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INSECT RESISTANCE IN FIELD CROPS

CH PADMAVATHI* AND **P G PADMAJA**[1]

ICAR-Indian Institute of Rice Research, Rajendranagar, Hyderabad 500030, Telangana, India
[1]ICAR-Indian Institute of Millets Research, Rajendranagar, Hyderabad 500030, Telangana, India
*Email: ch.padmavathi@icar.gov.in (corresponding author)

ABSTRACT

Insect resistant crop plants form the core component of Integrated Pest Management (IPM) due to their ability to reduce the crop losses and associated insecticide costs in addition to protecting the environment. In this review, various types of resistance being cited, resistance mechanisms and causal factors responsible with examples were discussed. Traits associated with resistance, genetics and inheritance patterns were listed. Several sources of resistance including crop varieties, wild relatives, QTLs identified and mapped for major insect pests so far were elaborated along with steps in the development of a resistant variety. Advantages and limitations of insect resistance were also discussed with emphasis on the development of insect biotypes. Novel strategies in molecular approaches like marker assisted selection, gene pyramiding, RNAi approach along with genome editing strategies were emphasized. The development of insect resistant crops is a sustainable way to manage pests and hence emphasis need to be given to breed trait specific insect resistant cultivars utilizing the novel approaches in the future breeding programs.

Key words: Insect pests, resistant variety, trait, mechanisms, biotypes, causal factors, QTLs

Global food production must increase dramatically by 2050 to feed projected population of 9.3 billion (Audsley et al., 2009). Presently, application of chemical pesticides is the widely prevalent strategy to reduce crop losses caused by insect pests and diseases and is valued at over US$ 250 billion annually. Indiscriminate application of the toxic chemicals has led to the development of resistance in target pests, resurgence of non-target pests and serious environmental hazards. Host plant resistance (HPR), plays a vital role in reducing crop losses and protecting the environment in most of the field crops. Growing insect resistant varieties does not need any extra skill for farmers and requires no additional cash investment. Considerable progress has been made in developing crop cultivars with resistance to the major insect pests in different field crops.

Insect resistant crop plants continue to be the foundation of food production due to their ability to increase yields and decrease insecticide costs (Wiseman and Webster, 1999). Earlier, farmers recognized plants that were able to withstand insect pest damage and adverse environmental conditions. The plants that were susceptible to pests were generally eliminated, and only resistant plants survived leading to the natural selection of plants with an ability to withstand pest damage. The first resistant wheat cultivar (cv. Underhill) against *Mayetiola destructor* was grown in New York in 1780's (Panda and Khush, 1985). Breeding for resistance to insect pests commenced formally after the rediscovery of Mendel's law of heredity in 1900 and evolved as a field of research with the work of Painter (1951) during 20th century. Over the past few decades, insect resistant varieties were developed by collaborative research between plant breeders and entomologists, and have contributed significantly to major yield increases in maize, rice and wheat (Smith, 2005; Brummer et al., 2011).

A number of indigenous cultivars and landraces selected by farmers hoarded genes conferring resistance to pests. The best examples of this process are brown planthopper resistant landrace Salkathi (Mohanty et al., 2017) and Rathuheenathi (Padmavathi et al., 2007), shoot fly resistant sorghums (landrace variety Maldandi) cultivated during the postrainy season in India, and head bug resistant guinea sorghums cultivated in West Africa (Sharma, 1993). There are many such examples of existence of plants resistant to pests in landraces and wild species of various crops. Host plant resistance (HPR), therefore, forms the backbone of any pest management strategy.

Using the conventional and molecular tools, resistance genes to major insect pests have been mapped, and some of these resistance genes have been, and are being transferred into agronomically elite and high-yielding varieties. Genes from the wild relatives of crops, and novel genes, such as those from *Bacillus thuringiensis* are also introgressed into different crops to make plant resistance an effective method in pest management. Development of pest-resistant varieties and their utilization will not only cause a major reduction in pesticide use and slowdown the rate of development of resistance to pesticides. Growing a resistant variety also increases activity of beneficial microorganisms and reduces pesticide residues in food and food products in some crops with a much safer environment to live.

Host plant resistance includes those characteristics of a plant to avoid, tolerate or recover from the attack of insects under conditions that would cause greater injury to other plants of the same species. Painter (1951) defined plant resistance as the relative amount of heritable qualities possessed by a plant which influence the ultimate degree of damage done by the insect. According to Kogan (1998), resistance to insects is the heritable property that enables a plant to restrain the growth of insect populations or to recover from injury caused by populations that were not restrained. Smith (2005) described host-plant resistance as sum of the constitutive, genetically inherited qualities that result in a plant of one cultivar or species being less damaged than a susceptible plant lacking these qualities. According to Panda and Khush (1995), plant resistance has four major features by which resistance can be assessed, viz., i) Resistance is heritable and controlled by one or more genes, ii) Resistance is relative and measured by comparison with a susceptible cultivar of the same plant species, iii) Resistance is measurable by standard scoring systems and iv) Resistance is variable and can be modified by the biotic and abiotic components of the environment.

Based on these characteristics, resistance can be classified genetically and epidemiologically. Genetically, there are three main types of resistance i.e, monogenic, oligogenic and polygenic. Monogenic resistance is controlled by a single major gene. Oligogenic resistance is controlled by several genes. Polygenic resistance is the result of many genes and is more difficult to incorporate into a plant breeding program. In epidemiological terms, resistance is classified as horizontal or durable resistance, with a long lasting effect and effective against all genetic variations of a particular pest and vertical or transient resistance that is effective for a short period and against certain variants only. Qualitative resistance applies when the frequency distribution of resistant and susceptible plants in a population is discontinuous and the plants are easily categorized as either resistant or susceptible. Quantitative resistance is used when a crop shows continuous gradation between resistant and susceptible plants within a population.

RESISTANCE MECHANISMS AND CAUSAL FACTORS

The most widely accepted mechanisms of insect resistance were given by Painter (1951) which includes

i) Antixenosis (Non-preference)
ii) Antibiosis
iii) Tolerance

Antixenosis refers to plant characteristics that deters insects away from a particular host and can be expressed in a cultivar either through morphological characters or allelochemicals. It affects the behavior of an insect in such a way it makes the plant unattractive for oviposition, feeding and shelter. Absence of physicochemical stimuli that are involved in selection of host plant or presence of repellents, deterrents, and antifeedants contribute to the antixenosis mechanism of resistance. Allelochemic non-preference is common among plants causing them totally rejected by insects. For example, Brown planthopper resistance in Mudgo variety is mainly due to the absence of asparagine resulting in gustatory non-preference to feeding (Sogawa and Pathak, 1970). Morphological non-preference is mostly due to plant structural characteristics which disrupt the normal behavior of an insect (Table 1).

Antibiosis is the adverse effect the plant exerts on the growth and survival of the insect. It affects the biology of the insect resulting in increased mortality or reduced longevity and fecundity of the insect leading to reduced pest abundance and damage to the resistant plants. Allelochemicals are generally involved in antibiosis. Best known examples include DIBOA in maize and gossypol in cotton (Table 1). Tolerance refers to the ability of the plant to withstand or recover from the damage by the insect. It is a plant response to the insect damage. Many factors are involved in tolerance leading to increased plant vigour, compensatory growth in plants, wound healing etc. In the crop varieties with a combination of three mechanisms of resistance, tolerance increases yield stability by providing at least a moderate level of resistance, when vertical genes providing a high level of resistance through antixenosis and antibiosis succumb to the new biotype.

The insect resistance in host crop may be due to the morphological, biochemical or physiological characteristics (Fig.1). Anatomical and physiological defense mechanisms of plants play a major role in defending themselves against insect attack. Anatomical defense mechanisms include specialized morphological structures produced by plants, while physiological mechanisms include secondary metabolism activated in plants (Fig. 1). The defensive leaf structures of the plant safeguards itself by the development of dense trichomes, spines, setae, as well as leafy toughness, cuticular thickness, and release of waxy epicuticles (Peterson et al., 2016). Trichomes, negatively influences the ovipositional sites and feeding behavior of insect pests and obstruct the movement over the plant surface (Sánchez and Morquecho-Contreras, 2017). Trichomes tend to hinder sap-feeding or leaf-chewing insects in some grasses (Hartley et al., 2015). Pigeonpea genotypes (ICPH 3461, ICPH 3762, BSMR 853, ICPL 332 WR, ICPH 2740, and ENT 11) with better pod wall thickness and high non-glandular trichome density showed improved tolerance to pod borer complex (Ambidi et al., 2021).

PHENOTYPING FOR RESISTANCE TO INSECT PESTS

The first step in any breeding program for the development of insect resistant varieties is to identify sources of resistance through evaluation using reliable phenotyping methodologies. Plant phenotyping for insect pests includes quantifying plant traits that contain insect infestations. For pests which are easy to mass rear, usually those with several generations/year and with no obligatory diapause, phenotyping techniques at seedling stage in laboratories and/or green-houses have been developed and used successfully. For pests with obligatory diapause and one generation/year on a host, the development and use of molecular markers to breed for resistance becomes a necessity. Once a marker is identified, breeders would use it in their breeding programs to screen their germplasm and make selection for resistance to these types of pests. A number of phenotyping methods have been developed, standardized and are being used for screening for resistance against major insect pests in various field crops (Kavitha and Reddy, 2012; IRRI, 2013; Sharma et al., 1992; Padmavathi et al., 2017). Most of these phenotyping techniques are laborious and time consuming relying mostly on the visual estimations of damage and has become a major bottleneck in breeding

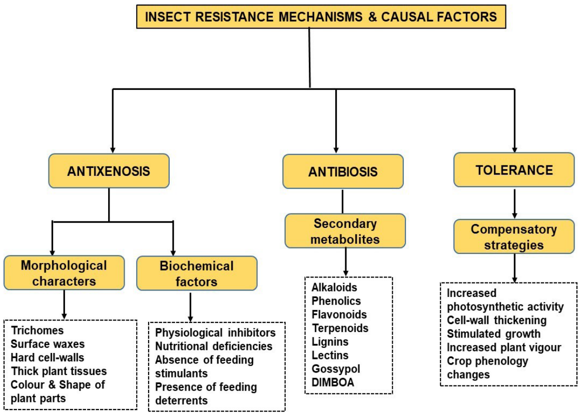

Fig. 1. Insect resistance mechanisms and causal factors in plants

Table 1. Traits associated with insect resistance in crop cultivars

Trait	Crop - Pest	Character	Reference
Morphological factors	Rice - BPH	Surface waxes	Woodhead and Padgham, 1988
	Rice - Stem borers	Small lumen, tight leaf-sheaths, tough tissues, ridged stems and high silica content & stem diameter, leaf number, flag leaf length and width, second leaf length and width and life duration of rice plant	Pathak, 1973; Shahjahan and Hossain, 2003
	Rice - Leaf folder	Leaf length and leaf width	Javvaji et al., 2021
	Sorghum - Shoot fly	Leaf glossiness, plant vigor, trichomes, and leaf-sheath pigmentation	Mohammed et al., 2016; Arora et al., 2021
	Sorghum - Aphid	Greater plant height and greater distance between two leaves and the presence of waxy lamina	Mote and Shahane, 1994
	Sorghum - Midge	Long glumes that do not open during anthesis, fast ovary growth in sorghum panicle, short floral parts, short glume length, short ovary girth	Rosetto et al., 1975 Jotwani, 1978
	Pearl millet - Head miner	Presence of involucral bristles, their density, length, and orientation	Youm and Kumar, 1995
	Sweet corn - Ear worm	Husk tightness	Wiseman and Davis, 1990
	Cotton - Jassid	Greater hair density on the mid rib and leaf lamina	Singh et al., 1972; Agarwal et al., 1987
	Cotton - Pink bollworm	High plant hair density	Wilson et al., 1980
	Cotton - Boll weevil	Fregobract	Jenkins and Parrot, 1971
	Wheat - Hessian fly	Pubescence	Roberts et al., 1979
	Wheat - Stem sawfly	Solid stem	Szczepaniec et al., 2015
	Chickpea - Aphids	Trichomes	Edwards, 2001
	Cowpea - Legume pod borer	long peduncles, podsheld over the plant canopy and at a wider angle	Singh, 1978
	Cowpea - Pod sucking bug	Trichomes on pods	Boukar et al., 2020
	Pigeon pea - *Helicoverpa*	High density of non-glandular trichomes on pods	Sharma et al., 2009
	Soybean - Beanflies, whiteflies & pod borers	Trichome length	Chiang and Norris, 1983; Lam and Pedigo 2002
	Groundnut - *H. armigera*, *S. litura*, and jassids	Stem thickness, leaflet shape, leaf length, leaf hairiness, standard petal length, stipule, and peg length	Sharma et al., 2003
Biochemical factors	Rice - BPH	Total sugars, phenols and protein content	Udaysree et al., 2020
	Rice - Stem borers, Leaf folders	Higher amount of phenolic compounds and high silica,	Israel and Kalode, 1966 Javvaji et al., 2021
	Rice - Stem borers	Low Oryzanone (p-methylacetophenone	Sadasivam and Thayumanavan, 2003
	Rice - Gall midge	Relative levels of free aminoacids, phenols and soluble sugars	Amudhan et al., 1999; Vidyachandra et al., 1981
	Rice - Leaf folder	Low nitrogen and high silica	Han et al., 2015; Javvaji et al., 2021

Trait	Crop - Pest	Character	Reference
	Sorghum - Shoot fly	Irregularly shaped silica bodies in the 4th to 7th leaf sheaths	Ponnaiya, 1951
	Sorghum - Stem borer	Surface waxes on the leaf and stem, high silica content, low sugar content, aminoacids, total sugars, tannins, total phenols, neutral detergent fibre, acid detergent fibre, lignin	Kalode and Pant, 1967 Jotwani, 1976
	Maize - Stem borers	DIMBOA	Butron et al., 2010
	Cotton - Whitefly and thrips	Gossypol glands on mid rib	Ahmed et al., 1987
	Cotton - Pink bollworm	High Gossypol	Ramalho et al., 1984
	Cowpea - *H. armigera*	High crude fibre and non reducing sugars with low per cent of starch, high per cent of cellulose, hemi celluloses and lignin in the pod wall.	Chhabra et al., 1990
	Cowpea - Aphid	Low sucrose levels and high levels of kaempferol and quercetin (aglycones of phenolic compounds	Togola et al., 2020
	Chickpea - *H. armigera*	High amount of malic acid	Rembold et al., 1990
	Pigeon pea - Podborer complex	High phenols, tannins, and flavonoids content	Ambidi et al., 2021
	Pigeon pea - *H. armigera*	high density of non-glandular trichomes on pods	Romeis et al., 1999

programs. However, in recent times, robust systems are being developed that can accurately screen many germplasm lines in a high-throughput manner (Goggin et al., 2015).

Considerable progress has been made in identification and utilization of crop germplasm for resistance to insect pests. Several sources of resistance to major insect pests and diseases have been identified, and the resistance transferred into high yielding varieties in different crops. Insect resistant cultivars have been developed in several crops, and released for cultivation by the farmers in India (Mahajan et al., 1997, Sharma and Ortiz, 2002). Host plant resistance has been a major component for minimizing losses due to insect pests in sorghum, chickpea and pigeonpea (Sharma and Ortiz, 2002). Development and release of midge-resistant cultivars in sorghum have been the major achievements towards developing crop cultivars with resistance to insect pests. Cultivars with moderate levels of resistance to shoot fly in sorghum, *Helicoverpa* in chickpea and pigeonpea have also been developed.

GENETICS AND INHERITANCE OF RESISTANCE

Genetically, there are three main types of resistance i.e, monogenic, oligogenic and polygenic. Monogenic resistance is controlled by a single major gene. Oligogenic resistance is controlled by few genes. Polygenic resistance is the result of many genes and is more difficult to incorporate into a plant breeding program.

A single recessive gene governs nonpreference for oviposition and two duplicate recessive genes govern the resistance to deadheart formation in sorghum by shoot fly (Sharma and Rana, 1985). The presence of trichomes on the abaxial surface of the leaf in sorghum is controlled by a single recessive gene and appears to be a highly heritable trait. Glossy leaves in sorghm are also governed by a single recessive gene (Table 2). Indirect selection through the component traits such as glossiness, and seedling height which are under the control of additive genes would be effective for improving shoot fly resistance in sorghum (Aruna et al., 2011). Resistance to stemborer in sorghum is additive and partially dominant over susceptibility (Pathak, 1985; Sharma et al., 2007). Inheritance of sorghum resistance to greenbug biotypes is relatively simple, while resistance to biotype C was determined to be dominant or incompletely dominant. Resistance derived from *Sorghum virgatum* (Hack.) Stapf was reported to be conferred by dominant genes at more than one locus (Hackerott et al., 1969). Resistance to head bugs showed dominance to partial dominance type of gene action and under the control of both additive and non-additive gene effects (Sharma et al., 2000).

SOURCES OF RESISTANCE FOR INSECT PESTS

Crop varieties resistant to insect pests

A number of insect resistant sources from cultivated varieties were identified for various insect pests in different crops (Table 3). Genetic diversity is available in the wheat genetic resources for resistance to the most economically important insect pests, Hessian fly, Russian wheat aphid and green bug. Many R genes including 37 genes for Hessian fly, 11 genes for Russian wheat aphid and 15 genes for green bug have been identified. Some of these have been deployed singly or in combination in the breeding programs to develop high yielding varieties with resistance to insects (Wuletaw et al., 2021). Three wheat genes (H5, H11, H13) were identified to be effective against the Hessian fly (EI Bouhssini et al., 1988). Screening of wild relatives of wheat showed large number of resistant accessions of *Aegilops taucshii* and very limited sources of resistance in wild *Triticum* (EI Bouhssini et al., 1998; EI Bouhssini et al., 2008). Several sources of resistance were also identified in primary synthetic hexaploid wheat lines for the Moroccan and the Syrian hessian fly biotypes (EI Bouhssini et al., 2013). Five wheat lines viz., Ferrugineum 205/ Frunsenskaya 60, Lutescencs 42/ Odesskaya krasno-kolosaya, Odesskaya, Erythrospermum 13 / Obriy and Frunsenskaya60/Tardo/Intensivnaya/ Eryt were identified as resistant to cereal leaf beetle. These lines expressed both antibiosis and antixenosis (Joukhadar et al., 2013).

Table 2. Inheritance of resistance

Crop	Insect	Trait	Inheritance	Reference
Rice	Brown planthopper	Damage score and resistance related traits	Of the 41 genes identified for resistnace to BPH, 31 genes are dominant and 10 genes are recessive	Jena and Kim, 2010; Akanksha et al., 2019; Wang et al., 2022
Rice	Gall midge	Gall formation	Of the 12 genes identified, 10 genes are dominant and 2 genes are recessive	Kumar et al., 2005, Sama et al., 2012; Bentur et al., 2016; Leelagud et al., 2020
Rice	White-backed planthopper	Damage score	Of the 15 genes identified, 11 genes are dominant and 4 genes are recessive	Padmavathi et al., 2017; Ramesh et al., 2014; Fujita et al., 2013
Sorghum	Shoot fly	Glossiness	Simple	Agarwal and House, 1982
			Single recessive	Tarumoto, 1980
			Additive and non-additive genes Non-additive genes	Agarawal and Abraham, 1985 Aruna and Padmaja, 2009
		Trichome density	Additive and non-additive genes	Halalli et al., 1982; Aruna and Padmaja, 2009
		Seedling height	Additive Non-additive	Sharma et al., 1977; Borikar and Chopde,1982; Halalli et al., 1983
		Deadhearts	Additive and non-additive components of heritable variation	Halalli et al., 1982; Biradar and Borikar, 1985; Dabholkar et al., 1989; Elbadavi et al., 1997

Crop	Insect	Trait	Inheritance	Reference
			Non-additive	Aruna and Padmaja, 2009
		Oviposition non-preference	Additive and non-additive	Halalli et al., 1982; Dabholkar et al., 1989; Agrawal and Abraham, 1985
		Recovery resistance	Additive and non-additive	Biradar et al., 1986
			Additive	Sharma et al., 1977; Starks et al., 1970; Borikar and Chopde, 1981a, 1982
		Tillering	Non-additive	Borikar and Chopde, 1981b; 1982; and Sharma et al., 1977
			Significant epistatic effects	Starks et al., 1970
Sorghum	Stemborer	Foliar damage Deadheart Stem tunneling Number of nodes	Additive	Nour and Ali, 1998
		Panicle initiation	Additive	Sharma et al., 2007
Sorghum	Greenbug	Recovery score	Single incompletely dominant gene	Weibel et al., 1972
		Stalk length	Dominant	Johnson et al., 1981
		Biotype C	Incompletely dominant and controlled by two genes	Tuinstra et al., 2001
Sorghum	Aphid	Biotype E Biotype I	Monogenic and controlled by a single dominant gene	Hsieh and Pi, 1982; Pi and Hsieh, 1982; Tan et al., 1985
Sorghum	Midge		Recessive trait and is controlled by two or more loci Additive and nonadditive genes	Boozaya-Angoon et al., 1984; Rossetto and Igue, 1983 Agarwal and Abraham, 1985
Sorghum	Headbug		Additive gene action	Widstrom et al., 1984; Sharma et al., 1996; 2000
Maize	Spotted stemborer	Leaf feeding, dead hearts and stem tunneling	Additive and non-additive gene effects	Pathak, 1991
Maize	Pink stemborer	Leaf and stem injury rating	Additive x additive (I) followed by dominance (D) and additive (A) gene effects	Sekhar et al., 2015
Maize	Maize weevil	Grain weight loss, progeny emergence	Additive and nonadditive genes	Zunjare et al., 2015

Table 3. Sources of resistance to major insect pests of field crops

Crop	Insect	Sources of resistance	Reference
Rice	Brown planthopper	Mudgo, ASD7, Rathu Heenati, Babawee, ARC10550, Swarnalata, T12, Chin Saba, Balamawee, N22, ARC10239, ADR52, PTB 33, Sinna Sivappu	Ling and Weilin, 2016
Rice	White backed planthopper	ADR 52, Podiwi A8, ARC 6650, ARC 5984, MO 1, Velluthecherra,	Padmavathi et al., 2017
Rice	Stem borer	W 1263, TKM 6, Ratna, Sasyasree, Vikas	Makkar and Bentur, 2017
Rice	Leaf folder	W 1263, TKM 6, ARC 10840, Darukasail	Bentur and Kalode, 1990
Sorghum	Shoot fly	IS 18551, ICSV 705, ICSV 708, SPSFR 94019, SPSFR 94006, SPSFR 94007, SPSFR 94011, SPSFR 94034, , SPSFR 96069, SPSFR 86065, PS 23585, ICSR 89058; PBMR3, PBMR7, PBMR8, NRCSFR09-3, GMR309,	IIMR, 2016
Sorghum	Stemborer	IS 1044, IS 1054, IS 2123, IS 2263, IS 2269, IS 5469, IS 5566, IS 12308, IS 13100, IS 18333, and IS 18573	Sharma et al., 2003
Sorghum	Aphid	HB 37, PE 954177, IS 8100C, R128, R131, and R133	Sharma, 1993
		SPS43, SLR37, TAM428, SLB81, KR191, Long SPS43, and SLR37	Bhagwat et al., 2011
Sorghum	Midge	IS 3461, IS 9807, IS 10712, IS 18563, IS 19476, IS 21873, IS 21881, IS 22806, PM 15936-2, and ICSV 197	Sharma et al., 2002
Pearl millet	Shoot fly	MH 1975, MH 1828, MH 195	AICPMIP, 2014
Pearl millet	Stem borer	Zongo	Gahukar 1984
Pearl millet	Sugar cane leafhopper	MH–1121, Saburi, CZP–9082	ICAR, 2002–07
Pearl millet	Chinch bug	07F-1226, 07F-1229, 07F-1231, 07F-1235, 07F-1238, 07F-1239, and 07F-1240	Ni et al., 2009
Foxtail millet	Shoot fly	SIA 1538, SIA 1533, SIA 1507, SIA 1581, SIA1566, SIA 1549	Kalaisekar et al., 2017
Kodo millet	Shoot fly	RPS 40-1, RPS 40-2, RPS 62-3, RPS 72-2, RPS 120-1, IPS 6, IPS 32, IPS 110, IPS 131, IPS 142, IPS 178, Keharpur	Murthy and Harinarayana, 1989
Wheat	Hessian fly	Triticum aestivum accessions Grant, Patterson, 86981RC1-10-3, 8268G1-19-49, KS89WGRC3 (C3), KS89WGRC6 (C6)	Dweikat et al., 1997
Wheat	Russian wheat aphid	Triticum aestivum genotypes PI 137739, PI 262660, PI 294994, PI 372129, PI 243781	Joukhadar et al., 2013
	Green bug	Aegilops tauschii accessions	Zhu et al., 2005
Chickpea	Podborer	Vijay, Vishal, ICCV 10, ICPL 88034, ICCL 86103	Sharma et al., 2014

Wild relatives as sources of diverse genes for insect resistance

Wild relatives of cultivated crops possess several desirable genes that can confer resistance to insects (Mammadov et al.„ 2018; Khan et al., 2020). Wild relatives of crops 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 (Table 4).

The two genes *zFPP* and *ShZIS* coding enzymes that synthesized the sesquiterpene 7-epizingiberene were transferred from tomato (*Lycopersicon esculentum*) wild variety to cultivated variety expressed in trichomes, the plant showed enhanced protection against multiple insects (Douglas, 2018). Arcelins are insecticidal proteins, obtained from wild accessions of the common bean (*Phaseolus vulgaris* Linnaeus), with resistance against bruchid beetles. Arcelin protein purified from hyacinth bean (*Lablab purpureus*) had the ability to manage storage pest in cereals transformed with *L. purpureus* defense related gene (Janarthanan et al., 2008). The chemical composition of arcelin has many similarities with lectin including agglutinating activity. Till date, different allelic variants (designated Arc-1–7) of arcelin proteins have been described, with molecular weight in the range of 27-42 kDa. Of great interest are the insecticidal properties of arcelin variants toward bruchid pests and, in particular, their inhibitory effect on the larval development of the Mexican bean weevil (*Zabrotes subfasciatus* Boheman) (Karuppiah et al., 2018).

Table 4. Wild relatives resistant to insect pests of field crops

Crop	Insect pests	Wild species	Reference
Rice	Brown planthopper	*Oryza eichingeri, O. minuta, O.latifolia, O. australiensis, O.nivara, O.rufipogon, O. longistaminata, O. glumaepatula,*	Khush and Brar, 1991; Ling and Weilin, 2016
		O. officinalis, O. australiensis, O. punctata, O. minuta, O. latifolia	Sarao et al., 2016
Rice	Whitebacked planthopper	*O.officinalis, O.latifolia*	Sanchez et al., 2013
Rice	Stemborer	*O. brachyantha, O. minuta*	Brar and Khush, 1997
Rice	Yellow stem borer	*O. glaberrima, O longistaminata*	Bhattacharya et al., 2006 Makkar and Bentur, 2017
Rice	Gall midge	*O. brachyantha, O. coarctata O. eichingeri, O. granulata, and O. ridleyi*	Israel et al., 1963
Rice	Leaf folder	*O. perennis, O. punctata, O. australiensis, O. nivara*	Khan et al., 1989
Sorghum	Shoot fly Spotted stemborer	*Sorghum laxiflorum, S. australiense S. brevocallosum, S. dimidiatum S. purpureosericeum*	Venkateswaran, 2003
Sorghum	Midge	*Sorghum angustum, S. amplum S. bulbosum*	Sharma and Franzmann, 2001
Wheat	Hessian fly	*Aegilopos tauschii, Triticum ventricosum, T. turgidum*	Clement, 2002
Wheat	Russian wheat aphid	*T. monococcum, T. turgidum*	Kaplin et al., 2015
Cotton	Helicoverpa armigera (Hubner)	*Gossypium thurberi, G. somalense G. armourianum, G. barbosanum*	Singh and Narayana, 1994
Pigeon pea	H.armigera	*Cajanus scarabaeoides C. sericeus, C. acutifolius*	Sharma et al., 2001 Green et al., 2006
Chickpea	H.armigera	*Cicer bijugum, C. reticulatum C. judaicum, C. microphyllum*	Sharma et al., 2005 a,b

Insect resistant QTLs identified in major field crops

A large number of insect pest resistance QTLs have been identified in major field crops. The gene mapping of *Bph7* can be utilized for map-based cloning and eventually in development of BPH-resistant lines in rice (Jaganathan et al., 2020). A joint analysis for *Busseola fusca* and *C. partellus* revealed that marker *CS132-2* was co-localized for leaf toughness and stem tunneling traits on two individual QTLs identified; thus, suggesting that the two traits can be improved using the same linked marker (Muturi et al., 2021).

However, only a limited number of actionable targets are known due to a lack of fine mapping and functional characterization. There is a rising need to clone and characterize the candidate genes underlying the identified QTLs, using fine mapping and map-based cloning approaches (Jaganathan et al., 2020). Such genes would shed light on the molecular mechanisms of insect resistance in crop plants. The ultimate objective of mapping and cloning insect pest resistance genes and unraveling the underlying defense mechanism is to facilitate the breeding of insect-resistant crop varieties, which represents an efficient, cost-effective, and environmental-friendly pest control strategy.

Over the past decade, QTL mapping has been used to characterize antixenotic, antibiotic resistance, and, to a lesser extent, plant tolerance, thereby increasing the possibility to develop arthropod-resistant germplasm with which to examine the individual effects of specific QTL (Table 5). Such knowledge about specific QTL provides the potential to broaden the genetic bases of arthropod plant defense and to develop more durable resistance

Use of the identified sources of resistance in breeding programs

A number of resistant sources were identified for different pests in various crops and theses were utilized for the development of an insect resistant variety (Fig. 2). The Hessian fly resistant varieties released in Morocco offer at least 32% higher grain yield than traditional varieties, under normal Hessian fly infestation levels (EI Bouhssini et al., 2021). Seven chickpea breeding lines with resistance to leaf miner and good agronomic characters were developed using two resistant parents (Malhotra et al., 2007) (Table 6).

Multiple insect pest resistance

Efforts have also been put in trying to find combined resistance to multiple insect pests in wheat-rye and *Aegilops speltoides* Tausch translocation and substitution lines. Three genotypes were identified with combined resistance to Hessian fly and three aphid species (*Sitobion avenae* Fabricius, *Rhopalosiphum padi* L. and *Schizaphis graminum* Rondani) and one genotype with resistance to Russian wheat aphid and to the same three aphid species. This is the first report of combined resistance to four pests. These sources are currently being used in the bread-wheat breeding programs at CIMMYT and ICARDA to transfer the multiple pest resistance to elite germplasm (Crespo-Herrera et al., 2019).

INDUCED RESISTANCE

The mechanisms of inducible plant defense responses are based on changes in gene expression. Zhu-Salzman et al. (2004) evaluated the transcriptional changes in a sorghum cultivar by comparing expression patterns of 672 cDNAs in the seedling tissues before and after infestation by greenbug or following treatment with defense signal components such as salicylic acid (SA) or methyl jasmonate (MJ). Their results indicated that activation of certain transcripts regulated exclusively by greenbug infestation was observed, and the expression patterns may represent unique signal transduction events independent of MJ- and SA-regulated pathways. More recently, the transcriptional changes in a parallel system was examined in greenbug-resistant and -susceptible genotypes of sorghum leading to detection of the abundance of the transcripts corresponding to 2,304 sorghum genes during the infestation by virulent greenbug biotype I (Park et al., 2006). The experiments showed comprehensive gene activation resulting from up-regulating, or activating existing defense pathways in sorghum seedlings in response to greenbug feeding. Among the induced genes identified, 38 genes exhibited threefold or higher abundance in their expression, and 26 genes were significantly repressed.

Table 5. QTLs mapped/ fine mapped/ cloned for insect pest resistance in some field crops

Crop	Insect	QTL/genes	References
Rice	BPH	*>40 genes/QTLs*	Zang et al. 2020; Li et al., 2019 Balachiranjeevi et al., 2019; Mohanty et al., 2017
Rice	WBPH	*23 genes/QTLs*	Yang et al., 2014; Fan et al., 2018
Rice	African rice gall midge	*qAfrGM4*	Yao et al., 2016
Rice	Asian rice gall midge	*12 genes*	Himabindu et al., 2010; Sama et al., 2014; Divya et al., 2015,2018; Leelagud et al., 2020; Bentur et al., 2021
Sorghum	Shoot fly	*SBI-05*	Satish et al., 2009; Aruna et al., 2011; Kiranmayee et al., 2015; Gorthy et al., 2017
Sorghum	Stemborer	*29 QTLs*	Vinayan, 2010
Sorghum	Midge	Two QTLs (SBI-03 and SBI-09)	Tao et al., 2003
Sorghum	Green bug	*9 QTLS*	Agrama et al., 2002
Wheat	Hessian fly	*H35* and *H36* *h4, H7* and *H8*	Zhao et al., 2020; Niu et al., 2020; Liu et al., 2020
Wheat	Russian wheat aphid	*QDn.unlp genes*	Ricciardi et al., 2010
Wheat	Sunn Pest	*Ei1*	Emebiri et al., 2017
Maize	Fall armyworm	62 QTNs	Badji et al., 2020
Maize	Corn leaf aphid	*HDMBOAGlc QTL*	Betsiashvili et al., 2015; Meihls et al., 2013
Soybean	Aphid	*Rag6* and *Rag3c* *R_P746* *QTL_13_1* and *QTL_13_2*	Zhang et al., 2017; Xiao et al., 2014 Jun et al., 2013
Soybean	Whitefly	*qRWF-1* and *qRWF-5-1*	Zhang et al., 2013
Chickpea	*Helicoverpa armigera*	9 QTLs	Barmukh et al., 2021

Table 6. Crop varieties resistant to Insect Pests

Crop	Insect Pests	Varieties	Reference
Rice	Brown planthopper	Jyothi in Kerala, Sonasali, Vajram, Chaitanya in AP, Neela and Udaya in Orissa and Manasarovar across the country	Jena et al., 2018
		Krishnaveni, Vajram, Pratibha, Mekom, Pavizham, Co-42, Chandana, Nagarjuna, Rasmi, Jyothi, Bhadra, Neela Annanga, Daya, Aruna, Kanaka, Remya, Bharatidasan, Karthika, Vijetha, Cotton Dora Sannalu	Pasalu et al., 2005
Rice	Yellow stemborer	Vikas, Ratna, Sasyasree	Bentur et al., 2021
Rice	Gall midge	Sneha, Pothana, Kakatiya Erramallelu, Kavya, Rajendradhan 202, Karna, Ruchi, Samridhi, Usha, Asha, MDU 3, Bhuban, Samalei, Orugallu, Abhaya, Shakti, Suraksha, Daya, Pratap, Udaya, IR 36, Shaktiman, Tara, Kshira, Sarasa, Neela, lalat, Phalguna, Mahaveer, Vibhava, Divya, Dhanya Lakshmi, Surekha, Vikram, Kunti, Triguna	Pasalu et al., 2005
Rice	Green leafhopper	Vikramarya, Lalat, Khaira, Nidhi	Pasalu et al., 2005
Chickpea	Leaf miner	FLIP 2005-1C, 2C, 3C, 4C, 5C, 6C, 7C	Malhotra et al., 2007

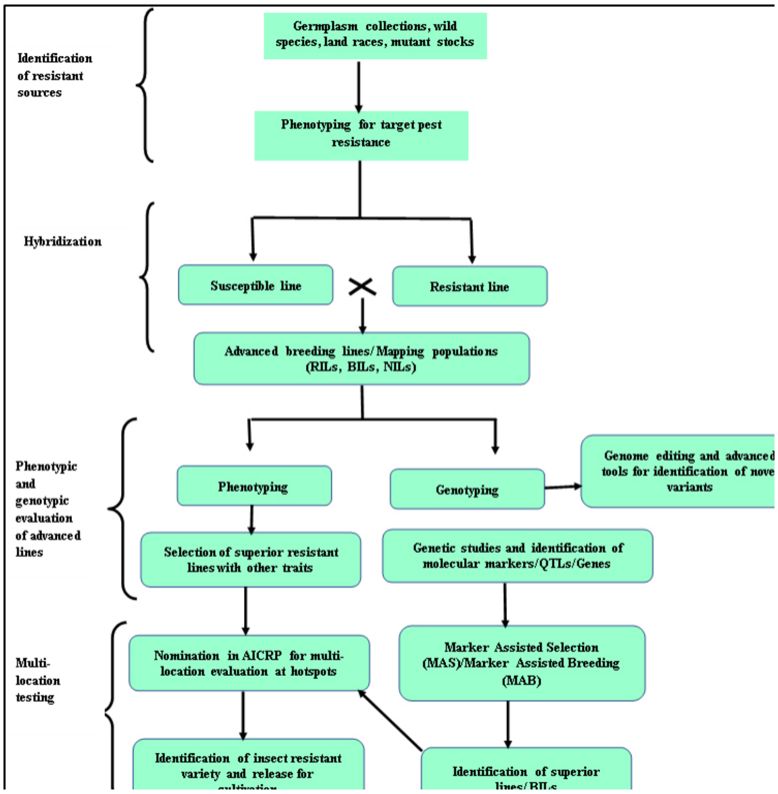

Fig. 2. Steps in the development of insect resistant variety

INSECT RESISTANCE - ADVANTAGES AND LIMITATIONS

Insect resistant varieties assume a central role in the Integrated Pest Management (IPM) aiming to increase production and productivity of crops by reducing the pest damage and protecting the environment. Major advantages include specificity, compatibility and environmental safety. Effects of plant resistance are cumulative over consecutive generations. Most of the insect resistant varieties express moderate to high level of resistance to target pests throughout the crop season. It is specific to the target pest and generally has no adverse effects on non-target organisms. Growing a resistant variety does not involve any additional costs to the farmers (Dar et al., 2006).

Development of pest-resistant varieties requires expertise and resources. Commitment of relatively long-term funding is a critical factor in the ultimate success of HPR. It takes relatively long time to identify and develop pest-resistant cultivars. This method is not suitable to solve sudden or localized pest problems. Absence of adequate levels of resistance in the available germplasm may deter the use of HPR for managing certain pests. Such limitations can now be overcome through the use of interspecific hybridization and genetic transformation. Occurrence of new biotypes of the target pests may limit the use of certain varieties in time and space. Under such situations, one has to continuously search for new genes, and transfer them into high yielding varieties. Certain plant traits may confer resistance to one pest, but render such plants more susceptible to other pests, e.g., hairiness in cotton confers resistance to jassids, but such varieties are preferred for oviposition by bollworms (*Earias vittella* and *Helicoverpa armigera*) (Sharma and Agarwal, 1983). Also, pubescence in soybean confers resistance to leafhoppers, but pod borer (*Grapholitha glycinivorella*) 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).

Insect biotypes

Painter (1941) defined the term "biotype" to situations where the insect response was indifferent to crop plants developed for their resistance to insect feeding. Biotypes represent evolutionary transients in the process of speciation and develop through natural selection acting upon genetic variations within the pest populations. The continous growing of insect resistant varieties may lead to certain physiological and biochemical changes in insect pests so that they are capable of feeding and developing on the resistant variety (Dhaliwal and Arora, 2009). Biotypes have been reported to occur in 36 crop pest species belonging to 17 arthropod families in six orders (Saxena and Barrion, 1987; Table 7). Almost 50% of these pest species with known biotypes are aphids. A disadvantage of both conventional and transgenic insect resistance is loss of function when insect strains evolve virulence to high levels of resistance genes. Virulence in brown planthopper *Nilaparvata lugens* and Hessian fly *Mayetiola destructor* is correlated with the genetic complexity of plant resistance, with varieties containing single resistance genes failing within 6-8 years after release years (Horgan, 2018; Johnson et al., 2017). More durable polygenic resistance has proven effective in several crops. Rice resistance to *N. lugens* and wheat resistance to wheat curl mite *Aceria toschiella*, has been shown to suppress virulence to these pests for >10 years (Mackill and Khush, 2018; Khalaf et al., 2019). In soybean plant resistance to damage by foliar feeding lepidoptera, a combination of both conventional and transgenic polygenic resistance has been developed. The soybean near-isogenic line Benning ME contains two major quantitative trait loci (one each from linkage group M and linkage group E) for effective field resistance to defoliation by soybean looper, *Chrysodeixis includens*, and Southern armyworm, Spodoptera eridania (Ortega et al., 2016). Further, Benning ME resistance is significantly greater in Benning ME plants that also contain the cry1Ac transgene. To slow down the process of biotype selection, crop cultivars with broad genetic bases are needed.

Table 7. Insect biotypes in field crops

Crop	Insect		No. of biotypes	Reference
Rice	Green leafhopper	*Nephotettix virescens* (Distant)	3	Rosida et al., 2020
Rice	Brown planthopper	*Nilaparvatha lugens* (Stal)	5	Jena and Kim, 2010
Rice	Gall midge	*Orseolia oryzae* (Wood Mason)	7	Vijayalakshmi et al., 2006
Sorghum	Green bug	*Schizaphis graminum*	11	Porter et al., 1997
Sorghum	Stem borer	*Chilo partellus*	4	Dhillon et al., 2021
Wheat	Hessian fly	*Mayetiola destructor* (Say)	16	Shukle 2008
Wheat/Barley	Aphid	*Sitobion avenae*	6	Wang et al., 2020
Wheat	Green bug	*Schizaphis graminum*	7	Kharrat et al., 2012
Corn	Corn leaf aphid	*Rhopalosiphum maidis* (Fitch)	4	

Evolution of biotypes among insect populations is a potential threat to the durability of host plant resistance. New insect biotypes can be tackled by pyramiding known resistance genes or QTLs. Due to the development of biotypes, successful cultivation of resistant varieties may be seriously constrained. Hence, identification of new genes by continuous and systematic evaluation of various germplasm resources should become a major program while developing insect resistant varieties. Breeders has to adopt a strategy of developing cultivars with polygenic resistance or search for new sources of resistance genes followed by their introgression into high-yielding popular cultivars (Jena and Kim, 2010). Additionally, cultivars having diverse mechanisms of resistance against prevalent insect biotypes should be utilized (Sharma, 2009).

NOVEL STRATEGIES IN DEVELOPING INSECT RESISTANT PLANTS

Marker assisted selection (MAS)

The typical breeding programme selection procedure is accelerated by MAS. Since the selection is based solely on particular genes, MAS frequently modifies the selection criteria (Francia et al., 2005). Because there are now a growing number of distinct molecular markers available, MAS can be used to pick both simple and quantitative features (Mohan et al., 1997).

The ultimate utility of identification of genomic regions conferring resistance to different insect pests in a breeding programme is to mobilize such specific QTLs into different genetic backgrounds via MAS to develop resistant cultivars (Fig. 2). Many resistant genes to BPH have been identified (*Bph1, Bph3, Bph14, Bph15, Bph17, Bph18*). Successful introgression of *Bph14* and *Bph15* (He et al., 2019; Wang et al., 2019); *Bph3* (Qing et al., 2019) have been reported to provide higher levels of resistance in the recurrent parent. Several gall midge resistance genes have been identified (*Gm1, Gm2, gm3, Gm4, Gm5, Gm6, Gm7, Gm8, Gm9, Gm10* and *Gm11*) and used in breeding rice against different biotypes of gall midge. The introduction of the gall midge resistance genes Gm4 and Gm8 for the enhancement of RPHR-1005 by marker-assisted backcross breeding (MABB) (Kumar et al., 2017) and the introduction of the *Gm1* and *Gm4* genes together with eight additional genes/QTLs for various traits in Improved Lalat via MABB are two examples of this (Das and Rao 2015).

Gene pyramiding

Using *Gm4* and *Gm8*, the research group at ICAR-IIRR (Kumar et al., 2017) has developed gene-pyramided lines in the genetic background of the elite restorer line RPHR1005R (restorer line for the popular rice hybrid DRRH3) through marker-assisted breeding. In another such effort, the high-yielding rice variety Akshayadhan has been improved for its resistance against gall midge by targeted transfer of *Gm4* and *Gm8* genes. Sama et al. (2014) introduced the recessive gene *gm3* into the genetic background of elite rice variety Improved Samba Mahsuri with the help of markers. In a recent report (Venkanna et al., 2018), two major resistance genes, *gm3* and *Gm8*, have been pyramided in the genetic background of the fine grain-type rice variety Kavya, which already possesses *Gm1*. Now that closely linked markers/functional markers are available for all the major gall midge resistance genes, selected gene combinations can be pyramided into elite genetic backgrounds (Divya et al., 2018c) easily through marker-assisted breeding for developing durable multiARGM biotype-resistant rice cultivars/hybrids.

RNAi Approach

In plant tissues consumed by insects, the double-stranded RNAs specific to important insect genes can be expressed persistently. This can cause the RNAi pathway to start degrading the mRNAs produced by the key insect genes (Price and Gatehouse, 2008; Agarwal et al., 2012). Targets of RNA interference (RNAi) for key genes in insects have been identified. These include genes encoding developmental proteins, digestive enzymes, salivary gland proteins, nervous system regulatory proteins, proteins involved in host-insect interaction, hormone receptors, gut enzymes, and metabolism-related proteins (Gatehouse, 2008; Huvenne and Smagghe, 2010; Kola et al., 2015). RNA-driven post-transcriptional homology-based gene silencing via the mRNA degradation pathway is known as the RNA interference (RNAi) strategy. This pathway is present in all eukaryotic organisms.

Double-stranded RNAs (dsRNA) that are processed by the protein Dicer, which resembles RNase-III, to form small interfering RNAs (siRNAs). An RNA-induced silencing complex (RISC) is directed to the target mRNA by the siRNA's guide strand. The use of the RNAi technology for insect resistance in rice is still in the early stages of development. The majority of studies on RNAi in rice focus on BPH and YSB (Zha et al., 2011; Zhou et al., 2013; Wang et al., 2018a; Renuka et al., 2017).

According to Li et al. (2015), dsRNAs are stable in a variety of conditions and can be ingested by the roots of crop plants. This discovery opens up the possibility of using dsRNAs as biopesticides. RNAi can be successfully employed as a control strategy against insect pests (Huvenne and Smagghe, 2010;). Upon feeding on plant parts, dsRNA enters into the insect gut, leading to the induction of RNAi machinery and then, silencing of the target gene in the insect pest. Kola et al. (2016) demonstrated that feeding YSB larvae with dsRNA of amino peptidase N (APN) and cytochrome P450 derivative (CYP6) lowered expression of target genes and increased larval mortality after 12–15 days. In a similar manner, Zeng et al. (2018) used the injection of dsRNAs to knock down three chemosensory protein (CSP) genes in rice leaffolder (*C. medinalis*), which decreased insect responsiveness to the particular chemicals.

To achieve an effective RNAi based insect pest control, careful identification of specific target insect enzymes and proteins, efficient delivery methods of introducing dsRNA into insect cells/bodies, and stabilization of dsRNAs during and after delivery are certain key issues which need immediate concern. In addition, RNAi technology coupled with Bt or other technologies offers a great choice in controlling the insect pests, which are prone to develop resistance against insecticidal proteins. However, to establish the true potential of host-induced RNAi to combat insect pests, further development and refinement of this technology in large-scale field tests are required.

Genetically modified crops

Transgenic technology has been effective against a wide range of pests including coleopteran, lepidopteran, hemipteran and dipteran pests. Major focus was laid predominantly on such genes that have demonstrated positive effects and proved to be of commercial success at the market primarily due to the development of pest-resistant transgenic food crops with expression of *Bacillus thuringiensis* toxins. In India, cotton (*Gossypium hirsutum* Linnaeus) and soybean (*Glycine max* Linnaeus) are the approved genetically modified crops. In 2014 GEAC (Genetic Engineering Appraisal Committee) approved 11 crops for the field trials which includes maize, rice, wheat, groundnut, sorghum and cotton (Table 8). A Moratorium was laid on Bt Brinjal in 2010 by the Indian Government which crippled the research on transgenic crops. The data generated by India was taken by the Bangladesh and 25,000 farmers cultivated Bt Brinjal and made it a success. USA, Brazil, Argentina, Canada, and India altogether have 91% of the global biotech crop area (Brookes and Barfoot, 2017). According to ISAAA (The International Service for the Acquisition of Agri-biotech Applications), the USA has 203 GM crops approved with 21 variants, cultivating food crops like maize, soybean, canola, sugar beet, papaya, squash, potato, livestock feed like alfalfa and a commercial crop cotton in nearly 70.1 million hectares in USA, followed by Brazil, Argentina, Canada and India. The information from ISAAA proclaims that around 2.7 billion hectares of biotech tech crops planted since 1996. Malawi, Ethiopia and Nigeria have planted Bt cotton for the first time in 2019. Recently, GEAC has approved genetically modified mustard (Dhara Mustard Hybrid – 11 (DMH-11)) for commercial cultivation, paving the way for India's first transgenic food crop (https://geacindia.gov.in/Uploads/MoMPublished/MoMPublishedOn20221025200345.pdf).

Out of 11 approved GM crop cultivars six are of cotton *Gossypium hirsutum* L. and the rest five are Soybean *Glycine max* L. But Intacta™ Roundup Ready™ 2 Pro is the only Bt gene incorporated crop. Continued use of transgenic crops is threatened by the evolution of resistance in insect populations. To overcome this, several research groups are assessing the potential of using non-Bt insecticidal proteins such as lectins (carbohydrate-binding proteins), vegetative insecticidal proteins (VIP), proteinase inhibitors (cowpea trypsin inhibitor), ribosome-inactivating proteins, secondary plant metabolites, small RNA viruses, and chemical elicitors that boost the signaling pathways (Makkar and Bentur, 2017; Sobhy et al., 2014; Bektas and Eulgem, 2015).

Genome editing strategies

Genome editing tools enable us to edit the genome or specifc genes of an organism by addition/deletion or replacement of nucleotides with high precision and with few off-target effects. Because of its simplicity and wider applicability, genome editing is being practiced in many laboratories for functional genomics and trait improvement (Zhu et al., 2020). In agriculture, the technology has immense potential to improve yield and abiotic and biotic stress tolerance of crops (Table 9).

Many insect pests identify host plants through the plants' volatile cues, morphological features, plant phenology, visual cues, odor and taste clues, and oviposition sites, among others (Larsson et al., 2004). An insect selects a particular plant for its oviposition site based on the availability of desired feed for its young ones. Plant morphological features play an important role in the ability of insect pests torecognize and damage a particular host. Modification in pigmentation of plants has been found to alter insect host preferences. Upregulation of anthocyanin pigmentation produced red leaves in a transgenic tobacco plant. This alteration in leaf color acted as a deterrent for the pests, *H. armigera* and *S. litura*, thereby confirming the significance of leaf color on host recognition in insect pests (Malone et al., 2009). Taken together, engineering of specific metabolic pathways in plants resulting in a change in plant visual appearance can be used as a plausible approach for CRISPR/Cas9-based editing for management of insect pests. CRISPR/Cas9 induced mutagenesis of vestigial gene (vest) developed wingless adults of Colorado potato beetle with no elytron formed (Gui et al., 2020). Targeting the genes responsible for mating partner identification and chemical communication using genome editing technology is another strategy to control insect pests. These two properties are very crucial to establish insect-plant interaction, like the olfactory receptors in insects that help to sense the odorant of a mating partner and to develop host-plant interaction via chemical signaling.

Table 8. Genetically modified crops approved in India with Bt genes incorporated

S. No.	Event name	Genes incorporated	Source	Function
1	BNLA-601	*cry1Ac*	*Bacillus thuringiensis* subsp. *kurstaki* strain HD73	Confers resistance to lepidopteran insects by selectively damaging their midgut lining
2	JK 1 TRADE NAME	*cry1Ac &nptII**	*Bacillus thuringiensis* subsp. *kurstaki* strain HD73	Confers resistance to lepidopteran insects & allows transformed plants to metabolize neomycin and kanamycin antibiotics during selection
3	GFM Cry1A	*cry1Ab-Ac* delta endotoxin (fusion protein) nptII* uidA*	Synthetic fusion gene derived from *Bacillus thuringiensis*	Confers resistance to lepidopteran insects & produces blue stain on treated transformed tissue, which allows visual selection
4	MLS 9124	*cry1C* delta endotoxin	Synthetic fusion gene derived from *Bacillus thuringiensis*	Confers resistance to lepidopteran insects, specifically *Spodoptera*
5	Bollgard II™ Cotton	*cry1Ac &cry2Ab nptII* uidA, aad**	*Bacillus thuringiensis* subsp. *kumamotoensis* & *Bacillus thuringiensis* subsp. *kurstaki* strain HD73	Confers resistance to lepidopteran insects by selectively damaging their midgut lining
6	Bollgard™ Cotton, Ingard™	*cry1Ac & cry2Ab nptII* aad**	*Bacillus thuringiensis* subsp. *kurstaki* strain HD73	Confers resistance to lepidopteran insects by selectively damaging their midgut lining
7	Intacta™ Roundup Ready™ 2 Pro	*cry1Ac & cp4 epsps**	*Bacillus thuringiensis* subsp. *kurstakistrain* HD73	Confers resistance to lepidopteran insects by selectively damaging their midgut lining, conferring increased tolerance to glyphosate herbicide

'*' are the marker/reporter genes incorporated in the event crop

Koutroumpa et al. (2016) mutated Or83b gene using CRISPR/Cas9 system, which caused defect in olfactory receptors and disturbed the selection of host for laying eggs. Insects produce unique enzymes that can be used to overcome the plant defense systems by releasing detoxification chemicals. Targeting these detoxification genes can increase the susceptibility of insects, especially in polyphagous species. CYP71A1 gene encodes tryptamine 5-hydroxylase that stimulates the production of serotonin from tryptamine, and plays a crucial role in stunted growth of plant hoppers. The mutant population showed increased resistance against striped stem borer (Chilo suppressalis) and brown planthopper (Nilaparvata lugens) in rice (Lu et al., 2018).

Table 9. Genome editing in insects for pest management

Trait	Target insect	Target gene	Reference
Body segmentation	*Spodoptera litura*	Slabd-A (*S. litura* abdominal-A) (targeted mutagenesis)	Sun et al., 2017
	Spodoptera frugiperda	Sfabd-A (indel mutations)	Wu et al., 2018
	Plutella xylostella	abdominal-A (gene knockout)	Sun et al., 2017
Mating time and partner	*Helicoverpa armigera*	OR16 (odorant receptor 16) (gene knockout)	Sun et al., 2017
	Spodoptera littoralis	Orco (olfactory receptor coreceptor) (gene knockout)	Koutroumpa et al., 2016
Regulation of detoxification enzymes	*Helicoverpa armigera*	CYP6AE gene cluster (gene knockdown)	Wang et al., 2018b

(Source: Tyagi et al., 2020)

CONCLUSIONS AND WAY FORWARD

Significant progress has been made in the breeding and commercial utilization of insect resistant varieties in various field crops. However, there are still numerous important insect pests throughout the World for which host plant resistance as a management tactic has not been adequately utilized. Innovative conventional breeding techniques and molecular genetic approaches may provide means for fully exploiting various resistant sources like wild species, land races and breeding lines in the development and utilization of durable and stable resistant cultivars for various insect pests.

Traditional breeding has been the sole approach used for breeding insect resistant plant varieties to cope with the losses caused by insect pests in various crops. However, emerging insect pests as well as unpredictable climate changes have forced scientists to search for alternative solutions to cope up these problems. Recent advances in biotechnological applications have provided a number of opportunities to breed trait specific insect resistant plants.

Integration of insect resistant varieties in IPM along with cultural, biological and chemical control tactics is the need of the hour not only to reduce crop losses caused by insect damage but also to reduce the use of toxic pesticides and protect the human and environmental health.

However, in order to fully exploit the enormous potential of biotechnology, appropriate biosafety regulatory frameworks and proper stewardship programs need to be effectively implemented. This integrated approach can promptly help respond to the ever-dynamic threat of pests and hence reliably combat food insecurity and ably contribute to sustainable development.

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