Journal of Environmental Biology
ISSN : 0254–8704

J.Environ.Biol.
23(2), 111-135 (2002)

Review article

Host plant resistance to insects : An eco-friendly approach for pest management and environment conservation.

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(Received : 08 March, 2001 ; Accepted : 15 June, 2001)

Abstract : *Host plant resistance (HPR) to insects is an effective, economical, and environment friendly method of pest control. The most attractive feature of HPR is that farmers virtually do not need any skill in application techniques, and there is no cash investment by the resource poor farmers. Considerable progress has been made in identification and development of crop cultivars with resistance to the major pests in different crops. There is a need to transfer resistance genes into high–yielding cultivars with adaptation to different agro–ecosystems. Resistance to insects should form one of the criteria to release varieties and hybrids for cultivation by the farmers. Genes from the wild relatives of crops, and novel genes, such as those from Bacillus thuringiensis can also be deployed in different crops to make HPR an effective weapon to minimize the losses due to insect pests. HPR will not only cause a major reduction in pesticide use and slowdown the rate of development of resistance to insecticides in insect populations, but also lead to increased activity of beneficial organisms and reduction in pesticide residues in food and food products.*

Keywords : *Host plant resistance, Insect, Pest management, Environment conservations.*

Introduction

Indiscriminate use of pesticides has led to serious concerns relating to their adverse effects on the non–target organisms, pesticide residues in food and food products, pest–resurgence, development of resistance in insects to insecticides, toxic effects on human beings, and environmental pollution (Metcalf and Luckmann, 1982). Insect pests have high reproductive rates, a fast generation turnover, wide genetic diversity across locations, and an ability to withstand, metabolize, and avoid toxic chemicals. As a result, it has become practically difficult to control several insect species through the currently available chemical pesticides. Therefore, it is important to adopt pest control strategies that are :

- Ecologically sound,
- Economically practical, and
- Socially acceptable.

Host plant resistance (HPR) along with natural enemies and cultural practices, is a central component of any pest management strategy. With the domestication of plants for agricultural purposes, farmers selected the plants that were able to withstand the adverse environmental factors, including insect pests and diseases. The plants that were susceptible to the herbivores were generally eliminated, and only resistant plants survived until the crop harvest. This process led to natural selection of plants having resistance to insect pests. Because of this unintentional, but continuous selection of plants over several hundred years, many landraces selected by farmers evolved as having or accumulating genes conferring resistance to insects. The best examples of this process are : shoot fly resistance in landraces of sorghum cultivated during the post–rainy season in India, and head bug resistance in *guineense* sorghums cultivated in western Africa (Sharma, 1993).

In spite of the importance of HPR as a component of integrated pest management (IPM), breeding for plant resistance to insects has not been as rapidly accepted, as has been the case in breeding disease–resistant cultivars. This was partly due to the relative ease with which insect control is achieved with the use of insecticides.

There has been a slow progress in developing insect–resistant cultivars because of the difficulties involved in ensuring adequate insect infestation for resistance screening. Insect–rearing programs are expensive; the technology development requires several years, and in some cases may not produce the behavioral or metabolic equivalent of an insect population in nature. However, with the development of insect resistance to insecticides, adverse effects of insecticides on natural enemies, and environmental pollution, there has been a renewed interest in the development of insect–resistant cultivars. The establishment of international agricultural research centers, and the collection and evaluation of existing germplasm for insect resistance has given a renewed impetus to the identification and use of HPR in pest management worldwide.

"Resistance of plants to insects enables a plant to avoid or inhibit host selection, inhibit oviposition and feeding, reduce insect survival and development, and tolerate or recover from injury from insect populations that would cause greater damage to other plants of the same species under similar environmental conditions" (Smith, 1989). Resistance of plants to insects is the consequence of heritable plant characters that result in a plant being relatively less damaged than the plant without these characters. This property is generally derived from physico–chemical characteristics of the plants, which influence the behavior and biology of insects. From an evolutionary point of view, resistance traits are pre–adaptive genetically inherited characters of the plant. Plants with such pre–adaptive genes resist the selective pressure of herbivore populations, and thus increase their chances of survival and reproduction.

Plant resistance to insects is relative, and the level of resistance is expressed in relation to resistant and susceptible genotypes under similar environmental conditions. This concept is important, since expression of resistance is dependent on insect density and environmental factors, both in time and space. Pseudo–resistance or false resistance may occur in normally susceptible plants through avoidance of insect infestation. Induced resistance may occur in plants because of variations in temperature, photoperiod, plant–water potential, and chemicals in the soil that induce the production and accumulation of secondary plant substances (phytoalexins) or affect the nutritional quality of the host plant. Associate resistance occurs when susceptible plants grow in association with resistant plants, and derive the protection for insect damage from the resistant plants. Associate resistance also occurs in multi–lines or synthetics as a result of diversion or delaying actions of mixture of plants resulting in slow development of an insect biotype that is capable of damaging the resistant cultivars. The role of host plant resistance in pest management has been discussed earlier by Painter (1951), Maxwell and Jennnings (1980), Smith (1989), Sharma and Kalode (1995), Smith *et al.* (1994), and Sharma *et al.* (1999b).

Identification and utilization of resistance

Newly developed cultivars fail to face the challenge of heterogeneous pest populations in the field, and consequently are rejected by the farmers. The products of crop improvement programs have to be viable under existing field conditions, while having the potential for increased yields under improved or high input situations. Sowing pest–resistant cultivars is especially useful under subsistence farming in the developing countries. Development and standardization of resistance screening techniques is the key for an effective resistance–breeding program. Knowledge concerning the periods of greatest insect density and 'hot–spots' is the first step to initiate work on screening for resistance to insects. Delayed plantings and use of infester rows of a susceptible cultivar are other effective means of augmenting insect populations to screen for insect resistance (Sharma *et al.,* 1992; Smith *et al.*, 1994; Kalode and Sharma, 1995). Information on population peaks, hot–spots, and use of infester rows need to be generated for insect pests of different crops.

Screening for insect resistance under natural conditions is a long–term process.

Because of variation in insect populations in space and time, it is difficult to identify reliable and stable sources of resistance under natural infestation. To overcome these problems, it is important to develop multi–or no–choice screening techniques where the test cultivars can be subjected to an uniform insect pressure at the most susceptible stage of the crop. For this purpose, it is important to have a reliable and regular supply of insects reared on natural hosts or on artificial diets. Artificial diets and rearing procedures have been developed for a number of insects (Singh and Moore, 1985). While screening under artificial infestation is a necessity for most insect pests, it may not be an absolute requirement for insects that occur in epidemic proportions over years or are endemic in particular areas, e.g., bollworms (*Pectinophora gossypiella* Saund., *Helicoverpa armigera* (Hub.), and *Earias vittella* Fab.) and jassids (*Amrasca biguttula biguttula* Ishida) in cotton, aphids (*Lipaphis erysimi* Kalt. and *Brevicoryne brassicae* L.) on cruciferous crops, and pod borers [*H. armigera* and *Maruca vitrata,* (Geyer)] in pigeonpea. Greater emphasis is needed on refining the resistance screening techniques, and develops uniform and standard procedures for evaluating insect populations and damage. Entomologists should be critical and vigilant in their screening and selection procedures to become an effective instrument in breeding crop cultivars resistant to insect pests.

Considerable progress has been made in identification and utilization of resistance for a number of insect pests. However, resistance–breeding programs are underway for a few crop pests only. This aspect needs greater emphasis and input from the entomologists, breeders, and the research planners. Insect resistance should be a major criterion in the development and release of new crop cultivars. Several sources of resistance to insects have been identified, and the resistance transferred into high yielding cultivars in different crops. Insect–resistant cultivars in desirable agronomic backgrounds have been developed in several crops, and some cultivars (marked with an * below) have been released for cultivation by the farmers in India. The most notable examples are :

Rice – Rice gall midge, *Orseolia oryzae* Wood–Mason (IR 36*, Kakatiya*, Dhanaya Lakshmi*, Surekha*, Phalguna*, Kunti*, Shakti*, Shamlei*, Asha*, Nandi*, Krishnaveni*, Pratibha*, Chaitanya*, Erra Malletu*, Kavya*, Orugattu*, Vajram*, Suraksha*, and Rajendradhan*); rice stem borer, *Scirpophaga incertulas* Walk. (Ratna*, Sasyasree*, Saket*, Suraksha*, ASD 20*, IET 3127, IET 2812, and MTU 5849*); rice leaf folder, *Cnaphalocrocis medinalis* Walk. (ASD 20* and VL Dhan 220*); brown planthopper, *Nilaparvata lugens* Stal. (Manasarowar*, Bhadra*, Jyoti*, Suraksha*, Co 42*, Co 46*, Aravindar*, IET 7575, IET 6315, and MTU 5249*); green planthopper, *Nephotettix* spp. (IR 20*, IET 7301, IET 7303, IET 7302, and Vani*); and whitebacked leafhopper, *Sogatella furcifera* Horvath. (AR 133, IC 25687, Tangner*, and Amelbero*) (Kalode, 1987; Kalode *et al.*, 1989; Nadarajan and Skaria, 1992; Krishanaiah, 1995; Rao *et al.*, 1992; Sharma *et al.*, 1993; Srinivasan *et al.*, 1996; Shanmugasundaram *et al.*, 1997; Rangasamy *et al.*, 1997; Reddy *et al.*, 1997; Suryanarayana *et al.*, 1997). Line R 650–1820 is resistant to brown planthopper, gall midge, and grain moth (Rana *et al.*, 1994).

Maize – Spotted stem borer, *Chilo partellus* Swin. (Ganga 4, 5, 7, and 9*; Ganga Safed 2*; Deccan 101 and 103*; Him 123*; Ageti* and Him129*); pink stem borer, *Sesamia inferens* Walk. (Kanchan*, Deccan 101 and 103*, and Kundan*); and maize shoot fly, *Atherigona* sp. (DMR 5, NCD, and VC 80) (Swarup, 1987; Mani *et al.*, 2000).

Sorghum – Sorghum shoot fly, *Atherigona soccata* Rond. (M 35–1*, Swati*, Phule Yashoda*, IS 18551, and ICSV 705); spotted stem borer, *C. partellus* (E 302, E 303, IS 2205, SPV 1015 and ICSV 700); sorghum midge, *Stenodiplosis sorghicola* Coq. (ICSV 197, ICSV 735, ICSV 745*, and ICSV 88032), and sorghum head bug, *Calocoris angustatus* Leth. [(IS 17610, IS 17645, CSM 388, BSR–1 (ICSV 239), and Chencholam*] (Sharma, 1993; Kishore 1993; Sundaram *et al.*, 1995).

Pigeonpea – Pod borer, *H. armigera* (ICPL 332*, PPE 45–2 (ICP 1964), MA 2, and ICPL 84060); spotted pod borer, *M. vitrata* (Pusa 855, Phule T 14, ICPL 980008, ICPL 87115, ICPL 90037, and ICPL 86020); pod fly, *Melanagromyza obtusa* Malloch (KM 7*, ICP 10531–E1, ICP 7941 E1, ICP 7946–E1, and ICP 7176–5 (Reed and Lateef, 1990; Kataria and Kandalkar, 1996; Sharma *et al.*, 1999a).

Chickpea – Pod borer, *H. armigera* (ICC 506, ICCV 7*, ICCV 10, ICC 6663, Dulia*, ICC 10667, and ICC 5264 (Lateef, 1985).

Cowpea – Pod borer, *M. vitrata* (Banswara*, G 20, C 55, CR 2–55, P 1461, and G7), jassid, *Empoasca kerri* Pruthi (JG 10–72, NS 19–4–1, C 152, and 3–779; aphid, *Aphis craccivora* Koch. (P 1473, P 1476, and MS 9369); stem fly, *Ophiomyia phaseoli* Coq. (Co 6*); and galerucid beetle, *Maduracia obscurella* Jacoby (5269 and Bundel Lobia 1*) (Lal, 1987; Vijaya Kuimar *et al.*, 1995; Kohli *et al.*, 2000).

Pea – Pod borer, *Etiella zinkenella* Triet. (EC 33860, Bonville*, T 6113*, PS 410, 2S 21, 172M, and PS 410); aphid, *A. craccivora* Koch. (Meteor*); stem fly, *O. phaseoli* (KS 252*); and leaf miner, *Phytomyza horticola* Goureau (P 402, PS 41–6, T 6113, PS 40, KMPR 9, P 402, and P 200 (Lal, 1987; Mahajan *et al.*, 1997; Gupta and Pandey, 1998).

Blackgram – Pod borer, *H. armigera* (Kalai*, 338–3, Krishna*, and Co 3*, 4*, and 5*); jassid, *E. kerri* (Sinkheda 1*, Krishna*, H 70–3, and UPB 1*); stem fly, *Ophiomyia centrosematis* de Merjere (Karaillel*, Killikullam*, 338/3, P 58, Co 3*, Co 4*, and Co 5*); and galerucid beetle, *M. obscurella* (Pusa 1*, KG 3, Krishna*, T 9, T 27, G 1*, and H 11* (Lal, 1987).

Greengram – Pod borer, *M. vitrata* (J1, LM 11, P 526, and P 336); white fly, *Bemisia tabaci* Gen. (ML 337, ML 5, MH 85–61, and ML 325); stem fly, *O. centrosematis* (Co 3); and galerucid beetle, *M. obscurella* (Jawahar 45*, PIMS 3, Gujarat 1*, R 12–16–3, S 9, ML 4, ML 6, PIMS 3, and PIMS 4* (Lal, 1987).

Groundnut – Leaf miner, *Aproaerema modicella* Duv. [ICGV 86031, ICGS 156 (M 13)*, FDRS 10*, and ICG 57, 156, 541, 7016, 7404, and 9883]; tobacco leaf caterpillar, *Spodoptera litura* F. (ICGV 86031 and FDRS 10*); jassid, *E. kerri* (NcAc 2230, M 13, ICG 5043, and ICG 5049); and thrips, *Thrips palmi* Karny (M 13*, Robut 33–1*, ICG 5043, and ICG 5044 (Wightman *et al.*, 1990).

Soybean – Leaf miner, *A. modicella* (PI 227687, Nimsoy*, PL 507, J9 75–1, and EC 18687) (Sundaram and Sundara Babu, 1992).

Rape and mustard – Mustard aphid, *L. erysimi* (C 294, Laha 101*, Pusa Kalyani*, RLM 84, 185, 195 and 185–59, 15, 34, and 52*, PBR 91*, and Pusa Jiakisan* in *B. juncea* Hooks f. & Thomas; Guilliver*, GSA, Regent*, GSV 2, V3, 6, 8 and 13; GS 47, 86, 123, 139, and 391, and V 3, 6, 8, and 13 in *B. napus* L.; Tora*, CDA–Span*, and Sariahi* in *B. campestris* Hooks f. & Thomas (Bakhetia, 1987; Dhillon *et al.*, 1993; Katiyar and Prasad, 1998).

Cotton – Pink bollworm, *Pectinophora gossypiella* Saund. (G 27, LD 135*, Lohit, Abadhita, MCU 7, Sujata, Digvijay, and Saguineum*); spotted bollworm, *Earias vittella* Fab. (L 1245*, JK 119–25–54, BCS 10, BCS 10–75, and Sanguineum*); cotton jassid, *A. biguttula biguttula* (Khandwa 2, Badnawar, MCU 5*, Krishna*, Mahalaxmi*, Sujay*, Sanguineum*, and Eknath*); and whitefly, *B. tabaci* (LK 861*, Amravathi*, Kanchan*, Supriya*, and LPS 141*) (Sundramurthy and Chitra, 1992).

Sugarcane – Stalk borer, *Chilo auricilius* Dudg. (Co 7302* and CoS 767); top borer, *Scirpophaga exerptalis* Wlk. (Co 7224, Co 67, Co 9302* and Co 1158); internode borer, *Chilo sacchariphagus indicus* (K.) (Co 6806, Co 6217, Co 975, and Co 77–1); sugarcane mealy bug, *Melanaspis glomerata* Green (CoS 671, Co 8014, Co 6217, Co 1132, Co 611, and Co 6907); whitefly, *Aleurolobus barodensis* Mask. (Co 671); and white grubs, *Holotrichia spp.* (Co 6304, Co 1158, and Co 5510 (David, 1987; Singh *et al.*, 1997).

Tobacco – Tobacco leaf caterpillar, *S. litura* (GT 4* and DWFC*); aphid, *Myzus persicae* Sulz. (Jamaica*, Cuban*, Fransons*, Little Rittendant*, and Sumatra*); and stem borer, *Scrobipalpa heliopa* Low (SBR 1* and SBR 2* (Chari, 1987).

Brinal – Shoot/fruit borer, *Leucinodes coronals* G. (Chaklasi Doli*, Doli 5*, Pusa Purple*, Pusa Purple Long*, Pusa Purple Round*, Pant Samrat*, SM 67 and SM 68); jassid, *A. biguttula biguttula* (Chaklasi Doli*, Doli 5*, and Pusa Purple*); coccinellid beetle, *Epilachna* sp. (Arka Kusumkar*, Arka Shirish*, Hisar Sel. 1–4*, and Vijay*); and whitefly, *B. tabaci* (Pusa Purple*) (Jiyani *et al.*, 1992; Mahajan *et al.*, 1997).

Tomato – Fruit borer, *H. armigera* (Punjab Kesri, BT 1, T 32*, and T 27*) (Mishra and Mishra, 1992; Mahajan *et al.*, 1997).

Onion – Thrips, *Thrips tabaci* Lind. (Punjab Selection (Mahajan *et al.*, 1997).

Chilli – Pod borer, *H. armigera* (HC 144*), white fly, *B. tabaci* (HC 144); aphid, *Aphis laburni* K. (HC 1444); thrips, *Scirtothrips dorsalis* Hood. (G 5, K 2, and X 235) (Mahajan et al., 1997).

Pumpkin – Fruit fly, *Dacus cucurbitae* Coq. (Arka Suryamukhi*) (Mahajan *et al.*, 1997).

Round melon – Fruit fly, *Dacus cucurbitae* Coq. (Arka Tinda*) (Mahajan *et al.*, 1997).

Lady's finger/okra – Shoot/fruit borer, *E. vittella* (AE 57, PMS 8, Parkins long green*, PKX 9275, and Karnual special*) (Ahmad and Rizvi, 1992).

Potato – Potato tuber moth, *Phthormoea opercullela* Zeller (QB 1A 21–29).

Cultivars with multiple resistance to insects and diseases will be in greater demand in future for sustainable crop production, and this requires a concerted effort from scientists involved in the crop improvement programs. There is great amount of variability in :

- emphasis placed on plant resistance in different crop improvement programs,
- availability of effective resistance screening techniques,
- progress made in identification and utilization of insect–resistant genotypes,
- multilocational testing to understand genotype x environment interactions,
- emphasis given to insect resistance in identifying and releasing new crop cultivars, and
- efforts made to spread and popularize insect–resistant cultivars in the farmers' fields.

Insecticides in general are quite effective in controlling insect pests. However, even if 90% of the insects are killed, the remaining population multiplies at a much faster rate in the absence of natural enemies (which are killed by the pesticides) (Knipling, 1979), and the farmers have to apply pesticides more frequently and at higher doses, which finally results in failure of control operations and environmental pollution. Heavy pesticide application has resulted in failure of insect control in several countries, and as a result, the farmers had to give up the cultivation of some crops in different regions. Some cotton farmers have even resorted to committing suicides in India. Heavy insecticide use has led an exponential growth in the number of insect species resistant to insecticides (Georghiou, 1986). Genetic, biological, ecological, and operational factors determine the rate of development of insect resistance to insecticides. The most effective strategy is to use selective pesticides at a low dosage in combination with HPR to slowdown the rate of evolution of insecticide–resistant populations. However, for the pest management strategies to be successful, it is important to deploy different methods of pest control for effective pest management.

Plant resistance has been used to suppress pest populations for many years. Host plant resistance has often been deployed alone as an approach for pest management. However, only a few pest species can be controlled by the use of resistant varieties alone. e.g., sorghum midge and green bug in sorghum; leafhoppers and gall midge in rice; jassids in cotton; jassids and thrips in groundnut; stem borers, scale insects, and whitefly in sugarcane; wheat stem fly, spotted alfalfa aphid, and cotton boll weevil (Sprague and Dahms, 1972; Kalode and Sharma, 1995). Cultivars with low to moderate levels of resistance can be extremely useful for insect population suppression over a period of time. The nature of deployment (alone or in combination with other methods of pest control) depends on the level and mechanism of resistance, and the crop production system (Kennedy *et al.*, 1987).

HPR and economic injury levels (EILs)

One of the first and most important adjustments to crop management recommendations that must be made relates to economic thresholds or action thresholds in relation to host plant resistance (Sharma and Teetes, 1995). In some cases, there are several cultivars of a crop with different levels of resistance. Experimental and empirical data should be generated to determine the level of resistance of a cultivar, which is critical in deciding the nature and timing of the intervention (insecticide application or release of natural enemies) needed to suppress an increasing pest population.

Because the term resistance conveys different expectations to different people and farmers desire no additional risk, the use of EILs to define the level of resistance of a newly released crop cultivar is critical in pest management. Insect–resistant cultivars not only decrease the density of pest populations, but also delay the time required by the pests to attain the EILs depending on the level and the mechanism of resistance. If the EIL is based on insect damage (e.g., percentage of deadhearts for sorghum shoot fly and stem borer, number of leaves damaged by aphids or percentage leaf area consumed by the armyworms), and the insect population increases over the season, then a susceptible cultivar will suffer economic loss in July, a moderately–resistant cultivar in August, and a resistant cultivar can withstand the pest density until the end of the season (Sharma, 1993). In case of insects in which the damage is limited to a particular stage and a short span of time (e.g., deadheart formation due to sorghum shoot fly and stem borers), a cultivar can be planted up to a period when insect density is expected to be below EIL. If EIL is based on adults, which is a non–damaging stage of the insect (e.g., sorghum midge adults or number of moths caught in pheromone or light traps), the EIL will increase with an increase in the level of insect resistance. The relationship between insect density and grain damage for sorghum midge changes with the level of resistance to this insect (Hallman *et al.*, 1984; Sharma *et al.*, 1993b). In the case of sorghum midge, the EIL is 1 adult per panicle on a susceptible cultivar (CSH 1), 25 adults per panicle on a moderately–resistant cultivar (ICSV 745), and > 50 adults per panicle on a highly–resistant cultivar (ICSV 197) (Sharma *et al.*, 1993b). If the EIL is based on adults, which also cause damage (e.g., head bugs in sorghum), and the resistance is based on non–preference and antibiosis (which will decrease the initial infestation and the rate of population increase), then the time taken by the insect to attain the EIL will also be extended by the resistant cultivars.

EILs for *C. angustatus* have been determined to be 0.2 to 0.9 bugs per panicle on CSH 11–a highly susceptible sorghum; 0.8 to 4.2 bugs on IS 9692–a susceptible sorghum; 0.5 to 1.3 bugs on IS 21443–a moderately resistant sorghum, and 10 to 15 bugs on IS 17610–a resistant sorghum (Sharma and Lopez, 1993). On chickpea, larval days for *H. armigera* needed to justify insecticide application (EIL) have been estimated to be 3.7 to 3.8 on Annigeri and ICCC 37 (susceptible cultivars) as compared to 2.7 larval days on ICC 506–a resistant cultivar (Wightman *et al.*, 1995). Thus, HPR has a great influence in EILs, and this information is very important in cropping systems involving insect resistance cultivars as a component of pest management.

HPR in Integrated Pest Management

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 pest–resistant cultivars should be aimed at conservation of the natural enemies and minimizing the number of pesticide applications. Use of insect–resistant cultivars also improves the efficiency of other pest management practices, including the synthetic insecticides (Adkisson and Dyck, 1980; Heinrichs, 1988; Sharma, 1993; Panda and Khush, 1995). Host–plant resistance can be used as :

- a principal component of pest control,
- an adjunct to cultural, biological, cultural, and chemical control, and
- as a check against the release of susceptible cultivars.

HPR as a principal method of insect control

HPR as a method of insect control in the context of IPM has a greater potential than any other method of pest suppression. In general, the use of pest–resistant varieties is not subjected to the vagaries of nature unlike chemical and biological control methods. Use of insect–resistant varieties has contributed immensely to sustainable rice production in Asia (Khush and Brar, 1991). Similarly, HPR is the major component of minimizing losses due to insect pests in sorghum (Sharma, 1993). Plant resistance as a method of pest control offers many advantages, and in some cases, it is the only practical and effective method of pest management. However, there may be problems if we rely exclusively on plant resistance for insect control, e.g., high levels of resistance may be associated with low yield potential or undesirable quality traits, and resistance may not be expressed in every environment wherever a variety is grown. Therefore, pest resistant varieties need to be carefully fitted into the pest management programs in different agro–ecosystems.

Insect–resistant varieties have now been deployed for the control a number of insect pests world- wide (Painter, 1951; Maxwell and Jennings, 1980; Smith, 1989; Sharma *et al.*, 1999b). Plant resistance to insects was a principal method of insect control before the advent of insecticides. Several insect pests have been kept under check through the use of insect resistant cultivars, e.g., grapevine phylloxera, *Phylloxera vitifoliae* (Fitch.)–resistant rootstocks from the United States (Painter, 1951); cotton jassid, *A. biguttula biguttula*–Krishna, Mahalaxmi, Khandwa 2, and MCU 5 (Sundramurthy and Chitra, 1992); wooly apple aphid, *Eriosoma lanigerum* (Hausm.)–Northern Spy rootstocks (Martin, 1973); Hessian fly, *Mayetiola destructor* (Say)–Pawnee, Poso 42, and Benhur (Maxwell *et al.*, 1972); rice gall midge, *O. oryzae*–IR 36, Kakatiya, Surekha, and Rajendradhan (Kalode, 1987), spotted alfalfa aphid, *Therioaphis maculata* (Buckton)–Lahontan, Sonora, and Sirsa 9 (Howe and Smith, 1957; Hunt *et al.*, 1966); sorghum shoot fly, *Atherigona soccata*–Maldandi and Swati (Sharma, 1993) and Phule Yashoda (Narkhede, B.N., personal communication); and sorghum head bug, *Eurystylus oldi* Poppius–*guineense* sorghums in West Africa (Sharma *et al.*, 1994).

The benefits of HPR depend on the pattern of insect invasion, e.g., many insects such as aphids, whiteflies, and mites invade the crop in low numbers, and their abundance increases over several generations before reaching the economic threshold levels. For such insects, even low levels of antixenotic and antibiotic resistance would be useful in delaying the time required to reach the damaging levels. Antixenotic resistance is likely to reduce the rate of both initial and successive insect populations build up. Antibiotic type of resistance decreases the rate of insect survival and reproduction, and also prolongs the generation time, while the recovery resistance can withstand the damage from an insect population, which is injurious to another cultivars without tolerance mechanism of resistance. Antixenotic resistance may shift the insect population to other fields of the same crop or to other crops, while antibiotic type of resistance can reduce the pest population within a few generations through cumulative effect (Knipling, 1979; Sharma, 1993).

The impact of insect–resistant varieties on pest populations can be demonstrated by making use of simple insect models of Knipling (1979) as adopted by Addison and Duck (1980), Teetes (1985) and Sharma (1985, 1993). Kennedy *et al.* (1987) demonstrated the usefulness of even low levels of resistance through simulation models. They suggested that maize with antixenotic resistance might not reduce the damage by *Helicoverpa zea* (Boddie), while the maize with antibiotic type of resistance could cause nearly 50% mortality in the first– and second–instar larvae. However, it will take the insect nearly 23 generations to overcome the antixenotic resistance by 50%, while it will require only seven generations to overcome the antibiotic type of resistance. A combination of antixenotic and antibiotic resistance is more durable (Gould, 1984). When the two types of resistances are combined, the insect would take 32 generations to overcome the antibiotic resistance, and over 100 generations to overcome the antixenotic resistance. If the insects are exposed to toxin producing plants, a biotype capable of overcoming the resistance can emerge quickly. Addition of 10% and 30% susceptible plants in the field can delay the development of a new biotype by 150 and 500 generations, respectively (Gould, 1986).

The impact of growing a resistant, a moderately–resistant, and a susceptible variety on insect populations over a period of time has been explained for the pod borer, *Helicoverpa armigera* on chickpea in Table 1. The effect of resistant cultivars would be similar for other insects depending on the level of resistance and the mechanisms involved. The mortality of *H. armigera* larvae is 15% in ICCV 37, 35% on ICCV 2, and 40% on ICC 506. If we assume that there are 10 female moths per ha in the beginning of the season, each female moth lays an average of 500 eggs, the sex ratio is close to 1 :1, and there are three generations in a cropping season; then there will be 1919,14,063 moths in an area planted with the susceptible cultivar, ICCV 37 as compared to 858,20,313 moths in the area planted to the moderately resistant cultivar ICCV 2, and 675,00,000 moths in the area planted to the resistant cultivar, ICC 506. Based on rates of insect multiplication, there would be 2.84 and 1.27 times as many insects in areas planted to ICCV 37 and ICCV 2, respectively, as compared with areas cropped with ICC 506. Thus, plant resistance has a great influence on insect populations, which is cumulative overtime. These models can also explain the situations where minor pests become very serious with the introduction of newly developed high–yielding insect susceptible cultivars.

Table – 1 : Population dynamics of *Helicoverpa armigera* on a susceptible (ICCV 37), a moderately–resistant (ICCV 2), and a resistant (ICC 506) chickpea cultivars–A hypothetical example based on the model proposed by Knipling (1979).

Generation		No. of *Helicoverpa armigera* moths ha^{-1}		
		ICCV 37	ICCV 2	ICC 506
Parent generation	P1	10	10	10
First generation	F1	4250	3250	3000
Second generation	F2	903125	528125	450000
Third generation	F3	191914063	85820313	67500000
Population ratio in relation to the resistant check (ICC 506)		2.84	1.27	1.00

It has been assumed that each female moth lays an average of 500 eggs, and the sex ratio is 1 :1. There are three generations in a cropping season. The *Helicoverpa armigera* population at the beginning of the season is assumed to be 10 female moths ha^{-1}. In each generation, the larval mortality is 15% in ICCV 37, 35% on ICCV 2, and 40% on ICC 506.

HPR and biological control

Plant resistance to insects, in general, is compatible with the natural enemies for pest management. Varieties with moderate levels of resistance that allow the pest densities to remain below economic threshold levels are best suited for use in pest management in combination with natural enemies. The natural enemies not only help to control the target pests, but also reduce the population densities of other insects within their host range (Maxwell, 1972). Insect–resistant varieties also increase the effectiveness of the natural enemies because of a favourable ratio between the densities of the target pest and its natural enemies. And such a combination is more effective in crops with tolerance mechanism of resistance (Kogan, 1982). Restless behavior of the insects on the resistant varieties also increases their vulnerability to the natural enemies (Pathak, 1970). Prolonged developmental period of the immature stages also increases the susceptibility period of the target pest to the natural enemies or result in synchronization of the insect developmental stages with the peak activity and abundance of the natural enemies. Plant resistance and biological control are the key components of integrated pest management (Starks *et al.*, 1972). Moderate levels of plant resistance in chickpea in combination with natural enemies (e.g., *Campoletis chlorideae* Uchida) can produce considerable effect on the population dynamics of *H. armigera* (Table 2). If we assume that there are 10 female moths per ha in the beginning of the season, each *H. armigera* female lays an average of 500 eggs, there are three generations in a cropping season, the larval parasite, *C. chlorideae* results in 20% larval mortality in each generation (based on information summarized by Romeis and Shanower, 1996), and the larval mortality is 15% in ICCV 37, 35% on ICCV 2, and 40% on ICC 506; then there would

Table – 2 : Population dynamics of *Helicoverpa armigera* on ICCV 37–susceptible, ICCV 2–moderately–resistant, and ICC 506–resistant chickpea cultivars in combination with the natural enemy, *Campoletis chloridae*–A hypothetical example based on the model proposed by Knipling (1979).

Generation		No. of *Helicoverpa armigera* moths ha^{-1}		
		ICCV 37	ICCV 2	ICC 506
Parent generation	P1	10	10	10
First generation	F1	3400	2600	2400
Second generation	F2	578000	338000	288000
Third generation	F3	98260000	43940000	34560000
Population ratio in relation to the resistant check (ICC 506)		2.84	1.27	1.00

It has been assumed that each female moth lays an average of 500 eggs, and the sex ratio is 1 :1. The larval parasite, *Campoletis chloridae* results in 20% larval mortality in each generation (based on information summarized by Romeis and Shanower, 1996). There are three generations in a cropping season. The *Helicoverpa armigera* population at the beginning of the season is assumed to be 10 female moths ha^{-1}. In each generation, the larval mortality is 15% in ICCV 37, 35% on ICCV 2, and 40% on ICC 506. The ratio between *Helicoverpa* population in areas with different cultivars + natural enemy and the cultivars alone is 0.51.

be 982,60,000 moths in an area planted with ICCV 37; 439,40,000 moths in the area planted to ICCV 2; and 345,60,000 moths in the area planted to the resistant cultivar, ICC 506. As compared to the resistant check, ICC 506; there would the 2.84 times more moths in the areas planted to ICCV 37 as compared to 1.27 times more moths in the areas planted to ICCV 2. There would be 5.55 times more insects in an area planted to a susceptible cultivar alone as compared to the areas having a resistant cultivar in combination with biological control with *C. chlorideae*. The ratio between *Helicoverpa* moth populations (across cultivars) in areas with different cultivars + control with the natural enemies as compared to those with the cultivars alone would be 0.51. Thus, natural enemies in combination with the natural enemies can have a dramatic effect on the population dynamics of the target pests.

The use of HPR and biological control brings together unrelated mortality factors, and thus reduce the pest population's genetic response to selection pressure from either plant resistance or from the natural enemies. Acting in concert, they provide a density–independent mortality at times of low pest density, and density–dependent mortality at times of pest abundance (Bergman and Tingey, 1979). In addition to the direct and indirect effects of plant resistance on insect pests, the selection pressure imposed by natural enemies can also result in magnification of the effects of plant resistance on insect density (Van Emden, 1990). In general, the rate of insect adaptation to a resistant cultivar is lower when the suppression is achieved by the combined action of plant resistance and natural enemies than by high levels of plant resistance alone (Gould *et al.*, 1991).

Biological control processes involve the tritrophic interactions between the plants, the target pests, and the natural enemies. These interactions are not limited to the impact of plant chemicals on the target pest and the effect of insect–fitness on natural enemies, but also include the direct effects of plants on the natural enemies. It is very likely that plants have evolved mechanisms to attract the natural enemies to reduce the extent of insect damage, e.g., the female parasitoid wasp, *Campoletis sonorensis* (Cam.) responds to the volatiles of cotton plant over a short distance while searching for its prey, *Heliothis virescens* (Fab.). It is easier for the wasp to find the host habitat first and then the prey within the vicinity of the host plant. Tobacco, cotton, and maize plants produce distinct volatile blends in response to damage by *H. virescens* and *H. zea* (Moraes *et al.*, 1998). The parpasitic wasp, *Cardiochiles nigriceps* (Vier.) exploits these differences to distinguish the plant infestation by *H. virescens* from that by *H. zea*, and selectively prefers the plants damaged by *H. virescens*. Therefore, the nature of insect–host plant interactions is critical in determining the extent of parasitization by the natural enemies. This type of strategy is compatible with biological control (Williams *et al.*, 1988). In contrast, plant secondary compounds such as tomatine in insect host's diet may affect the parasitization. In other cases, changes in host suitability due to insect host's diet can influence the developmental rate, size, percentage emergence, parasitization success, sex ratio, fecundity, and lifespan of the parasitoids (Vinson and Barbosa, 1987).

Compatibility of plant resistance and biological control : Insects feeding on a resistant plant generally have a slower growth and extended developmental period. Poorly developed insects are more vulnerable to natural enemies for a longer period, and this increases the probability of mortality due to biotic and abiotic factors. Insects developing slowly on resistant varieties are more effectively regulated by the predators than those feeding on the susceptible varieties (Price *et al.*, 1980). In certain cases, the plant secondary compounds imparting resistance to insects are compatible with the performance of natural enemies, e.g., *Cotesia congregata* (Say) (monophagous parasitoid of *Manduca sexta*) shows no detrimental effects on exposure to nicotine in tobacco. (Barbosa *et al.*, 1986). Gossypol in the pigment glands of cotton ingested by *H. virescens* has no adverse effect on *C. sonorensis*. Larger adults of *C. sonorensis* are produced on insect larvae fed on low concentrations of gossypol than those fed on gossypol–free diets (Williams *et al.*, 1988). Plant resistance and biological control are compatible in case of greenbug (Starks *et al.*, 1972). The movement of the greenbugs on the resistant sorghum cultivars increases the parasitization (Starks and Burton, 1977). Since insecticides are generally not used on resistant cultivars, the natural enemies of the greenbug are also protected.

Reduced rate of multiplication of aphids on the moderately resistant varieties can magnify the plant resistance in the presence of natural enemies (Van Emden and Wearing, 1965). Voraciousness of a given predator fails to control the aphid population daily multiplying by a factor of 1.2 on a susceptible cultivar, but is adequately controlled if the aphid population growth rate decreases to 1.15 on a resistant cultivar (Bombosch, 1963). Low levels of plant resistance also have a positive interaction with the predators of *B. brassicae* on Brussels sprouts. A moderate level of resistance in rice varieties IR 46 and Utri Rajapan effectively increases the predation rate by the spiders (*Lycosa* spp.) on the brown planthopper (Kartohardjono and Heinrichs, 1984).

A number of predators and parasitoids including *C. sonorensis* and *C. nigriceps* attack early instars of *H. virescens,* but generally do not attack bigger larvae. Because of a low level of antlibiosis in moderately resistant plants, the larvae of *H. virescens* remain in early instars for longer periods and are more likely to be parasitized (Danks *et al.*, 1979). The antixenotic factor may decrease or increase the pest fitness due to density and/or frequency–dependent predation. In avoiding plants or plant parts with antixenotic resistance, young larvae become aggregated at a limited number of feeding sites, and this situation is more favorable for natural enemies while screening for their prey (Gould *et al.,* 1991). Compatibility between moderate levels of plant resistance and natural enemies has also been reported in case of sorghum midge (Sharma, 1994). A synergism between plant resistance and biological control of the kind observed above is likely to be a valuable phenomenon in the development of practical insect pest management programs.

Resistant varieties of barley and sorghum complement the activity of the parasite, *Lysiphlebus testaceips* (Cresson) in reducing the damage by the greenbug, *Schizaphis graminum* Rondani (Starks *et al.*, 1972; Salto *et al.*, 1983). *Aphidius matricariae* Hal. is effective in controlling *M. persicae* on aphid–resistant chrysanthemums (Wyatt, 1970). Levels of parasitization of sorghum midge (*S. sorghicola)* by *Neotrichoporoides (Tetrastichus) diplosidis* Crawford were higher on the moderately resistant genotypes IS 10132 and PM 9760 compared to that on the highly resistant genotypes such as IS 3461, IS 7005, IS 9807, IS 19512, and AF 28 (with colored grain and high tannin content) (Sharma, 1994). However, Duale and Nwanze (1997) did not observe any significant differences in parasitization of sorghum midge larvae on different genotypes. Five parasitoid species have been observed on spotted stem borer larvae [*Cotesia* spp., *Sturmiopsis inferens* (Thn.), *Temelucha* spp., and *Glyptomorpha deesae* (Cam.)]. In general, parasitoid activity increased with crop age, and was highest at 40 days after emergence. Higher levels of parasitization were recorded on stem borer–resistant genotypes than on susceptible ones, irrespective of the time and method of infestation (Duale and Nwanze, 1997).

Incompatibility of plant resistance and biological control : Plant morphological characteristics and secondary plant substances sometimes may have an adverse effect on the natural enemies. Leaf hairs and trichomes offer an effective plant defense mechanism against arthropods, but it can interfere with the mobility of natural enemies (Stipanovic, 1983). Genotypes of tobacco with hooked and/or glandular trichomes severely limit the parasitization of the tobacco hornworm eggs by *Telenomus* sp. and *Trichogramma minutum* Riley (Rabb and Bradley, 1968). In case of pigeonpea and chickpea, the presence of trichomes and exudates hamper the parasitization of eggs of *H. armigera* by the egg parasitoid, *Trichogramma chilonis* Ishii (Romeis *et al.*, 1997), Increased trichome density on cotton leaves reduces the ability of the parasitoids *T. pretiosum* Riley and *Chrysopa rufllabris* (Burm.) to find and parasitize corn earworm eggs (Treacy *et al.,* 1985). The development rate is impaired in parasitoids fed on corn earworm larvae reared on artificial diets containing nicotine, tomatine, and gossypol (Vinson and Barbosa, 1987). Some of the midge–resistant sorghum lines with coloured grain and high tannin content have lower levels of parasitization by *N. diplosidis* than in the midge–resistant or susceptible sorghum genotypes having white grain and low or no tannins (Sharma, 1994). Tomatine also affects the egg predators, *Coleomegilla maculata* (DeGeer) and *Geocoris puctipes* (Say) adversely when *H. zea* is fed on the foliage of wild tomato line PI 134417 (Barbour *et al.,* 1993). In tomato, tomatine is absorbed by the endoparasitoid, *Hyposoter exiguae* (Vier.) from its host, *H. zea,* which prolongs the parasitoid larval period, reduces pupal eclosion and adult size, and shortens its longevity and fecundity (Campbell and Duffey, 1979; Herzog and Funderburk, 1985). Secondary plant substances can prolong postembryonic development (Isenhour and Wiseman, 1987, 1989) or reduce the number of adult parasitoids arriving on the host (van Emden, 1978). Plant characteristics can also be manipulated to promote the effectiveness of natural enemies. For example, the hairiness of cucumbers interferes with the biological control of the greenhouse whitefly by the parasite wasp, *Encarsia formosa* (Gahan). Cucumber hybrids now have half the number of hairs, and consequently, the movement of *E. formosa* is 30% higher, and the parasitism levels are significantly greater on these experimental hybrids (van Lenteren, 1991). Similarly the development of pigeonpea lines without glandular trichomes may lead to greater parasitization of *H. armigera* eggs on this crop (Sharma, H.C., unpublished).

Plant resistance–insect pathogen interaction. Plant resistance may improve or reduce the effectiveness of insect pathogens depending on the nature of plant resistance (Schultz, 1983; Barbosa, 1988). The effectiveness of *Bacillus thuringiensis* is greater on insect pests adapted to high tannin content (with a gut pH of 8.0 to 9.5). Secondary plant substances alter the pathogenicity of *B. thuringiensis* on *M. sexta* and *Trichoplusia ni* (Hub.) (Krischik *et al.*, 1988). *Manduca sexta* can tolerate higher levels of toxins such as nicotine and gain protection from entomogenous bacteria. However, when *T. ni* is reared on diets with higher concentrations of *B. thuringiensis*, the presence of dietary nicotine increases the insect mortality. The pathogenicity of the fungus, *Nomuraea ridleyi* is reduced if corn earworm larvae ingest tomatine from tomato plants (Gallardo *et al.*, 1990). A synergistic interaction has been observed between maize cultivars resistant to the fall armyworm, *Spodoptera furgiperda* (J.E. Smith) and the nuclear polyhedrosis virus (NPV) (Hamm and Wiseman, 1986). Rutin and chlorogenic acid inhibit the infectivity of NPV against *H. zea* (Felton and Duffey, 1990). Thus, insect pathogens can be more effective in a pest management program if antibiosis factors of host resistance are compatible with insect pathogens.

HPR and cultural control

Insect–resistant cultivars, including those that can escape pest damage, are highly useful in pest management in combination with cultural practices. This will have the same effect on the population dynamics of the pest species in question as the combined action of insecticides and resistant cultivars. For example, late planting of M 35–1 and Phule Yashoda sorghum cultivars during the postrainy season can reduce the shoot fly damage substantially. Cultural control is a powerful tool to suppress insect pests in agro–ecosystems. This technique involves two basic approaches :

- to make the environment less favorable to the pest, and
- to make the environment more favorable to the pest's natural enemies.

Cultural control by itself may not reduce the pest populations to below economic threshold levels, but aid in reducing losses though interaction with plant resistance (Glass, 1975). Plant resistance in concert with cultural control can drastically reduce the need for pesticide application.

Asynchrony between plant growth and insect populations : Insect–resistant varieties in combination with early planting, early–maturity, defoliation, destruction of stalks, and deep ploughing can be used effectively to control boll weevil and bollworms in cotton (Adkisson and Gaines, 1960). This not only reduces the pest damage, but will also decrease the over–wintering population of these pests, and thus result in reduced crop loss in the following seasons. The nectariless cotton varieties can reduce the pink bollworm infestation by 50% (Wilson and Shaver, 1973), and this in combination with cultural practices can reduce the pink bollworm infestation by 16–fold (Adkisson and Dyck, 1980). Through careful planning, the cropping pattern can be adjusted such that the most susceptible stage of the crop avoids the peak periods of insect activity. A combination of plant resistance and short–duration cotton varieties has been quite effective for controlling the bollworms (Walker and Niles, 1971). The short–season, rapid–fruiting cotton varieties mature 2 to 3 weeks earlier than the long–duration varieties. Early harvest coupled with areawide stalk destruction re‚uces the overwintering population of diapausing insects by 90% (Adkisson and Dyck, 1980). Such a system not only suppresses the pest population, but also restores the biological control and significantly reduces the need for insecticide application.

Genetic diversity : Genetic diversity can play a key role in pest management. Polyculture (growing more than one crop in the same area) is one way of increasing crop diversity. Polycultures are ecologically complex because of interspecific and intraspecific competition with the insects, and the natural enemies (Van Emden, 1965). Elimination of alternate habitats may lead to decreased predator and parasite populations and an increase in insect abundance (Southwood, 1975). Population densities of insect pests are frequently lower in polycultures (Risch *et al.*, 1983), because of associational resistance or resource concentration (Roots, 1973), and the action of natural enemies (Russell, 1989). Specialist insects are generally less abundant in diverse habitats because of low concentration of their food in the habitant and increased activity of natural enemies. Plant diversity may also provide important resources for the natural enemies such as alternative prey, nectar, pollen, and breeding sites. In diverse plant communities, a specialist insect is less likely to find its host because of the presence of confusing or masking effect of chemical stimuli from the non–host plants, physical barriers to movement, and changes in the micro–environment of the target insect. Consequently, insect survival may be lower in polycultures than in the monocultures (Baliddawa, 1985). *Diaphania hyalinata* (L.) population density is lower in polyculture (maize–cowpea–squash) than in monoculture (squash alone) (Letourneau, 1986). The total crop yield in polycultures is greater when estimated as a land equivalent ratio. However, the role of polycultures or plant diversity should be carefully assessed for its effects on insect damage, and the activity and abundance of natural enemies. Also, the effects of plant diversity on pest damage can change over time and locations, depending on the herbivore diversity and interactions among the harmful and beneficial insects.

Multilines / synthetics : The feeding preference of polyphagous insects can be altered by including genetically different genotypes with similar maturity and height. Biological control of the cereal leaf beetle, *Oulema melanopus* (L.) has been achieved with mixed cropping of beetle–resistant and beetle–susceptible wheat varieties than with pure stand of either one of the varieties on a region wide basis (Casagrande and Haynes, 1976). Simulated growth of aphid predators on the susceptible plants in variety mixtures also slows down the rate of development of virulent aphid biotypes (Wilhoit, 1991). The combined effect of varietal mixtures and natural enemies are very effective in suppressing the pest populations.

Trap crops : Cultural practices cause specific physiological changes that reduce the suitability of host plants for phytophagous insects (Hare, 1983). Most of these practices are compatible with other pest control tactics including HPR, and have long been associated with subsistence farming. Trap crops attract insect pests or other organisms so that pest incidence on the target crop is minimized. Reduction in pest damage is achieved either by preventing the pests from infesting the target crop or by concentrating them in a certain part of the field where they can be easily destroyed (Hokkanen, 1991). The principle is similar to associational resistance, in which the insect pests show a distinct preference for certain plant species, cultivars, or a crop stage. Crop stands can be manipulated in time and space so that attractive host plants are offered to the insect pests at a critical stage of insect development. The insects concentrate at the desired site on the trap crop, and as a result, the main crop seldom needs to be treated with insecticides and thus, the natural control of insect pests remains operational in most of the field. Trap cropping is particularly important in subsistence farming in the developing countries, and its application in cotton and soybean has been very successful (Newsom *et al.*, 1980). In cotton/sesame intercrop, row strips of sesame (constituting 5% of the total area) can be used as a trap crop to attract *Heliothis* spp. from the main crop of cotton. Sesame, which is highly attractive to *Heliothis* species (from the seedling stage to senescence), attracts large numbers of insects away from the cotton. It also attracts the parasitoid *C. sonorensis*, which parasitizes large numbers of *Heliothis* larvae (Pair *et al.*, 1982). Several cultural practices in combination with HPR can be used to suppress pest abundance or to allow the crop to escape pest damage.

Table – 3 : Population dynamics of *Helicoverpa armigera* on ICCV 37–susceptible, ICCV 2–moderately-resistant and ICC 506–resistant chickpea cultivars in combination with one insecticide spray–A hypothetical example based on the model proposed by Knipling (1979).

Generation		No. of *Helicoverpa armigera* moths ha^{-1}		
		ICCV 37	ICCV 2	ICC 506
Parent generation	P1	10	10	10
First generation	F1	850	650	600
Insecticide spray (80% larval mortality)				
Second generation	F2	180625	105625	90000
Third generation	F3	38382813	17164063	13500000
Population ratio in relation to the resistant check (ICC 506)		2.84	1.27	1.00

It has been assumed that each female moth lays an average of 500 eggs, and the sex ratio is 1 :1. One application of insecticide results in 80% mortality in first generation. There are three generations in a cropping season. The *Helicoverpa armigera* population at the beginning of the season is assumed to be 10 female moths ha^{-1}. In each generation, the larval mortality is 15% in ICCV 37, 35% on ICCV 2, and 40% on ICC 506. The ratio between *Helicoverpa* population in areas planted with different cultivars + one insecticide spray in the first generation and the cultivars alone is 0.20.

Nutrient application and plant resistance

Expression of resistance to insects changes with the availability of nutrients. Sorghum shoot fly incidence decreases with an increase in application of nitrogenous fertilizers (Reddy and Narashima Rao, 1975; Sharma, 1985). Crop susceptibility to different insect pests changes with the amount and type of fertilizers applied. Therefore, care should be taken to apply appropriate combination of nutrients to minimize pest damage and realise maximum crop yield.

Plant resistance and chemical control

Synthetic insecticides are quite effective for the control of many insect pests. Insecticides are most effective to obtain immediate control of pest outbreaks. However, their broad–spectrum mode of action destroys the beneficial insects as well, and thus leads to adverse effects in the environment. The suppressive action of insecticides is independent of the pest density. The same level of mortality can be expected from a given dose whether the pest population is high or low, and this characteristic is important in applying pest management, i.e., the use of insecticides to reduce populations to levels that can subsequently be controlled by other pest control techniques. The integration of other methods of insect control with different modes of action would lead to minimal use of insecticides for sustainable crop protection.

The most common form of integrated control involves the use of insect–resistant cultivars and insecticides. The pest numbers are reduced in each generation and this process slows down the rate of population growth of the target insects (Painter, 1951). Even a moderately resistant cultivar in combination with insecticides can bring about a substantial reduction in pest numbers (Table 3). If we assume that there are 10 female moths per ha in the beginning of the season, each *H. armigera* female lays an average of 500 eggs, there are three generations in a cropping season, one insecticide application in the first generation results in 80% larval mortality, and the larval mortality is 15% in ICCV 37, 35% on ICCV 2 and 40% on ICC 506 then there would be 383,82,813 moths in an area planted with ICCV 37, 171,64,063 moths in the area planted to ICCV 2, and 135,00,000 moths in the area planted to the resistant cultivar, ICC 506. In relation to ICC 506, there would the 2.84 times more moths in the area planted to ICCV 37 and 1.27 times more moths in the area planted to ICCV 2. There would be 14.22 times more insects in an area planted to a susceptible cultivar alone as compared to the areas having a resistant cultivar + one insecticide application in the first generation. The ratio between *Helicoverpa* moth populations (across cultivars) in areas planted with different cultivars + one insecticide spray in the first generation compared to those with cultivars alone would be 0.20. Plant resistance may also enhance the effectiveness of the insecticides through :

- better insecticide coverage of the plant parts to be protected through modified plant canopy, e.g., loose panicles in sorghum and frego–bract in cotton,
- imbalanced nutrition or toxic substances having an adverse effects on insect growth and development, which may increase the insect susceptibility to insecticides, and
- easy access to the parasites and predators through changes in plant canopy.

Rice varieties with resistance to stem borer (*C. supressalis*) and brown plant hopper (*N. lugens*) have been widely grown in South India, South East Asia, and require fewer insecticidal applications than the varieties susceptible to these pests (Pathak *et al.*, 1973). Several other varieties with resistance to different insects have been used in integrated pest management in rice, cotton, sorghum groundnut, tobacco, soybean, etc. (Kalode and Sharma, 1995).

Plant resistance may also enhance the effectiveness of the insecticides through better penetration of the insecticides to the target insect through modified plant morphology, e.g., loose panicles in sorghum (Sharma *et al.*, 1994a) or open canopy in cotton. Such traits also allow an easy access to parasites and predators, Moderate resistance based on imbalanced nutrition or toxic substances may increase the susceptibility of insects to insecticides. Insect–resistant corn hybrids require less insecticide application than the susceptible ones (McMillan *et al.*, 1972). In sorghum, maximum grain yield has been realized with four sprays of demeton–S–methyl against sorghum head bug, *C. angustatus* in IS 9692 and CSH 11, whereas only 1 to 2 sprays are sufficient to realize the maximum yield potential of the head bug–resistant genotypes, IS 17610 and IS 21443 (Sharma and Lopez, 1993). Head bug–resistant genotypes not only reduce the rate of population increase of the insect, but also tolerate greater head bug densities. Chemical control (carbofuran) in combination with host plant resistance is effective in reducing the shoot fly, *A. soccata* infestation in sorghum (Sharma *et al.*, 1999b).

Interaction between antixenosis mechanism of resistance and chemical control : In the antixenosis type of resistance, repellent chemicals and/or morphological traits may be effective either at the egg laying or feeding stage of the insect. In frego–bract cottons, the square has a rolled, twisted, and open bract (unlike in normal cotton where the bract is flat and encloses the square). Insecticide application is not required for boll weevil control on frego–bract cotton varieties where up to 94% of the weevil population was suppressed. This also reduces the over wintering weevil population (Jenkins and Parrot, 1971). A high level of oviposition suppression can be very useful in an eradication programs. As boll weevils feed and oviposit on the cotton buds, the exposed buds in the frego–bract cotton can ideally be covered with insecticides. When sprayed with methyl–parathion, frego–bract buds have seven times more deposits of insecticide residue than those with normal bracts. A combination of the okra–

leaf (open types) and frego–bract characteristics improved the efficiency of chemical control in cotton (Jones *et al.*, 1986). In sorghum, better control of head bugs and head caterpillars can be obtained in genotypes with open and semi–compact panicles (Sharma, *et al.*, 1994a).

A two–locus model has been developed for resistance–avoidance to illustrate that insect resistance can be managed in the field by the use of insecticides having insect–repellent properties (Gould, 1984). Insecticides reduce pest damage and decrease the population of the target pest, whereas repellency is likely to be effective in limiting pest damage to treated crops as it may keep the pests away from the target crop and reduce the pest incidence. Repellency is equivalent to using low doses of insecticides along with the repellent properties of the host plant. Insecticide formulations having noninsecticidal compounds with repellent properties (naturally derived or synthetically developed products) could lower the rate of insect adaptation to an insecticide. Insects lack the sensory apparatus to respond to most of the insecticides, but they have evolved the ability to respond to the volatile secondary plant compounds produced by the plants. Therefore, the selective pressure due to insecticides without antixenosis is likely to be much stronger than in populations faced with a resistant host plant with antixenosis mechanism of resistance (Pluthero and Singh, 1984).

Interaction between antibiosis mechanism of resistance and chemical control : Plant resistance reduces the rate of insect population increase, which is cumulative overtime. Insecticides kill the target pest while the antibiosis component of resistance aims at decreasing the rate of population increase through reduced vigor, longer development period, and reduced fecundity. This prevents the insect population from attaining the economic threshold levels. Because the toxicity of an insecticide is influenced by the insect body weight, it is expected that a lower concentration is needed to control the insects feeding on a resistant variety than those feeding on a susceptible variety. Nymphs of wheat grain aphid, *Sitobion avenae* (F.) reared on resistant wheat variety (Altar) possessing the antibiosis compound DIMBOA (2, 4–dihydroxy–7–methoxy 1, 4–benzoxazin–3–one) were significantly more susceptible to deltamethrin than the nymphs reared on the susceptible wheat variety (Dollar bird). The LD_{50} value (adjusted for weight) was reduced by 91% for nymphs reared on the aphid–resistant cultivar (Nicol *et al.*, 1993). In concentrations as low as one–hundredth of those affecting the survival and reproduction of the aphid, DIMBOA strongly inhibited detoxifying enzymes (peroxidase, polyphenol oxidase, N–demethylase, glutathione S–transrase, and UDP–glucose transferase) (Leszczynski *et al.*, 1993).

Moderate levels of resistance and chemical control : Moderate levels of resistance to the target pest can be used effectively in combination with insecticides to keep the pest density below economic threshold levels. A rational combination of moderate levels of plant resistance and insecticides reduces the chances of insect resurgence and helps to conserve the natural enemies, preserves environmental quality, slows down the rate of selection for insecticide–resistant insect strains, and increases the profitability of crop production (Adkisson and Dyck, 1980). Population of *M. persicae* on partially–resistant varieties has been observed to be about 85% of that on the susceptible varieties. However, LD_{50} of malathion for the aphid on the partially–resistant cultivar was about 55% compared to that of the aphids on the susceptible variety. Pesticide requirement was much less on the partially–resistant variety than that on the susceptible variety. The increased susceptibility to malathion on the partially–resistant variety appeared to be due to the interaction of the insecticide with insects of low vitality. Even with small levels of plant resistance, insecticide concentration can be reduced to one–third of that required on a susceptible variety (Van Emden, 1990). A half dose of chlorfenvinphos gave equal or better control of the turnip rootfly, *Delia floralis* (Fall.) on resistant cultivars of Swede (Cruciferae) variety S 7790 than the full dose on the susceptible cultivar Ruta. The reduction in indices of fly damage and the increase in percentage of marketable roots were more pronounced in the resistant than in the susceptible cultivar (Taksdal, 1993). Insecticide application did not result in a substantial increase in grain yield of ICC 506, while 4 to 5 sprays were needed to realize the maximum yield potential of Annigeri and ICCC 37 (Wightman *et al.*, 1995). The reduced pesticide use on vegetables for controlling insects not only benefits the agroccosystem and the natural enemies, but also results in lower pesticide residues in the food.

The susceptibility of the white backed planthopper and brown planthopper to insecticides is affected by the level of plant resistance in the rice cultivars. Planthoppers reared on moderately resistant rice varieties had lower LD_{50} values when placed on sprayed plants than those reared on the susceptible varieties (Heinrichs *et al.*, 1984). The LD_{50} of the whitebacked planthopper was 9.4 on the susceptible variety TN 1 treated with ethylan, but only 2.8 on the moderately resistant variety N 22. A combination of moderate resistance and low dosage of the pesticide resulted in effective hopper control.

High levels of plant resistance and chemical control : The resistant untreated maize hybrid 471–U6 x 81–1 had 48% more undamaged ears under artificial infestation (heavy population pressure) than the susceptible hybrid treated with seven applications of Gardona. However, one insecticide application on the resistant hybrid gave earworm control equal to that achieved with seven applications on the susceptible hybrid (McMillian *et al.*, 1972; Wiseman *et al.*, 1973). One of the most successful examples of drastic reduction in insecticide use with resistant varieties is the large–scale planting of rice gall midge–resistant varieties in India (Panda and Khush, 1995).

Advantages of HPR

Utilization of plant resistance as a control strategy has enormous practical relevance and additional emotional appeal (Davies, 1981). 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 of :

Specificity : It is specific to the target pest or a group of pests, and generally has no adverse effects on the non–target organisms.

Cumulative : 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.

Persistence : Most of the insect–resistant varieties express moderate to high levels of resistance to the target insect pests throughout the crop–growing season, except under certain environmental conditions or occasional occurrence of the new biotypes/high pest densities. In contrast, the pesticides have to be applied repeatedly to achieve satisfactory control of the pest populations.

Compatibility : It is compatible with other methods of pest control, and also improves the efficiency of other methods of pest management.

Environmental safety : There are no harmful effects of HPR on nontarget organisms, humans, and the environment.

Ease of adoption : It does not involve any costs to the farmers. Also, the farmers do not have to have knowledge of the application techniques.

Very high levels of resistance may neither be attainable nor required. A variety capable of reducing the pest population by 50% in each generation can be quite useful in reducing the damage below economic threshold levels within a few generations (Painter, 1951). The cumulative and persistent effect of plant resistance are quite contrasting to the explosiveeffects of insecticides, where the insect population multiplies at a much faster rate after the insecticide application because of the absence of natural enemies. One of the notable examples of use of HPR is the near elimination of Hessian fly by the use of resistant varieties in United States, and that of gall midge and brown plant hopper in rice in Asia (Panda and Khush, 1995). The advantages of growing pest–resistant varieties far outweigh their limitations.

Limitations of HPR

Plant resistance is not a panacea for solving all the pest problems. Certain limitations and problems will always beset any insect control program, and HPR is no exception. Development of plant varieties resistant to insect pests takes a long time. It took 15 years to develop the sorghum midge–resistant variety, ICSV 745 (Sharma, 1993). In contrast, only 3 to 5 years were needed to develop the spotted alfalfa aphid–resistant Cody, Moapa, and Lahontan varieties (Panda and Khush, 1995). Developing insect–resistant crop varieties requires a great deal of expertise and resources. It is usually necessary to organize a well–planned multidisciplinary team of entomologists and plant breeders. Commitment of relatively long–term funding is a critical factor in the ultimate success of plant resistance programs. 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 (Mooney *et al.*, 1983). Although concentration of defence chemicals responsible for resistance is low in plant tissues, the total amount per hectare may be high. The production cost of 34 kg of gossypol in terms of glucose equivalent in cotton will be 70.7 kg of glucose ha^{-1} (Mitra and Bhatia, 1982). The genetic, biochemical, and physiological mechanisms involve the initial cost of resistance as well as the extent to which they can be modified by screening and selection. Some mechanisms are less costly whereas others involving high costs cannot be modified. More information is needed on mechanisms of resistance, the genetic regulation of resistance traits, and biochemical pathways and their physiologic effects (Simms, 1992). One might expect a negative correlation between the potential yield of a cultivar and its level of resistance to the target pest. This is illustrated by the failure to evolve insect–resistant varieties of soybean, pigeonpea, chickpea, etc. Although HPR promises to contribute a great deal to pest management in several crops, progress has been slow mainly because of low yield potential of the resistant varieties (Newsom *et al.*, 1980, Sharma, 1993). Yield of promising soybean lines at the advanced stages of testing usually falls short of the performance of commercial varieties. The growers are not willing to plant an insect–resistant variety unless it can yield about as much without insecticide treatment as susceptible varieties with insecticide treatment. However, the fundamental objective of breeding for insect resistance in crop plants is to reduce the amount of pesticides needed to achieve satisfactory control of the target pests, and an acceptable level of sustainable resistance, compatible with yield and quality of the produce.

Despite many dramatic successes in HPR, there still are cases where plant resistance to one insect leads to increased susceptibility to another insect. Cotton varieties with high levels of gossypol are resistant to *Heliothis* spp. and blister beetles, but gossypol at concentrations found in most cotton plants attracts boll weevils (Bell *et al.*, 1987).

Secondary plant substances have a negative effect on the fitness of herbivores. However, many herbivores possess remarkable potential for utilizing or metabolising the toxic plant chemicals and their role as plant defence chemical is not sacrosanct. Thus, insects can evolve into biotypes to overcome antibiosis resistance. However, partially resistant varieties would probably last longer in the field than those with high levels of resistance (Lamberti *et al.*, 1983). The current theories on plant defence strategies do not take into account the complexity of tritrophic interactions. Plant resistance based on antibiosis may not always be compatible with biological control (Boethel and Eikenbary, 1986). Elucidation of these interactions can further our understanding, and provide greater potential for the manipulation of these systems to specific crop species and varieties. The possibility of using compounds from plants to reduce herbivore damage and increase the effectiveness of biological control agents is quite attractive. Ideally, plant resistance should strive to reduce substances attractive to herbivores, while increasing the substances attractive to the natural enemies.

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 carbaryl to *Heliothis* (Brattesten, 1988). Some plant defence chemicals also affect the food quality. Gossypol and related compounds that confer resistance to insects in cotton are toxic to non–ruminant vertebrates (Lambou *et al.,* 1966). Rutin, cholorogenic acid, tomatine, and phenols have toxic effects on humans. Some of these compounds may also be carcinogenic and mutagenic (Armes *et al.*, 1996). Insect–resistant tomato plants when ploughed into the fields after crop harvest may lead to build–up of allelopathic compounds in the soil and may affect the growth of the subsequent crop. The accumulation of such chemicals in the soil may alter the nature of the rhizosphere. Therefore, all such interactions should be kept in mind while developing and deploying the insect–resistant cultivars for pest management. The major limitations of plant resistance are :

Time for development : It takes a longtime to identify and develop insect–resistant cultivars. This method is not suitable to solve sudden or localized pest problems. It takes 5 to 15 years to identify sources of resistance and transfer the resistance traits into cultivars with high yield potential, and desirable quality traits.

Genetic limitations : Absence of adequate levels of resistance in the available germplasm may deter the use of plant resistance for managing certain pests. Such limitations can now be overcome through the use of interspecific hybridzation, mutations, and genetic transformation.

Occurrence of insect biotypes : Occurrence of new biotypes of the target pest may limit the use of certain insect–resistant varieties in time and space. Under such situations, one has to go for polygenic resistance or continuously search for new genes, and transfer them into high yielding varieties.

Conflicting resistance traits : Certain plant characteristics may confer resistance to one pest, but render such plants more susceptible to other pests, e.g., hairiness in cotton confers resistance to jassids (*A. bigullula biguttula*) (Sharma and Agarwal, 1983a), but such varieties are preferred for oviposition by spotted bollworm (*E. vittella*) (Sharma and Agarwal, 1983b). Also, pubescence in soybean confers resistance to leafhoppers, but pod borer (*Grapholitha glycinivorella* Matsumura) prefers pubescent varieties for oviposition (Nishijima, 1960). Varieties with high levels of resistance to sorghum midge are susceptible to head bugs, shoot fly, and stem borer (Sharma, 1993).

Plant resistance at times may be associated with low yield or factors resulting in poor or unacceptable produce, e.g., sorghum genotypes with high tannin content are resistant to sorghum midge (*S. sorghicola*) and birds, but such a grain has poor nutritional quality. Similarly, gossypol and other torpenoids in cotton confer resistance to bollworms (Sharma and Agarwal, 1982), but high gossypol content spoils the quality of cottonseed oil. In such situations, one has to break the linkage between the factors conferring resistance to the target insects and the low yield potential or arrive at a threshold levels for the resistant traits (secondary metabolites) that result in reduced pest susceptibility, and at the same time do not have an adverse effect on the quality of the produce.

Conclusions

Considerable progress has been made in developing techniques to screen for resistance to insects under natural and artificial infestation. There is a need to establish insect rearing facilities to undertake screening and breeding for resistance to insects in different crops. Multilocational testing of the identified sources and breeding material need to be strengthened to identify stable and diverse sources of resistance or establish the presence of new insect biotypes.

Resistance to insects should be given as much emphasis as yield to identify new varieties and hybrids for cultivation by the farmers. Insect–resistant varieties exercise a constant and cumulative effect on insect populations over time and space, have no adverse effects on the environment, reduce the need to use pesticides, have no extra–cost to the farmers, and does not require inputs and application skills by the farmers. Plant resistance to insects will form the backbone of pest management programs in future for sustainable crop production and environment conservation.

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