Host plant resistance to insect pests in pigeonpea: Potential and limitations

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Abstract: Host plant resistance to insects is one of the components of pest management in pigeonpea. Considerable progress has been made in developing techniques to screen for resistance to *Helicoverpa armigera*. However, some of these techniques cannot be used to evaluate material for resistance to spotted pod borer, *Maruca virtrata*, pod fly, *Melanagromyza obtusa*, pod wasp, *Tanaostigmodes cajaninae* and the pod bugs, *Clavigralla* spp. Genotypes with resistance to *H. armigera*, *M. vitrata*, *M. obtusa*, and *C. chinensis* have been identified, but the levels of resistance are low to moderate in the cultivated germplasm. However, high levels of resistance have been identified against *H. amigera* in wild relatives of pigeonpea. Considerable information has been generated on mechanisms of resistance to *H. armigera* and *M. vitrata*, but there is limited information on inheritance of resistance, and the molecular markers associated with resistance to insects. The progress in transferring insect resistance into the improved varieties has been limited, and there is a need to introgress resistance genes from the wild relatives into the culigen and/or develop pigeonpea cultivars expressing *Bt* genes to confer resistance to pod borers. Cultivars with moderate levels of resistance in combination with other components of pest management will play a major role in increasing the productivity of pigeonpea.

Key words: insect pests, pigeonpea, plant resistance

Insect pest problems in pigeonpea

Over 150 insect species damage pigeonpea, of which the legume pod borer, *Helicoverpa armigera* Hübner, spotted pod borer, *Maruca vitrata* Geyer, pod fly, *Melanagrmyza obtusa* Malloch, pod wasp, *Tanaostigmodes cajaninae* La Sale, spiny pod borer, *Etiella zinckenella* Triet and pod sucking bug, *Clavigralla gibbosa* Spin. are the major pests. Black bean aphid, *Aphis craccivora* Koch, Leafhoppers, *Empoasca* spp. and green bugs, *Nezara viridula* L. are the occasional pests (32, 39). The bruchids, *Collasobruchus chinensis* L. cause extensive losses in storage. Insect pests in India cause an average of 30% loss in pulses valued at 815 million USD. The pod borer, *H. armigera* - the single largest yield reducing factor in pigeonpea, causes an estimated loss of 317 million USD in the semi-arid tropics. Globally, it causes an estimated loss of over 2 billion USD annually, despite over 1 billion USD worth of insecticides used to control this pest (1).

Techniques to screen for resistance to insects in pigeonpea

Screening for resistance to insects in pigeonpea under natural conditions is a long-term process because of the variations in flowering times of pigeonpea genotypes and the insect populations over space and time (Fig. 1). As a result, it is difficult to identify reliable and stable sources of resistance under natural infestation (39). Therefore, there is a need to develop techniques to screen for resistance to insects under uniform insect pressure at the most susceptible stage of the crop. The following techniques can be adopted to maximize the effectiveness of screening for resistance to insects in pigeonpea.

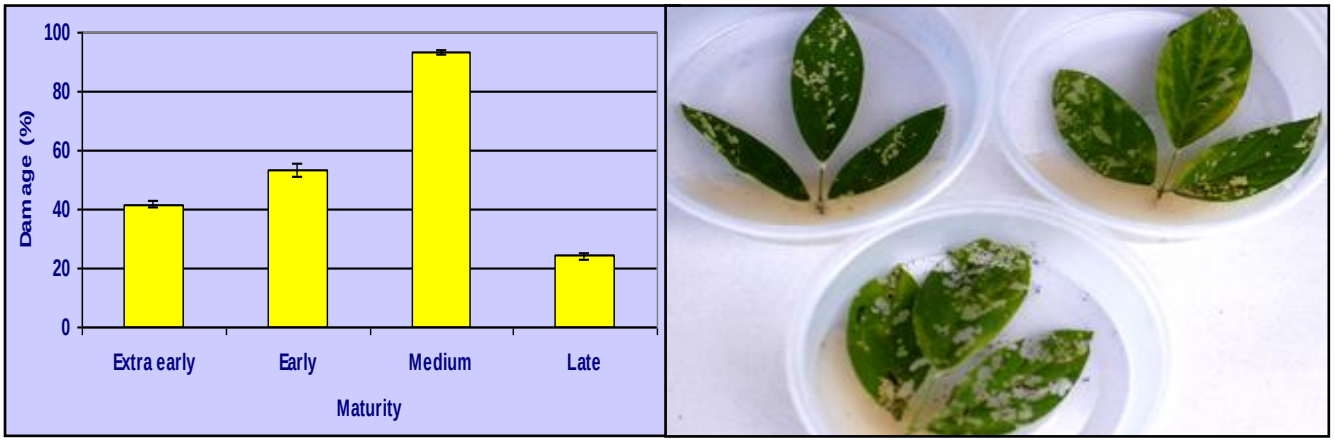

Figure 1. Pod borer damage in pigeonpea lines belonging to different maturity groups under natural infestation (left) and detached leaf assay to screen pigeonpea lines for resistance to *Helicoverpa armigera* (right)

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Planting times and use of hot-spot locations. The test material should be planted such that the most susceptible stage of the crop is exposed to optimum insect pressure. Most of the crops planted during June - July are exposed to heavy infestation by the pod borers in South central India during the rainy season, while the crops that have pods during December - January are exposed the heavy pod fly infestation (39). Hot-spots are the locations where the insects are known to occur regularly in optimum numbers across the seasons. Many locations in South Central India are hot-spots for *H. armigera* and *M. vitrata* and *M. obtusa*, which can be used to screen a large number of genotypes for resistance to insects.

Grouping the test material according to maturity and height. Because of fluctuations in insect populations over the crop-growing season, it becomes difficult to obtain uniform insect damage on genotypes flowering at different times under natural infestation (37). The early and late flowering lines escape insect damage, while those flowering in the mid-season are exposed to heavy insect pressure. To overcome this problem, it is important to group the test material according to their maturity and height. It is equally important to include resistant and susceptible checks, and/or commercial cultivars of similar maturity in each trial for proper comparisons.

Augmenting insect populations in the field. Insect density in the field can be augmented with field collected or lab reared insects to ensure optimum damage in the test material. Insect population can be augmented by placing non-destructive light, pheromone or kairomone traps. Indigenous insect populations can also be collected from the surrounding areas and released in the test plots. Kairomones present in the leaves of susceptible pigeonpea varieties are attractive to the egg-laying females of *H. armigera*, and such attractants can be used to increase insect abundance in the resistance screening nursery.

Tagging the plants/inflorescences. The test material flowering at the same time can be tagged with similar-colored labels or marked with paint. This enables the comparison of the test material flowering at the same time with the resistant and susceptible controls of similar duration. For comparisons to be meaningful, the inflorescences at flowering (between 30 cm and 45 cm long) at a particular point of time can be marked with a twine or with colored ribbons. The data on insect damage should be recorded in the tagged portion of inflorescence, and comparisons made amongst the genotypes flowering during the same period. For this purpose, 3 to 5 inflorescences may be tagged in each plot.

Artificial infestation in the field. Insects reared on artificial diet in the laboratory can be released on the test material in the field (34). Manual infestation with neonate larvae is quite effective, but it is cumbersome and time consuming. Eggs suspended in 0.2% agar-agar solution can also be spread on plants in controlled amounts through hypodermic syringes or pressure applicators. Field infestation should be carried out at the most susceptible stage of the crop. However, this technique cannot be used effectively in pigeonpea as there in no distinct plant whorl where the larvae can be released (32).

Caging the plants with insects in the field. Caging the test plants or inflorescences with insects in the field is another method of screening for resistance to insects (37). This prevents the insects from migrating away from the test plants. The cages/nylon bags (60 mesh) can be designed to cover 25 cm - 30 cm portion of the inflorescences. For valid conclusions, resistant and susceptible checks of appropriate maturity should also be included, and infested at the same time as the test genotypes. Because of large size of pigeonpea plants and the propensity of insects to lay eggs on the nylon net, it is not very effective for screening pigeonpa for resistance to pod borers.

Detached leaf assay. Detached leaf assay can be used quite successfully to screen pigeonpea plants for resistance to insects (38). The first fully expanded terminal trifoliate leaf with petiole can be placed into agar-agar (3%) in a small plastic cup or a glass jar (250 ml capacity). Ten to 20 neonate larvae are released on the test material, and data are recorded on larval survival and larval weights at 4 to 5 days after infestation, when there are maximum differences between the resistant and susceptible genotypes (Fig. 1). This test is easy and quick, and can be carried out with different parts of the same plant at different growth stages. However, results of detached leaf assay may not correspond to genotypic resistance to pod damage by the insects because of differences on physico-chemical characteristics between the leaves and the flowers/pods, as most of the pests of economic importance in pigeonpea feed on flowers and pods.

Diet incorporation assay. Incorporation of lyophilized leaves or flowers/ pods into the artificial diet can be used to assess antibiosis component of resistance to insects in pigeonpea (17, 39). Antibiosis can be assessed in terms of larval mortality, larval and pupal weights, adult emergence, and duration of development. Incorporation of 10 g of lyophilized leaf or pod powder into the artificial diet (300 ml) of diet results in maximum differences in survival and development of *H. armigera* larvae between the resistant (ICPL 332) and susceptible (ICPL 87) genotypes (29). However, there are subtle differences in larval weight and mortality between the insects reared on fresh leaves and pods and those fed on diets with lyophilized leaf or pod powder possibly because of effect of nutrients in the artificial diet on the biological activity of secondary metabolites in pigeonpea.

Measurement of resistance

Percentage damage to pods is the most common criterion for evaluating genotypic susceptibility to pod borers, *H. armigera* and *M. vitrata*. However, this criterion often leads to unreliable results due to variations in insect population over space and time, damage to flowers, dropping of the reproductive parts as a result of early infestation, and the genotypic ability to produce a second flush in case the first flush is lost due to pod borer damage. The second flush at times may escape insect damage, resulting in erroneous results. To overcome these problems, the test material can be evaluated on a 1 to 9 damage rating scale, taking into consideration the numbers of fruiting bodies retained on the plant, distribution of fruiting bodies throughout the plant canopy, and the proportion of the pods damaged by *H. armigera* and *M. vitrata* (1 = plants with little damage during the vegetative stage or showing good recovery from damage, large numbers of fruiting bodies retained on the plant with uniform distribution throughout the plant canopy, and < 10% damage to the fruiting bodies; and 9 = plants with poor recovery from damage, fewer fruiting bodies retained on the plant, uneven distribution of the fruiting bodies, and > 80% of the fruiting bodies damaged by the larvae) (32). Pod fly, *M. obtusa* and pod wasp, *T. cajaninae* damage can be evaluated by counting the number of pods infested, and the proportion of locules /seeds damaged. Pod bug damage is difficult to assess. Counting the proportion of pods

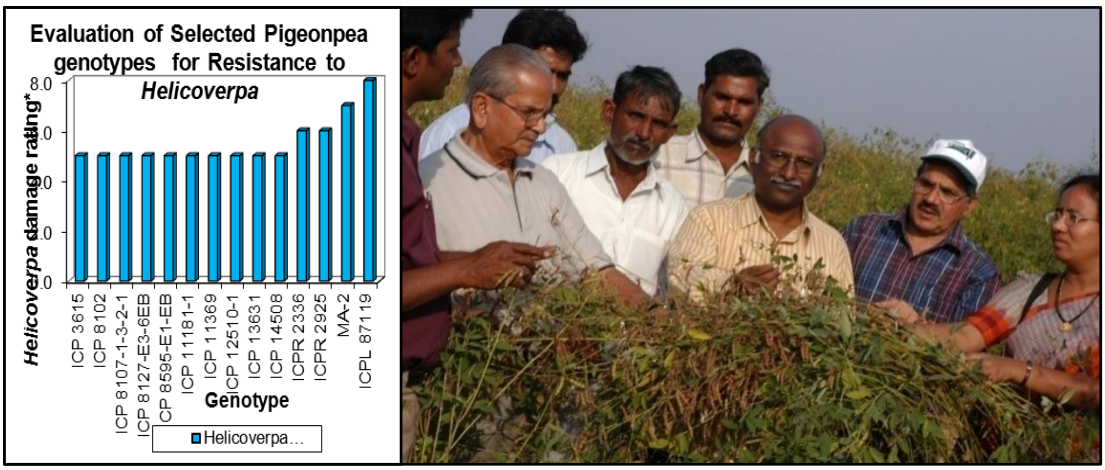


Figure 2. Relative resistance/ tolerance of pigeonpea genotypes for resistance to pod borer, *Helicoverpa armigera* (left); pod borer tolerant genotype ICPL 332WR grown on farmers fields in Telangana, India

infested, and the number of shrivelled seed can be used to assess pod bug damage. The bruchid damage can be assessed by the proportion of seeds damaged or increase in bruchid population per unit of seed weight over 30 days. The resistance/ tolerance to pod borers can also be measured in terms of loss in yield under unprotected conditions in relation to the plots maintained under protected conditions (14).

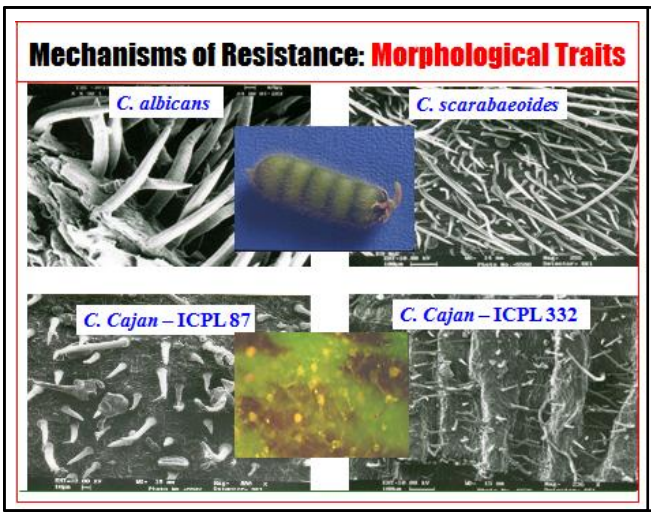
Identification and utilization of resistance

Screening of entire germplasm collections of pigeonpea (over 15,000 accessions) has led to identification of a few accessions with moderate levels of resistance to *H. armigera* (Fig. 2). However, lack of precision in evaluating thousands of accessions for resistance to the target pests probably resulted in missing many potentially good sources of resistance. In general, extra-early and determinate type genotypes are more susceptible to pod borer damage (24). P 54(b) (43); ICPL 5EB-EB (24), Phule T 1, Prabhat, T 21, Phule T 3 and 7411 (25); DL-78-1, ICPL 155, TAT 9 and TAT 10 (3); ICPL 1, H 79-6, UPAS 120, GP Nos. 17, 20, 24, 33, 30, 40, 43 and 45 (18); Bahar, ICPL 94, ICPL 154 and ICPL 85059 (10), ICPL 332, PPE 45-2 (ICP 1964), MA 2 and ICPL 84060 (28); ICPL 6, PPE 45-2, ICP 1903, MA 1, ICPL 187-1, ICPL 288, T 21, ICP 909, ICPL 86040, MAZ, ICPL 2, TA 10, ICPL 1, Pant A1, ICP 7345-1-5, BDN 7, DA 2, ICP 4070, ICP 3615, BSMR 1, ICP 10531, ICPL 201, ICP 109BB, (AUT 82-1), ICPX 77303, ICPL 87089, Bahar, ICPL 87088, ICP 7946-E and ICP 9889 (30); ICPL 7035, GAUT 85, ICPL 87075 and ICPL 151 (2); HPA 92 (13), Bori (27) and T 21 (23), PDA 88-2E and PDA 92-1E (5), PDA-92-3E, PDA-89-2E and SL-21-9-2 (4), GAUT 85035 and BDN 2 (12) and ICPL 4 (44) have been reported to be relatively resistant to *H. armigera*.

Short-duration genotypes ICP 7, ICP 13011, ICPB 2089, ICPL 187-1, ENT 11 and ICPL 98008 have moderate levels of resistance to pod borer damage (scores 6.0 to 8.0 compared to 9.0 in ICPL 151). In the medium duration, the genotypes ICP 995, ICP 1071, ICP 3046, ICP 6128, ICP 8793, ICP 9414, ICP 10397, ICP 13633, ICP 16264, ICPR 3461, ICPR 3472, ICPR 3491, ICPL 96058, ICPR 2913, ICPL 20097, ICPL 20099 and ICPL 332 WR suffered low pod damage and yielded > 1,500 kg ha^{-1}. In the long duration group, the genotypes ICP 8266, ICP 8102, ICP 8595-E1-EB, ICP 12510-1, ICP 12759, ICPL 20120, ICP 8087 and ICPL 332 WR suffered low pod damage by pod borer, *H. armigera*, and/or pod fly, and pod bug, and also exhibited high yield potential (> 1,000 kg ha^{-1}) under unprotected conditions. In the international pigeonpea *Helicoverpa* nursery, twenty-five genotypes, including the resistant and susceptible checks, were evaluated for resistance to pod borer, *H. armigera* in field trials. ICPHaRL 4985-1, ICPHaRL 4985-11, ICPHaRL 4989-7, and ICPL 332 WR showed moderate levels of resistance to pod borer damage, and exhibited yield potential of > 1,500 kg ha^{-1}.

In Tandur Region, Telangana, the yields of ICPL 332 WR ranged from 812 kg ha^{-1} to 1,250 kg ha^{-1}, and of Asha (ICPL 87119) varied from 875 kg ha^{-1} to 1,865 kg ha^{-1} and of Maruti (ICP 8863) from 780 kg ha^{-1} to 1,076 kg ha^{-1}. Most of the farmers reported a better control and lower insecticide use in ICPL 332 WR than on Asha. In Gulbarga region, Karnataka, the average grain yields were 1,127 kg ha^{-1} in ICPL 332 WR, 1,171 kg ha^{-1} in Asha and 970 kg ha^{-1} in Maruti. Among the improved varieties ICPL 84060, ICPHaRL 4985-4, ICPHaRL 4985-11, ICPL 20058 and ICPHaRL 4989-7 yielded 1,049 kg ha^{-1}, 1,050 kg ha^{-1}, 1,084 kg ha^{-1}, 1,106 kg ha^{-1} and 1,122 kg ha^{-1} respectively.

Wild relatives as sources of resistance to insects. Wild relatives of pigeonpea such as *C. scarabaeoides* (L.) Thouars, *C. sericeus* (Benth. ex Baker) Maesen, and *C. acutifolius* (F. Muell.) Maesen are highly resistant to *H. armigera* (9, 40), while ICPW 141, ICPW 278, and ICPW 280 (*C. scarabaeoides*), ICPW 214 (*Rhynchosia bracteata* Baker), ICPW 14 (*C. albicans* (Wight & Arn.) Maesen) and ICPW 202 (*Flemingia stricta* Roxb.) showed resistance to both *M. obtusa* and *T. cajaninae* (36; Fig. 3). Attempts have also been made to transfer pod borer resistance from the wild relatives into the cultigen (11, 19, 20).



Survival and Development of *Helicoverpa armigera* on Flowers and Pods of Wild Relatives of Pigeonpea

Accession	Species	Larval wt. (mg) 15 days	Larval mortality (%) 20 days	Larval period (days)
ICPW 1	*Cajanus acutifolius*	154.5	62	25.4
ICPW 159	*Cajanus sericeus*	112.1	58	22.7
ICPW 125	*Cajanus scarabaeoides*	46.4	62	33.7
ICPW 152	*Cajanus scarabaeoides*	112.1	48	36.1
ICPL 87	*Cajanus cajan*	325.2	36	21.7
ICPL 332	*Cajanus cajan*	294.5	46	24.3
SE ±		0.006	5.63	1.63

Figure 3. Trichomes on the leaf/pod surface of pigeonpea and its wild relatives influence the genotypic resistance to *Helicoverpa armigera* (left); the wild relatives of pigeonpea affect the survival and development of pod borer (right)

Transgenic plants. While several transgenic crops with insecticidal genes have been introduced in the temperate regions, very little has been done to use this technology for improving crop productivity in the harsh environments of the tropics, where the need for increasing food production is most urgent (19). Transgenic pigeonpea plants with *cry1Ab* and soybean trypsin inhibitor (*SBTI*) genes have been developed (41), but are ineffective for controlling *H. armigera* (6).

Morphological and biochemical traits associated with insect resistance

Morphological (trichomes, cell wall lignification, branching and podding habit, and podwall hairs and trichomes) and biochemical factors associated with insect resistance can also be used as selection criteria. This permits the rapid determination of potentially resistant plant material. This also removes the variation associated with insect density, and the effect of environmental factors on the expression of resistance to insects.

Phenological traits. Pigeonpea genotypes with determinate growth habit, clustered pods, and dense plant canopy are more susceptible to pod borers, *H. armigera* and *M. vitrata* than those with non-clustered pods (33, 35, 39), while the genotypes with smaller pods, pod wall tightly fitting to the seeds, and a deep constriction between the seeds are less susceptible to *H. armigera* (23). Plant growth types and maturity also influence genotypic susceptibility to pod fly, *M. obtusa*. Podwall thickness, trichome density, and crude fiber content are associated with resistance to this insect in pigeonpea.

Leaf hairs and trichomes. Leaf hairs (that do not produce glandular secretions) play an important role in host plant resistance to insects. Wild relatives of pigeonpea such as *C. scarabaeoides* and *C. acutifolius* with non-glandular trichomes are not preferred by *H. armigera* females for egg laying (42), while glandular trichomes in pigeonpea are linked to susceptibility to *H. armigera*.

Secondary metabolites. Secondary metabolites influence host finding, oviposition, feeding, and survival and development of insects, and play an important role in host plant resistance to insects in grain legumes. Quercetin, quercetrin, and guercetin-3-methyl ether in the pod surface exudates of pigeonpea, play an important role in food selection behavior of *H. armigera* larvae in pigeonpea (7, 8). Total phenols and tannins in the podwall of pigeonpea are negatively associated with pod fly damage. Stilbene - a phytoalexin occurs at high concentrations in pigeonpea cultivars with resistance to *H. armigera* (8).

Nutritional factors. Nutritional factors such as sugars, proteins, fats, sterols, and essential amino acids, and vitamins also influence host plant suitability to insect pests. Total soluble sugars in pigeonpea podwall influence pod damage by *H. armigera*. Protein content of the podwall is associated with susceptibility, while total sugars are associated with resistance to *M. obtusa* in pigeonpea. Amylase and protease inhibitors in pigeonpea and its wild relatives have been shown to have an adverse effect on growth and development of *H. armigera* (26).

Mechanisms and inheritance of resistance

Antixenosis, antibiosis and tolerance are the major components of resistance to *H. armigera* and pigeonpea (15, 16). Numbers of *H. armigera* larvae can be estimated by sampling at the plant site where the damage has taken place, and at the appropriate phenological plant stage and time. Shaking the plants, use of sampling nets or actual counts are used to obtain an estimate of larval abundance. Numbers of larvae should be recorded in 3 to 5 plants at random in the center of each plot at 10 to 15 days after flowering. Larval mortality and prolongation of the larval period are the main components of resistance to *H. armigera* in the wild relatives of pigeonpea (31, 42).

The levels of resistance to *H. armigera* in the germplasm accessions are low to moderate. This has necessitated the need for selecting genotypes with greater ability to tolerate or recover from the pod borer damage. Since it is almost impossible to get high levels of resistance against *H. armigea* in any legume crop, search for genotypes with recovery resistance through their ability to have more pods and recover from initial damage would be more rewarding.

There is little information on inheritance of resistance to insects in pigeonpea. Trichomes in pigeonpea, which are associated with resistance/ susceptibility to *H. armigera* has been studied in interspecific crosses involving *C. cajan* × *C. scarabaeoides*. The trichomes in the wild parent (high density of the non-glandular trichomes C and D, and low density of glandular trichome A) were dominant over the trichome features of *C. cajan,* suggesting dominance of resistance over susceptibility in wild relatives, and a single gene governed this character (1).

Potential and limitations of HPR in pest management in pigeonpea

Host-plant resistance can be used as a principal component of pest control, as an adjunct to cultural, biological and chemical control and as a check against the release of susceptible cultivars. High levels of plant resistance are available against a few insect species only. However, very high levels of resistance are not a pre-requisite for use of HPR in integrated pest management. Varieties with low to moderate levels of resistance or those which can avoid the pest damage can be deployed for pest management in combination with other components of pest management. Deployment of *Helicoverpa*-resistant cultivars in pigeonpea should be aimed at conservation of the natural enemies and minimizing the number of pesticide applications. Use of the pigeonpea cultivars resistant to *Helicoverpa* will also improve the efficiency of other pest management practices, including the synthetic insecticides.

Utilization of plant resistance as a control strategy has enormous practical relevance and additional emotional appeal. It is in this context that host-plant resistance assumes a central role in our efforts to increase the production and productivity of crops. Plant resistance to insects is the backbone of any pest management system because: i) it is specific to the target pest or a group of pests, and generally has no adverse effects on the non-target organisms in the environment, ii) effects of plant resistance on insect population density are cumulative over successive generations of the target pest because of reduced survival, delayed development, and reduced fecundity, iii) most of the insect-resistant varieties express moderate to high levels of resistance to the *Helicoverpa* throughout the crop-growing season. In contrast, the pesticides have to be applied repeatedly to achieve satisfactory control of the pest populations, iv) HPR is compatible with other methods of pest control, and also improves the efficiency of other methods of pest management, and v) it does not involve any costs to the farmers.

However, plant resistance is not a panacea for solving all the pest problems. Development of plant varieties resistant to insect pests takes a long time. Some mechanisms of plant resistance may involve the diversion of some resources by the plant to extra structures or production of defence chemicals at the expense of other physiological processes including those contributing to yield (22). Although concentration of defence chemicals responsible for resistance is low in plant tissues, the total amount per hectare may be high, e.g. production cost of 34 kg of gossypol (which imparts resistance to *Helicoverpa*/*Heliothis* in cotton) in terms of glucose equivalent in cotton will be 70.7 kg of glucose ha^{-1} (21).

Chemical basis of plant resistance to insects at times can modify the toxicity of insecticides to insects, e.g., 2-tridecanone in wild tomato reduces the toxicity of carboryl to *Heliothis* (22). Some plant defence chemicals also affect the food quality. Most of the pigeonpea and chickpea (*Cicer arietinum* L.) genotypes with resistance to *H. armigera* are susceptible to *Fusarium* wilt (32), There is a need to break the linkage between the factors conferring resistance to the target insects and the low yield potential or arrive at threshold levels for the resistant traits (secondary metabolites) that results in reduced pest susceptibility, and at the same time do not have an adverse effect on the quality of the product.

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