Chapter 15
Challenges in Molecular Insect Resistance Studies for Crop Improvement

Amarjit S. Tanda and Ravneet Kaur

15.1 Introduction

Crop plants are always exposed to different biotic stresses including insect pests and diseases which suppress their growth and development. Insect herbivory mostly compromises host plant balance and growth, ultimately killing the plant. A number of plants with great economic value are attacked by many insect pests globally, causing big reduction in yields of billions of dollars (Cheng et al. 2013a; Satyabrata et al. 2021). Hypersensitive responses (HR), organized cell killing, tissue augmentation at the site of injury, and expression of defense-responsive genes are related to defensive mechanisms against insect pests (Cheng et al. 2013b). Insect attack results in oxygen burst inside the tissues discharging intermediate signal molecules, for instance, reactive oxygen species (ROS), superoxides (O_2^-), nitric oxide (NO), and hydrogen peroxide (H_2O_2) which in turn produces the defense reaction through activation. Many plant hormones like abscisic acid (ABA), salicylic acid (SA), jasmonic acid (JA), ethylene (ET), and gibberellins (GA) (Fig. 15.1) govern defense responses and regulate expression of several downstream target genes (Berens et al. 2017). In addition, calcium-reliant protein kinase (CDPK), cyclin-dependent protein kinase (CDK), and mitogen-stimulated protein kinase (MAPK) act as a significant factor of the defense signaling forces (Berens et al. 2017). Furthermore, plant defense reactions against insect herbivory can be more varied and may be engaged constitutively or transiently. Additionally, host plant defense responses against insects show temporal dynamics with some defense reactions being obtained within

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A. S. Tanda (✉)
School of Horticulture, University of Western Sydney, Richmond, NSW, Australia

R. Kaur
Department of Zoology, Post Graduate Govt. College for Girls, Chandigarh, India

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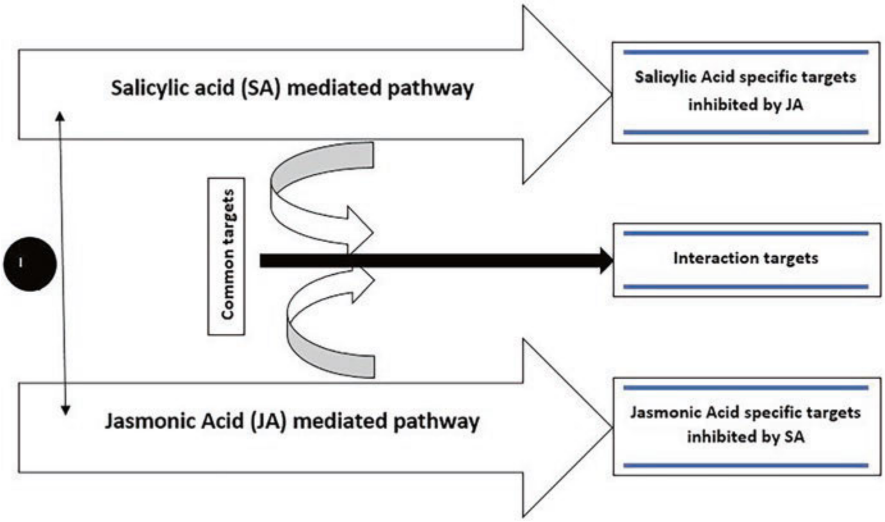

Fig. 15.1 Impact of phytohormones like jasmonic acid and salicylic acid on targets like herbivores

minutes of insect attack while others being exhibited later on (Fürstenberg-Hägg et al. 2013). Few years back, important progress has been made in comprehending insect pest defense methods, insect-resistant gene identification, and solving the molecular procedure of host-insect interaction in crops. All these defense plans used by plants are yet to be distinguished and classified depending on the elicitation nature. In this chapter, we have highlighted several plant defense reactions against insect attack and grouped them as per their defensive mechanism. Moreover, we offer a genetic and molecular mechanism description of insect resistance in detail and the implementation of multiple genomic bio-techniques for further improvement in insect resistance in the newly designed cultivars.

15.2 Host Plant Reactions to Insect Attack

The counter-defense reactions against insect herbivory can be of different nature such as integral, induced, direct, or indirect. Plants have developed multi-layered defense mechanisms to prevent insect damage. This diverse defense structure shows preventive procedures beginning with physical barriers to phyto-metabolites including inducible/adaptive defense structures. Sometimes, when the direct defense via secondary metabolites against the insects fails, plants hide substances that allure the scavengers of the insect herbivory (Erb and Reymond 2019). During this indirect defense, plants harbor the scavengers of pests to decrease the insect attack. A plant can be regarded as resistant, relying on modifying strategies for self-defense. When the physical and chemical responses of a host plant can alarm insects and subside

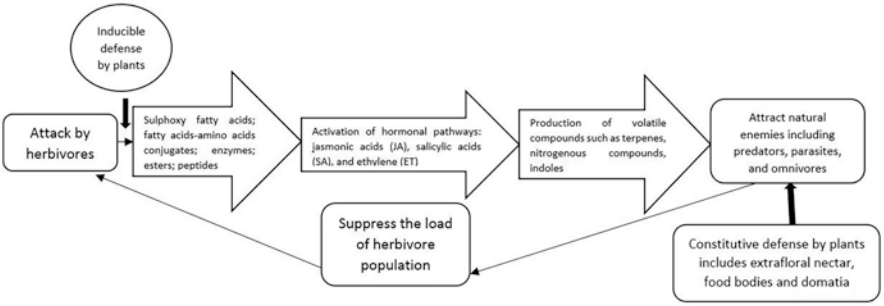

Fig. 15.2 Induced and constitutive defense by plants in response to herbivores attack and their neutralization by natural enemies

the damage caused by herbivory, it is considered to be resistant or tolerant (Fig. 15.2). The resistant crops try to discourage insect development and mostly foist strong selection pressure on the pest. Contrastingly, tolerant crops are helpless to deter the insects but can decrease the harmful effects of insect attack. Tolerant plants apply less selection pressure, and the growth and multiplication of the insects are undisputed. Insect attack, egg laying, and settlement can bring about many plant defense reactions, for example, building up or adapting physical barriers, release of antagonistic secondary substances, discharge of herbivore-induced plant volatiles (HIPVs), HR/ROS generation, defense gesturing, and exhibition of defense-associated genes. In addition, the briefing of plant defense against insects eases fast activation of defense responses (Blenn et al. 2012). Consequently, plants react to insect herbivory by starting any one kind or a cocktail of the procedures to reduce insect attack.

15.3 Insect Attack and Physical Plant Defenses

To prevent the insects of various nourishing guilds, crops have evolved modified structural characteristics, for example, trichomes, waxes, cuticle depositions, and spines, that act as physical barriers against insect attack and egg laying. The epicuticular wax layer inhibits insects to stay, feed, or oviposit on the leaves (Blenn et al. 2012). The wax production in the plant system differs from its natural traits under various insect-induced stresses. For instance, the egg laying of a cabbage white butterfly on *A. thaliana* activates the change in wax make-up by raising the concentration of tetratriacontanoic acid (C34) and decreasing tetracosanoic acid (C24) (Bricchi et al. 2012). This alteration in the wax composition allures the egg parasitoid wasps *Trichogramma brassicae*. Likewise, plants discourage insects by increasing the leaf and root rigidity. The strengthening of plant epidermis prohibits the feeding by herbivores. The roots' rigidity is built up mostly by the lignin polymer accumulation to discourage insect feeding. Additionally, accumulation of silica, suberin, callose, and cellulose culminates in cell wall bracing which limits herbivore attack. Crops also encourage extensive root regrowth under insect attack which encourages root density and number of roots. Adaptation of leaves to thorns and spines and trichomes also limit the crop from herbivory. Although thorns and spines prevent the bigger insects from attacking the plants, the trichomes stop the insect mobility and connection1. Glandular and non-glandular trichomes help in pest management, by reducing the plant taste and insect movement. The glandular trichomes in *N. attenuate* manufacture sufficient amounts of *O*-acyl sugars that indirectly encourage the larvae of *M. sexta* to liberate volatile metabolites, which results in alluring its predators (Cheng et al. 2013b). Likewise, in raspberries, the more leaf trichome density repulses and decreases egg laying by the mite *Tetranychus urticae* (Karley et al. 2016).

15.4 Host Plant Metabolites and Insect Damage

Numerous bioactive substances and secondary metabolites are manufactured by the plants which are antagonistic to herbivory. These metabolites not only minimize the insect attacks but also reduce the extent of insect damage and regulate subsequent plant defense systems. These secondary chemicals mainly help in direct defenses and, however, can also contribute in indirect defenses like dwelling the predators of the specific herbivory (Erb and Reymond 2019). Many plant-synthesized bioactive compounds work as toxins to insect pests and influence their digestive and nervous system, affecting development or death. Moreover, they control the taste, odor, and color of a host plant or its parts (Kessler et al. 2006). Almost in all plants, alkaloids are present and contribute to the defense mechanism against herbivory. Aphid attacks were limited in *Festuca arundinacea* due to the presence of pyrrolizidine alkaloids (PA) by the endophytic fungi *Acremonium coenophialum* (Johnson 2011). The PAs get converted to a toxic nature, as they access the alkaline digestive system of insects, empowering PAs as potent anti-feeders which generally debar aphids and other insects (Johnson 2011). Deglycosylation of 2-β-ᴅglucopyranosyloxy-4,7-dimethoxy-1, and 4-benzoxazin-3-one glucoside (HDMBOA-Glc) procreates HDMBOA, which limits damages by the moths *S. frugiperda* and *S. littoralis* (Glauser et al. 2011). Moreover, the glucosinolate derivatives, for example, the indole glucosinolate in *Arabidopsis*, give out more resistance to *M. persicae* (Erb and Reymond 2019). Plant terpenoids serve as toxins, insect repellents, and anti-feeders as a plant defense system. When these terpenoids are found as volatile compounds, resins and vital components of plant essential oils also influence the herbivory adversely. Several plant peptides and other chemicals assist in the plant defense system by damaging the insect digestion. Lectins, chitinases, and α-amylase inhibitors in plants work as anti-digestive proteins by impeding the digestion of the consumed plant or as anti-nutritive by interfering with the consumption of plant parts by the insects. Proteinase inhibitors (PIs) produced by the plants assist to impair the digestive process in the herbivory. Cysteine proteases and metalloproteinase are major enzymes available in *Hemiptera*, and suppression of these enzymes in the guts of insects can lead to mortality (Erb and Reymond 2019). Similarly, the plant α-amylase inhibitors (α-AI) chunk the αamylases of attacking insects, limiting their starch catabolism. The α-AIs were observed to hinder the mealworms in wheat, beetles, and wheat weevils from damaging the crop and cereals (Fürstenberg-Hägg et al. 2013). The heterologous expression of bean αamylase inhibitor1 in *Pisum sativum* established resistance against the weevil *Bruchus pisorum* (Morton et al. 2000). In addition, plants synthesize chitinase to neutralize insect attacks as chitin is a main compound in the exoskeleton of insects. The transgenic tomato lines having poplar chitinase found resistance to the beetle, *Leptinotarsa decemlineata*, by restricting their growth (Lawrence and Novak 2006). Likewise, polyphenol oxidase (PPO) enzymes also help in plant defense, regularly on mechanical damage or injury. During insect attack, the plant cell disruption produces PPOs which consecutively release ROS (Mahanil et al. 2008). In tomato, overexpression of PPO resulted in increased resistance to the moth *S. litura* by reducing its growth and enhancing its mortality rate (Mahanil et al. 2008). Numerous plants acquire laticifers and resin ducts which stock latex and resins. These ducts get punctured and the latex is discharged at the site of injury to hinder or to trap the herbivory during an attack. In addition, being sticky to entrap insects, the latex of few plants can also be lethal. The latex of *A. cannabinum* possesses phenolics, alkaloids, terpenoids, and PIs, which work as toxins or anti-feedants when ingested by herbivory (Erb and Reymond 2019).

15.5 Insect Pest Attack and Chemical Defense Mechanisms

Plants manufacture several metabolites, for example, the VOCs, food bodies, and nectars which allure, nurture, and accommodate the insect scavengers, thus encouraging insect's defense. VOCs are synthesized mainly in flowers and roots to entice crop pollinators (Tanda, 1983, 1984, 1985, 2019a, b, c, 2020, 2021a, b, c, d, e, f, g) and insect scavengers. About 30 volatile compounds, for example, sesquiterpenes, (*E*)-α-bergamotene, and other aromatic chemicals, were released by the attack of leaf-worm *S. littoralis* in maize (Erb and Reymond 2019). Oddly, the VOCs or HIPVs also help in intra- and inter-communication in crops and briefing the defense reactions against herbivory. The plants *Artemisia tridentata* and *N. attenuate* were found to share this behavior, where attacked *A. tridentata* plants produced VOCs provided chemical defense in *N. attenuate* (Kessler et al. 2006). Likewise, exposure of volatiles in the not-harmed leaves produced from injured leaves showed elevated defensive reactions against the moth *Lymantria dispar* (Maffei et al. 2012). Plants release food bodies (FBs) rich in nutrients to begin a mutualistic relation with other organisms which result in prevention against herbivory. The connections between *Piper fimbriatum* and *Pheidole bicornis* ants are mutualistic as the ants prevent the plant from many insects while nourishing on its FBs (Fischer et al. 2002). Several plants release nectars to allure pollinators, predators of insects and pests, and parasitoids which help greatly in indirect defense (Tanda, 2019a, b, c, 2020, 2021a, b, c, d, e, f, g; Erb and Reymond 2019). Nevertheless, nectars are manufactured by flowers; EFNs are released and put down on shoots and leaves of plants. The production and secretion of these EFNs enhance when the plant is attacked by herbivory. Gall formation was inhibited on excised roots of okra by co-culturing with sesame. Sesame callus reduced penetration, discouraged nematode build-up in okra, and caused an increase in numbers of males showing antagonism of sesame to root-knot nematode on okra (Tanda and Atwal 1988; Tanda et al. 1988, 1989).

15.6 Intrinsic Physiological Processes and Response to Herbivory

Apace with structural and chemical defense mechanisms, crop plants depend on several intrinsic physiological procedures like identification of insect effectors, ion flux gradients across the plasma membrane, Ca^{2+} burst, ROS generation, or oxidative burst and gesturing cascades for acumen and reaction to insects. This signaling afterwards influences the deposition of plant hormones, defense genes expression, biosynthesis of phytohormone genes, and plant hormone-controlled genes (Blenn et al. 2012). The acumen of the herbivory attack and stimuli is mostly at the site of the injury but can disperse to adjoining cells and start systemic defense reactions. The insects produce oral secretions (OS) or elicitors frequently into the plant system. To discern these secretions, many specific receptors are found on the cell membrane (Maffei et al. 2012). The signals produced by insects include change of the plasma membrane, ionic influxes or effluxes, and oxidative or Ca^{2+} ruptures. Many insect OS consists of fatty acid-amino acid conjugates (FACs) which work as potential elicitors for defense mechanisms. Feeding on leaves and OS by cotton leaf worm in lima beans quickly produced the depolarization of plasma membrane potential, thus starting defense reactions against the herbivory (Bricchi et al. 2012). Mousavi et al. (2013) described the role of change of membrane potentials and specific membrane proteins like glutamate receptor-like (GLRs) proteins in regulating the JA-induced gene expressions and signaling of wounds. The OS and FACs successively stimulate the kinase signaling cascades that act in regulating defense against herbivory. For example, in case of *N. attenuata*, the exogenous action of *Manduca sexta* obtained FACs to the injured cells induced MAPKs, wound-activated protein kinase (WIPK), salicylic acid-induced protein kinase (SIPK) and led in the deposition of plant hormones such as JA, SA and ET (Wu et al. 2007). Likewise, the attack of brown plant hoppers in rice activated the expression of multiple OsMPKs (Nanda et al. 2018). Oxidative production or burst of ROS is another quick response of plants against herbivory. ROS contribute in modulating anti-insect plant defense via redox potential-based signaling (Erb and Reymond 2019). The part of ROS in insect defense has been well established in *N. attenuata* (Wu et al. 2013). Injury of the *N. attenuata* plants caused production of NaRBOHD, a member of the respiratory rupture oxidase homolog (RBOH) family. Additionally, the treatment of OS from *M. sexta* led to elevated transcription of NaRBOHD. The ROS induction even after the OS treatment was significantly reduced in the NaRBOHD-silenced plants, and they were more susceptible to insect pests. The plant oxidases such as RBOHs have the capacity to combine with Ca^{2+} and MAPK signaling alongside ROS generation, showing its nexus in insect-induced defense reactions. Amalgamation of ROS release and Ca^{2+} signaling has been established already in *Arabidopsis* where the combining of Ca^{2+} synergistically stimulates RBOH12. ROS-mediated defense mechanism against phloem and sap-sucking herbivory is often registered through the collection of H_2O_2 and increased task of peroxidases (POD), superoxide dismutases (SOD), and catalases (CAT) in a number of crops (Kerchev et al. 2012). In many ion species, Ca^{2+} ion contribute to the change of cell membrane potential and signal alteration during insect attack. The concentration of Ca^{2+} ions in the cytoplasm and in the apoplast remains in the nanomolar and micromolar range, respectively, under normal conditions (Dodd et al. 2010). The Ca^{2+} homeostasis gets disrupted, and a gush of Ca^{2+} ions runs into the cytosols during insect injury. This change of the ionic concentrations by the Ca^{2+} burst starts downstream signaling cascades for defense reactions (Drerup et al. 2013). The Ca^{2+} signals are mostly observed by calcium sensor proteins, for example, calmodulin (CaM) and CDPKs, which further connect with downstream targets to spread the acquired signal to the nucleus (Du et al. 2011). The Signal responsive1 (AtSR1) transcription factor protein to CaM activates insect resistance in *Arabidopsis thaliana*, while the atSR1 mutants are susceptible to insects (Laluk et al. 2012). The defense feedbacks against aphid attack in *Arabidopsis* (vs. *Myzus persicae*) and wheat (vs. *Diuraphis noxia*) were observed to be controlled by the expression of CaM-binding proteins (Smith and Boyko 2007). Similarly, AtCPK3 and AtCPK13 regulated the CPK-mediated Ca^{2+} signaling, modulating the defense responses against *S. littoralis* (Kanchiswamy et al. 2010). Phytohormones contribute to the fine-tuning of plant defense mechanisms. JA works as a main participant in regulating defenses against herbivory by playing as direct and indirect defenses (Yang et al. 2019). Insect injury of leaves causes the rise of intracellular concentration and collection of JA in the plant tissues. Plant defense reactions activated by JA accumulation may be like the formation of trichomes to the liberation of volatile organic compounds (VOCs), production of extra foliar nectars (EFNs), secretion of secondary substances, and expression of JA-responsive genes (Wasternack and Hause 2013). In addition, the SA pathway is omnipresent in vascular plants and plays an important part in quick adaptation to insect infestation. SA regulates the defense reaction against the bollworm *Helicoverpa armigera* in tomatoes by producing ROS (Peng et al. 2004). SA-activated H_2O_2 collection also stops insect feeding as higher concentration of H_2O_2 adversely influences the insect digestion and growth (Maffei et al. 2007). Likewise, ET signaling works with JA and/or SA to induce or suppress defense responses to herbivory. For example, ethylene biosynthesis helped the development of fall armyworm *Spodoptera frugiperda* in maize (Harfouche et al. 2006). On the other hand, the deterioration of ethylene signaling aiding poor aphid development in tomato and more resistance to *S. littoralis* in *Arabidopsis* (Mantelin et al. 2009). In addition, ET is answerable for the activated emission of several VOCs in plant-insect interplay as observed in the European alder plants, lima beans and maize (Erb and Reymond 2019).

15.7 Insect Resistance and Molecular Strategies in Field Crops

Insect resistance in crops mostly includes two main defense mechanisms. On the other hand, constitutive defenses save crops from insect herbivory by setting up various physical barriers and chemical metabolites, activated defense ease perception of insect elicitors or effector molecules inducing the secretion of specific chemicals, induction of downstream signaling modules, and genetic rearranging of transcriptional methods (Du et al. 2020). Numerous insect resistance genes in crops convert plasma membrane-localized/intracellular-localized receptors implying that activated defense is important to crop resistance against herbivory (Du et al. 2020). Namely, plant defense response against insect injury shows a high similarity to that against the disease. Many important investigations have made it possible to comprehend the perceptions of the molecular mechanism of resistance to insect pests in crops in the last decade. Plant resistance to many insects and diseases is mostly elucidated by a zig-zag model (Jones and Dangl 2006). Nevertheless, such a system is not completely accepted for the host plant-insect interplay and the degree up to which it is applicable for the same, is yet unrevealed.

15.8 Molecular Patterns and Herbivory

Insect attack mostly induces the secretion of conserved molecules called as herbivore-associated molecular patterns (HAMPs) or damage-associated molecular patterns (DAMPs), which are resembling the pathogen-associated molecular patterns (PAMPs). Such molecules can be identified by the pattern recognition receptor (PRRs) in crops and trigger the PTI (PRR-triggered immunity), which is identical to that of the PAMP-activated resistance (Cheng et al. 2013b). HAMPs comprise secretory proteins from insect pest saliva, oral secretions (OS), and egg laying fluid containing fatty acid-amino acid conjugates (FACs), volicitin, alkaline phosphatase carliferins, bruchins, and glucose oxidase that activate defense reaction via JA signaling pathway (Erb and Reymond 2019). In addition, the DAMPs produced from the injured cells on insect attack contain oligogalacturonides, cutin monomers, and endogenous peptides comprising systemin, VOC, HypSys, and RALF. Alongside HAMPs and DAMPs, insect-released effectors, for example, endo-β-1,4-glucanase N1EG1 from brown plant hoppers (BPH) or HARP1 from cotton ballworm, can subdue or surpass the PTI to activate the effector-triggered susceptibility (ETS) (Malik et al. 2020).

Opposite to this, plant induces specific receptors or resistance (R) proteins that can identify these insect effector molecules, thus stimulating the effector-triggered immunity (ETI). In rice, Bph (Du et al. 2011) converts a NB–LRR protein that serves as a specific receptor for the effectors from BPH in rice-BPH interplay

(Du et al. 2020). Especially, when the PTI found the response to herbivory in a plant comprises cell wall callose deposition (structural), induction of ROS signaling (chemical) and causing signaling cascades (MAPK), ETI includes a more like gene-for-gene interaction for defense reaction via the stimulation of specific genes or transcription elements (Du et al. 2020). Depending upon the research on transcriptome and proteome dynamics, many genes found in insect tolerance have been cloned and distinguished in myriads of crop species. Although these few genes show a clear gene-for-gene association with the insect effectors, others do not advance by this theory. For example, NB-LRR class R-gene Mi-*1.2* from tomato and *vat* from melon convert protein that directly bestows immunity to *Macrosiphum euphorbiae* and *Aphis gossypii*, respectively (Rossi et al. 1998; Villada et al. 2009).

On the other hand, a rice long-chain-based gene *OsLCB1*a aided defense against insect feeding not by directly interplaying with the elicitor but by enhancing the concentration of the defense protein across the cell membranes (Begum et al. 2016). Nonetheless, plants do acquire many genes that contribute in the plant-insect interactions and modulate plant defenses disregarding their connection with the insect effectors. Three lectin receptor kinases (*OsLecRK1*, *OsLecRK2*, and *OsLecRK3*) and multiple *OsMPKs* were found to be engaged in rice resistance against BPH attack (Liu et al. 2015). Likewise, *LecRK1* in *N. attenuata* works as an important player in defense against *M. sexta* by stopping the collection of SA and raised concentration of nicotine, diterpeneglucosides, and trypsin protease inhibitors (Gilardoni et al. 2011).

A leucine-rich repeat receptor-like kinase, *OsLRR-RLK1*, in rice was observed to start defense responses against the *Chilo suppressalis* (Hu et al. 2018). While the transcription of *OsLRR-RLK1* was highly down-regulated by the insect injury, gene silencing revealed lessened resistance to *C. suppressalis*. Additionally, the MAPK cascade works downstream to *OsLRR-RLK1* and is positively controlled by *OsLRR-RLK1* regulating the expressions of MAPK and WRKY transcription factors (Hu et al. 2018). Similarly, the recognition of specific effectors in herbivory and their utilization through various functional genomic methods demonstrated new intuitions in plant-insect interplays. In earlier reports, the transcriptome analysis of the salivary glands of the pea aphid *Acyrthosiphon pisum* has led to the identification of C002, a key effector of insect attack (Mutti et al. 2008). The silencing of C002 resulted in enhanced aphid mortality as the aphids were unable to access the plant sieve tube components. Intriguingly, when the C002 ortholog MpC002 from green peach aphid was upregulated in transgenic *Arabidopsis* plants, it encouraged aphid severity establishing its role in plant defenses. Also, overexpression of candidate aphid effectors Me10 and Me23 also helped in the increased aphid virulence in *N. benthamiana* (Atamian et al. 2013). Insect attack produces jasmonic acid resulting in important transcriptional reprogramming, proposing the participation of multiple transcription factors (TFs) in activating herbivory resistance (Du et al. 2020).

15.8.1 Transcription Factors (TF'S)

It is demonstrated that combining jasmonate-isoleucine (JA-Ile) to coronatine-insensitive 1 (COI1) leads to the degradation of JAZ proteins and induction of the basic helix loop helix (bHLH) TF MYC2 during jasmonate signaling (Pauwels and Goossens 2011). The latest research has shown new insights into the role of various TFs in transcriptional reprogramming during JA signaling. MYC2 along with MYC3 and MYC4 has an extra defense against insect attack (Fernández-Calvo et al. 2011). Schweizer et al. (2013) established a systemic transcriptome profiling to illustrate the resistant result of nine TFs counting WRKYs, NACs, and ERFs in resistance to *S. littoralis*. Nevertheless, in comparison to myc234 triple mutant, the knockout lines of these TFs were moderately sensitive to *S. littoralis*, *showing* that MYC2, MYC3, and MYC4 are the main controllers of resistance to insects in *Arabidopsis*. On the contrary, in rice, the WRKY TFs were reported to be mainly responsible for generalist insect resistance. *Os*WRKY89 established increased WBPH resistance via more accumulation of leaf waxes, culm lignification, and SA deposition (Wang et al. 2007). *Os*WRKY70 observed increased resistance to striped stem borer with control of JA synthesis and susceptibility to BPH via negative management of gibberellic acid (GA) (Li et al. 2015a). Likewise, *Os*WRKY45 eased BPH resistance through enhanced accumulation of H_2O_2 and in rice ET29 and *Os*WRKY53 established SSB resistance through negative control of OsMPK3/6 signaling (Hu et al. 2016). In rice, *Os*bHLH61 and *Os*bLHL96 found great defense-responsive genes resulting in resistance to BPH (Wang et al. 2018). These investigations demonstrated the participation of multiple novel TFs in host plant defense mechanisms against insect infestations. RNA interference or the antisense arbitrated homologous gene silencing using double-stranded RNA (dsRNA) intermediates is an important reverse genetic technology that has been manipulated to comprehend the working of genes and bio-control of major crop insect pests (Zhang et al. 2017). dsRNA addressing important genes in herbivory have been instituted into crops which when consumed by the insects cause poor development or kill of the insect (Zhang et al. 2017). Since the first proof of concept study toward the usage of RNAi towards growth retardation and death of the Western corn rootworm (WCR) *Diabrotica virgifera virgifera*, the technology has been effectively employed towards development of resistance against multiple Coleopteran and Lepidopteran insects. Li et al. (2015b) have observed that BPH or Asian corn borers fed with rice or maize treated with a solution having dsCes (carboxylesterase gene) or dsKTI (Kunitz-type trypsin inhibitors gene) established significant decrease in their survival. Likewise, in rice, the expression of dsNlMLP (mucin-like protein gene) prevented it from BPH attack due to impairment of salivary sheath and decreased survival rate of insects when nourished on its plant parts (Shangguan et al. 2018).

An RNAi-based insecticide named SmartStax Pro has been manufactured by Monsanto and Dow Agrosciences in a new development. In maize, possessing a protectant utilizing a pyramided process engaging multiple Bt proteins and dsRNA targeting the WCR *Snf7* gene provided a good management of *Diabrotica virgifera*

virgifera (Head et al. 2017). In maize, possessing a protectant utilizing a pyramided process engaging multiple Bt proteins and dsRNA targeting the WCR *Snf7* gene provided a good management of *Diabrotica virgifera virgifera* (Head et al. 2017).

15.8.2 Interference RNA (RNAi)

Though the conveyance of RNAi in transgenic plants is sure, it is also anticipated that the RNA-built products are involved in a non-transformative way to prevent the controlling matter connected with GM goods. A report described the exogenous application of siRNA molecules against the diamondback moth *Plutella xylostella*.

15.8.3 siRNAs

Brassica spp. leaves treated with siRNAs targeting the acetylcholine esterase genes AchE2 of *Plutella xylostella* resulted in higher than 60% of the larval feeding (Gong et al. 2013). Likewise, the foliar spray of naked dsRNA aiming at the actin gene led to notable management of the Colorado potato beetle, *Leptinotarsa decemlineata* (San Miguel and Scott 2016). These investigations reveal that RNAi-based gene silencing is a practicable and an effective method to switch off important genes in plant protection against herbivory. The microRNAs (miRNAs), the endogenous small RNAs that negatively control gene expression, are incriminated in multiple biological procedures such as plant growth, development, and defense reactions to environmental pressures (Khraiwesh et al. 2012).

15.8.4 miRNAs

Similarly, siRNAs and miRNAs have also been related in insect-associated responses in crops. The fecundity of aphids was extremely oppressed in *Arabidopsis thaliana* lines mutated with DCL1 and ARGONAUTE1 (AGO1), the two key enzymes engaged in miRNA conversion (Kettles et al. 2013). More studies also show that miRNAs operate as the controlling modulators of herbivory tolerance in major field crops. About 32 resistant line-specific miRNAs were established via high-throughput sequencing of *Solanum lycopersicon* post attack with whitefly, *Bemisia tabaci* (Wang et al. 2018). Resistance-specific miRNAs have been described in response to *Aphis gossypii* aphid infestation in *Cucumis melo* (Sattar et al. 2012). Similarly, more than 150 miRNAs were distinctively identified in response to insect attack in the tea plant, *Camellia sinensis* by the moth *Ectropis oblique* (Jeyaraj et al. 2017). About 104 resistance-specific and 80 basal defense-responsive miRNAs were found post infection with brown plant hopper (BPH) under compatible and noncompatible interplay in rice (Weinhold and Baldwin 2011). In miRNAs, *Os*miR156 and *Os*miR396 have been identified as basic regulators of BPH resistance in rice crop. *Os*miR156 negatively controls BPH resistance by controlling the JA biosynthetic process (Fürstenberg-Hägg et al. 2013). OsmiR396 enhances rice response to BPH by managing the expression of the *Os*F3H (flavanone 3-hydroxylase), the rate limiting enzyme in the flavonoid biosynthetic routes (Dai et al. 2019). Recently, in rice small RNA profiling line integrated with the BPH-resistant gene, BPH6 found 29 opposite identified and 9 specifically identified miRNAs in early or late infesting stages showing their engagement in BPH6-mediated tolerance to BPH (Tan et al. 2020). These studies establish that plant miRNAs are significant in the resistance response against herbivory and function as a beneficial resource in comprehending the contribution of post-transcriptional silencing elements in host plant-insect defense responses. The modern tool of genome editing technologies (GETs) has revealed new avenues for insect resistance studies in key field crops. GETs are constituted by a number of advanced molecular bio-techniques that empower targeted alteration of genomic loci in a precise and effective way (Zhang et al. 2018).

15.8.5 CRISPR/Cas9

CRISPR/Cas9 is the most facile and revolutionary technology with broad application in crop improvement programs (Zhang et al. 2018). Though many plant species have been improved by this methodology for multiple trait improvements such as resistance to bacterial, viral, and fungal plant diseases, its utilization for insect resistance is being manipulated in recent studies. Important research has been recently carried out inducing BPH and SSB resistance in rice using CRISPR/Cas9-mediated suppression of serotonin (Lu et al. 2018). In rice crop, the cytochrome P450 monooxygenase gene *CYP71A1* incites the act of tryptamine 5-hydroxylase enzyme and catalyzes the transformation of tryptamine to serotonin. A CRISPR/Cas9 mutation of *CYP71A1* gene in rice led to greater SA levels, no serotonin production, and increased resistance to SSB and BPH (Lu et al. 2018). Genome editing biotechnology basically targets editing of susceptible genes that help the herbivory. The gene editing tool has the potential to change susceptible alleles into resistant types averting the requirement of traditional backcross breeding systems for resistance introgression. Recently, GETs are increasingly being studied to design gene drives in herbivores to avoid them from insect attack. However, more investigations are needed to completely use this biotechnology in insect resistance in field crops.

15.9 Challenges and Conclusions

The interactions between host plant-insects are greatly intricate and multi-faceted. The co-evolution of crops and herbivory and their challenging arm races for survival are very interesting. The multi-level defense plans as described are used by plants to manage herbivory. Important advances have been achieved recently to comprehend the molecular technology of insect resistance in field crops and its use in the resistance breeding projects. The transgenic cultivars with raised callose depositions have been observed to show enhanced resistance against the sucking insects, especially plant hoppers. Overexpression of specific metabolite genes has also caused better insect resistance. An important biotechnological development has been demonstrated in comprehending crop and insect genomes, proteomes, and transcriptomes. The useful genomic procedures and genetic engineering methods have aided the cloning and description of resistance genes, identification of supposed insect effectors, and exploration of signaling routes in plant-insect responses. The genetic program of plant-insect interaction is still insufficient in several crops. For example, as in few plants insect resistant R genes have been cloned, however, their putative effector is unrevealed. In many plant herbivory structures, the effector molecules have been established while the R-genes have not been distinguished. In future more comprehensive and exhaustive research is needed to be carried out in identification of host plant genes and insect-produced effectors to evolve a distinctive regulatory network related with effector-activated signaling-mediated resistance against herbivory. Modern arising biotechnologies, for example, RNAi and CRISPR/Cas9 genome editing are encouraging methods for crop insect pest management. However, many limitations make them impossible to utilize beyond the research laboratories. For instance, greater genetic variations in the natural pest abundance could lead to more varying results for RNAi under field environments. Additionally, high concentration of dsRNA may not be feasibly dispensed into herbivory in spite of its needs for gene silencing as it may result in imbalanced dietary options (Satyabrata et al. 2021). RNAi demands more in-depth research dealing with dsRNA stability and field-applicable efficient experiments to be regarded as effective against insect pest management programs. Similarly, GETs need precise understanding about plant susceptibility elements which would be efficiently mutated for use in insect pest control strategies. Nonetheless, all such bio-tools will be crucial for unravelling the significance of plant R-genes and insect effectors in the transformation of crop resistance to herbivory.

In the field, as several pests are present at the same time, the indiscriminate application of chemicals for pest control is more applicable, economical, and efficient than developing insect-resistant crop cultivars. Thus, insect resistance breeding programs must require the incorporation of broad-spectrum resistance genes to reduce the investment in crop management programs, designing a new technique more suitable for the future crop improvement strategies. Newly developed biotechnologies, for example, CRISPR/Cas9 gene editing to alter insect susceptible alleles to insect resistance alleles, as well as changing the levels of specific secondary metabolites in vivo, encourage the potential to develop field crops that can be repaired. Moreover, these emerging molecular tools will be invaluable for uncovering the contributions of insect effectors and plant target proteins in the regulation of crop immune systems.

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