysis of variance by using Genstat release 8.2. Data on number of eggs laid were converted to square root values before analysis of variance. Significance of differences between the genotypes in dual-choice tests was subjected to paired *t*-tests. The significance of differences between the genotypes was judged by *F*-test, and the treatment means were compared by least significant difference (LSD) at $P \leq 0.05$.

Results

Antixenosis for oviposition to Helicoverpa armigera

Under no-choice conditions, there were significant differences in oviposition between the different host plant species (56–425 eggs), and even within

different accessions of the same species, e.g. between ICPW 1 (151 eggs) and ICPW 2 (236 eggs) of *C. acutifolius*, ICPW 13 (65 eggs) and ICPW 14 (150 eggs) of *C. albicans*, ICPW 28 (258 eggs) and ICPW 29 (347 eggs) of *C. cajanifolius*, ICPW 41 (132 eggs) and ICPW 40 (425 eggs) of *C. lineatus*, and ICPW 159 (161 eggs), ICPW 160 (250 eggs) of *C. sericeus*, and ICPW 94 (76 eggs) and ICPW 281 (245 eggs) of *C. scarabaeoides* (Table 1). *C. scarabaeoides* accessions ICPW 90, 94, 116 and 137 showed very high levels of oviposition non-preference to *H. armigera* (76 to 89 eggs per female compared with 334 eggs on the susceptible check ICPL 87). Some of the accessions belonging to *C. acutifolius* (ICPW 1), *C. albicans* (ICPW 13 and 14), *C. lineatus* (ICPW 41), *C. sericeus* (ICPW 159), *F. stricta* (ICPW 202), *C. platycarpus* (ICPW 68), and *R. aurea* (ICPW 210), were also non-preferred for oviposition. The *H. armigera* females laid 190 eggs per five inflorescences on the resistant *C. cajan* check (ICPL 332), compared with 334 eggs on the susceptible *C. cajan* check (ICPL 87), indicating that oviposition nonpreference is an important mechanism of resistance to this insect in pigeonpea.

Under multi-choice conditions, *C. cajanifolius*, *C. lineatus* and *F. stricta* were as much preferred for oviposition as the susceptible check, ICPL 87 (Table 1). Accessions belonging to *C. albicans* (ICPW 13 and ICPW 14), *C. sericeus* (ICPW 159 and 160), *C. scarabaeoides* (ICPW 90, ICPW 125, ICPW 137 and ICPW 281), *R. aurea* (ICPW 210), *F. bracteata* (ICPW 192), *P. scariosa* (ICPW 207), and *R. bracteata* (ICPW 214) had 50% less eggs than the susceptible pigeonpea check ICPL 87. Under dual-choice conditions, significantly lower oviposition was recorded on the wild species than on the susceptible *C. cajan* check ICPL 87, except on *F. stricta* (ICPW 202). Accessions belonging to *C. acutifolius* (ICPW 1), *C. albicans* (ICPW 13 and 14), *C. scarabaeoides* (except ICPW 116) and *P. scariosa* (ICPW 207) showed high levels of antixenosis for oviposition to *H. armigera*.

Antibiosis to *Helicoverpa armigera*

Larval survival and development on leaves and pods. The larval and pupal weights of *H. armigera* were significantly lower when reared on leaves of *C. acutifolius* (ICPW 2), *C. cajanifolius* (ICPW 29), *C. sericeus* (ICPW 160), *C. scarabaeoides* (ICPW 83, 116 and 125) and *P. scariosa* (ICPW 207) when compared with the insects reared on the susceptible *C. cajan* check ICPL 87 (Table 2). The larval mortality was significantly greater on the wild relatives of pigeonpea compared with that on the susceptible pigeonpea check ICPL 87 (except for *C. lineatus* – ICPW 40). The larvae took >35 days to complete development when reared on the leaves of *C. albicans* (ICPW 13 and 14) and *C. scarabaeoides* (ICPW 83, 94, 116, 130, 137, 141, 152, 280 and 281) compared with 24.1 days on the susceptible *C. cajan* check (ICPL 87) and 29.1 days on the resistant pigeonpea check (ICPL 332). The pupal period lasted for >18 days when the larvae were reared on the leaves of *C. albicans* (ICPW 13), *C. scarabaeoides* (ICPW 83 and 130), *D. ferruginea* (ICPW 178), *F. stricta* (ICPW 202) and *P. scariosa* (ICPW 207) compared with 14.7 days on ICPL 87 and 17.2 days on ICPL 332.

The weights of *H. armigera* larvae were significantly lower (<50 mg per larva) in insects reared on flowers/pods of *C. acutifolius* (ICPW 1), *C. sericeus* (ICPW 159 and 160) and *C. scarabaeoides* (all the 12 accessions tested) compared with 237.7 mg on ICPL 87 at 10 days after initiating the experiment (Table 2). Larvae took 32.7–42.5 days to complete development on *C. scarabaeoides* accessions compared with 24.3 days on ICPL 332 and 21.7 days on ICPL 87. Differences in larval period on flowers/pods of *C. acutifolius*, *C. albicans*, *C. cajanifolius*, *C. sericeus*, *F. bracteata*, *F. stricta*, *P. scariosa* and *R. bracteata* were not significant.

Development of Helicoverpa armigera *larvae on artificial diets with lyophilized leaf or pod powder.* There were significant differences in larval and pupal weights of insects reared on artificial diets having different amounts of lyophilized leaf powder of ICPL 87, 332 and ICPW 83 (Table 3). The larvae weighed 9.4 mg per larva when reared on artificial diet with 10 g leaf powder of ICPW 83 compared with 47.1 and 57.0 on ICPL 332 and 87, respectively. The pupal weight (260.7 mg) was significantly lower on diets with 10 g leaf powder of ICPW 83 compared with that on the standard artificial diet (295.9 mg). Pupal weights of insects reared on diets with ICPL 87 leaf powder were significantly higher (315.4 mg) compared with those with ICPL 332 (293.2 mg). There was a gradual decrease in larval and pupal weights with an increase in the amount of lyophilized leaf powder in the artificial diet. A significant prolongation of larval period was observed with an increase in the amount of leaf powder in the artificial diet.

The larvae weighed 34.5, 140.0 and 314.6 mg on diets with 10 g pod powder of ICPW 83, ICPL 332 and 87, respectively (Table 3). The larval period was 26.3, 21.7 and 16.0 days in larvae reared on diets with 10 g pod powder of ICPW 83, ICPL 332 and 87, respectively. Pupal period ranged from 12 to 14 days in insects reared on the three artificial diets. Maximum differences in insect development between the resistant and susceptible genotypes were observed on diets containing 10 g of leaf or pod powder, and, therefore, 10 g of lyophilized leaf or pod powder was used to assess antibiosis to

Table 2. Survival and development of *Helicoverpa armigera* on the leaves and flowers/pods of wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Species	Accession number	Larval weight (mg; 10th day)		Pupal weight (mg)		Larval period (days)		Pupal period (days)	
		Leaves	Flowers/Pods	Leaves	Flowers/Pods	Leaves	Flowers/Pods	Leaves	Flowers/Pods
Cajanus acutifolius	ICPW 1	11.0	26.8	153.3	140.5	29.9	25.4	17.3	12.2
C. acutifolius	ICPW 2	7.2	51.8	142.1	162.2	32.8	24.7	16.9	12.4
C. albicans	ICPW 13	8.0	57.2	261.2	189.3	38.4	27.3	18.5	12.8
C. albicans	ICPW 14	15.0	87.8	279.0	241.4	35.2	25.5	17.6	13.2
C. cajanifolius	ICPW 28	64.3	109.4	164.3	205.1	30.8	21.8	17.1	12.2
C. cajanifolius	ICPW 29	11.7	100.3	125.2	169.1	34.6	24.1	17.6	12.8
C. lineatus	ICPW 40	82.3	85.4	270.9	232.4	31.4	29.9	17.5	13.6
C. lineatus	ICPW 41	31.4	59.2	266.3	219.3	33.5	32.5	16.7	13.8
C. sericeus	ICPW 159	13.8	39.6	183.6	165.8	26.3	22.7	15.8	12.2
C. sericeus	ICPW 160	8.0	25.9	137.1	148.5	30.7	26.4	16.2	12.2
C. platycarpus	ICPW 68	17.0	53.2	129.0	160.7	30.4	24.8	16.4	12.8
C. scarabaeoides	ICPW 83	17.8	13.2	126.8	127.6	39.6	42.5	17.9	13.6
C. scarabaeoides	ICPW 90	51.1	11.0	114.2	134.0	33.2	37.3	16.9	13.8
C. scarabaeoides	ICPW 94	35.4	9.2	123.1	92.5	34.9	32.7	17.1	13.8
C. scarabaeoides	ICPW 116	20.8	10.0	137.8	124.1	35.4	39.8	17.7	12.6
C. scarabaeoides	ICPW 125	24.2	17.6	150.0	140.6	33.9	33.7	17.4	12.2
C. scarabaeoides	ICPW 130	33.2	16.6	145.0	124.6	37.4	39.8	18.1	13.0
C. scarabaeoides	ICPW 137	28.8	17.0	112.0	123.7	36.1	40.0	17.2	13.0
C. scarabaeoides	ICPW 141	36.9	22.1	136.0	126.1	37.3	37.9	14.9	12.2
C. scarabaeoides	ICPW 152	32.1	28.4	150.1	123.2	34.9	36.1	14.5	12.8
C. scarabaeoides	ICPW 278	40.6	19.6	137.4	134.2	32.1	42.1	16.0	12.8
C. scarabaeoides	ICPW 280	33.1	14.0	142.0	128.5	36.9	36.2	13.5	13.0
C. scarabaeoides	ICPW 281	41.1	23.2	160.6	131.6	35.8	38.1	16.6	13.2
Dunbaria ferruginea	ICPW 178	38.2	51.4	194.3	147.6	33.4	36.0	18.0	12.8
Flemingia bracteata	ICPW 192	26.2	72.2	144.7	227.9	32.9	24.1	17.0	12.4
F. stricta	ICPW 202	100.2	105.4	212.9	248.0	25.7	26.4	18.3	12.6
Paracalyx scariosa	ICPW 207	11.4	134.9	124.7	175.8	34.3	27.1	18.2	13.6
Rhynchosia aurea	ICPW 210	15.0	11.5	129.0	125.2	33.6	35.0	16.8	14.0
R. bracteata	ICPW 214	15.0	140.8	167.3	233.7	32.2	25.9	17.2	12.0
C. cajan (S)	ICPL 87	78.3	237.7	252.8	271.2	24.1	21.7	14.7	10.8
C. cajan (R)	ICPL 332	72.1	181.5	227.4	245.4	29.1	24.3	17.2	12.8
SE ±		4.22	3.00	2.43	7.00	0.49	1.63	0.97	1.28
LSD at $P = 0.05$		14.7	8.34	8.5	19.46	1.91	4.50	2.02	9.92
Fp		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.01	<0.001

ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; S, susceptible check; R, resistant check; SE, standard error; LSD, least significant difference.

Table 3. Expression of antibiosis to *Helicoverpa armigera* in artificial diet having different amounts of lyophilized leaf and pod powders of cultivated and wild pigeonpeas (ICRISAT, Patancheru, India)

	Larval weight (day 10; mg)		Pupal weight (mg)		Larval period (days)		Pupal period (days)	
Accession	Leaf powder	Pod powder	Leaf powder	Pod powder	Leaf powder	Pod powder	Leaf powder	Pod powder
Test genotype								
ICPW 83 (5 g)	30.7	97.9	255.4	308.2	24.0	20.0	12.7	11.7
ICPW 83 (10 g)	9.4	34.5	260.7	296.3	27.0	26.3	15.0	14.0
ICPW 83 (15 g)	5.6	8.3	124.8	160.9	34.3	35.3	14.3	15.0
ICPW 83 (20 g)	2.4	4.0	66.7	—	39.7	38.0	—	—
Resistant check								
ICPL 332 (5 g)	51.7	244.4	290.3	307.9	21.7	18.3	12.3	11.7
ICPL 332 (10 g)	47.1	140.0	293.2	327.4	25.7	21.7	13.7	12.3
ICPL 332 (15 g)	6.6	78.8	141.2	276.8	26.3	25.0	12.3	13.7
ICPL 332 (20 g)	4.0	12.1	109.4	223.0	25.3	27.0	12.7	16.0
Susceptible check								
ICPL 87 (5 g)	71.7	329.5	313.3	344.5	16.3	14.3	10.7	9.3
ICPL 87 (10 g)	57.0	314.6	315.4	326.5	17.7	16.0	12.3	12.0
ICPL 87 (15 g)	15.4	109.3	231.3	291.5	21.7	18.7	11.7	11.7
ICPL 87 (20 g)	8.6	57.6	169.6	229.2	20.0	21.7	12.3	11.7
Artificial diet	237.2	347.7	295.9	278.5	11.7	12.3	10.3	9.7
SE ±	7.22	84.7	3.78	14.45	0.49	0.78	0.39	1.52
LSD at $P = 0.05$	21.07	247.1	9.73	42.37	1.44	2.29	1.13	NS
Fp	<0.001	0.018	<0.001	<0.01	<0.001	<0.01	<0.001	0.117

ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; —, not observed; NS, not significant; SE, standard error; LSD, least significant difference.

H. armigera in different accessions of wild relatives of pigeonpea.

The weights of the larvae reared on artificial diets with 10 g leaf powder of wild relatives of pigeonpea were significantly lower (<25 mg per larva) compared with the larvae reared on diets with leaf powder of cultivated pigeonpea (44.0 and 53.3 mg for ICPL 332 and 87, respectively), and the standard artificial diet (469.6 mg) (Table 4). Larvae weighed <20 mg when reared on diets having leaf powder of *C. acutifolius*, *C. sericeus* (ICPW 160), *C. scarabaeoides* (except for ICPW 137, 141 and 152), *C. platycarpus* and *P. scariosa* compared with the 53.3 mg in the ICPL 87 diet. The pupae weighed >300 mg when the insects were reared on diets with leaf powder of *C. albicans* (ICPW 13), *C. cajanifolius* (ICPW 28 and 29), *C. lineatus* (ICPW 41), *C. scarabaeoides* (ICPW 125, 130, 141 and 152), *D. ferruginea* (ICPW 178), *F. stricta* (ICPW 202), *R. bracteata* (ICPW 214), *C. platycarpus* (ICPW 68), and *C. cajan* (ICPL 332 and 87) compared with <250 mg in insects reared on diets containing leaf powder of *C. sericeus* (ICPW 159 and 160) and *C. scarabaeoides* (ICPW 137). The larvae took >25 days for pupation when reared on diets with leaf powder of *C. cajanifolius*, *C. lineatus*, *C. sericeus*, *C. scarabaeoides* (except on ICPW 125), *D. ferruginea*, *F. bracteata*, *F. stricta*, *C. platycarpus*, *R. aurea* and *P. scariosa* compared with 18.7, 25.3 and 12.3 days on ICPL 87 and 332, and the standard artificial diet, respectively.

Larval weights were <50 mg in insects reared on artificial diets with lyophilized pod powder of *C. acutifolius* (ICPW 1), *C. lineatus* (ICPW 40 and 41), *C. scarabaeoides* (ICPW 83), *C. platycarpus* (ICPW 68) and *R. aurea* (ICPW 210) compared with 339.6 mg on diet with pod powder of ICPL 87, 137.1 mg on diet with pod powder of ICPL 332, and 407.7 mg on the standard artificial diet (Table 4). Weights of the larvae reared on diets with pod powder of *F. stricta* (ICPW 202) and *R. bracteata* (ICPW 214) were similar to those reared on cultivated pigeonpea. Larvae took >25 days to complete the development when reared on artificial diets with pod powder of *C. acutifolius* (ICPW 2), *C. lineatus* (ICPW 41), *C. sericeus* (ICPW 159 and 160), and *D. ferruginea* (ICPW 178), *C. platycarpus* (ICPW 68), *C. scarabaeoides* (except on ICPW 125), *P. scariosa* (ICPW 207) and *R. aurea* (ICPW 210), compared with 15.7 days on diet with pod powder of ICPL 332, and 12.7 days on the standard artificial diet. Pupal period was 14.7 days on diets with pod powder of ICPW 83 and 14.0 days with ICPW 280 (*C. scarabaeoides*) compared

Table 4. Survival and development of *Helicoverpa armigera* on artificial diet with lyophilized leaf and pod powder of wild relatives of pigeonpea (ICRISAT, Patancheru, India)

		Larval weight (mg; day 10)		Pupal weight (mg)		Larval period (days)		Pupal period (days)	
Species	Accession number	Leaves	Pods	Leaves	Pods	Leaves	Pods	Leaves	Pods
Cajanus acutifolius	ICPW 1	12.5	32.6	288.3	284.8	19.3	23.3	12.5	11.3
C. acutifolius	ICPW 2	12.6	52.5	254.6	299.5	21.0	26.0	13.3	12.3
C. albicans	ICPW 13	34.3	137.5	300.1	324.8	22.0	21.0	12.7	11.3
C. albicans	ICPW 14	37.6	127.6	266.0	323.4	23.3	24.0	14.0	12.3
C. cajanifolius	ICPW 28	41.4	120.6	317.4	318.5	24.7	20.0	11.3	11.0
C. cajanifolius	ICPW 29	26.8	131.1	313.9	300.7	25.7	21.3	12.3	8.7
C. lineatus	ICPW 40	27.4	45.0	297.1	272.7	26.0	23.7	12.3	13.7
C. lineatus	ICPW 41	22.3	40.4	310.6	291.5	25.7	26.0	13.3	12.3
C. sericeus	ICPW 159	24.0	58.5	230.4	320.5	26.0	28.0	13.3	11.3
C. sericeus	ICPW 160	12.5	54.4	243.9	311.3	27.3	30.0	13.3	12.3
C. platycarpus	ICPW 68	15.0	27.9	307.7	302.6	26.0	28.0	13.3	13.3
C. scarabaeoides	ICPW 83	9.5	31.9	289.9	314.6	27.7	28.3	14.3	14.7
C. scarabaeoides	ICPW 90	10.4	58.0	278.1	283.1	27.3	25.7	12.3	13.3
C. scarabaeoides	ICPW 94	14.1	71.9	292.0	299.7	26.7	27.0	12.7	13.3
C. scarabaeoides	ICPW 116	13.2	60.2	275.3	334.2	25.0	24.7	12.7	13.3
C. scarabaeoides	ICPW 125	14.5	87.0	301.7	312.6	24.7	23.7	11.3	12.3
C. scarabaeoides	ICPW 130	12.1	108.0	305.3	277.5	27.0	28.0	13.3	13.0
C. scarabaeoides	ICPW 137	22.6	78.0	213.5	311.3	25.3	25.3	12.3	13.7
C. scarabaeoides	ICPW 141	28.1	64.2	307.9	288.6	27.3	27.0	13.0	12.0
C. scarabaeoides	ICPW 152	38.1	105.4	311.4	304.1	25.7	25.0	12.7	13.3
C. scarabaeoides	ICPW 278	17.2	54.6	299.4	300.0	26.7	26.0	12.3	12.3
C. scarabaeoides	ICPW 280	18.2	74.6	267.7	308.2	28.7	26.7	13.0	14.0
C. scarabaeoides	ICPW 281	15.5	77.4	267.2	258.7	27.0	25.3	13.0	13.0
Dunbaria ferruginea	ICPW 178	26.8	104.6	312.1	312.1	27.0	25.0	13.0	13.3
Flemingia bracteata	ICPW 192	27.2	97.9	296.7	303.3	28.3	24.3	11.3	12.0
F. stricta	ICPW 202	48.1	216.0	325.6	317.8	28.0	23.3	12.3	12.0
Paracalyx scariosa	ICPW 207	12.0	95.9	270.7	281.5	33.3	25.0	13.7	14.3
Rhynchosia aurea	ICPW 210	39.8	26.5	296.0	281.4	27.7	28.7	13.7	13.0
R. bracteata	ICPW 214	13.1	215.7	322.7	355.5	23.3	19.0	11.7	11.3
C. cajan (S)	ICPL 87	53.3	339.6	352.5	385.7	18.7	15.7	12.3	12.0
C. cajan (R)	ICPL 332	44.0	137.1	341.8	328.1	25.3	23.3	13.7	11.7
Artificial diet		469.6	407.7	334.4	324.0	12.3	12.7	10.7	10.7
SE ±		6.85	40.00	19.93	9.71	0.66	0.48	0.46	0.90
LSD at $P = 0.05$		19.00	114.00	56.00	28.00	1.91	1.34	1.27	2.55
Fp		<0.001	<0.001	<0.001	<0.001	<0.001	0.001	<0.001	0.002

ICRISAT, International Crops Research Institute for the Semi-Arid Tropics; S, susceptible check; R, resistant check; SE, standard error; LSD, least significant difference.

with 12 days in diets with pod powder of ICPL 87 and 10.7 days on the standard artificial diet.

Discussion

Female *H. armigera* oviposit in captivity even on inert substrates. However, under natural conditions, the pod borer females prefer to lay eggs on the host plant during the flowering stage (Firempong and Zalucki, 1990), which could be due to an increase in chemical attractiveness of the crop and availability of fruiting bodies for feeding by the neonate larvae (Zalucki *et al.*, 1986; Hartlieb and Rembold, 1996). In pigeonpea, *H. armigera* prefers to lay eggs on flowers, while the leaves are preferred least. Pigeonpea genotypes showing resistance to *H. armigera* under field conditions also exhibit oviposition non-preference under laboratory conditions (Kumari *et al.*, 2006), suggesting that laboratory tests can be used to assess antixenosis for oviposition to *H. armigera*.

The no-choice, dual-choice and multi-choice cage tests conducted in this study to assess the level of

antixenosis to *H. armigera* revealed significant differences in number of eggs laid on different species, and within different accessions of the same species. All the accessions of wild relatives of pigeonpea showed antixenosis for oviposition under multi-choice (except in *F. stricta*) and dual-choice (except for *F. stricta*) conditions, of which accessions belonging to *C. acutifolius*, *C. albicans*, *C. sericeus*, *C. scarabaeoides*, *F. stricta*, *P. scariosa*, *R. aurea* and *R. bracteata* also showed antixenosis for oviposition under no-choice conditions. Presence of non-glandular trichomes in these accessions/species might be one of the reasons for oviposition non-preference (Peter *et al.*, 1995; Romeis *et al.*, 1999). *C. acutifolius* (ICPW 2), *C. cajanifolius* (ICPW 28 and 29), *C. lineatus* (ICPW 40), *D. ferruginea* (ICPW 178) and *F. bracteata* (ICPW 192), which have a high density of glandular trichomes, were preferred as a substrate for oviposition (236–425 eggs per female). The accessions exhibiting high levels of antixenosis for oviposition under no-choice, dual-choice and multi-choice conditions, i.e. *C. acutifolius* (ICPW 1), *C. albicans* (ICPW 13 and 14), *C. sericeus* (ICPW 159 and 160), *C. platycarpus* (ICPW 68), *C. scarabaeoides* (ICPW 83, 90, 94, 125, 137, 141 and 280), *P. scariosa* (ICPW 207) and *R. aurea* (ICPW 210), can be exploited for developing pigeonpea cultivars with stable resistance to *H. armigera*.

Expression of antibiosis to *H. armigera* varied significantly among the wild relatives of pigeonpea. Lower larval weights and prolonged post-embryonic development were observed in insects reared on leaves when compared with those reared on flowers and pods of wild relatives of pigeonpea, which could be due to poor nutritional quality of the leaves and/or due to high concentration of secondary metabolites in the leaves. Compared with the susceptible cultivated–susceptible pigeonpea check, the larval and pupal weights of *H. armigera* were significantly lower when reared on the leaves and/or pods of several wild relatives of *C. cajan*. Similarly, the larval and/or pupal periods were also prolonged significantly in insects reared on leaves or pods of several wild relatives of pigeonpea, indicating high levels of antibiosis to *H. armigera* in some accessions of the wild pigeonpeas. Maximum differences in insect development between the resistant and susceptible genotypes were observed on diets containing 10 g of lyophilized leaf or pod powder, suggesting that diet incorporation assay can be used to assess antibiosis to *H. armigera* under uniform conditions in the laboratory. Very high levels of antibiosis to *H. armigera* were observed in artificial diets containing leaf and/or pod powder of several wild relatives of *C. cajan*.

Under natural conditions, *H. armigera* larvae feed on leaves only when no flowers or pods are available (Sison and Shanower, 1994). Mortality of early instars and prolonged development are good indicators of antibiosis against insect pests (Dahms, 1972; Slansky, 1982). Adverse affects of *C. scarabaeoides* accessions and their F_1 derivatives have been observed earlier on *H. armigera* larvae (Dodia *et al.*, 1996). Antibiosis to *H. armigera* in wild relatives of pigeonpea was also confirmed by incorporating lyophilized leaf and pod powders into the artificial diet. Incorporation of 10 g of lyophilized leaf or pod powder was sufficient to assess antibiosis to *H. armigera*. Larval and pupal weights and larval survival were greater in insects reared on diets containing lyophilized leaf or pod powder compared with larvae reared on the intact leaves, flowers and pods. This may be due to the availability of more nutrients in the artificial diet. Similar results were earlier observed in diets containing *C. scarabaeoides* pod powder (Yoshida and Shanower, 2000). The levels of resistance to *H. armigera* observed in the artificial diets with lyophilized leaf or pod powder were slightly different than those observed on the intact plant parts, suggesting that physical factors such as trichomes and pod wall toughness may also contribute to host plant resistance to *H. armigera*.

Wild relatives of pigeonpea such as *C. scarabaeoides*, *C. acutifolius*, *C. sericeus*, *C. cajanifolius* and *C. platycarpus* can be crossed easily with the cultivated pigeonpea, and hence there is considerable potential to exploit them for crop improvement. Some of the wild relatives of pigeonpea have already been exploited for developing cytoplasmic male-sterile lines for hybrid production (Saxena *et al.*, 2006). The accessions of wild relatives of pigeonpea that can be easily crossed with the cultivated pigeonpea, and showing high levels of antixenosis and antibiosis to *H. armigera*, can be used to increase the levels and diversify the bases of resistance to this insect in cultivated pigeonpea, both in the self-pollinated varieties as well as in hybrid parents for sustainable crop production.

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