

Paradigm Shifts in Research on Host Plant Resistance to Insect Pests

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Abstract

Conventional breeding in conjunction with molecular techniques and transgenic approaches have a great promise to reduce pest associated crop losses, and accelerate the progress in developing cultivars with resistance to insects. Although, considerable progress has been made over the past two decades in manipulating genes from diverse sources to develop plants with resistance to insect pests, deployment of molecular techniques for insect resistance, understand nature of gene action and metabolic pathways, but rapid and cost effective development and adoption of biotechnology-derived products will depend on developing a full understanding on the interaction of genes within their genomic environment, and with the environment in which their conferred phenotype interact. A good beginning has been made in developing genetic linkage maps of many crops, but the accuracy and precision of phenotyping for resistance to insect pests remains a critical constraint in many crops. Improved phenotyping systems will have substantial impact on both conventional and biotechnological approaches to breed for resistance to insect pests, in addition to the more strategic research that feeds into these endeavors.

Keywords: Host plant resistance, insect pests, molecular markers, genetic transformation, gene pyramiding, RNAi

Introduction

Host plant resistance (HPR) assumes a central role, and is the backbone of pest management in order to increase production and productivity of the crops, to meet the increasing demand for food, feed, fodder, and fuel. In spite of the importance of HPR as an integral part of integrated pest management (IPM), breeding for resistance to insects has not been as successful as breeding for disease resistance because of the relative ease with which insect control is achieved through insecticide use, slow progress in developing insect-resistant cultivars as a result of the difficulties involved in ensuring adequate insect infestation for resistance screening and slow transfer of insect resistance traits due to complex and polygenic inheritance. With the development of insect resistance to insecticides, adverse effects of insecticides on natural enemies, and public awareness of environment conservation, there has been a renewed interest in the development of crop cultivars with resistance to insect pests. The insect resistant varieties have been deployed as principal method of insect control in several parts of the world, for example, corn varieties with resistance to corn borer, *Ostrinia nubilalis* (Hubner) and corn earworm, *Helicoverpa zea* (Boddie), sorghum to green

bug, *Schizaphis graminum* (Rondani), and alfalfa to aphids - *Therioaphis maculate* (Buckton) and *Acyrtosiphon pisum* (Harris] in USA; cotton to jassid, *Jacobiella facialis* (Jacobi) in Africa; sorghum to midge, *Stenodiplosis sorghicola* (Coquillett) in India; and rice to brown planthopper, *Nilaparvata lugens* (Stal) and green leaf hopper, *Nephotettix virescens* (Distant), and wheat to Hessian fly, *Mayetiola destructor* (Say) and wheat stem fly, *Cephus cinctus* Norton in several parts of the world (Stoner, 1996). The quest to break yield plateau for sustainable increase in crop productivity of field crops through use of hybrid technology has diluted the emphasis on development of insect-resistant cultivars. Moreover, the levels of insect resistance in most of the recently released varieties/hybrids are inadequate, and therefore recent years have observed a paradigm shift in advocacy and deployment of techniques to diversify the bases of resistance through gene pyramiding from cultivated germplasm, closely related wild relatives of crops, and transfer of insect resistance genes in parental lines for developing insect-resistant hybrids (Kameshwara Rao *et al.*, 2005, Dhillon *et al.*, 2008, Sharma, 2009).

Last two decades have seen a rapid progress in deployment of molecular techniques and marker systems in agricultural

sciences to understand gene and genome organization and function of crop plants, and revolutionized the understanding to manipulate traits contributing to crop productivity, and the genes associated with resistance to insect pests. High-density genetic linkage maps of several crops such as barley, maize, potato, rye, sorghum, soybean, tomato, and wheat have been developed, and molecular markers in many of these crops have also been found to be linked to genes expressing resistance to insect pests, which can be used to accelerate the process of transferring insect resistance into improved cultivars (Sharma, 2009). The ability to isolate and manipulate single genes through recombinant DNA technology together with the ability to insert specific genes into cultivars with desirable agronomic traits, and adaptation to environmental conditions in a particular region has added new chapter to crop improvement. Significant progress has been made in over the past two decades in introducing foreign genes into plants, and provided opportunities to modify crops to increase yields, impart resistance to biotic stresses (insect pests, diseases, and weeds), and improve nutritional quality and yield (Sharma *et al.*, 2004). Genes from bacterium, *Bacillus thuringiensis*, non-selective herbicide resistance genes, protease inhibitors, plant lectins, ribosome inactivating proteins, secondary plant metabolites, and small RNA viruses have been used alone or in combination with conventional host plant resistance to develop crop cultivars that suffer less damage from insect pests (Sharma, 2009). Although, the *Bt* genes conferring resistance to insects have been inserted into several crop plants, genetically transformed cotton, maize, rice, tomato, and potato for the management of insect pests with *Bt* genes alone or stacked with herbicide resistance genes, have been deployed for commercial cultivation in several countries of the world (James, 2009). The crops, which initiate a gene-silencing response (RNAi), are a step ahead of existing genetically modified crops that produce toxic proteins, and now lots of emphasis is being given on deployment of this technology for producing insect-resistant crop plants. This paper overviews the paradigm shifts in research on different components of HPR to insect pests over the last two decades.

Identification and utilization of insect resistance sources

Several thousands of germplasm collections have been evaluated for the identification of accessions with resistance against several insect species in different crops in the last two decades (Panda and Khush, 1995, Clement and Quisenberry, 1999, Sharma *et al.*, 2003, Dhaliwal *et al.*, 2004, Smith, 2005, Sharma, 2009), and several insect-resistant cultivars have been released for cultivation in many crops in India (Table 1). Several new sources of insect resistance have been identified and supplemented to the existing resistance

sources against corn earworm, *H. zea*, corn borer, *O. nubilalis*, sugarcane borer, *Diatraea grandiosella* (Dyar), fall armyworm, *Spodoptera frugiperda* (J.E. Smith), and spotted stem borer, *Chilo partellus* (Swinhoe) in maize (Kanta *et al.*, 1997); brown planthopper, *N. lugens*, gall midge *Orseolea oryzae* (Wood-Mason), and stem borers, *Scirpophaga incertulas* (Walker) and *Chilo suppressalis* (Walker) in rice (Smith *et al.*, 1994); Hessian fly, *M. destructor* and greenbug, *S. graminum* in wheat (Smith, 2005); sorghum shoot fly, *Atherigona soccata* (Rondani), spotted stem borer, *C. partellus*, sorghum midge, *S. sorghicola*, and head bug, *Calocoris angustatus* (Lethiery) in sorghum (Sharma *et al.*, 2003, Sharma *et al.*, 2005c); and Oriental armyworm, *Mythimna separata* (Walker) in pearl millet (Sharma and Sullivan, 2000). Sources of resistance have also been identified against cotton bollworm, *Helicoverpa armigera* (Hubner), and leafhopper *Amrasca biguttula biguttula* Ishida in cotton; legume pod borer, *H. armigera* in chickpea and pigeonpea (Sharma *et al.*, 2005a); spotted pod borer, *Maruca vitrata* (Geyer) in pigeonpea and cowpea (Sharma *et al.*, 1999, Sharma and Franzmann, 2000); and pea weevil, *Bruchus pisorum* L. in pea (Clement *et al.*, 1994). Insect-resistant cultivars with desirable agronomic backgrounds have been developed in several crops, and cultivars with multiple resistance to stresses will be in greater demand in future for sustainable crop production, and this requires a concerted effort from the scientists involved in crop improvement programs.

Genetics of resistance to insect pests

Information on genetics and inheritance of resistance to insect pests is important for crop improvement, which indicates the degree of ease or difficulty involved in incorporating resistance genes into the improved cultivars. Many genes have been identified in rice that contribute for resistance to brown planthopper, green leafhoppers, gall midge, white backed planthopper, and yellow stem borer (Khush and Brar, 1991). Both dominant and recessive genes control the inheritance of resistance to brown plant hopper, white backed plant hopper, and gall midge (Khush and Brar, 1991, Katiyar *et al.*, 2001), while resistance to yellow stem borer is polygenic, and exists in many genotypes of rice (Khush and Brar, 1991). Evaluation of germplasm for resistance to Hessian fly has reported 29 genes that control resistance to this insect (Smith, 2005). All the genes (except *h4*) are inherited as dominant or partially dominant traits, and several of these genes have been deployed in response to evolution of Hessian fly biotypes. Eleven dominant genes control the expression of resistance to green bug (Zhu *et al.*, 2004), while twelve genes (both dominant and recessive) control resistance to the Russian wheat aphid, *Diuraphis noxia* (Kurdj.) in wheat (Saidi and Quick, 1996, Liu *et al.*, 2001). Resistance to *D. noxia* biotype I in barley is

Table 1. Insect-resistant cultivars of major food crops released for cultivation in India

Insect pests	Cultivars
Rice	
Brown planthopper	Manasarowar, Bhadra, Jyoti, Co 42, MTU 5249, Co 46, Shyraksha, and Dhanya
White backed planthopper	Tangner and Amelbero
Gall midge	IR 36, Kakatiya, Surekha, Phalguna, Kunti, Shakti, Shamlei, Asha, Rajendradhan, Sharaksha, and Kavya
Green leafhopper	IR 20 and Vani
Leaf folder	ASD 20
Yellow stem borer	Ratana, Sasyasree, Saket, and MTU 5849
Maize	
Pink stem borer	Deccan 101 and Deccan 103
Spotted stem borer	Ganga 4, 5, 7 and 9, Ganga safed 2, Deccan 101, 103, Ageti, Kanchan, Kundan
Sorghum	
Shoot fly	M 35-1, Swati, SPV 491, ICSV 700, ICSV 705, Phule Yashoda, SPV 1015
Spotted stem borer	E 302, E 303, ICSV 700, ICSV 705, SPV 101
Midge	DJ 6514, AF 28, ICSV 197, ICSV 745, ICSV 88032
Head bug	CSM 388, Chencholam, ICSV 239
Groundnut	
Leaf miner	ICGV 86031, IGCS 156 (M 13), FDRS 10
Thrips	M 13, Robut 33-1
Tobacco caterpillar	ICGV 86031, FDRS 10
Rapeseed and mustard	
Mustard aphid	PBR 91, Pusa Jai Kisan, C 294, Laha 101, Pusa Kalyani, Regent, Tora, Sariahi
Soybean	
Leaf miner	Nimsoy
Chickpea	
Pod borer	C 235, PantG 114, Anupam, JG 74, ICCV 10, Dulia, Pusa 261, Vijay, Vishal
Pigeonpea	
Pod borer	T 21, Bori, BDN 2, ICPL 332, MA 2, Bahar, ICPL 84060, Pant A1, BSMR 1
Pod fly	KM 7

Source: Dhaliwal et al. (2004)

controlled by dominant alleles at two loci (Momhinweg *et al.* 1995). Resistance to ear damage by European corn borer in sweet corn involves multiple genes, and is controlled by epistatic as well as additive-dominance effects (Warnock *et al.*, 1998). Both GCA and SCA effects explain significant amounts of variation in different maize populations for resistance to fall armyworm and southwestern corn borer (Williams *et al.*, 1995, 1998). Inheritance of maysin content

in maize imparts resistance to corn earworm, and is governed by the presence of a major modifier gene (Widstrom and Snook, 2001). Stalk resistance to the stem borer, *Sesamia nonagrioides* (Lefebvre) is quantitatively inherited, and additive, dominant and epistatic effects control the gene action (Cartea *et al.*, 2001). Both additive and dominant effects explain the variation in expression of resistance to corn leaf aphid, *Rhopalosiphum maidis* (Fitch.) (Bing and

Guthrie, 1991), and to *C. partellus* (Pathak, 1991). Resistance to shoot fly is inherited by additive gene action (Dhillon *et al.*, 2006e), while additive and non-additive gene effects govern resistance to spotted stem borer in sorghum (Sharma *et al.*, 2007). Resistance to sorghum midge is inherited as a recessive trait, and is controlled by additive gene effects (Sharma *et al.* 1996). However, resistance to sorghum head bug, *C. angustatus* is inherited as a partially dominant trait controlled by both additive and non-additive gene action (Sharma *et al.*, 2000), while resistance to African head bug, *Eurytulus oldi* (Poppus) is largely controlled by additive type of gene effects (Ratnadass *et al.*, 2002). Most of the characters associated with resistance to *H. armigera* in cotton are governed by oligogenes, and can be transferred into locally adapted cultivars. Inheritance of gossypol containing glands, which are associated with resistance to bollworms in cotton, is due to *G 13* allele (Calhoun, 1997). Trichome density in *Gossypium* species, which is associated with resistance to leafhoppers, is governed by five genes t_1-t_5 (Lacape and Nguyen, 2005). Resistance to *H. armigera* is controlled by multiple genes, and inheritance of resistance to pod borer in *desi* chickpea is governed by additive gene effects, while non-additive type of gene action was observed in *kabuli* types (Gowda *et al.*, 2005). Verulkar *et al.*, (1997) indicated the involvement of a single dominant gene in antixenosis mechanism of resistance in *C. scarabaeoides* to *H. armigera* and *Melanagromyza obtusa* Malloch. Inheritance of hooked trichomes responsible for *Empoasca kraemeri* Ross and Moore resistance in Lima bean is complex, and is controlled by additive, dominant, and epistatic gene effects (Park *et al.*, 1994). Resistance to bean weevil, *Acanthoscelides obtectus* (Say), is derived from a wild *Phaseolus* accession, and is inherited as a complementary effect of two recessive genes (Kornegay and Cardona, 1991). Resistance in mungbean, *Vigna radiata* to the Azuki bean weevil, *Callosobruchus chinensis* L., and the cowpea weevil, *C. maculatus* (F.) is derived from the wild mungbean, *Vigna radiata* var. *sublobata*, and is inherited as a simple dominant trait (Tomaka *et al.*, 1992).

Exploitation of cytoplasmic male-sterility systems for insect resistance

Considerable information has been generated on the effects of cytoplasmic male-sterility (CMS) on morphological and physiological characteristics in different crop plants, and on the influence of CMS on expression of resistance to insect pests. Most of the sorghum hybrids grown to date are based on *Milo* (A_1) cytoplasm, except a few hybrids based on A_2 cytoplasm in China (Shan *et al.*, 2000). The A_1 cytoplasm based hybrids have been reported to be highly susceptible to insect pests (Sharma, 2001, Dhillon *et al.*, 2005, Dhillon *et al.*, 2008). The expression of nonpreference and antibiosis

components of resistance to *D. grandiosella* and *D. saccharalis* was higher in resistant inbred lines based hybrids than the inbreds (Kumar and Mihm, 1996). Expression of different mechanisms and traits associated with resistance to shoot fly, midge, shoot bug, and sugarcane aphid have been found to be significantly lower in CMS as compared to the maintainer lines of sorghum (Dhillon *et al.*, 2006b, c, d). Hybrids based on shoot bug, sugarcane aphid, midge, and shoot fly-resistant CMS and restorer lines suffered less damage than the hybrids based on susceptible CMS and resistant or susceptible restorer lines, suggesting that expression of resistance to these insects is influenced by the genetic background of the CMS lines, and resistance is needed in both the parents to produce insect-resistant hybrids (Sharma *et al.*, 1996, Dhillon *et al.*, 2006c, Sharma *et al.*, 2006). Furthermore, the A_4M cytoplasm was found to be comparatively less susceptible to *A. soccata* damage than the A_1 , A_2 , A_3 , A_4G , A_4VzM cytoplasm (Dhillon *et al.*, 2005). The analyses of literature available on different CMS systems in cereals suggests that the genetic background of CMS, cytoplasmic factors, the interactions of the factors in the cytoplasm of maintainer lines with the nuclear genes and the restoration abilities of the restorers influences the expression of resistance to insect pests and diseases depending on the crop and the pest species involved; and therefore, there is a continuing need to evaluate different cytoplasmic factors for their effects on cultivar susceptibility to insect pests, and transfer insect resistance genes into A-, B-, and R-lines to develop hybrids with multiple resistance to insect pests for sustainable crop production (Dhillon *et al.*, 2008).

Search of insect resistance genes from wild relatives of crops

Wild species of crops are important sources of genes for resistance to biotic and abiotic constraints. Genotypes showing high levels of resistance to insects can be used in wide-hybridization to increase the levels and diversify the basis of resistance to the target insects. Last two decades have observed a paradigm shift in identification and deployment of wild species of several crops as sources of genes for resistance to insects, for example, wild relatives of cotton for resistance to pink bollworm, cotton bollworm, white fly, and leafhoppers; tomato for fruit borer; pigeonpea for pod borer, pod fly, and pod wasp; chickpea for pod borer and bruchids; groundnut for leaf miner, leaf hoppers, pod borer, and armyworms; pea for bruchid; cowpea for spotted pod borer and pod sucking bug; sorghum for shoot fly, stem borer, and sorghum midge; rice for brown planthopper, green leaf hopper, yellow stem borer, and

striped rice stem borer; and wheat for resistance to Hessian fly and Russian wheat aphid (Table 2).

Deployment of molecular markers for host plant resistance to insects

A wide variety of techniques have been developed in the past few years to detect DNA sequence polymorphism, characterization of genetic diversity, genome fingerprinting, genome mapping, gene localization, genome evolution, population genetics, taxonomy, plant breeding, and diagnostics. Whole genome sequencing of a number of model organisms and deployment of different types of molecular markers for the development of high-density genetic linkage maps of several crops such as barley, maize, rice, potato, rye, sorghum, soybean, cowpea, tomato, and wheat are some of the recent biotechnological developments in agriculture (Sharma, 2009). It takes five to six generations to transfer insect resistance traits into the high-yielding cultivars through conventional breeding, while gene transfer from wild relatives may take considerably longer time due to the complexity of achieving interspecific hybrids on a sufficiently large scale to identify stable progeny with an acceptable combination of traits. Near isogenic lines (NILs), F_2 and backcross populations, doubled haploids, and recombinant inbred lines (RILs) can be used for gene mapping in many crops (Mohan *et al.*, 1997). Mapping populations from interspecific crosses are often used for genetic linkage studies due to high level of detectable polymorphism, but linkage maps derived from such crosses may have limited relevance in crop breeding programs due to different recombination patterns (Fulton *et al.*, 1997). However, markers developed from such maps may be valuable tools for introgression of genes of interest from the wild relatives into the cultigen. Furthermore, marker

assisted selection (MAS) has shown the potential to dramatically speed up the process by reducing the number of generations and the size of the populations required to identify individuals with appropriate combination of genes, with minimal amount of linkage drag from the wild relatives.

Considerable progress has been made in the recent past in identifying genomic regions and genes associated with resistance traits in several crops to different insect pests (Smith, 2005). Several types of molecular markers have been used to evaluate DNA polymorphism, and for developing genetic linkage maps of different crops, to identify quantitative trait loci (QTLs) associated with resistance to insects. Molecular markers linked to yellow stem borer resistance (Selvi *et al.* 2002), and QTLs and genes conferring resistance to rice gall midge and its biotypes (Mohan *et al.*, 1994, Biradar *et al.*, 2004, Jain *et al.*, 2004), leaf hoppers (Wang *et al.*, 2004, Fujita *et al.*, 2006), and brown plant hopper (Sharma *et al.*, 2003, Jena *et al.*, 2006), have been mapped and deployed in MAS for developing insect-resistant rice. Several polymorphic markers and genes responsible for resistance to Hessian fly and its different biotypes (Dweikat *et al.*, 2004, Wang *et al.*, 2006), Russian wheat aphid (Ma *et al.*, 1998), and green bug (Zhu *et al.*, 2005), have been mapped and used in wheat breeding for insect resistance. The corn earworm resistance QTLs depicting change in maysin concentration in maize silk have been reported by Byrne *et al.*, (1996). Although, a few QTLs have been found for resistance to borers, the QTLs found responsible for resistance to stem boring by *O. nubilalis*, *D. grandiosella*, and *D. saccharalis* share some common genomic regions, and play a major role for resistance in

Table 2. Wild species of different crops identified as sources of genes for resistance to different insect pests

Crop	Wild species	Insect pests
Tomato	<i>Lycopersicon esculantum</i> , <i>L. hirsutum</i> , and <i>L. hirsutum</i>	<i>Helicoverpa armigera</i>
Cotton	<i>Gossypium thurberi</i> , <i>G. somalense</i> , <i>G. armourianum</i> , <i>G. gossypoides</i> , <i>G. capitata viridis</i> , <i>G. raimondii</i> , <i>G. trilobum</i> , <i>G. sinense</i> , <i>G. latifolium</i> and <i>G. barbosanum</i>	bollworms and sucking insect pests
Pigeonpea	<i>Rhynchosia aurea</i> , <i>R. bracteata</i> , <i>Cajanus scarabaeoides</i> , <i>C. sericeus</i> , <i>C. acutifolius</i> , <i>C. albicans</i> and <i>Flemingia bracteata</i>	<i>Helicoverpa armigera</i>
Chickpea	<i>Cicer bijugum</i> , <i>C. cuneatum</i> , <i>C. pinnatifidum</i> , and <i>C. judaicum</i>	<i>Helicoverpa armigera</i>
Groundnut	<i>Arachis cardenasii</i> , <i>A. duranensis</i> , <i>A. kempffmercadoi</i> , <i>A. monticola</i> , <i>A. stenoperma</i> , <i>A. paraguariensis</i> , <i>A. pusilla</i> , and <i>A. triseminata</i>	leafminer, <i>Helicoverpa armigera</i> , <i>Spodoptera litura</i> , and <i>Empoasca kerri</i>
Sorghum	<i>Sorghum australiense</i> , <i>S. purpureosericeum</i> , <i>S. brevicullosum</i> , <i>S. timorense</i> , <i>S. versicolor</i> , <i>S. matrankense</i> , <i>S. nitidum</i> , <i>S. angustum</i> , <i>S. ecarinatum</i> , <i>S. extans</i> , <i>S. intrans</i> , <i>S. interjectum</i> , and <i>S. stipodeum</i>	<i>Atherigona soccata</i> , <i>Chilo partellus</i> , and <i>Stenodiplosis sorghicola</i>
Rice	<i>Oryza officinalis</i> , <i>O. minuta</i> , <i>O. latifolia</i> , <i>O. australiensis</i> , <i>O. granulata</i> , and <i>O. brachyantha</i>	<i>Sogatella furcifera</i> , <i>Nilaparvata lugens</i> , and <i>Scirpophaga incertulas</i>

Source: Sharma (2009)

maize (Khairallah *et al.*, 1997, Butron *et al.*, 2005). Resistance to *O. nubilalis* appears to be controlled by QTLs for neutral detergent fiber, acid detergent fiber in leaf-sheaths, leaf-sheath acid detergent lignin, starch concentration in the stalk, and stem tunneling by European corn borer (Krakowsky *et al.*, 2007). Several QTLs have also been found associated with resistance to green bug and its I and K biotypes (Agrama *et al.*, 2002, Nagaraj *et al.* 2005), and two different mechanisms of resistance to midge have been mapped in sorghum (Tao *et al.*, 2003). The QTLs associated with phenotypic traits responsible for resistance to shoot fly have been identified in sorghum (Folkertsma *et al.*, 2003, Hash *et al.*, 2003, Dhillon *et al.*, 2006a). Two BAC libraries of wild Mexican diploid potato, *Solanum pinnatisectum*, have been constructed where fifteen BAC clones harbored polyphenol oxidase loci for Colorado potato beetle, *Leptinotarsa decemlineata* (Say) resistance (Chen *et al.*, 2004), which might be useful for BAC contig construction and map-based cloning of genes responsible for resistance to this insect. The QTLs for resistance to leaf miner, *Liriomyza trifolii* (Burgess) have also been identified in tomato (Moreira *et al.*, 1999). A mapping population based on *C. cajan* x *C. scarabaeoides* has been developed, and is under evaluation for resistance to *H. armigera* and identify QTLs linked to pod borer resistance in pigeonpea (Sharma, 2009). Mapping for resistance to pod borer in chickpea is only just beginning, and the efforts are underway to evaluate inter-specific mapping populations to identify QTLs linked to various components of resistance to *H. armigera* in chickpea (Sharma *et al.*, 2005b, Sharma, 2009). Eight markers associated with resistance to potato leafhopper, *Empoasca fabae* (Harris), four markers to *E. kraemeri*, and three markers to both species have been reported in common bean (Murray *et al.*, 2004). A major QTL for *Thrips palmi* Karny resistance has also been reported in Mesoamerican bean (Frei *et al.*, 2005). Two major QTLs have been identified in soybean for antibiosis mechanism of resistance to *H. zea*, and *Pseudoplusia includens* (Walker) (Terry *et al.*, 2000). Resistance to aphid, *Aphis craccivora* Koch has been identified in the groundnut breeding line ICG 12991, which is controlled by a single recessive gene (Herselman *et al.*, 2004).

Genetic transformation and gene pyramiding for insect resistance

Recombinant DNA technology has opened up new vistas to isolate and manipulate genes for crop improvement. Significant progress has been made over the past two decades in isolation, cloning, and introduction of foreign insecticidal genes into crop plants to impart resistance to insect pests and widen the pool of useful genes. The *Bt* genes conferring resistance to insects have been inserted into several crop plants such as maize, rice, wheat, sorghum, sugarcane,

cotton, potato, tobacco, broccoli, cabbage, chickpea, pigeonpea, cowpea, groundnut, tomato, brinjal, and soybean (Hilder and Boulter, 1999, Sharma *et al.*, 2004). Combining conventional/marker assisted host plant resistance with insertion of insect resistance genes through genetic transformation can provide a germplasm base to achieve durable resistance to insect pests. For example, MAS has been used to track the antibiosis/antixenosis resistance linked QTLs during and after the two backcrosses in soybean to develop a series of BC₂F₃ plants with or without *cryIAc* transgene, for *Bt* and QTL conditioning resistance against corn earworm (Walker *et al.*, 2002), indicating that *Bt*-transgene and QTL-mediated resistance can be combined for a viable insect control strategy. Transgenic plants of cotton with *Bt* + *GNA* conferred resistance to *H. armigera* and cotton aphid, *Aphis gossypii* Glover (Liu *et al.*, 2003). Till date, a total of 14 *Bt* genes have been deployed through 31 events of genetically modified cotton, 40 events of maize, three events of rice, one event of tomato, and 28 events of potato for the management of lepidopteran and coleopteran insect pests (Table 3), alone or stacked with herbicide resistance genes, and these genetically modified crops are under commercial cultivation in several countries of the world. The benefits of growing transgenic crops to growers have been higher yield, lower input costs in terms of pesticide use, reduction in harmful effects of insecticides on non-target organisms, reduced amounts of insecticide residues in food and food products, and easier crop management (Qaim and Zilberman, 2003, Dhillon and Sharma, 2009).

Deployment of RNA interference (RNAi) technology in host plant resistance

A conserved biological response to double-stranded RNA, often known as RNA interference (RNAi) or post-transcriptional gene silencing, mediates resistance to both endogenous parasitic and exogenous pathogenic nucleic acids, and regulates the expression of protein-coding genes (Hannon, 2002). Recently, the RNAi technology has been demonstrated to be helpful in understanding the functional genomics of valuable crop traits for resistance against insect pests (Gordon and Waterhouse, 2007). In RNAi technology, the dsRNA of insect's gene is expressed in plants by using transgenic technique, and then the interfering RNAs are formed in the plants. The interfering RNAs then enter into insects' bodies after being ingested by the insect that eats the plant, and conduct RNAi against the target gene, thereby expression of the target gene is suppressed by RNAi. Transgenic corn plants engineered to express WCR dsRNAs have shown a significant reduction in western corn rootworm, *Diabrotica virgifera virgifera* LeConte feeding damage, suggesting that the RNAi pathway can be exploited to control insect pests via in planta expression of a dsRNA

Table 3. Commercially deployed *Bacillus thuringiensis* genes through genetically modified crops for resistance to insect pests

Crop	No. of events	Insect pests	Gene(s)
Cotton	31	Lepidopteran	<i>cryIAC</i> , <i>cry2Ab2</i> , <i>cryIAb</i> , <i>cryIC</i> , <i>cryIA</i> , <i>vip3A(a)</i> , <i>cryIF</i> , and <i>flcryIAb</i>
Maize	40	Lepidopteran and Coleopteran	<i>cryIAb</i> , <i>cryIAC</i> , <i>cry9C</i> , <i>cry34Ab1</i> , <i>cry35Ab1</i> , <i>cryIF</i> , <i>cry3Bb1</i> , <i>cryIA.105</i> , <i>cry2Ab2</i> , <i>cry3A</i> , and <i>vip3Aa20</i>
Rice	3	Lepidopteran	<i>cryIAC</i> and <i>cryIAb</i>
Tomato	1	Lepidopteran	<i>cryIAC</i>
Potato	28	Coleopteran	<i>cry3A</i>

Source: CBD (2010); ILSI Research Foundation (2010)

(Baum *et al.*, 2007). Cytochrome P450 gene (*CYP6AE14*) the first gossypol-inducible P450 gene from bollworms, is directly involved in the ability of cotton bollworm to tolerate gossypol. When *CYP6AE14* expression is suppressed, as achieved by plant-mediated RNAi, the larval tolerance to gossypol is greatly reduced (Mao *et al.*, 2007). The ability to down-regulate *CYP6AE14* and *GSTI* expression in the midgut by feeding cotton bollworms dsRNA-producing leaves, suggests that plant-mediated RNAi may be a general approach for gene-silencing in herbivorous insects. However, the passage of years without reports of success using this approach seemed to suggest that simply expressing hairpin RNA in plant material to be ingested by an insect would not provide sufficient levels of intact dsRNA to trigger potent RNAi in the pest. RNAi provides a unique mode of action for the control of insect pests that could complement the current strategy of expressing *Bt* insecticidal proteins in crops such as corn, cotton and soybeans, and as the new crops target particular genes in particular insects, they will be safer and less likely to have unintended effects than other genetically modified plants.

Conclusions

Augmentation of conventional breeding with the use of molecular techniques and transgenic approaches have a great promise to reduce pest associated crop losses, and accelerate the progress in developing cultivars with resistance to insects and increase crop productivity. Although, considerable progress has been made over the past two decades in manipulating genes from diverse sources to develop plants with resistance to insect pests, deployment of molecular techniques for insect resistance, understand nature of gene action and metabolic pathways, but rapid and cost effective development, and adoption of biotechnology-derived products will depend on developing a full understanding on the interaction of genes within their genomic environment, and with the environment in which their conferred

phenotype interact. A good beginning has been made in developing genetic linkage maps of many crops, but the accuracy and precision of phenotyping for resistance to insect pests remains a critical constraint in many crops. Improved phenotyping systems will have substantial impact on both conventional and biotechnological approaches to breed for resistance to insect pests, in addition to the more strategic research that feeds into these endeavors. Marker-assisted selection has had a dramatic impact, particularly in the private sector, in breeding for disease-resistance and quality traits where simply inherited components could be readily identified. The same potential may be achieved in case of more complex traits such as resistance to insect pests and abiotic stresses. Therefore, there is a need to use molecular techniques to develop cultivars with improved resistance to insect pests, and to strengthen *Bt* transgenic crops for other components of plant resistance through precise mapping of the QTLs associated with resistance to insects, and development of new paradigms in breeding based on re-engineered breeding programs to make best use of biotechnological tools.

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