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Host Plant Resistance to Insects: Modern Approaches and Limitations*

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Abstract

Large scale application of pesticides to reduce the losses due to insect pests has not only led to serious environmental hazards, but has also has resulted in development of resistance in pest populations. It is in this context that varieties capable of resisting pest damage would play a vital role in pest management in future. Considerable progress has been made in identification of sources of resistance to the insect pests in different crops. However, there is a need to transfer the resistant 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. Genes from the wild relatives of crops, and novel genes from un-related species such as Bacillus thuringiensis, *protease inhibitors, and lectin genes can also be inserted into crop plants to make plant resistance an effective weapon in pest management. In addition, molecular techniques such as marker assisted selection, changing of metabolic pathways, and gene switches can also be used for accelerating the pace of developing crop cultivars with resistance to insect pests. Development of insect-resistant varieties will not only cause a major reduction in pesticide use, but also lead to increased activity of beneficial organisms, and a safer environment to live.*

Keywords: Host plant resistance, insect pests, modern approaches, wild relatives, genetic engineering, inducible resistance

Introduction

Large scale and indiscriminate use of insecticides has led to adverse effects on the non-target organisms, pesticide residues in food, pest-resurgence, development of resistance, toxic effects on human beings, and environmental pollution. As a result, it has become quite difficult to control certain insect pests through currently available chemical insecticides. Therefore, it is important to develop alternative methods of pest management involving host plant resistance (HPR) to insect pests. Host plant resistance along with natural enemies and cultural practices should form the backbone of pest management in different agro-ecosystems. Despite 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 is partly due to the relative ease with which insect control is achieved with the use of insecticides. However, with the development of insect resistance to insecticides, there is an urgent need to develop crop cultivars with resistance to insect pests in different crops.

Host plant resistance to insects: Conventional approaches

Considerable progress has been made in identification and utilization of crop germplasm for resistance to insect pests (Smith, 2005). However, resistance-breeding programs are underway for a few crop pests only. Slow progress in developing insect-resistant cultivars has mainly been due to the difficulties involved in ensuring adequate insect infestation for resistance screening, in addition to low levels of resistance to certain insect species in the cultivated germplasm (Sharma and Ortiz, 2002). Under natural conditions, the insect infestation is either too low or too high, and as a result, it becomes difficult to make a meaningful selection. Therefore, it is important to develop techniques to screen for resistance to insect pests under optimum levels of infestation and under similar environmental conditions. However, insect-rearing programs are expensive and technology development may take several years. Techniques to screen for resistance to insects have been developed against some insect species (Smith *et al.*, 1994, Sharma *et al.*, 1992). However, there is

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a need to develop systems for insect rearing, refine the resistance screening techniques, and establish long-term programs to screen and breed for resistance to several insect species that are important crop pests. However, insect-resistant cultivars in desirable agronomic backgrounds have been developed in a few crops only (Panda and Khush, 1995; Mahajan *et al.*, 1997; Sharma and Ortiz, 2002). Cultivars with multiple resistance to insect pests 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 worldwide.

Wild relatives of crops as sources of diverse genes for insect resistance

Wild relatives of crops are important sources of genes for resistance to insects. Wild relatives have shown high levels of resistance, and also have different mechanisms/genes conferring resistance to insect pests, and can be exploited to diversify the basis and increase the levels of resistance to insect pests in different crops.

In cotton, resistance to *Helicoverpa armigera* (Hubner) has been reported in wild species such as *Gossypium thurberi*, *G. somalense*, *G. armourianum*, and *G. barbosanum* (Singh and Narayanan, 1994). Similarly, *Solanum brachistotrichum* – a wild relative of potato, is resistant to green peach potato aphid, *Myzus persicae* (Sulzer). Wild relatives of tomato such as *Lycopersicon hirsutum* f. *glabratum* and *L. hirsutum* are resistant to *H. armigera* (Kashyap *et al.*, 1990). Wild relatives of pigeonpea such as *Cajanus scarabaeoides*, *C. sericeus*, and *C. acutifolius* are highly resistant to *H. armigera* (Sharma *et al.*, 2001; Green *et al.*, 2006); while the wild chickpea species, *Cicer bijugum*, *C. reticulatum*, *C. judaicum*, and *C. microphyllum* have high levels of resistance to *H. armigera* (Sharma *et al.*, 2005d,e). *Arachis cardenasii*, *A. duranensis*, and *A. paraguariensis* - wild relatives of groundnut, have shown levels of resistance to leaf miner, *Aproaerema modicella* (Deventer), *H. armigera*, and *Empoasca kerri* Pruthi (Sharma *et al.*, 2003). Wild relative of cowpea, *Vigna vaxillata* is resistant to spotted pod borer, *Maruca vitrata* (Geyer) and the pod sucking bug, *Clavigralla tomentosicollis* Stal. (Jackai and Oghiakhe, 1989).

In sorghum, accessions belonging to *Sorghum laxiflorum*, *S. australiense*, *S. brevocallosum*, *S. dimidiatum*, and *S. purpureosericeum* are highly resistant to sorghum shoot fly, *Atherigona soccata* (Rondani) and spotted stem borer, *Chilo partellus* (Swin.) (Venkateswaran, 2003). *Sorghum angustum*, *S. amplum*, and *S. bulbosum* are resistant to sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Sharma and Franzmann, 2001). In case of rice, *Oryza eichingeri* has shown high levels of resistance to brown plant hopper, *Nilaparvata lugens* (Stal.), while *O. brachyantha* and *O. minuta* are resistant to yellow stem borer, *Chilo suppressalis* Walker (Khush and Brar, 1991; Brar and Khush, 1997). In case of wheat, the wild relatives such as *Aegilopos tauschii*, *Triticum ventricosum*, and *T. turgidum* are resistant to Hessian fly, *Maytiola destructor* (Say) and *T. monococcum* and *T. turgidum* are resistant to the Russian wheat aphid, *Diuraphis noxia* (Mord.) (Clement, 2002).

Genetic engineering of crop plants for insect resistance

Significant progress has been made over the past three decades in handling and introduction of exotic insecticidal genes into crops plants. Genes from bacteria such as *Bacillus thuringiensis* have been used successfully for insect control through transgenic crops on a commercial scale (Hilder and Boulter, 1999). Trypsin inhibitors, lectins, ribosome inactivating proteins, secondary plant metabolites, vegetative insecticidal proteins, and small RNA viruses can be used alone or in combination with *Bt* genes to impart resistance to insect pests (Sharma *et al.*, 2004). The area planted to transgenic crops increased from 1.7 million ha in 1996 to 100 million ha in 2006 (James, 2006). In addition to the reduction in losses due to insect pests, the development and deployment of transgenic plants with insecticidal genes will also lead to: i) a major reduction in insecticide sprays, ii) reduced exposure of farm labor and nontarget organisms to pesticides, iii) increased activity of natural enemies, iv) reduced amounts of pesticide residues in the food and food products, and v) a safer environment to live. The benefits to growers would be higher yields, lower costs, and ease of management, in addition to reduction in the number of pesticide applications (Sharma *et al.*, 2002).

In the diverse agricultural systems such as those prevailing in the tropics, it would be important to understand the biology and behavior of all the insect species in the ecosystem so that informed decisions can be made as to which crops to transform, and the toxins to be deployed. It is also important to consider the resistance management strategies, economic value, and environmental impact of the exotic genes in each crop, and whether a crop serves as a source or sink for the insect pests and their natural enemies.

Inducible resistance: Gene switches

Induced resistance results in changes in a plant that produce a negative effect on herbivores (Karban and Baldwin, 1997). Chemically induced expression systems or "gene switches" enable temporal, spatial, and quantitative control of genes introduced into plants or those that are already present in the plants to impart resistance to insects. A number of inducible genes have been identified in plants based on endogenous chemical signals such as phytohormones, responses to insect and pathogen attack, or wounding. Effectiveness of the chemical injury inducer, Actigard™ in providing resistance to various insect pests and pathogens in the tomato has been demonstrated by Inbar *et al.*, (1998). Proteinase inhibitors and oxidative enzymes such as polyphenol oxidase, peroxidase, and lipoxygenase persist for at least 21 days after induction in damaged tomato leaflets (Stout *et al.*, 1996). Exogenous application jasmonic acid and salicylic acid has also been shown to induce resistance to several insect pests. The best-studied system utilizes the *PR1-a* promoter from tobacco, which is induced during systemic resistance response following pathogen infection (Uknes *et al.*, 1993). Another system in yeast uses a copper dependent transcriptional activation system, which consists of *ace1* gene encoding a metalloresponsive factor expressed constitutively. Activation of the reporter gene (*ace1*) is achieved in the presence of copper (Mett *et al.*, 1993).

Utilization of molecular approaches for improving HPR to insects

Marker-assisted selection. Recombinant DNA technologies, besides generating information on gene sequences and function, allows the identification of specific chromosomal regions carrying genes contributing to traits of economic interest (Karp *et al.*, 1997). Once genomic regions contributing to the trait of interest have been assigned and the alleles at each locus designated, they can be transferred into locally adapted high-yielding cultivars by making requisite crosses. The offspring with a desired combination of alleles can then be selected for further evaluation using marker assisted selection (MAS). The quality of a marker assisted selection program can only be as good as the quality of the phenotypic data on which the development of that marker was based. It is therefore essential to use large mapping populations, which are precisely and accurately characterized in many locations across several years. The selective power of markers must then be verified in a range of populations representing the diversity of current breeding populations. Only then it will be possible to identify markers, which can be effectively and robustly applied to assist the selection of complex characters.

Marker-assisted selection can be used to accelerate the pace and accuracy of transferring insect resistance genes into improved cultivars. Narvel *et al.*, (2001) used microsatellite markers to identify soybean QTLs for resistance to foliar feeding lepidopteran insects, to determine the degree to which different QTLs have been transferred into soybean cultivars. In contrast to the markers linked to resistance genes inherited as simple dominant traits, the improvement of polygenic traits (QTLs) through MAS is difficult due to involvement of a number of genes, and their interactions (epistatic effects). Several studies on QTLs linked to stem borer resistance in maize underscore the problems involved in using QTLs in MAS. The relative efficiency of phenotypic and MAS has been found to be similar (Willcox *et al.*, 2002). However, phenotypic selection was more favorable due to lower costs. Maximum progress has been made in breeding for insect resistance in common bean by using a combination of phenotypic performance and QTL-based index, followed by QTL based index, and conventional selection (Tar'an *et al.*, 2003).

Gene sequence and function. Genes can be discovered using a variety of approaches (Shoemaker *et al.*, 2001), but a routine large-scale approach can commonly be followed by generating and sequencing a library of expressed genes. A large number of ESTs are now available in the public databases for several crops such as *Zea mays*, *Arabidopsis thaliana*, *Oryza sativa*, *Sorghum bicolor,* and *Glycine max.* A comparison of the EST databases from different plants can reveal the diversity in coding sequences between closely and distantly related species, while mapping of ESTs may elucidate the synteny between those species. For understanding gene functions of a whole organism, functional genomics technology is now focused on high throughput methods using insertion mutant isolation, gene chips or microarrays, and proteomics. These and other high throughput techniques offer powerful new uses for the genes discovered through sequencing (Hunt and Livesey, 2000).

Metabolic pathways. Genetic engineering can be used to change the metabolic pathways to increase the amounts of secondary metabolites, which play an important role in host-plant resistance to insect pests and diseases, e.g., medicarpin and sativan in alfalfa, cajanol and stilbene in pigeonpea, deoxyanthocyanidin flavonoids (luteolinidin, apigenindin, etc.) in sorghum, and stilbene in chickpea (Sharma *et al.*, 2002). The expression of phytoalexins in transgenic plants may be difficult due to complexities involved in their biosynthesis. Expression of a bacterial cytokinin biosynthesis gene (*PI-II-ipt*) in *Nicotiana plumbaginifolia*) plants have been correlated with enhanced resistance to *M. sexta* and *M. persicae* (Smigocki *et al.*, 2000). Molecular mechanisms underlying the activation of defense genes implicated in phytoalexin biosynthesis are quite common in a large number of plant species. Biotechnology offers the promise to increase the production of secondary metabolites in plants that are used in medicine, aromatic industry, and in host resistance to insect pests, or inhibit the production of toxic metabolites in crop produce meant for food, feed, and fodder.

Potential for utilization of HPR in integrated pest management

High levels of plant resistance, that are effective in providing optimum control of the target insect pests, 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 insect damage can be deployed for insect control in combination with other components of pest management. Deployment of insect-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 management practices, including the synthetic insecticides (Sharma, 1993; Panda and Khush, 1995). Host-plant resistance can be used for pest management as: i) a principal component of pest control, ii) an adjunct to cultural, biological, and chemical control, and iii) check against the release of susceptible cultivars.

Plant resistance to insect pests as a method of insect control in the context of IPM has a greater potential than any other method of insect suppression (Adkisson and Dyck, 1980.). 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, e.g., expression of resistance to *H. armigera* in chickpea in North India. Therefore, insect-resistant varieties need to be carefully fitted into the cropping system for pest management in different agro-ecosystems. Several insect pests have been kept under check through the use of insect-resistant cultivars, e.g., cotton jassid, *Amrasca biguttula biguttula* Ishida - Krishna, Mahalaxmi, Khandwa 2, and MCU 5 (Sundramurthy and Chitra, 1992); rice gall midge, *Orseolia oryzae* (Wood Masson)- IR 36, Kakatiya, Surekha, and Rajendradhan (Kalode, 1987); sorghum shoot fly, *Atherigona soccata*- – Maldandi, Swati, and Phule Yashoda (Sharma, 1993); and sorghum midge, *Stenodiplosis sorghicola*- – ICSV 745 (Sharma, 1993).

HPR and biological control. Plant resistant varieties 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 favorable ratio between the densities of the target pest and its natural enemies. 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 increases the susceptibility period of the target pest to the natural enemies or results in synchronization of the insect developmental stages with the peak activity and abundance of the natural enemies. 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 abundance. In general, the rate of insect adaptation to a resistant cultivar is much 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).

Advantages of HPR

Plant resistance to insects is the backbone of any pest management system because it is: i) specific to the target pest or a group of pests, and generally has no adverse effects on the non-target organisms; ii) its effects on insect populations are cumulative over successive generations because of reduced survival, delayed development, and reduced fecundity; iii) it is persistent, except under certain environmental conditions, while pesticides have to be applied repeatedly to achieve satisfactory control of the pest populations; iv) it is compatible with other methods of pest control, and v) it does not involve any costs to the farmers. 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 pest damage to below economic threshold levels within a few generations. The cumulative and persistent effect of plant resistance are quite contrasting to the explosive effects of insecticides, where the insect population multiplies at a much faster rate after the insecticide application because of the absence of natural enemies.

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 insect-resistant varieties requires a great deal of expertise and resources. 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. The major limitations of plant resistance are: i) it takes a longtime to identify and develop insect-resistant cultivars, ii) absence of adequate levels of resistance in the available germplasm may deter the use of plant resistance for managing certain pests, iii) occurrence of new biotypes of the target pest may limit the use of certain insect-resistant varieties, and iv) certain plant characteristics may confer resistance to one pest, but render such plants more susceptible to other pests.

Conclusions

Considerable progress has been made in identification of sources of resistance to insect pests in different crops. However, genes conferring resistance to insects need to be transferred into high-yielding cultivars with adaptation to different agro-ecosystems. Resistance to insect pests 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 pest populations and have no adverse effects on the environment. Therefore, there is a need to exploit plant resistance to insects in integrated pest management for sustainable crop production with a safe environment to live.

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