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Morphological and chemical components of resistance to pod borer, *Helicoverpa armigera* in wild relatives of pigeonpea

H. C. Sharma · G. Sujana · D. Manohar Rao

Abstract Host plant resistance is an important component for minimizing the losses due to the pod borer, *Helicoverpa armigera,* which is the most devastating pest of pigeonpea. An understanding of different morphological and biochemical components of resistance is essential for developing strategies to breed for resistance to insect pests. Therefore, we studied the morphological and biochemical components associated with expression of resistance to *H. armigera* in wild relatives of pigeonpea to identify accessions with a diverse combination of characteristics associated with resistance to this pest. Among the wild relatives, oviposition non-preference was an important component of resistance in *Cajanus scarabaeoides,* while heavy egg-laying was recorded on *C. cajanifolius* (ICPW 28) and *Rhynchosia bracteata* (ICPW 214). Accessions belonging to *R. aurea, C. scarabaeoides, C. sericeus, C. acutifolius*, and *Flemingia bracteata* showed high levels of resistance to *H. armigera,* while *C. cajanifolius* was as susceptible as the susceptible check, ICPL 87. Glandular trichomes (type A) on the calyxes and pods were associated with susceptibility to *H. armigera,* while the non-glandular trichomes (trichome type C and D) were associated with resistance to this insect. Expression of resistance to *H. armigera* was also associated with low amounts of sugars and high amounts of tannins and polyphenols.

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Accessions of wild relatives of pigeonpea with non-glandular trichomes (type C and D) or low densities of glandular trichomes (type A), and high amounts of polyphenols and tannins may be used in wide hybridization to develop pigeonpea cultivars with resistance to *H. armigera.*

Introduction

More than 200 species of insects feed on pigeonpea, of which the pod borer, *Helicoverpa armigera* (Hubner) (Lepidoptera: Noctuidae), is the most damaging pest. Since *H. armigera* has developed high levels of resistance to insecticides, it has become difficult to control this pest on pigeonpea and several other crops with conventional insecticides (Kranthi et al. 2002; Sharma 2005). Losses due to this pest in pigeonpea have been estimated at US$317 million in the semi-arid tropics (ICRISAT 1992). Farmers often resort to heavy use of insecticides to control this pest, and therefore, there is a need to develop alternative methods to minimize the extent of losses. Development of insect-resistant cultivars has a considerable potential for use in integrated pest management, particularly under subsistence farming conditions in developing countries (Sharma 2005). However, screening of more than 14,000 accessions of pigeonpea for resistance to *H. armigera* has revealed low to moderate levels of resistance in the cultivated genotypes (Reed and Lateef 1990). However, a few accessions of the wild relatives of pigeonpea have shown high levels of resistance to *H. armigera* (Sharma et al. 2001; Green et al. 2006).

Several morphological traits such as pod toughness, structure of pod wall, and trichomes on the pod surface have been reported to be associated with resistance to *H. armigera* (Shanower et al. 1997). The nature and density of trichomes on the pods of different accessions of wild relatives of pigeonpea and their association with insect resistance are yet to be investigated, although some information has been generated on pigeonpea and the closely related wild species, *Cajanus scarabaeoides*. Besides the morphological traits, chemical compounds in trichome exudates and on pod wall surface also influence the host plant selection and colonization by *H. armigera* (Hartlieb and Rembold 1996; Green et al. 2002, 2003). Dense nonglandular trichomes (type C) on pods of wild pigeonpea possibly act as a physical barrier to the feeding by the young *H. armigera* larvae (Romeis et al. 1999), while the glandular trichomes (type A) in *C. cajan* act as attractants (Hartlieb and Rembold 1996) or phagostimulants for *H. armigera* (Green et al. 2003). Chemicals extracted in acetone from *C. scarabaeoides* pod surface result in feeding inhibition, whereas compounds extracted in methanol from the pod surface of cultivated pigeonpea act as phagostimulants (Romeis et al. 1999; Green et al. 2003). In addition, pigeonpea also contains anti-nutritional factors such as proteinase inhibitors, oligosaccharides, phenols, tannins, and phytic acid (Singh 1988), which may influence the host plant suitability to *H. armigera*. Therefore, the present studies were undertaken to ascertain the role of trichomes, and the amounts of soluble sugars, proteins, polyphenols, and tannins in the pods of wild relatives of pigeonpea in relation to expression of resistance to *H. armigera*.

Materials and methods

Plant material

Twenty-nine accessions belonging to 12 species of wild relatives of pigeonpea were evaluated for resistance to *H. armigera* along with cultivated pigeonpea (ICPL 87—susceptible check and ICPL 332—resistant check). The wild species included 12 accessions of *Cajanus scarabaeoides* (ICPW 83, ICPW 90, ICPW 94, ICPW 116, ICPW 125, ICPW 130, ICPW 137, ICPW 141, ICPW 152, ICPW 278, ICPW 280, and ICPW 281), 2 accessions each of *C. cajanifolius* (ICPW 28 and ICPW 29), *C. sericeus* (ICPW 159 and ICPW 160), *C. albicans* (ICPW 13 and ICPW 14), *C. acutifolius* (ICPW 1 and ICPW 2), and *C. lineatus* (ICPW 40 and ICPW 41), and one accession each of *C. platycarpus* (ICPW 68), *Rhynchosia bracteata* (ICPW 214), *R. aurea* (ICPW 210), *Dunbaria ferruginea* (ICPW 178), *Flemingia bracteata* (ICPW 192), *F. stricta* (ICPW 202), and *Paracalyx scariosa* (ICPW 207). The

seeds of these accessions, along with those of cultivated pigeonpea genotypes were sown on deep black soils (Vertisols) during the rainy season. To improve seed germination, the seed testa was cut at one end with a sharp knife, soaked in water overnight, and treated with thiram (1 g per 100 seeds). The test genotypes were grouped into three sets based on maturity (early = ≤60 days, medium = 60–120 days, and late = ≥120 days to flowering). There were three replications for each genotype, and the genotypes in each maturity were planted in a randomized complete block design. The seeds were sown on ridges 75 cm apart, and there were four rows in each plot, 2 m long. The plants were thinned to a spacing of 30 cm between the plants 30 days after seedling emergence. The experiments were repeated during the 2001–2003 rainy seasons. The experiments were planted so that the test genotypes were exposed to the peak abundance of *H. armigera* during November–December (Srivastava and Pimbert 1990). The annual species with short maturity cycle, including the cultivated pigeonpea, were planted twice at monthly intervals during June–July, while the perennial ones were planted only once in June with the onset of monsoon season so as to have the leaves, flowers, and the pods from all the accessions during the same period in December. Standard agronomic practices were followed for raising the crop, including application of basal fertilizer [N:P:K::100:60:40 kg ha^{-1}] and top dressing (urea 50 ha^{-1}). A fungicide (metalaxyl) spray (1.0 kg active ingredient (*ai*) ha^{-1}) was applied to control *Fusarium* wilt. The crop was raised between June and mid-October under rainfed conditions, and irrigated at monthly intervals between November and February. Wooden pegs (1.5 m high) were used to provide support for *C. scarabaeoides* and *C. platycarpus* accessions, which have a creeping habit.

Oviposition, larval density, and pod damage by *H. armigera* under natural infestation in the field

The test material was evaluated for oviposition, larval density, and pod damage under natural infestation in the field. Data were recorded on the numbers of eggs, larvae, and pod damage on inflorescences from five plants (that were at the flowering stage during the same period). For this purpose, five inflorescences (20 cm long) from five plants were tagged with a ribbon at the pre-flowering stage in each plot. Numbers of eggs and larvae were recorded on the tagged portion (20 cm) of the inflorescences at 5, 7, 9, 20, and 30 days after tagging the inflorescences. The numbers of eggs and larvae recorded in each plot across observation dates were pooled (as the numbers of eggs and larvae on some of the test entries were quite low), and then subjected to analysis of variance. The total number of pods and the pods damaged by *H. armigera* were recorded at

maturity in pods harvested from tagged inflorescences in each plot.

Trichome types and their density on calyxes and pods

Trichome types and their density on different accessions of wild relatives of pigeonpea were recorded on the pods and calyxes of different accessions of wild relatives of pigeonpea (Shanower et al. 1997; Romeis et al. 1999). For this purpose, 5 flowers or pods were collected from five plants in each plot, and preserved in acetic acid:ethanol (1:3). To record the trichome types and their density, the calyxes and the pods were examined at a magnification of 32× under a stereomicroscope (Carl Zeiss, Inc., Thornwood, New York), with an ocular measuring grid. Data were recorded on the numbers of different types of trichomes (type A, B, C, and D) and their density within the microscopic field. Type A trichomes are glandular and secrete a liquid, which is present in the form of droplets at the tips of these trichomes (Fig. 1). Type B trichomes contain an oily substance, and are globular in structure. Type C and D trichomes are non-glandular, but the type D trichomes are much longer than the type C trichomes. Type E trichomes are multi-lobed and glandular, but their numbers were too low and were not counted in the present studies.

Biochemical composition of leaves and pods

To determine the amounts of total soluble sugars, soluble proteins, condensed tannins, and polyphenols, the leaves and pods of each accession were collected from the five plants tagged at random in the field, and oven dried at 55°C for 3 days. The oven-dried material was powdered in a Willey mill and defatted by using hexane solution (100 ml g^{-1}). The amounts of sugars, proteins, condensed tannins, and polyphenols were determined for each accession. There were three replicates for each estimation in a completely randomized design.

For estimating total soluble sugars, 100 mg of defatted leaf or pod powder was used. The material was extracted with hot aqueous-ethyl alcohol. On treatment with phenol–sulfuric acid, the sugars produced a stable golden yellow color (Dubois et al. 1956). Absorbance of the golden yellow color was measured at 490 nm. Glucose standards with concentrations of 25, 50, 75, 100, and 125 mg ml^{-1} were used to prepare the standard curve for estimating the sugar content in the test material. Protein content in the pods was estimated by using Lowry's method (Lowry et al. 1951). A total of 300 μl of sample was prepared, and 20 μl of the supernatant was taken for estimating the proteins. The absorbance was recorded at 600 nm. Bovine serum albumin (BSA) was used as a standard at a concentration of 2 mg ml^{-1}.
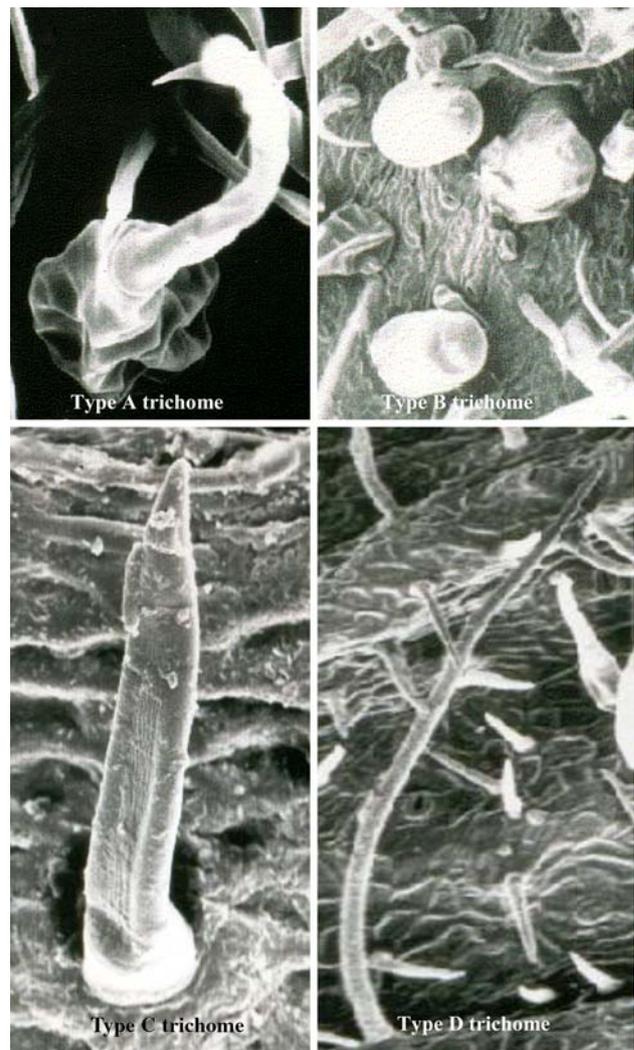
Fig. 1 Trichome types (A, B, C, and D) on the pod and leaf surfaces of pigeonpea and its wild relatives. *Type A* Long tubular glandular trichomes which secrete a liquid present in the form of droplets at the tips. *Type B* Globular in structure and contain an oily substance. *Type C* Short and non-glandular trichomes. *Type D* Longer than the type C trichomes, and are non-glandular

The amounts of polyphenols (which included tannins and low molecular weight phenolics) present in the leaves and pods of pigeonpea and its wild relatives were estimated by Folin Denis method (AOAC 1984). For this purpose, 100 ml of methanol–HCl (1 ml HCl in 99 ml of methanol) was added to 200 mg of defatted material. The absorbance was read at 760 nm using a spectrophotometer (Spectronic 21, Bausch and Lomb). A standard curve was prepared by adding 0–1 ml aliquots of standard tannic acid in HCl (with increments of 0.2 ml). Total phenolics were expressed as mg tannic acid equivalent g^{-1} dry matter of leaves or pods. The amounts of condensed tannins present in the leaves and pods of wild relatives of pigeonpea were estimated by vanillin–hydrochloric acid method (Price et al. 1978).

From the defatted material (leaf or pod), 100 mg sample was transferred to a centrifuge tube containing 2 ml of 1% acidic-methanol. Individual blanks were prepared for each extract by adding 5 ml of 4% HCl in methanol to 1 ml aliquot. The absorbance was recorded at 500 nm against the reagent blank in a spectrophotometer (Spectronic 21, Bausch and Lomb). Standard curve was prepared by plotting the average absorbance readings of the duplicate determinations of catechin concentrations, and expressed as mg tannic acid equivalents g^{-1} of dry matter.

Statistical analysis

The data for the two seasons were subjected to homogeneity test, and it was observed that there were no significant genotype × season interaction, and hence, pooled data across seasons was subjected to analysis of variance (ANOVA). The ANOVA was carried out by using Genstat Release 8.2. The significance of differences between the accessions was tested by F-test, and the treatment means were compared by least significant difference (LSD) at $P \leq 0.05$. Association of different morphological and chemical factors with the egg and larval numbers, and pod damage was determined by correlation analysis.

Results

Oviposition, larval density, and pod damage by *H. armigera* under natural infestation in the field

There was no egg laying on ICPW 137, ICPW 152 (*C. scarabaeoides*), and ICPW 210 (*R. aurea*), while a few eggs (0.1 eggs per 5 inflorescences) were recorded on ICPW 94 and ICPW 130 (*C. scarabaeoides*) compared to 6.4 eggs per 5 inflorescences of the pigeonpea variety, ICPL 87 (Table 1). There were no *H. armigera* larvae on *C. scarabaeoides* accessions ICPW 94, ICPW 137, and ICPW 152; while less than one larva per 5 inflorescences was recorded on *R. aurea* (ICPW 210) and *C. platycarpus* (ICPW 68) compared to 8.40 larvae on ICPL 87. *Helicoverpa armigera* damage in the pods of early duration accessions of the wild relatives ranged from 0.0% in *C. scarabaeoides* (ICPW 137) to 4.12% in *C. platycarpus* (ICPW 68) compared to 83.8% damage in the pods of cultivated pigeonpea cultivar, ICPL 87.

In the medium-duration group, there was no egg laying on *C. scarabaeoides* accessions ICPW 83, ICPW 90, ICPW 116, ICPW 125, ICPW 141, ICPW 278, ICPW 280, and ICPW 281. Egg-laying was quite high on *C. cajanifolius* [ICPW 28 (10.6 eggs per 5 inflorescences)] and the cultivated pigeonpea variety, ICPL 87 (4.5 eggs) (Table 2). There were no larvae on ICPW 90, ICPW 125, ICPW 278, ICPW 280, and ICPW 281; while 0.1 larvae per 5 inflorescences were recorded on ICPW 83 and ICPW 141 (*C. scarabaeoides*) compared to 4.7 larvae on ICPL 87. Pod damage was quite high in the cultivated pigeonpea, ICPL 87 (83.0%) and ICPW 28 (93.3%) of *C. cajanifolius;* while no damage was observed on ICPW 83 (*C. scarabaeoides*).

In the long-duration group, no egg-laying was observed on *C. acutifolius* (ICPW 2), while low egg-laying (<0.5 eggs per 5 inflorescences) was recorded on *C. acutifolius* (ICPW 1), *C. albicans* (ICPW 14), *C. lineatus* (ICPW 40 and ICPW 41), *F. bracteata* (ICPW 192), and *P. scariosa* (ICPW 207) as compared to that on ICPL 87 (1.8 eggs; Table 3). Less than one larva was recorded on *C. acutifolius*, *C. albicans*, *C. lineatus*, *F. bracteata*, *F. stricta,* and *P. scariosa* accessions compared to 1.9 larvae on ICPL 87.

Table 1 Oviposition, larval numbers, and pod damage by *H. armigera* in short-duration wild relatives of pigeonpea under natural infestation (ICRISAT, Patancheru, India)

Species	Accession	No. of eggs*	No. of larvae*	Pod damage (%)
Cajanus platycarpus	ICPW 68	1.00[b]	0.87[b]	4.12[a]
C. scarabaeoides	ICPW 94	0.07[a]	0.00[a]	0.43[a]
C. scarabaeoides	ICPW 130	0.07[a]	0.20[a]	0.91[a]
C. scarabaeoides	ICPW 137	0.00[a]	0.00[a]	0.00[a]
C. scarabaeoides	ICPW 152	0.00[a]	0.00[a]	0.60[a]
Rhynchosia aurea	ICPW 210	0.00[a]	0.34[ab]	1.07[a]
C. cajan (S)	ICPL 87	6.38[c]	8.40[c]	83.83[b]
F-test (df 6, 12)		10.22**	7.14**	47.53**
LSD at *P* 0.05		0.48	0.59	31.36

S Susceptible check

* Number of eggs or larvae per five inflorescences across five observation dates. Figures followed by the same letter within a column are not significantly different at $P \leq 0.05$

** F-test significant at $P < 0.01$

Table 2 Oviposition, larval numbers, and pod damage by *H. armigera* in medium-duration wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Species	Accession	No. of eggs*	No. of larvae*	Pod damage (%)
C. cajanifolius	ICPW 28	10.60[c]	4.33[b]	93.33[e]
C. cajanifolius	ICPW 29	5.47[b]	1.67[a]	65.83[d]
C. sericeus	ICPW 159	0.93[a]	0.80[a]	0.27[a]
C. sericeus	ICPW 160	0.20[a]	0.27[a]	0.16[a]
C. scarabaeoides	ICPW 83	0.00[a]	0.07[a]	0.00[a]
C. scarabaeoides	ICPW 90	0.00[a]	0.00[a]	0.34[a]
C. scarabaeoides	ICPW 116	0.00[a]	0.13[a]	0.24
C. scarabaeoides	ICPW 125	0.00[a]	0.00[a]	0.57[a]
C. scarabaeoides	ICPW 141	0.00[a]	0.07[a]	0.13[a]
C. scarabaeoides	ICPW 278	0.00[a]	0.00[a]	0.58[a]
C. scarabaeoides	ICPW 280	0.00[a]	0.00[a]	0.17[a]
C. scarabaeoides	ICPW 281	0.00[a]	0.00[a]	0.26[a]
Dunbaria ferruginea	ICPW 178	0.07[a]	0.20[a]	27.47[b]
C. cajan (S)	ICPL 87	4.53[b]	4.73[b]	83.02[e]
C. cajan (R)	ICPL 332	0.40[a]	0.93[a]	49.00[c]
F-test (df 14,28)		3.00**	4.36**	18.24**
LSD at *P* 0.05		1.82	2.13	10.0

S Susceptible check, *R* Resistant check

* Number of eggs or larvae per five inflorescences across five observation dates. Figures followed by the same letter within a column are not significantly different at $P \leq 0.05$

** F-test significant at $P < 0.01$

Pod damage was quite low (0–7.1%) in the wild relatives compared to 80.0% pod damage in the pigeonpea cultivar, ICPL 87.

Trichome types and their density on calyxes and pods

The density and distribution of trichomes (type A, B, C, and D) varied significantly on the calyxes among the species, but there was little variation within the species (Table 4). There was no significant variation in the density of type A trichomes between *C. acutifolius* (ICPW 1 and ICPW 2), *C. cajanifolius* (ICPW 29), *C. lineatus* (ICPW 41), and the cultivated pigeonpea, ICPL 87. Very high trichome density of type A trichomes was observed in cultivated pigeonpea variety, ICPL 332. The density of type A trichomes was very low on *C. albicans* (ICPW 14), *C. scarabaeoides* (ICPW 116, ICPW 141, ICPW 152, ICPW 280, and ICPW 281), *R. aurea* (ICPW 210), *C. albicans* (ICPW 13), and *C. sericeus* (ICPW 159). The density of type B trichomes was lower compared to other types of trichomes in all the species, except in *C. albicans* and *R. bracteata*. The highest numbers of type B trichomes were recorded on ICPL 332, but were absent in *D. ferruginea* and *C. scarabaeoides* (except ICPW 152). Density of type C type trichomes was high in *C. scarabaeoides* (ICPW 281), followed by *C. albicans* (ICPW 13 and ICPW

14). The density of type C trichomes was lowest in the cultivated pigeonpea varieties ICPL 87 and ICPL 332. Density of type D trichomes was lowest in *R. aurea* (ICPW 210), followed by *C. platycarpus* (ICPW 68), and *P. scariosa* (ICPW 207). The type D trichome density was high in *C. sericeus* (ICPW 159), and *C. scarabaeoides* (ICPW 94, ICPW 116, and ICPW 137) as compared to that on the cultivated pigeonpea. Type D trichomes were absent in *C. acutifolius* and *R. bracteata*.

Four types of trichomes (A, B, C, and D) were recorded on the pods of wild species of pigeonpea. Type A trichomes were absent in *C. sericeus* and *C. scarabaeoides* (Table 4). Density of type A trichome was significantly greater on the pods of *R. bracteata* (ICPW 214) and *C. platycarpus* (ICPW 68) compared to that on the pods of *P. scariosa* (ICPW 207), *F. stricta* (ICPW 202), and the cultivated pigeonpea varieties ICPL 332 and ICPL 87. Significantly lower numbers of type B trichome were observed on the pods of *C. platycarpus* (ICPW 68) and *F. bracteata* (ICPW 192) as compared to that on the pods of *C. lineatus* (ICPW 40 and ICPW 41), *C. albicans* (ICPW 13, and ICPW 14), *C. cajanifolius* (ICPW 28 and ICPW 29), and the cultivated pigeonpea variety, ICPL 87. The density of type C trichomes was quite low on the pods of *C. albicans* (ICPW 13) and *C. acutifolius* (ICPW 1) as compared to that on the pigeonpea variety, ICPL 87. The

Table 3 Oviposition, larval numbers, and pod damage by *H. armigera* in long-duration wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Species	Accession number	No. of eggs*	No. of larvae*	Pod damage (%)
C. acutifolius	ICPW 1	0.13[a]	0.07[ab]	1.32[a]
C. acutifolius	ICPW 2	0.00[a]	0.00[a]	0.45[a]
C. albicans	ICPW 13	0.68[a]	0.33[d]	0.30[a]
C. albicans	ICPW 14	0.14[a]	0.14[b]	0.00[a]
C. lineatus	ICPW 40	0.47[a]	0.40[d]	3.90[a]
C. lineatus	ICPW 41	0.27[a]	0.14[b]	3.27[a]
Flemingia bracteata	ICPW 192	0.13[a]	0.20[c]	0.38[a]
F. stricta	ICPW 202	0.54[a]	0.20[c]	0.64[a]
Paracalyx scariosa	ICPW 207	0.07[a]	0.13[bc]	3.61[a]
R. bracteata	ICPW 214	0.97[a]	1.06[e]	7.14[a]
C. cajan (S)	ICPL 87	1.81[b]	1.87[f]	80.00[b]
F-test (df 10, 20)		3.20**	6.55**	13.98**
LSD at *P* 0.05		0.78	0.09	11.04

S Susceptible check

* Number of eggs or larvae per five inflorescences across five observation dates. Figures followed by the same letter within a column are not significantly different at $P \leq 0.05$

** F-test significant at $P < 0.01$

density of type C trichomes on accessions of *C. scarabaeoides* was very high (>100 in all the accessions). Density of type D trichome was high on the pods of *C. sericeus*, followed by *R. aurea*, *C. lineatus,* and *C. scarabaeoides*. Density of type D trichomes was very low on the pods of *C. acutifolius, C. albicans, C. cajanifolius*, *F. bracteata, F. stricta, P. scariosa*, and *R. bracteata*.

Biochemical composition of leaves and pods

Total soluble sugars

The amounts of total soluble sugars were less than 5% on dry weight basis in accessions of *C. acutifolius* (ICPW 1 and ICPW 2), *C. albicans* (ICPW 13), *C. scarabaeoides* (ICPW 130, ICPW 137, ICPW 280, and ICPW 281), *C. cajanifolius* (ICPW 28), and *P. scariosa* (ICPW 207) compared to 5.62% in the leaves of ICPL 87 (Table 5). In case of pods, the sugar content was more than 5% in *C. albicans* (ICPW 13 and ICPW 14), and *R. bracteata* (ICPW 214), and less than 2.5% in *C. cajanifolius* (ICPW 28 and ICPW 29), *C. lineatus* (ICPW 40), *C. sericeus* (ICPW 159), *C. scarabaeoides* (except ICPW 125, ICPW 130, ICPW 278), *R. aurea* (ICPW 210), and *C. platycarpus* (ICPW 68). Sugar content in pods of all the accessions of wild relatives was significantly lower than that in the cultivated pigeonpea variety, ICPL 87 (7.1%). Sugar content in the leaves and pods of the *H. armigera* resistant cultivar, ICPL 332 was also significantly lower than that in the susceptible check, in ICPL 87.

Soluble proteins

Soluble protein content was lower (<2.0%) in the leaves of *C. lineatus*, *C. scarabaeoides* (except ICPW 83, ICPW 90, and ICPW 116), *F. bractaeta*, and *P. scariosa* than in the susceptible check, ICPL 87 (3.7%; Table 5). The accessions of *C. cajanifolius*, and *C. scarabaeoides* (except ICPW 125, ICPW 141, and ICPW 158) had more proteins (>2.95%) in the pods compared to that of the cultivated pigeonpea cultivar, ICPL 87 (1.94%). Protein content was low in the pods of *C. albicans* [ICPW 13 (0.8%) and ICPW 14 (0.9%)], and *R. aurea* [ICPW 210 (1.14%)]; while high amounts of proteins were recorded in the pods of *C. scarabaeoides* [ICPW 83 (4.2%) and ICPW 281 (4.2%)] compared to that in ICPL 87 (1.9%) and ICPL 332 (2.0%).

Total polyphenols

The concentrations of polyphenols were 83.7–177.4 mg g^{-1} (on dry weight basis) in the leaves of wild relatives of pigeonpea compared to 82.5 mg g^{-1} in ICPL 87 and 115 mg g^{-1} in ICPL 332. High amounts (>150 mg g^{-1}) of polyphenols were observed in the leaves of *C. scarabaeoides* (ICPW 94, ICPW 125, ICPW 137, and ICPW 281), and *F. stricta* (ICPW 202; Table 5). Amounts of polyphenols were greater (>100 mg g^{-1}) in the pods of *C. acutifolius, C. albicans, C. cajanifolius, C. lineatus* (ICPL 41), *C. sericeus, C. scarabaeoides* (ICPW 83, ICPW 90, ICPW 94, and ICPW 137), *D. ferruginea*, and *F. stricta* as compared to the cultivated pigeonpea (43.0 and 56.0 mg g^{-1} in ICPL 87 and ICPL 332, respectively).

Table 4 Density of different types of trichomes on calyxes and pods of wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Accession	Calyxes				Pods			
	A	B	C	D	A	B	C	D
ICPW 1	27.70^c	7.33^g	47.33^{ab}	0.00^a	21.33^{de}	5.00^{bc}	21.00^a	1.33^a
ICPW 2	27.30^c	5.00^f	42.00^{ab}	0.00^a	14.33^{cd}	5.33^{bc}	31.33^{bc}	1.00^a
ICPW 13	0.70^a	2.67^e	61.67^b	25.33^{abc}	4.33^a	36.67^h	18.67^a	2.33^{ab}
ICPW 14	0.30^a	1.67^d	67.67^b	32.00^{abcd}	2.67^a	25.67^g	27.67^{ab}	1.00^a
ICPW 28	29.30^c	1.33^{bc}	32.67^{ab}	16.33^{ab}	23.00^{def}	23.67^g	28.33^{ab}	0.22^a
ICPW 29	27.00^c	1.00^{bc}	27.67^a	25.33^{abc}	20.33^{de}	23.33^g	36.00^{bcd}	0.33^a
ICPW 40	34.00^c	1.33^{bcd}	59.33^b	16.00^{ab}	23.33^{def}	61.33^k	52.67^e	26.67^{gh}
ICPW 41	29.70^c	4.33^f	50.67^{ab}	22.33^a	20.67^{de}	48.33^j	42.33^{cde}	29.00^h
ICPW 159	0.70^a	0.67^{abc}	26.67^a	86.00^{ef}	0.00^a	17.67^f	26.67^{ab}	141.67^k
ICPW 160	1.00^a	0.33^{ab}	32.67^{ab}	66.00^{def}	0.00^a	13.33^e	28.00^{ab}	122.33^j
ICPW 68	5.00^{ab}	0.67^{abc}	33.67^{ab}	0.67^a	26.33^f	0.33^a	31.67^{bc}	7.67^{bc}
ICPW 83	0.00^a	0.00^a	46.00^{ab}	71.00^{ef}	0.00^a	5.67^{bcd}	141.67^{ij}	22.30^{efg}
ICPW 90	0.00^a	0.00^a	35.33^{ab}	76.33^{ef}	0.00^a	4.67^{bcd}	138.33^{ij}	25.00^{fgh}
ICPW 94	0.00^a	0.00^a	52.67^b	99.33^f	0.00^a	2.67^{ab}	117.00^{gh}	20.26^{ef}
ICPW 116	0.70^a	0.00^a	46.67^a	84.00^{ef}	0.00^a	7.33^d	148.67^j	22.42^{efg}
ICPW 125	1.00^a	0.00^a	42.00^{ab}	49.00^{bcd}	0.00^a	5.00^{bcd}	134.67^i	15.63^{de}
ICPW 130	0.00^a	0.00^a	56.67^b	63.67^{cdef}	0.00^a	2.00^{ab}	150.00^j	28.26^{gh}
ICPW 137	0.00^a	0.00^a	33.00^{ab}	82.00^{ef}	0.00^a	1.33^{ab}	102.00^f	15.52^{de}
ICPW 141	0.70^a	0.00^a	31.33^{ab}	66.00^{def}	0.00^a	4.00^{abcd}	156.33^j	16.85^{de}
ICPW 152	0.30^a	0.67^{abc}	55.33^b	36.00^{abcd}	0.00^a	4.67^{bcd}	152.00^j	18.53^e
ICPW 278	2.30^{ab}	0.00^a	32.67^{ab}	53.33^{bcde}	0.00^a	3.00^{abc}	118.33^{gh}	17.53^e
ICPW 280	0.30^a	0.00^a	52.00^b	72.33^g	0.00^a	7.00^{cd}	140.33^i	15.63^e
ICPW 281	0.70^a	0.00^a	70.33^b	48.67^{bcde}	0.00^a	5.33^{bcd}	133.33^i	22.15^{ef}
ICPW 178	5.00^b	0.00^a	31.33^{ab}	3.33^a	11.67^{bc}	41.00^i	52.00^e	22.33^{efg}
ICPW 192	12.00^c	2.67^e	40.33^{ab}	1.33^a	8.67^b	0.33^a	53.67^e	0.33^a
ICPW 202	2.30^{ab}	4.33^f	34.67^{ab}	2.33^a	1.00^a	22.33^g	123.67^g	0.00^a
ICPW 207	2.00^a	1.67^d	41.33^{ab}	0.67^a	0.67^a	3.33^{abc}	108.00^{fg}	1.00^a
ICPW 210	0.30^a	5.00^f	40.67^{ab}	0.33^a	4.33^a	9.33^{de}	37.00^{bcd}	49.67^i
ICPW 214	5.00^{ab}	4.67^f	40.67^{ab}	0.00^a	53.33^g	11.33^e	51.00^{de}	1.33^a
ICPL 87	27.33^c	1.00^{bc}	10.00^a	30.67^{abcd}	21.67^{def}	5.33^{bcd}	40.33^{cd}	8.00^{bc}
ICPL 332	47.00^d	15.00^h	12.33^a	56.67^{cde}	18.67^{de}	26.67^g	135.67^i	10.50^{cd}
F-test (df 30, 60)	210.71**	20.49**	70.32**	91.78**	119.64**	124.95**	199.30**	245.58**
LSD at *P* 0.05	10.13	1.98	41.53	38.29	4.81	4.11	10.21	6.49

S Susceptible check, *R* Resistant check

* Trichome density in the microscopic field at 32×. Figures followed by the same letter within a column are not significantly different at $P \leq 0.05$. For description of trichomes types, see Fig. 1

** F-test significant at $P < 0.01$

Condensed tannins

The levels of condensed tannins in the leaves were greater than those in the pods (Table 5). Amount of condensed tannins on dry weight basis in the leaves of ICPL 332 (0.1%), ICPL 87 (0.9%), and *C. cajanifolius* (ICPW 29) were quite low (0.32%), while high amounts of condensed tannins were observed in the leaves of ICPW 40 (18.4%) and ICPW 41 (13.2%) of *C. lineatus*. Higher amounts (>5%) of condensed tannins were recorded in the leaves of *C. acutifolius*, *C. lineatus*, *C. platycarpus*, *C. scarabaeoides* (except ICPW 83, and ICPW 152), *D. ferruginea*, *F. bracteata*, *F. stricta*, *P. scariosa*, and *P. aurea* as compared to that in the cultivated pigeonpea (0.88% in ICPL 87 and 0.08% in ICPL 332). Amounts of condensed tannins in the pods were high (>4%) in *C. acutifolius*, *C. albicans*, *C. cajanifolius*, *C. lineatus* (ICPW 41), *S. sericeus*, *C. scarabaeoides* (ICPW 83, ICPW 90, ICPW 94), *D. ferruginea*, *F. stricta*, *P. scariosa*, *R. bracteata* and the cultivated pigeonpea. The amounts of condensed tannins were greater in the

Table 5 Amounts of soluble sugars and proteins, polyphenols, and condensed tannins in the leaves and pods of wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Accession	Soluble sugars (% of dry matter)		Soluble proteins (% of dry matter)		Polyphenols (mg g^{-1} dry matter)		Condensed tannins (tannic acid equivalent g^{-1} dry matter)	
	Leaves	Pods	Leaves	Pods	Leaves	Pods	Leaves	Pods
ICPW 1	5.25^h	1.68^{fg}	3.44^{jk}	2.19^{bcde}	115.0^d	236.7^l	8.60^{def}	26.9^e
ICPW 2	5.12^{gh}	2.62^j	2.28^f	2.47^{cde}	130.0^{fg}	270.0^m	5.79^{abcde}	22.5^{cd}
ICPW 13	5.12^{gh}	5.25^n	3.51^{jk}	0.78^a	101.7^c	135.0^{hi}	3.24^{abdc}	61.0^e
ICPW 14	4.25^{def}	5.12^n	2.81^{hi}	0.95^{ab}	127.9^{ef}	173.3^k	1.21^{ab}	77.1^f
ICPW 28	5.37^h	2.14^h	2.19^e	3.31^{ef}	83.7^a	100.0^g	1.37^{ab}	5.8^a
ICPW 29	2.22^a	1.20^{cde}	3.62^{jk}	3.20^{ef}	103.3^d	110.0^g	0.32^a	7.9^a
ICPW 40	4.12^{de}	1.50^{ef}	2.00^{ef}	1.81^{abcd}	133.8^g	80.0^{ef}	18.36^g	3.2^a
ICPW 41	3.44^{bc}	3.37^k	2.01^{ef}	1.93^{abcde}	145.3^h	110.0^g	13.15^i	4.6^a
ICPW 159	4.68^{fg}	2.32^n	3.90^{kl}	1.62^{abcd}	104.2^c	145.0^j	3.27^{abc}	14.6^{bc}
ICPW 160	4.87^{gh}	4.50^l	3.68^{jk}	1.56^{abcd}	147.5^h	173.3^k	2.93^{abcd}	19.9^{bcd}
ICPW 68	3.87^{cd}	0.71^{ab}	2.41^{fgh}	1.65^{abcd}	105.0^c	55.3^b	7.57^{cdef}	3.7^a
ICPW 83	2.25^a	1.83^g	2.59^{gh}	4.17^f	123.0^{ef}	118.3^g	3.36^{abcd}	4.3^a
ICPW 90	3.12^b	1.15^{cd}	2.35^f	2.95^{def}	144.3^h	110.0^g	7.71^{cdef}	4.2^a
ICPW 94	3.87^c	1.05^{bc}	0.81^{ab}	3.08^{ef}	156.7^i	110.0^g	12.42^{fg}	4.3^a
ICPW 116	4.50^e	1.34^{de}	2.64^{gh}	3.69^f	113.3^d	80.0^{ef}	5.34^{abcd}	1.4^a
ICPW 125	4.62^{ef}	4.00^m	1.64^{cde}	2.67^{de}	177.4^k	52.7^{bc}	12.62^{fg}	1.9^a
ICPW 130	5.25^h	3.31^k	0.62^a	3.60^f	143.3^h	80.0^{ef}	11.53^{ef}	1.9^a
ICPW 137	5.25^h	1.99^h	1.89^{def}	2.97^{de}	175.0^k	100.0^g	10.47^{eff}	3.0^a
ICPW 141	3.35^b	0.86^b	1.89^{def}	2.82^{de}	127.5^{ef}	65.0^{cd}	7.13^{bcde}	2.7^a
ICPW 152	4.12^d	1.81^{gh}	1.67^{cde}	2.80^{de}	130.0^{fg}	46.7^{ab}	3.50^{abcd}	3.8^a
ICPW 278	4.50^{ef}	3.87	1.69^{cde}	3.49^f	127.5^{ef}	66.7^{cde}	11.23^{ef}	3.7^a
ICPW 280	5.37^h	1.91^{gh}	0.79^a	2.97^{def}	142.5^h	35.0^a	10.21^{ef}	2.7^a
ICPW 281	5.25^h	0.45^a	1.12^{abc}	4.17^f	162.5^j	67.0^{cde}	12.8^f	2.7^a
ICPW 178	4.00^d	4.87^m	2.22^{efg}	1.65^{abcd}	129.2^{efg}	110.0^g	5.99^{abcde}	4.6^a
ICPW 192	2.21^a	3.50^{kl}	1.39^{bcd}	1.87^{abcd}	92.5^b	35.0^a	6.50^{bcdef}	2.3^a
ICPW 202	2.28^a	4.50^m	3.23^{ij}	2.09^{bcd}	160.0^j	123.0^{gh}	6.52^{bcdef}	26.0^d
ICPW 207	5.12^g	3.68^l	1.67^{cd}	1.82^{abcd}	141.3^h	82.0^f	10.92^{ef}	12.8^b
ICPW 210	2.12^a	1.47^{ef}	2.68^{gh}	1.14^{abcd}	112.5^d	44.3^{ab}	6.79^{bcdef}	1.2^a
ICPW 214	3.25^b	5.62^o	4.41^l	2.25^{bcd}	110.0^d	73.7^{def}	2.15^{abc}	4.9^a
ICPL 87	5.62^h	7.12^p	3.66^{jk}	1.94^{abcd}	82.5^a	43.0^{ab}	0.88^{ab}	4.9^a
ICPL 332	4.87^g	3.00^j	2.86^h	1.98^{abcd}	115.0^d	56.0^{bc}	0.08^a	17.9^{bcd}
F-test (df 30, 60)	17.35**	229.22**	22.61**	428.52**	134.88**	214.32**	99.38**	210.00**
LSD at P 0.05	0.52	0.28	0.58	1.40	4.93	13.99	6.27	3.40

S Susceptible check, *R* Resistant check

Figures followed by the same letter within a column are not significantly different at $P \leq 0.05$

** F-test significant at $P < 0.01$

H. armigera resistant pigeonpea cultivar, ICPL 332 (17.9%) than in the susceptible cultivar (ICPL 87 (4.9%).

Correlation of morphological and biochemical traits with expression of resistance to *Helicoverpa armigera*

A significant and positive correlation was observed between the numbers of eggs and larvae of *H. armigera* and pod damage with the density of glandular (type A) trichomes on the calyxes and pods of wild relatives of pigeonpea (Table 6). Numbers of eggs and larvae and pod damage were significantly and negatively correlated with density of non-glandular (type C) trichomes. There was no association between type B trichomes and egg laying, larval abundance, and pod damage; while the density of type D trichomes on the pods was negatively correlated with pod damage. Concentration of polyphenols in the leaves was negatively correlated with egg and larval

Table 6 Correlation coefficients between densities of different trichome types on calyxes and pods and densities of *H. armigera* eggs and larvae, and pod damage in wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Parameter	Trichomes on calyxes				Trichomes on pods			
	A	B	C	D	A	B	C	D
No. of eggs	0.45**	−0.06	−0.39*	−0.18	0.36*	0.13	−0.36*	−0.16
No. of larvae	0.42**	0.00	−0.51**	−0.15	0.40*	0.02	−0.32*	−0.11
Pod damage	0.61**	0.17	−0.56**	−0.18	0.43*	0.20	−0.27*	−0.22*

*, ** Correlation coefficients significant at $P \leq 0.05$ and 0.01, respectively

Table 7 Correlation coefficients between biochemical components of leaves and pods and numbers of eggs, larvae, and pod damage in wild relatives of pigeonpea (ICRISAT, Patancheru, India)

Parameter	Polyphenols		Soluble proteins		Soluble sugars		Condensed tannins	
	Leaves	Pods	Leaves	Pods	Leaves	Pods	Leaves	Pods
Eggs	−0.56**	−0.12	0.45**	−0.04	−0.11	0.04	−0.44*	−0.05
Larvae	−0.51**	−0.19	0.34	−0.06	−0.34	0.12	−0.42*	−0.09
Pod damage	−0.29	−0.15	0.27	0.05	−0.21	0.04	−0.50**	−0.10

*, ** Correlation coefficients significant at $P \leq 0.05$ and 0.01, respectively

numbers, and pod damage under field conditions (Table 7). Protein content of leaves and pods was positively correlated with egg and larval numbers, and pod damage, but the correlation coefficients were non-significant (except with eggs). Soluble sugars showed no association with expression of resistance to *H. armigera*. The condensed tannins in the leaves also showed a significant and negative association with *H. armigera* damage under field conditions.

Discussion

Wild relatives of pigeonpea are useful sources of resistance to *H. armigera* (Romeis et al. 1999; Sharma et al. 2001). The present study showed that there was a significant variation in egg-laying, numbers of larvae, and pod damage among the wild relatives of pigeonpea under field conditions. Among the short-duration accessions, oviposition non-preference and antibiosis were important components of resistance to *H. armigera* as evidenced by low egg and larval numbers. Egg-laying was quite high on *C cajanifolius* (ICPW 28), which is the progenitor of cultivated pigeonpea, and it was as susceptible to *H. armigera* damage as the cultivated pigeonpea cultivar, ICPL 87. There was considerable variation in pod damage among different accessions of *C. scarabaeoides*, suggesting that it is important to evaluate the available accessions for resistance to insect pests before selecting a particular accession for use in breeding for resistance to insect pests. In several accessions, the numbers of eggs or larvae recorded on the marked portion of the inflorescences were nil (zero),

although some amount of pod damage was recorded in most of the accessions tested. The *H. armigera* moths have the choice to lay the eggs on other inflorescences at the flowering stage in the same plant, the larvae from the neighboring branches migrate to others and cause the pod damage, resulting in differences in egg laying, larval numbers, and pod damage. Accessions belonging to *R. aurea, C. scarabaeoides, C. sericeus, C. acutifolius*, and *F. bracteata* showed high levels of resistance to *H. armigera,* while the accessions belonging to *C. cajanifolius* were as susceptible to *H. armigera* as the cultivated pigeonpea. Among the cultivated pigeonpea genotypes, ICPL 332 (the resistant check) was consistently less damaged than the susceptible check, ICPL 87.

Trichome types, their orientation, density, and length influence host plant resistance/susceptibility to insect pests (Jeffree 1986; David and Easwaramoorthy 1988; Peter et al. 1995; Valverde et al. 2001; Gurr and McGrath 2001). However, trichomes at times also impart susceptibility to insects, e.g., to whitefly, *Bemisia tabaci* (Gen.) in cotton (Chu et al. 2000). Specifically, glandular trichomes and their exudates act as an important resistance mechanism to insects owing to the compounds exuded by them (Peter et al. 1995; Ranger and Hower 2001; Frelichowski and Juvik 2001). Density of glandular trichomes (type A) was high on the pods of *C. cajan, R. bracteata,* and *C. platycarpus*, and a significant and positive correlation was observed between the number of eggs laid and the density of type A trichomes. Hartlieb and Rembold (1996) suggested that glandular-secretions from trichomes in pigeonpea act as attractants to the adults of *H. armigera*.

Exudates from glandular trichomes (type A) in pigeonpea contain factors that also are phagostimulants towards the *H. armigera* larvae (Green et al. 2002, 2003). Significantly higher numbers of type B trichomes were observed on the pods of *C. lineatus, C. albicans,* and *C. cajanifolius* as compared to those on the pigeonpea cultivar, ICPL 87. The function of type B trichomes is not well known. However, Bisen and Sheldrake (1981) suggested that they are a source of the characteristic fragrance of pigeonpea. The fragrance of the pods of *C. lineatus* might also be due to the presence of high density of type B trichomes. The contents of type B trichomes are liberated only when the cell wall is ruptured. This could be caused by chewing by the insects such as *H. armigera* or by abiotic factors such as high temperatures or low air humidity (Ascensao et al. 1995). Density of non-glandular trichomes (type C and type D) was greater on the calyxes and pods of *C. scarabaeoides* than that on the pods of other species. The non-glandular trichomes, which were present at much higher densities on wild relatives of pigeonpea than on the cultivated pigeonpea, may also act as a physical barrier to feeding by the *H. armigera* larvae. The results suggest that non-glandular trichomes (type C and D) have a significant influence on genotypic susceptibility to *H. armigera* in wild relatives of pigeonpea, and these can be used as marker traits to breed for resistance to *H. armigera* in pigeonpea.

In addition to morphological traits, biochemical constituents present in the cells and tissues of the host plant exert a profound influence on biology of insect pests (Beck 1965; Smith 1989; Sharma 2009). Total soluble sugars were higher in the pods of cultivated pigeonpea than in the wild relatives, and this may be one of the factors leading to greater feeding by *H. armigera* larvae on the pods of cultivated pigeonpea compared to that on the accessions of wild pigeonpeas. MacFoy et al. (1983) recorded high concentrations of sugars and amino acids in the cowpea cultivar Vita-1, which is susceptible to spotted pod borer, *Maruca testulalis* (Geyer).

Low amounts of polyphenols in the cultivated pigeonpea might be another reason for their high susceptibility to *H. armigera.* Low amounts of phenols in pigeonpea flowers are also associated with susceptibility to spotted pod borer, *M. testulalis* (Ganapathy 1996). Soluble protein content was significantly higher in the pods of *C. scarabaeoides* compared to those of ICPL 87. High amounts of polyphenols were recorded in resistant (late-maturing) wild relatives of pigeonpea as compared to the cultivated pigeonpea. Similar observations have earlier been reported by Mukerji et al. (1993) and Sahoo and Patnaik (2003). Condensed tannins in plants often act as insect growth inhibitors owing to their presumed binding to the proteins (Smith 1989). However, Martin et al. (1987) indicated that there is little evidence to suggest that condensed tannins inhibit digestion in insects, but the adverse effects of condensed tannins might be due to their role as feeding deterrents. Wild pigeonpea accessions exhibiting high levels of resistance to *H. armigera* had low densities of glandular trichomes and high density of non-glandular trichomes and high amounts of condensed tannins and polyphenols, and these can be used in wide hybridization to increase the levels and diversify the bases of resistance to *H. armigera.*

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