Molecular mechanisms, genetic mapping, and genome editing for insect pest resistance in field crops

Shabir H. Wani1 · Mukesh Choudhary2 · Rutwik Barmukh3 · Pravin K. Bagaria2 · Kajal Samantara4 · Ali Razzaq5 · Jagdish Jaba6 · Malick Niango Ba7 · Rajeev K. Varshney3,8

Received: 23 June 2021 / Accepted: 11 February 2022 / Published online: 10 March 2022
© The Author(s) 2022

Abstract

Key message Improving crop resistance against insect pests is crucial for ensuring future food security. Integrating genomics with modern breeding methods holds enormous potential in dissecting the genetic architecture of this complex trait and accelerating crop improvement.

Abstract Insect resistance in crops has been a major research objective in several crop improvement programs. However, the use of conventional breeding methods to develop high-yielding cultivars with sustainable and durable insect pest resistance has been largely unsuccessful. The use of molecular markers for identification and deployment of insect resistance quantitative trait loci (QTLs) can fasttrack traditional breeding methods. Till date, several QTLs for insect pest resistance have been identified in field-grown crops, and a few of them have been cloned by positional cloning approaches. Genome editing technologies, such as CRISPR/Cas9, are paving the way to tailor insect pest resistance loci for designing crops for the future. Here, we provide an overview of diverse defense mechanisms exerted by plants in response to insect pest attack, and review recent advances in genomics research and genetic improvements for insect pest resistance in major field crops. Finally, we discuss the scope for genomic breeding strategies to develop more durable insect pest resistant crops.

Introduction

Insect damage is one of the major biotic constraints limiting the productivity and production of major field-grown crops. Besides feeding on several plant parts, insects also act as carriers or vectors for various plant parasitic viruses
(Chang et al. 2021) and cause extreme plant damage. Despite extensive efforts of plant breeders, over US $70 billion are invested annually world-wide for the management of insect pest damage (Bradshaw et al. 2016). Heavy reliance on chemical pesticides may not be feasible as they provide temporary benefits, often with adverse environmental hazards and in some instances can worsen farmer’s overall pest problems (Akhtar et al. 2009). One alternative to chemical control of insect pests is host plant resistance (HPR). Although the potential of HPR has not been fully explored, it is environmentally friendly and compatible with other control means. The major challenge today is to develop insect pest resistant varieties that can increase and sustain crop productivity, in a rapidly changing world.

Crop wild relatives (CWRs) and/or non-domesticated species possess several desirable genes that can confer resistance to insects (Mammado et al. 2018; Khan et al. 2020). However, introgression of valuable insect resistance genes into an elite cultivar preferable for commercial release is usually a time-consuming and laborious task. Specifically, if a wild relative or non-domesticated crop species is the donor genetic material, the process of gene introgression can take more than a decade (Plaisted et al. 1992). A focus on genomics-assisted breeding holds potential to address many of these challenges and the data to support this is beginning to arise in several crop species (Varshney et al. 2021a). Genomics-assisted breeding technologies are increasingly being utilized to enhance the yield, resistance to biotic and abiotic stresses, and quality traits of crops. For instance, dissection of QTLs can help to identify and develop molecular markers specific for target traits. By utilizing such markers, marker-assisted selection strategy provides a platform for deployment of identified QTLs to develop insect pest resistant crops (Varshney et al. 2014). Technological advances in such modern breeding techniques facilitate the use of wild species, landraces, and traditional varieties as sources of desirable genes for crop improvement (Pandey et al. 2016; Bohra et al. 2021). Introgression of these resources in cultivated gene pool will ultimately help in increasing the genetic diversity of cultivated crop germplasm together with providing agronomically beneficial traits (Varshney et al. 2019). Complementary to breeding strategies, targeted genome editing facilitated by clustered regularly interspaced short palindromic repeats (CRISPR)/CRISPR-associated nuclease protein (Cas) systems has enabled precise, efficient, and targeted manipulation of target genes associated with insect resistance and agronomically important traits (Gui et al. 2020; Wang et al. 2018a).

In this review, we highlight recent advances in mapping and genome editing of insect pest resistance loci in major crops. We first describe diverse resistance mechanisms employed by plants against insect pest attack. We then provide an overview of recent advances in the identification and map-based cloning of insect resistance QTLs in major cereal and pulse crops. Further, we describe the use of CRISPR/Cas9-mediated genome editing in overcoming certain long-standing issues in breeding for insect resistance. We conclude by highlighting some new research areas that are now becoming active, and which can be explored for enhancing insect pest resistance.

**Plant resistance mechanisms against insect pests**

One of the important factors influencing crop productivity in controlled and natural vegetation is the arms race between plant and insect pests. To counteract insect herbivory, a wide array of defenses are imparted by crop plants to decrease the risk of impairment and reduction in productive capacity (Mitchell et al. 2016). Plant defense mechanisms include various direct and indirect approaches to defend themselves against insect attack. Direct defense mechanisms include specialized morphological structures produced by plants, while indirect mechanisms include secondary metabolism activated in plants. Few examples of defense mechanisms observed in field-grown crops in response to insect pest attack are provided in Fig. 1.

**Morphological barriers**

The plant morphological structures significantly contribute toward host plant resistance in response to pest herbivory. 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). In particular, morphological traits such as leaf glossiness, plant vigor, and leaf-sheath pigmentation are responsible for imparting resistance against Sorghum shoot fly, Atherigona soccata, in sorghum (Mohammed et al. 2016; Arora et al. 2021). In sweet corn, husk tightness showed significant resistance against corn ear worm, Helicoverpa zea (Cameron and Anderson 1966; Wiseman and Davis 1990). Trichomes adversely impact the ovipositional sites and feeding behavior of insect pests and block their mobility to leaf epidermis by obstructing their movement over plant surface (Sánchez and Morquecho-Contreras 2017). Trichomes on cowpea pods were also found to confer resistance to the pod sucking bug, Clavigralla tomentosicollis Stål (Hemiptera, Coreidae) (Boukar et al. 2020). In some grasses, trichomes tend to hinder sap-feeding or leaf-chewing insects to a greater extent (Hartley et al. 2015).
Plant secondary metabolites

The host plant species induces a response upon insect attack to decline the survival of the insect and its reproductive rate (War et al. 2012). There are two major pathways through which plants recognize insect attack, viz. oral secretions (OS) of insects and ovi-positional fluids (Karban and Baldwin 1997). The OS of insects is composed of certain compounds which are recognized by the host plant cells. These compounds are known as elicitors or herbivore-associated molecular patterns, which trigger plant defense mechanism upon insect attack. A specific class of elicitors in plants called herbivore-associated elicitors (HAEs) are responsive toward folivorous insects (Bonaventure et al. 2011). During insect folivery, the HAEs can act in a diversified manner ranging from different structures to varied enzymes and in modified forms of lipids [e.g. fatty acid–amino acid conjugates] (Mattiacci et al. 1995; Eichenseer et al. 1999). For example, a compound named volicitin from the oral secretions of beet armyworm caterpillars induced maize seedlings to emit volatile compounds which can attract several parasitic wasps and other natural enemies of caterpillars. Shinya et al. (2016) demonstrated that the entire action of Mythimna loreyi OS, is significantly contributed by high molecular mass elicitor(s) fraction. The accumulation of reactive oxygen species (ROS) and phytoalexins were detected in the cells of rice, which were strongly induced by the high molecular mass elicitor(s) containing fraction. The HAEs can also act as modified forms of sulfur-containing fatty acids (caeliferins). For instance, the 16-carbon analog of caeliferin is responsible for induction of volatile organic compounds (VOCs) in maize upon herbivory of grasshopper species (Schistocerca Americana) that decoys the regular enemies of herbivores (Alborn et al. 2007). An apterous Aphis craccivora was attracted to cowpea leaves pre-infected with low population density (~10 individuals) of both alate and apterous aphid forms, but they were repelled if plants were pre-infected with higher population density groups (>50 individuals) of aphids. This represents a natural adaptation to colonize fresh leaves or those with the least population of conspecifics, to avoid intraspecific competition (Jaba et al. 2010).

The persistent contact of insect eggs and their ovipositional fluids on plant surface can induce defense responses. Plants are very sensitive to ovipositional fluids which elicit defense responses upon its attachment to plant surface. For instance, in rice, hypersensitive responses were noticed after the attachment of lepidopteran, hemipteran, and coleopteran insect eggs, which led to desiccation and detachment of the eggs from the plant surface (Shinya et al. 2016). The presence of predator (ladybird beetle, Cheilomenes sexmaculata) eggs on aphid-infested cowpea failed to attract its own species of other ladybird beetles. This might be due to the presence of marker pheromone/spacing pheromone-like chemicals, which are released from the egg mass deposited in aphid colonies (Jaba et al. 2013). Furthermore, plants can also get rid of insect eggs through secretion of ovicidal substances. Salerno et al. (2013) showed that maize leaves elicit defense by retaining egg parasitoids upon the secretion of accessory reproductive glands of Sesamianon agrioides. Yang et al. (2014) reported a natural defense mechanism
which induced watery lesions and high egg mortality against the whitebacked planthopper (*Sogatella furcifera*) in rice.

The major role of flavonoids in plants lies in providing defense against abiotic or biotic stresses. For instance, a plant strengthener named 4-FPA (4-fluorophenoxyacetic acid) regulates peroxidases, H$_2$O$_2$, and flavonoid production that directly cause flavonoid polymer formation. The rise in phenolic polymer accumulation in rice parenchyma cells was found to be closely related to a declining ability of the whitebacked planthopper (WBPH) *Sogatella furcifera* to reach the plant phloem (Wang et al. 2020). Notably, pigeonpea genotypes (ICPH 3461, ICPH 3762, BSMR 853, ICPL 332 WR, ICPH 2740, and ENT 11) with better pod wall thickness, high non-glandular trichome density, and high phenol, tannins, and flavonoids content showed improved tolerance to pod borer complex (Ambidi et al. 2021). In a recent study, the resistance of cowpea to aphids, *Aphis craccivora* (Koch), was found to be linked to their low sucrose levels and high levels of kaempferol and quercetin (aglycones of phenolic compounds) (Togola et al. 2020).

**Phytohormones and herbivore-induced plant volatiles**

To confront challenges of biotic stress from herbivores, plants have refined their defense strategies. Jasmonic acid (JA), salicylic acid, and ethylene as phytohormones contribute towards inducing indirect plant defense mechanisms (Thaler et al. 2012; Zhang et al. 2013). The lipid-derived phytohormone, jasmonate, proved to be very important in inducing defense responses toward the insect. For instance, quick jasmonate synthesis was consistently elicited upon insect herbivory which was then sensed by the F-box protein COI1 to promote recruitment of Jasmonate Zim Domain repressors for ubiquitination and degradation purpose. These activities stimulated the transcriptional factor release and thereby triggered defense against insect attack (Wang et al. 2019). The JA content in plants draws the attention of several parasitoids and predators on insects. According to Ye et al. (2019), rice leaves emit the indole volatile upon fall armyworm (*Spodoptera frugiperda*) caterpillar attack. As a result, OsMPK3 gets primed by indole activity that leads to transcription of OsWRKY70 and other jasmonate biosynthesis genes. This overall activity results in further assembly of bioactive oxylipins viz., JA precursor OPDA (12-oxophytodienoic acid) and JA and consequently declines larval growth, weight gain and damage. Salicylic acid elicitation has obvious implications toward plants, pathogens, insect pests, and their natural enemies. The release of volatiles related to salicylic acid defenses can draw attention of natural enemies both above- and below-ground, and can assist in reducing insect pest populations on crop (Filgueiras et al. 2019). In maize, application of foliar methyl salicylate attracted the subterranean entomopathogenic nematode *Heterorhabditis amazonensis*, which recruited herbivore-induced cues, infected insect larvae feeding on plant roots and enhanced the biological control of corn, which is fed by adult *Diabrotica speciosa*, the corn rootworm pest (Filgueiras et al. 2016).

Specified mixtures of herbivore-induced plant volatiles (HIPVs) (such as phenylpropanoids, terpenoids, sulphur containing compounds, nitrogen containing compounds, fatty acid-derived compounds, and isothiocyanates) are emitted by plants upon insect herbivores’ attack (Aartsma et al. 2017; Dicke and Lucas-Barbosa 2020). HIPVs can promote defense priming by stimulating quick response in intact tissues of plants (Erb et al. 2015; Mauch-Mani et al. 2017). Further, HIPVs can also attract parasitoids and predators that can contribute toward controlling the attacking insect (Aartsma et al. 2017; Xi et al. 2019; Mbaluto et al. 2020). According to Aljborj and Chen (2018), about 24 species of predators and 34 species of parasitoids were attracted to volatiles emitted from plants infested by herbivory insect pests. The egg parasitoid *Cotesia sesamiae* (Cameron) (Hymenoptera: Braconidae) is attracted to volatiles emitted by maize plants on which *Chilo partellus* (*Swinhoe*) (Lepidoptera: Cramidae) lays its eggs. The genetic basis for *C. partellus* induced indirect defense attracting *C. sesamiae* was investigated in maize genotypes (Tamiru et al. 2020). A genome-wide association study revealed 101 single nucleotide polymorphisms (SNPs) strongly associated with the trait. Within a 10 Mb region of the genome next to these SNPs, 33 candidate genes were found that may code for the trait, of which 7 were terpene synthase genes (*tps2, tps3, tps4, tps5, tps7, tps9*, and *tps10*) (Tamiru et al. 2020).

**Defensive proteins**

The requirement of nutrition for insect is quite comparable to other animals, and any disparity in the absorption and usage of plant proteins by insect herbivores causes harsh impact on insect physiology. The biotic stress resulting from insect attack stimulates gene alteration, which consequently alters the proteins both qualitatively and quantitatively. These changes significantly contribute in signal transduction as well as oxidative defense. The infestation by spotted stem borer (*Chilo partellus*) was found to induce more protein suppression but selective defensive protein aggregation in *Sorghum bicolor*. These proteins were mainly concerned with stress and defense, small molecule biosynthesis, amino acid metabolism, catalytic and translation regulation activities (Tamhane et al. 2021). The vegetative insecticidal protein (VIP), e.g., VIP1 and VIP2, present in the supernatant of vegetative *Bacillus cereus* culture, have been demonstrated to confer toxic effects on insects (Gupta et al. 2021). The VIP3 isolated from *B. thuringiensis* supernatant, which
is similar to Cry proteins in terms of toxicity potential, possess insecticidal activity against Lepidopteran pests. These proteins stimulate gut paralysis, and then total lysis of gut epithelium cells, leading to larval death (Gupta et al. 2021). The endochitinases, peroxidases, and glutathione S-transferase produce over catalytic activities of these defensive proteins (Alseekh et al. 2020). Likewise, another protein called superoxide dismutase was found at a high concentration in wheat, and showed strong colinearity with high resistance against invading aphids (Lightfoot et al. 2017).

Plant protease inhibitors are small proteins that naturally occur in plants (especially leguminous plants) and provide defense against a certain number of insect pests. They bind to trypsin in the insect gut that affects the synthesis and regulation of alimentary proteases. Ultimately, digestion and absorption of nutrients are disrupted leading to the death of the insect. For instance, protease inhibitors from cowpea (cowpea trypsin inhibitor) and soybean conferred resistance to a wide range of insect pests including lepidopterans (Zhao et al. 2019).

**Plant lectins**

Plant lectins are proteins that promote carbohydrate ligand binding, which aid in obtaining the sensations from environmental signals and convert them into phenotypic responses. The down-stream signaling cascades are required for these processes to arise, usually mediated by interacting proteins. Together, all these processes play a significant role in plant resistance mechanism (Esch and Schaffrath 2017). In recent past, the use of proteins carrying jacalin-related lectins gained importance into the plant resistance research areas. In a recent study, transgenic tobacco plants expressing Hvt-lectin resulted in 100% mortality of Helicoverpa armigera and Spodoptera litura within up to 96 h after infestation (Rauf et al. 2019). A jacalin-related lectin, Orysata from rice species was found to be antagonistic against Spodoptera exigua and Acrystosiphon pisum by lowering larval weight gain and obstructing development (Atalah et al. 2014). Hence, it is predicted that Orysata could be effectively used against biting-chewing and piercing-sucking insect pests.

**Defensive enzymes**

The phyto-enzymes impair nutrient uptake of insects through electrophile formation and have become one of the key attributes of plant defense against insects. One of the most crucial enzymes is chitinase, which is also an integral component of insect integument. A soybean seed coat chitinase fraction incorporated in artificial cotyledons resulted in up to 90% mortality and up to 87% decrease in larval mass of the insect Callosobrachus maculatus (Silva et al. 2018). Lipoxygenase is the first enzyme in the octadecanoic pathway which is a prominent link for the synthesis of the signaling molecule, which is associated in plant defense stimulation. The lipoxygenase-encoding gene was down-regulated in a susceptible genotype, while the basal expression remained level in the wheat genotype showing resistance against Rhopalosipnium padi (Correa et al. 2020). The accumulation of green leaf volatiles aided in declining the aphid preference, and the action of non-glandular trichomes as a physical barrier enabled uninterrupted lipoxygenase-encoding gene expression (Correa et al. 2020).

**Insect resistance QTLs identified in major field crops**

**Rice**

Brown planthopper (BPH) is one of the most destructive pests that reduces rice production in Asia. Qiu et al. (2014) carried out genetic mapping for brown planthopper resistance in 93–11/T12 F2 population and located Bph7 gene on the long arm of chromosome 12, between SSR markers RM28295 and RM313. Bph7 is responsible for 38.3% phenotypic variation of BPH resistance in the F2 population. 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). Similarly, a F2:3 population developed from a cross between BPH susceptible (Zhenshan 97) and BPH resistant (IR65482-17) genotype was utilized for mapping three QTLs for seedling resistance and feeding rate to BPH. Among the identified QTLs, qBph4.2 on chromosome 4 (between SSR markers, RM261 and SNP S1) exhibited the largest effect by contributing phenotypic variation of about 36–44% (Hu et al. 2015a). Further, Wu et al. (2014) mapped Bph28(t) between markers Indel55 and Indel66 in two different F2 mapping populations developed by crossing the common resistant parent, DV85 with susceptible japonica variety Kinmaze and Indica 9311. Fine mapping of such genes using advanced genomics technologies (Jaganathan et al. 2020) will greatly contribute toward marker-assisted gene pyramiding programs for insect resistance. Recently, Yuxing et al. (2020) and Yang et al. (2020) mapped Bph35 and Bph38, respectively, on chromosome 4 in rice. These studies indicated the importance of chromosome 4 in rice, which consists of a large number of QTLs mapped for BPH resistance (Table 1). QTL mapping studies using a RIL population led to the identification of three QTLs, namely qSBPH2, qSBPH3, and qSBPH7.1 located on chromosomes 2, 3, and 7, respectively, for small brown planthopper (SBPH) resistance that exhibited a cumulative phenotypic variation of 35.1% (Wang et al. 2013).

Van Mai et al. (2015) used two independent F2 populations derived from a cross of ASD7×Taichung 65 and mapped
Table 1  A list of key QTLs mapped/ fine mapped/ cloned for insect pest resistance in some field crops

| Crop | QTL     | Mapping population | Cross | Marker type | Environment | Chromosome/linkage group | Stress                              | References             |
|------|---------|--------------------|-------|-------------|-------------|--------------------------|-------------------------------------|------------------------|
| Rice | Bph38   | F₂,₃               | 9311 × RBPH327 | SSR (RM16563 and RM16763; YMI12 and YMI90) | Greenhouse | 4 | Brown planthopper (BPH) and whitebacked planthopper (WBPH) | Yang et al. (2020) |
| Rice | Bph35   | F₂,₃               | 9311 × RBPH660 | InDel (PSM16 and R4M13) | Greenhouse | 4 | BPH | Yuexiong et al. (2020) |
| Rice | Bph36 and Bph27 | F₂,₃, BC₁,F₂ | KW × RBPH16 and HHZ × RBPH17 | InDels (S13 and X48), RM16766 and RM17033 | Greenhouse | 4S and 4L | BPH | Li et al. (2019) |
| Rice | Bph38(t) | BC₁,F₅            | Khazar × Huang–Huan–Zhan | SNP (693, 369) | Greenhouse | 1L | BPH | Balachiranjeevi et al. (2019) |
| Rice | Bph39(t) and bph40(t) | BC₁,F₂ | [RPBio4918-230S line-(IRGC81848×Swarna)] × Swarna | – | Greenhouse and field | – | BPH biotype 4 | Akanksha et al. (2019) |
| Rice | Bph37   | F₂,₃               | KWQZ × IR64 | RM302 (SSR) and YM35 (InDel) | Greenhouse | 1 | BPH biotype 2 | Yang et al. (2019) |
| Rice | Bph34   | F₂, F₂,₃           | PR122 × IRGC104646 | SNP (AX-9592039 and AX-95921548), SSR (RM16994 and RM17007) | Field and greenhouse | 4L | BPH | Kumar et al. (2018) |
| Rice | Bph30   | BC₁,F₂, BC₂,F₂, NILs | AC–1613 × 9311 | SSR-28 and SSR-69, RM16278 and RM16425, RM16294 and RM16299 | Field | 4S | BPH | Wang et al. (2018b) |
| Rice | Bph33   | NILs, F₂,₃         | Kolayal × 9311 and Poliyal × 9311 | InDels (H25 and D17), SSR (RM551 and RM335, RM3335 and RM5633) | Greenhouse | 4S | BPH | Hu et al. (2018) |
| Rice | Two QTLs (qBph4.3 and qBph4.4) | F₄ RILs | TN1 × Salkathi | SSR (RM551 and RM335, RM3335 and RM5633) | Greenhouse | 4S | BPH biotype 4 | Mohanthy et al. (2017) |
| Rice | 10 QTLs | F₂,₃               | MR276 × RathuHeenati | RM231, RM588 and RM204 | Greenhouse | 1, 3, 6, 7, 9, 10, 12 | BPH biotype 3 | Shabanimofrad et al. (2017) |
| Rice | Bph31   |! F₂               | Jaya × CR2711–76 | InDels (PA26 and RM2334) | Glasshouse | 3L | BPH biotype 4 | Prahalada et al. (2017) |
| Rice | Bph32   | F₁,₄               | Ptb33/163B//163B | SSR (RM19291 and RM8072) | Greenhouse | 6S | BPH | Ren et al. (2016) |
| Rice | qBPH6 and qBPH12 | F₂ | ASD7 × Taichung 65 | SSR-RM5120 and RM8200 (qBPH6), RM3326 and S20103 (qBPH12) | NM | 6S and 12L | BPH | Van Mai et al. (2015) |
| Rice | QBph3 and QBph4 | BC | IR02W101 × Zhenshan 97 | SSR-RM514 and J412 (QBph3), RM261 and RM307 (QBph4) | Greenhouse | 3L and 4S | BPH | Hu et al. (2015b) |
| Crop | QTL | Mapping population | Cross | Marker type | Environment | Chromosome/linkage group | Stress | References |
|------|-----|---------------------|-------|-------------|-------------|-------------------------|--------|------------|
| Rice | QBph4.2 | F2,3 and BC | IR65482-17×Zhenshan 97 | Co-segregate with Indel XCA-27 (between SSRs RM261 and SNP S1) | Greenhouse | 4S | BPH | Hu et al. (2015a) |
| Rice | bph29 | NILs | TR539×TN1 | InDels (BYL8 and BID2) | Greenhouse | 6S | BPH | Wang et al. (2015) |
| Rice | Bph26/bph2 | NILs | ADR52×Taichung 65 | SNP (DS-72B4 and DS-17B) | NM | 12L | BPH | Tamura et al. (2014) |
| Rice | bph7 | F2 and BC | 93–11×T12 | SSR (RM3448 and RM313) | Greenhouse | 12L | BPH | Qiu et al. (2014) |
| Rice | Bph28(t) | F2 | DV85×Kinmaze (japonica) and DV85×93-11 (indica) | InDels (InDel 55 and InDel 66) | Greenhouse | 11 | BPH | Wu et al. (2014) |
| Rice | Bph3 | BC and F2 | RathuHeenati×02428 | SSR (RH078, W4, RM8213, RM16533 and RM5953) | Greenhouse | 4 | BPH | Liu et al. (2015) |
| Rice | Bph27 | BC | Teqing×GX2183 | SSR (RM16846 and RM16888) | Greenhouse | 4L | BPH | Huang et al. (2013) |
| Rice | Bph27(t) | F2,3 | Balamawee×japonica cv. 02428 | InDels (Q52 and Q20) | Greenhouse | 4L | BPH | He et al. (2013) |
| Rice | Bph25 and Bph26 | F3 and NILs | ADR52×Taichung 65 | SSR (S00310 and RM5479) | NM | 6S and 12L | BPH | Myint et al. (2012) |
| Rice | Bph6 | F2 and NILs | Swaralata×93–11 | STS (Y19 and Y9) | Greenhouse | 4 L | BPH | Qiu et al. (2010) |
| Rice | bph4 | F2 and NILs | TN1×Babawee, Babawee×KDML105 | SSR (RM589 and RM586) | NM | 6S | BPH | Jairin et al. (2010) |
| Rice | qSBPH7.1 | RILs | N22×USSR5 | SSR (RM234 and RM429) | Greenhouse | 2.3 and 7 | Small BPH | Wang et al. (2013) |
| Rice | qSBPH12-a1 | BC and F2 | 02428×RathuHeenati | SSR (RM519 and RM331) | Greenhouse | 12L | Small BPH | Tuyen et al. (2012) |
| Rice | Qsph3b, Qsph11d and Qsph11e | BC | Nipponbare×Kasalath | SSR (C80–C1677, R1506–C950 and S2260-G257) | Greenhouse | 3 and 11 | Small BPH | Duan et al. (2010) |
| Rice | qWDS-6 and qWNS-12 | F2,3 | TN1×SinnaSivappu | SSR (RM589-RM539 and RM519-RM28487) | Greenhouse | 6 and 12 | WBPH | Ramesh et al. (2014) |
| Rice | Four QTLs (qGRH2, qGRH4, qGRH5, qGRH11) | Five BC,F3 and seven BC,F3 | O. sativa ssp. japonica cv. ‘Nipponbare’×African wild rice O. longistaminata accession W1413 | SSR | Greenhouse | 2L, 4S, 5S and 11L | Green rice leafhopper (GRH) | Thein et al. (2019) |
| Rice | qGRH5 | F2 | ASD7×Taichung 65 | SSR (RM6082 and RM3318) | NM | 4S | GRH | Van Mai et al. (2015) |
| Rice | gm12 | F2,3 | KDML105×MN62M | SNP markers (S2,76222 and S2_419160) | Greenhouse | 2S | Asian rice gall midge | Leelagud et al. (2020) |
| Crop | QTL | Mapping population | Cross | Marker type | Environment | Chromosome/linkage group | Stress | References |
|------|-----|---------------------|-------|-------------|-------------|--------------------------|--------|------------|
| Rice | gm3 | RILs                | TN1 × RP 2068-18-3-5 | SSR (RM17480 and gm3SSR4) | Greenhouse | 4L | Gall midge | Sama et al. (2014) |
| Rice | Gm8 | RILs                | TN1 × Aganni | SSR (RM22685 and RM22709) | Greenhouse | 8 | Gall midge | Sama et al. (2012) |
| Rice | Gm1 It | RILs | TN1 × CR57-MR 1523 | SSR (RM28574 and RM28706) | Greenhouse | 12 | Gall midge | Himabindu et al. (2010) |
| Rice | Gm10 | F2_3 | BG 380–2 × Susceptible cv | – | Natural condition | – | Asian rice gall midge | Kumar et al. (2005) |
| Rice | Gm 9 | F2_3 | Madhuri Line 9 × MW10 | – | Natural condition | – | Asian rice gall midge | Shrivastava et al. (2003) |
| Rice | qAfrGM4 | BC | ITA306 × BW348-1, ITA306 × TOG7106 and ITA306 × TOS14519 | SNP using KASP assay | Greenhouse | 4 | African rice gall midge | Yao et al. (2016) |
| Wheat | H35 and H36 | RILs | SD06165 × OK05312 | SNP (SDOKSNP7679, SDOKSNP1618, SDOKSNP8089) | Greenhouse | 3BS and 7AS | Hessian fly | Zhao et al. (2020) |
| Wheat | h4 | RILs | Bobwhite × Java and Overley × Java | KASP (KASP3299 and KASP1871) | Greenhouse | 1AS | Hessian fly | Niu et al. (2020) |
| Wheat | H7 and H8 | F5_6 and F4_5 | Bobwhite × Seneca | KASP6A205 and KASP6A215 | Greenhouse | 6AL and 2B | Hessian fly | Liu et al. (2020) |
| Wheat | H34 | RILs | Ning7840 × Clark | SSR and SNP (Xnsnp921-Xnsnp274) | Greenhouse | 6B | Hessian fly | Li et al. (2013) |
| Wheat | QHf.osu-1A6d and QHf.osu-1A74 | DH | Duster × Billings | SSR—Xcfd15 and PCR based-OPRA1, Genotyping-by-sequencing (GBS07851 and GBS10205) | Greenhouse | 1A | Hessian fly | Li et al. (2013) |
| Wheat | QHf.osu-1A, QHf.osu-2A | RILs | Jagger × 2174 | SSR (Xcfa2153) | Greenhouse | 1A, 2A | Hessian fly | Tan et al. (2013) |
| Wheat | QHf.uga-6AL (HR61) and QHf.uga-3DL | RILs | 26R61 × AGS 2000 | SSR (Xgwm427-5Pr731936 and Xcfd4b-Xgwm52, respectively) | Green House | 6AL and 3DL | Hessian fly | Hao et al. (2013) |
| Wheat | QDn.unlp genes | DH | Spark × Rialto | SSR (Xpsp3103, Xgdm3 and Xpsp3094) | Greenhouse | 4DS, 5DS and 7AL | Russian wheat aphid | Ricciardi et al. (2011) |
| Wheat | Ei1 | DH | Cham6 × IG139883, Cham6 × IG139431 | SNP iSelect assay and Candidate gene-based KASP markers (IWB661338 and BS0022785) | Artificial screen cages | 4BS | Sunn Pest | Emebiri et al. (2016) |
Table 1 (continued)

| Crop          | QTL        | Mapping population      | Cross                                | Marker type     | Environment | Chromosome/linkage group | Stress                     | References                  |
|---------------|------------|-------------------------|--------------------------------------|-----------------|-------------|-------------------------|----------------------------|----------------------------|
| Maize         | 62 QTNs    | Association mapping panel | 341 tropical maize lines             | DArTseq markers | Field       | All 10                  | Maize weevil and fall army-worm | Badji et al. (2020)         |
| Maize         | 15 QTLs    | RILs                    | Population 84 × Kilima               | SSR             | Field       | 1, 2, 3, 4, 8, and 10   | Maize weevil               | Castro-Álvarez et al. (2015) |
| Maize         | Aphid resistance QTL | RILs | B73 and Mo17                 | AC213878 and AC204415 | Greenhouse | 4                       | Corn leaf aphid            | Betissi et al. (2015)       |
| Maize         | 4 Major QTLs for root damage, root regrowth, and root size traits | IRIL–IBM Reombinant Inbred Line | IBM – Intermated B73 × Mo17 | SSR and SNP | Field       | 1 and 6                  | Western corn rootworm      | Brikic et al. (2020)        |
| Maize         | 4 and 3 putative QTLs for RDR, RRG and RSZ | DHLs | (NGSDCRW1 × AG1 and LH51 × CRW8-1) top crossed with PHZ51 | SNP             | Field       | 7, 9, 10 and 6, 8, respectively | Western corn rootworm | Bohn et al. (2018)         |
| Maize         | c3 NI (q03.165) | F₂, BC, and DH | FS8B × B86, UR2 × Mo47 | SNP             | Artificial cages | 3                       | Western corn rootworm      | Hessel (2014)               |
| Maize         | Six QTLs (three for tunnel length, one each for kernel resistance, stalk damage, and yield) | RIL | A637 × A509                  | SNP             | Field       | 5, 8, 9, and 10          | Mediterranean corn borer    | Jimenez-Galindo et al. (2017) |
| Maize         | 8 QTLs for resistance traits like tunnel length, stalk damage, stalk lodging, kernel resistance, and grain yield | RILs | B73 × CML103                | SNP             | Artificial | 1, 5 and 6               | Mediterranean corn borer    | Samayoa et al. (2015)       |
| Maize         | HDMBOAGlc QTL | RILs | B73 × CML322                | PZA03189.4 and PMHS098.25 | Greenhouse | 1                       | Corn leaf aphid            | Mehls et al. (2013)         |
| Soybean       | Raso2      | RILs                    | Williams 82 × PI 366121             | SNP using Golden Gate assay (BARC-042815–08424 and BARC-015945–02020) | Plant growth chambers | 7                       | Foxglove aphid             | Lee et al. (2015)           |
| Soybean       | Raso1      | BC                      | Toyomusume × Shokukei-10            | SSR             | Plant growth chambers | 3                       | Foxglove aphid             | Ohnishi et al. (2012)       |
| Soybean       | Rag6 and Rag3c | F₃,₄                  | E08934 × E00003                  | MSUSNP08-2 and Sat209; MSUSNP16-10 and Sat370 | Field and greenhouse | 8 and 16                  | Aphid                     | Zhang et al. (2017)         |
### Table 1 (continued)

| Crop       | QTL          | Mapping population | Cross                        | Marker type                        | Environment               | Chromosome/linkage group | Stress          | References               |
|------------|--------------|--------------------|------------------------------|-----------------------------------|---------------------------|--------------------------|----------------|--------------------------|
| Soybean    | R_P746       | F_{2,3}            | P746 × Dongnong 47          | SSR (Satt335 and BARC-SOYSSR_{13,1508}) | Greenhouse                | 13                       | Aphid          | Xiao et al. (2014)       |
| Soybean    | QTL_{13,1} and QTL_{13,2} | RILs              | Wyandot × PI 567324         | Oligo Pool Assay containing SNPs   | Greenhouse and field environment | 13                       | Aphid          | Jun et al. (2013)        |
| Soybean    | rag3 and rag1b | F_{4,5}            | IA2070 × E06902             | SSR and SNP (Gm16_6262227_C_T–Gm16_6424067_A_G and Satr435-BARC-SOYSSR_{07,0295}) | Field and greenhouse | 16 and 7                  | Aphid          | Bales et al. (2013)      |
| Soybean    | Rag1         | BC_{1,2}           | Dowling × Dwight            | SNP markers (46169.7 and 21A)      | Plant growth chambers     | 7                        | Aphid          | Kim et al. (2010a)       |
| Soybean    | Rag2         | F_{2,3}            | LD02-4485 × (Ina × PI 200538) | SNP (KS9-3 and KS5)               | Green House               | 13                       | Aphid          | Kim et al. (2010b)       |
| Soybean    | Rag3         | F_{4} derived lines| PI 567543C × E00003         | SSR (Sat_{339} and Satt_{414})    | Greenhouse and field environment | 16                       | Foxglove aphid | Zhang et al. (2010)      |
| Soybean    | qRWF-1 and qRWF-5-1 | F_{2}              | Huapidou × Qihuang 26       | SSR (satt071-satt147 and satt619-satt545) | Field environment, and controlled conditions | 1 and 5                  | Whitefly       | Zhang et al. (2013)      |
| Chickpea   | Nine main-effect QTLs for H. armigera resistance component traits | RILs | ICC 4958 × PI 489777 | Axiom®CicerSNP Array | Field environment, and controlled conditions | CaLG01, CaLG03, CaLG04, and CaLG07 | Helicoverpa armigera | Barmukh et al. (2020) |
| Cowpea     | Thr-1, Thr-2, and Thr-3 | RILs              | IT93K503-1 × CB46           | AFLP (ACC-CAT7, ACG-CTC5, and AAG-CAT1) | Field environment | 5 (Thr-1, Thr-2) and 7 (Thr-3) | Thrips         | Muchero et al. (2010)   |
| Cowpea     | QAc-vu7.1    | RILs              | CB27 × IT97K-556–6         | SNP (T_{0912–1,0391})            | Field environment         | 7                        | Aphid          | Huynh et al. (2015)     |
| Mungbean   | Two QTLs for bruchid resistance and one QTL for pod sucking bug | F_{2,3} | Sunhwa × Jangan, Sunhwa × TC1966 | SSR (MB87 and COPU11), and COPU06 | Field environment         | –                        | Bruchid and Pod sucking bug | Hong et al. (2015) |
| Rice bean  | Cmpd1.5 and Cmpd1.6 | F_{2,3}   | LRB238 × LRB26, JP100304 × LRB26 | SRAP markers (E2M9–270 and E12M7311), and SRAP marker and SSR-CEDG259, respectively | Controlled conditions-growth chambers | 4 and 9                  | Bruchid         | Venkataramana et al. (2016) |
| Pea        | 4 QTLs (BpSL.I, BpSL.II, BpSL.III and BpLD.I) | F_{3,4} | P. sativum ssp. syriacum accession P665 × P. sativum ssp. sativumcv. Messire | DaRTseq markers | Field environments | LGI, LGII, LGIV and LGV, respectively | Pea weevil | Aznar-Fernández et al. (2020) |
two QTLs (qBPH6 and qBPH12) for BPH resistance and one QTL (qGRH5) for green rice leafhopper (GRH) resistance. Recently, Thein et al. (2019) identified four major QTLs, namely qGRH2, qGRH4, qGRH5, and qGRH11 in African wild rice O. longistaminata accession W1413 derived backcross populations, with qGRH2 being a novel QTL for GRH.

Rice gall midge (RGM) is another important pest of rice affecting its production globally. Sama et al. (2014) carried out the mapping of QTLs for gall midge resistance in RILs developed from a cross between TN1 (susceptible) × RP2068-18-3-5 (resistant) using SSR markers. A significant association was observed between gene and phenotype based on flanking markers, RM17480 and gm3SSR4. Based on the sequence polymorphism, ‘gm3del3’ was cloned and efficiently utilized as a functional marker for introgressing gm3 gene in the elite bacterial blight resistant cultivar Improved Samba Mahsuri (B95-1), via marker-assisted selection (MAS) approach. Leelagud et al. (2020) mapped gm12 on chromosome 2 in the F2:3 population derived from the cross of KDML105 and MN62M, wherein SNP markers (S2_76222 and S2_419160) were found to flank gm12. This gene can be extensively used for the identification of RGM biotypes in Thailand and Southeast Asia. African rice gall midge (AfRGM) has proved to be a very destructive pest in the areas of irrigated and lowland African ecologies. Three independent bi-parental rice populations (ITA306 × BW348-1, ITA306 × TOG7106, and ITA306 × TOS14519) were developed for the identification of QTLs resistant to AfRGM, followed by meta QTL (mQTL) analysis studies to identify the conserved genomic regions across different genetic backgrounds. Out of the total 28 QTLs identified, a major QTL qAfrGM4 was mapped on chromosome 4 in ITA306 × TOS14519 population, and this QTL exhibited 34.1% phenotypic variation. Meta-analysis revealed that most of the mQTLs were background specific, except one minor effect mQTL (chromosome 1) that was common in the TOS14519 and TOG7106 genetic backgrounds. This is the first reported QTL for AfRGM resistance and further fine mapping is under process for its efficient utilization in MAS (Yao et al. 2016).

### Wheat

Sunn Pest (Eurygaster integriceps) is a pest of serious concern in wheat. Mapping studies with 90 k SNP iSelect assay and candidate gene-based KASP markers in two separate DH populations derived from Cham6 × IG139431 and Cham6 × IG139883, respectively, led to the identification of a major QTL for resistance to sunn pest, Ei1 on chromosome 4BS (Table 1). The Ei1 was mapped on chromosome 4B between markers, IWB66138 and BS00022785, and was found to be very close to other agronomically important genes like GA-insensitive dwarfing gene, Rht-B1.

| Crop          | Mapping population | Cross                  | Environment          | Markertype        | Chromosome/linkage group | Stress References |
|---------------|-------------------|------------------------|----------------------|-------------------|--------------------------|------------------|
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Pennant × P. fulvum (ATC113) | Glasshouse 2 and 4 Pea weevil | DArTseq markers | SSRs (A179-A180, A190) | Aryamanesh et al. (2014) |
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Messire; P. fulvum accession, P060×P651 | Field environments 2 and 4 Pea weevil and aphid, rust | DArTseq markers | SSRs (AA179-AA180, A190) | Barilli et al. (2019) |

### Table 1 (continued)

| Crop          | Mapping population | Cross                  | Environment          | Markertype        | Chromosome/linkage group | Stress References |
|---------------|-------------------|------------------------|----------------------|-------------------|--------------------------|------------------|
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Messire; P. fulvum accession, P060×P651 | Field environments | SSRs (AA179-AA180, A190) | - | Barilli et al. (2019) |
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Messire; P. fulvum accession, P060×P651 | Field environments | SSRs (AA179-AA180, A190) | - | Barilli et al. (2019) |
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Messire; P. fulvum accession, P060×P651 | Field environments | SSRs (AA179-AA180, A190) | - | Barilli et al. (2019) |
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Messire; P. fulvum accession, P060×P651 | Field environments | SSRs (AA179-AA180, A190) | - | Barilli et al. (2019) |
| Pea           | F2 F3              | P. sativum ssp. sativum cv. Messire; P. fulvum accession, P060×P651 | Field environments | SSRs (AA179-AA180, A190) | - | Barilli et al. (2019) |

- Barilli et al. (2019): Identification of major QTLs for gall midge resistance in rice using DArTseq markers.
- Aryamanesh et al. (2014): Development of a functional marker for introgressing gm3 gene in rice.
- Leelagud et al. (2020): Mapping of gm12 on chromosome 2 in rice.
- Yao et al. (2016): Identification of a major QTL for AfRGM resistance in rice.
(Emebiri et al. 2016). Hessian fly (HF), *Mayetiola destructor* is a destructive pest of wheat globally. Gene pyramiding is the best approach to achieve resistance to HF owing to the availability of multiple biotypes that are virulent to different wheat HF resistance genes, and this approach relies upon the identification of linked DNA-based markers. Li et al. (2013) developed a RIL population by crossing Ning7840 with the HF resistant genotype Clark for identification of QTLs governing HF resistance. A major QTL designated *H34* for resistance to fly biotype *GP* exhibiting 37.2% phenotypic variation was mapped on chromosome 6B, between markers Xsnp921 and Xsnp2745. Further, a major QTL for Hessian fly resistance, *QHf.osu-1A*, was mapped on chromosome 1A using SSRs in hexaploid wheat RILs derived from a cross between Jagger and 2174. This was followed by the identification of two new loci for HF resistance namely *QHf.uga-3DL* and *QHf.uga-1AL* (HR61) on chromosome 3 and 6, respectively, in RILs derived from a cross of 26R61 with AGS 2000 (Hao et al. 2013). Recently, Zhao et al. (2020) mapped a major QTL, *H35* on chromosome 3BS in SD06165 × OK05312 RIL population. Niu et al. (2020) mapped a recessive gene, *h4* on chromosome 1AS in RILs derived from two separate crosses (Bobwhite × Java and Overley × Java) using KASP markers.

**Maize**

Maize leaf aphid (*Rhopalosiphum maidis*) is one of the most destructive pests affecting maize production globally. A RIL mapping population developed by crossing B73 and CML322 was used to map QTLs for leaf aphid resistance. This study led to the identification of *HDMBOAGlc* on the chromosome 1 between markers, PZA03189.4 and PMHS098.25 (Meihs et al. 2013). Castro-Álvarez et al. (2015) carried out QTL mapping for maize weevil resistance in RILs derived from a cross between population 84 and Kilima. A total of 15 QTLs for maize weevil resistance mapped on 6 different chromosomes exhibited a range of phenotypic variation between 14% and 51%. These QTLs hold potential to be utilized for tropical maize improvement through MAS. Mediterranean corn borer (MCB), *Sesamia nonagriptera*, is a major pest of maize, in Mediterranean countries. Jiménez-Galindo et al. (2017) mapped six QTLs (three for tunnel length, and one each for kernel resistance, stalk damage, and yield) for MCB resistance on chromosomes 5, 8, 9, and 10 in A637 × A509 based RILs. A double haploid (DH) population developed by crossing UR2 with Mo47 was used to map QTLs for resistance to western corn rootworm. Among a total of 21 QTLs identified, a major QTL *c3 NI* (*q03.165*) was mapped on chromosome 3 between SNPs, MAGI_14202 and MAGI_72398. It was also found that a herbivore stress response governing *sp2* gene lied within the identified QTL interval (Hessel 2014). Recently, Brkić et al. (2020) mapped four major QTLs for root damage, root regrowth, and root size traits on maize IBM Interned RILs (B73 × Mo17 based). These QTLs were found to co-locate with genomic regions governing plant defense against herbivory.

**Sorghum**

Sorghum shoot fly, *Atherigona soccata* (Rondani) is one of the most damaging pest affecting world-wide sorghum production. A total of four QTLs were identified, and SBI-05 was found to contain the major QTL for non-preference to oviposition; while SBI-01, SBI-07, and SBI-10 contributed to shoot fly resistance (Kiranmayee et al. 2015). Furthermore, assessment of phenotypes led to the identification of two resistant lines for each QTL region present on chromosomes SBI-01, SBI-07, and SBI-10 in ICSB 29004 × Parbhani Moti (Gorthy et al. 2017). In another study, 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).

**Soybean**

The soybean aphid (*Aphis glycines* Matsumura) is an important pest of soybean [*Glycine max* (L.) Merr.]. Jun et al. (2013) mapped two major QTLs, namely *QTL_13_1* and *QTL_13_2*, for aphid resistance on chromosome 13 using RILs developed from a cross between Wyandot and PI 567324. The study revealed that *QTL_13_1* and *QTL_13_2* were mapped very close to already reported loci, *Rag2* and *Rag4*, respectively (Jun et al. 2013). Xiao et al. (2014) mapped *R_P746* between SSRs, *Satt334*, and *Satt335*, on chromosome 13 in a P746 × Dongnong 47 derived *F₂* population comprising of 312 individuals. These linked markers will prove to be valuable in MAS-based aphid resistance breeding program in soybean. Further, Zhang et al. (2017) mapped two QTLs, *Rag6* and *Rag3c*, on chromosomes 8 and 16, respectively, and these QTLs were validated in two related populations with different genetic backgrounds. These QTLs were contributed by E08934, an advanced breeding line derived from the wild soybean *Glycine soja* 85-32; thereby indicating the importance of wild relatives in conferring tolerance to biotic stresses. Foxglove aphid, *Aulacorthum solani* (Kaltenbach), is a hemipteran insect of destructive nature in soybean. RILs derived from a cross between Williams 82 and PI 366121 were used for mapping of foxglove aphid resistance through antibiosis and antixenosis. Mapping was carried out with the help of Golden Gate assay-based SNP markers. This study resulted in the identification of a major QTL on chromosome 7 which
was later named as Raso2 to differentiate from the earlier reported QTL, Raso1 (Lee et al. 2015).

**Chickpea**

In chickpea, Helicoverpa armigera (Hübner) causes up to 100% yield losses in the tropical regions of the world (Patil et al. 2017). In a recent study, Barmukh et al. (2020) used an intraspecific RIL population (ICC 4958 × PI 489777) to map QTLs for *H. armigera* resistance component traits (Table 1). A total of nine main-effect QTLs and 955 epistatic QTLs explaining up to 42.49% phenotypic variation were mapped for multiple *H. armigera* resistance component traits. Interestingly, a QTL cluster on linkage group CaLG03 harboring main-effect QTLs for three component traits, was predicted to be of particular relevance for improving *H. armigera* resistance in elite chickpea cultivars (Barmukh et al. 2020).

**Cowpea**

Thrips, Megalurothrips sjostedti Trybom and aphid, Aphis craccivora Koch are among the most damaging insect pests of cowpea in Africa (Kusi et al. 2019). SNP-based mapping of QTLs for thrips resistance identified major QTLs such as Fthp28, Fthp87, and Fthp129 on chromosomes 2, 4, and 6 accounting for 24.5%, 12.2%, and 6.5% of the total phenotypic variation, respectively. Transgressive segregation was observed toward the susceptible phenotype. Both additive and non-additive effect QTLs were observed, with additive effects being predominant (Sobda et al. 2017). Furthermore, SNP-based mapping of QTLs for aphid resistance was carried out in a RIL population developed from a cross between California blackeye cultivar (CB27) and a resistant African breeding line (IT97K-556-6). This study resulted in the identification of a major QTL on chromosome 7, which was validated in a related F₂ population (Huynh et al. 2015).

**Mungbean**

Bruchid (Callosobruchus chinensis L.) and pod sucking bug (Riptortus clavatus Thunberg) are pests of serious concern in mungbean during the reproductive stage and seed storage. Two QTLs for bruchid resistance and one QTL for pod sucking bug resistance were identified in two independent F₂ populations derived from a cross of Sunhwa with Janganand, and Sunhwa with TC1966. The linked SSR markers hold promise to be successfully utilized for cloning of bruchid and bean bug resistant genes (Hong et al. 2015).

**Rice bean**

Bruchids (Callosobruchus maculatus) is a major pest of stored seeds in rice bean (Vigna umbellata), Venkataramana et al. (2016) identified QTLs for damage caused to the seed related to bruchid resistance in two F₂ populations derived from the cross of a common susceptible parent, LRB26 with LRB238 and JP100304. SSR and SRAP based genotyping resulted in the mapping of two major QTLs, Cmpd1.5 and Cmpd1.6 exhibiting 67.3 and 77.4% phenotypic variation, respectively.

**Pea**

Pea weevil, Bruchus pisorum, is one of the most destructive pests decreasing the production of field pea (Pisum sativum) globally. QTL mapping for traits associated with pea weevil resistance, such as cotyledon and pod wall/seed coat resistance, was performed in an interspecific population derived from a cross between the cultivated field pea and *P. fulvum* (resistance source) (Aryamanesh et al. 2014). This study led to the mapping of three major QTLs on linkage groups LG2, LG4, and LG5 for cotyledon resistance, and two major QTLs for pod wall/seed coat resistance on LG2 and LG5 exhibiting up to 80 and 70% phenotypic variation, respectively. These identified QTL markers may prove to be crucial in the screening of pea germplasm for pea weevil resistance genes (Aryamanesh et al. 2014). Recently, Aznar-Fernández et al. (2020) used DArTseq markers to map four QTLs, BpSI.I, BpSI.II, BpSI.III, and BpLD.I for weevil seed infestation and larval development on linkage groups LGI, LGII, LGIV and LGIV, respectively.

**Breeding crops for insect pest resistance**

Over the past decades, a large number of insect pest resistance QTLs have been identified in major field crops. 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. Recent advances in genomics and sequencing technologies have opened new avenues for rapid identification of genetic variation underlying crop performance and have improved the efficiency of breeding. The significance of sequence variations in the ability of the plants to regulate specific traits has been further uncovered by digging deeper into the genomes (Varshney et al. 2021b). This has facilitated the initiation of
the next level of biotechnological intervention, referred to ‘Genome editing’. This engrossing strategy enables modifications in the genome by adding, deleting, or editing specific DNA sequences, thereby presenting opportunities for use in plants, animals, and humans. In the current scenario of limited agricultural land and a higher load of insect pests on crop plants, genome editing holds enormous potential in combating insect pests and expediting crop improvement for future food security.

**Genome editing strategies for engineering insect pest resistance**

In recent years, genome editing has emerged as the most promising technology to cope up with the challenges associated with agriculture production. This technology has provided unprecedented opportunities to develop improved crop genotypes having higher yield and better adaptability under increasing environmental fluctuations. Among several other plant genome editing technologies, the CRISPR/Cas system has emerged as one of the most widely used systems due to its cost-effectiveness, simplicity, and high efficiency (Zhu et al. 2020). CRISPR/Cas9 is continuously expanding its toolbox with new discoveries and innovations (Razzaq et al. 2019). Till date, several insect resistance QTLs have been identified in crops (Table 1), with each QTL having only a small effect on the phenotype while interacting with each other. Moreover, QTLs do not follow a simple Mendelian pattern of inheritance and are extremely difficult to study and manipulate. Genome editing holds promise in overcoming these limitations by offering tools to associate genetic polymorphisms with phenotypic variations. CRISPR-based QTL editing can be utilized to incorporate numerous preferred quantitative trait alleles directly into elite crop varieties, thereby preventing the need for intensive crossing (Shen et al. 2018). This strategy will be particularly suitable for editing QTLs that are present in low recombination regions of the genome. Importantly, the CRISPR multiplex technique can be used to manipulate a blend of candidate QTLs or all target genes present within the QTL region, resulting in alterations to measurable phenotypes.

An interesting aspect of managing insect pests via genome editing has the benefit of altering both plants and insects pests (Fig. 2). While recent advances in genome editing have transformed insects to make them less effective toward crop damage, plant genomes are being modified to make plants more effective in repelling insect pests. Here, we discuss some key research efforts being pursued and those which can be anticipated toward genome editing in crops for insect management.

![Fig. 2](image.png)

Fig. 2 The CRISPR/Cas9-mediated genome editing applications for insect pest resistance in plants. The Cas9-gRNA complex targets desired sequence in the DNA and produces a double stranded break (DSB) at the 3’ upstream PAM sequence. This results in gene insertion/deletion through non-homologous end joining (NHEJ) mechanism, while gene insertion via homology directed repair (HDR) process. Different genes and receptor genes can be knocked-out to control the insect pest population. gRNA Guide RNA, NHEJ Non-homologous end joining, HDR Homology directed repair, DSB double stranded break, pgSIT precision guided sterile insect technique.
Genome editing in insects to alter and attenuate pest population

The utilization of CRISPR/Cas-based gene editing techniques to develop insect-resistant plants and also for targeting the insect pest/pathogens to reduce their destructive abilities has conversely been limited. CRISPR-enabled tools have increasingly advanced their ability and versatility to target multiple genes and to modify specific traits within the insect genome. The major focus on the design of sophisticated techniques for vector delivery includes binary vectors to assist in precise genome editing in insect pests. It provides an excellent platform for addressing several environmental problems and public health concerns in sustainable way (Gantz and Akbari 2018). An interesting feature of insect pest management via genome engineering has significant benefits of altering both plants and insect genomes. Innovative investigations are being performed to modify plant genomes for enhancing their capability to limit insect pests from feeding on plants and disarmed insects to avert their attack (Tyagi et al. 2020). Kandul et al. (2019) reported a precision guided sterile insect technique (pgSIT) based on CRISPR/Cas9 mediated genome editing in Drosophila. The sterile insect technique (SIT) is an ecologically secure and well-established approach to repress insect populations. Multiple pgSIT systems were engineered efficiently in Drosophila to constantly produce 100% sterile male population. This model population of pgSIT was competitive and offered great ability to suppress disease vectors and insect pests (Kandul et al. 2019). Another pest management strategy induced via CRISPR/Cas9 technology was demonstrated by Gui et al. (2020) to study the biology of Colorado potato beetle (CPB), Leptinotarsa decemlineata, an important pest of Solanaceae family, including potatoes. CRISPR/Cas9 induced mutagenesis of vestigial gene (vest) developed wingless adults of CPB with no elytron formed. This study provides an excellent way forward to control the CPB in environmentally safe manner (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. 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. Likewise, Orco (olfactory receptor coreceptor) gene was disrupted in Spodoptera litura, which resulted in impaired selection ability of host plant and distraction of insect from finding a mating partner (Koutroumpa et al. 2016). 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. A CRISPR/Cas9 based genome editing in H. armigera was conducted to knock-down CYP6AE gene cluster, which led to detoxification of these harmful chemicals (Wang et al. 2018a). Taken together, such techniques of insect pest management have great potential to deter the insect from crops and avoid yield loss.

Genome editing in plants for insect pest management

Editing plants against multiple fungal, viral, and bacterial diseases has been successful in several agricultural crops (Vats et al. 2019). However, genome editing in plants for insect pest management has been comparatively less explored. Here, we discuss some key examples of targeting plant genes via CRISPR-based editing for insect management and highlight the possibilities of potential plant defenses that can be engineered for editing-based crop protection. In some instances, insect behavior, immunity, and even development depend on vital chemical substances (VOCs, secondary metabolites, etc.) produced and secreted by the plants. This has been successfully reported in rice by mutating the CYP71A1 gene through CRISPR/Cas9 nucleases. This 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).

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 VOCs contain a mixture of volatiles, among which only some are detected by insects as cues for selection of hosts and oviposition site. Recent study demonstrates that a particular volatile blend can be utilized as a kairomone-mediated lure to attract the predator Nesidiocrosis tenuis, for the biological control of major tomato pest Tuta absoluta (Meyrick) and Trialeurodes vaporariorum (Westwood) (Ayelo et al. 2021). Modifications of plant volatile blends via genome editing can serve as an effective strategy for insect pest management. That said, utmost care needs to be taken to ensure that the manipulation of volatile blends do not cause deleterious impact on beneficial insect/natural enemy population.

Plant morphological features play an important role in the ability of insect pests to recognize and damage a particular host. For instance, modification in pigmentation of plants...
has been found to alter insect host preferences. This phenomenon was demonstrated in a study by Malone et al. (2009), in which 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. littura*, thereby confirming the significance of leaf color on host recognition in insect pests. 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.

The CWRs have a wide range of pest resistance traits but lack desired agronomic traits such as high yield, fruit/grain size, preferable plant structure, among others (Bohra et al. 2021). For example, the wild tomato *Solanum pimpinellifolium* has been reported to be resistant to a wide range of arthropod pests including spider mites (Rakha et al. 2017). Multiplex CRISPR/Cas9 editing of six different genes in *S. pimpinellifolium* resulted in high yielding tomato lines with additional resilience properties from wild tomato, in a single generation (Zsögön et al. 2018). Based on the characteristics and molecular processes underpinning the target organism, this technique can be meticulously applied to different CWRs. Notably, de novo domestication of CWRs can be a game-changing method for the development of crops with improved insect pest management features.

**Conclusion and future perspectives**

Recent advances in molecular breeding of major crops such as rice, maize, and wheat, have resulted in better yield, good quality, and biotic and abiotic stress resistance. Major emphasis should now be given to develop improved crop varieties that hold the best genotypic combinations and also contain broad-spectrum resistance to both insect pests and diseases. Importantly, the role of microbiomes (for instance, bacteria, fungi, endophytes, floral microbes, etc.) on plant resistance to insect pests can also be explored. On-going developments in plant genetics and biotechnology provide exciting possibilities for the control of pest populations in an environment-friendly manner. Stacking of multiple genes has increased the protection power against multiple harmful organisms, and has the added advantage of durability and reduced risk of emergence of new herbivore resistance. Insect resistance to transgenic crops can be delayed using strategies such as refuge crops, and high toxin expression, among others.

The use of modern genomic breeding technologies offer enormous potential to design insect resistant crops for the future. For instance, adoption of genomic selection, and haplotype-based breeding strategies will facilitate the assembly of superior haplotype combinations of insect resistance alleles in elite cultivars, thereby enabling informed decision-making in breeding programs (Bohra et al. 2020). Genetically modified crops are also being adopted in several countries but special attention should be given to food safety and resistance management. Local systems, their constraints and socio-economic implications should be strictly considered before the adoption of such genetically modified materials. Importantly, there is a growing need to pursue management strategies that reflect the pest biology, plant–insect interactions, and their effect on the natural enemies to prolong the usefulness of the resistant crops.

**Author contribution statement** SHW and RKV conceived the idea and coordinated writing the article. SHW, MC, RB searched literature and made substantial contribution in writing of the article. PKB, KS, AR, JJ and MNB contributed to writing special sections. All authors read and approved the manuscript.

**Funding** Open Access funding enabled and organized by CAUL and its Member Institutions. RKV is thankful to International Atomic Energy Agency (IAEA), Bill & Melinda Gates Foundation for supporting research and to Science & Engineering Research Board (SERB) of Department of Science & Technology (DST), Government of India for providing the J C Bose National Fellowship (SB/S9/Z-13/2019). RB acknowledges funding support from the Council of Scientific and Industrial Research (CSIR), Government of India, for the award of a research fellowship.

**Availability of data and material** Not applicable.

**Declarations**

**Conflict of interest** The authors declare that they have no conflict of interest.

**Code availability** Not applicable.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

**References**

Aartsma Y, Bianchi FJJ, van der Werf W, Poelman EH, Dicke M (2017) Herbivore-induced plant volatiles and tritrophic interactions across spatial scales. New Phytol 216:1054–1063
Akanksha S, Lakshmi VJ, Singh AK, Deepthi Y, Chirutkar PM, Balkrishnan RD, Sarla N, Mangruthia SK, Ram T (2019) Genetics of novel brown planthopper Nilaparvata lugens (Stål) resistance genes in derived introgression lines from the interspecific cross O. sativa var. Swarna × O. nivara. J Genet 98:113

Akhtar MW, Sengupta D, Chowdhury A (2009) Impact of pesticides use in agriculture: their benefits and hazards. Interdiscip Toxicol 2:1–12

Alborn HT, Hansen TV, Jones TH, Bennett DC, Tumlinson JH, Schmizl EA, Teal PEA (2007) Disulfoxoxy fatty acids from the American bird grasshopper Schistocerca americana, elicitors of plant volatiles. Proc Natl Acad Sci USA 104:12976–12981

Aljboroy Z, Chen M-S (2018) Indirect plant defense against insect herbivores: a review. Insect Sci 25:2–23

Alseekh S, Perez de Souza L, Benina M, Fernie AR (2020) The style genes in derived introgression lines from the interspecific cross of novel brown planthopper Schistocerca americana, elicitors of plant plant resistance in two populations of doubled haploid lines in maize (Zea mays L.). J Econ Entomol 111:435–444

Bohra A, Jha UC, Godwin ID, Varshney RK (2020) Genomic interventional for sustainable agriculture. Plant Biotechnol J 18:2388–2405

Bohra A, Kilian B, Sivasankar S, Caccamo M, Mba C, McCouch SR, Varshney RK (2021) Reap the crop wild relatives for breeding future crops. Trends Biotechnol. https://doi.org/10.1016/j.tibte.2021.08.009

Bonaventure G, VanDoorn A, Baldwin IT (2011) Herbivore-associated elicitors: FAC signaling and metabolism. Trends Plant Sci 16:294–299

Boukar O, Abberton M, Oyatomi O, Togola A, Tripathi L, Fatokun C (2020) Introgroom breeding in cowpea [Vigna unguiculata (L.) Walp.]. Front Plant Sci 11:567425

Bradshaw C, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Morgane B, Salles J, Simard F, Couchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. Nat Commun 7:12986. https://doi.org/10.1038/ncomms12986

Brière A, Simić D, Jambrović A, Zdunić Z, Ledenčan T, Rasupid E, BrnMJ, Brički, M, Brički, J, Mazur M, Galic V (2020) QTL analysis of Western corn rootworm resistance traits in maize IBM population grown in continuous maize. Genetika 52:137–148

Cameron JW, Anderson LD (1966) Husk tightness, earworm egg numbers, and starchiness of kernels in relation to resistance of corn to the corn earworm. J Econ Entomol 59:556–558

Castro-Alvarez FF, William M, Bergvinson DJ, García-Lara S (2015) Genetic mapping of QTL for maize weevil resistance in a RIL population of tropical maize. Theor Appl Genet 128:411–419

Chang X, Wang F, Fang Q, Chen F, Yao H, Gatehouse AMR, Ye G (2021) Virus-induced plant volatiles mediate the olfactory behaviour of its insect vectors. Plant Cell Environ. https://doi.org/10.1111/pce.14069

Correa JI, Maciel OVB, Bückner-Neto L, Pilati L, Morozini AM, Faria MV, Da-Silva PR (2020) A comprehensive analysis of wheat resistance to Rhopalosipham padi (Hemiptera: Aphididae) in Brazilian wheat cultivars. J Econ Entomol 113:1493–1503

Dicke M, Lucas-Barbosa D (2020) Herbivore-induced plant volatiles as a source of information in plant–insect networks. In: Pichersky E, Dudareva N (eds) Biology of plant volatiles. CRC Press, Cham, pp 327–346

Duan CX, Su N, Cheng ZJ, Lei CL, Wang JL, Zhai HQ, Wan JM (2010) QTL analysis for the resistance to small brown planthopper (Laodelphax striatellus Fallen) in rice using backcross inbred lines. Plant Breed 129:63–67

Eichenseer H, Matthews MC, Bi JL, Murphy JB, Felton GW (1999) Salivary glucose oxidase: multifunctional roles for Helicoverpa armigera (Hübner) resistance component traits in chickpea (Cicer arietinum L.). Plant Genome 14:e20071

Betsiashvili M, Ahern KR, Jander G (2015) Additive effects of two quantitative trait loci that confer Rhopalosipham maidis (corn leaf aphid) resistance in maize inbred line Mo17. J Exp Bot 66:571–578

Bohn MO, Marroquin JJ, Flint-Garcia S, Dashiel K, Willmot DB, Hibbard BE (2018) Quantitative trait loci mapping of western corn rootworm (Coleoptera: Chrysomelidae) host plant resistance in two populations of doubled haploid lines in maize (Zea mays L.). J Econ Entomol 111:435–444

Varshney RK (2021) Reap the crop wild relatives for breeding future crops. Trends Biotechnol. https://doi.org/10.1016/j.tibtech.2021.08.009

Bonaventure G, VanDoorn A, Baldwin IT (2011) Herbivore-associated elicitors: FAC signaling and metabolism. Trends Plant Sci 16:294–299

Boukar O, Abberton M, Oyatomi O, Togola A, Tripathi L, Fatokun C (2020) Introgroom breeding in cowpea [Vigna unguiculata (L.) Walp.]. Front Plant Sci 11:567425

Bohra A, Kilian B, Sivasankar S, Caccamo M, Mba C, McCouch SR, Varshney RK (2021) Reap the crop wild relatives for breeding future crops. Trends Biotechnol. https://doi.org/10.1016/j.tibtech.2021.08.009

Bonaventure G, VanDoorn A, Baldwin IT (2011) Herbivore-associated elicitors: FAC signaling and metabolism. Trends Plant Sci 16:294–299

Boukar O, Abberton M, Oyatomi O, Togola A, Tripathi L, Fatokun C (2020) Introgroom breeding in cowpea [Vigna unguiculata (L.) Walp.]. Front Plant Sci 11:567425

Bohra A, Jha UC, Godwin ID, Varshney RK (2020) Genomic interventions for sustainable agriculture. Plant Biotechnol J 18:2388–2405

Bohra A, Kilian B, Sivasankar S, Caccamo M, Mba C, McCouch SR, Varshney RK (2021) Reap the crop wild relatives for breeding future crops. Trends Biotechnol. https://doi.org/10.1016/j.tibtech.2021.08.009

Bonaventure G, VanDoorn A, Baldwin IT (2011) Herbivore-associated elicitors: FAC signaling and metabolism. Trends Plant Sci 16:294–299
Esch L, Schaffrath U (2017) An update on jacalin-likelectins and their role in plant defense. Int J Mol Sci 18:1592

Filgueiras CC, Willett DS, Pereira RV, Moino Junior A, Pareja M, Dun- can LW (2016) Eliciting maize defense pathways: overhead ground versus infrared ground biocontrol agents. Sci Rep 6:36484

Filgueiras CC, Martins AD, Pereira RV, Willett DS (2019) The ecology of salicylic acid signaling: primary, secondary and tertiary effects with applications in agriculture. Int J Mol Sci 20:8581

Gantz VM, Akbari OS (2018) Gene editing technologies and applications for insects.Curr Opin Insect Sci 28:66–72

Gorty S, Narasu L, Gaddameedi A, Sharma HC, Kotla A, Deshpande SP, Arc AK (2017) Introduction of flowering time (Atherigona soccata L. Moench) resistance QTLs into elite post-rainy season sorghum varieties using marker assisted backcrossing (MABC). Front Plant Sci 8:1494

Gui S, Taning CNT, Wei D, Smagghe G (2020) First report on CRISPR/Cas9-targeted mutagenesis in the Colorado potato beetle. Leptinotarsa Decemlineata. J Insect Physiol 121:104013

Gupta M, Kumar H, Kaur S (2021) Vegetative insecticidal protein (Vip): A potential contender from Bacillus thuringiensis for efficient management of various detrimental agricultural pests. Front Microbiol 12:659736

Hao Y, Cambrons E, Chen Z, Wang Y, Bland DE, Buntin GD, Johnson JW (2013) Characterization of new loci for Hessian fly resistance in common wheat. Theor Appl Genet 126:1067–1076

Hartley SE, Fitt RN, McLarnon EL, Wade RN (2015) Defending the leaf surface: intra and inter-specific differences in silicon deposition in grasses in response to damage and silicon supply. Front Plant Sci 6:35

He J, Liu Y, Liu Y, Jiang L, Wu H, Kang H, Liu S, Chen L, Liu X, Cheng X, Wan J (2013) High-resolution mapping of brown planthopper (BPH) resistance gene Bph27(t) in rice (Oryzasativa L.). Mol Breed 31:549–557

Hessdal DA (2014) Deciphering the genetic architecture of native resistance and tolerance to western corn rootworm larval feeding. Graduate theses and dissertations. Paper 13874

Himabindu K, Sunetha K, Sama VSAK, Bentur JS (2010) A new rice gall midge resistance gene in the breeding line CR57-MR1523, mapping with flanking markers and development of NILs. Euphytica 174:179–187

Hong MG, Kim KH, Ku JH, Jeong JK, Seo MJ, Park CH, Kim YH, Kim HS, Kim YK, Baek SH, Kim DY (2015) Inheritance and quantitative trait loci analysis of resistance genes to bruchid and bean bug in mungbean (Vigna radiata L. Wilczek). Plant Breed Biotechnol 3:39–46

Hu J, Xiao C, Cheng MG, Gao GJ, Zhang QL, He YQ (2015a) A new finely mapped Oryza australiensis derived QTL in rice confers resistance to brown planthopper. Gene 561:132–137

Hu J, Xiao C, Cheng MG, Gao G, Zhang Q, He YQ (2015b) Fine mapping and pyramiding of brown planthopper resistance genes QBph3 and QBph4 in an introgression line from wild rice O. officinalis. Mol Breeding 35:3

Hu J, Chang X, Zou L, Tang W, Wu W (2018) Identification and fine mapping of Bph33, a new brown planthopper resistance gene in rice (Oryza sativa L.). Rice 11:55

Huang D, Qiu Y, Zhang Y, Huang F, Meng J, Wei S, Li R, Chen B (2013) Fine mapping and characterization of BPH27, a brown planthopper resistance gene from wild rice (Oryza rufipogon Griff.). Theor Appl Genet 126:219–229

Huynh BL, Ehlers JD, Ndeve A, Wanamaker S, Lucas MR, Close TJ, Roberts PA (2015) Genetic mapping and legume synteny of aphid resistance in African cowpea (Vigna unguiculata L. Walp.) grown in California. Mol Breeding 35:1–9

Jaba J, Hasena B, Tripathy S, Hosamani AC, Amareys YS (2010) Olfactory response of cowpea aphid, Aphis craccivora Koch, to host odours and population of conspecifics. J Biopestic 3:405–407

Jaba J, Bhaskar H, Ranjith AM (2013) Behavioural response of Cheilomenes sexmaculata (Fabricius) to natural enemy and pest mediated semiochemicals. J Biol Cont 21:58–60

Jaganathan D, Bohra A, Thudi M, Varshney RK (2020) Fine mapping and gene cloning in the post-NGS era: advances and prospects. Theor Appl Genet 133:1791–1810

Jairin J, Sansen K, Wongboon W, Kothcharer T (2010) Detection of a brown planthopper resistance gene bph4 at the same chromosomal position of Bph3 using two different genetic backgrounds of rice. Breed Sci 60:71–75

Jiménez-Galindo JC, Ordás B, Buttrón A, Samayoa LF, Malvar RA (2017) QTL mapping for yield and resistance against Mediterranean corn borer in maize. Front Plant Sci 8:698

Jun TH, Mian MR, Michel AP (2013) Genetic mapping of three quantitative trait loci for soybean aphid resistance in PI 567324. Heredity 111:16–22

Kandul NP, Liu J, Wu SL, Marshall JM, Akbari OS (2019) Transforming insect population control with precision guided sterile males with demonstration in flies. Nat Commun 10:1–12

Karban R, Baldwin IT (1997) Induced responses to herbivory. University of Chicago Press, Chicago

Khan A, Garg V, Roorkiwal M, Golicz AA, Edwards D, Varshney RK (2020) Super-pangenome by integrating the wild side of a species for accelerated crop improvement. Trends Plant Sci 25:148–158

Kim KS, Bellendir S, Hudson KA, Hill CB, Hartman GL, Hyten DL, Hudson ME, Diers BW (2010a) Fine mapping the soybean aphid resistance gene Rag1 in soybean. Theor Appl Genet 120:1063–1071

Kim KS, Hill CB, Hartman GL, Hyten DL, Hudson ME, Diers BW (2010b) Fine mapping of the soybean aphid-resistance gene Rag2 in soybean PI 200538. Theor Appl Genet 121:599–610

Kirman, RN, KNSU, Kishor PKB, Hash CT, Deshpande SP (2015) Evaluation of QTLs for shoot fly (Atherigona soccata) resistance component traits of seedling leaf blade glossiness and trichome density on sorghum (Sorghum bicolor) chromosome SBI-10L. Trop Plant Biol 9:12–28

Koutroupa FA, Monsempees C, François MC, De Cian A, Royer C, Concordet JP, Jacquin-Joly E (2016) Heritable genome editing with CRISPR/Cas9 induces anoxia in a crop pest moth. Sci Rep 6:29620

Kumar A, Jain A, Sahu RK, Shrivastava MN, Nair S, Mohan M (2005) Genetic analysis of resistance genes for the rice gall midge in two rice genotypes. Crop Sci 45:1631–1635

Kumar K, Sarao PS, Bhatia D, Kumar N, Kaur A, Mangat GS, Brar DS, Singh K (2018) High-resolution genetic mapping of a novel brown plant insect resistance locus, Bph34 in Oryza sativa L. x Oryza nivara (Sharma & Shastri) derived interspecific F2 population. Theor Appl Genet 131:1163–1171

Kusi F, Nboyine JA, Abudulai M, Seidu A, Agyare YR, Sugri I, Zakaria M, Owusu RK, Ntsugah SK, Asamoah L (2019) Cultivar and insecticide spraying time effects on cowpea insect pests and grain yield in northern Ghana. Ann Agric Sci 64:121–127

Larsson MC, Domingos AI, Jones WD, Chiappe ME, Amrein H, Voßshall LB (2004) Or83b encodes a broadly expressed odorant receptor essential for Drosophila olfaction. Nature 427:703–714

Lee JS, Yoo MH, Jung JK, Bilyeu KD, Lee JD, Kang S (2015) Detection of novel QTLs for foxglove aphid resistance in soybean. Theor Appl Genet 128:1481–1488

Leeagul P, Kongsa K, Vejchasarn P, Darwell K, Phansawee Y, Suthanthangjai A, Uparang C, Kawichai R, Boonsanga K, Chamarek V, Jairin JS (2020) Genetic diversity of Asian rice gall midge based on mtCOI gene sequences and identification of...
apath (Diuraphis noxia) in wheat (Triticum aestivum L.). Crop Past Sci 61:970–977

Salerno G, De Santis F, Iacovone A, Bin F, Conti E (2013) Short-range cues mediate parasitoid searching behavior on maize: the role of oviposition-induced plant synomones. Biol Control 64:247–254

Sama VSAK, Himabindu K, Naik SB, Sundaram RM, Viraktamath BC, Bentur JS (2012) Mapping and MAS breeding of an allelic gene to the GmB spot resistance to Asian rice gall midge. Euphytica 187:393–400

Sama VSAK, Rawat N, Sundaram RM, Himabindu K, Naik BS, Sundaram RM, Viraktamath BC, Bentur JS (2014) A putative candidate for the recessive gall midge resistance gene gmr3 in rice identified and validated. Theor Appl Genet 127:113–124

Samayo LA, Malvar RA, McMullen MD, Battrón A (2015) Identification of QTL for resistance to Mediterranean corn borer in a maize tropical line to improve temperate germplasm. BMC Plant Biol 15:1

Sánchez H, Morquecho-Contreras A (2017) Chemical plant defense against herbivores. In: Shields VDC (ed) Herbivores. Cham, IntechOpen. https://doi.org/10.5772/67346

Shabanimoofrad M, Rafii MY, Ashkani S, Hanafi MM, Adam NA, Harun AR, Latif MA, Miah G, Sahebi M, Azizi P (2017) Mapping of QTLs conferring resistance in rice to brown planthopper, Nilapavarta lugens. Entomol Exp Appl 162:50–68

Shen L, Wang C, Fu Y, Wang J, Liu Q, Zhang X, Yan C, Qian Q, Wang K (2018) QTL editing confers opposing yield performance in different rice varieties. J Integr Plant Biol 60:89–90

Shinya T, Hojo Y, Desaki Y, Christeller JT, Okada K, Shibuya N, Galis I (2016) Modulation of plant defense responses to herbivores by simultaneous recognition of different herbivore-associated elicitors in rice. Sci Rep 6:32537

Shrivastava MN, Kumar A, Bhandarkar S, Shukla BC, Agrawal KC (2003) A new gene for resistance in rice to Asian rice gall midge (Orseolia oryzic Wood Mason) biotype 1 population at Raipur, India. Euphytica 130:143–145

Silva NCM, Conceição JG, Ventury KE, De Sá LFR, Oliveira EAJ, Santos IS, Gomes VM, Costa MN, Ferreira ATS, Perales J, Xavier-Filho J, Fernandes KVS, Oliveira AEIA (2018) Soybean seed coat chitinase as a defense protein against the stored product pest Callosobruchus maculatus. Pest Manag Sci 74:1449–1456

Sobda G, Boukar O, Tongoona PB, Ayertz J, Oiffe KS (2017) Quantitative trait loci (QTL) for cowpea resistance to flour bud thrips (Megalurothrips soshi) Trybom). Int J Plant Breed Genet Sci 74:292–299

Tamhane VA, Sant SS, Jadhav AR, War AR, Sharma HC, Jaleel A, Kashkar AS (2021) Label-free quantitative proteomics of Sorghum bicolor reveals the proteins strengthening plant defense against insect pest Chilo partellus. Proteome Chem 19:6

Tamiru A, Paliwal R, Manthi SJ, Odeny DA, Midega CAO, Khan ZR, Pickett J, Bruce TJ (2020) Genome wide association analysis of a stemborer egg induced “call-for-help” defense trait in maize. Sci Rep 10:11205

Tamura Y, Hattori M, Yoshioka H, Yoshioka M, Takahashi A, Wu J, Sentoku N, Yasui M (2014) Map-based cloning and characterization of a brown planthopper resistance gene BPH29 from Oryza sativa L. CYP6AE Y (2018a) Identification of quantitative trait loci associated elicitors in rice. J Integr Plant Biol 60:89–90

Tan C, Carver BF, Chen MS, Gu YQ, Yan L (2013) Genetic association of OPR genes with resistance to Hessian fly in hexaploid wheat. BMC Genom 14:1

Thaler JS, Humphrey PT, Whitman NK (2012) Evolution of jasmonate and salicylate signal crosstalk. Trends Plant Sci 17:260–270

Thein HW, Yamagata Y, Mai TV, Yasui H (2019) Four resistance alleles derived from Oryza longistaminata (A. Chev. & Roehrich) against green rice leaffhopper, Nephotettix cincticeps (Uhler) identified using novel introgression lines. Breed Sci 69:573–584

Togola A, Boukar O, Servent A, Chamartthi S, Tamo M, Fatokun C (2020) Identification of sources of resistance in cowpea mini core accessions to Aphis craccivora (Homoptera: Aphiidae) and their biochemical characterization. Euphytica 216:1–15

Tuyen LQ, Liu Y, Jiang L, Wang B, Wang Q, Hanh TT, Wan J (2012) Identification of quantitative trait loci associated with small brown planthopper (Laodelphax striatellus Fallén) resistance in rice (Oryza sativa L.). Hereditas 149:16–23

Tyagi S, Kesiraju K, Saakre M, Rathinam M, Raman V, Pattanayak D, Sreevaths R (2020) Genome editing for resistance to insects: an emerging tool for crop improvement. ACS Omega 5:20674–20683

Van Mai T, Fujita D, Matsumura M, Yoshimura A, Yasui H (2015) Genetic basis of multiple resistance to the brown planthopper (Nilapavarta lugens Stål) and the green rice leaffhopper (Nephrotettix cincticeps Uhler) in the rice cultivar ‘ASD7’ (Oryza sativa L. ssp. indica). Breed Sci 65:420

Varshney RK, Pandey MK, Bohra A, Singh VK, Thudi M, Saxena RK (2019) Toward the sequence-based breeding in legumes in the post-genome sequencing era. Theor Appl Genet 132:797–816

Varshney RK, Bohra A, Yu J, Graner A, Zhang Q, Sorrells ME (2021a) Designing future crops: genomics-assisted breeding comes of age. Trends Plant Sci 26:631–649

Varshney RK, Rooikwal M, Sun S, Bajaj P, Chitikineni A, Thudi M, Singh NP, Du X, Upadhyaya HD, Khan AW, Wang Y, Garg V, Fan G, Cowling WA, Crossa J, Gentzibettl L, Voss-Fels KP, Valluri VK, Sinha P, Singh VK, Ben C, Rathore A, Punna R, Singh MK, Tar’an B, Bharadwaj C, Yasin M, Pithia MS, Singh S, Soren Kr, Kudapa H, Jarquin D, Cubby P, Hickey LT, Dixit GP, Thuillet AC, Hamwiah A, Kumar S, Desokar AA, Chaturvedi SK, Francis A, Howard R, Chattopadhyay D, Edwards D, Lyons E, Vigoiroux Y, Hayes BJ, von Wettberg E, Datta SK, Yang H, Nguyen HT, Wang J, Siddique KHM, Mohapatra T, Bennetzen JL, Xu X, Liu X (2021b) A chickpea genetic variation map based on the sequencing of 3,366 genomes. Nature. https://doi.org/10.1038/s41586-021-04066-1

Varshney RK, Teraiuchi R, McCouch SR (2014) Harvesting the promising fruits of genomics: applying genome sequencing technologies to crop breeding. PLoS Biol 12:e1001883

Vats S, Kumawat S, Kumar V, Patil GB, Joshi T, Sonah H, Sharma TR, Deshmukh R (2019) Genome editing in plants: exploration of technological advancements and challenges. Cells 8:1386

Venkataramana PB, Gowda R, Somma P, Ramesh S, Rao AM, Bhanu Prakash K, Srinives P, Gireesh C, Pramila CK (2016) Mapping of quantitative trait loci (QTLs) for resistances to small brown planthopper and rice stripe virus in rice using recombinant inbred lines. Intl J Plant Breed Genet 10:1135–147

Wang Q, Liu Y, Hu J, Zhang Y, Xie K, Wang B, Tuyen LQ, Song Z, Wu H, Liu Y, Jiang L (2013) Detection of quantitative trait loci (QTLs) for resistances to small brown planthopper and rice stripe virus in rice using recombinant inbred lines. Int J Mol Sci 14:8406–8421

Wang Y, Cao L, Zhang Y, Cao L, Fu H, Huang F, Qiu Y, Li R, Lou X (2015) Map-based cloning and characterization of BPH29, a B3 domain-containing recessive gene conferring brown planthopper resistance in rice. J Exp Bot 66:6035–6045

Wang H, Shi Y, Wang L, Liu S, Wu Y, Yang Y, Feyereisen R, Wang Y (2018a) CYP6AE gene cluster knockout in Helicoverpa armigera reveals role in detoxification of phytocarcinogens and insecticides. Nat Commun 9:4820

Wang H, Shi S, Guo Q, Nie L, Du B, Chen R, Zhu L, He G (2018b) High-resolution mapping of a gene conferring strong antibiosis to brown planthopper and developing resistant near-isogenic lines in 9311 background. Mol Breed 38:107

Wang J, Wu D, Wang Y, Xie D (2019) Jasmonate action in plant defense against insects. J Exp Bot 70:3391–3400
Wang W, Yu Z, Meng J, Zhou P, Luo T, Zhang J, Wu J, Lou Y (2020) Rice phenolamindes reduce the survival of female adults of the white-backed planthopper *Sogatella furcifera*. Sci Rep 10:5778

War AR, Paulraj MG, Ahmad T, Buhroo AA, Hussain B, Ignacimuthu S, Sharma HC (2012) Mechanisms of plant defense against insect herbivores. Plant Signal Behav 7:1306–1320

Wiseman BR, Davis FM (1990) Plant-resistance to insects attacking corn and grain-sorghum. Fla Entomol 73:446–458

Wu H, Liu Y, He J, Liu Y, Jiang L, Liu L, Wang C, Cheng X, Wan J (2014) Fine mapping of brown planthopper (*Nilaparvata lugens* Stål) resistance gene *Bph28(t)* in rice (*Oryza sativa* L.). Mol Breed 33:909–918

Xiao L, Zhong YP, Wang B, Wu TL (2014) Mapping an aphid resistance gene in soybean (*Glycine max* (L.) Merr.) P746. Genet Mol Res 13:9152–9160

Xiu C, Dai W, Pan H, Zhang W, Luo S, Wyckhuys KAG, Yang Y, Lu Y (2019) Herbivore-induced plant volatiles enhance field-level parasitism of the mirid bug *Apolygus lucorum*. Biol Control 135:41–47

Yang M, Cheng L, Yan L, Shu W, Wang X, Qiu Y (2019) Mapping and characterization of a quantitative trait locus resistance to the brown planthopper in the rice variety IR64. Hereditas 156:22

Yang M, Lin J, Cheng L, Zhou H, Chen S, Liu F, Li R, Qiu Y (2020) Identification of a novel planthopper resistance gene from wild rice (*Oryza rufipogon* Griff.). Crop J 8:1057–1070

Yang Y, Xu J, Leng Y, Xiong G, Hu J, Zhang G, Huang L, Wang L, Guo L, Li J, Chen F, Qian Q, Zeng D (2014) Quantitative trait loci identification, fine mapping and gene expression profiling for ovicidal response to whitebacked planthopper (*Sogatella furcifera* Horvath) in rice (*Oryza sativa* L.). BMC Plant Biol 14:145

Yao N, Lee CR, Semagn K, Sow M, Nwilene F, Kolade O, Bocco R, Oyetunji O, Mitchell-Olds T, Ndjiondjop MN (2016) QTL mapping in three rice populations uncovers major genomic regions associated with African rice gall midge resistance. PLoS ONE 11:e0160749

Ye M, Glauser G, Lou Y, Ehr M, Hu L (2019) Molecular dissection of early defense signaling underlying volatile-mediated defense regulation and herbivore resistance in rice. Plant Cell 31:687–698

Yuexiong Z, Gang Q, Qianqian M, Minyi W, Xinghai Y, Zengfeng M, Haifu L, Chi L, Zhenjing L, Fang L, Dahui R, Rongbai L (2020) Identification of major locus *Bph35* resistance to brown plant hopper in rice. Rice Sci 27:237–245

Zhang G, Gu C, Wang D (2010) A novel locus for soybean aphid resistance. Theor Appl Genet 120:1183–1191

Zhang J, Li W, Zhang L, Dai H, Ci D, Xu R (2013) QTL mapping of soybean resistance to whitefly (*Bemisia tabaci* Gennadius) under multi-environment conditions. Aust J Crop Sci 7:1212

Zhang S, Zhang Z, Bales C, Gu C, DiFonzo C, Li M, Song Q, Cregan P, Yang Z, Wang D (2017) Mapping novel aphid resistance QTL from wild soybean, *Glycine soja* 85–32. Theor Appl Genet 130:1941–1952

Zhao H, Ullah H, McNeill MR, Du G, Hao K, Tu X, Zhang Z (2019) Inhibitory effects of plant trypsin inhibitors Msti-94 and Msti-16 on *Therioaphis trifolii* (Monell) (Homoptera: Aphididae) in *Alfalfa*. Insects 10:154

Zhao L, Abdelsalam NR, Xu Y, Chen MS, Feng Y, Kong L, Bai G (2020) Identification of two novel Hessian fly resistance genes *H35* and *H36* in a hard winter wheat line SD06165. Theor Appl Genet 133:2343–2353

Zhu H, Li C, Gao C (2020) Applications of CRISPR-Cas in agriculture and plant biotechnology. Nat Rev Mol Biol 21:661–677

Zsögön A, Čermak T, Naves ER, Notini MM, Edel KH, Weinl S, Freischl L, Voytas DF, Kudla J, Peres LEP (2018) *De novo* domestication of wild tomato using genome editing. Nat Biotechnol 36:1211–1216

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.