Sarwan Kumar
Michael Furlong *Editors*

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Preface

Insects have long been a significant challenge for farmers and agricultural systems worldwide. As the global population continues to expand, the demand for food production has risen dramatically. However, the success of major field crops is threatened by the ever-present and evolving threat of insect pests. This book, '*Plant Resistance to Insects in Major Field Crops*', delves into the crucial topic of plant-insect interactions and the development of resistance mechanisms in crops.

The concept of plant resistance to insects is not new; farmers have been observing and selecting pest-resistant plants for centuries. However, with advances in scientific research and technology, our understanding of these complex interactions has deepened. The integration of classical breeding techniques with molecular and genetic tools has enabled us to unravel the intricacies of plant defense mechanisms, laying the foundation for the development of sustainable pest management strategies.

This book aims to provide a comprehensive overview of the current knowledge and advancements in the field of plant resistance to insects in major field crops. It brings together a diverse group of researchers, scientists, and experts who have contributed their expertise and insights to the different chapters of this volume. Their collective efforts have resulted in a rich compilation of information, covering various aspects of plant resistance, including plant-insect interactions, resistance mechanisms, host-plant resistance breeding, and practical implementation of insect-resistant crops.

The chapters in this book explore a wide range of major field crops, such as maize, rice, wheat, oilseeds and pulses, cotton, and more, highlighting the specific challenges posed by insect pests in each crop and the strategies employed to develop resistant varieties. Additionally, the book explores the roles of molecular biology, genomics, biotechnology, and high-throughput phenotyping in enhancing our understanding of plant resistance mechanisms, offering exciting prospects for future research and development. High-throughput phenotyping has revolutionized the field of plant research by enabling scientists to rapidly and accurately assess the resistance traits of a vast array of crops. By leveraging cutting-edge technologies and advanced imaging systems, this method offers unprecedented speed, precision, and scalability in evaluating the intricate interactions between plants and insect pests.

We recognize that this book is just a snapshot of the vast and ever-evolving field of plant resistance to insects. It is our hope that the knowledge and insights shared within these pages will inspire further research, facilitate collaborations, and aid in the development of sustainable and effective pest management strategies. We also aim to provide valuable information to students, researchers, entomologists, plant breeders, agronomists, and policymakers who are invested in addressing the challenges posed by insect pests in major field crops.

We extend our sincere gratitude to all the authors who have contributed their expertise and knowledge to this book. Their dedication and commitment to advancing the field of plant resistance to insects have made this volume possible.

Finally, we hope that '*Plant Resistance to Insects in Major Field Crops*' serves as a valuable resource for anyone interested in understanding and addressing the complex interactions between plants and insects. Together, let us strive to develop resilient and sustainable agricultural systems that can withstand the challenges of insect pests while ensuring global food security.

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About the Editors

Sarwan Kumar is Senior Entomologist at Punjab Agricultural University (PAU), Ludhiana, India, and holds a PhD in entomology (2005) from CCS Haryana Agricultural University, Hisar, India. He has more than 17 years of experience as an entomologist at PAU, Ludhiana. His research interests include host plant resistance, insect-plant interactions, plant defense, and pest management in oilseed crops with special reference to oilseed *Brassica*. Before being appointed as Assistant Professor of Entomology at PAU in 2006, he worked as Senior Research Fellow (2005–2006) in the Department of Entomology, PAU, and worked on dissemination of pest management strategy in cotton. Dr. Sarwan Kumar has nearly 84 publications, including 45 research articles in journals of national and international repute and 26 conference/symposia presentations. He has authored eight book chapters in edited books published by leading publishers and three scientific reviews. He has guided the research work of more than 15 PG students in entomology and plant pathology. He is an active member of 'All India Coordinated Research Project on Rapeseed-Mustard' and is coordinating the entomology program of the project. He is the recipient of Australian Government's Prestigious Endeavour Research Fellowship (Australia Awards) and Fellow of Indian Society of Oilseeds Research. Besides this, he is editor of Journal of Insect Science (India) and Journal of Oilseed Brassica and member of the Society of Chemical Industry, UK, and Entomological Society of Iran.

Michael Furlong is Professor of Insect Ecology and Biological Control at the University of Queensland, Australia. He completed his PhD at Imperial College, London, in 1993 and took up Postdoctoral Research Fellow positions at Rothamsted Research, UK (1993–1997); the University of Maine, ME, USA (1997–1999); and the University of Queensland (1999–2005) where he was appointed to a teaching and research lectureship in 2005. Professor Furlong leads large teams of researchers at the UQ and in international collaborations, and his work in the South Pacific has led directly to improved pest control and documented reductions in hazardous pesticide use, providing clear benefits for the environment and society. He studies how pest species interact with crop plants and how ecosystem services can be sustained and enhanced when they are stressed by agricultural intensification and climate change. His research and outreach in the Pacific engage national governments and local communities to develop novel extension strategies to provide vocational training that directly impacts resource-poor rural communities.

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Introduction

1

Neha Panwar, Lukesh Bansal, Michael Furlong, and Sarwan Kumar

Abstract

Growing world population and changing climate pose a significant threat to food security. A number of biotic and abiotic constraints further aggravate this challenge by reducing the crop productivity. Out of the various biotic stresses faced by plants, insects are the major constraints which are largely managed by synthetic chemical pesticides. This approach comes along with several associated risks like environmental degradation, pesticide residues in food chains, non-target effects, health hazards to the persons applying pesticides, and many more. To address these concerns, there is a growing need to shift towards more sustainable management practices which are safer to the environment as well as human health. Host plant resistance has the potential to provide sustainable solution to pest problems which offers economical, effective, easy, and environment friendly option to manage pests. Plants utilize a plethora of biophysical and biochemical defenses that can be harnessed to develop insect resistant cultivars. Conventional breeding techniques take longer time to develop resistant cultivars but they can be easily integrated with modern breeding techniques to develop resistant cultivars in a shorter period of time. Cultivars with even moderate level of resistance can be integrated into IPM system which can help reduce pesticide load.

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The global population is rapidly growing resulting in increased demand for food. This demand can be met either by increasing cropped area or by increasing productivity per unit area. Since, there is a limited scope for horizontal area expansion; increased requirements can be met by improving the productivity of agriculturally important crops. This can be challenging due to various biotic and abiotic constraints that limit production. It is believed that about 20–40% crop losses occur due to diseases and pests, with insects being a major contributor to this loss (FAO, Food and Agriculture Organization of the United Nations 2009). Insect pests are a major cause of agricultural losses worldwide caused directly by crop damage and indirectly by the diseases that some species transmit. Farmers often use synthetic insecticides to manage pests, prolonged use of these chemicals can lead to many problems such as insecticide resistance, pest resurgence, detrimental effects on non-target beneficial species, residual activity, human health effects, and environmental pollution. To achieve sustainable food production, it is imperative that innovative techniques that complement or replace the use of broad-spectrum chemical pesticides are adopted. Host plant resistance has the potential to contribute to sustainable food production as well as reduce the use of insecticides (Wiseman and Webster 1999). The earliest examples of utilizing a crop resistant variety date back to 1780s when the "Underhill" variety of wheat (Havens 1792), resistant to Hessian fly, *Mayetiola destructor* (Say) and the "Winter Majetin" variety of Apple (Lindley 1831) resistant to the wooly apple aphid, *Eriosoma lanigerum* (Hausmann), were developed. Application of Mendelian rules of heredity further played a crucial role in the systematic development of resistant breeding programs (Panda and Khush 1995). Successful examples of the development of many insect and disease resistant varieties during green revolution like IR-36 variety of rice further sparked interest of breeders and growers in this field (Smith 2005).

Host plant resistance can offer sustainable solutions to pest management problems with many advantages. Research on host plant resistance has led to the development of arthropod resistant crop varieties resulting in significant improvements in food production, alleviation of hunger, and improved nutrition (Khush 1995). In the past few decades, genetic engineering has further expanded the horizons of plant resistance science. Introgression of genes from crop wild relatives (CWRs) and gene transfer from organisms of non-plant origin like the bacterium *Bacillus thuringiensis* have revolutionized breeding for resistance. Novel techniques like genome editing using CRISPR further hold great potential in achieving the sustainability goal of host plant resistance. In this chapter, we discuss how host plant resistance can be efficiently utilized against insect pests.

1.1 The Types of Host Plant Resistance

Painter (1951) defined host plant resistance as “the relative amount of heritable qualities possessed by a plant which influence the ultimate degree of damage done by an insect.” It is very important to note that resistance should always be measured on a relative scale by comparing the amount of resistance in a given variety to that of susceptible control plants that experience more damage under similar experimental settings. Host plant resistance can be categorized into three types: non-preference, antibiosis, and tolerance.

Kogan and Ortman (1978) introduced the term “antixenosis” in place of non-preference as it refers to a plant’s ability to resist being a host for insect herbivores, which compels the pests to choose a different host plant. This term describes how the presence of specific plant characteristics, such as chemical or physical factors, can alter insect behavior. Antibiosis refers to the negative effects on the insect lifecycle that occur when an insect feeds on a resistant host plant (Painter 1951). It can be caused by both chemical and physical plant defenses, and severity can range from mild to fatal. The effects of antibiosis include mortality in early life stages, extended periods of development, decreased adult lifespan and fertility, and/or abnormal behavior. Tolerance refers to a plant’s inherent genetic capacity to continue growing and reproducing while supporting herbivore population roughly equivalent to that which harms a susceptible plant. Unlike antibiosis, it does not exert any selection pressure on the insect population, reducing the probability of selecting for resistant insect biotypes. To determine if tolerance exists, damage levels, plant growth, and yield can be compared between insect infested and uninfested hosts. However, developing crops/hosts that are tolerant to insects requires that tolerance mechanisms are identified and characterized and that genetic basis that underpins tolerance is understood (Peterson et al. 2018). Additionally, it is very difficult to educate farmers to understand that damage caused to crops by pests doesn’t always result in economic losses. Apart from this, tolerant varieties may serve as a reservoir for insect populations that may damage the other non-tolerant crops growing in the vicinity. However, modern precision breeding methods, like gene editing and marker-assisted selection, offer the possibility of achieving greater resistance levels while producing high-quality and high-yielding crops. It is crucial to thoroughly investigate these mechanisms because of the advantages that resistant plants can offer in Integrated Pest Management (IPM) systems. Ideally, cultivars which demonstrate a combination of resistance mechanisms should be developed.

1.2 Bases of Host Plant Resistance

Plants and insects have been engaged in a co-evolutionary arms race for millions of years. As plants have evolved new defenses to protect themselves from herbivores, insects have evolved new adaptations to overcome those defenses. These plant defenses can be either constitutive or induced. Constitutive defenses are expressed in plants even in the absence of herbivores, whereas, induced defenses are generally activated by interactions with herbivores. Plant defenses can also be classified as direct, including physical defenses such as spines, thorns, and tough leaves, and chemical defenses such as toxic compounds, or indirect such as the production of volatile compounds that attract natural enemies of the herbivorous insects. These defenses can make it more difficult for herbivorous insects to feed on the plants, or can make the insects less fit, reducing their ability to reproduce and survive.

1.2.1 Biophysical Bases

A plant's suitability as a host for insect pests is in part governed by a number of physical plant characteristics (in addition to biochemical characters) including leaf waxiness, trichomes, plant shape and size, toughness, etc. Trichomes are short hair-like structures present on plant parts which help plants to defend themselves against different insect pests. Different trichome characteristics like shape, length, density of trichomes, etc. play a crucial role in determining the extent of protection offered against different insect pests. These trichomes generally make the plant unsuitable/less suitable for oviposition and/or feeding and, therefore, provide protection to plants against herbivory (Dalin et al. 2008). Trichomes are of two types, simple or glandular, depending on whether they secrete defensive fluids or not. Simple trichomes serve as a physical barrier, whereas, glandular trichomes secrete repellant or toxic chemicals to ward off the pests (Handley et al. 2005).

Epicuticular waxes can act as biophysical barriers to herbivores by making it difficult for them to attach to and feed on plant surfaces (Jeffree 1986). They serve as a barrier for insect feeding by eliciting negative tactile and chemical reactions in insects' mechano- and chemoreceptors.

Plant toughness or rigidity can also prove useful in defending plants against various insects. Because of the presence of substances like lignin, cellulose, callose, etc., it becomes extremely difficult for herbivores to pierce plant tissue for oviposition or feeding. For instance, the solid-stemmed variety of wheat and rind hardness of sugarcane imparts resistance against stem fly and internode borer, respectively (Platt and Farstad 1946; Martin et al. 1975).

1.2.2 Biochemical Bases

Plants generate a wide range of secondary metabolites, which are believed to number over 200,000 molecules belonging to different classes such as alkaloids, cyanogenic alkaloids, glucosinolates, phenylpropanoids, terpenes, and aromatic polyketides (Mithofer and Boland 2012). These chemicals can be involved either in direct defenses that are toxic or repellant to herbivores or indirect defense that attract the natural enemies of phytophagous insects. However, some insects have evolved to detoxify or tolerate these secondary metabolites and utilize them as cues for oviposition and/or feeding (Schoonhoven et al. 2005). These secondary metabolites can be either phytoanticipins such as tannins (constitutively present) or phytoalexins such as isothiocyanates (induced after herbivory) in nature (Morant et al. 2008).

Plants may also release volatile organic compounds (VOCs) which play a key role in regulating plant–insect interactions (Blande et al. 2007). Herbivore-induced plant volatiles (HIPVs) are one such example of VOCs which have been implicated in indirect defenses. Upon herbivory, plants may produce volatile compounds which can be utilized by natural enemies to detect the likely presence of herbivore host/prey (Furlong et al. 2018). These chemical signals have been referred to as ‘Call or cry for help’ (Dicke and Baldwin 2010), and they are integral to indirect defenses that attract parasitoids and predators to herbivore damaged plants.

1.3 Breeding for Insect Resistance

1.3.1 Conventional Breeding

A source of resistance is the first requirement in any breeding programme aimed at development of insect resistant cultivar. For the development of an effective standardized screening protocol to detect resistance, thorough knowledge about pest infestations, seasonal history, as well as pest hot-spot regions is required. The screening for insect resistance is a very long process and since pest infestation may show temporal variations, it becomes very challenging to identify reliable and durable source(s) of resistance.

After the identification of the insect resistance trait, it is transferred to the cultivated background. When the trait of interest in plants is present in plants of the same species or closely related species, traditional breeding methods can be used. A number of breeding methods like selection, pedigree method, hybridization, induced mutagenesis, etc. can be utilized for transferring the desired resistance trait into the cultivated background. However, these methods take a long time to develop resistant varieties, though, marker-assisted selection can aid in accelerating breeding programme (Collard and Mackill 2008). Kumar et al. (2011) attempted to introgress resistance to turnip aphid, *Lipaphis erysimi* (Kaltenbach) from wild *Brassica fruticulosa* to *B. juncea*. Rigorous phenotyping over the years led to identification of resistant introgression lines though with some linkage drag with some undesirable traits. More recent research has attempted to remove this drag through the use of γ-irradiation (Agrawal et al. 2021).

Earlier efforts by plant breeders largely focused on the development of high-yielding cultivars with little attention paid to insect or disease resistance. This led to the loss of many defense-related genes in many of the high-yielding varieties compared to their crop wild relatives (Chen et al. 2015). Most cultivated crops produce fewer plant secondary metabolites (PSMs) and are less toxic to herbivores than their wild relatives (Olsen and Wendel 2013). For example, domestication of tomato has led to the loss of two genes, zFPP and ShZIS, which are known to code for enzymes involved in production of sesquiterpene 7-epizingiberene which has a role in plant defense (Olsen and Wendel 2013). When these genes were reintroduced into the cultivated tomato, the plants became more resistant to various insect pests.

1.3.2 Modern Breeding

For crops that have limited genetic variation in the desired traits, genetic technologies such as genetic transformation and genome editing can expedite the development of cultivars with insect resistance. Researchers studying plant resistance are now utilizing genotyping by sequencing technologies to quickly and accurately discover and map resistance genes. Also, this technique can efficiently track resistance genes during the breeding and selection process (Campbell et al. 2018). While it is important to keep uncovering new sources of resistance, it is equally crucial to maintain resistant genotypes that have already been developed. For example, maize breeding lines developed in the 1970s with polygenic resistance to the fall armyworm are currently being used to address the pest's recent invasion in Sub-Saharan Africa (Feldmann et al. 2019).

Over the last few decades, there has been increased focus on the use of some defense-related genes in the development of transgenic plants resistant to insects. Genes coding for plant lectins are one such example. Plant lectins are a diverse class of proteins which can be utilized to induce defense responses in plants against insect pests. These lectins serve as feeding deterrents for herbivores by binding to the carbohydrate molecules on the insect gut leading to cessation of feeding, diarrhea, and ultimately death (Esch and Schafrath 2017). Rauf et al. (2019) reported that transgenic tobacco plant upregulating Hvt-lectin caused complete mortality of *Spodoptera litura* and *Helicoverpa armigera*.

Protease inhibitors (PIs) are another class of proteins present naturally in plants that defend them against herbivory by inhibiting the activity of digestive proteases in the insect gut. These PIs bind to the active site of digestive proteases leading to inhibition of protein digestion. This is manifested in reduced utilization of protein by insects leading to adverse effect on its development and increased susceptibility to other stress factors such as pathogens and predators. Plant protease inhibitors such as cowpea trypsin inhibitor (CpTI) and soybean trypsin inhibitor (STI) have been widely explored for their involvement in host plant defense to insect herbivores. CpTI and STI both inhibit the action of trypsin-like enzymes in the guts of insect herbivores, resulting in decreased feeding and development (Zhao et al. 2019).

Bacillus thuringiensis (Bt) and *Bacillus sphaericus* have been the most successful group of organisms identified for use in genetic transformation of crops for pest control on a commercial scale (Schuler et al. 1998). Generally, these plants express Bt toxins at levels sufficient to cause high mortality of target pests in the field. Though Bt genes have been found to be successful and hence commercialized, there is a fear of insects developing resistance to Bt gene products (Estruch et al. 1997; Tabashnik et al. 2023). To overcome this difficulty, gene pyramiding (more than one gene) is advocated. Just as it is important to rotate crops in the farm for maintaining a dynamic ecosystem, gene rotation is necessary in biotechnology-based agriculture.

Ribosome-Inactivating Proteins (RIPs) are plant proteins that inhibit protein synthesis in eukaryotic cells by catalyzing the removal of adenine from ribosomal RNA, causing depurination and prevent the production of functional ribosomes (Stirpe 2013). They can be utilized by plants against different insect pests because of their insecticidal properties. When an insect is exposed to RIPs, the RIPs penetrate the insect's cells and limit protein synthesis, resulting in their death. Moreover, RIPs can activate a variety of defense-related genes and pathways in the host plant, resulting in the synthesis of additional defensive chemicals such as phytohormones and plant secondary metabolites. For example, transgenic tobacco plants which upregulated the RIP production genes reported both sublethal and aphicidal effects against *Myzus persicae* (Hamshou et al. 2016).

RNA interference (RNAi) allows for the development of transgenic plants that are more flexible than protein toxins in terms of their selectivity and mode of action. To achieve this, essential gene-specific double-stranded RNA (dsRNA) from an insect pest is taken up into cells, where Dicer enzymes break it down into small interfering RNA (siRNA) molecules. These molecules then direct the RNA-induced silencing complex (RISC), which contains the Argonaute protein, to degrade complementary mRNAs, and sometimes prevent the target mRNA from being translated (Scott et al. 2013). The delivery of dsRNA is typically achieved through plant genetic manipulation (Price and Gatehouse 2008). However, topical application of dsRNA through sprays or drenches can control lepidopteran and hemipteran pests (Li et al. 2015). RNAi can be used for developing insect resistant plants, for example, Pitino et al. (2011) reported that RNAi resulted in reduced feeding of green peach aphids due to silencing of Rack-1 and COO2 gene in transgenic *Arabidopsis* and tobacco plants.

Genome editing technologies like CRISPR (clustered regularly interspersed short palindromic repeats) can also be used to incorporate resistance characteristics into crops (Georges and Ray 2017). The CRISPR/Cas9 bacterial defense against viruses is the most extensively used CRISPR system in eukaryotes, including plants. The Cas9 protein is essentially a nuclease enzyme that cuts DNA at a specific place indicated by a synthesized guide RNA. There are several CRISPR techniques available, some of which can induce site-specific modifications in DNA, such as indels (which frequently result in frameshift mutations), replacement or insertion of particular sequences, and gene expression suppression through the use of a deactivated Cas9. CRISPR is the most preferred method for creating new varieties in response to resistant insect strains that overcame plant resistance. This is due to the fact that there is only a difference of a single or few nucleotides between susceptible and resistant alleles of plant resistance genes. With the help of CRISPR, the susceptible allele can be edited to become a resistance allele, reducing the requirement for traditional approaches which involve extensive crossing and backcrossing.

1.3.3 Potential of Plant Resistance

Resistant cultivars provide an economic advantage to growers as they offer genetically built-in control against pests for only the cost of the seed and no special application technique is required to utilize them. Even when a moderately resistant variety is combined with pesticide treatment, the costs of insecticidal control can be decreased considerably. Moreover, such reduced pesticidal applications provide added ecological benefits such as lower pesticide residues, cleaner water supplies, and less harm to beneficial natural enemies (Smith 2005).

Host plant resistance can serve as a foundation to and be integral component of IPM. Insects that feed on resistant plants generally experience reduced vigor, which can make them more vulnerable to insecticides and ultimately reduce the amount of insecticide required for successful pest control (Stout 2014). Due to reduced insecticidal usage, the economic threshold (ET) for resistant varieties is comparatively higher than that for susceptible varieties of the same crop (van den Berg et al. 1997). This threshold is frequently reached later in the crop growth season, resulting in lower insect populations on these plants throughout the season. Tolerant plants that are resistant to insects work very well in integrated pest management (IPM) programs because they raise the economic threshold without exerting any kind of selection pressure on the pest populations (Peterson et al. 2018).

Resistant varieties can also be integrated with biological control in IPM programs. Their integration can be either additive or synergistic. It is generally believed that resistant varieties may have a negative impact on natural enemies as the pest population is lowered, however, this is largely offset by decreased chemical pesticide usage, which ultimately increases predator and parasitoid populations. Further, moderately resistant varieties which can tolerate pest damage and maintain pest populations offer sufficient food and shelter for beneficial natural enemies (Stout and Davis 2009). Rand et al. (2020) demonstrated that even minimal parasitism (22%) along with solid-stemmed resistant wheat cultivars can effectively manage wheat sawfly.

Insects can cause indirect damage to plants by serving as a vector for diseases, especially viruses. It is very uncommon for plants to be resistant to both a virus and the vector that transmits it, but vector resistance can greatly decrease the incidence and spread of the virus. In the U.S. High Plains, wheat varieties that contain gene (s) for resistance to the wheat curl mite *Aceria tosichella*, the vector for wheat streak mosaic virus (WSMV), have continuously reduced WSMV epidemics for more than 40 years, as about 30% of wheat varieties have this resistance (Carver et al. 2016).

1.3.4 Challenges for Host Plant Resistance

It takes a lot of money, time (years), and expertise to develop a single resistant variety by traditional methods. Alone, such resistant varieties are not able to compete with high-yielding varieties for grower demand. Sometimes, it is very difficult to make growers understand that primary objective of host plant resistance is ecological sustainability which can be achieved by utilizing it as a component of IPM-a method to reduce insecticidal inputs. Modern techniques like market-assisted selection, genetic engineering, genome editing, etc. have significantly reduced the time required to develop a resistant cultivar. Further, the growing demand for sustainable and organic solutions has led to increased interest in this eco-friendly approach.

Both conventional and transgenic insect resistant cultivars may lose their efficacy when insects evolve to feed on these insect resistant cultivars, leading to the development of new insect biotypes. For example, varieties with a single resistance gene to Hessian fly, *M. destructor* and brown planthopper, *Nilaparvata lugens* (Stål) are vulnerable to failure 6–8 years after release (Johnson et al. 2017; Horgan 2018). On the other hand, efficacy of polygenic resistance is long-lasting in most crops. For example, polygenic resistance in raspberry plants has suppressed virulence of raspberry aphid, *Amphorophora idaei* Borner for about 30 years (Jones et al. 2000). Another strategy to prevent or delay virulence in insects can be the use of a combination of conventional and transgenic polygenic resistance. This approach has been used in soybean against lepidopteran insects. Benning ME, a soybean near-isogenic line, has two significant quantitative trait loci, one from linkage group M and one from linkage group E, which provide field resistance against soybean looper, *Chrysodeixis includens* (Walker) and Southern armyworm, *Spodoptera eridania* (Cramer). Moreover, resistance in Benning ME plants is much higher when the cry1Ac transgene is present (Ortega et al. 2016).

1.4 Conclusion

Repeated attempts to control insect pests have shown that there can never be a permanent solution because high selection pressure on insects results in the development of new ways to overcome control measures, whether they are insecticide based or based on host plant resistance (Thrall et al. 2011). A highly or completely resistant variety is neither practical nor desirable. Instead efforts should be directed to how we can utilize moderately resistant varieties which are components of IPM approaches. However, we can still improve the durability of resistance traits in plants by implementing effective resistance management strategies. Polygenic resistance, refugia crops, and gene pyramiding can prove useful in this regard (Carriere et al. 2015). These resistance management strategies can be used along with the newer technologies like genome editing to develop crops that can be modified in real time to combat with evolving insect pests.

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Unraveling the Coevolutionary Arms Race: Insights into the Dynamic Interplay of Plants, Insects and Associated Organisms

2

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Abstract

Insect–plant interactions are complex and dynamic relationships that have evolved over millions of years. Plants have developed various adaptations to deter insect herbivores, including physical, chemical, and induced defences. In response, insects have evolved detoxification mechanisms, behavioural adaptations, and physiological adaptations to overcome these defences. This coevolutionary arms race has shaped the interactions between plants and insects, leading to a diverse array of strategies and counter-strategies. Additionally, other associated organisms such as endosymbionts and rhizosphere microbes have been shown to play a critical role in these interactions. Endosymbionts can alter the nutritional quality of plant tissue and confer resistance to environmental stressors, while rhizosphere microbes can influence plant growth and nutrient uptake. Understanding the coevolutionary arms race and the role of associated organisms in insect–plant interactions has important implications for plant protection and management. By leveraging these relationships, we can develop sustainable and eco-friendly approaches to crop protection and pest management.

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Keywords

Insect–plant interactions · Plant defence · Induced defence · Endosymbionts · Rhizosphere · Crop protection

2.1 Introduction

2.1.1 Overview

The term ‘Coevolution’ was introduced by Ehrlich and Raven (1964) to describe the close interaction between two or more species in an ecosystem, resulting in genetic adaptations in one or both species due to natural selection imposed by the other interacting species. This process is a product of evolution and can have reciprocal impacts (Janzen 1980; Berenbaum and Zangerl 1998; Woolhouse et al. 2002). The interaction between any groups of interacting species, including mutualists, pathogens, competitors, and predators and prey, can lead to coevolution. The nature and intensity of their interaction determine the selection pressures exerted by each species on the other. Previous research has demonstrated the significance of the relationship between two species in determining the selection pressures on each other (Hochberg et al. 2000; Thompson and Cunningham 2002).

Interaction between plants and insects is a constantly changing system. These interactions have a long history of coevolution, with each group engaged in an ongoing arms race, thus influencing the other’s evolutionary trajectory (Labandeira 1998). The theory of coevolution developed by Ehrlich and Raven (1964) forms the foundation for the current understanding of the dynamic interplay between plants and insects. The relationship between insects and plants has been dynamically occurring for over 400 million years, resulting in a complex system of interactions that includes herbivory, pollination, and other mutualistic relationships (Labandeira 2013). Insects perform essential functions for plants, such as defence and pollination, while plants provide critical resources such as shelter, oviposition sites, and food for insect growth and reproduction. Nonetheless, herbivores can pose a significant threat to plants and exert strong selection pressure to evolve strategies to tolerate or resist them (Panda and Khush 1995).

The coevolution of insect–plant interactions has resulted in a complex system of adaptations and counter-adaptations, with each group influencing the other’s evolutionary trajectory. This ongoing process has led to the diversity and complexity of the natural world we see today, with insects and plants playing critical roles in ecosystem function and biodiversity.

2.1.2 Coevolution in Shaping Various Insect–Plant Interactions

One of the most prominent examples of coevolution between insects and plants is the evolution of morphological adaptations and specialized feeding strategies. Many insects have evolved to feed on specific plants. For example, some insects have evolved specialized mouthparts to pierce and suck plant tissue, while others have developed chewing mouthparts to consume leaves (Krenn 2019). However, excessive herbivory on leaves, stems, flowers, and other plant parts can lead to reduced growth and reproduction, and in some cases, can even kill the plant. Accordingly, plants have evolved specific mechanisms to deter or tolerate herbivory. They have evolved various structures such as thorns, spines, tough leaves, and other physical barriers to deter herbivores (War et al. 2012). Some plants also produce/increase toxic chemicals that are harmful to herbivores, in response to which insects have developed mechanisms to detoxify these chemicals (Gatehouse 2002). This arms race between plants and insects has resulted in evolution of a vast array of chemical compounds and biochemical pathways (Schoonhoven et al. 2005; Howe and Jander 2008). Plants also recruit other organisms such as predators or parasitoids to attack the herbivores.

The coevolution of insect–plant interactions has also resulted in various mutualistic relationships (Bronstein and Huxman 1997). Many plants rely on insects for pollination, and in return, provide them with a source of nectar or pollen. This mutualistic relationship has led to the coevolution of floral morphology and insect behaviour. Plants have evolved to form floral structures, shapes and colours (Willmer 2011), and chemical signals (Raguso 2008) to attract specific pollinators. Accordingly, insect pollinators perceive and interpret these signals by using their visual and olfactory sense organs (Chittka and Raine 2006). These insects feed on the nectar produced by plants (Heil 2011) and aid in pollination by developing specialized adaptations for collecting and transferring pollen, such as long tongues or hairy bodies (Johnson and Steiner 2000).

Coevolutionary mutualistic relationships between insects and plants can extend beyond just pollination. In some cases, insects live in close association with the plant and providing the plant with protection from predators in exchange for nutrients (Bronstein et al. 2006). This type of relationship has led to the evolution of specialized structures in plants to accommodate the insects.

One such structure is called a gall, which is a growth on the plant caused by the interaction between the plant and an insect, mite, or other arthropod. Gall-forming insects, such as wasps and flies, lay their eggs in plant tissues, which induces the plant to form a protective structure called a gall around the developing insect. The gall provides a safe environment for the insect to develop and feed, and in exchange, the insect secretes chemicals that alter the physiology of the plant to make it more suitable for its needs (Stone and Schönrogge 2003; Jansen-González et al. 2012). Another specialized structure is the domatia, which are small cavities or pouches that are formed in the leaves or stems of some plants, and are inhabited by mutualistic arthropods such as mites, spiders or insects, which provide plant with protection (Agrawal and Karban 1997). Similarly, many ant species depend on plants for food and housing in exchange for protection against predators (Heil and McKey 2003; Nelson et al. 2019).

Furthermore, the coevolution of insect–plant interactions has also driven the evolution of mimicry. Some insects have evolved to mimic the physical appearance or chemical signals of other insects to avoid being detected by predators or to attract prey. In turn, some plants have evolved to mimic the physical appearance or scent of other plants to deceive herbivores or attract specific pollinators (Schaefer and Ruxton 2009).

These types of plant–insect relationships have likely evolved through a process of coevolution, where the plants and insects have adapted to each other's presence over time. As with pollination, the specific details of these relationships can vary widely depending on the species involved. However, in this review, we will focus on the coevolutionary dynamics of herbivore insect–plant relationship.

2.2 Coevolutionary Arms Race during Insect Herbivory

The concept of coevolutionary arms race describes the evolutionary adaptations that occur between two species, where each species is under selective pressure to evolve in response to the adaptations of the other. In the context of plant–insect herbivore interactions, this refers to the adaptations that occur between plants and the insect herbivores that feed on them (Ehrlich and Raven 1964).

Insect herbivory has been one of the major driving forces in the evolution of plant defence mechanisms. Plants have developed a variety of physical and chemical defences to deter herbivores, including thorns, spines, tough fibrous leaves and toxic secondary metabolites, such as alkaloids and terpenoids (Hanley et al. 2007; Wöll et al. 2013). Moreover, depending on the intensity and kind of an insect damage, plants modify the synthesis and distribution of these defence chemicals. Insects, in turn, have evolved mechanisms to overcome these defences, such as specialized mouthparts for feeding, specific digestive enzymes, detoxification mechanisms, and behavioural adaptations (War et al. 2018). This dynamic relationship between insects and plants has driven the coevolution of traits in both groups, resulting in a diverse array of interactions (Sharma et al. 2021).

The interaction between *Asclepias syriaca* (milkweed) and *Danaus plexippus* (monarch butterfly) is a typical example involving coevolution through toxic cardenolides. Milkweed plants produce toxic cardenolides that deter most insect herbivores, while monarch butterflies have evolved to store these toxins in their bodies, making them unpalatable to predators. As a response, milkweed plants have evolved to produce more complex mixtures of cardenolides, making it harder for monarch butterflies to sequester them (Agrawal et al. 2012).

Thus, many herbivores have evolved the ability to break down and detoxify plant toxins. In response, plants have evolved more complex and diverse chemical defences to counteract these adaptations. In some cases, plants have even evolved mutualistic relationships with other organisms, such as parasitoids, ants or fungi, which provide additional protection against herbivores (Ali and Agrawal 2012; Mathur et al. 2013a).

2.3 Plant Adaptations to Insect Herbivory

The coevolution of insects and plants results in plants acquiring adaptations that improve their own chances of surviving and reproducing in an environment with multiple kinds of herbivory. Plant defence against insect herbivory can be broadly classified into two genetic strategies, namely resistance and tolerance mechanisms. These strategies enable plants to protect themselves from damage caused by herbivorous insects through the production of chemical or physical barriers, as well as by regenerating lost or damaged tissues (Agrawal 2000; Stowe et al. 2001).

Resistance mechanisms involve the production of compounds that deter or harm herbivores, such as toxic chemicals, physical barriers or structural defences. These compounds may be constitutive, meaning they are present in the plant at all times, or induced, meaning they are produced in response to herbivory (Karban and Myers 1989). Plants have evolved various physical features, such as resins, wax, silica and lignins, which serve as direct defence mechanisms against herbivorous insects. These morphological traits, together with secondary metabolites, constitute a crucial aspect of the plant–insect interaction (Hanley et al. 2007; Belete 2018).

Tolerance mechanisms involve the ability of plants to recover from herbivory by regenerating damaged tissues, reallocating resources to compensate for lost tissues, or by increasing photosynthesis to produce more energy. Tolerant plants can often withstand higher levels of herbivory without experiencing significant reductions in growth or reproduction (Strauss and Agrawal 1999). For example, some plants may increase the growth rate of undamaged leaves after herbivory to compensate for the loss of damaged leaves (Garcia and Eubanks 2019).

Plants may use a combination of resistance and tolerance mechanisms to defend themselves against insect herbivores. The specific mechanisms used by a plant depend on factors such as the type of herbivore, the intensity of herbivory, and the availability of resources for growth and repair.

In addition, plants employ indirect defence systems such as the production of extrafloral nectaries and volatile chemicals to attract predators and other enemies of herbivores to assist in their defence (Heil and Karban 2010). Over time, the diversity and complexity of plant secondary metabolites have increased, placing increased adaptive pressure on herbivores.

2.3.1 Morphological Features

Plants possess a cuticle covered by epicuticular waxes which form films and crystals (Koch et al. 2004). These waxes provide protection against desiccation and pathogens, as well as increasing the slipperiness of the cuticle, discouraging non-specialized insects from populating leaf surfaces (Muller et al. 2007). The biosynthesis and composition of these waxes vary during plant development, and their physical–chemical properties respond to changes in temperature and season (Howe and Schaller 2008). Even changes in the wax composition due to egg deposition were found to increase fatty acid tetratriacontanoic acid (C34) and a decrease tetracosanoic acid (C24), thereby attracting the egg parasitoid (Blenn et al. 2012).

Moreover, plants have various structures such as thorns and spines that protect them mainly from mammals, and hairs called trichomes that protect against insects (Karban and Myers 1989). When trichomes are removed, herbivorous insects feed and grow more easily. Insect feeding has been observed to cause an increase in trichome density (Fordyce and Agrawal 2001; Mathur et al. 2011).

Scientific evidence suggests that the toughness of leaves can prevent the penetration by insects with piercing-sucking mouthparts, while increasing the wear and tear on the mandibles of herbivores with biting-chewing mouthparts (Raupp et al. 2008). While younger leaves may contain higher levels of chemical defences, mature leaves can be strengthened with various macromolecules such as lignin, cellulose, suberin, and callose, as well as small organic molecules like phenolics and even inorganic silica particles (Schoonhoven et al. 2005). When roots are consumed by insect herbivores, they exhibit significant regrowth in both density and quantity. Furthermore, genotypes with long and fine roots are less susceptible to herbivory than those with short and thick roots (Belete 2018).

Many plant species have laticifers and resin ducts in their vascular tissues that store latex and resins under internal pressure. When the channels are broken, the substances are secreted and can entrap or intoxicate the herbivore (Pickard 2008). Laticifers are found in over 10% of angiosperms and are most common in tropical regions (Agrawal and Konno 2009). Among more than 50 plant families that are known to produce latex, Asclepias, commonly referred to as milkweed, stands out as one of the most extensively studied plant groups (Dussourd and Hoyle 2000; Buttery and Boatman 1976). Specialist herbivores that feed on latex-producing plants can block the flow of latex by cutting veins or trenches in the leaves (Carroll and Hoffman 1980). Conifers produce oleoresins which are mixture of terpenoids and phenolics stored in high pressurized intercellular spaces called ducts (Phillips and Croteau 1999). According to scientific studies, when herbivores cause damage to a tree, the flow of resin can remove stem-boring bark beetles from the borehole (Mumm and Hilker 2006). The resin acids contain highly volatile monoterpenes and sesquiterpenes, which can deter insects while the wound is healing. However, specialist insects have evolved to overcome this defence mechanism by cutting across resin ducts, and some even use the resin as an olfactory cue to locate and select their preferred host plant (Raffa et al. 2016).

2.3.2 Chemical Defences

Plants synthesize a variety of chemical compounds that are categorized into primary and secondary metabolites based on their biological roles. Primary metabolites are essential for basic life processes such as growth, development, and reproduction. Conversely, secondary metabolites, also known as bioactive compounds, serve several ecological functions such as defence against herbivores and microbial pathogens, attraction of pollinators and seed-dispersing animals, and facilitation of competitive and symbiotic interactions with other plants and microbes (Jain et al. 2019; Salam et al. 2023). These chemical compounds have evolved to specifically target the unique biological systems of herbivores, such as their nervous, digestive, and endocrine organs, and can be produced either constitutively or upon induction (Senthil-Nathan 2013; Karban and Myers 1989). Additionally, they contribute significantly to the sensory properties of plants, including their odours, tastes, and colours. Generally, bioactive specialized compounds act as repellents for generalist insects while attracting specialist insects. Toxic compounds are more likely to intoxicate generalist herbivores, while specialists will need to allocate resources to detoxify them, thereby slowing down their growth and development (Kessler and Baldwin 2002; Macel 2011).

More than 100,000 plant secondary compounds, such as phenolics, terpenoids, alkaloids, cyanogenic glucosides, and glucosinolates have been identified (Hadacek 2002; Howe and Schaller 2008), with each plant species produces only a small, but unique combination of these compounds. While many secondary metabolites are found in multiple plant families, some compounds are specific to certain plant families or genera. A good example of this is the Solanaceae family, which contains alkaloids such as nicotine and solanine that are not commonly found in other plant families (Fiesel et al. 2022). Similarly, the Brassicaceae family contains glucosinolates such as sinigrin and brassicanapin that are not typically found in other plant families (Nguyen et al. 2020). The presence of unique secondary metabolites in different plant families can be attributed to their evolution and adaptation to specific environmental pressures and ecological niches. For instance, certain plant families may have evolved unique secondary metabolites to defend themselves against specific herbivores or pathogens that are prevalent in their native habitats.

2.3.2.1 Alkaloids

Alkaloids are bioactive natural products that are widely distributed and can be found in over 15,000 different plants. They are primarily found in Leguminosae, Liliaceae, Solanaceae, and Amaryllidaceae and have evolved as a defence against insect herbivory (Wink 2020). They are characterized by their alkaline properties and nitrogen-containing heterocyclic rings, which are synthesized from amino acids in the roots and then accumulated above ground. The heterocyclic ring structure includes pyridines, pyrroles, indoles, pyrrolidines, isoquinolines, and piperidines. Some alkaloids, such as caffeine and solanidine, are alkaline but not derived from amino acids, while others like mescaline are alkaline and derived from amino acids but do not contain nitrogen in a heterocycle (Thawabteh et al. 2019; Phukan et al. 2023). Plants containing demissine and solanine alkaloids have been found to be resistant to certain herbivores, although some can detoxify them. Pyrrolizidine alkaloids (PAs) occur naturally in many plants as non-toxic N-oxides but become toxic when reduced in the digestive tracts of certain insect herbivores. Some herbivores, such as *Utetheisa ornatrix*, can detoxify PAs and use them as a defence against their own predators (Wink 2019; Bezzerides et al. 2004).

2.3.2.2 Cyanogenic Glucosides

Cyanogenic glucosides (CNglcs) are present in various plant species, including angiosperms, monocotyledons, dicotyledons, gymnosperms, and pteridophytes, with more than 2600 species from over 550 genera and 150 families (Yulvianti and Zidorn 2021). These amino acid derived glucosides come from tyrosine, valine, isoleucine, and phenylalanine and are stored in vacuoles (Gleadow and Møller 2014). Damage of plant tissue due to insect herbivory causes exposure to β-glucosidases leading to hydrolysis and the formation of toxic hydrogen cyanide (HCN) and a ketone or aldehyde (Boter and Diaz 2023). HCN is a potent toxin that can disrupt cellular respiration by inhibiting cytochrome c oxidase in the mitochondrial respiratory pathway. This can result in severe health complications and even death in high enough concentrations (Manoj et al. 2020). In addition to their toxic properties, CNglcs can also serve as nitrogen storage compounds or osmoprotectants, and their presence may increase a plant's resistance against certain herbivores while acting as phagostimulants or oviposition cues for others. However, the production of CNglcs comes at a cost, as it can be energetically expensive and may hinder plant growth and development. Additionally, the release of HCN during CNglc production can harm the plant itself by inhibiting the production of phytoalexins, which are essential for defending against microbial pathogens (Vetter 2000).

2.3.2.3 Glucosinolates

Glucosinolates (GLS) are compounds containing sulphur and nitrogen that are found in Brassicaceae and Capparales. They are derived from amino acids, and there are over 200 different known structures (Ishida et al. 2014; Rosa-Téllez 2023). They are categorized into four groups based on their amino acid precursor of the side chain: aliphatic glucosinolates (50%) derived from methionine, indole glucosinolates (10%) synthesized from tryptophan, aromatic glucosinolates (10%) derived from phenylalanine or tyrosine, and structures synthesized from several different amino acids (30%) or with unknown biosynthetic origin (Hopkins et al. 2009). These compounds are more abundant in roots than in shoots, and different tissues have different dominant glucosinolates (Van Dam et al. 2009). When they are hydrolysed by myrosinases upon tissue disruption, they break down into toxic breakdown products such as isothiocyanates, nitriles, and thiocyanates, which are responsible for the flavours of several vegetable foods (Eisenschmidt-Bönn et al. 2019; Wieczorek et al. 2018). These breakdown products act as both herbivore toxins and feeding repellents (Jeschke et al. 2016). Different insects respond to glucosinolates differently (Mathur et al. 2013b). The metabolic diversity in toxin production by individual plants can also provide defence against herbivores with different feeding strategies or resistance mechanisms (Speed et al. 2015; Wittstock et al. 2003).

2.3.2.4 Phenolics

Phenolics of several classes are synthesized by a wide variety of plants. This group comprises approximately 10,000 distinct chemical entities such as tannins, vanillin, ferulic acid, and caffeic acid (Alamgir and Alamgir 2018; de la Rosa et al. 2019). They can be synthesized using either the malonic acid pathway or the Shikimic acid pathway (Saltveit 2017). Phenols serve numerous functions for plants, such as herbivore defence, pollinator attraction, mechanical support, systemic acquired resistance (SAR), and allelopathy (Divekar et al. 2022). There are multiple examples of phenolic compounds acting as defence mechanisms against insects. They can act as feeding deterrents by reducing the palatability and digestibility of plant tissues or directly inhibit insect growth and development or even cause mortality. Additionally, some phenolics attract natural enemies of insect herbivores, such as parasitoids or predators, which can help to reduce insect populations (Rehman et al. 2012).

2.3.2.5 Terpenoids

Terpenoids are a class of organic compounds synthesized in plants from either acetyl-CoA or glycolytic intermediates. They are classified based on the number of isoprene units they contain, ranging from monoterpenes with ten carbons to polyterpenes with more than 40 carbons (Ninkuu et al. 2021). Terpenes play various roles in plants, including defence against herbivores and pathogens, attraction of pollinators, response to abiotic stress, synthesis of plant hormones, and release of volatile organic compounds (Abbas et al. 2017). These functions contribute to the adaptation and survival of plants in different environments (Aharoni et al. 2005). Essential oils, a blend of volatile monoterpenes and sesquiterpenes with well-known insecticidal properties, are found in many plants. Leafcutter ants are repelled by the terpenoid limonene, which citrus trees generate (Fürstenberg-Hägg et al. 2013). Coniferous plants generate monoterpenes, which are poisonous to many insects, including bark beetles. While certain terpenoid amide derivatives can function as insect juvenile hormone analogs, phytoecdysones, which are steroids found in common fern, prevent insect moulting by imitating moulting hormones (Canals et al. 2005). Additionally, when combined, several terpenoids have synergistic effects that have a higher impact on insect fatality rates.

Many secondary metabolites are constitutively present in a certain amount irrespective of presence of herbivorous insects or other stressors. However, upon herbivore attack, plants may recognize elicitor molecules, which are then transduced into the cell to activate specific genes for the biosynthesis of diverse defensive chemicals with unique chemical activities. This process is mediated by complex cellular transduction mechanisms that regulate the genetic expression of biochemical pathways (Bonaventure et al. 2011; Maffei 2010; Maffei et al. 2012; Mithoefer and Boland 2012). These routes can diversify since they are not required for growth and development (Hartmann 2007). The diversity of metabolic products in plants can be attributed to several molecular processes such as gene and genome duplications, accumulation of point mutations, and multi-loci control. These mechanisms result in variations in gene expression, enzyme activity, and substrate specificity, leading to the production of diverse secondary metabolites (Kroymann 2011; Weng et al. 2012; Moore et al. 2014).

2.4 Insect Adaptations to Plant Defences

Insect herbivores have evolved various adaptations to cope with the complex challenges posed by their plant hosts, including the timing of plant growth and reproduction, the specific nutrient composition, and the chemical and physical defences of the plant. As a consequence of this coevolution, herbivorous insects have developed specialized feeding behaviours and are often restricted to a narrow range of host plants that are related phylogenetically and/or share similar biochemical compositions. This adaptation enables herbivorous insects to efficiently feed on their host plants, while minimizing the risks of consuming toxic or unsuitable plant material (Simon et al. 2015; War et al. 2018).

In response to selective pressure from plants that produce direct defence compounds, specialist herbivores have evolved various defence mechanisms to mitigate the toxicity of these compounds. Unlike generalist herbivores, they have developed the ability to detoxify the hazardous chemicals through enzymatic inactivation or sequestration. This adaptation allows them to tolerate the ingestion of plant material that would otherwise be toxic to them (Nishida 2002; Peng et al. 2007; Petschenka and Agrawal 2016). Additionally, specialized herbivores can use certain compounds, such as phagostimulants, to locate suitable host plants (del Campo et al. 2001; Picaud et al. 2003). Some herbivores can even store these protective compounds and use them for defence against predators and parasites or to attract mates (Cogni et al. 2012). This pattern of specialization highlights the strong evolutionary relationship between host plants and specialized herbivores and has been observed in numerous studies (Becerra 2007; Bandeili and Müller 2010; Richards et al. 2010; Agrawal et al. 2012).

2.4.1 Behavioural Adaptations

Insects have the ability to avoid consuming poisonous plants by utilizing either genetically predetermined or learned avoidance mechanisms that are triggered through visual, olfactory, or tactile exposure (Chapman 2003). Female insects possess genetically programmed oviposition behaviour that can prevent them from laying eggs on unsuitable plants (Fox et al. 2004). However, in some cases, larvae may need to migrate to locate a suitable host plant (Cotter and Edwards 2006). Furthermore, insects may consume non-toxic parts of plants or seek out environments that are free from toxins, as well as utilizing plants that are not currently producing toxins (Nealis and Nault 2005). Insects can exhibit diverse responses to toxins depending on their surrounding environmental conditions. For instance, solitary phase locusts are deterred by a bitter-tasting plant alkaloid, whereas gregarious-phase locusts are attracted to it. This difference in feeding behaviour is reflective of various anti-predator strategies, such as changes in colouring and grouping tendencies (Glendinning et al. 2002; Despland 2021; Després et al. 2007).

Insects utilize chemosensation as a means of detecting and avoiding potentially harmful secondary compounds present in their environment. Gustatory and olfactory receptor neurons allow insects to detect these poisons through their senses of taste, smell, and touch. Gustatory receptors are categorized into sweet, bitter, umami, salt, and carbon dioxide receptors, and bitter receptors are involved in sensing secondary compounds that inhibit insect intake by activating downstream signaling pathways. This aversive mechanism may be inherited or acquired (Zunjarrao et al. 2020). Some insects limit their diet to organs of non-toxic plants or eat only on plants with low levels of toxins to avoid hazardous substances (Fox et al. 2004). However, insects also avoid bitter substances even though they are not always harmful, which limits their host plant options and increases the cost of avoidance (Pelden and Meesawat 2019). To circumvent plant defences, insects have developed various strategies, such as recognizing previously induced reactions, feeding on diverse plant tissues, weaving silk over spines, making trenches across leaves before eating, and puncturing leaf veins to block the passage of poisons (Perkins et al. 2013).

2.4.2 Manipulation of Plant Chemical Defences

While avoiding plant allelochemicals is generally the most effective way for insects to minimize their exposure to harmful compounds, they have evolved additional mechanisms to cope with occasional consumption of toxic substances.

Many insects can affect a plant's chemical defences by making tunnels in leaves to release pressure in secretory canals and remove poisonous exudates near their feeding spot (Helmus and Dussourd 2005; Becerra 2003). Insects have developed the ability to inhibit the plant's defence mechanisms by secreting elicitors that can lower the expression of regulatory genes that are crucial for initiating the plant's defences. This allows the insects to better exploit the plant and continue feeding on it without triggering a defensive response (Bede et al. 2006; Divekar et al. 2022). Gall-inducing insects, such as sawflies, have developed the ability to reduce the levels of toxic phenolic chemicals found in the galls where their larvae grow. This adaptation is thought to facilitate frequent switching between host plants, which can increase the survival and reproductive success of these insects (Nyman and Julkunen-Tiitto 2000). By reducing the levels of toxic chemicals in their feeding sites, gall-inducing insects can better tolerate a wider range of plant species and exploit new host plants as they become available, ultimately enhancing their ecological flexibility and evolutionary potential.

2.4.3 Sequestration of Plant Defence Compounds by Insects

Sequestration is a common defence strategy employed by insects that can have significant impacts on their interactions with plants. This strategy involves the selective absorption, transport, endogenous metabolism, and excretion of plant chemicals into different organs of the insect. Through this process, insects can accumulate and store large quantities of plant compounds, often in specialized tissues, for use in a variety of contexts, such as chemical defence against predators or as a source of nutrients. The sequestration of plant chemicals can also lead to coevolutionary dynamics between insects and plants, as insects may evolve mechanisms to overcome or exploit plant defences, while plants may evolve counter-strategies to defend against insect herbivory (Pentzold et al. 2014; Nishida 2002). Insects are known to sequester a diverse array of compounds from their host plants, including aromatic compounds, nitrogen-containing secondary compounds such as alkaloids, cyanogenic glycosides, glucosinolates, and isoprenoids such as cardiac glycosides, cucurbitacins and iridoid glycosides (Opitz and Müller 2009). These sequestered compounds can serve various functions, including as defensive agents against predators or parasites, as feeding stimulants or repellents, and as precursors for the biosynthesis of sex pheromones or other signaling molecules (Dobler 2001). The specific suite of sequestered compounds can vary widely among insect taxa, reflecting differences in the evolutionary history, feeding behaviour, and ecological pressures faced by each group.

Studies have revealed numerous mechanisms by which insects can acquire and store plant chemicals, including a shift from de novo synthesis of detoxifying compounds to sequestration of host phytochemicals. Sequestration is widespread in several insect groups because it is thought to have a lower metabolic cost than de novo production (Beran and Petschenka 2022). In spite of this, there has been limited experimental research on it since the evolutionary background and natural history of the study system aren’t well known.

Insects that sequester defence compounds from plants have evolved diverse mechanisms to accumulate these compounds in various parts of their bodies, such as the haemolymph, defence glands, or integument. Insects absorb plant defence chemicals from the gut lumen into the hemocoel through the peritrophic matrix and gut epithelium. The type of absorption mechanism depends on the chemical properties of the substances, with absorption occurring either through passive diffusion or carrier-mediated transport. The permeability of the epithelial layer also plays a role in absorption and may be modulated by efflux pumps that restrict the uptake of certain substances (Dobler et al. 2015; Sorensen and Dearing 2006). This selective accumulation is achieved through processes such as selective absorption through the gut, transport within the body, endogenous metabolism, and excretion via the malpighian tubules (Petschenka and Agrawal 2016). The cardiac glycoside digitoxin is one example. It was discovered to passively diffuse over the midgut of the milkweed insect *Oncopeltus fasciatus*, but not across the midguts of the desert locust *Schistocerca gregaria* and the American cockroach, *Periplaneta americana* (Scudder and Meredith 1982). This suggests that mechanisms that either aid or hinder the absorption of plant defence compounds across the gut are a key factor in the development of sequestration. It was demonstrated that the cytochrome P450 monooxygenases, a different group of membrane proteins, are implicated in nicotine transportation from the gut into the haemolymph of the tobacco hornworm, *Manduca sexta* (Kumar et al. 2014).

In addition, insects may modify the amounts and composition of sequestered defence chemicals based on the chemical composition of their food plant. For example, some insects can selectively sequester certain types of glucosinolates or iridoid glycosides depending on the plant species they consume (Baden et al. 2013; Beran et al. 2014; Yang et al. 2020). Nevertheless, because the processes of sequestration have only been studied in a small number of insect species, the significance of each of these aspects is not entirely known.

2.4.4 Detoxification

Insects have developed sophisticated detoxification mechanisms to biotransform and excrete secondary metabolites, which have the potential to cause toxicological harm (Erb and Robert 2016). This enables insects to minimize the deleterious effects of these compounds and maintain their ability to feed on plants that contain secondary metabolites. Some insects have specialized gut enzymes or gut microorganisms that detoxify ingested plant chemicals, allowing them to consume otherwise toxic plant material (van den Bosch and Welte 2017).

Insects possess a variety of enzymes that aid in detoxifying plant toxins through oxidation, reduction, hydrolysis, or conjugation of molecules (Birnbaum and Abbot 2018). The three primary types of enzymes involved in detoxification are cytochrome P450 monooxygenases (also known as CYPs or P450s), glutathione S-transferases (GSTs), and carboxylesterases (COEs) (Feyereisen 2005). Berenbaum and Zangerl (1998) demonstrated that the ability of insects to metabolize furanocoumarins, a class of compounds produced by plants, was found to be associated with the varying levels of furanocoumarin production among different plant species. This suggests a tight genetic linkage between the genes responsible for the insect's capacity to utilize host plants and those involved in metabolizing these chemical compounds. The cytochrome P450-dependent monooxygenase gene is a notable example of a gene implicated in both plant–insect interactions and insect physiology. Insects, such as *Papilio polyxenes*, have developed adaptations to thrive on host plants that contain toxins by undergoing diversification of P450 enzymes, which play a key role in the detoxification process (Scott and Wen 2001).

2.4.5 Further Processing of Plant Toxins

A multitude of insects have developed the ability to eliminate or excrete detrimental plant compounds, and in some instances, these compounds are sequestered and utilized for diverse purposes, such as synthesizing pheromones, defending against infections or predators, and generating pigments for adult coloration (Beran and Petschenka 2022; Robinson et al. 2023). Selective transport and storage mechanisms that keep the poison from interfering with the insect's physiological functions are necessary for sequestration (Kuhn et al. 2004). Molecular studies on leaf beetles have shown that a minor modification in ancestral defence mechanism has facilitated the utilization of plant components for predator defence. This adaptation has emerged convergently in multiple leaf beetle lineages and is metabolically advantageous due to its low energy cost (Kuhn et al. 2004; Termonia et al. 2001).

2.5 Involvement of Higher Trophic Level

Insects that feed on plants release volatile organic compounds (VOCs) and extrafloral nectar as a signal to be found and attacked by parasitoids and other natural enemies of the insect (Heil 2008, 2015; Shah et al. 2015). Insect-caused plant damage results in the induction of volatile and nectar and extrafloral nectar secretion to entice the herbivore's natural enemies, such as ants, wasps, and parasitoids (Heil 2011, 2015; Mathur et al. 2013a, b). These natural enemies may exert selective pressure on insect herbivores, resulting in the evolution of various traits, such as behavioural changes or morphological adaptations that enable herbivores to avoid predation (Dicke and Baldwin 2010). These changes, in turn, can influence herbivore feeding behaviour and plant defence strategies, potentially leading to coevolutionary interactions between herbivores and their host plants (Vale et al. 2018). In contrast, when predators consume herbivores that are not well adapted to the plant's chemical defences, it can lead to the selection for herbivores that can more efficiently detoxify or sequester plant compounds. This can result in an arms race between herbivores and plants, where plants evolve more potent chemical defences, and herbivores continue to adapt their detoxification and sequestration mechanisms to overcome them. The pressure from predators can, therefore, indirectly impact the coevolutionary dynamics between herbivores and their host plants, driving the evolution of novel traits that can enhance herbivore fitness and promote coevolutionary interactions between plants and insects.

2.6 Role of Symbiotic Microorganisms

Insects and plants have a mutually beneficial relationship with their symbiotic microorganisms. This relationship creates a complex web of interactions that have both ecological and evolutionary implications. These microbes are critical components of the intricate relationships among plants, insects, and their environments. The interaction between insects and plants involves an indirect interaction with the microorganisms that inhabit each other. In other words, insects and plants have a shared relationship with the microorganisms living within them, which plays a critical role in shaping their interactions and the broader ecological and evolutionary consequences (Sharma et al. 2021; Sugio et al. 2015). The microorganisms that inhabit both plants and insects are highly diverse and can be found in various parts of their respective hosts. Endophytes, microorganisms that live within the tissues of plants, can be found in the roots, stem, leaves, seeds, and fruits of plants, while insects harbour the symbiotic microorganisms throughout their bodies (Compant et al. 2021; Provorov and Onishchuk 2018).

Endophytes are known to play a crucial role in insect–plant interactions by influencing the behaviour, fitness, and survival of their insect hosts (Shikano et al. 2017; Grunseich et al. 2019). Endophytes can produce various secondary metabolites that have insecticidal properties, which can help to deter herbivorous insects from feeding on the plant. The interdependent relationship between plants and endophytes has been demonstrated to promote plant growth and improve their physiological condition, as well as providing a vital defence mechanism against harsh environmental conditions (Malinowski et al. 2000; Peschiutta et al. 2018; Mathur and Ulanova 2022). They contribute to not only growth-promoting phytohormones such as indole acetic acid and gibberellic acids, but also various metabolic compounds such as alkaloids, terpenoids, and flavonoids (Mukherjee et al. 2022; Sharma et al. 2023; Tan and Zou 2001). Endophytes can also influence the nutritional quality of the plant for insect herbivores, by altering the levels of carbohydrates, proteins, and other nutrients in the plant tissue. This can affect the performance and development of herbivorous insects that feed on the plant. Furthermore, endophytes can also confer resistance to environmental stressors such as drought, salinity, and temperature fluctuations, which can improve the overall health and survival altering the levels of carbohydrates, proteins, and other nutrients in the plant tissue and its associated insect community (White et al. 2019). Root-associated microorganisms also contribute to the increased emission of volatiles. The rhizospheric microbiome is susceptible to changes caused by herbivory, which, in turn, can affect the relationship between the plant microbiome and the herbivore (Venturi and Keel 2016).

Insects harbour microorganisms both internally and externally that may be divided into two categories: primary and secondary symbionts. Primary symbionts are crucial for the survival and reproduction of insects and are typically obligatory and vertically transferred from mother to offspring (Bright and Bulgheresi 2010; Szklarzewicz and Michalik 2017). Secondary symbionts, on the other hand, are not essential for host survival and can reside in various insect tissues. They provide a range of benefits to their hosts, such as protection against environmental stresses, natural enemies, and plant toxins (Brownlie and Johnson 2009; van den Bosch and Welte 2017). Secondary symbionts reproduce only in association with their hosts, but they can undergo horizontal transfer. Many studies have highlighted the importance of secondary endosymbionts in insect–plant interactions, including recognition, defence, digestion, and fitness of the insect (Frago et al. 2012; Paniagua Voirol et al. 2018).

Microbial symbionts play a crucial role in insect–plant interactions in several ways. They are known to aid in the recognition of host plants by altering the sensory abilities of insects, such as their ability to detect plant volatiles. Moreover, they can provide protection against natural enemies of insects, such as predators, parasites, and pathogens, which can increase the survival and fitness of the insect. They also help insects to digest plant material and extract nutrients from it, which can be difficult to break down without the aid of microorganisms. Additionally, they confer resistance against plant toxins, allowing the insect to consume a wider range of plant species. These symbiotic microorganisms can also contribute to the overall health and fitness of the insect, which can affect its reproductive success and ability to survive in its environment (Frago et al. 2012; Frago and Zytynska 2023; Hansen and Moran 2014). Overall, microbial symbionts have a significant impact on the interactions between insects and plants, and understanding these relationships can provide insights into the ecology and evolution of both groups of organisms.

2.7 Role of Rhizosphere in Shaping Insect–Plant Interactions

Rhizosphere is a complex and dynamic system that plays a crucial role in shaping insect–plant interactions. One way in which the rhizosphere influences these interactions is by providing a habitat for beneficial microorganisms, such as bacteria and fungi, that can promote plant growth and health. These microorganisms can produce plant growth-promoting substances, such as phytohormones and enzymes, that stimulate plant growth and increase the nutritional quality of the plant for herbivorous insects (Berendsen et al. 2012). As a result, plants growing in healthy and diverse rhizospheres can be more attractive to herbivorous insects, which can lead to increased herbivory and pest pressure. However, these rhizosphere microbes can modulate insect herbivory in different manners and are powerful drivers of insect–plant coevolution (Rasmann et al. 2017; Van der Putten et al. 2001).

In contrast, studies have reported that by creating volatiles, the microbial populations found in the roots help plants survive a variety of biotic and abiotic stressors (Garbeva and Weisskopf 2020). Depending on the insect's feeding guild and specialization, these microorganisms have varying effects on insect herbivory (Pineda et al. 2010). By boosting sugar and protein production, causing metabolic changes, and lowering root pathogen infestation, these bacteria give the plant a selective advantage during insect attacks (Westman et al. 2019). Studies have demonstrated that in order to survive without their insect prey, soil-dwelling entomopathogenic fungi like *Metarhizium* and *Beauveria* have evolved a symbiotic association with plants (Hu and St. Leger 2002). It is hypothesized that other fungi connected to plants may have provided these microorganisms with the genes for insect disease. Rhizospheric microbial communities, such as PGPR, PSB, and VAM, have been reported to boost the antioxidant activity of plants after insect damage (Song et al. 2014; Kousar et al. 2020; Sharma and Mathur 2020).

Thus, interactions between plants, insects, and the rhizosphere can provide insights into the ecology and evolution of these organisms and can help to develop sustainable strategies for managing insect pests in agricultural and natural ecosystems.

2.8 Conclusion

Over the period of 400 million years, several strategies for dealing with chemical defences of their hosts have been developed by insects that feed on plants. The response of plants to insect herbivores has significant implications not only for the interacting players themselves but also for the interactions between responding plants and other organisms associated with plants. This coevolutionary arms race between plants and insect herbivores can have significant ecological consequences. It can influence the structure and diversity of plant communities, as well as the evolution of insect herbivore species. The interactions between plants, insects, and their biotic and abiotic factors such as parasitoids and predators, endosymbionts, and the rhizosphere associated with them are shaped by coevolutionary processes, which have driven the adaptation of these organisms to each other over time. Plants and insects have co-evolved complex mechanisms of defence and counter-defence that allow them to interact in a dynamic and constantly evolving way. It can also have economic impacts, as some insect herbivores are pests that can cause significant damage to crops.

In summary, the coevolutionary arms race between plants and insect herbivores is an ongoing process of adaptation and counter-adaptation, where each species evolves in response to the adaptations of the other. This process can have significant ecological and economic implications and provides a fascinating example of the complexity of evolutionary interactions between species. Understanding the coevolutionary dynamics between plants, insects, and the rhizosphere can provide valuable insights into the ecology and evolution of these organisms and can help to develop sustainable strategies for managing insect pests in agricultural and natural ecosystems.

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Host Plant Resistance to Insects in Cotton

3

Lucy Egan, Qian-Hao Zhu, Iain Wilson, and Warwick Stiller

Abstract

Across the globe, cotton production is limited by endemic and introduced insect pests. The incorporation of host plant resistance (HPR), defined as the ability of a plant to defend itself against targeted biotic stresses, has been a key breeding target for many cotton breeding programs. The development of resistant cultivars provides a cost effective and environmentally sustainable solution for cotton growers. The key insect pests to cotton production include *Helicoverpa* spp., pink bollworm, *Spodoptera* spp., silverleaf whitefly, various plant and stink bugs, aphids, and thrips. Cotton plants have a range of native and genetically modified traits that infer HPR. However, breeding for HPR in cotton is a slow and complex process, with cultivar development commonly requiring more than 15 years to reach the market. Often, the incorporation of native HPR traits has a negative impact on yield and important agronomic characteristics, so it is not economically viable. Therefore, determining the value of a native HPR trait under multiple scenarios is a critical element for research and development investment. This chapter aims to review the major pests to cotton production and the current status of native HPR in commercial cultivars to each pest, outline the process of breeding for HPR in cotton, and discuss the economic value of HPR traits.

Keywords

Gossypium · Host plant resistance · Breeding · Germplasm · Native traits · Economic value

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Abbreviations

ASAL	*Allium sativum* leaf agglutinin
Bt	*Bacillus thuringiensis*
DNA	Deoxyribonucleic acid
dsRNA	Double-stranded RNA
GM	Genetically modified
HMGS	Host-mediated silencing of insect genes
HPR	Host plant resistance
miRNA	Micro RNA
mRNA	Messenger RNA
RNA	Ribonucleic acid
RNAi	RNA interference
ROI	Return on investment
SAT	Shoot apical meristem transformation
siRNA	Small interfering RNA
SLW	Silverleaf whitefly
tasiRNA	Trans-acting siRNA
T-DNA	Transfer DNA
TSSM	Two-spotted spider mite
USA	United States of America

3.1 Introduction

Cotton is an important global crop and is grown in over 70 countries for fibre, oil, and protein (Leff et al. 2004). The cotton genus, *Gossypium*, includes >50 species. Out of these, four species are cultivated for cotton production: *Gossypium arboreum* (Desi cotton), *Gossypium herbaceum* (Levant or Arabian cotton), *Gossypium barbadense* (Pima, Egyptian, or Sea Island cotton), and *G. hirsutum* (Upland cotton) (Wendel et al. 2009; Constable et al. 2015). The most predominant species for commercial production is *Gossypium hirsutum,* and primary, secondary, and tertiary gene pools for the *Gossypium* genus are based on crossing compatibility with *G. hirsutum.* Over 90% of global cotton production utilises *G. hirsutum* (Constable et al. 2015).

The *Gossypium* genus consists of diploid (A–G and K genomes, $2n = 2x = 26$) and tetraploid species (AD genomes, $2n = 4x = 52$) (Lubbers and Chee 2009). The genetic resources of cotton are spread across five continents, and Munro (1994) suggests that the difference in genomes is due to the geographical isolation. The A, B, and E genomes are found across Africa and Asia, the C, G, and K genomes are confined to Australia, the D genomes to America, and the F and G genomes are only found in a single species each (Stiller and Wilson 2014).

On average, the annual global yield of cotton cultivars is increasing. The increase is due to a range of factors including improved farming management practices and improved higher performing cultivars (Liu et al. 2013; Voora et al. 2020). However contrary to the global trend, yields in Pakistan are decreasing (Shahzad et al. 2022; USDA 2022). China, India, the United States of America (USA), Pakistan, Uzbekistan, and Brazil are the leading producers of cotton by volume, but the Australian cotton industry has the highest yields of any production region in the world (Constable and Bange 2015).

Under current cotton management systems, a large proportion of the global crop is grown with cultivars expressing genetically modified (GM) traits developed by multinational corporations such as Bayer, BASF, Corteva, and Syngenta. These GM cultivars express insecticidal protein(s) encoded by gene(s) from *Bacillus thuringiensis* (Bt), a gram-positive soil bacterium. The technology has provided a sustainable solution for the control of major Lepidopteran cotton insect pests, including cotton bollworm (*Helicoverpa* spp.) that became increasingly difficult to control during the late 1980s and the early 1990s due to increased insect populations and resistance to insecticides (Wilson et al. 2018). For example, in Australia, between 1993 and 2019, pesticide use to control *Helicoverpa* reduced by 95% due to the uptake of GM cotton cultivars (Constable et al. 2011; Cotton Australia 2023a). The successful deployment of GM cotton cultivars has been aided by the constant monitoring of resistance development of targeted insects and the planting of conventional cotton to allow for the dilution of resistant alleles (Downes et al. 2017). However, GM cotton is not the 'silver bullet' for pest management. Bt cotton does not control all pests, and the uptake of GM cotton cultivars has increased the threat of previously categorised 'secondary pests' to cotton. The rise in secondary pests is largely due to the reduction in broad-spectrum pesticides used to control Lepidopteran pests which provided some control against secondary pests. Trapero et al. (2016) stated that host plant resistance (HPR) traits may help support the resistance management of the Bt cottons, largely due to the Lepidopteran species interaction with secondary pests that could be controlled by HPR traits.

Although the GM trait packages are critical to the cotton industry, the backbone of cotton breeding programs is conventional (non-GM) germplasm enhancement. Advances in breeding techniques and the uptake of molecular tools have facilitated increases in yield and fibre quality characteristics in cotton (Liu et al. 2013). However, despite the advancement of the crop, yield is often limited by pest damage (Egan and Stiller 2022). Cotton has seven major pests that impact production: Lepidopteran spp. (*Helicoverpa*, *Heliothis,* and *Spodoptera*), plant bugs, stink bugs, silverleaf whitefly (SLW), aphids, and thrips (Luttrell et al. 1994; Trapero et al. 2016; Cotton Australia 2023b). These pests are present across cotton production regions globally, and the severity of the pests changes due to differing environmental conditions across geographical areas. Egan and Stiller (2022) stated that when a pest is widespread, causing significant yield loss, and there is no cost effective or durable management solution, HPR (where available) is the most appropriate method of control.

HPR is commonly defined as the plant's ability to defend itself against a biotic stress, namely a pest or disease (Stout 2014). HPR traits can be in the form of native, from the primary, secondary, or tertiary gene pools, or GM traits. The types of plant resistance to pests have been categorised into three major groups: antibiosis, antixenosis (non-preference), and tolerance (Koch et al. 2016). Antibiosis induces resistance through the plant's biology to negatively impact the pest's biology and can result in pest death. Non-preference trait is a host trait that negatively impacts the pest, but the pest can still survive on the host, or makes the host become less attractive to the pest. Tolerance traits reduce the impact/damage to the plant by the pest whilst maintaining pest population levels similar to those seen on susceptible plants. A key example in cotton is the correlation between the number of extrafloral nectaries and the indirect defence of the plant (Llandres et al. 2019). Whilst the three groups of resistance are beneficial for reducing yield loss due to pest damage, there is concern that it could lead to pest populations that develop resistance to one or more mechanisms. Due to the fast life cycle of many pests and the slow nature of plant breeding, there is an increased opportunity for the evolution of resistance in pest populations. However, this is heavily dependent on the nature of the insect resistance mechanism.

This chapter aims to outline the major pests to cotton production and their current HPR status, summarise the process of breeding for HPR in cotton, and discuss the economic challenges when breeding for HPR. The content will take a somewhat narrow view of HPR and focus on the native or non-GM traits that are available to infer resistance but will briefly discuss GM approaches when necessary and how GM could be a guide as to what needs to be targeted via native HPR.

3.2 Major Pests to Cotton Production

The types of sucking and chewing pests that affect cotton differ throughout the world. Several reviews summarise the major pests to cotton and the available sources of resistance and different traits that could be utilised in incorporating HPR (Jenkins and Wilson 1996; Trapero et al. 2016). Specifically, Trapero et al. (2016) summarised the genetic sources of HPR and identified traits in cotton that provide resistance to secondary pests. Therefore, building on those reviews, the major pests and the current status of HPR in commercial cultivars to each pest are summarised below, and Table 3.1 provides a summary of whether the HPR traits were commercially released in a cultivar.

3.2.1 *Helicoverpa* Species

Helicoverpa is a major pest to conventional (non-GM) cotton (Downes et al. 2017). The two *Helicoverpa* species that impact cotton are *H. armigera* and *H. punctigera* and cause similar damage to cotton crops. However, *H. armigera* has developed a high level of resistance to insecticides and is of growing concern to the industry

Table 3.1 The native host plant resistance (HPR) traits available to the major cotton pests and the associated commercially released variety (if applicable)

Insect	Native HPR trait	Deployed into a variety (✓/×)	Name of variety and who released it
Helicoverpa species	Increased gossypol	×	
	Biochemical compounds	×	
	Yellow/orange pollen	×	
	Frego bract	✓	• **Sicot 3**, CSIRO (Thomson 1984)
	Nectariless and glabrous	×	
	Red plant colour	×	
	Extreme hairiness	×	
	Nectariless	✓	• **Stoneville 731N**, Stoneville Pedigreed Seed Company (USDA 2016) • **Stoneville 825**, Stoneville Pedigreed Seed Company (USDA 2016) • **DP 0935 B2RF**, Monsanto Technology LLC (USDA 2016)
Pink bollworm	Nectariless	✓	• **Stoneville 731N**, Stoneville Pedigreed Seed Company (USDA 2016) • **Stoneville 825**, Stoneville Pedigreed Seed Company (USDA 2016) • **DP 0935 B2RF**, Monsanto Technology LLC (USDA 2016)
	Okra	×	
	Glabrous	×	
Spodoptera species	Increased gossypol	×	
Silverleaf whitefly	Okra leaf shape	×	
	Reduced leaf trichomes	×	
	Increased phenolic compounds	✓	• **Ravi**, Cotton Research Institute, Pakistan (Perveen et al. 2001; Yasmin et al. 2008)
	Reduced soluble sugars and proteins	✓	• **Niab-Kiran**, Nuclear Institute for Agriculture and Biology, Pakistan (Rizwan et al. 2021; Nuclear Institute for Agriculture and Biology 2022)
Plant and stink bugs	High gossypol	×	
	Nectariless	✓	• **Stoneville 731N**, Stoneville Pedigreed Seed Company (USDA 2016) • **Stoneville 825**, Stoneville Pedigreed Seed Company (USDA 2016)

(continued)

Table 3.1 (continued)

Insect	Native HPR trait	Deployed into a variety (✓/×)	Name of variety and who released it
			- **DP 0935 B2RF**, Monsanto Technology LLC (USDA 2016) - **UA212ne**, Arkansas Agricultural Experiment Station (Bourland and Jones 2020)
	Frego bract	×	
	Leaf hair	×	
	Glandless	×	
Aphids	Reduced leaf hair	×	
Thrips	Pubescence	×	
	Glandless	×	

The name of the variety is emboldened in the last column

(Joußen et al. 2012). The species composition in the crop varies with seasonal fluctuations, time of the year, and location. Often the *H. armigera* population overwinter towards the end of the season and emerge in the early stages of the next growing season. *H. punctigera* is often the dominant species in the early stages of the growing season but depending on the season, *H. armigera* can have early infestations and become the dominant species (Cotton Australia 2023b). The *Helicoverpa* adults produce a large number of eggs and are mobile, which under favourable conditions can lead to a rapid population growth. *Helicoverpa* attacks all stages of plant growth, and the chewing damage can lead to secondary plant infections (Riaz et al. 2021). Key damage symptoms include chewing holes on soft leaves, squares, and bolls and often lead to shedding off of fruiting bodies. Recent reports show that hybridisation has occurred between *H. armigera* and *H. zea* (native to Brazil) in South America (Cordeiro et al. 2020; Rios et al. 2022). This hybrid breeding between the native and invasive pest could severely impact the current resistance management strategies in cotton (Cordeiro et al. 2020).

Currently, *Helicoverpa* is well controlled due to the deployment of Bt cotton. Three generations of Bt cotton (Bollgard I, II and III) have been developed and commercially adopted. Bollgard I (BG I) contains a single Bt gene Cry1Ac, whereas BG II and III contain two (Cry1Ac and Cry2Ab) and three (Cry1Ac, Cry2Ab, and Vip3A) Bt genes, respectively, providing a higher level and broader spectrum of protection from Lepidopteran pests than BG I. Transgenic cotton cultivars co-expressing Cry1A and CpTI, a cowpea-derived gene encoding trypsin inhibitor, are also being used in commercial cotton production in China (Cui et al. 2011; Li et al. 2020). However, if resistance management protocols such as a requirement for refuge cotton (cotton crops that are planted to generate numbers of susceptible moths that have not been exposed to the Bt proteins in cotton) are not followed correctly, then there will be a need for increased HPR through either native or GM traits.

Before Bt cotton was deployed, large research efforts were invested into finding native traits that conferred resistance and focused on traits such as high gossypol (Jenkins and Wilson 1996), biochemical compounds (Jenkins and Wilson 1996), yellow or orange pollen (Bailey 1981), nectariless (the removal of the nectaries) (Lukefahr et al. 1971), glabrous leaves (Lukefahr et al. 1971), and varying gland densities (Scheffler et al. 2012). Most of these traits confer similar levels of resistance across the Lepidopteran spp. that affect cotton (Jenkins and Wilson 1996) and are summarised below.

- Gossypol, a yellow pigment that is produced in the glands of the plant, is an important allelochemical that confers resistance. Bottger et al. (1964) were the first to report the effect of gossypol in relation to pest resistance and found that cotton germplasm that lacked gossypol glands suffered increased damage from bollworms. Breeding lines with high levels of gossypol have shown reduced insect damage and slower larval growth, and it is largely attributed to the toxicity of gossypol to Lepidopteran species (Lukefahr and Houghtaling 1969; Parrott 1990).
- Biochemical compounds that provide resistance from plant defence mechanisms are commonly identified in the literature. Bi et al. (1997) showed that the biochemical defence compounds of peroxidase, ascorbate oxidase, lipoxygenase, and diamine oxidase are found in higher levels after foliar and pest damage. Therefore, genetic manipulation to overexpress the genes involved in biosynthesis of those defensive compounds could enhance resistance.
- Pollen that is yellow or orange has been shown to reduce the growth of *Heliothis* larvae (Hanny et al. 1979; Bailey 1981). There are no known breeding efforts to use these in the development of cultivars. However, since most Upland cotton cultivars have cream pollen, it may indicate that other pollen colours have a detrimental effect on yield (Jenkins and Wilson 1996).
- Frego bract (narrow and twisting flower bract) has been reported in the literature to provide resistance through the reduction in bollworm oviposition (Maxwell et al. 1969; Lincoln et al. 1971; Thomson 1984). However, there are conflicting reports to the validity of the resistance, and it has been concluded that frego bract is not preferred by the bollworm when other food sources are available. However, in the absence of other food sources, the bollworm will still overwhelm the crop and overcome the resistance. Furthermore, the frego bract trait increases the susceptibility of the genotypes to the ‘plant bug’ complex. To the best of our knowledge, there has only been one commercially produced cultivar with frego bract; Sicot 3 (Thomson 1984).
- The traits of nectariless and glabrous (reduced or no leaf trichomes) leaves reduce the oviposition of the *Heliothis* moths (Lukefahr et al. 1965, 1971). Lukefahr et al. (1965) identified that nectariless cotton genotypes had a reduction of up to 60% in egg deposition by *Heliothis* spp. Genotypes that were both nectariless and glabrous had up to an 80% reduction.
- Red plant colour is a minor researched trait, but Hunter et al. (1965) identified that non-preference resistance was inferred in red leaf types compared to green

foliage. The resistance was largely related to the intensity of the red; the darker the red, the less preference by the pest (Jones et al. 1970, 1989).
- Wannamaker (1957) was one of the first to evaluate the effect of leaf hair density in relation to feeding and reproduction of the boll weevil (Jenkins and Wilson 1996). Extreme hairiness significantly reduces damage from the boll weevil and the plant bug complex. However, although the trait provides resistance, it is of limited value due to the mechanical complications of harvesting hairy leaves. Further, increased hairiness is preferred by the bollworms complex. Hairy leaves have also been associated with short, coarse fibres that are less desirable for spinning.

3.2.2 Pink Bollworm

Pink bollworm (*Pectinophora gossypiella*) is a critical pest to the global cotton industry. The pest is native to Asia but is now present in many of the global cotton producing regions. The pest damages squares and bolls resulting in severe yield and fibre penalties. The pest became present in the USA in 1917 but has since been eradicated through the use of Bt cotton and release of sterile males (Tabashnik et al. 2021). In cotton producing areas of India, pink bollworm has become resistant to the first release of Bt cotton, which can be attributed to the lack of adoption of refuge cotton to some extent (Tabashnik and Carrière 2019).

Bolls of nectariless plants have been noted to have significantly less damage from pink bollworm and have provided a low but consistent level of resistance (Niles 1980; Adjei-Maafo et al. 1983). On the other hand, the glabrous trait is not sufficient to provide resistance (Wilson and George 1981). Wilson and Flint (1987) suggested that the okra leaf shape could provide resistance to pink bollworm as it changes the microclimate around the boll which negatively impacts the pest. In the USA, several okra leaf and nectariless cultivars have been commercially released, but were largely targeted for growing areas where pink bollworm is not a major problem.

3.2.3 *Spodoptera* Species

The *Spodoptera* spp. pests are of growing concern to cotton production (Barros et al. 2010). Cluster caterpillar (*Spodoptera litura*) is found frequently in tropical and coastal environments from India to the Pacific (Maes 2014). The common name comes from the caterpillar's high-density clustering of young larvae up to the first three instars. The young larvae feed on the surface of the leaf and scrape the leaves, whilst the older larvae can completely devour the leaves, they often feed on reproductive tissue of cotton. Large infestations of the cluster caterpillar can lead to total defoliation and have a severe impact on production (Bhattacharyya et al. 2007; Maes 2014). A clear example of this is the collapse of the cotton industry in Northern Australia in the 1970s of which *Spodoptera* spp. were a key pest. Currently, control is provided by Bt cotton through Cry1Ac and Cry2Ab.

Lesser armyworm (*Spodoptera exigua*) originated from Southeast Asia and is now found in several cotton producing countries. The pest activity is impacted heavily by climatic conditions and is more prevalent in warmer climates. Although it is considered a minor pest for young cotton crops, the lesser armyworm can be a severe defoliator to fruiting cotton by chewing all of the green tissue of leaf lamina except the veins. Fall armyworm (*Spodoptera frugiperda*) is a tropical insect that is an endemic pest to many cotton producing regions of the world. Damage by fall armyworm can range from minimal to severe, and fruiting bodies are often the most damaged part of the crop. De-topping of cotton plants and total defoliation can occur under high infestation levels (Vyavhare 2017).

HPR research against *Spodoptera* spp. has not been as focused as for *Helicoverpa* spp. However, traits such as increased levels of terpene and aldehydes, e.g. gossypol, can be deployed in management programs for *S. frugiperda* (Jesus et al. 2014). Cotton cultivars containing only Cry1Ac have been shown to be not much more efficient in controlling *S. frugiperda* (Adamczyk Jr et al. 1998) and can increase tolerance of individuals feeding on the cultivar (Adamczyk Jr and Sumerford 2001).

Although the above-mentioned native traits were developed in an attempt to provide resistance to Lepidopteran pests, they were largely unsuccessful as the level of resistance they provided was simply not high enough to prevent significant pest damage to the crop. Given that Bt cotton provides stable and robust resistance to Lepidopteran pests, developing HPR cotton cultivars in the form of GM has by far seen the largest investment and is the most successful deployment of an HPR trait in cotton. In 2019, 18 countries cultivated genetically engineered Bt cotton with a total area of ~25.7 million hectares (ISAAA 2019). The major insecticidal Bt genes that are deployed in commercial cotton cultivars are Cry1Ac, Cry2Ab, and Vip3A. But, in the past decade, several new entomotoxic Cry proteins from Bt have been expressed in cotton individually or in different combinations with other insecticidal proteins to evaluate their efficacy in resistance to different species of insect pests; including non-lepidopteran insects that are not targeted by the Bt genes currently used (Table 3.2). For instance, transgenic cotton plants expressing Cry10Aa are highly resistant to *Anthonomus grandis* (cotton boll weevil), with a mortality rate of 90–100% (Ribeiro et al. 2017). For the Bt proteins with low insecticidal efficacy, amino acid optimisation has been used to change the protein characteristics and to enhance their efficacy. A good example of such optimisation is the creation of Cry51Aa2.834_16, a new variant of Cry51Aa2 (Gowda et al. 2016). The transgenic cotton plants expressing Cry51Aa2.834_16 can reduce populations of both *Lygus hesperus* and *L. lineolaris* more significantly than those expressing Cry51Aa2. Commercially acceptable transgenic events have been identified and will be introgressed into elite commercial cotton cultivars for release. However, the Bt genes have specificities which only allows it to be a good defence against specific classes and is not a silver bullet for pest management.

Table 3.2 Genes from *Bacillus thuringiensis*, plants and insects being evaluated for insect resistance in cotton

Transgene	Recipient cultivar	Target pests	Transformation approach	References
Insecticidal genes				
Single gene				
Vip3A or *tvip3A*	Zhongmiansuo 35	*Spodoptera frugiperda*, *S. exigua*, and *Helicoverpa armigera*	AMT	Wu and Tian (2019)
ASAL	NC-601	*Amrasca devastans* and *Bemisia tabaci*	SAT	Vajhala et al. (2013)
Cry51Aa2.834_16	DP393	*Lygus hesperus* and *L. lineolaris*	AMT	Gowda et al. (2016)
Cry2AX1	Coker 310	*H. armigera*	AMT	Dhivya et al. (2016)
Cry1Ac	Coker 310FR	*H. armigera*	AMT	Singh et al. (2016)
Cry1Ia12	BRS Cedro	*S. frugiperda* and *A. grandis*	PMT	de Oliveira et al. (2016)
Tma12	Coker 312	*B. tabaci*	AMT	Shukla et al. (2016)
Cry10Aa	BRS 372	*Anthonomus grandis*	AMT	Ribeiro et al. (2017)
S. rolfsii lectin	Sahana	*Aphis gossypii* and *S. litura*	SAT	Vanti et al. (2018)
Cry2ax1	Coker 310	*H. armigera*	AMT	Jadhav et al. (2020)
Cry1AcF or *Cry2Aa*	Pusa 8–6	*H. armigera*	SAT	Karthik et al. (2021)
Cry5Aa	n/a	*H. armigera*	PMT	Zhao et al. (2021)

Cry1Ia12	GS-01	*Pectinophora gossypiella*	SAT	Tariq et al. (2022)
Multiple genes				
Vip3A or Vip3a + Cry1Ab	n/a	*H. zea* and *H. virescens*	AMT	Bommireddy et al. (2011)
Cry1Ac + CpTI	CRI23	*H. armigera*	PMT	Cui et al. (2011)
NaPI + StPin1A	Coker 315	*H. armigera*	AMT	Dunse et al. (2010)
Cry9C + Cry1Ac or Cry9C + Cry2A	Simian 3	*S. litura*	AMT + cross	Li et al. (2014)
Vip3AcAa + Cry1Ac	Coker 312	*S. litura, S. exigua,* and *Agrotis ipsilon*	AMT	Chen et al. (2017)
Cry1Be + Cry1Fa	n/a	*S. litura and Ostrinia nubilalis*	AMT	Meade et al. (2017)
Vip3AcAa + Cry1Ac	Coker 312	*H. armigera*	AMT	Chen et al. (2018)
Cry1Ac + GNA	GSN-12	*A. gossypii* and *S. littoralis*	SAT	Khabbazi et al. (2018)
Cry1Ac + Cry2Ab	Coker 312	*Spodoptera litura*	AMT	Siddiqui et al. (2019)
Cry2Ab + Cry1F + Cry1Ac	Narasimha	*H. armigera* and *S. litura*	SAT	Katta et al. (2020)
Vip3Aa + ASAL	CEMB33	*B. tabaci*	SAT	Din et al. (2021)
Cry1Fa + Cry32Aa + AtPME + AnPME	Eagle-2	*H. armigera, P. gossypiella,* and *Earias fabia*	SAT	Razzaq et al. (2021)
Cry3Bb1 + Cry3	Eagle-2	*P. gossypiella* and *H. armigera*	SAT	Zafar et al. (2022)
Vip3Aa	CKC-01 (with *Cry1Ac + Cry2Ab*)	*H. armigera*	SAT	Shad et al. (2021)
Host-mediated gene silencing (HMGS) by RNAi				

(continued)

Table 3.2 (continued)

Transgene	Recipient cultivar	Target pests	Transformation approach	References
Single gene				
dsCYP6AE14	R15	*H. armigera*	AMT	Mao et al. (2011)
dsHMG-CoA reductase	YZ1	*H. armigera*	AMT	Tian et al. (2015)
dsNDUFV2	R15	*H. armigera*	AMT	Wu et al. (2016)
dsCYP392A4	Jimian 14	*Tetranychus cinnabarinus*	AMT	Shen et al. (2017)
dsHaHR3	F15	*H. armigera*	PMT	Han et al. (2017)
JHMT or *JHBP*	W0	*H. armigera*	AMT	Ni et al. (2017)
Ghr-miR166b	HS6	*B. tabaci*	SAT	Wamiq and Khan (2018)
dsAILIM	Jin668	*Apolygus lucorum*	AMT	Liang et al. (2021)
dsAgCYP6CY3-P1	n/a	*A. gossypii*	n/a	Zhang et al. (2023)
Multiple genes				
dsCYP6AE14 + *GhCP1*	R15	*H. armigera*	AMT	Mao et al. (2013)
JHMT or *JHBP* + *Cry1Ac*	W0	*H. armigera*	AMT	Ni et al. (2017)
COPβ + *EcR*	Pusa8–6	*A. biguttula*	SAT	Karthik et al. (2023)

AMT Agrobacteria-mediated transformation followed by tissue culture, *PMT* pollen-tube-mediated transformation, *SAT* shoot apical meristem transformation, *n/a* not available

3.2.4 Silverleaf Whitefly

SLW (*Bemisia tabaci* B-biotype) is a serious pest to cotton due to its resistance to many insecticides and ability to vector serious cotton viruses. SLW feeds on the plant sap and causes wilting, dropping of leaves, and in extreme cases, may result in death of the plant. However, the primary damage is caused by sucking large quantities of plant sap and excretion of honeydew which contaminates the lint and creates problems during processing, and ultimately results in an economic loss to the grower (Johnson et al. 1982; Rao et al. 1989; Hequet and Abidi 2002).

There is currently no known resistance to SLW in current commercial cotton cultivars. Morphological resistance has been identified through an okra leaf shape (deeply invaginated leaf lobes) and reduced leaf trichomes (Thomson et al. 1987; Butter and Vir 1989; Fitt et al. 1992; Miyazaki et al. 2013). Although the resistance has been identified, the deployment of the non-preference trait is limited by the impact on yield. An okra leaf shape has less leaf area and consequently reduced photosynthetic capacity and can result in a yield penalty. Whilst the literature supports the possibility of a yield reduction associated with the okra-glabrous trait, Thomson (1994) showed that high-yielding okra leaf breeding populations could be developed. High-yielding commercial okra leaf cultivars have also been released (Reid 1998). Several studies have identified that resistance can also be conferred by an increase of phenolic compounds, tannins (Perveen et al. 2001), flavonoids, and a reduction in soluble sugars and proteins (Rizwan et al. 2021). Breeding for increases in phenolic compounds has seen some success in the literature in other crops (Balyan et al. 2013; Atak et al. 2021), yet is often correlated with a negative impact on other commercially important traits (Kaushik et al. 2015). Leaf gossypol glands have also been linked with increased resistance to whitefly (Khalil et al. 2017; Rizwan et al. 2021).

3.2.5 Plant and Stink Bugs

A range of various bugs (Suborder Heteroptera) can cause damage to cotton, including *Lygus, Creontiades, Nezara, Campylomma,* and *Dysdercus.*

Lygus (*Lygus* spp.) feed on cotton terminals and fruiting bodies. Several *Lygus* species can occupy a cotton crop which include the western tarnished plant bug (*Lygus hesperus*), tarnished plant bug (*Lygus lineolaris*), and the pale legume bug (*Lygus elisus*). The damage to cotton includes stunted growth, deformed bolls, shedding of squares and bolls, and damaged seed (Layton 2000).

Mirids (*Creontiades* spp.) are a sucking pest to cotton and both the adults and nymphs feed by piercing the plant tissue and releasing a chemical that damages the nearby cells and results in a wide variety of symptoms including leaf damage, wilting, deformity, shedding and deformity of bolls, and reduced yield and fibre quality. Mirids are a challenging pest to control as they are extremely mobile, and the population numbers can fluctuate rapidly (Cotton Australia 2023b).

Three stink bug species primarily affect cotton; the green stink bug (*Acrosternum hilare* Say), the southern green stink bug [*Nezara viridula* (L.)], and the brown stink bug [(*Euschistus servus* (Say)]. Population levels of the three species vary extensively across geographical regions and are widely distributed throughout the world. Due to the reduction in applications of broad-spectrum insecticides to control *Lepidopteran* pests, the stinkbug has increased in prevalence in recent years. They feed on bolls of cotton plants, and the majority of the yield loss comes from damage to the younger bolls (<10 days old). Excessive stink bug damage can cause a reduction of fibre quality, in the form of stained lint and poor colour grades (Kamminga et al. 2012).

There are very few commercial cultivars with targeted incorporated HPR to plant bugs (Jenkins and Wilson 1996). Germplasm has been identified that is resistant to *L. hesperus* which includes species related to *G. hirsutum* (Tingey et al. 1975) and germplasm with high gossypol content (Tingey et al. 1975; Schuster and Frazier 1976). Benedict et al. (1983) confirmed that the absence of gossypol in seeds and plant tissues increased the susceptibility to plant bugs. The nectariless trait has conferred some resistance to plant bugs by causing reduced oviposition and reduced nectar as a food source for the nymphs (Schuster et al. 1976; Bailey et al. 1984; Jenkins and Wilson 1996). Attempts to combine the frego bract trait with the nectariless trait have shown increased resistance to plant bugs (Jones et al. 1989), although the frego bract trait by itself increases susceptibility to plant bugs (Milam et al. 1985). The incorporation of the nectariless trait has shown promise in the past as there has been no major negative impact on agronomic or fibre quality characteristics linked with the trait (Meredith Jr and Bridge 1977; McCarty Jr et al. 1983).

As mentioned previously, the development of *Lygus* resistant cultivars has shown promise through a transgenic approach (Gowda et al. 2016). Transgenic cotton that expressed a variant of a Bt crystal protein (Cry15Aa2) significantly reduced the *Lygus* spp. in field trials, and the germplasm containing the variant has been moved forward to the cultivar development pipeline. The trait has been named 'ThryvOn'™ (Bayer 2023).

3.2.6 Aphids

The cotton aphid (*Aphis gossypii*) causes damage to all plant parts and is known to transmit various viral diseases including the economically devastating cotton blue disease (Aboughanem-Sabanadzovic et al. 2019; Bag et al. 2021; Parkash et al. 2021; Tarazi and Vaslin 2022) and cotton bunchy top disease (Reddall et al. 2004; Ellis et al. 2013, 2016). Similar to SLW, aphids also secrete honeydew which causes lint contamination and challenges for lint processing. If large aphid populations are left uncontrolled for several weeks, significant yield loss can occur. Dunnam and Clark (1939) reported that the number of aphids increased in correlation with the number of trichomes on the lower leaf surface and concluded that a reduced hair pattern on the leaf could be a potential HPR trait.

3.2.7 Thrips

A number of thrips species cause damage to cotton, including *Frankliniella* spp. and *Thrips* spp. They are commonly early seedling pests, and primarily feed on the leaves and early squares. Damage can result in silvering of the leaves and damage to the plant terminal (Cotton Australia 2023b). Under some conditions, heavy infestations may reduce stands, stunt plants, and delay fruiting and maturity. However, under favourable growing conditions, cotton can often recover completely from early thrips damage. In areas where seedling emergence typically occurs under warm conditions, thrips are usually of little concern. Despite being a pest, thrips are a useful control of two-spotted spider mites (TSSM) as they predate on TSSM eggs.

Pubescence (the presence of trichomes) is associated with resistance to thrips at the seedling stage (Jenkins and Wilson 1996). However, the deployment of the trait increases oviposition of bollworms and whitefly and has been associated with trash and mechanical harvesting issues (Byrd et al. 2016), so is not an effective nor practical HPR solution in countries that use mechanical harvesting. Miyazaki et al. (2017) identified that some diploid cottons provide resistance to thrips.

3.3 Breeding for Host Plant Resistance to Pests in Cotton

3.3.1 Breeding HPR Traits by Conventional Approaches

Modern cotton breeding programs aim to exploit novel variation for breeding targets and select stable cultivars that are adapted to the local environment. The overarching themes of most cotton breeding programs are similar—increase yield and fibre quality, increase pest and disease resistance, and enhance adaptation to regional constraints. Primarily, yield is the most prominent breeding target in cotton breeding programs as this is what the grower is paid for. The breeding methodology depends on the breeding target, heritability of the trait, technology available for phenotypic and genotypic assessments, and available germplasm. Pure line development is a key goal and results in stable and uniform cultivars. India and China engage in cotton hybrid development, but the majority of programs in other countries focus on pure line development. The generalised cotton breeding methodology begins with the recombination of desired traits from individual lines by hybridisation (pedigree and backcross breeding methods are the most common) and consequent inbreeding to create variation within a population. Successive rounds of selections are performed to select for the desired phenotype and to fix traits. The breeding lines are then evaluated across multiple environments (or multiple different sites within a target environment) and compared to current commercial cultivars. Breeding lines that outperform (for one or more traits) what is currently available on the market are commercially released to the industry.

Breeding for HPR to a biotic stress is generally only considered if there is no other suitable management strategy due to the time and cost it takes to identify and introgress the resistance into an elite background. Egan and Stiller (2022) outlined the factors that must be present for HPR to be considered as a viable investment decision. In summary, the pest or pathogen must be widespread, causes significant yield loss and there be no cost effective and durable management strategy. For a HPR trait to be pursued by a breeder, there has to be native genetic variation for the trait. Commonly for polygenic traits such as pest resistance, variation in resistance is often continual rather than discrete. If there is no variation present in the germplasm, then it must be attempted to be created through mutagenesis or molecular techniques, e.g. gene editing. In the situation where a breeder is unable to identify HPR in their germplasm, they may look to import/exchange germplasm with international genebanks or institutions. However, licensing and biosecurity requirements can make this process long and complex.

Traits that provide resistance to pests include one or more defence mechanisms that often function in a complex manner and have strong interaction with the environment. Resistance is often defined as chemical or morphological, or genomic regions are identified that control the resistance. Chemical resistance is often observed with compounds such as flavonoids, tannins, and terpenoids (Wink 1988; Hagenbucher et al. 2013), while morphological resistance has been seen in plant architecture and trichome manipulation, such as the okra leaf shape (Miyazaki et al. 2013).

The most common approach to the development of a resistant cultivar can be categorised into three steps: (1) evaluate germplasm to identify sources of resistance, (2) introgress the resistance into an elite background, and (3) deploy the cultivar into current crop management systems. Due to the long timelines and large investment associated with integrating HPR into an elite background, the selection pressure for resistance in the material is high to ensure that only the most resistant material is moved forward for advancement.

In the case of pest resistance, the first step is to thoroughly understand the interaction of the crop and pest. Once this is understood, a wide screen of germplasm (often from diverse genetic backgrounds and includes landraces, international cultivars, and related species) is conducted in a field trial that is purposefully infested with the pest. This is the most efficient way of identifying if any genetic background has resistance to the pest. If a breeder is unsuccessful in identifying resistance to the pest, they may look outside of their available germplasm collection for resistance alleles. Trapero et al. (2016) summarised the genetic sources of HPR and identified traits employed in cotton against pests that are traditionally considered secondary.

Once resistant material is identified, a high-throughput screening method (often in a glasshouse or growth cabinet) is developed to accurately screen for resistance that is reflective of field observations. The methods often involve uniformly infesting the germplasm with the pest and evaluating survival, damage, and other phenotypic scores. High-throughput screening methods allow germplasm to be accurately screened at scale and aid in decreasing the long timelines associated with HPR breeding activities. However, it is critical that the results from the controlled environment screening method are reflective of field resistance. Field resistance is defined as the ability of germplasm to resist a stress compared to control cultivars. However, this can be complex to replicate in a glasshouse environment, and in some case not possible, as often pest behaviour differs in controlled conditions in comparison to the field. Although resistance is often genetically controlled, it is heavily influenced by environmental conditions, including temperature, rainfall, light intensity, crop nutrition, genotype, plant growth stage, and the presence of other pests. The breakdown or lack of identified field resistance in controlled conditions could be attributed to the plant being stressed by factors that are not present in the field. In controlled environment pest screenings, often the intensity of the pest infestation is higher than what is seen under commercial production conditions, and this could cause the resistance to breakdown. Despite the challenges, several screening techniques have been developed to identify resistance to different insects in cotton; thrips (Conzemius et al. 2023), Jassid (Batra and Gupta 1970), whitefly (Sukhija et al. 1986; Butter and Vir 1989), and leafhopper (Mekala 2004).

The ease of the introgression of resistance into an elite background is largely determined by where the source of the resistance originated from, i.e. primary, secondary, or tertiary germplasm, in combination with any ploidy differences of the elite background and the source of resistance, and the genetic complexity of the trait. In cotton, resistance to a pest is commonly polygenic, and often the variation in the level of resistance is continual. The introgression is complicated by the environmental interaction between the resistance traits and the genetic variability of the pest. Due to the polygenic nature of many resistance traits, during the recombination process, resistance may be partially or completely lost, and segregating generations may have to be regenerated to recover the resistance in an elite background.

To aid in the efficiency and speed of HPR breeding activities, molecular tools, such as deoxyribonucleic acid (DNA) markers, can be developed once a source of resistance and a desired phenotype have been identified. One of the approaches that can rapidly locate the genetic region(s) responsible for the resistance is mapping-by-sequencing, which uses two DNA samples pooled separately from the resistant and susceptible individuals of a segregating population. Molecular markers within the genetic region(s) and linked to the resistance are then designed and adopted to guide selection of resistant progeny (Zhu et al. 2017). Egan and Stiller (2022) stated that as pest resistance is often found in wild or unadapted germplasm, the development and uptake of molecular markers are beneficial for breeding efforts—particularly with the introgression into elite backgrounds that contain industry relevant GM trait packages. As GM trait packages with resistance to target pests and herbicides are critical in many cotton producing countries, the introduction of the GM package can only begin once the source of resistance is introgressed into the predominantly cultivated species, *G. hirsutum*, and has stable inheritance.

The current genetic limitations on the use of HPR may be overcome by new genetic engineering techniques. These tools will be helpful to create new diversity in germplasm but will likely add to the already long breeding timeline (Maxwell 1985).

3.3.2 Incorporating HPR Traits in Cotton by Genetic Engineering

The incorporation of genes encoding insecticidal proteins or of ribonucleic acid (RNA) molecules generating small RNAs targeting genes essential for pest survival into crop genomes by genetic engineering provides crops resistance against insect pests. Genetic engineering is thus the fast track for improving HPR of crops, including cotton, to insect pests. But successful implementation of genetic engineering for HPR in cotton requires information on the genes encoding insecticidal proteins and the genes critical for the growth and development of the pests, as well as efficient gene transformation technologies.

Apart from Bt entomotoxic Cry proteins, plant-derived insecticidal proteins have been expressed in cotton to confer resistance to insect pests (Table 3.2). Protease inhibitors (e.g., CpTI) and lectins (e.g., *Allium sativum* leaf agglutinin, ASAL) are the two major types of proteins being used in cotton, because they have been shown to confer resistance to major sap-sucking insects in other plants. A recent study has also investigated the insecticidal efficacy of pectin methyl esterase (PME) in cotton. PME catalyses de-esterification of pectin in cell wall to regulate the response of plants to insect infestation. Bioassay using transgenic cotton expressing two PME genes (from *Arabidopsis thaliana* and *Aspergillus niger*) and two Cry genes (Cry1Fa and Cry32Aa) showed 100%, 95%, and 70% mortality rate for larvae of *H. armigera*, *Earias fabia* (spotted bollworm), and *Pectinophora gossypiella* (pink bollworm), respectively, which was higher than the transgenic cotton expressing only the two Cry genes (Razzaq et al. 2021). Another study found that constitutive expressing Tma12, a chitin-binding domain containing protein from the fern *Tectaria macrodonta*, in cotton can control >99% of a whitefly population. However, it is unclear whether the insecticidal activity of Tma12 is contributed by its chitinase activity (Shukla et al. 2016).

RNA interference (RNAi) is a sequence-specific gene silencing mechanism by which small RNAs repress the activity of target gene post-transcriptionally by cleavage or translational repression of messenger RNA (mRNA). Host-mediated silencing of insect genes (HMGS) by RNAi for control of insect pests is achieved by insect ingestion of host plant tissue containing RNA molecules generating small RNAs that target essential insect genes. The first commercial transgenic double-stranded RNA (dsRNA) product is maize SmartStax® Pro that is engineered to express dsRNA targeting *Diabrotica virgifera* Dvsnf7 and was approved in Canada (2016) and the United States (2017) (Head et al. 2017). The success of using HMGS in pest control depends on the choice of target genes that are critical for the survival of insect pests, the adoption of suitable RNA precursors for generating small RNAs required for RNAi and ensuring high expression of the small RNAs in insect cells.

Many insect genes have been investigated for their suitability to be used as RNAi targets in cotton, such as genes encoding juvenile hormone methyltransferase (Ni et al. 2017) and a subunit of mitochondrial complex I that catalyses NADH dehydrogenation in respiratory chain (Wu et al. 2016). Effectors are released by insects upon feeding on host plants to conquer host defence. Repressing the effector genes abolishes the insect's anti-defence capability against host defence, so insect genes encoding effectors, such as Highly Accumulated Secretory Protein1 and R-like Protein 1 from *H. armigera* (Chen et al. 2019, 2023), are potentially ideal targets of HMGS. Other potential target-insect-genes of HMGS are those acquired by insects from other species via horizontal transfer, because the horizontally transferred genes tend to be insect unique and important for growth and survival of insects, such as the gene encoding squalene synthase in whitefly (Feng et al. 2022).

The most commonly used RNA molecule for delivering RNAi small RNAs in cotton is double-stranded RNA (dsRNA) (Table 3.2). Upon intake transgenic cotton tissues and/or sap by insects, dsRNA is processed by the insect RNA machinery to generate small RNAs to silence the target insect gene. But several other types of RNA precursors have been tested for their efficacy in HMGS by RNAi in cotton. Overexpressing the cotton endogenous microRNA (miRNA) (ghr-miR166b) that is predicted to target mitochondrial ATP synthase of *B. tabaci* (whitefly) in cotton has been shown to reduce the whitefly population and to suppress the spread of viral disease transmitted by whitefly (Wamiq and Khan 2018). A recent study also demonstrated the possibility of using artificial trans-acting siRNAs (tasiRNAs) in simultaneous control of multiple pests and pathogens in cotton. In the study, the Arabidopsis miR173 and the target-insect-genes engineered with a 22-nt upstream sequence recognised by miR173 were integrated into a single construct and overexpressed in cotton, and the endogenous target-insect-genes are repressed by the artificial tasiRNAs generated from the overexpressed target-insect-genes as a result of miR173-mediated cleavage of the engineered target-insect-genes (Karthik et al. 2023).

For HMGS by RNAi to be effective in insect pests, a high quantity of the RNA precursors needs to be delivered into insect cells. One way to achieve that is to mitigate and/or avoid degradation of the RNA precursors by host plant RNAi machinery. Expressing RNA precursors from the chloroplast genome can escape degradation imposed by host plant RNAi machinery that is present in nuclei but absent in chloroplast, leading to accumulation of RNA precursors (Jin et al. 2015; Wu et al. 2022). Alternatively, the small RNA, such as artificial miRNA, targeting insect genes can be incorporated into RNA precursor from insects to avoid host plant RNAi machinery and to deliver the intact RNA precursors into insect cells, ensuring production of high quantity of small RNAs in insect cells to effectively repress target-insect-genes (Bally et al. 2020).

Pest control by genetic engineering requires the transfer DNA (T-DNA) containing the insecticidal gene and/or the RNA precursor generating siRNA (small interfering RNA), miRNA, or tasiRNA targeting insect gene to be stably integrated into the host plant genome. Thereby, generation of transgenic cotton expressing insecticidal gene and/or RNA precursor is the first step to fulfill the goal. Production of transgenic cotton plants involves two major processes: gene transformation and plant regeneration, both are the bottlenecks for genetic engineering in cotton when using *Agrobacterium*-mediated transformation followed by tissue culture, as cotton is a plant species recalcitrant for *Agrobacterium*-mediated gene transformation and plant regeneration, and only few genotypes are transformable. Genotype dependency of cotton transformation hinders direct application of genetic engineering in elite commercial cotton cultivars. As a result, all commercial Bt cotton cultivars were bred by introgression of the Bt gene(s) from transgenic donors into conventional commercial cotton cultivars through a backcross breeding strategy, which usually takes several years to accomplish, compromising rapid adoption of novel gene technologies.

Deploying tissue-culture independent *in planta* transformation methodologies bypasses genotype dependency of cotton transformation. One such methodology is the shoot apical meristem transformation (SAT) that targets T-DNA to the growing shoot apical meristem in vitro by co-cultivation of mature embryos with *Agrobacterium* and allows the generation of transgenic plants ex vitro (Vajhala et al. 2013). This approach has been adopted by the cotton community, particularly in the past a few years, to investigate the functionality of insecticidal genes and the efficiency of HMGS by RNAi in diverse cotton genotypes (Table 3.2), including commercial Bt cotton cultivar with *Cry1Ac* and *Cry2A* (Shad et al. 2021). The major disadvantage of SAT is the low frequency of transgenic events, which can be compensated by using an increased number of mature embryos.

Pollen magnetofection is a novel gene transformation methodology developed recently and has been successfully used to integrate transgenes into cotton genome without tissue culture (Zhao et al. 2017). This approach uses positively charged magnetic nanoparticles as the cargos of recombinant DNA and magnetic field as the force to deliver the recombinant DNA into pollen grains, which are then used in pollination to produce transgenic seeds. Like SAT, this approach suffers from low transformation rate. But with the rapid advancement in the development of diverse nanomaterials, pollen magnetofection or similar technologies is anticipated to be widely adopted by the cotton community for gene transformation because of their relatively low technique demand compared to the approach of *Agrobacterium*-mediated transformation followed by tissue culture.

3.4 How Valuable Is an HPR Trait?

Determining the value of a HPR trait can be complex. Breeding for HPR is a long-term and large investment for a breeding program. There is substantial literature published that highlights the basic research of identifying a trait the confers resistance, but the follow through of the incorporation of these traits into commercial cultivars is minimal. The lack in uptake of the resistance traits is largely governed by the efficacy of the trait together with the practicality of deploying the trait, i.e. the associated deleterious effects and/or negative impact on yield and/or agronomic performance. As previously discussed, the HPR traits that provide resistance can increase susceptibility to other pests or have a severe impact on yield. The impact that a trait has on overall performance is deemed the 'trait trade-off'. Trait trade-offs are common when breeding for novel breeding targets, and the value is ultimately decided by the return on investment (ROI).

Private breeding programs and companies are all largely driven by revenue, so the economic incentive of pursuing a trait is a key factor in their decision-making. The driver of investment decisions in breeding programs and companies is most commonly yield. For pests that do not cause significant damage and for which sustainable control options are in place, the breeding programs are more likely to breed for better local adaption and higher yield. The incentive to develop HPR to a pest has to be large enough that it would cause a loss of revenue for the company, or in a public breeding program, the benefit has to be large enough to justify the time and resources. The seasonal variation of pest/host–plant complexes can complicate the landscape when justifying the ROI for a HPR trait. All breeding programs and companies have defined resources and they must allocate them when and where appropriate. Three scenarios are outlined below to illustrate.

- Scenario 1: HPR to a pest is coming from a species related to *G. hirsutum* and is going to take 15+ years to incorporate the resistance and develop an elite line. The pest is seasonally variable, and in seasons where there is high pest abundance, chemistry is used as a control method. At worst, a 5% yield penalty occurs. In this situation, it would be exceptionally hard for a breeding program to justify the ROI for this trait under the current cotton production system.
- Scenario 2: HPR to a pest has been identified in a *G. hirsutum* landrace cotton and will take 5–8 years to incorporate the resistance and develop an elite line. The pest is consistently present in most seasons and the chemistry used to control it is expensive and unsustainable for growers. Yield penalties of up to 15% have been reported. In this situation, due to the shorter timeline and cost of other control methods, it would be likely that a breeding program could justify the ROI for this trait under the current cotton production system.
- Scenario 3: HPR to a pest has been identified in a species related to *G. hirsutum* and will take 15+ years to incorporate the resistance and develop an elite line. The pest is devastating to the majority of cotton production areas in a large geographic area and has started to become resistant to chemistries used as a control method. Yield penalties of up to 40% are common. In this situation, the development and deployment of the HPR trait are critical for the survival of the industry and would heavily justify the ROI for this trait under the current cotton production system.

However, the suggested outcome of all the above-listed scenarios is dependent on the current control method and the social perception of the control method. Therefore, in some situations, environmental and social pressures may influence the justification of the HPR trait deployment.

The loss of an industry is the biggest imperative for breeding companies to pursue HPR traits. If a pest is damaging enough to collapse an industry, whether it be because the pest has become resistant to chemistries normally used to control them or there are no other available control options, the financial incentive for breeding companies to invest money into identifying and incorporating HPR traits is critical. Potential changes in legislation on the use of certain chemistries could result in an HPR trait becoming easier to justify the ROI. However, it is unlikely that a chemistry would be completely banned, rather restrictions on the timing and conditions of when it could be sprayed would be imposed largely for environmental/sustainability reasons.

3.5 Conclusions

The success of cotton production since the inception of the global industry has been laced with the parallel success of pests. As the effects of climate change alter the environments that we currently grow cotton and previously deemed unsuitable areas to grow cotton become suitable, new pests will consequently move into areas where they were not seen before.

HPR is commonly agreed upon as the most desirable means to control insect pests in cotton crops. HPR will remain a critical component of the production system for cotton, and resistant cultivars will remain the foundation upon which all other components of the crop production and pest control systems operate. Historical breeding efforts have identified HPR traits in cotton germplasm but very few have been advanced through to be incorporated into a commercial cultivar. The deployment of Bt cotton is one of the great GM success stories but does indicate both the frailties of relying on native HPRs, i.e. it was not successful, and the risks associated if Bt resistance occurs.

The continued success of HPR breeding in cotton will rely heavily on the continued screening of germplasm and the parallel development of biotechnological tools that can increase accuracy and speed of breeding decisions. However, the enormity of the work for HPR breeding should not be underestimated, and the adaptation of the pest to resistant breeding lines and the changing seasonal environment must always be revisited and evaluated. Furthermore, there is a never-ending list of insects that cause economic damage to cotton, and it is often questioned why there are not pest-resistant cultivars to all critical insects. Often it is overlooked that an increase in yield potential is a pest tolerance mechanism, and it is commonly forgotten about that current cotton cultivars carry a significant increase in resistance to many of the critical cotton pests.

The ever-advancing molecular tools are making breeding activities easier to deploy HPR through marker-assisted trait introgression to avoid time-consuming, and sometimes not so accurate, phenotyping-based trait selection. Once the causative mechanism is known, the HPR trait can be replicated in the elite genetic background by genotype-independent genetic engineering. The bottleneck limiting the adoption of molecular tools in breeding HPR traits in cotton is lack of target genes, so screening all three gene pools (primary, secondary, and tertiary) for pest resistance is highly encouraged.

To help aid in accommodating for HPR trait development, it is critical that the economic value of the HPR trait is estimated under both infested and non-infested environments so that growers can see the economic benefit. Loss of an industry, pest resistance to chemistries or previously resistant cultivars, and to a lesser extent, legislation that restricts chemical application are the three largest incentives to validate a ROI for an HPR trait.

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Current Status of Host Plant Resistance to Insects in Rice and Future Perspectives

4

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Abstract

Rice is grown in diverse ecologies, and the crop is attacked by large number of insect pests of which planthoppers, stem borers, leaf folders and gall midge cause considerable yield losses, which may vary from 10% to 90%. This chapter reports the current status of research in host plant resistance (HPR) to major rice pests, as HPR is considered as the most economical and eco-friendly component of insect pest management. The journey from various phenotyping techniques to identification of resistant sources from diverse gene pools, through precise studies on mechanisms and genetics of resistance to genes, etc., is discussed at length. For pests like yellow stem borer, where very few sources of tolerance are available, novel strategies that have been developed for tackling this insect pest, like exploitation of host plant susceptibility, induced resistance, Bt transgenic and use of RNAi tools for pest suppression are discussed. In pests like gall midge and brown planthopper, HPR has an influence on the evolution of biotypes and on the symbionts that are harboured. To address the problem of multiple biotic stresses, marker-assisted backcross breeding is considered a potent tool, which helps in introgression of known resistance genes in the desired varietal background. With the availability of genomics resources for both rice host and insect pests like brown planthopper, white-backed planthopper, gall midge, leaf folder, yellow and striped stem borer, novel techniques like genomic selection, gene editing to address the issue of pest resistance in some of the incalcitrant traits are also discussed. Though development and deployment of a durable resistant variety with phenotypically acceptable traits are the need of the hour, the dire need for precision phenotyping keeping in view the pest behaviour and the target traits to

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address the location-specific needs is emphasized. Further, the need for a designer rice, addressing the location-specific needs, which involves both development of a resistant variety on one hand followed by strategic deployment of resistance genes as per the pest population prevalent in a location, consumer preference and market demands are emphasized in this chapter.

Keywords

Rice · Insect pests · Damage · Host plant resistance · Screening protocols · Molecular tools · Breeding strategies · Resistant varieties · IPM

4.1 Introduction

Rice is grown in several countries across the globe and is the staple cereal for teeming billions, and for many Asian countries including India, it is a way of life. With the rapid increase in the population growth, and the responsibility to feed the mankind with nutritious diet, there lies an unprecedented challenge for the rice workers to meet the demands for higher production, productivity and nutritious diets to cater to the needs of the increasing needs of the poverty stricken, malnourished mankind. Achieving food security through rice is challenged by insect pests, which reduce yields by up to 90%.

4.1.1 Insect Pests of Rice

Among the various pests attacking the rice plant, namely planthoppers, stem borers, leaf folders are universal and infest the rice crop at all stages of crop growth, i.e., from nursery to grain-filling stage causing significant economic loss to the crop. There are other pests like rice gall midge, thrips, leaf mites, which cause economic loss at vegetative phase (Plate 4.1). Some of the pests like gundhi bug, ear-cutting caterpillar attack the crop at reproductive phase. Of the many pests that infest the rice crop, most important are stem borers: yellow stem borer (YSB), *Scirpophaga incertulas* (Walker); striped stem borer (SSB), *Chilo suppressalis* (Walker); and pink stem borer (PSB), *Sesamia inferens* (Walker); planthoppers: brown planthopper (BPH), *Nilaparvata lugens* Stål; white-backed planthopper (WBPH), *Sogatella furcifera* Horvath; and small brown planthopper (SBPH), *Laodelphax striatellus*; leafhoppers: green leafhopper (GLH), *Nephottetix virescens* (Distant); green rice leafhopper (GRL/GRH), *Nephotettix cincticeps* Uhler and zigzag leafhopper (ZLH), *Recilia dorsalis* (Motchulsky); gall midges (GM): Asian rice gall midge (ARGM), *Orseolia oryzae* (Wood–Mason); and African rice gall midge (AfRGM), *Orseolia oryzivora* Harris & Gagné; and leaffolders: *Cnaphalocrocis medinalis* (Guenée) and *Marasmia* spp. In the USA, the fall armyworm, *Spodoptera frugiperda* (J.E. Smith), rice water weevil, *Lissorhoptrus oryzophilus* (Kuschel) and Mexican rice borer, *Eoreuma loftini* (Dyar) are the serious pests.

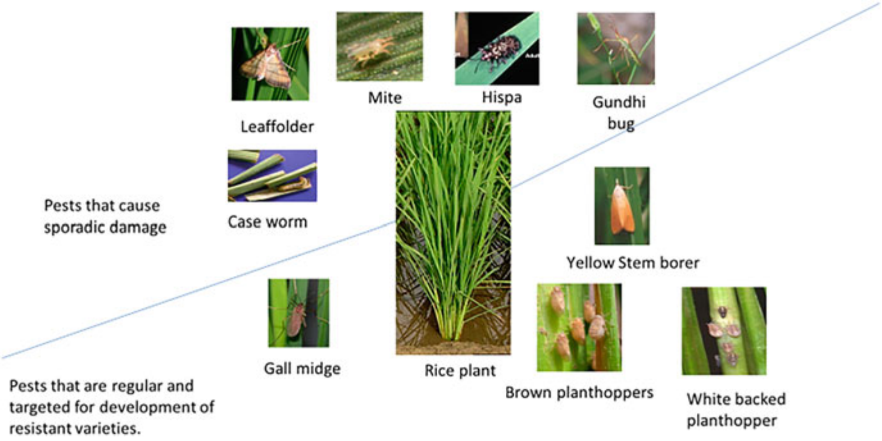

Plate 4.1 Major insect pests of rice crop

Despite the dynamic nature of pest infestations, stem borers and rice brown planthopper continue to be the two regular and major threats limiting rice production across the Asian countries. Both these pests inflict damage to the crop at all crop growth stages. Yellow stem borer (YSB), *Scirpophaga incertulas* (Walker), a monophagous pest with exclusive host specificity towards rice, is considered to be a dominant pest across the rice-growing regions. Some of the other stem borers like striped stem borer, *Chilo suppressalis* Walker, dark headed striped stem borer (DHSB), *Chilo polychrysa* Meyrick; gold fringed borer (GFB) *Chilo auricilius* Dudgeon; spotted stem borer, *Chilo partellus* Swinhoe and other *Scirpophaga* spp. are either specific to particular crop stage or are reported from rice and rice-based cropping systems. Apart from these two, there are pests like leaffolders, gall midge, rice hispa, caseworm, thrips and gundhi bugs which do cause economic losses but are endemic to certain pockets. Planthoppers and leafhoppers are also vectors of many plant viruses.

4.1.2 Losses Caused by Insect Pests in Rice

Oerke (2006) estimated 37.5% losses at global level due to animals, weeds, pathogens and viruses in rice crop. Average annual losses to rice borers in China, India, Bangladesh and Southeast Asia were approximately 5–10%, though losses in individual fields may reach 50–60% (Rahman et al. 2004). The losses in the rice crop due to animal pests increased from 15% in pre-green revolution era to 25% in the post-green revolution era in India, though at global level there was a decrease in the crop losses (Dhaliwal et al. 2007). Dhaliwal et al. 2010 estimated 25% crop loss due to insect pests in rice crop. The yield losses vary from one region to another, but range from 1.2 to 2.2 tons/ha due to the combined attack of diseases, insects and weeds in Asia (Savary et al. 2012). It is common to note that though infestation/

damage to rice appears high, the losses may be limited and control measures, sometime would be uneconomical. The intensity and effect of damage depend on the stage of the crop and confluence of the many biotic and abiotic factors that influence crop growth. Pest profile varies with the location, cultivation practices, nutritional profile of the crop, adopted management practices and the prevailing cropping system. Hence, insect pest management should be addressed based on the location-specific requirements. The losses caused by insect pests are very high when the yield components like productive tiller or grain yield are affected as in the case of BPH, WBPH, SB or GM or when the quality of the grain is affected as in the case of gundhi bug or stored grain pests. Nymphs and adults of planthoppers suck phloem sap (Auclair and Baldos 1982; Khan and Saxena 1984) from leaves and leaf sheaths turning them yellow and reducing plant height, tillering and filled grains. Plants infested by the BPH before maximum tillering usually have fewer panicles per unit area and fewer grains per panicle; a planthopper attack after the heading stage affects the percentage of ripened grain and grain weight. The time of insect attack in relation to plant growth, intensity of injury (or the population density of insects), duration of the attack and environmental factors affecting both insect activities and plant growth influence the relationship between an insect infestation and its effect on yield. Severe infestation of the insect leads to hopper-burn resulting in complete drying and death of the crop. Based on 770 experimental units from 28 years' data (All India Coordinated Rice Improvement Project from 1965 to 1992), empirical yield loss estimates caused by stem borers over various rice ecosystems due to 1% dead heart or white ear head or to both phases of damage were 2.5% (or 108 kg/ha), 4.0% (174 kg/ha) and 6.4% (278 kg/ha), respectively (Muralidharan and Pasalu 2006). White earhead damage had a much greater impact on rice yield in the irrigated ecosystem than due to dead heart, as it occurs later in the crop stage when no compensation is possible, thus resulting in direct loss of a yielding panicle. The grain yield loss from damage at the two phases, namely, dead heart and white earhead, is more than additive. On the other hand, potential yield gains of at least 10–20% of the current yields may be achieved through effective pest management techniques (Oerke 2006; Savary et al. 2012). Puri and Mote (2003) predicted that brown planthopper and gall midge in rice and pink stem borer in sorghum would assume serious proportions in future due to changes in the ecosystems and habitats. Deutsch et al. (2018) predicted that with every degree Celsius of increase in temperature, the loss caused by insects would increase by 10–25% which is more pronounced in temperate climates. This is imminent and evident with the impact of climate change on the crop growth life cycles and availability of the host plants beyond the traditional seasons, thus ensuring survival and multiplication of the pests.

4.1.3 Status of Host Plant Resistance in Rice IPM

In an agro-ecological system, the growth of insect pest population depends on the initial colonization, natural population growth rate and the impacts of control measures. Pest management strategies should focus on limiting the initial pest recruitment, colonization and build-up of the population (Cheng et al. 2008) before reaching the economic threshold level. Pest management strategies may include genetic resistance, acquired resistance during cultivation practices, improved environmental resistance, augmentative and inundative release of selected natural enemies. Host plant resistance is a built-in approach which is inherently the genetic makeup of the plant. It is environmentally safe, mostly compatible with other components of pest management and does not require additional equipment or cost except for the initial cost of development of the variety/breeding line. Large variation exists in the reaction of the rice pests to germplasm, breeding lines and varieties. A wealth of literature and information are available on the resistance mechanisms, genes conferring resistance to BPH, WBPH, GLH, ARGM, AfRGM, leaf folder and to some extent for pests like rice hispa, gundhi bug and thrips. Thus, integrated pest management through deployment of host plant resistance should be thought of within the context of crop management. Litsinger (2005) opined that with the advances in the breeding methodology and change in plant type with high tillering capacity and improved yield potential as compared to traditional varieties, the capacity for compensation from insect pest damage is enhanced. Appropriate crop management practices also supplement the compensatory ability. Prior knowledge on the crop compensatory ability and severity of crop stress acting on it would help the farmers in accurate decision-making to take up control measures.

4.2 Phenotyping for Insect Resistance

Accurate phenotyping for insect resistance, elucidating the mechanisms and genetics, serves as a back bone on which all the modern biotechnological tools and breeding programmes depend upon. So, a precise phenotyping of a resistant source is very much essential and is the base on which all the further studies and results rely upon.

4.2.1 Screening Methodology

Germplasms from various sources, breeding material at different stages of development with known sources of resistance, are evaluated to identify resistance for various pests. Standard screening protocols are available for various rice pests. Protocols for screening and identifying sources of resistance and studying various mechanisms of resistance were reviewed at length for all the rice pests, namely plant and leafhoppers, stem borers, gall midge, leaf folders, rice thrips, gundhi bug, case worm, whorl maggot, etc., by many rice workers (Heinrichs et al. 1985; Panda and Khush 1995; Bentur et al. 2011), and the protocol for screening and scoring for damage by rice pests was summarized in IRRI (2013) which till date is followed by rice workers all over the world. Later on, based on the need, many protocols were designed, developed, revised and improvised for deeper understanding of rice–pest interactions and studying their mechanisms of resistance. Some of these techniques are detailed below:

4.2.1.1 Field Screening Techniques

Screening of large quantum of material can be taken up at "hot spots" or endemic areas where occurrence of natural populations is regular. Infestation by natural populations helps to identify the promising lines which are further retested under stringent conditions to identify the resistant cultures (Plate 4.2a). Field screening requires thorough knowledge of the pest incidence pattern so as to adjust the time of sowing/planting in order to ensure pest infestation at the right crop stage. The major limitations of evaluating germplasm in the field are seasonality, unpredictability with reference to incidence of the insect pests, uneven distribution of the pest, asynchrony between insect pest incidence and the stage of the crop for effective screening, interference from other biotic and abiotic factors rendering field screening unreliable at times. Under most of the field conditions in production systems, it is common to have two or more biotic stresses at the same time. For example, WBPH colonizes the plant first, but as the crop advances, BPH takes over. Therefore, in some of the locations there would be a mixture of both BPH and WBPH, and the resultant phenotype would be due to damage by both the insect pests. To address the issue of uneven infestation, staggered sowing to coincide with the time of the specific pest incidence in the field, followed by supplementing the infestation, is suggested.

4.2.1.1.1 Augmentative Releases

Augmentative release of insects at specific stage can be carried out so as to ensure reliable screening of the material. These techniques are currently available for BPH, gall midge, yellow stem borer, leaffolder and hispa (Plate 4.2b). To develop screening techniques, a deeper understanding of the insect biology, behaviour and its interaction with the host is very much essential. Under All India Coordinated Research Programme on Rice (AICRPR) in NARS, India, multi-location evaluation of rice lines is carried out for major pests like planthoppers, GM, YSB, LF and rice hispa. Details of phenotypic screening protocols for the major rice pests are described below:

BPH

A susceptible variety is raised as infestor rows around the test material. A polythene sheet barrier of 2.5 ft height is erected all around the planting area within 15 days after planting. For better results, it is desirable to plant test entries in longitudinal strips not wider than 2 m and each strip separately covered around with polythene sheet. Currently, TN1 is used as the susceptible check. PTB 33 and RP2068-18-3-5 are the resistant checks for BPH and MO1 for WBPH screening. Adults and nymphs of planthoppers collected from adjacent areas or greenhouse culture are released to build up the pest pressure. A spray of Deltamethrin (0.002%) is given on infestor/feeder rows to ensure further build-up of the pest population. Field screening can identify field tolerance of the genotypes.

Plate 4.2 (**a**) Field screening of rice lines based on natural pest incidence at hot spots. Damage by (A) Gall midge (courtesy: Dr Atanu Seni); (B) Planthoppers (courtesy: Dr Mallikarjuna Rao); (C) Stem borer—dead heart (Dr AP Padmakumari); (D) Stem borer (white ear: Dr Sanjay Sharma). (**b**) Screening of rice lines through insect augmentation. (A) Screening against BPH (photo courtesy: Dr JS Bentur); (B) Release of GM adults in cages at IIRR (photo courtesy: Dr AP Padmakumari); (C) Release of leaffolder adults (photo courtesy: Dr Ch. Padmavathi); (D) Augmenting with YSB egg mass (photo courtesy); (E) Release of two neonate YSB larvae per tiller to augment the infestation, E-1 in pot, E-2 in field (Dr AP Padmakumari); (F) Screening in net house against adult rice hispa (F2)-F1-hispa damage (photo courtesy: Dr A Srivastava)

Plate 4.2 (continued)

Yellow Stem Borer

Augmentative release is carried either through pinning of the egg mass at black head stage or release of two neonate larvae per tiller at maximum tillering stage in vegetative phase for dead heart damage and at booting stage in reproductive phase for white ear damage as the damage by the pest differs between crop phases. The material thus infested is scored for dead heart, white ear damage and grain yield in the infested plants (Bentur et al. 2011; Padmakumari and Ram 2012; Padmakumari and Katti 2018; Jeer et al. 2018). Pusa Basmati 1 is the susceptible check; TKM6, Sasyasree and W1263 are the resistant checks used for comparison. The methodology is highly dependent on availability of adult YSB in the field. In order to synchronize the infestation at appropriate crop stage, staggered sowings are suggested. It should be noted that the resistance/tolerance to YSB can be at both vegetative and reproductive phase or only at vegetative phase and susceptible at reproductive phase or vice versa. This protocol is useful to screen any material for yellow stem borer.

Gall Midge

The material to be screened can be raised in two rows. Generally, late planting is preferred in hot spot areas to ensure sufficient infestation and catch up with the pest incidence. For phototropic insects like gall midge, it is suggested to deploy incandescent bulb around the field to attract adults for oviposition. TN1 is the susceptible check.

Leaffolder

In case of leaffolder, field-collected adults are released on to the screening material covered by nylon net at 40–60 days after transplanting (DAT). The damaged leaves are counted at 60–80 DAT (in the reproductive phase) or 20 DAT after release of the adults. TN1 is the susceptible check, and W1263 is used as a resistant check (Bentur et al. 2011). Bentur and Kalode (1990) studied the mechanism of resistance through a feeding test which involved caging of individual V instar larvae for 48 h on 30–45-day-old plants of test varieties with PTB12 as resistant check and recording area of leaf damage when the leaf nitrogen content varied from 2% to 3.4%. As leaffolder has a behaviour to undergo precocious pupation when exposed to nutritional stress (resistant variety), a rapid screening test was developed wherein single third instar leaffolder larva reared on TN1 in greenhouse was released on to the leaves of test entries and allowed to feed for 48 h (Chintalapati et al. 2017). After 48 h of confinement, the larvae were collected back and the leaf damage was scored for extent of feeding. Using this technique, promising RILs developed from W1263/TN1 were screened and identified for leaffolder resistance (Chintalapati et al. 2019). A study using a doubled haploid population of CJ06/TN1 uncovered five QTLs for rice leaffolder (RLF) resistance on chromosomes 1, 2, 3, 4, and 8. The effect of a single locus is limited, but QTLs pyramiding markedly improved leaffolder resistance in rice (Rao et al. 2010).

Rice Hispa

The adult and grubs of this pest cause extensive damage. Srivastava and Kamini (2020) identified resistant lines by collecting adults from field and releasing @40 adults/m^2 on the test material at maximum tillering phase and scoring for leaf damage by the adults.

4.2.1.2 Greenhouse Techniques

Screening for BPH, WBPH and GLH is carried out as per the Standard Seed box Screening Technique (SSST) (Heinrichs et al. 1985). It is to be noted that the status of resistance is dependent on crop age. In order to characterize resistance for a particular pest, it is most appropriate to go in for screening of the shortlisted entries under greenhouse conditions through modified seed box screening technique (MSST). MSST provides a reliable method of identifying field resistance under greenhouse conditions and is expected to be a useful tool in breeding high-yielding rice cultivars with durable resistance to BPH (Velusamy et al. 1986). A rapid and quick mass screening technique at seedling stage against brown planthopper by following the standard evaluation system (SES) was employed by Soundararajan and Jeyaprakash (2019). Through this technique all the susceptible lines can be identified so that large germplasm can be screened within a short time. Gall midge is maintained on susceptible rice cv. TN1 plants, and screening is carried out as per Vijayalakshmi et al. (2006). Cheng et al. (2021) reported that 24 seedlings treated with at least five female ARGM adults were efficacious and could offer adequate samples for insect development observation or molecular biological studies.

Though greenhouse screening is a fool-proof method, it is highly labour-intensive and laborious. The basic requirement for greenhouse screening is the continuous maintenance of insect population conditioned on a susceptible check entry and infestation of the test material at the right stage of the plants with right stage of the insect. Therefore, depending on the need of experimentation, the desired number of insects can be maintained.

Kobayashi (2015) emphasized the role of development and maintenance of a virulent population on susceptible host from single progeny in characterizing resistance so that the base line data related to identification of resistant sources would be accurate. This rule would apply to all insects in the screening programme and caution should be exercised in the maintenance and release of the avirulent test insect populations as the reaction to a particular genotype would vary with the virulence of the insect. Authenticity of the variations exhibited is highly dependent on the different seed sources, their purity and/or accessions used in these evaluations.

4.2.2 Mechanisms of Resistance

Host plant resistance mechanisms are primarily categorized as antixenosis, antibiosis and tolerance (Painter 1968). Antixenosis is mainly due to host-plant characters which are responsible for non-preference by the insects for shelter, oviposition and/or feeding because of the presence of morphological or chemical factors. Antibiosis denotes the adverse effect of the biochemical and biophysical factors of the host plant on the biology (survival, development and reproduction) of the insect pests and their progeny. Both non-preference and antibiosis interfere with insect behaviour and metabolism.

Tolerance is the ability of the host plant to grow and produce satisfactory yield in the presence of pests that would cause loss in a susceptible plant. The phenomenon of tolerance is generally cumulative and a result of interacting with the host plant. These include general vigour, inter- and intra-plant compensatory growth, wound compensation, mechanical strength of tissues and organs and nutrient and growth regulator partitioning (Velusamy and Heinrichs 1986). This mechanism does not provide any selection pressure on the insect pests that can lead to the development of insect biotype. Tolerant varieties have higher decision thresholds than susceptible varieties resulting in reduction of insecticide usage and enhanced natural enemy activity (Panda and Heinrichs 1983). Usually, vertical resistance governed by single/major genes leads to development of biotypes. If this first line of defence provided by major genes breaks down, the tolerance mechanism becomes a secondary line of defence and will continue to function while efforts can be directed towards the release of a new resistant variety (Litsinger 2005).

4.2.2.1 Planthopppers

The predominant mechanisms operating for planthoppers are non-preference for oviposition; for feeding quantified through honey dew tests, days to wilt and functional plant loss index and the tolerance mechanism (Heinrichs et al. 1985; Panda and Khush 1995) which operates with age and plant damage. Biochemical factors like phenols, salicylic acid, shaftosides and sucking inhibitors like oxalic acid, soluble silicic acid, were attributed to lowering the damage in rice by BPH and WBPH. Various studies pointed out the significance of feeding behaviour of planthoppers in quantifying resistance. Use of the electrical penetration graph (EPG) technique has revealed details of host plant suitability and feeding behaviour, including probing frequency, duration of stylet insertion, duration of phloem or xylem feeding and honeydew secretion (Velusamy et al. 1986; Walling and Thompson 2013). Host searching and feeding behaviour of BPHs on rice were implicated in host resistance together with flavonoid glycosides, which are phloem secondary metabolites that have anti-feeding activity against BPH (Grayer et al. 1994), the resistance factors are thought to occur within the phloem and in the pathways to the vascular system (Walling and Thompson 2013). BPH feeding up-regulated callose synthase genes and induced callose deposition in the sieve tubes at the point where the stylets were inserted. In the resistant plants, the compact callose remained intact while in susceptible plants, genes encoding β-1,3-glucanases were activated, causing unplugging of the sieve tube occlusions (Hao et al. 2008). Shen et al. (2022) reported that the plant elicitor peptide (Pep), rice PEP RECEPTORs (PEPRs) and PRECURSORs of PEP (PROPEPs), particularly *OsPROPEP*, were transcriptionally induced in leaf sheaths upon BPH infestation conferring resistance to BPH. Knockout of *OsPEPRs* impaired rice resistance to BPH, whereas exogenous application of *OsPep3* improved the resistance. Hormone measurement and co-profiling of transcriptomics and metabolomics in *OsPep3*-treated rice leaf sheaths suggested potential contributions of jasmonic acid biosynthesis, lipid metabolism and phenylpropanoid metabolism to OsPep3-induced rice immunity. In case of BPH, primary tiller not infested by the brown planthopper translocates nutrients and assimilates into the main shoot, to reduce the effects of brown planthopper feeding on the main shoot (Rubia-Sanchez et al. 1999). Our own studies identified that some of the lines damaged by brown planthopper at reproductive phase recover back, but continue to remain in the vegetative phase without putting forth any grain. This phenotype which appears to be resistant in terms of plant stand is not useful for the farmers. Application of nitrogenous fertilizers did not confer or improve plant tolerance against BPH attack as hoppers being phloem feeders utilized the extra nutrients before they are used by host plant (Horgan et al. 2016).

4.2.2.2 Gall Midge

It is well established that nature of resistance to ARGM is antibiosis and is governed by a single gene^{-}. The death of the maggot occurs due to feeding on the meristem which is often associated with the induction of a hypersensitive reaction where there is browning of the tissue due to phenols (i.e. HR^{+}) or only dead maggots without browning (HR^{-}) which is mostly constitutive in nature. Amudhan et al. (1999) implicated the role of phenols in conferring HR^{+} resistance. Agarrwal et al. (2014) identified biomarkers for gall midge infestation. Trehalose was classified as an infestation feature and linoleic acid, as a resistance feature accumulated in higher levels in infested tissues as compared to uninfested tissues of Kavya (*Gm1*) but not in RP2068 (*gm3*). Levels of glutamine were significantly lower in infested tissues during compatible interaction as compared to its levels in uninfested tissues, thus suggesting that depleted levels of glutamine in gall midge infested tissues as compared to uninfested played a role in the plant's susceptibility to gall midge. Furthermore, Agarrwal et al. (2016) studied the transcriptome and metabolome of RP 2068-18-3-5 (*gm3* and HR^+) infested with gall midge biotype1 (GMB 1) and implicated the involvement of reactive oxygen species, i.e. singlet oxygen and accumulation of azelaic acid, a marker metabolite of lipid peroxidation (LPO)-mediated cell death leading to induced HR^+ reaction. This coincided with a greater accumulation of GABA (a neurotransmitter and an insect antifeedant) at the feeding site which could have resulted in maggot morality. Microarray data revealed deregulation of carbon (C) and nitrogen (N) metabolism causing a C/N shift; up-regulation of tetrapyrrole synthesis and down-regulation of chlorophyll synthesis and photosynthesis which manifests as tissue necrosis.

4.2.2.3 YSB

YSB moths do not exhibit any ovipositional preference. TKM6 was reported to confer non-preference mechanism of resistance. Padhi (2004) worked on the biochemical basis of resistance in rice to *S. incertulas* and reported that rice varieties TKM 6 and PTB 18 recorded lower borer incidence, larval survival and sugar content, but higher quantity of total phenols, ortho-dehydroxy phenol and silica indicating their resistance to yellow stem borer as compared to Jaya, the susceptible check. Rubia et al. (1996) through simulation studies reported that dead heart damage by stem borer could be compensated up to 10%. The response of varieties to YSB damage is diverse. The response of a variety to stem borer damage was calculated from the observed dead hearts and their regeneration capacity. In majority of the varieties, the first and fourth tillers were damaged. Regeneration capacity varied from 4% to 80% in the varieties studied (Padmakumari et al. 2008). The study show that compensation through the recovery resistance is the major mechanism operating in rice against yellow stem borer at the vegetative phase. Varieties/breeding lines, wherein panicles were produced without any delay soon after damage by YSB and among those wherein grain filling is not affected despite borer damage, can be graded as tolerant lines. Recovery resistance at vegetative phase and low level of antibiosis with tolerance could be the possible mechanisms of resistance in IR64/*O. glaberimma* lines, Swarna^{*2}//*O. longistaminata* introgressed lines (Padmakumari and Ram 2012; Padmakumari et al. 2015). Selvi et al. (2002) identified four phenotype-specific RAPD markers through Random Amplified Polymorphic DNA (RAPD) analysis, in conjunction with bulked segregant analysis in an F_2 mapping population of Co43 (susceptible parent)/W1263 (resistant parent). The markers $C1_{320}$ and $K6_{695}$ (at 12.8 cM) were linked with resistance and $AH5_{660}$ and $C41_{300}$ with susceptibility. However, the marker $K6_{695}$ was consistently found to be associated with resistance. Bose et al. (2015) introgressed yellow stem borer (YSB) resistant traits like short stature, increased tiller number and reduced stem diameter from the wild rice species *Oryza brachyantha* and BPH resistance from *O. rufipogon* to the high-yielding durable BPH resistant varieties.

4.2.2.4 Leaffolder

In the case of the rice leaffolder, both antixenosis and antibiosis as mechanisms of resistance were reported (Khan et al. 1989; Ramachandran and Khan 1991; Dakshayani et al. 1993; Xu et al. 2010; Punithavalli et al. 2014). Bio-physical plant factors like trichomes, leaf length are associated with resistance to leaffolder. Different genotypes had varying effects on leaf folding behaviour by the larvae (Punithavalli et al. 2013). The time taken by the larva to fold the leaves or developmental time for the larvae to complete one generation is one of the criteria developed based on the insect behaviour to evaluate the resistance (Javvaji et al. 2021).

4.2.3 Sources, Genes and Genetics of Resistance

Heinrichs et al. (1985) reported various sources of resistance to BPH, WPH, GRH, GLH, YSB, LF and other minor pests like hispa from land races, wild rices, breeding lines and cultivars. However, the levels of resistance were not good enough to confer resistance to all the major pests in one varietal background. With the improvement of techniques to identify the resistance, developments in sources of tolerance have been reported for many pests which were earlier reported that no sources of resistance were available. The details of sources of resistance, markers and genes identified against BPH, WBPH. GLH, GRH and GM are detailed in Table 4.1.

BPH

Around 40 BPH resistance genes have been identified so far in indica, African rice varieties along with wild germplasms such as *O. nivara* (AA), *O. officinalis* (CC), *O. minuta*, *O. punctata* (BB and BBCC), *O. rufipogon*, *O. australiensis* (EE) and *O. latifolia* (CCDD) (Jena and Kim 2010; Muduli et al. 2021). Genes/QTLs involved in BPH resistance, including *Bph1*, *bph2/BPH26*, *Bph3*, *bph4*, *Bph6*, *bph7*, *BPH9*, *Bph12*, *Bph14*, *Bph15*, *Bph17*, *BPH18*, *bph19*, *Bph20*, *Bph21(t)*, *Bph27*, *Bph27(t)*, *Bph28(t)*, *BPH29*, *QBph3*, *QBph4*, *QBph4.2*, *Bph30*, *Bph32*, *Bph33*, *Bph35 and Bph36*, have been fine-mapped by different researchers across the globe. The majority of genes/QTLs are located on rice chromosomes 1, 3, 4, 6, 11 and 12 (Sarao et al. 2016; Muduli et al. 2021). However, there are inconsistencies in assigning gene number and locating their position on the chromosome. Fujita et al. (2013) detailed on the confusions and anomalies in the naming of the *Bph* genes and suggested that CGSNL convention (McCouch and CGSNL 2008) of naming may be adopted to avoid confusions in future. Of the total BPH genes identified for resistance, 14 genes have been identified through map-based cloning (Yang et al. 2020; Du et al. 2020). *BPH1*, *bph2*, *bph7*, *BPH 9*, *BPH10*, *BPH18*, *BPH21*, *BPH26* encoded for CC-NB-NB-LRR protein localized in the endomembrane bundles. *BPH3* and *BPH15* encoded for leptin receptor kinases localized in plasma membrane; BPH6 for atypical LRR protein; *BPH 14* encoded for CC-NB-LRR and localized in LRR nucleus and cytoplasm; *bph29* encoded for DNA-binding domain, and *BPH32* for unknown SCR domain though localized in nucleus and plasma membrane, respectively. It is interesting to note that despite their subcellular

Table 4.1 List of insect resistance genes identified in rice germplasm against major pests

Pest	Source of resistance	*Gene/QTL*	Chromosome	Associated marker(s)	Reference
Brown planthopper (BPH)	Mudgo, TKM6	*Bph1*[a]	12	BpE18-3	Kim and Sohn (2005)
	ASD7	*bph2*[a]	12	RM463, RM7102	Sun et al. (2007)
	Rathu Heenati	*Bph3*[a]	6	RM469, RM588	Jairin et al. (2007a)
	Babawee	*bph4*	6	RM190, C76A	Kawaguchi et al. (2001)
	ARC10550	*bph5*	–	–	Khush et al. (1985)
	Swarnalata	*Bph6*[a]	4	Y19, RM119	Qiu et al. (2010)
	T12	*bph7*[a]	12	RM3448, RM313	Qiu et al. (2014)
	Chinsaba (Acc. no. 33016)	*bph8*	–	–	Nemoto et al. (1989)
	Kaharamana	*BPH9*	12	RM463, RM5341	Su et al. (2006)
	Pokkali	*BPH9*[a]	12	OPR04, S2545	Murata et al. (2001)
	O. australiensis	*BPH10*[a]	12	RM260, RM313	Ishii et al. (1994)
	O. officinalis	*bph11*	3	–	Hirabayashi et al. (1998)
	B14 (*O. latifolia*)	*Bph12*	4	RM16459, RM1305	Qiu et al. (2012)
	IR54745-2-21 (*O. officinalis*)	*Bph13(t)*	3	AJ09b230, AJ09c	Renganayaki et al. (2002)
	B5 (*O. officinalis*)	*BPH14*[a]	14	–	Huang et al. (2001)
	B5 (*O. officinalis*)	*Bph15*[a]	4	RM261, S16	Lü et al. (2014)
	M1635–7	*Bph16*	12	RM6732-R10289	Hirabayashi et al. (2004)
	RathuHeenati	*Bph17*	4	RM8213, RM5953	Sun et al. (2005)
	IR65482-7-216 (*O. australiensis*)	*BPH18(t)*[a]	12	RM463, S15552	Jena et al. (2006)
	AS20-1	*bph19*	3	RM6308, RM3134	Chen et al. (2006)
	IR71033-121-15 (*O. minuta*)	*Bph20(t)*	4	MS10, RM5953	Rahman et al. (2009)

	IR71033-121-15 (*O. minuta*)	*Bph21(t)*[a]	12	RM3726, RM5479	Rahman et al. (2009)
	IR 75870-5-8-5-B-1-B (*O. glaberrima*)	*Bph22(t)*	–	–	Ram et al. (2010)
	IR 71033-121-15 (*O. minuta*)	*Bph23(t)*	–	–	Ram et al. (2010)
	IR 73678-6-9-B (*O. rufipogon* (Acc. 106412))	*Bph24(t)*	–	–	Deen et al. (2010)
	ADR52	*BPH25*	6	S00310	Myint et al. (2012)
	IR1154-243	*bph2/Bph26*[a]	12	KAM4	Murai et al. (2001)
	GX2183 (*O. rufipogon*)	*Bph27*	4	RM273, RM471	Huang et al. (2013)
	Balamawee	*Bph27(t)*	4	RM471, RM5742	He et al. (2013)
	DV85	*Bph28(t)*	11	Indel55, Indel66	Wu et al. (2014)
	RBPH54 (*O. rufipogon*)	*BPH29*[a]	6	BYL7, BID2	Wang et al. (2015)
	AC-1613 (*O. indica*)	*Bph30*	4	RM16294, RM16299	Wang et al. (2018)
	CR2711-76 (indica)	*BPH31*	3	PA26, RM2334	Prahalada et al. (2017)
	Ptb33	*Bph32*[a]	6	RM19291, RM8072	Ren et al. (2016)
	RP2068	*Bph33(t)*	1	RM488, RM11522	Naik et al. (2018)
	Kolayal and Poliyal	*Bph33*	4	H99, H101	Hu et al. (2018a)
	IRGC104646 (*O. nivara*)	*Bph34*	4	RM16994, RM17007	Kumar et al. (2018)
	RBPH660	*Bph35*	4	PSM16, RM413	Zhang et al. (2020)
	O. rufipogon Griff	*Bph36*	4	S13, X48	Li et al. (2019)
	IR64	*BPH37*	1	RM302	Yang et al. (2019)
	Khazar	*BPH38(t)*	1	SNPs 693, 369	Balachiranjeevi et al. (2019)

(continued)

Table 4.1 (continued)

Pest	Source of resistance	*Gene/QTL*	Chromosome	Associated marker(s)	Reference
	[RPBio4918-230S line-(IRGC81848 × Swarna)] × Swarna	bph39(t) and bph40(t)	–	–	Akanksha et al. (2019)
	RathuHeenati	*qBph3*	3	RM3180, RM2453	Kumari et al. (2010)
	IR02W101 (*O. officinalis*)	*QBph4.1*	4	P17, xc4-27	Hu et al. (2015b)
	IR65482-17-511 (*O. australiensis*)	*QBph4.2*	4	RM261, S1	Hu et al. (2015a)
White backed planthopper (WBPH)	N22 (IRRI Acc. no. 4819)	*Wbph1*		Genetic Analysis	Sidhu et al. (1979)
	ARC10239	*Wbph2*		Genetic Analysis	Angeles et al. (1981)
	ADR52	*Wbph3*		Genetic Analysis	Hernandez and Khush (1981)
	Podiwi A8	*wbph 4*		Genetic Analysis	Hernandez and Khush (1981)
	N′ Diang Marie	*Wbph 5*		Genetic Analysis	Wu and Khush (1985)
	Giu-yi-gu	*Wbph 6(t)*		Genetic Analysis	Brar and Khush (1991)
	B5 (*O. officinalis*)	*Wbph 7(t)*	3	R1925, G1318	Tan et al. (2002)
	B5 (*O. officinalis*)	*Wbph 8(t)*	4	R288, S11182	Tan et al. (2002)
	SinnaSivappu	*wbph 9(t)*	6	RM589-RM539	Ramesh et al. (2014)
	SinnaSivappu	*wbph10(t)*	12	SSR12-17.2-RM28487	Ramesh et al. (2014)
	SinnaSivappu	*wbph11(t)*	4	RM3643-RM1223	Ramesh et al. (2014)
	SinnaSivappu	*Wbph12(t)*	4	RM16913-RM471	Ramesh et al. (2014)
	Asonimori	Ovc	6	S1520, L688	Yamasaki et al. (2003)
	Asonimori	Ovc	6	R2373-C946	Yamasaki et al. (2003)
	Asonimori		1	XNpb346-C112	Yamasaki et al. (2003)

		qOVA-1-3 Asominori 1			
	Asonimori	*qOVA-5-1*	5	XNpb251-R331	Yamasaki et al. (2003)
	Asonimori	qOVA-5-2	5	C1268	Yamasaki et al. (2003)
	Asominori	Ovc	6	R2373-C946	Yamasaki et al. (2003)
	Asominori	qOVA-1-3	1	XNpb346-C112	Yamasaki et al. (2003)
	Asominori	qOVA-4	4	R1854	Yamasaki et al. (2003)
	Asominori	qOVA-5-1	5	XNpb251-R3313	Yamasaki et al. (2003)
	Asominori	qOVA-5-2	5	C1268	Yamasaki et al. (2003)
	O. rufipogon	qWPH2	2	RM1285-RM555	Chen et al. (2010)
	O. rufipogon	qWBPH5	5	RM3870-RZ70	Chen et al. (2010)
	O. rufipogon	qWBPH9	9	RG451-RM245	Chen et al. (2010)
	Chunjiang 06	qWL6	6	M3-M5	Yang et al. (2014)
	IR54751	qWBPH3.2	3	InDel3-23-InDel3-26	Fan et al. (2018)
	IR54751	qWBPH11	11	DJ53973-SNP56	Fan et al. (2018)
	Mudgo	WBPHM1, WBPHM2	–	–	Sidhu et al. (2005)
	MO1	*WBPH0*	–	–	Sidhu et al. (2005)
	NCS2041	*WBPHN*	–	–	Sidhu et al. (2005)
Green rice leafhopper (GRLH), *N. cincticeps*	Norin-PL2 (Pe-bi-hun), IR24	*Grh1*	5	XNpb260R2558, C309, R566	Tamura et al. (1999), Kadowaki et al. (2003)
	Lepedumai	*Grh2*	11	S723, G1465	Fukuta et al. (1998), Kadowaki et al. (2003)
	Aichi42	*Grh3(t)*	6	C288B, C133A, C81	Saka et al. (2006)
	DV85	*Grh4*	3	XNpb144	Kadowaki et al. (2003)
	W1962 (*Oryza rufipogon*)	*Grh5*	8		Fujita et al. (2006)

(continued)

Table 4.1 (continued)

Pest	Source of resistance	*Gene/QTL*	Chromosome	Associated marker(s)	Reference
				RM3754, RM3761	
	SML17	*Grh6*	4	RM5414, C60248	Fujita et al. (2004), Phi et al. (2019)
	IRGC104038 O. glaberrima	*qGRH9*	9	RM201, RM205	Fujita et al. (2010)
Green leaf hopper, *N. virescens*	*GLH1*	Pankahari 203	5	–	Athwal et al. (1971)
	GLH 2	ASD7	11	–	Athwal et al. (1971)
	GLH 3	IR8	6	–	Athwal et al. (1971)
	glh4	PTB8	3	–	Siwi and Khush (1977)
	GLH 5	ASD8	8	–	Siwi and Khush (1977)
	GLH 6 *GLH 7*	TAPL 796 MaddaniKaruppan	5 –	– –	Rezaul Karim and Pathak (1982)
	glh8	DV85	–	–	Ghani and Khush (1988)
	GLH 9, glh10t	IR28, IR36	–	–	Angeles and Khush (2000a)
	GLH 11t	IR20965-11-3-3	–	–	Angeles and Khush (2000a)
	GLH 12t	Hashikalmi, ARC10313, Ghaiya, Garia	–	–	Angeles and Khush (2000b)
	GLH 13	Asmaita	–	–	Angeles and Khush (2000b)
	GLH 14	Asmaita	–	–	Sebastian et al. (1996)
Gall midge (ARGM), *Orseolia oryzae*	W1263, Kavya	*Gm1*	9	RM23941, RM23956	Reddy et al. (1997), Sundaram (2007)
	Phalguna	*Gm2*	4	RM17473, RM17503	Mohan et al. (1994), Sundaram (2007)

	RP2068-18-3-5[a]	*gm3*	4	RM17480, gm3SSR4	Kumar et al. (1998a), Sama et al. (2014)
	Abhaya[a]	*Gm4*	8	RM22551, RM22562	Srivastava et al. (1993), Divya et al. (2015)
	ARC 5984	*Gm5*			Kumar et al. (1998b)
	Dukong 1	*Gm6*	4	OPM061400, RG2014, RG476	Katiyar et al. (2001)
	RP2333-156-8	*Gm7*	4	SA 598, F8	Kumar et al. (1999), Sardesai et al. (2002)
	Jhitpiti/Aganni[a]/INRC 3021	*Gm8*	8	RM22685, RM22709	Kumar et al. (2000), Sama et al. (2012)
	Madhuri-L9	*Gm9*	7	NA	Shrivastava et al. (2003)
	BG308	*Gm10*		NA	Kumar et al. (2005)
	CR57-MR1523	*Gm11*	12	NA	Himabindu et al. (2010)
	MN 62M	*gm12*		RM3340, S2-76222	Leelagud et al. (2020)

NA = marker details not available in the publication cited
[a] Cloned gene

variations, all these genes are expressed in vascular bundles, thus affecting the insect which is a phloem feeder. Ishwarya Lakshmi et al. (2022) validated *Bph17* and *Bph32* gene-specific SNPs and identified six SNPs, namely snpOS00912, snpOS00915, snpOS00922, snpOS00923, snpOS00927 and snpOS00929 through Kompetitive allele-specific PCR (KASP) assay and distinguished BPH resistant genotypes. This would help in the detection of SNPs with high precision and has potential usefulness in MAS related to many breeding programmes.

WBPH

Till date, 13 genes, 10 QTLs were identified to confer resistance to WBPH. Studies on the inheritance of WBPH resistance revealed eight major genes, i.e. *Wbph1* in N22 (Sidhu et al. 1979), *Wbph2* in ARC 10239 (Angeles et al. 1981), *Wbph3* in ADR 52 (Hernandez and Khush 1981), *wbph 4* in Podiwi A8 (Hernandez and Khush 1981), *Wbph 5* in N'Diang Marie (Wu and Khush 1985), *Wbph 6(t)* in Giu-yi-gu (Brar and Khush 1991), *Wbph 7(t)* and Wbph 8(t) in B5 (Tan et al. 2002), *wbph 9t*, *10t*, *11t*, and *WBPH 12t* from Sinnasivappu (Ramesh et al. 2014); Ovc gene, qOVA-4, qOVA-5-1, qOVA-5-2 from Asominori (Yamasaki et al. 2003); *qWPH2*, *qWBPH5*, *qWBPH9* from *O. rufipogon* (Chen et al. 2010); *qWL6* from Chunjiang 06; M3–M5 (Yang et al. 2014); qWBPH3.2 and qWBPH11 in IR54751 (Fan et al. 2018). The other sources of resistance include a single dominant gene in ADR 52; a single recessive gene in ARC 6650, ARC 5984 and Podiwi A8 (all allelic to each other); two dominant genes in Velluthecherra; and one dominant and one recessive gene in MO 1 though the dominant genes present in ADR 52 and Velluthacherra are different. The recessive gene of MO1 was non-allelic to that of Podiwi A8 (*wbph 4*). *Wbph 3* and *wbp4* can be effectively utilized in the breeding programme for development of resistant cultures (Padmavathi et al. 2007).

Leaf Hoppers

Leaf hoppers play a major role as vectors of viral diseases rather than causing damage as insect pests**.** Six dominant genes (GRH1–GRH6) and one minor QTL were identified for GRH. Against GLH, 14 genes were identified of which three were recessive (*glh* 4, 8, 10).

Gall Midge

Of the 12 gall midge resistance genes identified thus far, 10 (*Gm1*, *Gm2*, *gm3*, *Gm4*, *Gm5*, *Gm6*, *Gm7*, *Gm8*, *Gm11* and *gm12*) have been tagged and mapped with reported linked markers (Bentur et al. 2021). Among the 12 genes, only two genes *gm3* and *gm12* are recessive in nature. The recessive resistance gene, *gm3*, which displays HR^+, encodes an NB-ARC (NBS-LRR) domain-containing protein, while the dominant gene, *Gm4*, which also displays HR^+, encodes a leucine-rich repeat (LRR) protein, and *Gm8*, displaying HR^-, encodes a proline-rich protein (PRP). Of the 12 genes, *Gm2*, *gm3*, *Gm6* and *Gm7* are located on chr 4, *Gm4* and *Gm8* on chr 8, *Gm1* on Chr 9 and *Gm11* on Chr 12. So far, three gall midge resistance genes, *gm3* (Sama et al. 2014), *Gm4* (Divya et al. 2015) and *Gm8* (Divya et al. 2018b), have been cloned and characterized. *Gm2* has been reported to be allelic to *gm3*

(Sundaram 2007; Sama et al. 2014). Since resistance against gall midge is single gene-governed conferring antibiosis, it can break down within a short time. Hence, the strategy of pyramiding two or more genes with divergent mechanisms of resistance (i.e. HR^{+} and HR^{-}) has been advocated for durable resistance against this insect pest (Sundaram et al. 2013).

YSB

Yellow stem borer, *S. incertulas* is the most predominant stem borer species across rice ecosystems in India and infests rice crop from nursery to grain-filling stage. Conventional breeding has led to development of rice varieties like Ratna, Sasyasree and Vikas which derived moderate level of resistance from the donor source TKM6. Very limited information is available on the donors for stem borer resistance in the *sativa* germplasm. The progress in resistance breeding for yellow stem borer has been limited for most of the ecosystems due to polygenic nature of resistance. The wild species are a reservoir of useful genes for rice improvement. Wide hybridization and chromosome manipulation are the important techniques to transfer useful genes from wild to cultivated rice leading to rapid genomic changes like chromosomal rearrangements, genome expansion, differential gene expression and gene silencing. The tertiary gene pool was exploited for identification of resistant sources to BPH, gall midge and YSB. Wild rice germplasm has been screened against yellow stem borer. Protocols for extensive screening of material against yellow stem borer were standardized through utilization of field populations (Bentur et al. 2011; Padmakumari et al. 2015; Padmakumari and Katti 2018). *O. brachyantha*, *O. officinalis*, *O. ridleyi* and *Porteresia coarctata* were found to be resistant/tolerant against yellow stem borer (Padhi and Sen 2002) and the genes have been introgressed from *O. brachyantha* (Thapa 2008; Panda et al. 2011). *O. glaberrima*, *O. longistaminata* and *O. rufipogon* as sources of tolerance to yellow stem borer were identified (Padmakumari and Ram 2012) as a good source of resistance/tolerance to yellow stem borer. Cut stem assay of these tolerant lines with neonate larvae also revealed 30–100% larval mortality and delay in the larval growth as compared to 10% mortality in the recurrent parent (RP) IR 64 (Padmakumari, unpublished). In a novel method to address the issue of stem borer tolerance, intensive field screening of 4500 lines of EMS mutants of BPT 5204 against yellow stem borer at both phases of crop growth was carried out. This led to identification of 8 lines as tolerant to YSB with low level of antibiosis and recovery resistance (Padmakumari et al. 2017b; Potupureddi et al. 2021). Since stem borer is an internal feeder, the mechanism of resistance is always either low level of antibiosis or coupled with recovery resistance due to compensation. Hence, the yield would be almost at par with the national check variety or less than the wild type (Padmakumari and Ram 2016). Hence, while evaluating resistant varieties, it is pertinent to note that the economics need to be worked based on the ecosystem services, cost involved in raising the variety and cost towards the reduction in insecticide sprays so that proper deployment can be ensured.

4.2.3.1 Multiple Pest Resistance

Many donors were identified to possess multiple pest resistance to two or more pests. Some of the identified donors are listed in Table 4.2. These donors can be effectively utilized in the resistance breeding programmes.

4.2.3.2 Insect Virulence, Biotypes and Effective Genes

Here we discuss two important insects of rice BPH and GM where the concept of biotype with reference to the reaction of insect population to a set of host plant differentials is well established and would play a crucial role in the designing of location-specific breeding programmes and gene deployment for durable resistance.

4.2.3.2.1 BPH

Four biotypes were identified for BPH based on the virulence to the host plant differentials. Biotypes 1 and 2 are widely distributed in Southeast and East Asia, whereas biotype 3 was developed in the laboratory by rearing the insects on the resistant variety ASD7 which has the *bph2* gene for resistance (Panda and Heinrichs 1983) while biotype 4 or the South Asian biotype which is most destructive in nature occurs in the Indian subcontinent. Ferrater et al. (2013) reviewed the status of virulence in BPH populations. Using genome-wide scanning and interval mapping, the Qhp7 locus that governs preference for Bph1 plants was mapped to a 0.1 cM region of chromosome 7. In addition, two major QTLs that govern the rate of insect growth on resistant rice plants were identified on chromosomes 5 (Qgr5) and 14 (Qgr14) (Jing et al. 2014). Many salivary proteins have been identified using transcriptome and proteome techniques. The genetic loci of virulence were mapped in BPH genome based on the linkage map (Jing et al. 2017). Widespread virulence in South and SE Asia for *Bph1*, *Bph3* and *bph4*—India (Verma et al. 1979), Thailand (Thanysiriwat et al. 2009), *bph4* and *bph8*—China and *BPH26*—widespread in SE Asia (Myint et al. 2009b); *Bph5*, *Bph6*, Japan (Myint et al. 2009a); *BPH25* and *Bph7*, *bph8*, *Bph9*, *Bph10*, *Bph18*, *Bph20 and Bph21*—Philippines (Ferrater et al. 2013) was reported. From current literature on rice resistance to the brown

Table 4.2 Donors with multiple pest resistance

Insect pests	Donors/cross combination
BPH and WBPH	Mudgo, MO1, Podiwi A8
BPH and ARGM	RP 2068-18-3-5 (Swarnadhan × Velluthacheera)
BPH and GLH, LF	ASD7
BPH and ZLH	PTB33
GM and BPH, MR to SB	PTB21 (IRRI Acc. 6113)
GM and SB (MR)	PTB18
GM, SB (MR), LF, BPH (biotype1 & 3)	W1263 (MTU15 × Eswarakorra (*Gm1*))
GM, BPH (biotype1 & 3)	Suraksha
BPH and ARGM	Sinnasivappu (IRRI Acc. 15444)
BPH and ARGM	SuduHondrawala (IRRI Acc. 15541)
BPH and SB (MR)	RathuHeenati

Modified from Heinrichs et al. (1985)

planthopper, it is evident that newly identified resistant varieties and genes appear less effective than the varieties and genes that were identified in the 1970s and 1980s (Horgan et al. 2015). In a study on 39 rice accessions with 12 populations of BPH from South and South East Asia, only 6 varieties were less damaged than the susceptible check Taichung Native 1 (TN1). *Bph1*, *bph2*, *bph5*, *bph7*, *bph8*, *Bph9*, *Bph10* and *Bph18* were ineffective against most planthopper populations. *Bph20*, *Bph21* and *Bph17* have the potential to be used in resistance breeding in both South and South East Asia, whereas BPH25 and BPH26 have potential for use in South Asia (Horgan et al. 2015) suggesting pyramiding of two or more genes with different mechanisms could improve resistance level and durability. The variations in the reactions could be attributed to different seed sources or accessions used in these evaluations or the preconditioning of the insect used in evaluations. Horgan et al. (2015) reported that IR71033-121-15 (IRTP23991, a line introgressed with *Oryza minuta* from Philippines with *Bph20*, *Bph21* and MO1 (*WbphN*, *WbphO*) were apparently resistant to all South Asian populations and South East Asian populations of BPH though RathuHeenati (*Bph3*), Balamawee, Swarnalata and PTB33 showed resistance/tolerance across 4–6 populations tested. It is interesting to note that MO1 identified as resistant donor for WBPH is also tolerant to BPH. These can be used as differentials to check/monitor for the variation in virulence of the BPH populations. Genetic analysis revealed that BPH resistant genes are either linked with other gene or clustered together. BPH resistant genes are localized on 7 of the 12 chromosomes (1, 2, 3, 4, 6, 11 and 12) with several of the genes reported to be on chromosome 4 followed by chromosome 12. Kuang et al. (2021) in their studies on effect of climate change on the efficacy of BPH resistance genes in IR24-NILs reported that NIL-BPH17 has a strong inhibitory effect on BPH feeding on phloem and would be unaffected by environmental changes, while NIL-BPH20 would lose its ability during the environmental changes.

4.2.3.2.2 GM

Asian rice gall midge (GM), *O. oryzae* (Wood-Mason) is a serious pest in rice-growing countries, especially in China, India, Vietnam and Sri Lanka. Based on the reaction of the populations from endemic locations against a set of host plant differentials grouped into 4 categories, seven biotypes of rice gall midge were reported from India (Vijayalakshmi et al. 2006). Recent studies indicate that most of the gall midge populations in India are avirulent on *Gm1* and *Gm8* both with HR^{-} mechanism of resistance followed by *Gm4* and *virulent* on *Gm11*, *gm3* and *Gm4* (ICAR-IIRR, 2018–2021). Studies on inheritance of virulence in gall midge suggest that virulence against plant resistance gene *Gm2* is conferred by a single recessive gene (v*Gm2*) and is inherited in a sex-linked manner (Bentur et al. 1992), whereas virulence against *Gm1* gene is also conferred by a recessive gene (*vGm1*) but shows autosomal pattern of inheritance predicting the durability of *vGm1* as compared to *vGm2*. A simple modified F_2 screen method was developed and tested for estimating frequency of rare recessive alleles in pedigreed crosses of natural populations of gall midge (Bentur et al. 2008; Andow and Bentur 2010). Hence, it is very much essential to monitor the virulence of the major insect pests and generate more information on the insect virulence with respect to the effective plant resistance genes. This prior knowledge would aid in effective deployment of the plant resistance genes, thus aiding in durable resistance.

4.3 Breeding for Insect Resistance

4.3.1 Conventional Approaches

Owing to the prevalence and economic losses caused by insect pests across the world, concerted efforts were directed towards development of a resistant variety against either planthoppers/leaf hoppers, gall midge or stem borer which is the ultimate goal of host plant resistance in the service of mankind. Mudgo (*Bph1*), ASD 7 (*bph2*), RathuHeenati (*Bph3*) and Babawee (*Bph4*) were extensively utilized in breeding programmes as donors to develop BPH resistant varieties in Southeast Asia (Jairin et al. 2007b). Some of them were mega varieties for more than a decade before their breakdown due to development of new biotypes. Because of the high variability of BPH and the apparent specificity of BPH resistance, an understanding of the linkage and allelic relationship of resistance genes is particularly important for the development of BPH-resistant cultivars (Jena and Kim 2010). It is interesting to note that some of the cultures bred for resistance through conventional approaches are not under cultivation, but few varieties are still in the seed production chain for more than a decade in India (Table 4.3). This is mainly due to the patronage by the consumers in certain areas for their grain and cooking quality. But no information is available on the current status of pest incidence in these varieties.

4.3.2 Molecular approaches

4.3.2.1 Application of Molecular Markers in Breeding for Insect Resistance

Biotic stresses like stem borer, BPH, leaffolder, gall midge and among the diseases, blast, bacterial blight, sheath blight, false smut and rice tungro disease reduce rice

Table 4.3 Resistant varieties in seed production chain in India

Resistant variety	Seed production (no. of years)	Cultivation in India	Resistance trait
Jyothi	21	Kerala	Gall midge
Uma	15	Kuttanad area, Kerala	Gall midge
Phalguna	14	Andhra Pradesh	Gall midge
Danteshwari	14	Chhattisgarh	Gall midge
Ratna	18	Maharashtra	Stem borer
Erramallelu	11	Telangana	Gall midge
Surekha	11	Grown in Telangana but exported to Kerala	Gall midge
Karma Mahsuri	9	Chhattisgarh	Gall midge

production in India significantly. As chemical control of pests and diseases has several limitations as a strategy, and with the phasing out of many broad spectrum insecticides, deployment of host plant resistance has been advocated. BPH, gall midge, blast and bacterial blight can be effectively managed through deployment of resistant varieties. Availability of molecular markers facilitates easy identification of resistance genes and aids in the selection of good and relevant donors, thus saving the cost, time and energy involved in the rigorous phenotyping. Bentur et al. (2021) had reviewed at length the literature on the identified genes conferring resistance to BPH, WBPH, GLH, GRH and GM, the chromosome number, primer identity along with the forward and reverse sequences for the benefit of the molecular breeders. With the basic knowledge available on the mechanisms of resistance to all the effective genes, it is easy to breed a resistant/tolerant variety with desired genes. Hence, development of an insect resistant variety through any breeding programme for a specific location would involve selection of a good donor wherein these molecular markers can be effectively used to develop gene pyramids for wide spectrum and durable resistance. However, from the stand point of acceptability, when the same rice variety may not be grown across the length and breadth of the country, a single variety need not be pyramided to provide resistance to all the biotypes of gall midge. Instead, locally adopted rice varieties can be used to introgress two or more effective genes that will confer resistance against all the prevalent biotypes/pests in that area. Durability of resistance is influenced by initial frequency of alleles in the pest population that confer adaptation against the plant gene, nature of inheritance of this allele and possible cross-virulence (Cohen et al. 2004). Hence, it is suggested that deployment of two or more undeployed genes that differ in their mechanism of resistance is the ideal option. Figure 4.1 depicts the schematic representation of the work flow for the development of a durable pest resistant rice variety.

4.3.2.2 Gene Pyramiding Strategies for Durable Resistance

Pyramiding resistance genes is predicted to increase the durability of resistant rice varieties against phloem feeding herbivores and other rice pests. Attempts to pyramid insect resistance genes were initiated with GM genes as resistance is governed by a single gene with the availability of closely linked markers/functional markers for developing durable pest-resistant rice cultivars/hybrids. Sama et al. (2014) introduced the recessive gene *gm3* into the genetic background of elite rice variety improved Samba Mahsuri with the help of markers. A focussed molecular breeding programme, which is still ongoing, was initiated in 1999–2000 at IIRR, Hyderabad, for introgression of several genes conferring resistance against bacterial blight, blast, gall midge and BPH into elite Indica rice varieties and hybrid rice parental lines with the help of molecular markers. Samba Mahsuri, Swarna, Akshayadhan, few elite *Basmati* varieties along with the hybrid rice parental lines KMR3R, RPHR-1005R, IR58025 and DRR17B served as recipient varieties while several breeding lines/ genotypes possessing one or more genes conferring resistance against BB, blast, gall midge and BPH served as donors. The genes considered for introgression included *Xa21*, *xa13*, *xa5*, *Xa33*, *Xa38* for BB resistance, *Pi1*, *Pi2* and Pi54 for blast resistance, *Gm1*, *gm3*, *Gm4 and Gm8* for gall midge resistance and *Bph18* and

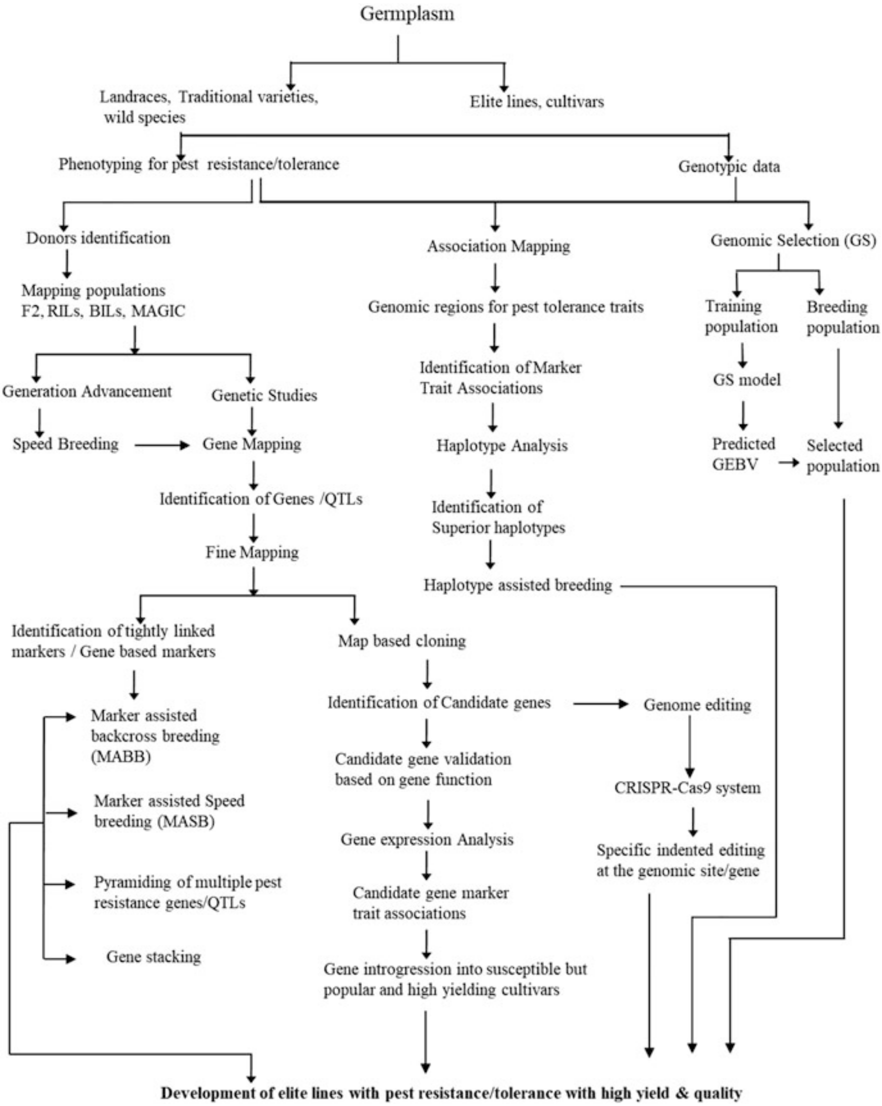

Fig. 4.1 Schematic representation depicting integration of breeding, molecular and genomic approaches for developing elite pest resistant lines. *RIL* recombinant inbred lines, *BIL* backcross inbred lines, *GEBV* genomic estimated breeding value, *GS* genomic selection, *MAGIC* multiparent advanced generation intercross, *QTLs* quantitative trait loci, *CRISPR* clustered regularly interspaced short palindromic repeats

Bph33 for BPH resistance. Two approaches, namely marker-assisted backcross breeding (MABB; i.e., 3–4 backcrosses), limited MABB (i.e. a single backcross) in conjunction with pedigree breeding were deployed for targeted resistance gene transfer. Recently, a novel BPH resistance gene, named *Bph33* was transferred along with the gall midge resistance genes, *gm3*, *Gm4 and Gm8* into improved Samba

Mahsuri through MABB (Naik et al. 2018). In another project funded by DBT, Govt. of India, initiated in the year 2009, a total of two genes each for resistance against BB (*Xa21* and*Xa33)*, blast (*Pi2* and *Pi54*), gall midge (*Gm4* and *Gm8*) and BPH (*Bph18*) have been transferred into the high-yielding rice variety Akshayadhan and hybrid rice parental line DRR17B. Backcross derived breeding lines possessing four, five and six resistance genes conferring tolerance to multiple biotic stresses have been developed and screened for their resistance against multiple biotic stresses.

Using *Gm4* and *Gm8*, the research group at ICAR-IIRR has developed gene-pyramided lines (PYL) in the genetic background of the elite restorer line RPHR1005R (restorer line for the popular rice hybrid DRRH3) (Abhilash Kumar et al. 2017) and into a high-yielding rice variety Akshayadhan through marker-assisted breeding. In another such effort, two resistance genes, *gm3* and *Gm8*, have been pyramided in the genetic background of the fine-grain-type rice variety Kavya, which is known to have *Gm1* (Venkanna et al. 2018). Multilocation studies on evaluation of gene PYL for gall midge resistance in India indicated that pyramided lines with two effective genes *Gm4* and *Gm8* were conferring resistance across 7–8 populations of gall midge (ICAR-IIRR, 2018–2021). But one of the major problems encountered in the development of rice varieties resistant to gall midge is that over a period of time, gall midge develops resistance against the deployed resistance genes, through the evolution of new biotypes. But later, it has been recorded from the research stations that only *Gm8* and *Gm1*, both with HR^{-} reaction, are holding promise across locations against gall midge populations in India (ICAR-IIRR 2018–2021).In another study from the Philippines, it was recorded that pre-conditioning of GLH, *N. virescens* on a pyramided line (PYL) with GRH2 and GRH 4-PYL gained partial virulence (feeding and development equal to that on T65) to the pyramided line within 10 generations and complete virulence (egg-laying equal to that on T65) within 20 generations. Studies with various rice pests suggest that previous long-term exposure to ineffective genes (including unperceived resistance genes) could dramatically reduce the durability of pyramided resistance (Horgan 2018). However, Gupta and Nair (2021) in her laboratory studies on BPH exposed to resistant rice variety, Rathu Heenati (*Bph 3*), observed that the epigenetic changes were induced in the context of DNA methylation levels. These epigenetic changes were reversible, i.e. the methylation levels, especially in CHG and CHH contexts reverted to its initial state once the stress was removed. The time taken for these epigenetic marks to “fade away” was shorter in case nutritional stress (resistant variety) as compared to pesticide stress. This information can be utilized in the effective deployment of a cafeteria of resistant genes.

4.3.2.3 Genomics-Assisted Breeding for Resistance/Tolerance Trait

It is interesting to note that though resistance breeding programme was in vogue since time immemorial, not many resistance varieties are under large cultivation. Of the many factors, it is pertinent that the final product/resistant variety will find a place in cultivation if it caters to the regional requirements of the farmers/consumers apart from possessing reasonable level of resistance to a particular pest(s). It is well known that resistance to insect pests is often associated with low yields. In this direction to address the issue, many of the BPH resistance genes have been introduced alone or in combination into modern rice varieties/parental lines of hybrids by marker-assisted selection. Wang et al. (2017a, 2017b) pyramided *Bph6* and *Bph9* into elite restorer line 9311, while Fan et al. (2017) developed three broad-spectrum BPH-resistant restorer lines by pyramiding big-panicle gene *Gn8.1*, BPH resistance genes *Bph6* and *Bph9* and fertility restorer genes *Rf3*, *Rf4*, *Rf5* and *Rf6* through molecular marker-assisted breeding. *Gm4* and *Gm8*, the effective genes, for conferring resistance to gall midge were incorporated into major mega varieties like MTU1010 (Duriseti et al. 2018), Swarna (Dixit et al. 2020), WGL 44 (Jai Vidhya et al. 2018); *Gm8* for gall midge (GM) in the background of Naveen (Janaki Ramayya et al. 2021); *Bph*20/21 into Krishna Hamsa (Badri et al. 2022) along with other genes for biotic (blast and BLB) and abiotic stresses (drought). To address this issue of both resistance and yield, care was taken to design the final product which has both insect resistance genes along with yield genes. Nagamani (2022) developed pyramided lines in the background of the elite variety MTU1010 through MABB conferring resistance to both blast and virulent population of gall midge and possessing high yield (*Ospl*4 and *Gna* genes). This involved intensive phenotyping under field conditions and selection for both resistance and yield in each generation of development for various stresses and advancement of promising material. In this endeavour, vast genetic resources with various gene combinations and different levels of expression were generated out of which pyramided lines with 3–7 genes under homozygous condition for gall midge resistance along with BLB genes and good grain yield ready for deployment are currently available. In this method, genotyping or presence of marker was correlated with the phenotypic data so as to ensure the presence of genes. However, the expression of genes under infested conditions in the finished product is not quantified. It is to be noted that the type of yield genes to be chosen would depend on the insect damage so that the gene would negate/compensate for the effect of insect feeding.

4.3.2.4 Molecular Cross Talks Between Insect Resistance/Susceptibility Pathways and Other Pathways

Plants are able to activate different types of induced resistance, depending on the organism that interacts with the plant. Well-studied examples of induced resistance are systemic acquired resistance, which is triggered by pathogens causing limited infection, such as hypersensitive necrosis. Wound-induced resistance, which is typically elicited upon tissue damage such as that caused by insect feeding (Kessler and Baldwin 2002; Howe 2004). Salicylic acid (SA), jasmonic acid (JA) and ethylene (ET) are recognized as key players in the regulation of the signalling pathways involved in conferring resistance (Howe 2004). It is generally stated that pathogens with a biotrophic lifestyle are more sensitive to SA-mediated induced defences, whereas necrotrophic pathogens and herbivorous insects are resisted more through JA/ET-mediated defences (Kessler and Baldwin 2002). In nature, however, plants often deal with simultaneous or subsequent invasion by multiple aggressors, which can influence the primary induced defence response of the host plant. Cross talk is the interaction between the signalling pathways which helps the plant to minimize energy costs and create a flexible signalling network that allows the plant to finely tune its defence response to the invaders encountered (Reymond and Farmer 1998; Pieterse et al. 2001; Bostock 2005). SA plays an important role in the regulation of systemic acquired resistance (SAR). Transduction of the signal leads to activation of the genes encoding pathogenesis related proteins. The regulatory protein Non expressor of PR genes 1 (NPR1), WRKY transcription factors are important factors in SA-dependent signalling. MAP kinases and Gluaredoxin GRX 480 are implicated in SA/JA cross talk. Highlight diversity in resistance pathways in rice against the gall midge triggered by different R genes has been reported by Divya et al. (2018a). Ample evidence is available on the interaction of SA, JA and ET pathways which could be either positive or negative. Although most reports indicate a mutually antagonistic interaction between SA and JA-dependent signalling, synergistic interactions have been described as well (Mur et al. 2006). As a result of negative cross talk between SA and JA, activation of the SA response should render a plant more susceptible to attackers that are resisted via JA-dependent defences and vice versa.

Usually under field conditions, the rice crop is challenged by many biotic stresses like insect pests, diseases or weeds. The challenge may vary. It could be one insect or many insects, or a disease and an insect at a particular crop stage. So a cautious deployment of a rice culture resistant to a single biotic stress/multiple biotic stresses is necessary. Though progress in tagging, mapping and cloning of several resistance (R) genes against various biotic stresses has led to marker-assisted multigene introgression into elite cultivars for multiple and durable resistance, no detailed studies on possible interactions among these genes when expressed simultaneously under combined stresses are available. Divya et al. (2018c) reported induction of several defence genes in response to attack by more than one biotic stress under controlled conditions through expression profiles of 14 defence-related genes in 11 rice breeding lines derived from Samba Mahsuri (BPT 5204), an elite cultivar with different combination of R genes against bacterial blight (BB), blast (BL) and ARGM. Cross response of *Pi54* and *Gm4* was observed, and inhibition of expression of *Pi54* by other target genes was indicated. In another study, marker-assisted intercross (IC) breeding involving multiple donors was used to combine three BB (bacterial leaf blight) resistance genes—*xa5*, *xa13* and *Xa21*, two blast resistance genes—*Pi9* and *Pi54*, two BPH resistance genes—*Bph20* and *Bph21* and four drought-tolerant quantitative trait loci (QTL)—qDTY1.1, qDTY2.1, qDTY3.1 and qDTY12.1—in the genetic background of the elite Indian rice cultivar ‘Krishna Hamsa’. It was observed that though introgressed lines (ILs) were marker-positive, there was a selective exclusion of BPH resistance genes especially when BB genes were present. However, such interactions were not observed with *Pi* genes (blast), and this requires further validation in different backgrounds to confirm the results (Badri et al. 2022). Multiple genes introgression in single background may result in the selective combination of compatible genes or selective exclusion of some combinations due to recombination events or chromosome-related factors (Haque et al. 2021). Significant variation was observed in the phenotypic response of the ILs in the background of Swarna despite the presence/absence of corresponding R genes and BPH susceptibility in ILs with *Bph3* and *Bph17* (Dixit et al. 2020) which could be due to the difference in the genome recovery and background interaction of genes/QTLs of the ILs. The study also reports that mere presence of markers would not ensure a positive phenotype. The negative phenotype in marker-positive plants can be the effect of varying expression of a specific gene in different background genomes. This could be the trade-off between the different signalling pathways associated with the genes that are operating. Expression profiling of stress-inducible genes was carried out in rice varieties and reported variability in gene expression patterns indicating the complex network of pathways for regulation of multiple stresses (Basu and Roychoudhury 2014). Detailed studies on cross talk between defence pathways are essential (Sharoni et al. 2011) when genes are pyramided to engineer plants resistant to multiple stress conditions (Saidi and Hajibarat 2019). So, it is important to know the pathways which are operating prior to the deployment of the varieties with various defence genes. To understand the functioning of the complex defence signalling network in nature, molecular biologists and ecologists should work in tandem to study molecular mechanisms of induced plant defences in an ecological perspective (Koornneef et al.2008).

4.4 Novel Methods to Identify and Characterize Resistance to Insect Pests

4.4.1 Susceptible Variety as Trap Crop for Stem Borer Management

It is an eco-friendly pest management strategy for small farmers where a susceptible cultivar was used to attract YSB larvae and minimize YSB damage. Growing one row of a susceptible aromatic variety (Pusa basmati 1) as an inter-crop/trap crop for every 9 rows of main crop (2.5–3 m) in east-west direction helps in reducing the damage by stem borer in the main crop by increasing the damage in the trap crop. The main crop variety can be of farmers' choice. The sowing date of aromatic variety has to be adjusted so as to flower a week before the main crop (Plate 4.3) (Padmakumari and Pasalu 2003). Under All India Coordinated Crop Improvement Programme for Rice, this concept was successfully tested in different regions for 3 years with a cafeteria of varieties like Swarna, MTU1010, BPT5204, HMT Sona, Tellahamsa, Krishna Hamsa, Jyoti, Rajendra Kasturi, TPS3, Karjat2, Karjat3 and ADT36 as main crop varieties in both wet and dry seasons (DRR 2009–2011). The grain yield in the treatments with main crop + trap crop was more than that in the treatment with main crop alone and the B C: ratio varied from 1.18 to 4.17 across locations and the monetary gain obtained varied from 3.27% to 8.25%. The damage in the main crop is reduced to half of that in the trap crop, thus avoiding one impulsive spraying of insecticide at the vegetative phase in a stem borer endemic area. No insecticide spray is required on main crop up to 25% dead heart damage in the trap crop (Padmakumari et al. 2017a).

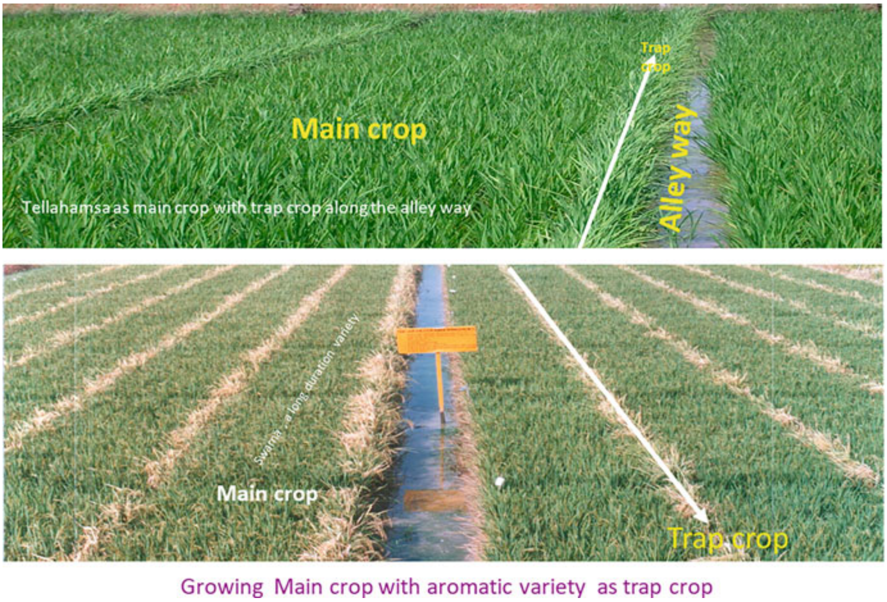

Plate 4.3 Host plant susceptibility for yellow stem borer management

4.4.2 Exploitation of Susceptibility Genes

Besides plant R-genes, plant susceptibility genes can be very useful in pest management. Some herbivorous insects have the ability to suppress effective defence responses of plants to their own advantage. It is hypothesized that these insects activate certain plant genes, the so-called susceptibility genes, to suppress or avoid the defence that antagonizes insect performance resulting in the susceptibility of the host plant (Walling 2008; Giordanengo et al. 2010). Knockdown of such susceptibility genes may be particularly interesting to control plant-manipulating insects. Therefore, investigating the potential to use susceptibility genes to control insect pests deserves to be explored though it was reported to confer resistance to certain pathogens (Lorang et al. 2007). It would be more appropriate to explore the mutagenic resources where both the reference genome and the lines susceptible for a particular trait are available. These lines can be further utilized to study the genetics, molecular and biochemical factors that confer susceptibility to a biotic stress and manipulate through gene editing to identify tolerant lines.

4.4.3 Induced Resistance

During the coevolution of plant–insect relationships, plants developed defensive strategies to minimize insect herbivory, which in turn led to the development of counter adaptations by herbivores. The plant hormone jasmonate (JA) plays a central role in regulating induced defence responses to a broad spectrum of herbivores.

4.4.3.1 Herbivore- and Elicitor-Induced Resistance

Bentur and Kalode (1996) observed that infestation of primary tiller induced HR^+ in resistant rice var. Phalguna, but mortality of gall midge maggots was induced in the secondary tiller without HR^+. The effects of prior herbivory by the fall armyworm, *Spodoptera frugiperda* and of exogenous applications of jasmonic acid (JA) on the resistance of rice plants to the rice water weevil, *L. oryzophilus*, manifested as reduced numbers of eggs and first instars associated with armyworm-injured or JA-treated plants relative to control plants (Hamm et al. 2010). In field experiments, there was a transient but significant reduction in the number of immature *L. oryzophilus* on JA-treated plants relative to untreated plants. The duration of effectiveness of such induced resistance varied with the sequence and time lag between infestations. Such studies are essential where induced resistance to same insect or different insects, to know the effectiveness of the genes under real-time situations where the sequence and intensity of insect infestations vary and are not under our control under field situations and also the exogenous application of methyl salicylate/jasmonate for pest management.

4.4.3.2 Silicon as Source of Resistance

Many elements that are considered as essential nutrients play a significant role in host plant–pest interactions. But silicon (Si) though not identified as an essential element was found to play a significant role in imparting biotic and abiotic stress resistance and had a predominant negative impact on herbivore performance (Ma 2004). The application of Si to crops is a viable component of an integrated management programme for insect pests and diseases as it is relatively less expensive, leaves no pesticide residue in food or the environment and could easily be integrated with other pest management practices (Laing et al. 2006). Extensive work on carrier-induced silicon transportation into rice in relation to yellow stem borer (Ranganathan et al. 2006) identified imidazole as the best carrier cum solubilizer for silicon of the many amino acids studied. The effect of imidazole, when applied in split doses at 1500 mmol of the carrier X four times in the field in lowering yellow stem borer damage in rice varieties (Voleti et al. 2008) due to accumulation of Si. Study by Jeer et al. (2017), the first study of its kind, demonstrated that application of imidazole, a solubilizer cum carrier, enhanced the uptake of Si, deposited in the stem region (2.1–5.3-fold), thereby increasing the abrasion of the larval incisors (mandibular wearing) and effected the YSB larval growth, larval recovery through effect on mandible wearing and inner lining of the midgut. The work has led to the identification of a novel class of bio-compatible molecules, which exhibited remarkable resistance to damage by yellow stem borer. Combined application of rice husk ash (a cheap source of Si) and imidazole reduced YSB damage with a benefit–cost ratio (1.16–1.31) which was at par with one granular insecticide application (Jeer et al. 2018). In BPH, Si acts as a sucking inhibitor (Yoshihara et al. 1979). Studies on BPH proved that Si amendment adds to fast and strong callose deposition in

BPH-infested plants, resulting in low feeding by BPH on Si-supplemented plants. Si amendment is involved in modulation of the gene expression of callose synthase and hydrolase triggered by BPH infestation and that high expression of the synthase gene *OsGSL1* and low expression of the hydrolase gene *Gns5* were recorded in Si-amended plants during the initial stages of BPH infestation (Yang et al. 2018). The reported relationships between soluble silicon and the jasmonic acid (JA) defence pathway and herbivore-induced plant volatiles (HIPVs) suggest that soluble silicon may enhance the production of herbivore-induced plant volatiles (HIPVs) (Reynolds et al. 2016).

4.4.4 Transgenics

Research in late 1990s explored various options for development of resistance to incalcitrant pests like stem borers where adequate sources of resistance in the gene pool were not available, and genetic engineering as a tool was explored and utilized to develop resistant lines. Among the widely used genes encoding insecticidal proteins/molecules against rice insect pests, endotoxin crystal proteins of *Bacillus thuringiensis*, digestive enzyme-specific protease inhibitors, plant lectins, α amylase inhibitors, insect chitinases and insecticidal viruses are important. Of these, Bt toxin genes (*cry1A*, *cry1B*, *cry1C*, *Cry1Aa*, *cry1Ab*, *cry1AC*, *cry1Aa*, *cry1Ac*, *cry2A*, *cry1C*, *cry1c* and *cry2A*) and protease inhibitors PINII (potato proteinase inhibitor) (cowpea serine P1) *Cry1AB*, *Cri Ac*, *Cry1A*, *Cry2Aa*, with CaMV 35S promoters were tested. Chimeric Bt gene, *cry1Ab*; *cry1Ab/cry1Ac* fusion gene against stem borer and lectin protein gene (gna, asa lectin, snowdrop lectin) against hoppers have been reported to be effective. Nayak et al. (1997) and Datta et al. (1998) were the first to report transformation of rice with the Bt gene against yellow stem borer. Research spanning more than two decades had resulted in many genes effective against stem borers, YSB and SSB which has been extensively reviewed (Makkar and Bentur 2017; Bentur et al. 2021).

Apart from YSB, genetic engineering approaches were also attempted for the most destructive pest brown planthopper in south and south-east Asia. Plant-derived lectins were utilized for engineering resistance to plant and leafhoppers. The snowdrop lectin gene, *Galanthus nivalis* agglutinin (*GNA*), conferred partial to complete resistance to planthoppers and leafhoppers in the rice varieties. Partial resistance to leafhoppers and planthoppers was demonstrated by rice transformation with a lectin gene from garlic (*Allium sativum* leaf agglutinin gene, *ASAL*; Rao et al. 1998; Saha et al. 2006). Bala et al. (2013) reported that *ASAL* interacts with NADH quinine oxidoreductase (NQO), a key player in the electron transport chain, and results in toxicity and increased mortality of BPH in transgenic rice lines. This study also demonstrated that, among all the transgenes available for control of sucking pests, *ASAL* holds significant promise, particularly against BPH. Yoshimura et al. (2012) developed transgenic rice possessing lectin1 gene from *Dioscorea batatas* under the control of a phloem-specific promoter (i.e. promoter of sucrose synthase-1gene) that showed a 30% decrease in the survival rate of BPH. Even though, in general, it is known that Cry proteins are ineffective against sucking pests, through loop replacements with gut-binding peptides in *Cry1AB* domain II, enhanced toxicity against BPH has been demonstrated (Shao et al. 2016). Liu et al. (2018) have shown the efficacy of Cry64Ba and Cry64Ca, two ETX/MTX2-type *Bt* proteins, against hemipteran pests. Boddupally et al. (2018) recently demonstrated that the expression of hybrid fusion protein (Cry1Ac::ASAL) in transgenic rice plants imparted resistance against multiple insect pests: BPH, stem borer and leaffolder.

Bt rice lines Huahui No. 1 (CMS restorer line) and *Bt* Shanyou 63 (a hybrid of Huahui No. 1 and Zhenshan97A, aCMS line), expressing *Cry1Ab/Ac* fusion gene, were developed in China (Chen et al. 2011) and earned biosafety certificates in 2009. However, because of political reasons, its commercialization in China has been postponed, and, to date, Bt rice is not grown in China. Some of the reasons for the delay in commercialization are (a) Bt rice was developed only for stem borer resistance and not any other rice pests. So, there is a need to develop insect resistance management strategies, (b) low level of understanding and acceptance of GM crops in China (Li et al. 2016), (c) resolving trade policy impediments (High et al. 2004; Liu et al. 2016). Jin et al. (2019) estimated the opportunity cost of postponement of Bt rice between 2009 and 2019 to be 12 billion US dollars per year.

4.4.5 RNA Interference (RNAi) for Plant Resistance to Insects

RNAi also known as post-transcriptional gene silencing (PTGS) is a novel method wherein gene expression of specific sequences is suppressed. Gene silencing mechanism is triggered by double-stranded RNA at the cellular level. The RNAi strategy for pest control is based on ingestion of double-stranded RNA (dsRNA) into the target pest system. After ingestion, dsRNA expresses either through hairpin or by other different means and spreads throughout the insect system (Katoch et al. 2013). Resistance to *C. suppressalis* was provided by rice knockdown lines TT51 (*cryAb* and *cry1Ac*) and T1C-19 (*cry1Ac*) with two aminopeptidase N genes (APN1 and APN2) (Qiu et al. 2017). Kola et al. (2016) demonstrated the silencing of CYP and APN genes of *S. incertulas* and knockdown of acetylcholine esterase gene (Ache) in rice lines which resulted in reduced larval length and weight of yellow stem borer within 15 days after exposure to dsRNA (Kola et al. 2019). However, they are still considered as genetically modified crops and more data need to be generated on specificity of dsRNA, fate of nanoparticle/dsRNA formulation in the environment, effects of RNAi-based products on non-target organisms, etc.

4.4.6 Genome Editing for Developing Resistance to Insect Pests in Elite Background

CRISPR gene editing is gaining prominence as an effective tool to tackle insect pest problems as it has the capacity to alter the specific gene of interest. In rice, the cytochrome P450 gene CYP71A1 encodes tryptamine 5-hydroxylase, which catalyses conversion of tryptamine to serotonin. In susceptible wild-type rice, planthopper feeding induces biosynthesis of serotonin and salicylic acid, whereas in mutants with an inactivated CYP71A1 gene, no serotonin is produced, but salicylic acid levels are higher. Insect-resistant rice plants with mutations in the cytochrome P450 gene accumulated high levels of salicylic acid but lacked serotonin. Suppression of serotonin confers resistance to planthoppers and stem borers, the two most destructive pests of rice (Lu et al. 2018). However, commercial use of CRISPR/Cas9 in insect pest management is still in its infancy. With the governments favouring SD2 genome-edited events, this method of genome editing is more appealing as compared to transgenic approach for the production of next-generation insect-resistant crops.

4.5 Role of Genomics in Insect Pest Resistance

4.5.1 Rice Genome

The 3k rice genome panel is a valuable resource which can be exploited for identification of genotypes with similar haplotypes. Once the haplotypes are identified, they may be evaluated for their phenotype. This will reduce the drudgery of screening large germplasm against the target pests. The work flow propounded by Varshney (2016) can be applied to the generation of re-sequencing and phenotyping data on 3000 rice genotypes. The re-sequencing data will be analysed for better understanding the rice genome and identification of structural variations in the germplasm collection. These structural variations together with phenotyping data will be analysed for establishing marker–trait associations for resistance traits of importance. The associated structural variations can be utilized for accelerating development of improved cultivars using genomics-assisted breeding. The availability of the rice genome sequence in conjunction with cutting-edge genomic technologies, including transcriptomics, proteomics and metabolomics, provides scientists an unprecedented opportunity to unravel the functions of rice defence genes against insects. The knowledge and molecular tools developed through these studies will undoubtedly facilitate the development of novel rice varieties with enhanced insect resistance (Chen et al. 2012).

4.5.2 Insect Genome and Transcriptome

The genome of BPH and its endosymbionts have been sequenced (Xue et al. 2014). It is a large genome (1141 Mb) with 27,571 protein-coding genes, of which 16,330 are specific to this species. In comparison, the WBPH genome is relatively smaller (720 Mb) with 21,254 protein-coding genes (Wang et al. 2017a), while the SBPH genome size is 541 Mb with 17,736 protein-coding genes (Zhu et al. 2017). Mitochondrial (mt) genomes of these three planthopper species have also been sequenced (Zhang et al. 2013, 2014). Draft genome (Kattupalli et al. 2021) and larval transcriptome (Renuka et al. 2017) of *S. incertulas*; chromosome level genome assembly of *C suppressalis* (Ma et al. 2020) and genome of *C. medinalis* (Zhao et al. 2021) are currently available. Transcriptomes of individual tissues like secretory salivary glands of GM with details on SSGPs in resistant and susceptible varieties (Sinha et al. 2012a, 2012b) and BPH (Ji et al. 2013) which have major implications in pest–rice interactions have been studied. Transcriptome analysis provides valuable information regarding BPH development, wing dimorphism and sex differences (Xue et al. 2010), which could facilitate further investigations on the detailed physiological mechanisms of BPH. Comparative analyses of the methylation patterns of Tf2 elements in BPH feeding on resistant- and susceptible-rice varieties confirmed that methylation, particularly in non-CG context, is involved in TE regulation and dynamics under nutritional stress which is reversible (Gupta and Nair 2022). These changes likely account for its capacity to thrive under unstable environments and its remarkable resilience to several stresses. Information on genes involved in sensory and chemoreception, those regulating metabolic pathways, detoxification genes, RNAi machinery in rice pests, can be further explored for developing pest-resistant crops.

4.5.3 Application of Structural and Functional Genomics in Genomics-Assisted Breeding

The insect genome and transcriptome databases of rice, the host plant and the insects have opened new vistas in the understanding of pest behaviour and can be exploited in future for developing pest-resistant lines. Deeper understanding of the pest–host interaction would help in manipulation of the signalling or metabolic pathways for conferring resistance.

4.6 HPR as a Component of Rice IPM

4.6.1 HPR with Biological Control

Earlier studies suggest that insect feeding on resistant varieties has delayed development and is more exposed to natural enemies. There are also some volatile organic compounds [*S*-linalool, caryophyllene, green leaf volatile (GLV) etc.] whose expression level in response to BPH attack determines the plant–pest interaction. *S*-linalool is one such volatile which is strongly induced by BPH attack (Cheng et al. 2007). Inducible *S*-linalool attracts predators and parasitoids but repels BPH. Similarly, GLV encoded by a gene HPL3 positively modulates resistance to BPH by modulating oxylipin pathway (Tong et al. 2012). Compared with rice plants exposed to the volatiles from uninfested plants, plants exposed to SSB-induced volatiles showed enhanced direct and indirect resistance to SSB. When subjected to caterpillar damage, the HIPV-exposed plants showed increased expression of jasmonic acid (JA) signalling genes, resulting in JA accumulation and higher levels of defensive proteinase inhibitors. Plants exposed to *C. suppressalis*-induced volatiles emitted larger amounts of inducible volatiles and were more attractive to the parasitoid, *Cotesia chilonis* (Yao et al. 2023) implicating the role of proteinase inhibitors. However, in-depth studies are essential to prove the effect and role of damage-associated molecular patterns (DAMP), HIV, green leaf volatiles (GLVs) in pest resistance and their utility in pest management.

4.6.2 HPR with Insecticides

Horgan et al. (2020) reported that BPH populations selectively reared on IR65482-4-136-2-2 (*Bph10* gene) had increased susceptibility to imidacloprid and fipronil, representing a possible trade-off with virulence. In contrast, a population with virulence to the highly resistant variety PTB33 was 4.88 times more resistant to imidacloprid and 3.18 times more resistant to BPMC compared to planthoppers of the same origin but reared on the susceptible variety IR22. Their experimental results suggest complex relations between insecticide resistance and virulence that vary according to insecticidal toxins and resistance genes and include potentially increased insecticide susceptibility (a trade-off) as well as common detoxification mechanisms (a benefit).

4.6.3 HPR and Endosymbionts

Symbionts influence the performance of herbivores on plants, to such an extent that they can ultimately determine whether a plant becomes a suitable host for an insect or not. In BPH, until 2000, yeast-like symbionts (YLS) were reported to be associated. But of late, other eukaryotic and bacterial symbionts have been reported to be associated with *N. lugens* and *N. cincticeps*. Ferrater et al. (2013) reviewed the complexity of the rice hopper symbiont interactions. He detailed on the nature of symbiont communities and their functions in planthoppers and leafhoppers—focusing on their likely roles in mediating adaptation to plant resistance. Evidence from a small number of experimental studies suggested that bacterial and eukaryotic (including yeast-like) symbionts can determine or mediate hopper virulence on rice plants and that symbiont functions could change over successive generations of selection on both resistant and susceptible plants. The role of symbionts in mediating virulence could differ depending on the strength of resistance in rice and the extent of planthopper exposure to the resistant variety or to varieties with similar resistance genes. Yeast-like symbionts (YLS) may mediate virulence adaptation in early generations of selection with the planthoppers themselves ultimately adapting to the novel resistance after several generations.

Preliminary mating studies with *N. lugens* have indicated that YLS did contribute to virulence on a resistant variety (IR62—*Bph3* gene), the male parent also influenced fitness on the resistant host, suggesting that other mechanisms (which may include bacterial symbionts) also played a role in virulence adaptation. Gupta et al. (2022) reported that *Pseudomonas* sp. in BPH microbiome varied with seasons and geographical locations and its composition and abundance correlated with BPH survivability. Environment-guided microbial shifts drive rapid stress adaptations in BPH.

Sinha et al. (2022) in their studies on analysis of rice tissues at the site of feeding of ARGM maggots revealed differential representation of the phylum Proteobacteria in the GM-infested and uninfested rice tissues. Analysis of the species diversity of *Pseudomonas* and *Wolbachia* supergroups at the feeding sites indicated the exchange of bacterial species between ARGM and its host, the rice upon infestation. In another study, sequencing of 16S rRNA bacterial gene (V3-V4 region) revealed differences in the microflora of the ARGM maggots feeding on susceptible (var. TN1) or resistant rice (RP 2068-18-3-5) hosts though *Wolbachia* sp. and *Pseudomonas* sp. formed the major constituents of the Proteobacteria in all the ARGM samples analysed. *Wolbachia* was the predominant bacterium in pupae and adults. *Pseudomonas* sp. was predominant in maggots. High species diversity in maggots isolated from susceptible rice and high representation of unclassified bacteria in maggots isolated from resistant rice was observed (Ojha et al. 2017). During the different stages of metamorphosis of an insect, there is a sterilization process at each stage, and insects acquire new set of microbes at each stage.

Symbionts do not work or have no role to play on mechanisms of resistance which are associated with plant surfaces, mechanical barriers, volatiles or chemicals that work on sensory features of the insect. Studies till date suggest an influence of endosymbionts on insect adaptation and virulence, but the mechanisms operating the adaptation are unclear. However, bacterial functions or the nature of the association between the bacteria and the insect pest (i.e. primary, secondary, internal or external) has not been established. The relative role of these symbionts in each of the insect pest–rice interactions needs more in-depth studies to actually define their role in insect survival and conferring virulence. Gupta and Nair (2020) opined that the gut microbiome can dramatically influence the physiology, behaviour and genetics of its insect host, and therefore, targeting the microbiome could be counted as an effective approach for developing an integrated, environment-friendly and a sustainable pest-management strategy.

4.6.4 Conclusion

IPM is the careful selection and intelligent deployment of the various proven and available strategies from the basket of options that are available for managing insect pests. It is solely based on location-specific needs of the farmers and not prescription-based. The current rice varieties developed and deployed for cultivation possess high tillering capacity with improvement in various yield components than traditional rice for compensation from insect pest damage and that capacity is enhanced by agronomic practices, thus integrated pest management should be thought of within the context of crop management (Litsinger 2005). Systems biology-guided analysis plays a major role in understanding the needs of plant–

insect interaction. The order of recruitment/colonization of insects in a field and understanding the relative importance of biotic and abiotic factors that affect insect community assemblages and species co-occurrence on plants is thus central to our understanding of insect–plant interactions (Trivellone et al. 2017). More careful, targeted and intelligent deployment (both temporally and spatially) of resistance genes together with crop management practices that avoid pest outbreaks will reduce the emergence of further virulent populations especially in the case of planthoppers which are widespread and gall midge which are endemic to certain pockets. So a thorough knowledge on the crop management practices and deployment strategies should be developed for rice lines with pyramided resistance, and the farmers need to be informed and educated thoroughly so as to avoid the build-up of virulent herbivore populations and increase the durability of resistance. Another opinion is that resistant varieties can be deployed to delay the outbreaks of the pests but not as an integral part of IPM (Horgan 2018).

4.6.5 Way Forward

Last decade witnessed a tremendous shift from exclusive selection of plants based on phenotype to section of plants based on molecular markers. Availability of trait-linked molecular markers and reduction in genotyping costs have facilitated better selection of lines in the breeding programmes. Most of the genotyping depends on the precise, reliable and repeatable phenotyping protocols with specific insect population. More accurate and precise phenotyping strategies are necessary to empower high-resolution linkage mapping and genome-wide association studies (GWAS) and for training genomic selection models in crop improvement (Varshney 2016). It is anticipated that selection of lines in breeding programmes will be predominantly based on genotyping/sequencing in the framework of genomic selection (GS). Cobb et al. (2013) reiterated that phenotyping is emerging as the major operational bottleneck limiting the power of genetic analysis and genomic prediction. To ensure relevance, the implementation of efficient and informative phenotyping experiments also requires familiarity with diverse germplasm resources, population structures and target populations of environments. Therefore, they proposed to establish next-generation phenotyping to increase the accuracy, precision and throughput of phenotypic estimation at all levels of biological organization while reducing costs and minimizing labour through automation, remote sensing, improved data integration and experimental design. Robust and field-relevant trait phenotyping systems are needed to characterize the full suite of genetic factors that contribute to quantitative phenotypic variation across cells, organs and tissues, developmental stages, years, environments, species and research programmes. Today, with the impact of climate change evident, there is a need to look for climate-resilient lines tolerant to insect pests. Varshney (2014) proposed the utility of NGS technologies combined with precise phenotyping methods, as tools that are powerful and rapid for identifying the genetic basis of agriculturally important traits and for predicting the breeding value of individuals in a plant breeding population. Unlike MAS, GS does not necessarily need QTL information before selection. GS uses reference population data containing phenotype and high-density marker data to predict breeding values for all the markers. Based on the predicted values, the breeding population data will be analysed to select the individual that possesses the desirable phenotype (Perez-de-Castro et al. 2012; Hu et al. 2018b). In this way, it is possible to introgress even minor-effect QTLs efficiently, as there are no biased marker effects, unlike with MAS.

As the plants and insects co-evolve, evaluation, identification and characterization of genetic resources are a continuous process. Finally, the age at which plants are attacked, how resistance manifests vis-à-vis over various stages of crop growth and how farmers manage their crop (vis-à-vis fertilizer and pesticide inputs), the knowledge level of the farmers, access to various pest management options will be the key determinants of pest population growth and damage responses in fields of resistant rice.

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Host Plant Resistance to Insect Pests in Wheat

5

Anamika Sharma, Venugopal Mendu, and Gadi V. P. Reddy

Abstract

Host plant resistance offers an excellent solution to pest problems, which reduces pesticide usage and environmental pollution. Host plant resistance to insect pests in wheat has enabled the management of major insect pests including *Mayetiola destructor*, *Cephus cinctus*, *Diuraphis noxia*, *Schizaphis graminum*, and *Rhopalosiphum padi.* The major sources of genetic diversity for pest resistance in wheat have been landraces cultivars of wheat and wild relatives. Several resistance genes have been identified and are incorporated into cultivated wheat (especially in *Triticum aestivum*). Nevertheless, scanty information is available about resistance to other economically important pests such as *Sitodiplosis mosellana* and *Oulema melanopus.* A coherent program to incorporate resistant varieties in the integrated pest management (IPM) of wheat pests is needed to better protect the crop and improve crop yields.

Keywords

Breeding · Transgenic wheat · Insect resistance · Hessian fly · Aphids · Wheat stem sawfly

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5.1 Introduction

Wheat (*Triticum* spp.) (Poaceae) is one of the widely consumed cereal grains in the world and is a staple food for over 30% of the world's population (FAO 2014). In terms of production, wheat is the second most-produced cereal after maize (FAO 2014). Wheat production increased in 2022 (FAO 2022) and is predicted to continue to expand due to its use in human and animal feeding purposes. Consumption has also increased due to the higher use of wheat in animal feed in China, the European Union, and the United States of America (FAO 2022), and demand is projected to rise at a rate of 1.6% annually until 2050 (FAO 2022). China remains the largest wheat producer in 2022 followed by the European Union, India, Russia, and the USA. The significant wheat exporters are Russia, Canada, Australia, and the USA, and the major importers are Egypt, Brazil, and Mexico.

Wheat is considered an environmentally friendly crop. In terms of climate change, emissions from cereals production are much lower than in the cattle and meat industries. Wheat emissions per hectare are about 20% of those of rice production, making wheat a desirable cereal crop (FAO 2022). There are several species of wheat, but those most widely cultivated are *Triticum aestivum* (common wheat, a hexaploid species, 95% of total wheat production), *T. durum* (durum or pasta wheat, a tetraploid species), and *T. dicoccum* (emmer wheat, a tetraploid species). Other less commonly cultivated species of wheat include *T. spelta* (spelt, a hexaploid species), *T. compactum* (club wheat, a hexaploid species), and *T. monococcum* (einkorn, a diploid species) (Moudrý et al. 2011). Species of wheat have different characteristics and uses and are adapted to various growing conditions and environments.

Both abiotic and biotic factors affect wheat yield and quality. Major abiotic stressors are drought, heat stress, cold stress, salinity, soil acidity, nutrient deficiency, water logging, and frost. Biotic stresses include pest species of fungi, bacteria, viruses, nematodes, weeds, and insects. Moreover, weather-related disorders, as well as chemical, genetic, and physiological problems also affect wheat production (Bockus et al. 2010). These stresses can act alone or in combination, leading to significant reductions in wheat yield and quality. Developing new wheat varieties more tolerant to stresses is a major goal of wheat breeding programs. Public and private organizations are working on developing insect-resistant wheat varieties, including the International Maize and Wheat Improvement Center (CIMMYT), the International Rice Research Institute (IRRI), the National Research Center for Wheat (NRCW), the United States Department of Agriculture (USDA), Agriculture and Agri-Food Canada (AAFC), and the China National Wheat Improvement Center (CNWIC).

Globally, insect losses in wheat are 5–35%, depending on the region and year (Dhaliwal et al. 2010). There are several research review articles available that comprise the basic details of insects, their biology, and insect resistance efforts. Some of the major articles in recent years are Luo et al. (2023), Sarthi et al. (2022), Arif et al. (2022), Mondal et al. (2016), Berzonsky et al. (2003). In this chapter, we are attempting to compile the basic mechanisms of producing resistant varieties, breeding methods, and the status of the current efforts.

5.2 Sources of Wheat Resistance to Arthropod Pests and Utilization in Breeding Programs

Plants naturally exhibit different levels of resistance to arthropods, which are categorized as *tolerance* (the ability of a plant to maintain its yield or quality under pest pressure) (Onstad and Knolhoff 2014), *antixenosis* (non-preference by a pest for a plant due to the plant's specific traits such as trichomes) (Gebretsadik et al. 2022; Achhami et al. 2020), and *antibiosis* (plant traits that interfere with the arthropod's physiological processes, such as plant chemistry) (Cao et al. 2015; El-Wakeil et al. 2010). Typically, antibiosis traits allow plants to actively resist predators and parasites but come with a plant fitness cost. These resistance traits evolve when the benefit is greater than the cost and may be used to produce resistant varieties. Such resistance traits create a strong selection pressure on the pest evolution to overcome the resistance. Plants then are selected to evolve different resistance traits, creating a cycle of resistance deployment followed by pest or pathogen adaptation (Smith 2005; Garcia et al. 2021; Tadesse et al. 2022a). Genetic diversity for pest resistance from wild species can be discovered by screening the germplasm collections. Increasing genetic diversity by incorporating genes from wild varieties could help improve the resistant traits of wheat (Moudrý et al. 2011). Finding potential sources of resistance to pests of interest proceeds through a series of steps as outlined here below.

5.2.1 Sources of Resistance

In developing new resistant varieties of a crop, the first step is to identify potential sources of resistance to the targeted stress. The level of resistance associated with sources must then be quantified, and the identified genetic factors used to modify crop genetic diversity (ideally enhancing the total number of genetic resistance characteristics), leading ultimately to crop improvement. New sources of genetic resistance are periodically re-collected over time because of the difficulties involved in carrying out systematic collections of new accessions and the decline in the condition of previously collected germplasm due to the deterioration during storage (Smith 2005). Wheat genetic resources are held at institutes such as GRIN (Germplasm Resources Information Network) maintained by the USDA-ARS, which has more than 400,000 wheat accessions from around the world, with information on the accessions' genetic and geographic origins, morphological and agronomic traits, and molecular data; IWIS (International Wheat Information System), which is an online platform maintained by CIMMYT that has information on wheat varieties, germplasm, and wheat genetic resources worldwide); WGRC (the Wheat Genetic Resource Center) of Kansas State University, USA, which has information on more than 26,000 wheat accessions from around the world); NCBI (the National Center for Biotechnology Information of the USA's National Library of Medicine), has information on wheat genome sequences and molecular markers for wheat germplasm characterization (Tadesse et al. 2019). However, only about 10% of the available wheat genetic resources have been used by breeders in their research programs. In part, this lack of use may be because some gene bank accessions are obsolete, and secondly, the germplasm collections of many accessions are poorly characterized or the available data might not be readily accessible. Such accessions cannot be easily matched with the interest of breeders. Finally, for some breeding objectives, there may be enough genetic diversity available in the best-studied, best-performing breeding lines and varieties (Tadesse et al. 2022a).

5.2.2 Screening Germplasm Collections and Identification of Resistant Varieties

Germplasm collections are repositories of genetic resources from a diverse collection of seeds from plants (landraces, wild relatives, cultivars, etc.) that can be used to identify potential sources of resistance. These collections can be screened for resistance to arthropod pests using various techniques, such as field observations, artificial infestations, and laboratory bioassays (Gebretsadik et al. 2022; Nasrollahi et al. 2019; Li et al. 2013; Luo et al. 2023). Varieties found in the above resources that appear to be resistant to a given arthropod pest can then be used as potential sources of resistance in breeding programs. Such candidate varieties can be identified through literature searches, expert consultations, and field observations (Xu et al. 2020).

5.2.3 Crossbreeding with Related Species and Genetic Mapping

When desired resistance traits are not located in wheat varieties as described, another approach is to crossbreed the crop with related species, such as wild wheat relatives, to introduce new genes and traits into the crop, which may confer resistance to arthropod pests. Advances in molecular biology, molecular genetics, and genomics allow scientists to map the genes that control resistance in wheat to specific locations on the genome. This information can be used to identify the source of observed resistance and to develop molecular markers that can be used to select the resistance traits in breeding programs to develop new wheat varieties with improved resistance to arthropod pests (Smith and Clement 2012; Smith 2005). Different types of markers can potentially be used for gene mapping, including RFLP, STS, RAPD, AFLP, SSRs, and SCAR (Smith 2005) for molecular breeding for rapid introgression of resistance traits.

5.3 Factors Influencing the Expression of Resistance in Wheat to Arthropods

The expression of resistance in wheat to arthropods is influenced by several factors, including genetic issues, environmental conditions, plant physiology, and the pest's traits.

5.3.1 Genetic Factors

Those that influence the level of resistance in wheat to a given pest can include (1) whether resistance is due to a single gene or by multiple genes, (2) the amount of gene expression, (3) whether the desired resistance is due to tolerance, non-preference, or antibiosis, and (4) the genetic background of the plant.

5.3.2 Environmental Factors

These include variables such as temperature, moisture, and light that can affect the expression of resistance in wheat to arthropods. For example, high temperature and low humidity may reduce the level of resistance in wheat to some pests (Tang et al. 2018), while moderate temperatures and adequate moisture can enhance the expression of resistance (Zhu et al. 2010).

5.3.3 Physiological Factors

These including the plant's physiological status can influence the expression of resistance in wheat to arthropods. For example, the level of resistance may be affected by the stage of plant growth, as well as by stress such as drought or nutrient deficiency (Zhang et al. 2017).

5.3.4 Arthropod Factors

Arthropod factors are those where an insect's biology or behavior influences the level of resistance in wheat. For example, the susceptibility of some arthropods to certain types of resistance may vary by pest species (Luo et al. 2023), and the resistance level may be affected by factors such as feeding behavior, mobility, and population dynamics (Smith and Clement 2012; Smith 2005).

5.4 Techniques Used to Measure Pest Resistance

The choice of technique to measure pest resistance in wheat depends on the type of resistance, the pest of interest, and the resources available for testing. A combination of techniques can be used to provide a more comprehensive assessment. Assessments often start with laboratory bioassays that expose plant varieties to the pest under controlled laboratory conditions. The insect responses are then measured, including variables such as insect oviposition responses, the number of insects that survive, and the developmental stage of the pest (Wu et al. 2003). Simultaneously, the effects on the plants are measured, such as the level and types of damage caused by the pest (Smith and Clement 2012). Bioassays of various designs can be used to test for various types of resistance, including antibiosis, antixenosis, and tolerance (Gebretsadik et al. 2022; Arif et al. 2022; Cao et al. 2015). Field observations can also be used to measure resistance based on monitoring the behavior and performance of arthropod pests on wheat plants under field conditions (Achhami et al. 2020; Xu et al. 2020; Gebretsadik et al. 2022). This type of information can provide information about the level of infestation, the timing of pest outbreaks, and the level of damage caused by the pests on different plant varieties. Both laboratory and field experiments involve visual rating scales to assess the level of damage caused by arthropod pests on wheat plants (Tadesse et al. 2022a, b). Molecular markers are then used to identify the genes that control resistance detected in plants and later track the presence or absence of these genes in different breeding lines. Another technique, the electrophysiological technique, measures the electrical activity of plant tissues in response to insect feeding (Arif et al. 2022). These techniques can provide a sensitive and rapid way to detect changes in plant physiology in response to insect feeding, which can be used to identify resistant varieties (Smith 2005; Smith and Clement 2012).

5.5 Inheritance of Arthropod Resistance in Wheat

The inheritance of arthropod resistance in wheat plants is a complex genetic process that can be influenced by various factors. The genetic basis of arthropod resistance in wheat plants is typically polygenic (controlled by multiple genes). The genes that control arthropod resistance in wheat plants can be inherited from both parents in breeding, and the inheritance pattern can be influenced by both the type of resistance and the genetic background of the plant. Some types of resistance, however, are controlled by single genes, such as the Hessian fly resistance gene (H6), which confers resistance to *Mayetiola destructor*. Inheritance of single-gene resistance follows Mendelian laws of inheritance, where resistance is associated with the dominant allele and susceptibility is associated with the recessive allele. Monogenic resistance is easier to introgress into varieties compared to polygenic resistance. Other types of resistance, such as antibiosis or tolerance, are controlled by multiple genes, and the inheritance pattern is more complex. In these cases, the expression of resistance is influenced by the interaction of multiple genes and environmental and physiological factors. Plant breeders use a variety of techniques, such as genetic mapping, marker-assisted selection, and genome editing, to identify and manipulate the genes that control arthropod resistance in wheat plants (Smith 2005; Smith and Clement 2012). These techniques can help to improve the effectiveness and durability of resistance in wheat plants (Smith 2005; Tadesse et al. 2022a).

5.6 Constitutive Versus Induced Host Resistance

Plants have evolved various resistance mechanisms to defend themselves from pests. Deploying resistance molecules is energy-intensive, hence some mechanisms are induced only in the presence of pests while others are constitutively active in the plants. Wheat resistance genes to arthropod pests can be classified as constitutive or induced. Constitutive resistance genes are always present in the plant and provide a baseline level of resistance. These genes can be inherited from naturally resistant parent plants or artificially introduced by breeders through genetic modification. For example, some wheat varieties may have constitutive resistance genes that produce toxic compounds or other defenses that deter or kill arthropod pests. Breeders apply techniques such as cloning, genetic engineering, or biotechnology to enhance constitutive resistance. In contrast, induced resistance genes are activated in response to arthropod infestations or other environmental cues. These genes are triggered by the presence of arthropod pests, damage to plant tissues, or exposure to other stress factors. Induced resistance genes can result in changes to plant physiology, such as enhanced production of defense compounds, or changes in plant morphology, such as increased trichome density or altered leaf shape. Induced resistance is accomplished by the induction of allelochemicals, elicitor proteins, or defense gene expression in arthropods-induced resistance plants. Some varieties of wheat also exhibit traits that enhance their tolerance to pests, for example, varieties that are tolerant to feeding byaphids (*Diuraphis noxia*; Aphididae), Hessian fly (*Mayetiola destructor*), or wheat stem sawfly (*Cephus cinctus*) (Onstad and Knolhoff 2014; Tadesse et al. 2022b).

5.7 Transgenic Approach for Arthropod Resistance

Transgenic resistance to pest arthropods involves the genetic modification of plants by introducing genes from other organisms (bacteria or other plants) that produce toxic compounds or other defense molecules harmful to pest arthropods. Currently, there are no transgenic varieties of wheat that are commercially approved for cultivation (Abbas 2018). Transgenic wheat has been developed and tested for insect resistance. Host-Induced Gene Silencing (HIGS)-mediated silencing of the Aphid gene resulted in reduced fecundity (Zhang et al. 2022). HIGS technology involves the expression of small RNAs in plants that target insect or pathogen genes (Koch and Wassenegger 2021; Qi et al. 2019). The small RNAs enter the insect and silence the host genes resulting in killing or weakening the insect's survival. Transgenic wheat expressing SmDSR33 RNA interference (RNAi) construct caused reduced expression of SmDSR33 in aphids resulting in resistance against aphids. Expression of barley trypsin inhibitor CMe (BTI-CMe) in wheat (Altpeter et al. 1999) resulted in a significant reduction in grain moth (*Sitotroga cerealella*). Expression of the Pinellia pedatisecta lectin gene in wheat showed enhanced resistance against wheat aphids (Duan et al. 2018). Successful insect resistance using transgenic and HIGS technologies suggests that it is possible to use transgenic technologies for arthropod insect resistance. In addition, potentially useful modifications include the incorporation of genes of *Bacillus thuringiensis* and genes that code for plant-derived insecticidal proteins such as lectins or protease inhibitors. A plant-derived insecticidal protein called cowpea trypsin inhibitor (CpTI and CpTI-Phyto) has been developed to enhance resistance to aphids and other sap-sucking insects. *Triticum aestivum*, the most widely planted wheat species, has a complicated hexaploid genome, and, therefore, its successful breeding and genetic manipulation will require a fundamental understanding of the resistance mechanisms using functional genomics.

5.8 Arthropod Biotypes and Development of Resistant Varieties

Insect biotypes evolve rapidly due to high fecundity and environmental/host pressure. Arthropod biotypes can affect the development of resistant varieties of wheat. Arthropod biotypes are subpopulations of arthropod species adapted to feed on specific host plants or overcome specific resistance mechanisms in their host plants (Smith 2005). In the context of wheat, different biotypes of arthropod pests may be able to overcome different types of resistance mechanisms in wheat plants. For example, specific biotypes of the *M. destructor* (Hessian fly) are able to overcome the resistance conferred by the wheat gene H13, which was previously considered to provide broad-spectrum resistance to the pest. This loss of efficacy led to developing new wheat varieties with resistance based on multiple genes (e.g., H5, H13, and H22 genes) to provide a more durable resistance (Tadesse et al. 2022b). Identifying arthropod biotypes in advance of crop resistance failure can help researchers anticipate such problems and prepare alternative resistant varieties. Visual or molecular tools can identify biotypes. Due to the low cost of sequencing technologies and the availability of reference genomes, in future, biotype identification by genome sequencing will help in the rapid identification of biotypes.

5.9 Historical Review of Plant Resistance to Wheat Pests

The first reports of wheat resistance to pest insects date back to the 1920s and 1930s, when researchers in the United States identified wheat varieties resistant to Hessian fly (*M. destructor*). In the 1970s, in response to problems with greenbug aphids, *Schizaphis graminum* (Aphidae), a major pest of wheat in the southern United States, a new resistant variety, “Greenbug Resistant 1,”was developed by USDA scientists (Royer et al. 2015). In the 1970s and 1980s, the use of resistant wheat varieties for pest management increased significantly in response to outbreaks of new and virulent insect pests (Armstrong and McNew 1976; Porter and Webster 1976). Since the 1980s, wheat breeding programs worldwide have developed insect-resistant varieties using traditional and molecular breeding methods based on naturally occurring resistance genes (Smith and Harris 1989; Porter and Webster 1982). More recently, molecular tools have been used to identify and introgress resistance genes from related species into desirable wheat varieties (Smith 2005; Smith and Clement 2012). Currently, there are several commercially available insect-resistant wheat varieties targeting the Hessian fly (*M. destructor*), green bug (*S. graminum*), and wheat stem sawfly (Tan et al. 2017; McCauley 2020; Peirce et al. 2022; Onstad and Knolhoff 2014). However, many of the varieties with resistance to Hessianfly or green bug are not resistant to important wheat diseases such as stem rust, leaf rust, and stripe rust and biotypes of Russian wheat aphid (*Diuraphis noxia*) (Zukoff et al. 2023). It is an ongoing challenge for researchers and breeders to identify new sources of resistance and develop effective strategies for managing insect pests in wheat production. There are many insect pests of wheat for which no known resistant variety is available (for example, wheat stem maggot (*Meromyza americana*) (Diptera: Chloropidae). In some cases, resistance has not yet been identified in wheat or its wild relatives. In other cases, resistant varieties may exist but have not yet been widely adopted by farmers due to various factors such as lack of availability or suitability to local growing conditions. It has been estimated that a new release of wheat varieties is needed every 5–10 years for a given pest just to overcome the development of resistant pest populations (Zhao et al. 2015).

5.10 Major Arthropod Pests of Wheat

Insect species or groups that often damage wheat include aphids (Homoptera: Aphididae), armyworms and cutworms (Lepidoptera: Noctuidae), leaf beetles (Coleoptera: Chrysomelidae), grasshoppers (Orthoptera: Acrididae), Hessian fly (Diptera: Cecidomyiidae), thrips (Thysanoptera: Thripidae), wheat curl mite (Acari: Eriophyidae), wheat jointworm (Hymenoptera: Eurytomidae), wheat stem maggot (Diptera: Chloropidae), wheat stem sawfly (Hymenoptera: Cephidae), wheat strawworm (Hymenoptera: Eurytomidae), white grubs (Coleoptera: Scarabaeidae), wireworms (Coleoptera: Elateridae), false wireworms (Coleoptera: Tenebrionidae), and stored-grain insects. Of these, pest management through host plant resistance has been considered for the following species.

5.10.1 Hessian Fly, *Mayetiola destructor* (Diptera: Cecidomyiidae)

This fly is an important pest of wheat in North Africa, North America, southern Europe, northern Kazakhstan, northwestern China, and New Zealand, attacking wheat, barley, and rye (Kamran et al. 2013). First instar larvae induce galls that function as feeding sites for all instars (Zhao et al. 2015). Third instars pupate inside the larval exuvia (the puparium, ashiny, protective case also known as flaxseed). The third instar enters a facultative diapause in which it overwinters inside wheat stubble or stems of volunteer wheat. Depending on environmental conditions, there are 2–5 generations/year (Tadesse et al. 2022b). Salivary secretions of this insect have a very high proportion of transcripts coding for Secreted Salivary Gland Proteins (SSGPs). Genome sequencing has identified many families of genes that collectively encode nearly 2000 putative active substances (effectors) in salivary secretion (Zhao et al. 2015; Aljbory et al. 2020). Plant resistance (*R*) genes encode proteins that elicit effector-triggered immunity (ETI) when they encountered SSGPs of Hessian fly (Zhao et al. 2015). So far, at least 34 genes conferring resistance to Hessian fly have been identified in wheat (numbered H1–H34) (Tan et al. 2017, 2018; Sardesai et al. 2005; Li et al. 2013). For example, the gene Hfr-2 expresses mannose-binding lectins in the lead sheath that have anti-insect properties and serve as storage proteins. Storage proteins that accumulate in the phloem sap in response to feeding by Hessian fly larvae includeWci-1 mRNAs and Hfr-1 (defender gene). These genes are used in resistant wheat varieties. The Hfr-1 gene is specifically active against Hessian fly and can protect crops from severe attack (Subramanyam et al. 2006).

Antibiosis as a basis for Hessian fly resistance includes the presence of elevated levels of silica in leaf sheaths and the production of free amino acids, organic acids, and sugars in plants. Novel jacalin-like lectin genes from wheat respond significantly to the infestation of Hessian fly larvae and could be used effectively in future breeding programs (Kamran et al. 2013). In areas where resistant varieties have been grown for several years, losses to Hessian fly have been reduced to <1%.

5.10.2 Aphids

Several aphid species, including greenbug (*Schizaphis graminum*), English grain aphid (*Sitobion avenae*), bird cherry-oat aphid (*Rhopalosiphum padi*), corn leaf aphid (*Rhopalosiphum maidis*), rose-grain aphid (*Metopolophium dirhodum*), grain aphid (*Sitobion miscanthi*), and Russian wheat aphid (*Diuraphis noxia*), are known to feed on different species of wheat. *Rhopalosiphum padi* and *D. noxia* are considered to be the most damaging of aphids to wheat (Kamran et al. 2013).

5.10.2.1 Russian Wheat Aphid, *Diuraphis noxia* (Hemiptera: Aphididae)

This aphid sporadically causes significant yield losses to wheat and is found in South Africa, the western United States, central, and southern Europe, and the Middle East (Berzonsky et al. 2003). Damage appears as longitudinal chlorotic streaking and leaf rolling, which reduces photosynthesis. Leaf rolls protect aphids from contact with insecticides and natural enemies. Its primary hosts are wheat, barley, triticale, rye, and oat, while alternate hosts are cool season (crested) and wheat grasses (*Agropyron* spp.) (Kamran et al. 2013). Yield losses of 20–90% have been reported in different parts of the world (Archer et al. 1998). Host plant resistance has been the most effective and economic control method, through induction of antixenosis, antibiosis, or tolerance against this pest. Several biotypes of Russian wheat aphid have been recognized. About 15 different Dn (*Diuraphis noxia*) resistant genes have been identified in various wheat cultivars (Kisten et al. 2020). Dn4 has been the gene most extensively used in breeding resistant cultivars. However, multiple genes are usually required for resistance to different biotypes of *D. noxia*. Within the same breeding line, certain biotypes require two genes for resistance, while others only required one resistance gene (Kisten et al. 2020). Rye and common progenitors of wheat (*Triticum tauschii*) have served as sources of a number of resistance genes. The inclusion of several resistance genes can slow the development of resistant aphid biotypes. Although several resistant wheat varieties are available, Russian wheat aphids continue to develop resistance toward them. Currently, this pest is damaging to all commercial wheat varieties in western Kansas, USA (Zukoff et al. 2023).

5.10.2.2 Greenbug, *Schizaphis graminum* (Hemiptera: Aphididae)

Greenbug is distributed in Asia, southern Europe, Africa, and North and South America. It feeds on many genera of Poaceae, including *Agropyron*, *Avena*, *Bromus*, *Dactylis*, *Eleusine*, *Festuca*, *Hordeum*, *Lolium*, *Oryza*, *Panicum*, *Poa*, *Sorghum*, *Triticum*, and *Zea*. This pest transmits the Barley Yellow Dwarf Virus (BYDV), especially the *Schizaphis graminum* strain (SGV). Feeding causes chlorosis and necrosis at the feeding sites (Porter and Webster 2000). In 1970, the first successful resistant wheat variety was developed (Royer et al. 2015). Several biotypes (C, E, I, and K) have been identified, of which biotype I is predominant and most severe (Onstad and Knolhoff 2014). Both dominant and recessive resistance genes for this pest are known in wheat. Multiple quantitative trait loci for greenbug resistance in different genetic resistance sources have been located for use against greenbug biotypes C, E, I, and K. Gb6 is the most effective gene, conferring resistance against biotypes B, C, E, G, and I. It was recovered from a wheat-rye translocation germplasm (Crespo-Herrera et al. 2019a). Gene combinations should conform broad spectrum and long-lasting resistance against greenbug in wheat. Sequential use of resistant genes, along with monitoring of prevalent greenbug biotypes, could be helpful (Porter and Webster 2000; Tan et al. 2017).

5.10.2.3 Bird Cherry-Oat Aphid, *Rhopalosiphum padi* (Hemiptera: Aphididae)

This aphid is distributed worldwide (Elek et al. 2009). It transmits Barley Yellow Dwarf (BYD) and can overwinter on plants outside the *Poaceae*. This pest shows high biological plasticity, in both its holocyclic and anholocyclic life cycles, which causes contrary results in terms of host plant resistance to both types of life cycles. *Rhopalosiphum padi* can reduce yield by 31–62%, especially when damage is combined with BYDV infection. Plant traits or mechanisms that induce aphid nymphal mortality, increase aphid developmental time at the wheat seedling stage, or reduce the aphid birth rate at wheat flowering are the most effective resistance mechanisms to help manage this pest (Kamran et al. 2013). Also, plant traits that prevent the bird cherry-oat aphid from inoculating wheat phloem with BYDV also reduce the development of the winged females, limiting dispersal of BYDV to other plants (Kamran et al. 2013). At least four different Dn genes have been identified in wheat to help manage bird cherry-oat aphid.

5.10.3 Sunnpest, *Eurygaster integriceps* (Hemiptera: Scutelleridae)

This true bug is the most important pest of wheat and barley in western and central Asia, eastern Europe, and North Africa (Nasrollahi et al. 2019). This univoltine pest feeds on various parts of its host cereal plants, including the leaves, stems, and kernels, creating various amounts of damage. Losses can reach 100% yield reduction under severe infestations (Nasrollahi et al. 2019). Prolyl endoproteases injected into the grain during the pest's feeding can severely harm the quality of the resulting flour by degrading gluten proteins (Tadesse et al. 2022a). Only a few resistance sources have so far been identified for *E. integriceps* in wheat or its wild relatives (El-Bouhssini et al. 2013). Identification and deployment of additional resistance genes could prevent the development of new biotypes of the test (Nasrollahi et al. 2019).

5.10.4 Cereal Leaf Beetle, *Oulema melanopus* (Coleoptera: Chrysomelidae)

This leaf-feeding beetle is distributed in Europe, North America, Africa, and Asia. Reduction in yield can be from 23% to 55% (Kher et al. 2011; Herbert et al. 2007). Adult beetles overwinter in protected areas such as wind rows, crop stubble, and tree bark crevices (Buntin et al. 2004). Host plant resistance, including trichomes (pubescence) on leaf surfaces, is an important resistant trait, useful in managing this pest. However, few efforts have been made to develop resistant varieties due to a general lack of resistance sources and a negative correlation between known resistance traits and crop yield (Buntin et al. 2004). Putative quantitative trait loci (QTL), such as Ppd-D1 and Ppd-D1a, have been identified as potential sources of resistance to cereal leaf beetles. Resistance might be increased by classical phenotypic selection in fields with natural infestation. Alternatively, genomic selection might be a productive avenue; it is, however, more expensive and probably only worth pursuing if marker profiles become available (Würschum et al. 2020).

5.10.5 Wheat Stem Sawflies, *Cephus* spp. (Hymenoptera: Cephidae)

Several sawfly species in this genus affect wheat in North America, Europe, North Africa, and Asia. *Cephus cinctus* is a major pest in Europe, North America, and Asia. *C. pygmaeus* is common in Europe, North Africa, and West Asia (Morrill and Weiss 2007). Host plants of this insect include wheat and other cereal crops including barley, rye, and triticale (Shanower and Hoelmer 2004). Larval feeding damages the insides of stems, reducing the nutrient transfer capability of the plant and weakening the stems. Major losses occur if stems are girdled and topple to the ground before harvest. Larvae pass through four or five instars. There is only one generation per year. During severe infestations, there can be 35% yield reductions (Shanower and Hoelmer 2004). Using varieties with resistant genotypes (plants having solid stems) minimizes this damage. Several studies have identified multiple QTLs (quantitative trait loci) associated with resistance to wheat stem sawfly (*C. cinctus*) in wheat. Resistance due to this trait appears to be controlled by multiple genes. A solid stem has been the only well-characterized wheat trait used in resistant varieties. Solid stems are due to undifferentiated parenchyma cells that create a solid pith. In solid stem genotypes, genes involved with cell wall modification and degradation and in the regulation of programmed cell death are suppressed (Nilsen et al. 2017). However, stems become less solid as the plant matures. A solid stem inhibits egg hatching and serves as a mechanical barrier to the larva's movement, and early drying of the pith causes larval desiccation and death. Solid-stemmed genotypes also reduce female body weights, sizes, and fecundity, sometimes delay adult emergence, and affect sex ratio. Under high wheat stem fly infestations, solid-stemmed genotypes can increase yield compared to hollow-stemmed susceptible genotypes (Peirce et al. 2022).

5.10.6 Orange Wheat Blossom Midge, *Sitodiplosis mosellana* (Diptera: Cecidomyiidae)

This midge is a major pest in North America, Europe, Asia, and Africa. It is a small (~3 mm long), mosquito-like, orange fly. There is a single generation each year. Adult emergence coincides with flowering, and the first two larval instars feed on the developing seeds, reducing yield and quality. Larger seeds, if harvested, show undesirable changes in germination, protein content, and dough strength (Arif et al. 2022). Host plant resistance, including genotypes that produce antitoxic substances, can minimize wheat blossom midge infestation rates. Sm1 is the only described resistance gene and is the foundation for managing orange blossom midge (Kassa et al. 2016). These genotypes alter oviposition rates in the field and reduce the egg densities resulting in a smaller midge population.

5.11 Incorporation of Resistant Wheat Varieties into IPM Programs

Integrated pest management programs for wheat include chemical pesticides, cultural controls, biological control, and resistant varieties. Major insect pests such as Hessian fly and aphids use volunteer wheat as a host before attacking new wheat stands. Cultural controls, such as eradication of volunteer wheat or alternate hosts, crop rotation, tillage, and change in planting dates, help suppress densities of these pests (Kamran et al. 2013; Zukoff et al. 2023). Conservation and release of natural enemies (parasitoids, predators, and entomopathogenic fungi) are possible means for biological control of wheat pests (Kamran et al. 2013). Using resistant wheat varieties as part of the IPM program can benefit farmers economically. However, resistant wheat varieties can negatively impact the management of other pest arthropods, such as arthropods that depend on the targeted pests and the overall biological community (Shelton et al. 2002). Over time, repeated use of resistant wheat varieties can stimulate the development of pest populations that are able to overcome host plant resistance. This can make the resistant varieties less effective over time and require additional management methods. Fewer management strategies (due to resistance) can make the wheat crop more vulnerable to sudden pest outbreaks. The use of resistant varieties may or may not have unintended impacts on non-target arthropods, including natural enemies. For example, when antibiosis is based on the expression of toxins, then host plant resistance can have negative impact on natural enemies (Van Emden 2017). Nevertheless, majority of the time parasitism in aphid–wheat–parasitoid interaction was enhanced on resistant plants (Zanganeh et al. 2015; Cai et al. 2009). When selecting for resistance to arthropods, breeders may need to make trade-offs with other desirable traits, such as yield potential, drought tolerance, or disease resistance (Peirce et al. 2022).

On the other hand, transgenic arthropod resistance has the potential to improve the control of arthropod pests in wheat crops, reducing the need for chemical pesticides and promoting more sustainable agricultural practices without impacts on yield. However, the development and use of transgenic crops are subject to a complex and lengthy process for approval (Abbas 2018). Previously, genetically modified wheat varieties with traits such as herbicide tolerance, disease resistance, and insect resistance have been developed. However, due to concerns about consumer acceptance and market rejection, these varieties were not commercialized. In addition, some countries have restrictions or bans on cultivating genetically modified crops (Domingo 2016). Further, information on GM wheat's long-term health effects, including mutagenicity, teratogenicity, and carcinogenicity tests, is needed (Abbas 2018).

5.12 Conclusion

Wheat host plant resistance plays a key role in arthropod pest management by reducing pest damage and the use of chemical insecticides. The use of resistant wheat varieties can lead to significant reductions in pest populations and damage to crops, which in turn can lead to higher yields and greater profitability for farmers (Shiferaw et al. 2013; El-Bouhssini et al. 2021). Developing new resistant varieties is, however, a long, complex process, and a new variety can become ineffective in as little as 7–10 years (Crespo-Herrera et al. 2019b). It is also essential to develop and deploy resistant varieties suited for precise growing regions. Wild wheat species or landraces of *Aegilops* and *Triticum* species are potential sources of host plant resistance to both biotic and abiotic stressors (Crespo-Herrera et al. 2019b). Using the genetic diversity in landraces and wild wheat species should also lead to the discovery of new traits for biochemical responses in wheat. Further, the introgression of traits from close crossable wheat relatives is an excellent option. It is possible to cross wheat, barley, and oats in different combinations to transfer genes across these genera (Fedak and Armstrong 1980). Current advances in wheat functional genomics, metabolomics, and genome editing could provide methods for the identification and rapid introgression of desirable traits. The authors believe that developing new varieties is an effective strategy to manage wheat pests; however, better incorporation of resistant varieties into IPM programs is needed. Combining resistant traits for biotic and abiotic factors, including insect pests, diseases, and drought, in one variety could enable better management and help avoid the failure of a variety that is effective against one, but not another, type of stress.

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Host Plant Resistance to Insect Pests in Maize

6

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Abstract

Maize, a potential global crop is attacked by a wide array of insect pests. Among them, spotted stem borer, pink stem borer, fall armyworm, and shoot fly are the major insect pests affecting maize productivity. Significant yield losses and environmental concerns necessitated the need to develop potential and safe management strategies against insect pests. Maize genotypes with improved insect pest resistance help in minimizing yield losses. Adoption of host plant resistance-based approaches not only sustains maize production in long run but is also environmentally friendly. Exploration of wild relatives in breeding programs increases the genetic diversity and sources of resistance to key insect pests. Conventional breeding in combination with molecular techniques speeds up the progress in developing insect pest-resistant genotypes. Understanding plant–insect interactions and elucidation of the molecular regulation of signaling networks is important for formulating novel pest control strategies. Various phytohormones such as jasmonic acid (JA) and salicylic acid (SA) and their derivatives, elicitors present in the saliva/oral secretions/regurgitant/frass of herbivores play an important role in modulating plant defenses. In this chapter, host plant resistance-based approaches including screening techniques, identification, and utilization of resistant sources, mechanisms and factors associated with plant resistance, induced defenses, the role of the microbiome in insect pest management, novel breeding strategies, namely quantitative trait loci (QTL) mapping, genetic engineering, genome editing to develop insect-resistant maize genotypes are discussed.

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Keywords

Maize · Stem borers · Fall armyworm · Shoot fly · Screening techniques · Host plant resistance · Wild relatives · Structural traits · Cell wall components · Genome editing

6.1 Introduction

Maize (*Zea mays* L.) is an international crop popularly known as the "Queen of Cereals" because of its high genetic yield potential. It has different types like field corn, sweet corn, and popcorn apart from different variants of field corn like high oil corn, quality protein maize, and baby corn. The total maize produced in the world is used for various purposes like poultry and animal feed, starch, food, biofuel, and raw material in several other allied industries. It is being grown in diverse environmental conditions across >170 countries in the world. Globally, 1210 million MT of maize is produced from 205 million ha with an average productivity of 5.8 t/ha). In India, maize is the third most important cereal after rice and wheat constituting 10% of the total food grain production of the country. Currently, India produces 31.51 million MT from 9.2 million ha with an average productivity of 3.1 t/ha, which accounts for nearly 4% of the global maize area and 2% of global production (DES 2021). However, the maize productivity in India is around half of the world average. The major yield-limiting factors that affect maize productivity in India are various biotic and abiotic stresses. The emerging challenges like changing climate and depletion of natural resources put additional pressure on the production and productivity of maize. On the contrary, the demand for maize is also increasing gradually across the globe and more specifically, in developing countries including India. In this context, appropriate interventions to reduce the losses caused by major biotic stresses like insect pests play a crucial role.

In general, maize is damaged by more than 100 species of insect pests under field and storage conditions. However, few insect pests are considered the major ones across different geographical regions of the world; for example, spotted stem borer (SSB), *Chilo partellus* (Swinhoe), pink stem borer (PSB), *Sesamia inferens* Walker, Fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith), Shoot fly, *Atherigona* spp., and *Helicoverpa armigera* are considered as the most economically important, which infest maize in one or the other growing seasons. The yield losses due to SSB (26–80%), PSB (25.7–78.9%), FAW (73%), and shoot fly (20–21.28%) in different agro-climatic regions have been reported (Moyal 1998; Panwar 2005; Rao 1983; Murua et al. 2006; Pathak et al. 1971).

Several approaches have been followed to reduce the losses caused due to insect pests in maize, and the most widely used method is the use of chemical insecticides. However, the use of chemicals on a sustainable basis, in the long run, is not a feasible option due to its inherent problems like increased cost of cultivation and adverse effects on humans, non-target organisms especially pollinators, and the environment. Further, continuous use of chemical insecticides may lead to the development of resistance in the insect pests against insecticides leading to the ineffectiveness of chemical control in long run. Apart from the above problems, the use of chemical insecticides increases the cost of cultivation and reduces the farmers' profitability. Therefore, novel, environmentally friendly, economical crop protection strategies are necessary to mitigate the negative impact of major insect pests in maize agro-ecosystems on a sustainable basis. In this context, the adoption of a host plant resistance approach can play an important role in effective insect pest management in maize.

6.2 Screening Techniques for Insect Resistance

Identification of resistant sources against insect pests is the first step before employing resistance sources for the management of insect pests. Evaluation of a large number of germplasm against different insect pests under artificial infested conditions in different locations over the years is necessary to identify reliable sources of resistant genotypes. The screening techniques have been developed for each of the major insect pests of maize. Screening maize germplasm for stem borer under artificial infestation is being done by releasing 10 neonate larvae into the whorl of a 10–12-day-old maize plant. Observation on leaf injury rating (LIR) is recorded at 30–35 days after infestation using a 1–9 scale. Based on LIR, the germplasm is classified into resistant (1.0–3.0), moderately resistant (3.1–6.0), and susceptible (6.1–9.0) (Sarup et al. 1978; Reddy et al. 2003). A detailed description of recording LIR by following a 1–9 scale for spotted stem borer and pink stem borer is given in Tables 6.1 and 6.2, respectively.

Similarly, the screening technique for FAW is also based on leaf damage rating (LDR) on a 1–9 scale, which was developed based on the number of shot holes/

Table 6.1 Leaf injury rating scale for *Chilo partellus* (Sarup et al. 1978)

Rating	Description
1.	Apparently healthy plant
2.	Plant with parallel, oval or oblong holes, slightly bigger than pin-sized (2–3 mm) on 1–2 leaves
3.	Plant with more elongated holes (4–5 mm or match stick head-sized) or shot holes on 3–4 leaves
4.	Plant with injury (oval holes, shot holes and slits of 1–4 cm) in about 1/3 of total number of leaves
5.	Plants with about 50% leaf damage
6.	Plants with a variety of leaf injuries in about two-thirds of the total number of leaves (ragged appearance) or one or two holes or slits at the base of the stem (>10 cm streaks are observed)
7.	Plants with every type of leaf injury and almost all the leaves damaged (ragged or crimpled appearance), with tassel stalk boring or circular dark ring at the base of stem
8.	Plants with stunted growth in which all the leaves are damaged
9.	Plants with dead heart

Table 6.2 Leaf injury rating scale for *Sesamia inferens* (Reddy et al. 2003)

Rating	Description
1.	Apparently healthy plant
2.	Plant with parallel, oval or oblong holes, slightly bigger than pin-sized (2–3 mm) on 1–2 leaves
3.	Plant with more elongated holes (4–5 mm or match stick head-sized) or shot holes on 1–2 leaves
4.	Plant with injury (oval holes, shot holes and slits of 1–4 cm) in about 1/3 of total number of leaves and midrib damage on 1–2 leaves
5.	Plants with about 50% leaf damage, oblong holes, shot holes, slits, and streaks of 5–10 cm and midrib damage on leaves
6.	Plants with a variety of leaf injuries to about two-thirds of the total number of leaves (ragged appearance) or one or two holes or slits at the base of the stem (>10 cm streaks are observed)
7.	Plants with every type of leaf injury and almost all the leaves damaged (ragged or crimpled appearance), with tassel stalk boring or circular dark ring at the base of stem
8.	Plants with stunted growth in which all the leaves are damaged
9.	Plants with dead heart

Table 6.3 Leaf Damage Rating (LDR) scale to categorize maize germplasm for resistance to FAW (Lakshmi Soujanya et al. 2022)

Rating	Description/symptoms
1.	Healthy plant/no damage/visible symptoms
2.	Few short /pin size holes/scraping on few leaves (1–2)
3.	Short/pin size holes/scraping on several leaves (3–4)
4.	Short/pin size holes/scraping on several leaves (5–6) and a few long elongated lesions (1–3 Nos) up to 2.0 cm length present on whorl and or adjacent fully opened leaves
5.	Several holes with elongated lesions (4–5 Nos) up to 4.0 cm length and uniform/ irregular shaped holes present on whorl and or adjacent fully opened leaves
6.	Several leaves with elongated lesions (6–7 Nos) up to 6.0 cm length and uniform/ irregular shaped holes present on whorl and adjacent fully opened leaves
7.	Several long lesions (>7 Nos) up to 10 cm length and uniform/ irregular shaped holes common on one-half of the leaves present on whorl and adjacent fully opened leaves
8.	Several long lesions >10 cm length and uniform/ irregular shaped holes common on one half to two-thirds of leaves present on whorl and adjacent fully opened leaves
9.	Complete defoliation of whorl of the plant

pinholes and lesion length to categorize maize genotypes based on their reaction to FAW infestation (Lakshmi Soujanya et al. 2022). In the case of FAW, 15–20 neonate larvae will be released manually into the whorl of each maize plant at the V_5 phenological stage as part of the artificial infestation. The degree of leaf feeding damage is visually rated thrice, i.e., on the 7th, 14th, and 28th day after infestation. Based on LDR, the genotypes are classified into resistant (1–4), moderately resistant (4.1–6.0), and susceptible (6.1–9.0). A detailed description of observation recorded on LDR for FAW in the 1–9 scale is given in Table 6.3.

Table 6.4 Modified rating scale of Sharma et al. (1992) for shoot fly in maize

S. no.	Damage symptoms/description	Response
1.	<10% plants with dead hearts	Resistant
2.	>10–20% plants with dead hearts	Moderately resistant
3.	>20–30% plants with dead hearts	Moderately susceptible
4.	>30–50% plants with dead hearts	Susceptible
5.	>50% plants with dead hearts	Highly susceptible

The screening of maize genotypes against shoot fly species is done under natural conditions but in hot spot locations only, because the occurrence of shoot flies is nearly uniform and also high in hot spot locations during a particular window of the spring season. In general, artificial infestation with the shoot fly is not followed while screening maize germplasm for shoot fly because of difficulties in rearing shoot fly in the laboratory. On the contrary, shoot fly occurrences are regular and also high during a particular window of the spring season in hot spot locations of north-west India including Punjab, Haryana, Delhi, western Uttar Pradesh, and Uttarakhand. Therefore, screening is done under natural conditions at hot spot locations. However, spreading of fish meal in and around the screening area (fish meal technique) is followed to attract a large number of shoot flies toward maize genotypes while screening to simulate artificial infested conditions. Observations are recorded on the number of plants with eggs, plants with dead hearts, the total number of eggs, and the total number of plants with dead hearts at 14 and 21 days after seedling emergence. Based on the percentage of dead hearts, the germplasm is grouped into resistant (<10), moderately resistant (>10–20), moderately susceptible (>20–30), susceptible (>30–50), and highly susceptible (>50) (Sharma et al. 1992) (Table 6.4).

6.3 Identification and Utilization of Resistant Sources including Wild Relatives

Repeated screening of maize germplasm with different and diverse genetic backgrounds for major insect pests, namely stem borers, FAW, and shoot fly has led to the identification of resistant/moderately resistant genotypes. In some cases, the probable reasons for plant resistance were also reported. Several promising germplasms, namely Antigua group 1 and Antigua group 2, CML 139, CML 67, PFSRS 2, AEBYC 534-1-1, P 390AM/CMLC4F230-B-2, AEBCYC534-3-1, CML 384X176F3-100-9, P 63C2-BBB-17B have been identified as resistant or moderately resistant sources to spotted stem borer (Chatterji et al. 1966; Panwar and Sarup 1980; Kumar et al. 2005).

Similarly, the following genotypes, namely CML 421, CAO 3141, CAO 3120, CAO 0106, WNZPBTL 9 (3.2), WNZPBTL 8 (3.5), CML 338 (3.6), WNZ EXOTIC POOL DC2 (3.1), CML 424 (3.2), WNZPBTL9-1 (3.4), BGS 86, CM111/*Zeadiploperennis*/CM111, CML 141, CML 33#-4 (2.4), DML 1432 (3.0), EC

619101 (2.5) are resistant to PSB (Sekhar et al. 2008, 2016a, b; Soujanya et al. 2019).

FAW was one of the serious insect pests in the maize-growing ecologies across different countries in the world. Previously, several efforts have been made elsewhere to identify the resistant sources against FAW. The previous efforts made by several researchers/breeders in maize have led to the identification and development of numerous FAW-resistant lines. Some of the FAW-resistant genotypes developed were Mp 496, Mp 703, Mp 704, Mp 705, Mp 706, Mp 707, Mp 701, Mp 702, Mp 713, Mp 714, Mp 716, Mp 708 (Williams et al. 1990); CML 333, CML 336, MP 708 (Ni et al. 2008); Mp 708, FAW 7061 (Ni et al. 2011); UR 11003:S0302, CUBA 164-1; DK 7 (Ni et al. 2014); CML 338, CKSBL 10008, CKIR 04002, CKIR 04005 (Prasanna 2019). It was interesting to note that most of the FAW-resistant maize lines were derived from Caribbean maize germplasm and Tuxpeño landrace accessions from Mexico (Mihm 1997). The introgression of insect-resistant maize populations and inbred lines in the regular breeding programs at CIMMYT and many African countries has led to the development of elite maize germplasm against lepidopteran insect pests (Murenga et al. 2015; Tefera et al. 2016a, b; Matova et al. 2020; Kasoma et al. 2020a).

In India, FAW being the recent invasive insect pest, several efforts have been made to identify the resistant sources against FAW based on leaf damage rating (LDR) under artificial infestation conditions during 2019–2022. Some of the promising germplasms with high resistance or moderate resistance to FAW are DMRE 63, DML163 1, CML 71, CML 141, CML 337, and CML 346 (Lakshmi Soujanya et al. 2022). The potential lines identified for resistance to PSB and FAW are being used in breeding programs at ICAR-IIMR and implementing extensive efforts to develop insect-resistant maize genotypes. Based on per cent dead hearts, five resistant germplasm lines against shoot fly have been identified, namely CML 420 (8.3%), ACC 263214 (9.1%), WINPOP 8 (9.1%) AEB(Y) (10.0%), and CML 49 (10%) (AICRP Annual Report IIMR 2015).

Efforts have been made to evaluate some of the most widely cultivated landraces to identify resistant sources. Meckenstock et al. (1991) reported that landraces of the Maicillo group (San Bernardo III, Pina61, Hilate179, and Lerdo104), close alternative hosts of FAW (like sorghum) from Honduras, exhibited antibiosis to FAW, which might be due to increased selection pressure on the landraces as a result of intercropped maize. Similarly, Zapalote Chico 2451F (ZC2451F), derived from Zapalote Chico landrace, ZM 4236 and ZM 7114 collected from Zambia are reported as improved sources of resistance to FAW (Nuessly et al. 2007; Widstrom et al. 2003; Kasoma et al. 2020b). Waiss et al. (1979) identified that part of the Zapalote Chico silk's resistance is due to the presence of maysin, which confers an antibiosis-based mechanism of resistance when FAW larvae fed on silk content (Byrne et al. 1996). Tamiru et al. (2011) observed that maize landraces emit herbivore-induced plant volatiles against egg deposition of SSB that attracted parasitic wasps, which was absent in commercial maize hybrids. Similarly, Luciano et al. (2018) observed reduced oviposition, delayed larval, and larva to an adult developmental period when FAW larvae fed on landrace Perola. In another study, abnormal growth, resulting in lower pupal weight (1.05-fold lower) and longer larvae-pupae development (1.12-fold), was observed when FAW fed on maize landrace Tuxpeno (De La Rosa-Cancino et al. 2016).

Apart from elite breeding material and landraces, several efforts have been made to evaluate wild relatives of maize against different insect pests to identify the resistance sources. Ramirez (1997) reported that wild relatives of maize, namely *Z. mays* ssp. mexicana, *Z. mays* ssp. diploperennis, and *Z. mays* ssp. perennis are resistant to Asian corn borer. Similarly, *T. dactyloides* exhibited resistance to corn rootworms via non-preferences and/or antibiosis (Branson 1971; Moellenbeck et al. 1995; Eubanks 2001). In a similar study, Mammadov et al. (2018) reported that morphological traits such as leaf toughness and leaf trichome density in *Z. mays* ssp. parviglumis are responsible for resistance to FAW. Further, Lakshmi Soujanya et al. (2022) also confirmed the finding that the wild relative maize, *Zea mays* ssp. parviglumis was found to be resistant to FAW. The in-depth analysis of resistance in some of the studies involving wild species has led to an understanding of the mechanism of resistance. For example, the higher expression of herbivore resistance genes, wound inducible protein (wip1), a maize protease inhibitor (mpi), and pathogenesis-related protein (PR-1) in *Z. mays* ssp. parviglumis impart resistance to FAW (Szczepaniec et al. 2012). In *Z. mays* ssp. diploperrennis, the chemical composition of leaves such as apimaysin and 3′-methoxymaysin in leaves or silks (Gueldner et al. 1992), caffeoylquinic acids, and other luteolin derivates (Farias-Rivera et al. 2003), wip1, PR-1, and chitinase gene, maysin, and chlorogenic acid (Szczepaniec et al. 2012) contribute resistance to FAW. In certain cases, the intercrosses between elite lines and wild relatives have led to the development and identification of resistance against insect pests. For example, a cross between maize × *Z. mays* ssp. mexicana showed some degree of resistance against European corn borer (*Ostrinia nubilalis*) (Pasztor and Borsos 1990).

6.4 Mechanisms of Resistance

The response of host plants upon infestation by insect pests is complex. However, the resistance reaction or response by the host plant to insect pests is categorized into three types such as antixenosis, antibiosis, and tolerance. Antixenosis resistance is defined as the non-preference of the pest for a resistant plant and influences the behavioral traits of a pest (Painter 1951; Smith 2005). Antibiosis resistance influences the biology of the pest to diminish its population and subsequent damage, resulting in higher mortality or reduced longevity and reproduction of the insect. Tolerance is a resistance where a plant can resist or recover from damage caused by the pest population (Smith 2005). Three types of resistance mechanisms are specific to target insect pests. Thus, the development of insect-resistant genotypes provides a stable and cumulative effect on the pests’ population and has no harmful effect on the non-target organisms and environment.

Several researchers observed oviposition behavior (indicative of antixenosis mechanism of resistance) of stem borers and FAW in field conditions by growing resistant and susceptible genotypes side by side or in construction cages under greenhouse conditions and observed significant differences in oviposition on resistant and susceptible genotypes (Ampofo 1985; Dubey and Sarup 1982). Oviposition for non-preference by SSB was shown in genotypes WNZPBTL 2, CM 500, WNZPBTL 6, AEB(Y)C5F38-1 under multi-choice conditions (Cholla et al. 2018a). The differential ovipositional behavior of SSB might be due to variations in the humidity stimuli in the vicinity of the plants. Due to contact-perceivable characters such as surface waxes, and trichomes, the lowest number of eggs were laid by the SSB females on the resistant maize genotypes compared to distance-perceivable characters (hygro, visual and olfactory stimuli) (Kumar and Saxena 1985). Divekar et al. (2019) recorded fewer eggs on resistant genotypes WP 21, E 63, and HKI 193-1 by PSB than on susceptible genotypes. Further, a significantly higher number of PSB eggs were deposited on the first leaf sheath followed by the second leaf sheath, basal leaf sheath, and then the third leaf sheath in susceptible ones. Minimum oviposition by FAW females was observed on the tolerant maize genotype CKH191221 compared to susceptible ones, which might be due to components of host plant quality such as carbon, nitrogen, and defensive metabolites, which directly affect the fecundity (Awmack and Leather 2002; Anyanda et al. 2022).

Antibiosis mechanisms of resistance express mainly through the plant's biochemical components such as the phenols, tannins, amino acids, and fiber content, which have adverse effects on the biological attributes of insect pests. Antibiosis is a component of resistance to stem borers and FAW. It affects survival, larval weight, pupal weight, and prolongation of larval and pupal periods. Antibiosis results in extended larval and pupal periods and a reduced percentage of pupation thus directly reflecting the resistance to SSB in maize (Arabjafari and Jalali 2007). The biological parameters of SSB have also been studied in an artificial diet through the impregnation of dry leaf powders of resistant and susceptible maize genotypes (Kumar 1993). Sekhon and Sajjan (1990) reported that the antibiosis mechanism of resistance depends upon plant age; it was observed that antibiosis became operative in a 15-day-old maize plant, and it increases with plant age. The mechanisms of antibiosis differ between genotypes. For example, AEB(Y) C5 55-1 (32 days), PFSR S3 (31 days), and HKIPC4B (31 days) genotypes showed antibiosis against PSB in terms of the prolonged larval period, whereas genotype E 30 showed antibiosis in terms of least larval weight (20.53 mg) (Kaur et al. 2016). Similarly, low larval viability, small larval weight, short adult longevity, and low emergence rates were found to impart an antibiosis form of resistance against FAW in maize when FAW was fed on resistant maize genotypes (Lima et al. 2006; de Paiva et al. 2016; Anyanda et al. 2022).

Tolerance refers to host plant's or cultivar's ability to yield well despite pest infestations that severely harm and lower the yield of susceptible host plants (Painter 1951). Genotypes CML 338 and Mp708 were classified as tolerant to FAW as uninfested and damaged plants did not exhibit any variations in photosynthetic rate and light response curves (Ni et al. 2008).

6.5 Factors Associated with Insect Resistance

Host plants respond to herbivore attacks by activating their native but complex defense mechanisms and in the process several changes either at structural and/or at biochemical and/or molecular levels.

6.5.1 Structural Traits

Among direct defense, plants can modify their morphology by increasing trichome densities that create a physical barrier for insects (Tian et al. 2012). Plant structural traits are the first line of defense against insect pests, which play a predominant role in plant resistance. It was reported that trichomes, surface wax, leaf thickness and toughness, and silica content result in avoidance behavior in insects (Gatehouse 2002; Schoonhoven et al. 2007). The role of trichomes in inhibiting oviposition by spotted stem borer was reported as a mechanism of antixenosis (Ampofo 1985; Kumar and Saxena 1985). The role of pith puncture resistance (PPR), rind puncture resistance (RPR), rind thickness, length of the meristematic area (LMA), and pith parenchyma inner lumen thickness (PPIT) was identified as resistance-imparting structures against PSB (Santiago et al. 2003). Similarly, Suby et al. (2020) reported the choice of second above ground internode by stem boring larvae in V6-10 stage maize and its pith and rind penetration resistance as the predictors of plant tolerance and antixenosis to SSB. Cholla et al. (2018b) reported that leaf damage as indicated by leaf injury rating (LIR) and stem tunneling are good indicators of resistance to SSB. The role of cuticular lipids in imparting resistance against FAW was also been reported. For example, FAW larvae fed on leaves free from cuticular lipids weighed more and developed faster as compared to larvae fed on leaves with cuticular lipids (Yang et al. 1993a). Further, it was also reported that FAW neonate larvae traveled longer distances on upper leaves, which have a smooth appearance, compared to lower leaves, which contain a dense array of wax crystals (Yang et al. 1993b). The other morphological traits attributed to FAW resistance include a thicker cell wall complex of the epidermal layer (Davis et al. 1995), a very tight husk cover, and kernel hardness that minimizes insect feeding. Whereas in shoot fly, seedling vigor, less leaf area, less number of leaves, and a thin stem are reported to impart resistance (Goyal et al. 2020).

6.5.2 Biochemical Constituents

Biochemical compounds in the host plants form the second level of defense mechanisms. An array of biochemicals such as nutritional compounds and secondary metabolites present in the different parts of plants (tissues/cells) either individually or in conjunction with other compounds contribute to imparting resistance to key insect pests of maize. The role of different biochemical compounds in plant defenses is discussed below.

6.5.2.1 Nutritional Factors

The crop plants are the primary source of energy for insect pests. The suitability of a plant or preference of crop plants by insect pests determines its status as the host plant. In most cases, insect pests derive their energy or depend on food from several types of crop plants. However, the preference of host plants by insect pests varies between crop plants and/or between different varieties of the same crop plant, which again depends on the nutritional status of host plants. For example, the suitability of host plants is influenced by some of the nutritional factors, namely nitrogen, phosphorous, total sugars, and amino acid content. Higher nitrogen (Haile and Hofsvang 2001) and low phosphorous contents (Sharma and Chatterji 1971) are attributed to the intensity of insect pest infestation. However, insect physiology and its overall biology are also responsible for differential preference to different genotypes. Since carbohydrates form the universal source of energy, simple sugars form the most preferred source of energy. It was reported that the stem borer–resistant maize genotypes contain lower reducing and total sugars because the reducing sugars and total sugars are found to be positively related to infestation by a stem borer. Similarly, higher protein content was found to be responsible for susceptibility to SSB in maize (Kabre and Ghorpade 1999). Thus, a positive correlation has been observed between the per cent SSB larvae completing the life cycle and major biochemical compounds (protein, total sugars, reducing sugars) and nutrient elements (nitrogen and phosphorus). Rao and Panwar (2002) reported that SSB-resistant genotypes possessed higher lignin content, which contributes toward the strengthening of stem tissues. On the contrary, the higher concentration of amino acids, namely aspartic acid and tyrosine, imparts resistance to FAW (Hedin et al. 1990). Goyal et al. (2020) reported that total soluble sugars (TSS), proteins, and amino acids influence dead heart incidence caused by shoot fly in maize. A positive correlation was observed between dead heart incidence and total soluble sugars (TSS), proteins, and amino acids in maize genotypes.

6.5.2.2 Secondary Metabolites

Total phenols and tannins and activities of defensive enzymes, namely phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO) are associated with resistance to shoot fly in maize genotypes. A similar negative correlation was found between potassium and total phenol content and SSB infestation (Lokesh and Mehla 2017). Phenolic compounds and hydroxamic acids are the most common groups of secondary metabolites identified as constitutive chemical compounds that are involved in resistance to stem borers (Ortego et al. 1998; Barros-Rios et al. 2015). DIMBOA, the major hydroxamic acid, and its degradation products, MBOA and HMBOA, were negatively associated with European corn borer (Barry et al. 1994); pink stem borer (Gutierrez et al. 1988); corn root worm (Xie et al. 1990). Wiseman et al. (1992) observed that maysin imparts resistance to FAW and corn earworm *Helicoverpa zea*. Genotypes CML 333 (with moderate silk maysin), CML 336 (with low silk maysin), and CML 338 (with high silk maysin) were identified as resistant to FAW, whereas CML 335 without silk maysin was found susceptible

(Ni et al. 2008). Santiago et al. (2006) reported that phenyl propanoids in pith tissues, *p*-coumaric acid, and ferulic acid impart resistance to *Sesamia nonagrioides*.

6.5.2.3 Cell Wall–Bound Components

Plant cell wall acts as a physical barrier against insect attack on the cell from the outside, it protects all the internal organelles and cytoplasm. The components of the cell wall play a major role in imparting resistance to insect pests (Read and Stokes 2006). Santiago et al. (2016) identified that the cell wall components, namely fiber and hydroxycinnamates impart resistance to feeding by several stem borers in maize. The fiber content in the cell wall disturbs feeding insect pests both from the nutritional and physical point of view. Tissue toughness is one of the important traits that regulate insect damage in plants (Raupp 1985). High content of lignin could make plants less palatable to herbivores (Zheng et al. 2021). The high levels of fiber content in the cell wall increase the bulk density of the diet, hence larvae are unable to ingest sufficient amounts of nutrients and water. Besides, tissues with high fiber content are tougher and more resistant to the cutting or chewing action of the mandibles. Therefore, maize genotypes with elevated levels of cell wall fiber and lignin (Beeghly et al. 1997) or fortification of the epidermal cell wall (Bergvinson et al. 1995) contribute resistance to the European corn borer, *Ostrinia nubilalis* in maize. Several researchers reported that variation in cell wall–bound phenolic constituents like *p*-CA and FA in resistant and susceptible maize genotypes contributes contrasting levels of resistance to stem borers (Bergvinson et al. 1997; Santiago et al. 2013; Lakshmi Soujanya et al. 2020). Lakshmi Soujanya et al. (2020) reported that the cell wall–bound *p*-CA and FA contribute resistance to PSB infesting maize. Similarly, Gundappa et al. (2013) identified through laboratory bioassays that *p*-CA was detrimental to SSB.

6.5.2.4 Induced Defenses

The presence of elicitors in the saliva/oral secretions/regurgitates/frass of insects or herbivores helps the plant sensors to perceive the physical and chemical signals (Wu and Baldwin 2009). As a result, the induced defense signaling process in the host plant is activated, leading to the production of defense chemical compounds through chemical changes in plants. The induced defense signaling processes triggered by the insect infestation serve as a powerful chemical weapon against insect pests. Plant response to insect pests is genotype-dependent and varies from one pest to another. It was reported that several plant defense mechanisms such as genes encoding jasmonic acid biosynthetic enzymes, proteinase inhibitors, defense-related transcription factors, and proteins involved in cell-wall reorganization activated due to Mediterranean corn borer attack (Rodríguez et al. 2012). Similarly, several studies have found that the accumulation of Benzoxazinoids increases due to insect attack. Malook et al. (2021) reported the accumulation of higher levels of benzoxazinoids in Chinese maize inbred line Xi 502 upon FAW attack. The first gene in the benzoxazinoid biosynthesis pathway, i.e., the transcript levels of *Bx1* increased after insect attack (Erb et al. 2009; Tzin et al. 2015). Further, insect feeding led to significant increases in DIMBOA and HDMBOA-Glc (the methylated form of

DIMBOA-Glc) and decreased levels of DIMBOA-Glc (Glauser et al. 2011). Tamayo et al. (2000) observed maize proteinase inhibitor accumulation in tissues adjacent to the wound site when fed by *Spodoptera littoralis* on maize leaves. Further, the level of inhibitor accumulation was higher in leaves chewed by larvae than in leaves that had been damaged mechanically.

Sometimes, the induced defense response of host plants upon insect attack provides resistance to multiple insects. For example, defense responses in the Mp708 genotype negatively impacted both European corn borer and Western corn rootworm larval weights providing evidence for changes in root physiology in response to ECB feeding on shoot tissues. In the genotype Mp708, resistance to insect pests is mediated by the defense proteins including Maize Insect Resistance1-Cysteine Protease (Mir1-CP) (Pechan et al. 2000, 2002); protease inhibitors, and peroxidases, which could hamper caterpillar growth (Castano-Duque and Luthe 2018). Lopez et al. (2007) reported an accumulation of Mir1-CP in the roots due to FAW infestation in the whorl regions of maize, which also provides enhanced resistance to root-feeding herbivores (Gill et al. 2011). Thus, the Mp708 genotype provides resistance to both above and below-ground feeding caterpillars (Gill et al. 2011; Castano-Duque et al. 2017). Significant downregulation of genes in the root tissues following short-term ECB feeding was observed (Pingault et al. 2021).

Mason et al. (2022) reported that the expression of plant resistance to insects varies with the fertilization regime. The study reported the increasing pattern in gene and protein expression with herbivory, but it varied between fertilization levels. For example, low fertilization reduced induced defenses in the resistant maize genotype. However, the soluble protein concentrations did not change with fertilization levels but were higher in the susceptible ones. Wang et al. (2022) reported that FAW attack and JA application enhanced the maize defense when supplemented with 156.6 mg/kg of N, which led to the decreased contents of amino acids and soluble sugars. Insect attack also led to increased levels of phenolics in the plants supplemented with 156.6 mg/kg of N and, thus, had negative effects on insects. Further, significantly higher volatiles of acrylic acid, indoles, and myristic aldehyde might be the reason for the reduced selection of maize supplemented with 156.6 mg/kg of N by FAW.

6.5.2.4.1 Elicitors and Signaling Regulation of Insect Resistance

Induced defense responses are complex; generally, they are initiated by wounding; the elicitors derived from insect-feeding herbivore-associated molecular patterns (HAMPS) or oviposition activate a complex regulatory network that mediates the biosynthesis of secondary metabolites. Among them, saliva, frass, oral secretions, and regurgitation of chewing insects play a major role in insect–plant interactions (Basu et al. 2018). To identify these insect HAMPS, plants utilize surface immune receptors and further induce a multitude of downstream defenses to impair insect development and/or colonization on host plants (Zogli et al. 2020). Some of the reported signaling molecules in different insects and the subsequent downstream processes are given below. In European corn borer (ECB), indole-3-acetic acid (IAA) present in its OS (Dafoe et al. 2013), saliva (Louis et al. 2013), frass (Ray et al. 2016) modulates maize defense responses. ECB saliva-induced defense-related transcripts including lipoxygenase (LOX) and 12-phytodienoic acid (OPR) genes are involved in the biosynthesis of jasmonic acid (Louis et al. 2013). The oral secretion of *Mythimna separata* feeding on maize contains more than ten kinds of fatty acid amino conjugates (FACs), the most abundant one is the hydroxylated FAC volicitin (Qi et al. 2016). The elevated levels of the hormones JA and its derivative JA-Ile were observed when the oral secretion of *Mythimna separata* was applied to maize wounds. Louis et al. (2015) reported that feeding by corn leaf aphids induces the rapid accumulation of *mir1* transcripts in the resistant maize genotype, Mp708, which is regulated by the ethylene signaling pathway. Furthermore, Mp708 provided elevated levels of antibiosis and antixenosis-mediated resistance to aphids compared to B73 and Tx601 maize susceptible lines. Block et al. (2019) observed elevated production of the defense hormone salicylic acid and an increase in FAW resistance to the combinatorial stress of flooding and infestation with FAW. In the same study, it was also observed the remodeling of phenylpropanoid pathways led to increased production of the C-glycosyl flavones (maysins) and the herbivore-induced volatile phenolics, benzyl acetate, and phenethyl acetate.

6.5.2.4.2 Phytohormones

Phytohormones play a key role in modulating maize defense against chewing insects. Among them, JA, salicylic acid (SA), and ethylene (ET) are the critical players in providing resistance to chewing pests (Erb et al. 2012). ECB feeding on maize foliage resulted in an increased accumulation of phytoalexins such as benzoxazinoids and kauralexins (Dafoe et al. 2011). Zhang et al. (2015) reported that MeJA-induced proteins, including pathogenesis-related protein 1 (PR1) and thioredoxin M-type chloroplastic precursor (TRXM), as the recombinant proteins of PR1 and TRXM inhibited the development of Asian corn borer larvae and pupa.

Similarly, ZmLOX10 (maize lipoxygenase) mutant, involved in maize JA biosynthesis, showed strongly reduced wounding-induced JA levels and reduced volatile emissions. Further, attractiveness to larval parasitoid wasps was observed. These results confirm that JA mediates direct and indirect defense responses in maize. Ethylene is also an important phytohormone that regulates *Mythimna separata* resistance in maize (Qi et al. 2011). In Mp708, a maize insect resistance1 (mir1) gene was identified that encodes a cysteine (Cys) proteinase, named Mir1-Cys protease, which disrupts the peritrophic matrix and thus reduces FAW growth (Pechan et al. 2002). It was observed that blocking ETH synthesis or perception in Mp708 reduces Mir1-Cys protease accumulation, resulting in more susceptibility to FAW and corn leaf aphids (Harfouche et al. 2006; Louis et al. 2015).

6.5.2.4.3 Plant Volatiles

Herbivore-induced plant volatiles (HIPVs) defend plants with the help of natural enemies of insect pests. Volatiles are also released by secondary metabolites that attract the insect's natural enemies. Plant volatiles from resistance and susceptible genotypes were equally effective in eliciting oviposition by SSB (Kumar 1994). Alborn et al. (1997) reported that the application of synthetic volicitin to maize attracts the predators of insects. In some maize landraces, oviposition by SSB induces the release of volatiles, which attract egg parasitoid *Trichogramma* spp. and larval parasitoids (*Cotesia sesamiae*) (Tamiru et al. 2011). Veyrat et al. (2016) reported that indole, a volatile aromatic compound, decreases insect food consumption and the survival rate of *Spodoptera littoralis*. Further, applying indole to maize elevates herbivory-induced JA and JA-Ile contents. Methyl salycilate (MeSA) is another aromatic compound that is released by maize after sensing insect feeding/ oviposition (Tamiru et al. 2011). Maize landrace Braz1006 releases eightfold of (*E*)-bcaryophyllene, owing to the higher TPS23 transcript levels, resulting in more attraction to egg parasitoid (*C. sesamiae*) of stem borer (SSB) (Tamiru et al. 2017). Similarly, maize landraces C-2101, B-3016, and H-2034 also release (*E*)-b-caryophyllene and other terpenes ((*E*)-4,8-dimethyl-1,3,7, nonatriene (DMNT) and (*E*,*E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene (TMTT)) after sensing SSB oviposition (Tamiru et al. 2011). Apart from these, maize can perceive other insect-derived elicitors, such as caeliferin and inceptin, but differences between genotypes do exist in their responses to these elicitors.

6.5.2.4.4 Kauralexins

Kauralexins are a group of maize diterpenoid phytoalexins that accumulate in response to insect infestation and phytohormone treatment, which are highly attractive to female parasitic wasps (Fontana et al. 2011). These volatile blends of herbivore-damaged maize are mostly dominated by sesquiterpenes (Degen et al. 2004). The herbivore-induced sesquiterpenes of maize are mainly produced by two terpene synthases, TPS10 and TPS23, in which TPS10 forms (*E*)-α-bergamotene and (*E*)-β-farnesene along with 13 minor sesquiterpenes in herbivore-damaged leaves (Schnee et al. 2006). The herbivore-induced sesquiterpene synthase TPS23 forms mostly (*E*)-β-caryophyllene, which can also attract parasitic wasps to leaf-feeding herbivores (Kollner et al. 2008), as well as the entomopathogenic nematodes to the root-damaging western corn rootworm (Rasmann et al. 2005; Kollner et al. 2008). These elicitations generally induce expression of genes of phytoalexin biosynthesis through transcriptional or translational regulation. Schmelz et al. (2011) observed that the accumulation of phytoalexins resulted in significant increase in antifeedant activity in *O. nubilalis*. The expression of TPS10 (terpene synthase) is highly induced by herbivory (Kollner et al. 2013) and also by MeJA treatment. Maize ZmWRKY79, a common transcription factor, physically binds to the W-boxes or WLE cis-elements in the promoters of terpenoid phytoalexin biosynthetic genes (An2 and ZmTPS6) in maize, regulating their expression (Fu et al. 2018). Li et al. (2015) reported that the MeJA- and herbivore-inducible transcription factor EREB58 directly promoted the expression of *TPS10*. In vivo and in vitro assays indicated that *EREB58* promotes *TPS10* expression by directly binding to the GCC-box within the region from −300 to −200 of the *TPS10* promoter.

6.6 Role of the Microbiome in Plant Resistance to Insect Pests

All plants are associated with both beneficial and pathogenic microbes, which play the predominant role in altering the expression of traits. Insect pests depend upon plant-produced cues to locate their hosts that provide information about suitable plant characters (Bruce et al. 2005). The microbes that establish mutualistic interactions with plants indirectly influence the plant–insect interactions and impact host-plant selection by insect pests (Hassani et al. 2018). The beneficial plant-associated microbes include plant growth-promoting rhizobacteria (PGPR), nitrogen-fixing rhizobia, arbuscular mycorrhizal fungi (AMF), and foliar and root endophytes. Root colonization by rhizobacteria induces plant resistance against insect pests in numerous crops (Dean et al. 2009). These microbes interact with both above- and below-ground plant organs and live endophytically/ectophytically, depending on the species of a microbe and the specificity or type of interaction (Gibert et al. 2019). Beneficial rhizobacterium, *Azospirillum brasilense* influences the host plant selection by the South American rootworm, *Diabrotica speciosa*, which infests maize roots. It is observed that the *A. brasilense* inoculation triggers higher emissions of (*E*)-β-caryophyllene as compared to non-inoculated plants. Non-preference of *D. speciosa* was observed for inoculated plants due to sesquiterpenes emission, which is a well-known compound to mediate belowground insect–plant interactions (Santos et al. 2014).

Arbuscular mycorrhizal fungi (AMF) also improve plant nutrient uptake and trigger defense responses. As a result, the ability of a plant to resist insect attack increases. The production of secondary metabolites and defense gene upregulation in plants enhance due to AMF colonization. Song et al. (2011) reported that 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one production increased in maize seedlings by AMF colonization. The AMF colonization increases the induced jasmonic acid pathway plant defense responses and reduces the rate of survival and development of European corn borer in maize. AMF colonization also upregulates induced defense production in response to insect attack that reduces the herbivore's performance and/or improves plant fitness (Karban and Myers 1989). Murrell et al. (2019) measured the cascading consequences of cover crop treatment (canola/radish/rye/oats) on maize root AMF colonization, maize growth, and performance of European corn borer.

6.7 Breeding for Insect Pests Resistance

Host plant resistance (HPR) breeding is an important component of IPM. HPR is the inherent ability of the host plant to resist insect pests' attack, and it is largely determined by its genetic makeup. Understanding the genetic basis of resistance is important to develop resistant maize genotypes. Conventional breeding for resistance is a bit challenging due to the nature of the inheritance of resistance to insect pests. Further, several efforts toward long-term planning and strategy are required for the successful development of resistant lines. Recently, success in identifying quantitative trait loci (QTL) in maize using various molecular markers provides an alternative approach for speeding up conventional breeding programs. Currently, several molecular-marker-based breeding techniques including mapping of QTLs, development of transgenics, and genome editing are being employed. A brief note on each of the approaches is described below.

6.7.1 QTL Mapping

As insect pests inflict significant yield losses, it is necessary to know the genetic mechanisms that regulate the resistance traits. Therefore, several researchers have tried to identify the genomic regions controlling resistance to stem borers in maize using quantitative trait loci (QTL) mapping. The QTL mapping studies have been reported in major insect pests of maize, namely spotted stem borer (Munyiri and Mugo 2017); Mediterranean corn borer (Santiago et al. 2016; Jimenez-Galindo et al. 2017); European corn borer (Papst et al. 2004); southwestern corn borer (Brooks et al. 2007); sugarcane borer (Groh et al. 1998). Willcox et al. (2002) performed QTL mapping to identify genomic regions for resistance to southwestern corn borer using BC_1F_2 mapping population. The study identified three putative QTLs on chromosomes 7, 9, and 10 together accounting for 28% of the total phenotypic variance. QTL mapping for resistance to Mediterranean corn borer (MCB) using two different recombinant inbred lines (RILS) mapping populations, namely EP42 × A637 (Samayoa et al. 2014) and A637 × A509 (Jimenez-Galindo et al. 2017) has led to the identification of genomic regions determining resistance to MCB. The studies have found that the favorable QTL alleles were contributed by the A637 genotype. Jimenez-Galindo et al. (2017) have identified 12 QTLs for both yield (agronomic) and resistance to MCB using 285 SNP markers. QTLs identified are based on phenotypic data of 171 RILs, evaluated along with the two parental inbred lines A637 and A509 in a 13 × 14 single lattice design for MCB. The QTL located at bins 1.10 and 5.04 improved both yield and insect resistance simultaneously. On the contrary, QTLs located in the region 8.04–8.05 showed opposite effects for yield and resistance. Further, several QTLs located in the region 10.02–10.03 were identified for indexes that combine yield and resistance traits.

Munyiri and Mugo (2017) identified QTL associated with resistance to SSB and *Busseola fusca* in maize. The study identified two QTLs for reduced stem tunneling on chromosome 4, one each for *B. fusca* and SSB and one QTL for reduced stem borer exit holes on chromosome 5. The study used 203 $F_{2:3}$ individuals, derived from a cross between CML 442 (susceptible) and CKSBL10026 (resistant) and 152 SNPs for mapping the QTLs. Badji et al. (2018) meta-analyzed QTLs for resistance to stem borers in maize and cell wall constituents imparting resistance using the IBM2 2008 Neighbors as a reference map. The study generated 24 leaf injury rating (LIR), 42 stem injury rating (SIR), and insect resistance meta-QTL (MQTL) of a diverse genetic background. Some of the LIR MQTLs such as LIR4, LIR17, and LIR22 involved in imparting resistance to the European corn borer, sugarcane borer, and southwestern corn borer. Eleven out of the 42 SIR MQTLs related to resistance to

European corn borer and Mediterranean corn borer. Samayoa et al. (2019) tested the suitability of marker-assisted selection (MAS) for improving resistance to stem tunneling by *S. nongrioides* without adverse effects on yield. The results revealed that marker information can be utilized for simultaneous improvement of resistance and yield especially if genome-wide approaches are applied.

Brooks et al. (2007) investigated genomic regions encoding resistance to FAW in maize using family-based QTL analyses. The cross of A619 (susceptible parent) and Mp708 (resistant parent) was mapped using 91 simple sequence repeat (SSR) markers and 213 $F_{2:3}$ families. The study has found QTLs determining resistance to FAW on chromosomes 1, 2, 6, 7, and 9. Womack et al. (2020) identified two major QTLs in bins 4.06 and 9.03 for resistance to FAW in maize. The linkage map was constructed using 1276 single-nucleotide polymorphisms and simple sequence repeat molecular markers.

Vikal et al. (2020) identified genomic regions associated with shoot fly resistance. A total of 107 F_2 population derived from the cross CM 143 (resistant) and CM 144 (susceptible) was genotyped with 120 SSR markers. The major QTLs determining shoot fly resistance, namely *qDH9.1* (dead heart) and *qEC9.1* (oviposition) were co-localized on chromosome 9. These QTLs are syntenic to regions of chromosome 10 of sorghum, which also accounted for dead heart and oviposition suggesting that the same gene block may be responsible for shoot fly resistance in maize. Some of the candidate genes predicted within the QTL region are cysteine protease, subtilisin-chymotrypsin inhibitor, and cytochrome P_{450}. The candidate genes are involved in the synthesis of allelochemicals, receptor kinases, *glossy15*, and ubiquitin-proteasome degradation pathways.

6.7.2 Transgenics

Globally, transgenic maize expressing *Cry* gene(s) of *Bacillus thuringiensis* (Bt), responsible for the production of insecticidal proteins (delta-endotoxins), has been adopted to provide resistance to insect pests, reduce the losses due to insect pests, and also sustain the productivity (James 2015; Ashfaq et al. 2010). *Bt* toxins act on epithelial cells of the gut of insects and promote osmotic disruption of these cells, leading to the death of the caterpillar (Gill 1995). Currently, around 208 events comprising various insect-resistant genes in maize have been approved for cultivation depending on the prevalence of insect pests (Kumar et al. 2020). Sun et al. (2015) developed transgenic maize with resistance to Asian corn borer and glyphosate tolerance by fusion gene transformation. Linker peptide LP4/2A was used in the study to connect the *Bt* cry1Ah gene with the 2mG2-epsps gene and combined the widely used manA gene as a selective marker to construct one coordinated expression vector called p2EPUHLAGN. Liu et al. (2018) developed transgenic maize event ZD12-6 expressing a *Bacillus thuringiensis* (*Bt*) fusion protein Cry1Ab/Cry2Aj and a modified 5-enolpyruvylshikimate-3-phosphate synthase (EPSPS) protein G10. Insect bioassays revealed that the transgenic plants are highly resistant to Asian corn borer (*Ostrinia furnacalis*), cotton boll worm (*Helicoverpa armigera*), and armyworm (*Mythimna separata*). Li et al. (2022) evaluated the lethal effects of the transformation events of DBN9936 (Bt-Cry1Ab), DBN9936 × DBN9501 (Bt-Cry1Ab + Vip3A), Ruifeng 125 (Bt-Cry1Ab/Cry2Aj), and MIR162 (Bt-Vip3A) on major lepidopteran pests, namely *Spodoptera frugiperda*, *Helicoverpa armigera*, *Ostrinia furnacalis*, *Conogethes punctiferalis*, *Mythimna separata*, *Leucania loreyi*, and *Athetis lepigone*, using an artificial diet containing lyophilized *Bt* maize tissue at a concentration representing a 25-fold dilution of tissue. The study found that the mortalities of DBN9936 (*Bt*-Cry1Ab), DBN9936 × DBN9501 (*Bt*-Cry1Ab + Vip3A), Ruifeng 125 (*Bt*-Cry1Ab/Cry2Aj), and MIR162 (*Bt*-Vip3A) to *Spodoptera frugiperda*, *Helicoverpa armigera*, *Ostrinia furnacalis*, *Conogethes punctiferalis*, *Mythimna separata*, *Leucania loreyi*, and *Athetis lepigone*, were in the range of 53.80–100%, 62.98–100%, 57.09–100%, and 41.02–100%, respectively. Even though *Bt* maize provides an area-wide suppression of insect pests, the development of resistance is a major threat to the durability of *Bt* crops (Huang et al. 2011). Insect resistance management strategies are to be implemented wherever *Bt* crops are being grown to slow down/minimize the development of resistance in insect pests.

6.7.3 Genome Editing

Genome editing of plants for the management of insect pests has been less exploited compared to diseases in various crops. It is a new technology that can serve as a potential tool to tackle insect pests as well (Razzaq et al. 2019; Vats et al. 2019). This technique utilizes either a sequence-specific nuclease (SSN) to produce precise gene knockout and knock-in edits or synthetic oligonucleotides to introduce specific point mutations in the target DNA region (Songstad et al. 2017). Recently, Gui et al. (2020) reported that genome editing facilitated by (CRISPR)/CRISPR-associated nuclease protein (clustered regularly interspaced short palindromic repeats) is precise, and efficient, for the manipulation of target genes associated with insect resistance. Herbivores identify host plants based on the plant's own volatile, gustatory clues, and the oviposition site's visual appearance (Larsson et al. 2004). Beale et al. (2006) identified that changes in volatile blends deter insects from host plants. Bringing changes in the blends of plant volatiles through genome editing is one of the promising approaches in insect pest management. However, utmost care is to be taken so that the changes will not result in deleterious effects on natural enemies. Infestation by aphids results in the emission of a sesquiterpene hydrocarbon (*E*)-β-farnesene (Eβf), which retracts feeding by other host populations and attracts a parasitic wasp *Diaeretiella rapae*, which manages aphid. Apart from plant volatiles, the visual appearance of host plants also plays an important role in the recognition of insects. Change in leaf color acted as a deterrent to the insect pests, *Spodoptera litura*, and *Helicoverpa armigera*. Malone et al. (2009) reported that alteration in plant pigmentation has been found to modify insect host preferences, which were observed in transgenic red-leaf tobacco, which was developed by the modification of the anthocyanin pathway.

6.8 The Way Forward

The development of sustainable integrated pest management is essential for strengthening the nation's food security. Host plant resistance forms the backbone of IPM for improved maize production. However, understanding insect pests' biology, herbivore–plant interactions, and their impact on natural enemies, i.e., multi-trophic interactions are vital to deploy defensive traits in pest management. To overcome insect pest attacks, manipulation and higher expression of plant secondary metabolites biosynthesis pathway-related genes could be advantageous. Further, the elicitors of induced defense can be exploited for pest management in maize. The deployment of modern breeding techniques provides enormous potential to develop insect-resistant maize. Wild relatives are important sources of insect-resistant traits, and through improved molecular technologies such as marker-assisted breeding and interspecific hybridization techniques, insect-resistant traits can be introduced into cultivated maize. Emphasis is to be given to unravel molecular regulation of host plant defense for the improvement of insect-resistant traits in maize so that the target genes could be identified and deployed for conferring resistance to insect pests through genetic transformation. Genome editing through CRISPR/CAS 9 also offers new opportunities and long-term solutions for reducing yield losses by insect pests.

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Host Plant Resistance to Insects in Pulse Crops

7

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Abstract

Pulses are important sources of protein, dietary fiber, vitamins, and minerals for human nutrition and are widely cultivated in many countries around the world. Crops belonging to pulse include mainly chickpeas, mung bean, lentils, pigeon peas, and cowpeas. Pulse production and storage are negatively affected by a variety of biotic and abiotic factors, such as insect pests, diseases, parasites, low soil fertility, heat, and drought. Among these, insect pests have the most significant impact on pulse productivity worldwide. The extent of insect pest damage is a major challenge for pulse farmers and can lead to significant quantitative and qualitative losses. While synthetic insecticides are commonly used to control insect pests in pulses, their harmful effects on humans, animals, and the environment, as well as the development of insecticide resistance in pests, have prompted research efforts to identify eco-friendly alternatives. One such alternative is host plant resistance, which involves developing pulses with genetic traits that make them resistant to insect pests. The chapter underlined the importance of host plant resistance as a sustainable approach to protecting pulse crops against insect pests. It reviews past and recent studies that have contributed to improving pulse crops and sustaining their production through host plant resistance measures. Genomic tools and resources could be further utilized to develop insect resistance in all types of pulses and accelerate the pace of research in this area.

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Keywords

Pulse crops · Vigna unguculata · Insect pests · Genetic traits · Eco-friendly alternatives · Crop improvement

7.1 Introduction

Pulses are important crops for human nutrition and food security in many countries around the world. They are a rich source of proteins, dietary fiber, complex carbohydrates, vitamins, and essential minerals (Patterson et al. 2009). However, pulses also contain enzyme inhibitors, lectins, oligosaccharides, polyphenols, phytates, and saponins that affect the digestibility and bioavailability of nutrients in humans and animals (Bressani 1993).

Despite their importance, pulse production and storage are highly challenged by many constraints leading to quantitative and qualitative losses. These losses are imputable to a complex of biotic and abiotic stress factors including insect pests, diseases, parasitic weeds, heat, low soil fertility, and drought. Above all, biotic stresses in general and insect pests in particular have the most negative impact on pulse productivity worldwide. The extent of insect pest diversity and the severity of their attacks in pulses vary from crop to another and also from one location to another. Average grain yield losses between 50 and 80% in untreated cowpea fields were reported by Singh and Allen (1979) that can go up to 90–100% under high insect infestation conditions, on susceptible varieties (Jackai and Daoust 1986; Singh and Singh 2014; Togola et al. 2017). Over 85 insect species attack cowpea (Singh et al. 1990) with about 20 of them having regular occurrence and being of economic importance in various cowpea production areas worldwide (Oyewale and Bamaiyi 2013). Legume pod borer (*Maruca vitrata* Fabricius), cowpea aphid (*Aphis craccivora* Koch), flower bud thrips (*Megalurothrips sjostedti* Trybom), pod sucking bugs (*Clavigralla tomentosicollis* Stål), and cowpea weevils (*Callosobruchus maculatus*) are the most widespread and damaging insect pests of cowpea (Hassan 2009; Tamò et al. 2019; Oyewale and Bamaiyi 2013; Togola et al. 2017, 2019, 2020).

Other pulses like chickpea are similarly damaged by some 60 insect species known to feed on this crop, of which cut worm *Agrotis* spp., beet armyworm *Spodoptera exigua,* leaf miner *Liriomyza cicerina*, aphid *Aphis craccivora*, pod borer *Helicoverpa armigera*, and bruchid *Callosobruchus chinensis* and *Callosobruchus maculatus* are the major pests worldwide (Sharma et al. 2007, 2014; Malo and Hore 2020). Also, *Liriomyza cicerina* (Rondani) is one of the devastating and dominant leaf miner species on the crop (Chrigui et al. 2020).

Among the devastating insect pests of lentil, there are legume pod borer *Helicoverpa armigera* (Hub.), spiny pod borer *Etiella zinckenella* (Treit.), aphids *Aphis craccivora* Koch and *Acyrthosiphon pisum* (Harris), pea leaf weevil *Sitona crinitus lineatus* and weevil *Bruchus lentis*, pod sucking bug *Clavigralla gibbosa* Spin (Clement et al. 1994; Erskine et al. 1994; Sharma and Crouch 2004; Malo and

Hore 2020). As for the pigeon pea, over 150 insect species damage the crop (Sharma 2016). According to Shanower et al. (1999), the most serious and primary insect pests of pigeon pea are those that attack reproductive structures, including buds, flowers, and pods. Nearly 30 species of Lepidoptera and a large number of Hemiptera feed on the reproductive structures of the crop. The legume pod borer *Helicoverpa armigera* (Hübner), the spotted pod borer *Maruca vitrata* Geyer, the pod fly *Melanagromyza obtusa* Malloch, the pod wasp *Tanaostigmodes cajaninae* La Salle, the spiny pod borer *Etiella zinckenella* Triet., the pod sucking bugs *Clavigralla* spp. and the bruchids *Callosobruchus chinensis* L. are the major pests (Sharma 2016). Similarly, pod borer and pod fly were reported as major insect pests affecting pigeon pea production (Malo and Hore 2020; Rajeswari and Jayamani 2020). A total of 64 insect species attacking mung bean in the field were reported by Lal (1985). However, the major insect pests are bean fly *Ophiomyia phaseoli* Tryon, stem fly *Melanagromyza sojae* Zehntner, thrips, *Megalurothrips* spp. and *Caliothrips indicus* Bagnall, aphids *Aphis craccivora* Koch, whitefly *Bemisia tabaci* Gennadius, pod borers *Helicoverpa armigera* (Hubner), spotted caterpillar *Maruca vitrata* Fabricius, pod sucking bugs *Clavigralla gibbosa* Spinola and bruchids *Callosobruchus maculatus* Fab., and *Callosobruchus chinensis* L. (Lal 1985; Yadav and Singh 2006; Gentry 2010; Swaminathan et al. 2012; Duraimurugan and Tyagi 2014; Mbeyagala et al. 2017; Laosatit et al. 2020; Pratap et al. 2020). According to Rana et al. (2016), insect pests alone can lead to a yield reduction of 20–55% on mung bean, depending upon the stage of the crop, the severity of the stress, and prevailing environmental factors.

Application of synthetic insecticides remains the most common measure used to control the insect pests in pulses. However, knowing the harmful hazards caused by chemicals to humans, animals, and environment and possible development of insecticide resistance in pests, many research efforts were made to seek eco-friendly alternative options such as host plant resistance. Varietal resistance appears to be the most cost-effective and environment friendly approach to mitigate pest damage in pulses. This chapter highlights the importance of the host plant resistance as sustainable protection measure of pulse crops against insect pests and reviews some achievements of past and recent studies to support pulse crops improvement and sustain their production.

7.2 Host Plant Resistance to Insects in Pulse Crops

Over the past decades, significant progress has been made in developing resistant varieties of pulse crops to insect pests. The research efforts of identifying resistant genotypes to insects went through the process of phenotypic screening where the genotypes were evaluated for their resistance to various insects of economic importance to pulses.

As a result, hundreds of insect tolerant/resistant pulse genotypes were identified, improved, or developed through field, laboratory and screen house screening, genetic improvement, and biotechnology applications to mitigate insect pests' effects while sustaining pulse production and value-chain.

7.2.1 Progress in Host Plant Resistance to Insect Pests of Cowpea

On cowpea (*Vigna unguiculata*), concerted efforts were undertaken to boost productivity through the development of resistant lines to insect pests and also the deployment of quantitative modern genetics and genomic tools (Boukar et al. 2016, 2019; Ongom et al. 2022). These are expected to accelerate the rate of genetic gain, allowing farmers to benefit from the full genetic potentials of the crop (Ongom et al. 2021).

In recent decades, three accessions of the International Institute of Tropical Agriculture (IITA) mini core collection (TVu6464, TVu1583, and TVu15445) were reported to be resistant to *Aphis craccivora,* all having a low sucrose content in the plant and a high kaempferol and quercetin content (Togola et al. 2020). Earlier studies found the cowpea wild relative, TVNu1158, as resistant to aphid in seedling stage (Boukar and Fatokun 2009; Souleymane et al. 2013; Boukar et al. 2020). Single dominant genes designated as *Rac1* and *Rac2* were identified to control aphid resistance in cowpea (Boateng 2015). Same efforts were made to identify sources of resistance to *Megalurothrips sjostedti* where Togola et al. (2019) identified four cowpea mini core accessions TVu8631, TVu16368, TVu8671, and TVu7325 as resistant to this pest. Other cowpea accessions reported to be resistant to *M. sjostedti* are Sanzisabinli (Abudulai et al. 2006; Alabi et al. 2011; Sobda et al. 2018), Moussa local, TVu1509, TVx3236 and Sewe (Alabi et al. 2004), and IT93K-452-1 (Dormatey et al. 2015).

The cowpea accessions IT06K-123-1, ALEGI*SECOW3B, IT86D-1038, WC35B, IT86D-1033, TOUMKALAM, KPLOBEROUGE, WC66*NE50, IT06K-270, IT84S-2246-4, WC36, and TVu1471 were identified to be resistant to *Callosobruchus maculatus* in Benin (Kpoviessi et al. 2019). Similarly, TVu13677, WC36, and WC66*5T were identified as resistant to *C. maculatus* (Kpoviessi et al. 2021). Dabire-Binso et al. (2010) identified IT86D-716 as resistant to *Clavigralla tomentosicollis* implying the presence of cyanogenic heterosides, flavonoids, tannins, and trypsin inhibitors in the pods.

Recent development of genomic resources will support the molecular breeding and facilitate the development of durable resistance to cowpea insect pests. To accelerate such breeding process, advanced biotechnology methods and tools are being explored. Gene pyramiding is being explored by IITA and associated national agricultural research systems (NARS) partners to develop high desired cultivars combining resistance genes to different insects of cowpea (Boukar and Fatokun 2009; Togola et al. 2017). Genetic engineering option had been undertaken for the development of Maruca resistant transgenic cowpea by inserting the Cry1Ab Bt gene (Popelka et al. 2006; Togola et al. 2017). The Bt gene has been transferred through backcrossing to some improved and released cowpea varieties in different countries.

7.2.2 Progress in Host Plant Resistance to Insect Pests of Lentil

Research efforts have made it possible to find sources of plant resistance to some important field and storage insect pests of lentil (*Lens culinaris* Medik) as reported by Clement et al. (1994). Field tests were conducted to successfully identify some lentil genotypes for resistance to attack by *Bruchus lentis* Froel, *Aphis craccivora* Koch, and *Sitona* sp. (Sedivy 1972; Chopra and Pajni 1987; Clement et al. 1994). However, host plant resistance to *Sitona* sp. has not yet received major focus as a control alternative (Erskine et al. 1994).

Genetic differences in resistance against aphid species such as *A. craccivora* and *Acyrthosiphon pisum* were reported but no strong resistant genotype was obtained. Although resistance against *Etiella zinckenella*, has been found, but no attempt has been made to breed for resistance (Erskine et al. 1994). Similarly genetic variations in response to seed weevils, *Bruchus lentis* have been found, but breeding for resistance has not been initiated (Erskine et al. 1994). Laserna-Ruiz et al. (2012) recorded lower infestation of seed by bruchids in *Lens culinaris* Medikus subsp. *culinaris*, *Lens culinaris* Medikus subsp. *orientalis* (Boiss.) Ponert, *Lens nigricans* (M. Bieb.) Godr., and *Lens lamottei* Cezfr., than the check.

Genotypes, ILL 9924, RL 83, ILL 10856, ILL 6458 and RL 67 were found to be less susceptible to *A. craccivora* and had higher grain yield (Neupane et al. 2020). Low aphid incidence was associated with green or yellowish green foliage and slightly pubescent leaves on lentil genotypes (Kumari et al. 2009; Neupane et al. 2020).

7.2.3 Progress in Host Plant Resistance to Insect Pests of Chickpea

In South Asia, progress was made to breed resistance or tolerance of chickpea to reduce losses caused by *H. armigera* in this crop (ICRISAT 1990). Since 1976 extensive germplasm collections have been screened at the International Crops Research Institute for Semi-Arid Tropics (ICRISAT), India, where more than 14,000 chickpea germplasm accessions were screened for resistance to *H. armigera* of which ICC 506EB, ICC 10667, ICC 10619, ICC 4935, ICC 10243, ICCV 95992, and ICC 10817 were found to be resistant to the pod borer (Lateef 1985; Sharma et al. 2014). Germplasm accessions such as ICC506, 10667, 10619, 6663, 10817, ICCX 730008-8, ICCX 730041-8, ICCX 730094-18, ICCX 730020-11-I, ICC 10870, and ICC 5264 have also been identified as borer-resistant (Lateef 1985; Ahmed et al. 1990). Similarly, Lateef and Sachan (1990) found good level of resistance of *H. armigera* in ICCV 7, ICC 6663, ICC 10817, ICCL 86102, CCL 86103, ICC 4935-E2793, PDE-2, and PDE-5 across the agroecological zones of India. Varieties such as ICCV 7, ICCV 10, and ICCL 86103 with moderate levels of resistance to *H. armigera* have been released for cultivation in India (Sharma et al. 2014). Accessions belonging to *Cicer bijugum* (ICC 17206, IG 70002, IG 70003, IG 70006, IG 70012, IG70016, and IG 70016), to *C. judaicum* (IG 69980, IG 70032, and IG 70033), to *C. pinnatifidum* (IG 69948), and to *C. reticulatum* (IG 70020, IG

72940, IG 72948 and IG 72949, and IG 72964) showed resistance to *H. armigera* as well (Sharma et al. 2014). Sarwar et al. (2009) found germplasm C-727 resistant to *H. armigera.* Salimath et al. (2008) found the least pod damage in chickpea genotypes ICCL 87317, ICC 12479, ICC506, ICC 86102, ICCV 95992, ICCV 96752, ICCL 87315, ICCL 87314, ICCL 87316 and ICC 12494, and ICCV 2. Most of these lines showed the highest content of lignin and cellulose in pod husk. In addition, the tolerant genotypes, viz. ICCL 87315, ICC 506, and ICC 12479 had higher number of trichomes and exhibited less percent pod damage to *H. armigera*. Ruttoh et al. (2013) found genotypes EC58318, ICCV10, ICC14831, EC583260, EC583264, and EC583250 resistant to *H. armigera* in Kenya.

Germplasm accessions ILWC 39, ILC 3800, ILC 5901, and ILC 7738 were identified as resistant to leaf miner damage (Chen et al. 2011; Sharma et al. 2014). Sharma et al. (2014) found that oxalic acid content in chickpea leaves was correlated with leaf miner resistance in this crop. Genotypes CPI 29973, CPI 29975, CPI 29976, NCS 960003, K 902, CM 72, CMN 122, and BG 372 have been reported to be resistant to *C. maculatus*. Apart from the cultigens, wild relatives of several grain legumes have shown high levels of resistance to bruchids (Lateef 1985). Lines showing resistance to bruchids usually have small seeds with a rough seed coat. Accessions belonging to *C. bijugum, C. pinnatifidum,* and *C. echinospermum* have shown resistance to the bruchid, *Callosobruchus chinensis* (Sharma et al. 2014).

Against *Liriomyza cicerina,* some genotypes with different degrees of resistance were available. Chrigui et al. (2020) found superior RILs with resistance to the leaf miner indicating that introgression of resistance to leaf miner from chickpea could be possible using interspecific crosses. The inheritance pattern of resistance to the leaf miner in RILs was shown to be quantitative. Succinic acid exhibited the highest direct effects on resistance to the leaf miner suggesting that a high level of this compound could be used as a potential biochemical selection criterion for resistance to leaf miner in chickpea.

Divija et al. (2020) found 5 germplasm accessions resistant to *C. chinensis* as well. These germplasms were ICC397375, ICC372351, ICC3552, ICC3089, and PG186. The resistance in ICC37235 was established to be an antibiosis implying high content of some secondary metabolites such as phenol, flavonoid, and trypsin (protease) inhibitor. As for germplasms ICC 397375 and ICC 3552, their resistance was associated with some seed characters (e.g., seed roughness, medium seed size) implying a non-preference mechanism (Divija et al. 2020). Also, a laboratory investigation conducted by Sathish et al. (2020) determined resistance in PI 599066 to *C. chinensis*. This genotype exhibited a complete resistance to *C. chinense* due to its small seed size and hairiness.

7.2.4 Progress in Host Plant Resistance to Insect Pests of Pigeon Pea

Host plant resistance to insects is one of the components of pest management in pigeon pea, and considerable progress has been made in developing techniques to screen for resistance to major insect pests (Sharma 2016). Genotypes with resistance to *H. armigera, M. vitrata, M. obtusa*, and *C. chinensis* have been identified, but the levels of resistance are low to moderate in the cultivated germplasm (Sharma 2016). Rathinam et al. (2020) reported that the wild relative of pigeon pea *Cajanus platycarpus* was resistant to the devastating pigeon pea pod borer *H. armigera.* Another wild relative of pigeon pea, *Cajanus scarabaeoides* was found to be resistant to the pod borer by Njaci et al. (2020). The mechanism of resistance was associated with an enhanced induction of phytohormone and calcium/calmodulin, plant volatiles, and secondary metabolites all showing an elevated pest-induced gene expression (Njaci et al. 2020). Kumar et al. (2020) found the pigeon pea genotypes LRG-208 and CRG 2015-007 to be the most resistant to *H. armigera.* Ngugi-Dawit et al. (2020) found good resistance in IBS 3471 to *H. armigera*. They found that the mechanisms of resistance in this genotype were both antibiosis and antixenosis by inhibiting the growth and development of *H. armigera*. Vanambathina et al. (2021) found a high level of resistance to *H. armigera* in 5 Australian Cajanus wild genotypes including *C. acutifolius* (AGG316925WCAJ1), *C. latisepalus* (AGG309208WCAJ1), *C. lanceolatus* (AGG300129WCAJ1), *C. pubescens* (AGG309206WCAJ1), and *C. reticulatus* var. *reticulates* (AGG300159WCAJ1). The resistance mechanism was driven by the total phenolic content in the wild genotypes of pigeon pea. The progress in transferring insect resistance into the improved pigeon pea varieties has been limited, and there is a need to introgress resistance genes from the wild relatives into the culigen and/or develop pigeon pea cultivars to confer resistance to pod borers (Sharma 2016). According to Naresh et al. (1993), extra-early and determinate types of pigeon pea genotypes are more susceptible to pod borer damage. Genotypes P54(b), ICPL 5EB-EB, Phule T 1, Prabhat, T 21, Phule T 3 and 7411, DL-78-1, ICPL 155, TAT 9 and TAT 10, ICPL 1, H 79-6, UPAS 120, GP Nos. 17, 20, 24, 33, 30, 40, 43 and 45, Bahar, ICPL 94, ICPL 154 and ICPL 85059, ICPL 332, PPE 45-2 (ICP 1964), MA 2 and ICPL 84060, ICPL 6, PPE 45-2, ICP 1903, MA 1, ICPL 187-1, ICPL 288, T 21, ICP 909, ICPL 86040, MAZ, ICPL 2, TA 10, ICPL 1, Pant A1, ICP 7345-1-5, BDN 7, DA 2, ICP 4070, ICP 3615, BSMR 1, ICP 10531, ICPL 201, ICP 109BB, (AUT 82-1) ICPX 77303, ICPL 87089, Bahar, ICPL 87088, ICP 7946-E, and ICP 9889 have been reported to be relatively resistant to *H. armigera* (Chauhan and Dahiya 1987; Kushwaha and Malik 1988; Reed and Lateef 1990; Gupta et al. 1990; Naresh et al. 1993; Sharma 2016). Also, short-duration genotypes ICP 7, ICP 13011, ICPB 2089, ICPL 187-1, ENT 11, and ICPL 98008 showed moderate levels of resistance to pod borer damage (Sharma 2016).

7.2.5 Progress in Host Plant Resistance to Insect Pests of Mung Bean

Various mung bean insect-resistant varieties have been identified through a series of screening methods. Against *Bemisia tabaci*, several varieties were identified. These resistant sources included ML 803, ML 839, PDM 91-249, and PBM 5 (Yadav and

Dahiya 2000); NM 92 (Khattak et al. 2004); ML 1265 and ML 1229 (Kooner and Cheema 2007); TMB 36 and RMG 1004 (Singh and Singh 2014); ML 1774 and ML 1779 (Cheema et al. 2015). Other mung bean resistant lines to *B. tabaci* comprise ML 1, ML 6, ML 7, P 290, P 292, P 131, P 293, P 325, P 364, and 11,148 (Kooner et al. 1997). Against bean blossom or flower thrips (*Megalurothrips distalis* Karny), some resistant sources were found including cultivars Co 3, Co 4, and Co 5 (Lal 1987); genotypes SML 77, UPM 82-4 and Pusa 107, MGG 347, SML 832 (Malik 1990; Laosatit et al. 2020), genotypes PIMS 2, PIMS 3, CO 3, ML 5 and ML 337 (Chhabra 2001); NM-92 (Khattak et al. 2004) and MH 3153 (Nadeem et al. 2014).

Against stem fly, *Ophiomyia* sp., sources of resistance comprise cultivars, viz. V2396, V3495 and V4281, G05253, G05776, G02005, and G02472 (Abate 1990; Talekar 1990). Against, *Aphis craccivora* Koch, the resistant genotypes identified include JRUM 1, JRUM 11, JRUM 33, DPI 703, LAM 14-2, UPM 83-6 and UPM 83-10, Pusa 115, PDM 116 and ML 353 (Sahoo and Hota 1991). Against *Helicoverpa armigera* (Hub.) resistant cultivars include J1, LM 11, P526 and Co3 (Lal 1987), ML 337, ML 423 and ML 428 (Chhabra et al. 1988). Against *Maruca vitrata,* resistant sources include LGG 505, ML 267, LGG 502, LGG 407, LGG 460 and LGG 485 (Swarnalatha 2007); MGG 364, MGG 365 and MGG 363 (Choragudi et al. 2012). A wild mung bean accession TC1966 (*V. radiata* var. sublobata Roxb.) was identified as a potential source of resistance to *Callosobruchus maculatus* (Fab.) and *C. chinensis* (Fujii et al. 1989; Lambrides and Imrie 2000). Similarly, accessions (V2802 and V2709) were confirmed to possess complete resistance to *C. chinensis* and *C. maculatus* (Somta et al. 2007). Also, bruchid resistant accessions comprise V2709, V2802, TC1966, ACC41, VC1973A, Jangan Mung (Laosatit et al. 2020). The first resistance source identified in wild mung bean accession was TC1966 that exhibited complete resistance to both *C. chinensis* and *C. maculatus* (Fujii et al. 1989). Other wild mung bean accessions such as ACC23 and ACC41 were reported to be resistant to *C. chinensis* and *C. maculatus* (Lambrides and Imrie 2000). Cultivated mung bean accessions V1128, V2709, V2802, and V2817 were resistant to *C. chinensis* and *C. maculatus* (Somta et al. 2007). Two breeding lines V-02-802 × DGGV-7 and V-02-802 × DGGV-2 from F_4 generation were reported to be resistant to *C. maculatus* (Majhi et al. 2020). Hema et al. (2022) found three inter sub-specific lines, viz. GGISC 124, GGISC 150, and GGISC 140 resistant to *C. chinensis*. Variety Pant Moong-1 was found to be resistant to *B. tabaci* by Khaliq et al. (2017). Three lines of Green Gram (*Vigna radiata*), namely GGISC-2, GGISC-21, and GGISC-49 were found resistant to *Callosobruchus chinensis* (Harshitha et al. 2022) in India. The mechanism of resistance in these lines was antibiosis affecting some biological parameters of the beetle (e.g., delayed adult emergence, uneven adult emergence, prolonged developmental period, small and malformed adults).

The recent release of a reference genome sequence of mung bean and current advanced sequencing technology has enabled fast and efficient DNA marker development; and fine-mapping and identification of candidate gene(s) for the biotic resistance in mung bean have been made possible (Laosatit et al. 2020). The resistance to *C. chinensis* in the wild mung bean TC1966 is controlled by a single dominant gene locus, designated Br, possibly in combination with minor gene(s), and the resistance is dependent on genotypes of the seeds (Kitamura et al. 1988; Fujii et al. 1989). Similarly, Miyagi et al. (2004) found that the resistance to *C. chinensis* in wild mung bean ACC41 was controlled by a single dominant locus. Secondary metabolites, storage proteins, and enzyme inhibitors in legume seeds are major biochemical compounds causing resistance (antibiosis) to bruchid (Laosatit et al. 2020). The cyclopeptide alkaloids (vignaticacids A and B) were isolated from BC20F4 isogenic lines carrying the Br gene from TC1966 (Sugawara et al. 1996).

7.3 Conclusion

Pulse crops play an important role in human and livestock nutrition worldwide but their production remains challenged by quantitative and qualitative losses due to insect pests. In this chapter, major insect pests of pulse crops were described and sustainable management focusing on host plant resistance was highlighted. Especially, past and recent achievements in plant breeding for genetic improvement as well as screening efforts to identify sources of resistance among existing germplasms were reviewed. Although advanced efforts and more research synergy are still needed, existing achievements are likely to mitigate insect pests' effects while sustaining pulse production and value-chain when adequately explored. Genomic tools and resources could still be exploited in all the pulses to accelerate development of insect resistance.

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Plant Resistance to Insects in Oilseed Crops

8

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Abstract

Oilseed crops are energy rich crops that are grown under energy deprived conditions. The demand for premium seed oils is increasing as the world's population grows. The attack of pests and diseases reduces the production potential of these crops. The cost of controlling insect pests by synthetic chemical insecticides in agriculture annually is billions of dollars worldwide. The overuse of insecticides has many associated ill effects. To maintain the ecological balance of the environment, it is imperative to develop alternative pest management systems that aim for minimal pesticide use and the conservation of natural enemies. Resistance in host plants is one such alternative strategy. Since one of the main bottlenecks in realization of full yield potential of oilseed crops is attack of insect pests, a traditional and effective alternative crop protection method serves as the fundamental tool of integrated pest management. Future development of insect-resistant oilseed crop cultivars will depend on the adoption of technologies and breeding techniques such as genomic selection, high-throughput phenomics, gene editing, and landscape genomics as well as the continuous use of sources of resistance from crop germplasm.

Keywords

Breeding · Defense · Insect–plant interactions · Phenotyping · Screening

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8.1 Introduction

Oilseed crops are widely grown across the world due to their versatility and high economic value. Due to a rise in the demand for vegetable oil, animal feed, medicines, biofuels, and other oleochemical industrial uses, oilseeds have recently gained increased attention. Over the past 30 years, the increased interest has led to an 82% rise in the area under oilseed cultivation and a roughly 240% increase in global production (El-Hamidi and Zaher 2018). Some of the major oilseed crops grown in the world include seven edible oilseeds (soybean, rapeseed-mustard, groundnut/ peanut, sunflower, sesame, safflower, and niger) and two non-edible oilseeds (castor and linseed) due to their diverse agroecological conditions. More than 180 million hectares of crop land are used for oilseeds cultivation in the world (Oerke et al. 2006). These crops are important source of income for farmers and contribute significantly to the global food and energy supply. There are several limitations in successful cultivation of oilseed crops that can impact output, including climate, soil quality, water availability, pests, diseases, etc. Pests are a significant barrier to the global expansion of area under oilseed crops. Insect pests pose a serious threat to food security and sustainable development, demanding the creation of efficient plant protection technologies to prevent and reduce pest-related crop losses (Oerke et al. 2006). Chemical pesticides are farmers' first line of defense against insect pests, but their widespread use has led to several problems, such as the killing of beneficial insects, environmental pollution, problems with human and animal health, and the development of pest resistance to pesticides (Pedigo and Rice 2006; Stevens et al. 2012; Nderitu et al. 2020). One strategy for addressing this problem is Integrated Pest Management (IPM). Modern and more sustainable agriculture methods must be adopted to address these problems. Further, these negative off-target impacts have inspired scientists to develop brand-new, environmentally benign approaches to manage insect pests. Host plant resistance has the potential to serve as the foundation for pest management in many agricultural systems (Sharma 2007; Kumari et al. 2022). The term host plant resistance (HPR) has many different definitions. In general, "the proportional amount of inheritable plant traits to counteract the activities of insects to cause minimum percent drop in yield" can be used to define plant resistance. The development of insect-resistant cultivars based on a thorough understanding of the many host plant resistance mechanisms is one of the key milestones in the HPR initiative. Antixenosis, antibiosis, and tolerance are three types of resistance mechanisms in plants that confer resistance to insect pests. Plant traits that prevent or restrict insect pests from coming, landing, settling, feeding, or ovipositing are known as antixenosis, also known as non-preference. This type of mechanism is based on both physical (visual cues, morphological traits) and biochemical (the presence of chemical molecules that function as anti-deterrent, antifeedants, etc.) properties of plants. Antibiosis is brought on by traits that impair an insect's biology, growth, and reproduction. The basis for tolerance in plants is their ability to continue to develop normally and sustain minor yield losses in the face of insect assault or other damage (Palaniswamy 1996). The intensity of both current and novel pests and illnesses that affect oilseed crops will grow as oilseed production intensifies and scales up. Although great emphasis is paid to locating sources and analysing the intricate mechanisms of insect resistance, it is important to keep in mind that the end objective is reducing pest damage in future crop types. Resistance must be considered, carefully assessed, and chosen among other criteria of the variety-to-be during the developmental process (selection and breeding). Sadly, not enough is frequently done during breeding to develop traits in the new variety that make it resistant to insects. Our objective is to give readers a better grasp of host plant resistance for the creation of genuinely ecological IPM techniques in oilseed crops. An overview of research and development on several oilseed crops with regard to HPR is provided in this chapter.

8.1.1 Soybean

The leading agricultural crop in the world, soybean is used for a variety of things, including food for humans and other animals, edible oil, biofuel, industrial products, and cosmetics. Many pests, such as fungi, bacteria, and insects, affect the production of the crop in soybean growing areas (Hartman et al. 2011). The methods and input prices for soybean pest management have changed dramatically over time (Ragsdale et al. 2011; Hodgson et al. 2012). The peculiar grain legume known as soybean, *Glycine max*, is well known for serving as both a pulse and an oilseed, having 38–44% protein and 18–22% oil. Moreover, soybean is listed as an important ingredient in a wide range of industrial goods, including insulating foams, adhesives, inks, lubricants, and solvents. In a country like India, where a sizable portion of the population is vegetarian, soybean plays a significant role as a rich source of protein. India is one of the top exporters of soy meal to other Asian nations and the third-largest importer of soy oil in the world.

8.1.1.1 Damage by Insect Pests

About a dozen of the 275 species of insect pests that infest soybean in India has acquired the status of important pests, including the girdle beetle, tobacco caterpillar, green semilooper, Bihar hairy caterpillar, stem fly, aphids, jassids, and whitefly. A total of 380 different kinds of insects have been found on soybean crop across the globe (Patel and Rahul 2020). The soybean looper, velvet bean caterpillar, beet armyworm, bean leaf beetle, stem borer, Mexican bean beetle, and soybean leaf miner are examples of lepidopteran and coleopteran pests that feed on soybean in the world (Higley 1995). The threat posed by the soybean aphid and stink bugs has the potential to increase quickly as their geographic ranges expand. For example, the soybean aphid, which was first detected in Wisconsin, expanded to 30 US states and three Canadian provinces in less than 10 years (Ragsdale et al. 2011) while the brown-marmorated stink bug (BMSB) has already been found in 38 US states since it was first found in Pennsylvania in 1996 (Leskey et al. 2012).

8.1.1.2 Role of HPR

To lessen the harm caused by insect pests, an Integrated Pest Management (IPM) programme should take advantage of host plant resistance in soybean cultivars. We attempt to assess recent advancements in the analysis of soybean resistance to different pests in this chapter. Several crop plants have been developed that are resistant to hemipteran insects (Smith 2005; Smith and Boyko 2007). From a historical perspective, HPR has been quite effective in controlling hemipteran insect pests of soybean. Due to the presence of pubescence on plant leaves, soybeans are now resistant to the potato leaf hopper (*Empoasca fabae*), a pest that was once a severe problem for the crop (Hollowell and Johnson 1934). The potato leaf hopper was relegated to a non-pest category after the pubescence trait was subsequently included into commercial varieties of soybean (Boethel 1999). Many crops, including cereals, vegetables, fruits, and forages, have been found to have aphid-specific resistance genes (Smith 2005). The first aphid resistance genes were discovered at the beginning of the twenty-first century, and resistant cultivars have been sold for 10 years, but they have been terribly underutilized. Screening for resistance genes in soybean lines commenced very soon after the first report of soybean aphid in North America. Hill et al. (2004) investigated 1530 cultivars between 2001 and 2002 and identified *Rag1*, a single dominant gene that confers antibiosis, as the first of numerous *Rag* genes (resistance to *Aphis glycines*). The ability of insects to develop virulence that allows them to overcome the resistance is the biggest limiting factor to the long-term utility of resistant cultivars, as it is with any sort of host plant resistance (Kelley et al. 2021). Since then, screening by several research programs (mostly in the public sector) has uncovered at least 11 naturally occurring *Rag* genes as well as four quantitative trait loci, all in various stages of evaluation and development (Natukunda and MacIntosh 2020). Researchers discovered aphid biotypes with varying degrees of virulence against *Rag* genes in test plots before the restricted commercial distribution of *Rag*-containing cultivars. Four biotypes referred to as biotypes 1–4 have been identified to date in the US, and their survivability varies based on the biotype and resistance gene. We are aware of no records of virulent biotypes in Asia, the aphid's natural habitat. Despite being widespread in the soybean aphid's range in the US (e.g. in Ohio, Illinois, Wisconsin, and South Dakota), virulent biotypes have not yet become prevalent or numerous enough to pose a threat to the usefulness of organic *Rag* soybean varieties. This is possibly because these varieties make up a relatively small portion of the soybean acreage (Kelley et al. 2021). Using insecticide resistance management (IRM), it may be possible to control how aphid biotypes evolve, encouraging more active commercial development of these varieties. We need data, models, and tactics to accurately predict changes in the incidence of virulent aphids and respond to them for an IRM strategy to provide sustainable use of *Rag* soybeans. In this quest, the use of genetic markers to categorize aphid lineages and determine virulence would be extremely helpful, especially when confirmed using aphids collected in the field. To increase the durability and shorten the development time of hemiptera resistant soybean, a combined approach will probably be required. In a similar manner, *Anticarsia gemmatalis* Hübner causes serious economic harm to soybean. Use of

Bt transgenic soybeans and chemical control are the main management tactics for this bug. In conjunction with other tactics as part of an integrated pest management (IPM) approach, alternative strategies like host plant resistance are seen as an effective and less-aggressive method. Using oviposition, attractiveness, and food consumption tests, Ongaratto et al. (2021) assessed 30 soybean genotypes for antixenosis expression and chose 13 promising genotypes to confirm the potential for antibiosis. Their findings imply that the genotypes "TMG 133" RR, "TMG 1179" RR, "IAC 19", "IAC 17", "IAC 100", D75–10169, and IAC 78–2318 have antixenosis. The genotypes IAC 74–2832, "IAC 19", "IAC 17", "IAC 100", and "PI 274454" were found to have antixenosis and antibiosis, which were characterized by an effect on behaviour and a detrimental effect on larval survival. It was discovered that the "TMG 7062" IPRO provided antibiosis resistance by adversely affecting larval survival and development. Antixenosis was advised for "IAC 24" due to the larvae's decreased feeding consumption. While developing soybeans with *A. gemmatalis* resistance, breeding programmes should take these genotypes into account (Ongaratto et al. 2021).

While much of the current research has been on conventional and traditional host plant breeding and screening techniques, novel genomic and molecular technology-based research is beginning to emerge. The vast array of signalling molecules produced by the plant's immune system, as well as morphological barriers, all contribute to HPR. These plant-defensive responses are linked to either constitutive, therefore always present, or induced plant features that are shaped by an attack or elicitation in the morphology, physiology, and/or chemistry of the plant, which produces plant secondary metabolites (Romero et al. 2020; Bravo et al. 2019). Both strategies result in direct or indirect consequences through the attraction of natural enemies and are not mutually incompatible. Breeding initiatives must place a strong emphasis on tolerant cultivars. As was already established, tolerant cultivars can tolerate or recover from damage brought on by insect populations comparable to those that affect susceptible cultivars. The adoption of host plant resistance is encouraged more by the growth of insect pest populations that are resistant to pesticides in soybean. A more extensive commercialization of this effective pest control technique may be encouraged by recent research on the genetics and markers of insects, plant gene expression, and in-plant refuges. These findings point to important directions for insect resistance management (IRM).

8.1.2 Rapeseed-Mustard

The second-most significant and well-known group of winter oilseed crops in India is rapeseed-mustard after soybean. These crops are primarily grown in India's northern plains, while there are some cultivated areas in the country's eastern region as well. *Brassica juncea* (Indian mustard) is the predominant oilseed Brassica crop in India, while *B. rapa* (*Toria*, Yellow *Sarson*, Brown *Sarson*), *B. napus* (*Gobhi Sarson* popularly known as Canola), and *B. nigra* (Black Mustard) are some of the other crops included in the rapeseed-mustard group. The defatted cake is fed to animals.

Lack of high-quality seed, diseases, and insect pests have significant impact on mustard yield if not controlled during the crucial crop growth period. Dealing with pest infestations is one of the main challenges in oilseed Brassica cultivation. Insecticides are frequently used to control insect pests; however, the socioeconomic and, environmental issues and the growing incidence of insecticide-resistant populations argue against their exclusive use. At present, oilseed Brassica pests are primarily controlled by synthetic chemical pesticides. In addition to concerns about how insecticides impact people and other non-target species, the formation and spread of pesticide resistance in populations of the oilseed Brassica pests is another barrier to their usage. Plant resistance is a historic and reliable alternative crop protection technique that is the cornerstone of integrated pest management. The diamondback moth (*Plutella xylostella*) has developed resistance to all major classes of insecticides including Bt, while the insecticide resistance in cabbage stem flea beetle (*P. chrysocephala*) is quickly expanding in the population (Furlong et al. 2013). *Lipaphis erysimi,* mustard aphid, is one of the primary and most problematic pests of rapeseed-mustard in Indian subcontinent (Bakhetia et al. 2002; Blackman and Eastop 2000). Continuous feeding by large colonies of nymphs and adults on aboveground plant parts results in drastic yield reduction. The productivity losses of up to 83% in India's rapeseed-mustard crops are attributable to this pest alone (Mandal et al. 2002). Oilseed Brassicas have evolved a number of biophysical and biochemical defense systems to ward-off these pests (Mitchell et al. 2016). Plant tissues contain constitutive defense mechanisms that serve as preventative protection against future damaging circumstances (Mertens et al. 2021). In response to herbivore attack, defense mechanisms may also be dynamic and created, depending on the age, developmental stage, and genetic makeup of the plant (Howe and Jander 2008; Brunissen et al. 2009; Chandrasekhar et al. 2018; Batyrshina et al. 2020). Variation in these systems at the spatial level (individual sections inside a plant) may be one of the main variables determining pest proliferation and feeding behaviour (Awmack and Leather 2002; Karley et al. 2002; Jakobs and Müller 2018). How closely related the defense systems are, how they differ in, how well they prepare for attacks, and how well they defend against aphids have not been fully explored. Researchers have examined the associations between several physiological and biochemical traits and the resistance of the mustard variety to *Lipaphis erysimi*. Many physical and chemical barriers have a significant impact on mustard aphid resistance (Sandeep et al. 2017; Hervé 2018). In contrast to chemical defenses, which frequently include the production of low molecular weight natural chemicals known as secondary metabolites that may be toxic to the creatures attacking plants, biophysical defenses include structures like prickles, thorns, and cuticular waxes (Vanetten et al. 1994; Maffei et al. 2007a). The variation found in the aphid population counts on various varieties of different species is attributed to the specific host–insect interactions. Insects prefer specific genotypes/species for feeding, which is influenced by several factors including environmental and chemical interactions between host plant and insect–pests. Hopkins and Huner (2004) reported that plants challenged by insects respond through changes in the composition and physical properties of the cell wall as well as the biosynthesis of secondary metabolites. Defensive chemicals may be constitutively present in the plant before an insect attack (phytoanticipins), or they may be induced after attack (phytoalexins). Trichomes are present on a variety of oilseed plant species and stop aphid migration and stylet insertion. Trichomes may or may not have glands. Non-glandular trichomes, specialized epidermal hair-like structures, may affect aphid movement and reproduction rates (Riddick and Simmons 2014). Although the specific mechanism of how glandular trichomes function is unknown, plants use them to defend themselves against insect attacks. Genetic differences among varieties resulted in significant diversity in surface wax concentration, which can be phenotyped for resistance to insects in relation to wax content. Waxes differ widely among the plant species and even in different parts of the same plant, attesting to the genetic diversity and developmental influences (Rutledge and Eigenbrode 2003). There is a lot of evidence that trichomes decrease feeding and motility, but it is unclear how they affect other aspects. Additionally, the glandular trichomes exude some toxic exudates that capture and ultimately kill small insects including aphids. Research on plant mutants with varied surface properties provided the first evidence, in terms of structural qualities, of the significance of surface layers for host acceptance. Wax on the leaf epicuticular surface protects plants from pathogen infection, insect pest attack, and desiccation (Trdan et al. 2004; Frati et al. 2013; Ni et al. 2014). According to Paré and Tumlinson (1999), chemicals on leaf surfaces can cause diverse responses in insects. Moreover, the wax can physically obstruct an insect's movement across the surface of a leaf. According to Bjorkman et al. (2011), there is a negative relationship between the number of insects and the amount of epicuticular wax in the leaves (Bjorkman et al. 2011). Several hydrocarbons, long-chain fatty acids, primary and secondary alcohols, fatty aldehydes, ketone esters, and primary and secondary alcohols make up the chemical composition of epicuticular waxes (Jenks et al. 1994; Alcerito et al. 2002). There are fewer plant species that exhibit glossy phenotypes (types with less epicuticular wax crystals) (Kanno and Harris 2000; Steinbauer et al. 2004). Yet, for eating and oviposition, many insect species favour glossy leaves or leaves with the waxes removed over the leaves with normal or high epicuticular wax loads (Stork 1980; Bodnaryk 1992; Brennan et al. 2001; Cervantes et al. 2002).

8.1.2.1 Plant–Herbivore Interactions in Oilseed Brassica

It has been estimated that at least one species consumes at least one kind of plant due to the prevalence of herbivory (Schoonhoven et al. 2005). The plant develops several defensive strategies in response to herbivore attack. There are various pest control uses for this plant–herbivore interaction. Transcriptomics has shown the mechanisms by which insects respond to plant protection and the survival strategies they use (Vogel et al. 2014; Thorpe et al. 2016; Schweizer et al. 2017). In-depth understanding of these underlying mechanisms is required to develop innovative pest management techniques that either strengthen plant defenses or thwart pest attempts to get around those defenses. In response to infestation or infection, different phytohormone-dependent processes are activated. Salicylate (SA)-dependent responses are induced by several necrotrophic diseases (Thomma et al. 2001), and sucking and chewing insects (Maffei et al. 2007b), whereas ethylene

(ET) and jasmonate (JA) pathways are induced by biotrophic pathogens and chewing insects (Thomma et al. 2001). These interactions result in the production of several defense-related proteins and secondary metabolites with antixenotic or antibiotic properties. It indicated that aphid infestation resulted in an SA-dependent response. JA-dependent genes, however, were inhibited (Zhu-Salzman et al. 2004; Thompson and Goggin 2006; Gao et al. 2007; Walling 2008). All these responses result in the modification of plant metabolism to ensure beneficial interactions between insects and plants. Source germplasm for insect resistance genes (especially aphids) in Brassica spp. is still mostly unavailable despite multiple prior attempts (Sekhon and Åhman 1993; Bhadoria et al. 1995). During the laboratory-based screening, the wild crucifer *Brassica fruticulosa* reportedly displayed effective antibiosis against *L. erysimi* and gene(s) for aphid resistance have been successfully introgressed in *B. juncea* background (Atri et al. 2012). Several attempts to produce aphid-resistant transgenic mustard have led to varied success but the field testing of these transgenics is still awaited (Kanrar et al. 2002; Hossain et al. 2006). When looking for increased transcripts in response to taxonomically diverse plant–aphid interactions in the absence of specific R genes, many orthologous transcripts were discovered. These transcripts result in the production of proteins that are essential for cell maintenance, general plant defense and signalling, reactive oxygen species (ROS) production, hypersensitive response, and photosynthesis (Boyko et al. 2006; Koramutla et al. 2014). Recently, Singh and Dhillon (2022) reported some of the *B. juncea* lines to show resistance against *L. erysimi* but all the lines fell under susceptible to highly susceptible category given the aphid resistance index, thus making their claims self-contradictory.

Herbivorous insects use various visual, tactile, and chemical cues in host plant selection. It is important to choose the right host plant for oviposition because this will affect the progeny’s survival and growth. A significant factor affecting how insects behave during oviposition is the presence of surface chemicals, plant volatiles, and trichomes (Hilker et al. 2002; Chamarthi et al. 2011). The most crucial defense mechanism for plants against insect herbivory is antixenosis for oviposition. The female moths use a variety of physical and chemical cues to choose an appropriate host plant for oviposition. Plants respond to insect oviposition by using direct and indirect defenses that try to kill or remove the insect eggs to prevent the larvae, that would hatch from them, from causing damage to the plant (Hilker and Meiners 2010). In reaction to oviposition, plants generate neoplasm at the egg deposition site, which lifts and lowers the eggs, as well as ovicidal substances, which kill the eggs (Doss et al. 2000; Seino et al. 1996; Yamasaki et al. 2003). Moreover, oviposition causes necrotic tissue to form at the oviposition site due to the plant tissues’ hypersensitive reaction, which separates the eggs (Petzold-Maxwell et al. 2011). Salicylic acid (SA) and jasmonic acid (JA) are crucial phytohormones that help plants defend themselves against insect herbivory (Stotz et al. 2002; Traw and Bergelson 2003; Bruinsma et al. 2007; Zhao et al. 2009). They cause plants to produce harmful antinutritive chemicals and poisonous secondary metabolites, which stunt larval growth and development and prevent adult moths from ovipositing (Bruinsma et al. 2007). Many intermediary substances are released by the octadecanoid and phenylpropanoid routes, respectively, which are mediated by JA and SA. Some of these substances have an antibiotic effect on pest insects, while others have an antixenotic effect on oviposition (Dicke and van Poecke 2002; Bruinsma et al. 2007). A negative crosstalk is known to exist between the JA and SA pathways (Traw and Bergelson 2003). Significantly less number of *Pieris rapae* and *P. brassicae* eggs were laid on plants treated with JA compared to untreated plants (Bruinsma et al. 2007). In addition, eggs had more JA content than plant tissues or larval diets do (Hilker and Meiners 2010).

8.1.2.2 Perspectives for Integrated Insect Pest Protection in Oilseed Brassica Breeding

In the past, plant breeding efforts to breed for insect-resistant cultivar generally lacked the focus to develop resistant cultivar for incorporation in an IPM module. Plants breeders always looked for high level of resistance in plants and often ignored moderate resistance. Due to the lack of effective strategies for crop rotation, tillage, biocontrol, and cultivar tolerance, the management of insect pests in oilseed rape has relied on pesticides in recent years (Zheng et al. 2020). The frequent use of a limited number of insecticides, many with common modes of action, resulted in insect populations with resistance against various classes of insecticides (e.g. pyrethroids) within the last decade worldwide including populations of the diamondback moth (*Plutella xylostella*), pollen beetle (*Brassicogethess aeneus*), cabbage stem flea beetle (*Psylliodes chrysocephala*) and cabbage seed weevil (*Ceutorhynchus obstrictus,* syn. *assimilis*) (Hervé 2018). The 2013 European Union ban on neonicotinoid seed treatments led to increased insect damage and decreased oilseed rape yields. Moreover, fewer conventional crop protection products are getting new product approvals (McDougal 2018). Insect pests are projected to move into previously unaffected oilseed rape production areas (range expansion) because of changes in insect populations brought on by climate change (Bale et al. 2002). The cultivation of oilseed rape is now threatened by these trends. A major shift towards creative and integrated management approaches is urgently needed since insect pest management strategies that just rely on insecticides are not viable. A significant problem is maintaining environmentally sustainable rapeseed production amid growing dangers from insect predation. There are about 40 kinds of insects that prey on rapeseed globally, and only a few effective control measures have been developed. Rapeseed also exhibits relatively little resistance to insect predation. It is difficult to phenotype for host plant resistance because resistances are often quantitative in nature. By focusing on a variety of potential insect control techniques, new, comprehensive protection measures for rapeseed will emerge throughout the short, medium, and long term, maintaining the output of this important oil crop species (Obermeier et al. 2022) (Fig. 8.1).

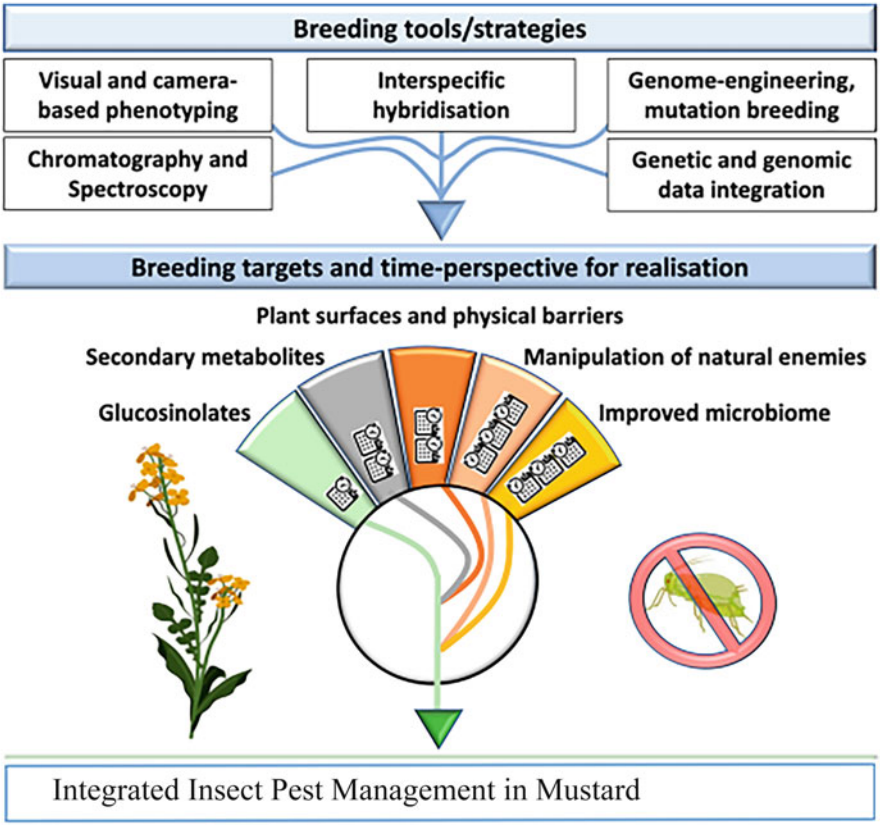

Fig. 8.1 Schematic representation of major breeding tools/strategies and breeding targets with time perspective for future realization and availability of insect-resistant breeding lines in integrated insect pest protection of mustard (Adapted from Obermeier et al. 2022)

8.1.3 Groundnut

A significant source of digestible proteins, cooking oil, and vitamins, groundnuts are a major oilseed crop in the world. Insect pests are the major biotic stressors in limiting peanut production. About 1.6 million tones of produce equal to US $ 30.9 million are lost each year in India due to groundnut production losses caused by insect infestations (Savage and Keenan 1994; Dhaliwal et al. 2010). Groundnut production during the *kharif* season is predicted to total 83.69 lakh tonnes in 2022–2023 as opposed to 83.75 lakh tonnes in 2021–2022 according to the first advance projections from the Government of India (Anonymous 2023). There are various biotic and abiotic stresses affecting the production of groundnut. Yield losses from pest attack are difficult to estimate because of the localized and sporadic nature of the outbreaks (Reddy and McDonald 1984). An estimated 15% of the groundnut crop's annual yield is lost to insect pest damage. According to Baskaran and Rajavel (2013), the tobacco caterpillar *Spodoptera litura* (Fabricius) is a significant groundnut pest that can lead to up to 47% production loss (Baskaran and Rajavel 2013). Larvae feed aggressively on vegetation at first, then completely defoliate the plants Furthermore, massive and careless use of pesticides has a negative impact on non-target organisms (predators and parasitoids), leads to pesticide residues in food, encourages the resurgence of pests, and leads to the development of insecticide resistance in insects in addition to adverse effects on human health and the environment (Sharma 2007). Given this, host plant resistance has the potential to offer sustainable solution to pest problems. Enhancing host plant defenses against insects will decrease losses from herbivores, reduce the need for insecticides, improve agricultural yields, and create a safer environment (Howe and Jander 2008). Host plant resistance is an important pest management tactic for *S. litura*, that significantly reduces groundnut harvests globally. Saleem et al. (2019) examined various biochemical (reducing, non-reducing and total sugars, proteins, and phenols content) and biophysical (trichome density, relative water content, specific leaf weight, epicuticular wax) parameters in the eight groundnut genotypes resistant to *S. litura* along with four controls and the wild species *Arachis monticola* L. There was a significant negative correlation of leaf damage with leaf weight, midrib, leaf lamina trichome density, wax content, proteins, and phenols content. ICG 928, one of the *S. litura* resistant genotypes, displayed higher leaf lamina (140 mm^{-2}) and midrib (180 mm^{-2}) trichome density, specific leaf weight (2.5 g dm^{-2}), wax content (0.36 g cm^{-2}), proteins (4.91 mg g^{-1}), and phenols content (3.77 mg g^{-1}) than the susceptible check JL 24, which displayed higher relative water content (73.3%), reducing sugars (11.32 mg g^{-1}). These biophysical and biochemical elements can be successfully used in groundnut breeding to develop cultivars resistant to *S. litura*.

During the time of seedling emergence and a few weeks thereafter, thrips feeding results in high damage. Early in the season, thrips feeding damage from high thrips pressure can cause yield loss and/or delayed maturity (Todd et al. 1995a; de Moraes et al. 2005; Funderburk et al. 2007). Thrips use a method of sex determination known as haplodiploidy, in which fertilized eggs develop into diploid females and unfertilized eggs into haploid males (Moritz 2002). They can quickly multiply due to their mode of reproduction and temperature-dependent life cycle. Breeding cultivars resistant to orthotospoviruses has received a lot of attention because it is difficult to control thrips, and the viral infection results in severe economic loss. Research with tomato spotted wilt virus (TSWV) in peanut undertaken in the United States and groundnut bud necrosis virus (GBNV) studies conducted in Asia provide a large portion of the knowledge on breeding for virus resistance. The Florunner and Southern runner cultivars were particularly vulnerable to the spotted wilt disease caused by TSWV in the Southern United States in the 1980s and early 1990s (Culbreath et al. 1992; Todd et al. 1995b). Most of the resistance was generated from a single genotype (PI 203363) that was brought from Brazil in 1953 because of screening and breeding activities (Culbreath et al. 2003). Since that the primary runner peanut cultivars contain a sizable percentage of PI203363 alleles, the introduction of this distinctive genotype had an immediate and considerable impact on American peanut breeding (Clevenger et al. 2017).

The current generation of 'third generation TSWV resistant' peanut cultivars has good level of field resistance to the disease, and losses caused by it have been reduced. Breeding initiatives have also identified some GBNV resistance in Asia (Amin et al. 1985; Dwivedi et al. 1995; Reddy et al. 2000; Kesmala et al. 2004; Mandal et al. 2012). Many of these lines have partial viral resistance and frequently involve the incorporation of other management techniques. Insecticides are still used, for instance, to lessen thrips feeding damage in early-season peanut (Mandal et al. 2012; Marasigan et al. 2016). Finding and implementing efficient thrips resistance in high yielding peanut cultivars can assist farmers financially and lessen the environmental impact of pesticide use.

Brar et al. (1994) attempted genetic transformation of peanut, but no resistance tests were carried out. Cry genes from *Bacillus thuringiensis* (Berliner), which confer resistance to a variety of insects, especially those of the order Lepidoptera, have been introduced into peanut (Krishna et al. 2015). However as per the available information, no transgenic peanut has been examined or found to be resistant to thrips. Transgenesis has been successful in transferring thrips resistance to other crops; for example, potato plants have been modified to resist the western flower thrips (Outchkourov et al. 2004). Stefin, potato cystatin, equistatin, and cystatin were combined, synthesized into a functional unit, and produced in potato plants as inhibitors of cysteine and aspartic proteases. Compared to non-transgenic control plants, the plants expressing these multidomain proteins had fewer larvae and adults (Outchkourov et al. 2004). Orthotospovirus resistance has been repeatedly attained in transgenic peanut (Li et al. 1997; Magbanua et al. 2000; Yang et al. 2004; Rao et al. 2013; Mallikarjuna et al. 2016). Valencia and runner genotypes were transformed using TSWV/GBNV N-gene or coat protein-based constructs in both the United States and India, and pathogen-derived resistance was attained in these transformants. Transformed peanut seedlings offered significant level of field or in vitro resistance against TSWV and GBNV (Li et al. 1997; Magbanua et al. 2000; Yang et al. 2004; Rao et al. 2013; Mallikarjuna et al. 2016). A transgenic peanut resistant to the peanut stem necrosis virus was also developed by Mehta et al. (2013). Hence, the possibility of viral resistance in peanut through transgenic technology cannot be ruled out.

RNAi is another technology that has the potential to offer resistance against viruses and insects (Whyard et al. 2009; Gan et al. 2010; Zhang et al. 2013). It involves the conversion of an invasive organism's dsRNA to short interfering (si) RNSs (20–23 nucleotides long) with the help of an enzyme complex. This siRNA, subsequently, prevents the translation of the mRNA (Fire et al. 1998; Pak and Fire 2007). In peanuts, the effectiveness of RNAi against viruses and/or thrips has not been proven. Yet, the effectiveness of RNAi has been established for *F. occidentalis,* where a considerable increase in reproductive fitness was seen after a double-stranded RNA (dsRNA) associated with an essential enzyme (vacuolar ATP-synthase or V-ATPase) was silenced (Badillo-Vargas et al. 2015). Developments in thrips genomics and transcriptomics have resulted in identification of several developmental genes linked to tobacco thrips and western flower thrips (Schneweis et al. 2017; Shrestha et al. 2017). It is important to first validate the use of these genes through in vitro assays before attempting to express and test the effectiveness of these genes against thrips in plants to assess the utility of RNAi as a management strategy. Although consumer preferences may prevent transgenic peanut from entering the market anytime soon, the transgenic technology that is currently accessible does present some extremely intriguing research opportunities. Plant-based transgene delivery could be avoided by making modifications to technologies like RNAi. In the first Genome Wide Association (GWA) investigation on seed composition attributes on the U.S. peanut small core collection, Zhang et al. (2021) found some important QTLs in peanut. GWAS and RNA-seq screening yielded a total of 282 differentially expressed genes (DEGs), and 16 genes substantially associated with seed composition features were also tested. These 16 genes' levels of expression were associated with five fatty acid and protein concentrations. Breeders looking to change the fatty acid ratios or boost the protein/oil content of peanut seeds may find the QTLs and genes discovered in this study valuable. These potential genes must be tested in the future against various biotic stressors, such as insect pests. In conclusion, groundnut plants have developed various biochemical and biophysical barriers to protect themselves against pests. Plants with high level of induced resistance to insect pests can offer resistance against insects which are not regular in occurrence and the attack is unpredictable (War et al. 2011). Groundnut develops numerous plant defense features after the exogenous application of jasmonic acid (JA) and salicylic acid (SA), which confer resistance to insect pests (War et al. 2011).

8.1.4 Sunflower

The consumer market recognizes sunflower as a significant oilseed crop which despite being used as oil crop also finds uses in roasted, confectionery, and bird feed products. Russian plant breeders increased the oil content of sunflower seeds, turning a common wayside plant into a well-known oilseed crop. The habitats in which sunflower species can be found include plains, deserts, and salt marshes. Because of their tolerance to a variety of ecological conditions, wild species can be seen as reservoirs of novel alleles to meet a variety of breeding objectives (Kantar et al. 2014). It has been widely documented that related species can be used in breeding programmes to produce different alleles (Seiler 1992, 2007), and this potential can be used to breed for pest and disease, drought, heat, and salinity resistance. Barriers made of phytomelanin and terpene repellents found in glandular trichomes are examples of known mechanisms for resistance in sunflower (Rogers et al. 1987). The presence of a phytomelanin layer may contribute to the pericarp's robustness (Seiler 1997; Rogers 2019). A single locus with a dominant allele has been postulated to be a genetic link to the phytomelanin layer, which has been investigated as a potential source of insect resistance (Johnson and Beard 1977). Development of resistant sunflower cultivars may be facilitated by identifying the genetics underlying the mechanisms. Phytomelanin barriers and terpene repellents located in glandular trichomes are two examples of sunflower host plant resistance features (Johnson and Beard 1977; Carlson 1971; Rogers and Kreitner 1983). Moreover, sunflower has morphological and physiological traits that may confer some tolerance. Based on different studies, it is hypothesized that the physical defense mechanisms of sunflowers against herbivory by sunflower moth late instar larval eating behaviour are significantly influenced by pericarp strength (Prasifka et al. 2014). More than 60 insects attack sunflowers in North America (Schulz 1978; Walker 1936; Phillips et al. 1973; Niide et al. 2006). The release of transgenics, particularly for weedy characteristics (herbicide resistance, illnesses, and insects), had an ecological impact due to the quick gene flow from cultivated to wild germplasm. The release of transgenic sunflowers in areas where wild populations coexist with cultivated fields carries a significant danger since natural gene flow between the two forms of sunflower happens quickly in these areas (Cantamutto and Poverene 2007; Gutierrez et al. 2010; Presotto et al. 2012).

8.1.5 Safflower

The safflower plant, *Carthamus tinctorius* L., is a bushy, herbaceous annual plant that is a member of the family Compositae. It is an important oilseed crop that is becoming more and more important in many countries of the world. The plant has historically been produced for its blossoms, which are used as a source of dye for colouring foods and textiles. Safflower oil has very high level of linoleic acid (78%). The safflower plant is known to be attacked by 101 different pests at various stages crop growth and development stages (Singh et al. 1999; Javed et al. 2013). Unfortunately, a variety of insect pests and diseases cause damage to safflower, resulting in significant productivity losses (Singh et al. 1999). The most devastating of these are insect pests, specifically the aphid, *Uroleucon compositae* (Theobald) and pod borer *Helicoverpa armigera* (Hubner) (Akashe et al. 2014). Nine different kinds of natural enemies and 20 insect pests have been identified on safflower in the Karnataka region (Mallapur et al. 2001). The aphid, *U. compositae* (Theobald) (Aphididae; Hemiptera), which attacks safflower, is one of the most destructive and persistent pests and infests crop, especially from its elongation stage until flowering phase (Akashe et al. 2014). Both nymphs and adults deplete the plants resources by sucking the cell sap from the underside of leaves and vulnerable shoots. Aphid performance on various genotypes can vary for a variety of reasons, including physical traits and the quality of the host plant. Since host plant suitability is influenced by the number of amino acids or nitrogen in the phloem sap and the secondary metabolites that affect aphid performance, host plant quality is a significant factor that contributes to the antibiotic resistance of plants (Gibson and Pickett 1983; Ave and Tingy 1986; Dixon 1998; Cisneros and Godfrey 2001; Karley et al. 2002). Different plant species exhibit variable suitability as hosts for diverse insects (Storer and van Emden 1995; Frei et al. 2003). Several genotypes of a plant species have various physical and chemical characteristics that influence its suitability as host (Ave and Tingy 1986). By analysing feeding deterrence and aphid settlement in a choice test, Saeidi (2020) studied safflower genotypes for antixenosis against *U. carthami* and found significant variations in the performance of the eight safflower genotypes examined. The genotypes with the fewest aphids present exhibit the highest antixenosis resistance. Thus, comparing the pest resistance of different genotypes considering the plant differences may provide crucial information about how suitable or unsuitable they are for insects.

Safflower fly, also known as shoot fly or capsule fly (*Acanthiophilus helianthi* Rossi), is another important insect pest of safflower in Asia and Europe (Talpur et al. 1995). This insect causes significant loss in most of the safflower producing areas in Iraq, Pakistan, and India in Asia (Al-Ali et al. 1977; Talpur et al. 1995; Verma et al. 1974). The insect heavily infests the plant throughout its reproductive phase with particular preference for egg laying during flowering and head development (Talpur et al. 1995). Hatched larvae break through the head bracts and consume the entire seed or the tissue that makes up the receptacle. According to Narayanan (1961), each larval or pupal stage lasts for 7 days, and eclosed flies can survive for up to 2 weeks before beginning a fresh cycle of oviposition. Significant reductions in seed weight, yield, and marketability are caused by larvae feeding on seeds (Ashri 1971). The most efficient and environment friendly approach to pest control should be to develop safflower cultivars that are resistant to different insects. Unfortunately, the lack of reliable sources of resistance has slowed down the development of breeding insect-resistant cultivars. It is important to note that out of 80 safflower germplasm accessions screened by Dambal and Patil (2016), 11 accessions reported foliage drying of 21–35% with aphid population on the central twig/plant. Ashri (1971) looked for fly resistance in more than 2000 cultivars of safflower, but no resistant genotype was found. Wild safflower species, on the other hand, demonstrated a moderate to high level of resistance to the safflower fly (Ashri 1971). Only two wild safflower cousin species, *Carthamus oxyacanthus* Bieb. and *Carthamus palaestinus* Eig., are easily crossable with the cultivated species and are resistant to safflower fly, making them suitable for safflower improvement (Ashri and Knowles 1960; Sabzalian et al. 2010). The development and deployment of resistant cultivars can be a successful technique to help decrease insect pest populations while minimizing the need for chemical crop treatments. Also, it can be combined with biological control and any other pest management technique used in IPM programmes.

8.1.6 Sesame

Sesame (*Sesamum indicum* Linn.), a member of the Pedaliaceae family, is a traditional and significant oilseed crop grown across the tropics and subtropics of India as well as other regions of the world. It was given a boost due to its high-quality edible oil. Sesame is also known as the “queen of oilseeds” and is a rich source of carbohydrates, protein, calcium, and phosphorus (Seegeler 1983). Moreover, it is used in the production of bread, cookies, cakes, margarine, and confections. Insecticides, cosmetics, fragrances, soaps, and pharmaceuticals are all made with the oil. The cake is also utilized as cattle feed (Mbah and Akueshi 2009). India has the largest area under sesame cultivation in the world, but yield is quite low (332 kg/ ha) compared to the global average (Singh et al. 2003). The major sesame-growing states in India are Rajasthan, Maharashtra, Gujarat, Madhya Pradesh, Andhra Pradesh, Karnataka, Uttar Pradesh, West Bengal, Orissa, Punjab, and Tamil Nadu. China, Myanmar, Sudan, Uganda, Nigeria, Pakistan, Ethiopia, and Bangladesh are the other sesame-producing countries (Ogbonna and Umar-Shaba 2012). Sesame yields in India are generally low for several reasons, but insect pests have a major role in reducing yield. The pest attack results in a significant decrease in seed production (25–90%) (Ahuja and Kalyan 2002). The crop is typically severely damaged by insect pests particularly at the flowering phase. Although the physical harm may be less than that caused by leaf pests, the impact on the production is enormous (Mahmoud 2013). The potential insect barrier to production from the seedling stage till maturity is the sesame leaf webber and capsule borer, *Antigastra catalaunalis* Duponchel (Lepidoptera: Pyraustidae) (Selvanarayanan and Baskaran 1996; Karuppaiah and Nadarajan 2011). Pesticide use has environmental concerns and unfavourable side effects on non-target organisms despite their effectiveness (Rai et al. 2002). For resource-constrained farmers, breeding for host plant resistance is thought to be the most effective, efficient, and practical control method (Bayoumi and El-Bramawy 2007). Karuppaiah et al. (2009) screened 21 sesame genotypes for resistance against *A. catalaunalis,* of which only four genotypes were less favoured for oviposition. The trichome density in the leaf had a positive correlation ($r = 0.749$) with the egg laying by *A. catalaunalis.* Comparison of growth index of this pest on different genotypes exhibited antibiosis mechanisms with significantly low growth index in resistant genotypes compared to susceptible ones. *A. catalaunalis* damage exhibited negative relationship with the total phenols content of leaves, flowers, and pods. Panday et al. (2021) identified several sources of resistance in sesame against leaf webber and capsule borer and found germplasm lines with inhibitory mechanisms of resistance to *Antigastra* that can be exploited to transfer the resistance into commercial varieties. Even cultivars that are only partially resistant could be able to offer sufficient control even when just sparingly using insecticides. By preventing the emergence of insecticide-resistant insect strains, it will aid in extending the usable commercial life of current pesticides. Choudhary et al. (2017) evaluated various sesame varieties and noted that the number of leaves, branches, capsules, and trichome density of these varieties had a negative relationship with the population of *A. catalaunalis.* The impacts of inducible defenses on phytophagous insects can include greater toxicity, a delay in larval development, or increased attack by insect parasitoids (Maleck and Dietrich 1999). Compared to constitutive defensive mechanisms, inducible defenses are thought to degrade plant fitness to a lesser extent and might be more robust (Agrawal 1998). The population dynamics of many herbivores depend heavily on the quality of the host plant, which is determined by the plant's nutritional condition (Sarwar et al. 2011). Several plant species have been demonstrated to benefit from salicylic acid in terms of the expression of dormant genes (Mahmoud 2013). The level of resistance in the cultivated sesame germplasm in India is quite low, and the available resistant germplasm has not been used to create resistant cultivars.

8.1.7 Castor

Castor is an important non-edible oilseed crop. Castor farming can be improved by growing it in areas with abundant rainfall (Cheema et al. 2013). Castor's genetic improvement has mostly been restricted to the exploitation of naturally occurring genetic variation present in the base population and limited to selection for high yield, desired branching type, non-shattering capsules, and seeds with better oil content. The types and hybrids have become more susceptible to a variety of biotic and abiotic challenges because of extensive production with high inputs, improper scientific management, and lack of crop rotation. About 100 species of insect pests have been reported on castor at different phonological stages, of which castor semilooper, capsule borer, *Spodoptera litura*, red hairy caterpillar, jassids, and whitefly are the most damaging (DOR 2005; Lakshminarayana and Sujatha 2005). According to yield loss estimates, loss in seed yield can range from 35 to 50% depending on the crop growth stage and the pest pressure. Nonetheless, complete losses have been reported in cases of significant outbreaks of red hairy caterpillar and castor semiloopers during the early stages of crop growth. Castor has the natural ability to withstand up to 25% of leaf damage without suffering a substantial loss in seed production; however, damage to the spikes and capsules causes a large yield loss (Sujatha et al. 2011). Breeders are constantly looking for new sources of pest resistance and stress tolerance. In contrast to plant disease resistance, resistance to insect pests is found to be transient and, for the most part, incomplete. There is evidence for both horizontal (polygenic) and vertical (single or few genes) disease resistance, although there is limited support for vertical resistance in terms of host–insect interactions. Insect resistance in castor has not yet been bred into any varieties or hybrids; breeding programmes aiming at introducing resistance to the main insect pests are still in their infancy. The production of cultivars for disease resistance is the focus of the parental-line and varietal front development programmes. Numerous reports on the resistance/tolerance of released varieties/hybrids—namely TMVCH-1, DCH-519, RHC1, DCH-32, GCH-4 to leaf hoppers; GCH-5 to jassids, whitefly and capsule borer; AKC1 to castor semilooper and capsule borer; TMV-6 to leaf hoppers, semilooper and capsule borer; and Kranti to semilooper—are based on field reaction to the pests. Except for the leaf miner, no systematic attempts are made to screen germplasm under consistent pest-load for the selection of promising genotypes. Castor germplasm has been tested for resistance to leaf miner, leading to the identification of the RG 1930 and RG 2008 lines, which have a purple morphotype and resistance to the miner with exceptionally low infestation compared to control plants (Anjani 2005). Resistance to leaf miner and its link to the purple colour phenotype showed uniparental inheritance (Anjani et al. 2007). Also, it was noted that cultivars SKI 73 and SKI 89 were very resistant to leaf miner infestation (Kapadia 1995). Low genetic variability for productivity attributes and sources of pest and disease resistance hinders the success of breeding for yield stability (Weiss 2000; Hegde et al. 2003). There are several opportunities for genetic enhancement of castor using traditional and biotechnological methods. Due to the lack of new sources of genes and germplasm, the main drawbacks of broad commercial production are unevenness and low yields. Castor genetic enhancement should focus on strengthening the composition against various biotic stresses as well as boosting castor productivity in a variety of conditions (Singh et al. 2015). For the establishment of newer lines and hybrids, molecular markers must be used in castor. However, the successful application of this information for development of DNA-based markers, understanding metabolic pathways of oil biosynthesis, toxins, biotic stress resistance, etc. still needs to be clarified.

8.2 Breeding for Host Plant Resistance

HPR offers a sustainable approach to manage insect pests (Stout 2014). This is especially true in underdeveloped nations (primarily tropical nations), where it is either impossible or inappropriate to use alternative control methods like pesticides. HPR is compatible with other management strategies, takes little from the farmer (other than the procurement of the proper variety of seed), has a cumulative effect frequently, and has no harmful effects on the environment. Additional forms of control must be integrated with HPR as a foundation. Nothing else will be required for economically viable crop production if the level is high enough. Development of pest-resistant cultivars may be the most effective and profitable to manage pests and diseases, but before making any research investments of this nature, several factors must be taken into account. First, think about how the pest or disease is spreading; if it is widespread, causes a considerable yield loss, and can only be successfully bred out from an agronomic standpoint, then that is a reasonable breeding goal. If an appropriate management strategy is in place, HPR is also considered a breeding goal, however it is costly and unreliable. For a pest or disease that is highly localized or temporally sporadic, has little impact on yield or quality, or is adequately controlled by conventional management measures, the time and expense of HPR breeding is not justified. The assessment of whether a resistant cultivar is the best method of controlling the pest or disease, however, must frequently be reviewed because the dynamics of the pest or disease and crop are constantly changing and because effective control chemicals can also be unexpectedly lost due to changes in government regulations. While breeding for HPR, it is important to consider the ability of the pest or pathogen to adapt to the developed lines, the improvement of the developed lines by additional recombination during breeding, and the changing environment from season to season. It frequently involves a high cost and a protracted timetable to justify the development of a resistant cultivar, especially from the secondary or tertiary gene pools. The normal process for developing resistant cultivars involves three steps: (1) identifying potential sources of resistance in the germplasm, (2) incorporating the source of resistance into an elite background, and (3) integrating the cultivar into current (or novel) crop management practices.

Every breeding programme has multiple competing objectives, so the selection criteria used to assess the resistance of germplasm must be stringent to ensure that only the most resistant material is advanced. How difficult it is to introduce new resistance into an elite background depends on the genetic distance between the source of the resistance and the cultivated species (i.e. whether it comes from primary, secondary, or tertiary germplasm), the genetic basis of the resistance, and any ploidy differences. Most of the polygenic resistance to a pest or pathogen occurs in oilseeds, although some, fortunately, are passed down by single genes. Finding germplasm with the proper level of resistance can be difficult because, like other polygenic traits, variation in resistance is typically continuous rather than discrete. It is also typical to find beneficial pest and disease resistance in the wild or unadapted genetics of plants. As a result, the process of eliminating poor alleles introduced by the resistant donor and enhancing the performance of the introgressed progeny is typically time-consuming when integrating resistance into top populations. Genetic markers connected to all the donor's key genomic regions that are sufficient to confer resistance are useful for assisting in the selection of lines with resistance and lowering the number of resources needed to create a resistant cultivar. The viability of molecular approaches has risen over the past 10 years with the adoption of low-cost, high-throughput sequencing technology known as 'next-generation sequencing'.

8.3 Genetic Engineering for Resistance to Insect Pests

In the current environment of a growing population and climate variations, increasing crop productivity is a crucial issue that needs to be addressed. Insect pests are one of the main biotic pressures that are holding back agriculture in the twenty-first century. The decrease in potential yields, which leads to stagnant productivity, is caused by insects. Despite the adoption of control measures, most of the commercially important crops experience a variety of yield losses. But, to combat insect pests, farmers have turned to chemical pesticides, their extensive usage has the potential to harm both people and the environment. Therefore, the main goal of modern agriculture has been to increase yields using the available resources and land to ensure food security for everyone throughout the world and agricultural sustainability. Genome editing is slowly and regularly becoming the tool of choice for laboratories all over the world for understanding gene function and its practical applications (Fig. 8.2). They are being used in a variety of crop development efforts to reduce biotic and abiotic stressors. Due to the editing strategies' great precision, effectiveness, cost, and time effectiveness, they have become useful tools. Significant phenotyping and enrichment of the resistance gene pool are crucial clues that demand novel approaches. To do this, it is necessary to evaluate the available germplasm, including wild relatives of crops, for pest response and to identify genes that respond to stress using multi-omics techniques. The details of genome editing for pest management involve multiplex editing of such identified resistance genes utilizing high-throughput transformation techniques. Targeted mutations

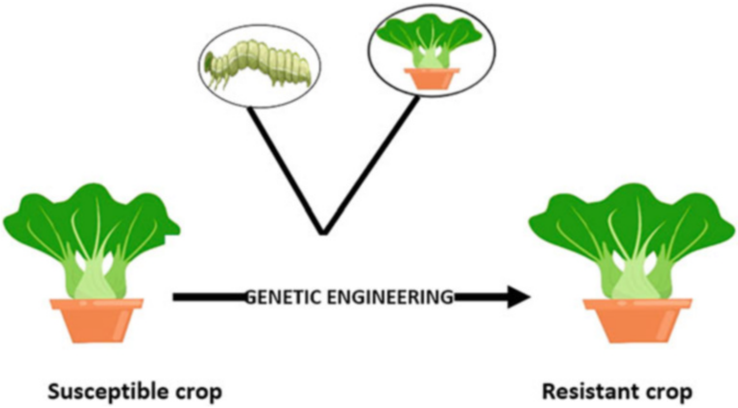

Fig. 8.2 Genetic engineering in plants

turning sensitive plants into ones that can control their pests are not far off in space or time with such studies presently in vogue. These factors, along with legislative restrictions on gene-edited crops, may help the technology succeed in terms of science.

Oilseed plants represent an important renewable source of fatty acids because they accumulate them in the form of triacylglycerol (TAG) as major storage components in seeds. In plants, two interconnected metabolic pathways—an acyl-CoA-dependent pathway and an acyl-CoA-independent pathway—lead to the export of processes for de novo fatty acid synthesis from plastids to the cytoplasm. The discovery and precise quantification of the expression of transcription factors and important genes associated with lipid metabolic pathways in soybean (Severin et al. 2010), *Jatropha curcas* (Costa et al. 2010), *Arabidopsis* (Beisson 2003), peanut (Gupta et al. 2016), and castor bean (Brown et al. 2012) have been made possible by high-quality RNA-seq data. Engineering plants to produce oilseed crops with higher yields and resilience to abiotic and biotic challenges make it possible to gather RNA-seq data and enhance plant transformation technology. To attain optimal metabolic flow, there are currently tactics that rely on more complicated methods that simultaneously overexpress or inhibit several genes. Knowing a metabolic network would enable predictable and beneficial natural product production and new chemical synthesis (Lu et al. 2006) that would help to improve the genetic makeup of oilseed crops. This is why, over the past 10 years, corporate and academic researchers have become interested in the metabolic engineering of oilseed plants.

8.4 Future Perspectives

Soon, oilseed crops and their products will account for a significant portion of global trade. These plants can be utilized for both food and non-food purposes. Gaining and maintaining future genetic gain require a thorough grasp of the development of oilseed crop breeding, including how breeding triumphs have been attained so far. The industry should feel confidence that our breeders can use a similar methodology for success in the future and the time limits involved if comparable obstacles are encountered. The effectiveness of using traditional breeding methods has been seen in oilseed breeding activities. The development of high-performing cultivars will depend on the native variation present in oilseed germplasm and potentially novel sources of additional genetically modified (GM) characteristics. Future traits must be able to take advantage of variation that is either already existing in germplasm or has been developed through recombination with closely related species or through transgenic methods. Recent developments in panomics suggest that these novel breeding tools should be kept in HPR oilseed breeding programmes together with new and existing crop management techniques and the ongoing search for new sources of resistance. Breeding for HPR will be crucial for future climates, even though crop management and precision agriculture are significant and should be considered if it is determined that a breeding solution is not the greatest path to success. For instance, using precision agricultural techniques enables farmers to adopt more effective management plans that are tailored to their individual circumstances by having a precise understanding of where a disease may emerge inside a field or throughout a farm. To lessen the impact of plant pests and diseases on the crop, techniques might range from using high level geospatial data to complex models of precise insecticide and fertilizer application (Shafi et al. 2019; Roberts et al. 2021).

8.5 Conclusion

One of the primary causes of falling agricultural output is insects. Farmers are more likely to use chemical insecticides because they offer an immediate solution to the insect pest problems. The potential deployment of alternative pest-control strategies has received increased attention because of the fast-growing public awareness of the risks indiscriminate pesticide usage poses to human and animal health as well as the environment. Host plant resistance is a pest management strategy that is safe for the environment and an important component of IPM (integrated pest management) programmes. Host plant resistance is an effective, economical, and environmentally friendly method of pest control. Because of its benefits to the economy, ecology, and environment, it has evolved into a crucial and important part of IPM methods against invertebrate pests in many agricultural systems (Teetes 1996). The most important feature of HPR is that farmers with limited resources practically never need technical know-how for application techniques and do not have to make any financial commitment. It has taken a lot of effort to find and develop agricultural cultivars that are resistant to the worst pests that affect different crops. It is essential to incorporate resistance genes into high yielding cultivars that can adapt to varied agroecosystems. Pest resistance should be one requirement for releasing varieties and hybrids for farmer use. The use of pesticide-resistant crop varieties can result in lower pesticide dosages and less frequent treatments, which lowers crop production costs and promotes biodiversity in the relevant agroecosystem. The prospects of using crop varieties resistant to invertebrate pests as a sole control method or as a supplement to other control strategies of IPM systems have also been demonstrated by empirical studies in oilseed crops, though more research is needed to elucidate the resistance mechanisms for the development and deployment of pest-resistant varieties in these crops. In fact, homogeneity is the worst thing from the standpoint of crop protection because it makes an area or time more vulnerable to stressors now or in the future (Grettenberger and Tooker 2015). It is now known that even the simplest form of diversity, such as the mixing of different genotypes in a field, can produce associational insect resistance in addition to several other advantages (Barot et al. 2017; Grettenberger and Tooker 2015; Tooker and Frank 2012). Consequently, it may be more effective (or long-lasting) to reconsider breeding techniques for complementary genotypes that produce associational resistance when grown in mixtures rather than aiming for a perfect genotype that would be entirely resistant in isolation. Future IPM strategies are also anticipated to heavily rely on genetically modified crops with improved insect resistance.

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Host Plant Resistance to Insects in Vegetable Crops

9

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Abstract

Host plant resistance is an effective approach to manage insect pests in vegetable crops. This approach involves the use of plant traits that deter or reduce insect feeding and reproduction involving the mechanisms of antibiosis, antixenosis, and tolerance. These traits affect plant–insect interactions through the production of metabolites and volatiles, which can modify insect behavior and physiology. Tri-trophic interactions between plants, insects, and natural enemies also protect plants from herbivory and increase insect parasitization. The use of transgenics and genome editing provides new opportunities to enhance host plant resistance

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by introducing or modifying genes involved in the production of insect-resistant traits. Understanding the mechanisms of host plant resistance and their interactions with insect pests and natural enemies is crucial for the development of effective pest management strategies that are environmentally friendly and economically sustainable. Overall, host plant resistance offers a promising approach to reducing reliance on synthetic pesticides in vegetable crop production, but continued studies are required to fully realize its potential.

Keywords

Antibiosis · Antixenosis · Tolerance · Plant-insect interactions · Constitutive and induced metabolites · Priming · Volatiles · Tri-trophic interactions · RNAi

9.1 Introduction

In nature, plants are exposed to a number of biotic and abiotic stresses that limit their productivity. In response to these stresses, they produce a variety of resistance mechanisms that allow them to avoid, withstand, or recover from the consequences of pest infestations (Hanley et al. 2007). Plant traits that influence herbivore biology, such as physical defenses on the plant's surface (hairs, trichomes, thorns, spines, and thicker leaves), are what mediate direct defenses and affect the herbivore growth (Samadia and Haldhar 2019). In order to reduce the likelihood of insects using a host plant for oviposition, food, or refuge, they exhibit antixenosis, which refers to potential plant qualities or attributes that affect or alter insect behavior (War et al. 2012).

Host plant resistance is considered the core component of any IPM module (Horgan et al. 2020; Mansour and Eryan 2022). Antibiosis, antixenosis (non-preference), and tolerance are three modalities of resistance that affect how an insect and a plant interact (Koch et al. 2016; Iqbal et al. 2018). Antibiosis resistance affects the pest biology, which ultimately leads to reduction in plant damage. According to Smith (2005), antixenosis resistance affects a pest's behavioral features by preventing it from favoring a resistant plant (Painter 1951). According to Smith (2005), tolerance is a form of resistance where a plant can withstand or recover from harm brought on by a pest population.

India has a relatively low share in vegetable exports due to a number of factors including high domestic consumption, more than 100,000 diseases caused by viruses, bacteria, fungi, and other microorganisms (Hall 1995; Dhaliwal et al. 2007). According to estimates by Pimentel and Levitan (1986), the total global food and preharvest losses resulting from insect pests and weeds were around 45% (of the total food production) and 30%, respectively. In order to manage insect pests in horticultural crops, such plant resistance mechanisms have been widely and successfully exploited (War et al. 2012; Haldhar et al. 2015). Long-term use of both indigenous and imported genetic materials from arid horticulture crops for breeding variations in the nation led to the creation of numerous new genotypes/lines through selection and, to a lesser extent, hybridization (Haldhar et al. 2017). By expediting the development of novel pest-resistant varieties in vegetable crops and even underutilized crops, modern biotechnology offered the finest possibilities for diversifying agricultural production (Abah et al. 2010). The systematic use of wild gene pool in strategic breeding for the development of genotypes with biotic and abiotic stress resistance or tolerance, as well as their conservation as related species, is therefore urgently needed (Samadia and Haldhar 2017).

Host plant resistance has occasionally provided a straightforward method for managing insect pests and insect vector transmissible diseases on a number of agricultural and horticultural crops. In this chapter, we have reviewed the plant–insect interactions, tri-trophic interactions, herbivore-induced metabolites/volatiles, transgenics, and genome editing approaches in vegetable crops against insect pests.

9.2 Importance of Host Plant Resistance

Synthetic pesticides have been widely used in agriculture for decades to control pests and increase crop yields. However, the indiscriminate use of these chemicals has led to several negative impacts on the environment, human health, and biodiversity (Aktar et al. 2009). To address these issues, host plant resistance has emerged as a viable alternative to synthetic pesticides, which is a natural defense mechanism that plants have developed over thousands of years to protect themselves from insect pests (Sharma and Ortiz 2002). By incorporating host plant resistance into pest management strategies, farmers can reduce their dependence on synthetic pesticides, thereby reducing the negative impact of these chemicals on the environment and human health. Moreover, host plant resistance has been shown to be effective against a wide range of insect pests, including those that have developed resistance to synthetic pesticides. This is because host plant resistance is a dynamic defense mechanism that can evolve and adapt to changing pest pressures over time (Huot et al. 2013). As such, it offers a sustainable and long-term solution to pest management that can help ensure the continued productivity of agricultural systems.

9.2.1 Mechanisms of Host Plant Resistance

Plants have evolved several mechanisms including antibiosis, antixenosis, and tolerance to defend themselves against insect pests. Each of these mechanisms involves different strategies that plants use to reduce the damage caused by insect pests. This section describes the mechanisms of host plant resistance to insect pests with reported examples in vegetable crops.

9.2.1.1 Antibiosis

Antibiosis is a term used to describe an organism's ability to restrict the growth or survival of another organism. This can be accomplished through the production of toxic or inhibitory substances, such as antibiotics or toxins. In relation to insect pests, antibiosis refers to the ability of specific plants to produce chemical compounds that can exterminate or suppress insect growth. Plants employ antibiosis as a defense mechanism, producing compounds that are harmful to insect pests, thus altering their growth, development, and survival (Bischoff et al. 2023). One example of antibiosis in plants is the production of toxic proteins including lectins produced by various plants such as beans, which can be toxic to insect pests such as aphids and caterpillars (Li et al. 2023). They bind to the digestive tract of the insects, causing damage and inhibiting their growth and survival. Another example of antibiosis is the production of protease inhibitors by plants. Protease inhibitors are compounds that inhibit the digestion of protein in insects, causing them to starve and ultimately die (Casaretto and Corcuera 1995). For instance, soybean plants produce a protease inhibitor known as Bowman–Birk inhibitor, which has been found to be effective against several insect pests such as corn earworm, tobacco budworm, and fall armyworm (Azzouz et al. 2005). The Bowman–Birk inhibitor targets digestive enzymes in the gut of these insects, which leads to reduced food digestion and eventually their death.

9.2.1.2 Antixenosis

Antixenosis refers to the ability of one organism to reduce the attraction or suitability of a habitat for another organism. In the context of insect pests, antixenosis is the defensive mechanism employed by plants to insect pests involving the production of chemical or physical barriers that discourage insects from feeding or ovipositing on the plant (Stenberg and Muola 2017). Essentially, it is the plant's ability to make its habitat less attractive or less suitable for the insects, which can be achieved through both physical and chemical barriers. Trichomes, spinescence, waxy cuticle, and sclerophyll in leaf and stem in plants act as physical barriers for insects (Mitchell et al. 2016; Xing et al. 2017). Leaves, stems, and even fruits of some plants showed an increase in trichome density and prevented the insects to attack the plants. Besides, the glandular trichomes secrete viscous fluids, which also prevent the insect's attack (Wheeler and Krimmel 2015). Due to the presence of trichomes, some plants also manipulate the host selectivity of herbivores. The presence of trichomes in kidney beans resulted in lowering the attack and life span of insects (Xing et al. 2017). For instance, some plants have developed physical barriers such as thorns, spines, or tough leaves to prevent insects from feeding or laying eggs on them. Others have developed chemical barriers such as the production of toxic or unpalatable substances that deter or repel the insects. For example, the presence of glandular trichomes on cucumber leaves can deter feeding by spider mites and whiteflies (Xue et al. 2019). Similarly, the production of volatile compounds by tomatoes and carrots can repel insect pests from laying eggs on the plant. For instance, tomato plants produce the volatile compound methyl salicylate, which has been shown to repel the whitefly, *Bemisia tabaci*, and the tomato fruit worm, *Helicoverpa zea* (Shi et al. 2016).

9.2.1.3 Plant Tolerance to Insects

Plant tolerance is one of the most important aspects of resistance against pests and pathogens where plants show their ability to withstand even though there are enough insects to cause severe damage to other susceptible plants. Tolerance enables the plant to continue its growth, and plants can complete their life cycle under insect attack. Plant alters its morphological features as a part of its defense against insect pests. Tolerance mechanisms employed by vegetable crops in defending insects are presented in Table 9.1. Besides the alteration in morphological changes, plants change their growth characters to reduce the damage caused by insect infestation. Delaying flowering, reduced growth, and delayed fruit setting are some of the tolerance characteristics in some plants to pass the insect attack (Stenberg and Muola 2017). However, the opposite characters are also observed in some plants such as higher number of branches, tillers, and higher number of roots and shoots to continue its growth under the insect attack (Koch et al. 2016). Breaking the dormancy under insect attack results in increase in the number of branches (Koch et al. 2016).

The continuous and increased growth of plants under insect attack has been correlated with the physiological basis of plant tolerance to insects. The increase in photosynthetic rate is common in several plants to adjust the growth under insect infestation, which also sustain the growth rate (Weintraub et al. 2018). Tolerant plants can increase the photosynthetic rate by increasing the photosynthetic pigments including the chlorophyll a, b and carotenoids and increase the enzymatic activities related to carbon capture and light harvesting systems such as RuBP and ATPase (Koch et al. 2016; Mitchell et al. 2016). An increase in photosynthesis under the insect infestation results in ensuring plant growth with higher vigor. Besides, the increase of carbon translocation to shoots from roots increases the sink strength to continue its growth and in some cases regrowth under insect infestation.

Over-accumulation of reactive oxygen species (ROS) under insect attack has been reported, which acts as signaling molecules for several defense systems. Though ROS lead to cell death, they activate several defense systems including hormonal regulation, metabolism, growth development, and gene expression having a negative impact on insects (Rashid and Chung 2017; Wani et al. 2022). Plants increase their antioxidative compounds including SOD, POD, APX, and proline to suppress the detrimental effect of ROS (Mansoor et al. 2022). However, the hormonal regulation, especially JA and SA translocate from the infested leaf to a distant leaf and activate the defense mechanisms, resulting in the activation of systemic acquired tolerance to insects (Divekar et al. 2022; Kumari et al. 2015; Zhang et al. 2019a, 2022a; Sahu et al. 2022). Besides, these events include the gene expression in systemic leaves, which are linked to plant defense against the insect.

Increase in metabolic biosynthesis is one of the tolerant mechanisms to insect attack. The most common metabolites are isoflavonoids, terpenoids, phenolics, alkaloids, and phytoalexins, which showed negative effect on insect performance and decrease in insect attack (Jeckel et al. 2022; Jha and Mohamed 2022; Divekar et al. 2022; War et al. 2012). Some of them have properties like feeding deterrence, releasing volatile compounds, direct toxins, and repellents having an overall

Table 9.1 Tolerance mechanisms to different insects in vegetable crops

Crop	Insect	Tolerance mechanism	Reference
Potato	*Leptinotarsa decemlineata*	Tolerance to beetle was attributed with higher doses of nitrogen which changed the leaf morphological features including leaf expansion, increased photosynthetic rate which led to tolerate defoliation.	Weintraub et al. (2018)
	L. decemlineata	Transgenic plant showed reduction in EcR transcripts in larvae.	Hussain et al. (2019)
	Myzus persicae	Tolerant potato cultivars showed lower infestation rate with higher leaf chlorophyll, photosynthesis, leaf hair density, and leaf hair number.	Quandahor et al. (2019)
	L. decemlineata	Plants overexpressed with Cry3A gene showed higher tolerance with higher mortality rate of insect, lower foliage consumption, and lower survival rates of insect.	Mi et al. (2015)
	Halyomorpha halys	Plants showed tolerance to herbivore insect through the increase biosynthesis of ROS.	Sperdouli et al. (2022)
Tomato	*Manduca sexta*	Changes in primary and secondary metabolites with a higher concentration in sink tissues showing the higher utilization to alleviate the attack.	Gomez et al. (2012)
	Helicoverpa armigera	Tolerance was attributed through the JA signaling pathway with an increase of photsynthetic rate, sucrose phosphate synthase, and flower and fruit biomass.	Guo et al. (2012)
	H. armigera	Heat shock protein (GroEL) enhanced the tolerance through the minimization of photo-oxidation of chlorophyll by increasing the activity of antioxidants and lower cell death.	Kumari et al. (2015)
	H. armigera	Overexpressed tomato lines with proteinase inhibitor gene showed antibiosis effect on insect with delayed growth rate.	Tanpure et al. (2017)
	Tuta absoluta	Cry1AC gene in plant showed higher mortality rate of insect.	Selale et al. (2017)
	Heliothis peltigera; *Spodoptera littoralis*	Overexpression of BnFAD3 enhanced the tolerance to both chewing insects through the JA signaling pathway.	Zhang et al. (2019a)
	H. zea	Tolerant plants showed higher trichomes and volatile organic compounds.	Paudel et al. (2019)
	T. absoluta	Tolerant tomato genotypes showed higher level of secondary metabolism, volatile organic compounds and higher level of SNP variation.	D'Esposito et al. (2023)
	Bemisia tabaci	siRNA transgenic lines showed higher mortality rate of whitefly.	Pizetta et al. (2022)

(continued)

Table 9.1 (continued)

Crop	Insect	Tolerance mechanism	Reference
	M. persicae and *B. tabaci*	Tolerant plants showed higher density of trichome with thick stem and increased concentration of phenols and tannins.	Anu et al. (2021)
Pepper	*B. tabaci*	Tolerant genotype was found to have higher level of resistance compounds with lower levels of nutrients.	Jiao et al. (2018)
	Spodoptera litura	Plant overexpressed with Cry2Aa2 gene showed tolerance to insect by increasing the photosynthetic pigments and rate, proline, soluble sugars, ROS with better growth and yield.	Zhu et al. (2015)
Broccoli	*Ascia monuste*	Tolerant character was associated with methyl jasmonate, and PR1 gene expression.	Venegas-Molina et al. (2020)
Cucumber	*Acalymma vitattum*	Tolerant plants showed higher germination rates, higher number of flowers and biomass, and higher JA and SA.	Rivera-Vega et al. (2022)
Common bean	*M. persicae*	PeBC1 elicitor protein triggered the biosynthesis of JA and SA by increasing the associated genes which resulted in lethality to aphids.	Basit et al. (2019)
Eggplant	*M. persicae*	Least susceptible plants showed lower number of adult aphids, lowest reduction in height and dry weight with greater plant resistance indices.	Raeyat et al. (2021)

negative effect on insects by disruption of their growth and development, ultimately leading to reduction in their number (Zhu et al. 2015).

Volatile organic compounds (VOCs) are plant-derived chemicals having deterrent effect on plant herbivores (Zhou and Jander 2022). They are the intermediate products of different metabolic pathways, which have diverse roles in plant defense against both biotic and abiotic stresses. VOCs play roles in ROS sequestration by membrane stabilization, inhibiting pathogen growth, attraction of parasitoids, and induction of systemic resistance (Brilli et al. 2019; Russo et al. 2022; MacDougall et al. 2022). A large number of vegetable crops including onion, potato, tomato, carrot, and other vegetables have been reported to contain several VOCs (Wang et al. 2019; Tiwari et al. 2020). A recent study showed that tomato and pepper increased the volatile synthesis after whitefly attack leading to disturbance of insect population (Ghosh et al. 2022).

A diverse range of proteins, transcripts, and gene expressions contribute to plant tolerance (War et al. 2012). Plant resistance proteins have been reported in vegetable crops including tomato, potato, pepper, and cucumber (Abuyusuf et al. 2022; Li et al. 2019; Leybourne and Aradottir 2022; Wani et al. 2022), which showed tolerance to insects such as *Manduca sexta*, *Spodoptera littoralis,* and *Macrosiphum euphorbiae*. Some proteins have functions like protease inhibitors, catalase, chitinase, and peroxidase, which suppress the growth and establishment of insects (Wang et al. 2018). Many of them are also related to the signaling cascade to activate systemic tolerance by activating the JA and SA signaling. Gene expression due to the insect attack is one of the most specific molecular defense mechanisms in plants including vegetables. Tomato overexpressed with Cry1A genes enabled it to reduce the damage against a diverse range of insects (Murata et al. 2021). Genes that encode the proteinase inhibitor, phytolectin, amylase inhibitor, and chitinase have been reported in plants, which contributed to the natural defense against insects and microbes (Wang et al. 2018, 2021a).

Crop improvement focusing on the tolerance mechanism has been used as a part of integrated pest control. Identification of metabolites, hormonal regulation, and plant volatile compounds for general and specific targets have great challenges to include them in pest control strategy. Due to their no effect on selection and reduction in the number of insect pests, tolerance can be a sustainable approach that can help to promote the effects of beneficial arthropods in agricultural practices.

9.2.2 Pseudo Resistance

Plants possess several traits that make them less vulnerable to insect attack. These mechanisms can occur at both spatial and temporal levels. In terms of spatial escape, plants may not be detectable by insects due to the plant alterations/changes in morphological features, whereas the temporal escape occurs due to lack of the synchronization of most susceptible stage(s) of plants with the peak pest activity period (Stenberg and Muola 2017). As a part of their indirect defense against insect pests, plants use spatial and temporal escape to sustain their growth and development. While host escape occurs at the individual level, host evasion happens at the population level. Plants pass through the most susceptible stage quickly or at a time when insects are less numerous. Plants may also alter their growth patterns to be asynchronous with the number of insect pests, further reducing their susceptibility to insect attacks.

Under insect pressure, plants modify their morphology, physiology, and biochemical synthesis, resulting in the activation of their defense systems. Escape can be attributed to morphological, physiological, and biochemical alterations in response to plant–insect interactions (Wani et al. 2022). For instance, plants may alter their leaf, flower, and vegetative growth to keep insects away. Changes in plant height and stature can also be considered escape traits. Mimicry can also be effective, whereby a plant may have leaves that are similar in shape and morphology to those of another species but differ in their chemical composition, helping the plant escape insect attacks (Stenberg and Muola 2017). Plants may also exhibit escape traits that increase their tolerance to insects. For example, some plants camouflage themselves to avoid herbivores by altering the appearance of their leaves. They may also change leaf traits such as trichome density, trichome number, and leaf thickness to prevent insect attack (Dominguez et al. 2017).

Associational resistance, also known as escape, can enable plants to remain undetected by insects and direct them toward neighboring plants. Additionally, some plants produce volatile organic compounds (VOCs), which serve as long-distance signaling molecules and act as insect repellents while also triggering plant immunity against insects (Conboy et al. 2020; Piesik et al. 2022; Nalam et al. 2019). Tomato plants, for instance, produce methyl salicylate (MeSA), which serves as both a repellent and an activator of plant defense mechanism when the plant is attacked by insects. VOCs have also been reported in other plant species such as potato, broccoli, eggplant, cucumber, and onion, among others, and have shown their efficiency in helping plants escape insect attacks (Darshanee et al. 2017; Steglińska et al. 2022; Murakami et al. 2019; Ahmed et al. 2021; Jo et al. 2022; Zhang et al. 2022a; Wang et al. 2019).

9.3 Plant–Insect Interactions

Plants interact with their environment, and the interactions with insects are regulated by a complex interplay between the systems that enable plants to detect insect attacks and coordinate the downstream signaling processes that activate plant defenses. In response to herbivory, plant defenses typically decrease the fitness of insects by reducing their survival and reproduction by triggering a cascade of resistance mechanisms. Plant–insect interaction is a two-way process, i.e., plants initiate a specific defense response after insect injury to protect themselves with a variety of induced chemical defenses that can act either directly or indirectly on herbivores.

9.3.1 Constitutive and Induced Defenses

Plants defend insects through constitutive and/or induced defenses. The constitutive defenses are the inherent defenses that are present regardless of herbivory/attack, and these defenses include the structures and compounds of primary and secondary metabolism (Bar and Shtein 2019). The constitutive defenses can work independently of one another, or they can act synergistically. For instance, a structural and chemical defense system is formed by glandular trichomes and their secretory canals (Glas et al. 2012; Wang et al. 2021b). Constitutive chemical defenses may be poisonous, repulsive, or antifeedant, and they may affect the growth of herbivores by altering their resistance, fecundity, and digestive capabilities.

By contrast, induced defenses are activated in response to herbivory or other biotic and abiotic stresses and consist of the structures, products, and compounds of the plant's secondary metabolism that are subsequently primed (Kersch-Becker et al. 2019). A sophisticated phytohormone system controls the layered set of responses known as induced defenses (Schuman and Baldwin 2016; Howe et al. 2018). The induced cellular mechanisms caused by interacting herbivores change the plant's metabolome, and insect herbivory activates defense metabolites to prevent pest invasion and the emergence of plant resistance (Maag et al. 2015; Jiang et al.

2019). Plants that have been damaged perceive a range of endogenous chemicals as danger signals, which are referred to as damage-associated molecular patterns (DAMPs), which also include secondary metabolites. Green-leaf volatiles are also DAMPs, and they respond to herbivory by activating both short-term and long-term defense mechanisms (Quintana-Rodriguez et al. 2018; Santamaria et al. 2018). Both constitutive and induced defenses can be direct and indirect, the direct ones include the buildup of toxins or the thickening of cell walls, which have an impact on the growth and performance of herbivore (Lin et al. 2020; Yang et al. 2020). Indirect defenses influence the behavior of herbivores, predators, or parasitoids by attracting them to the infested plant and/or to neighboring plants by sending out alarm signals (Coppola et al. 2017). Induced metabolites/volatiles of vegetable crops and their defense function against herbivores are presented in Table 9.2.

9.3.2 Herbivore-Induced Metabolites

The induced defenses are often controlled by metabolic pathways such as jasmonic acid (JA), salicylic acid (SA), and ethylene (ET)-mediated signaling, which may have a direct or indirect impact on the host choice by insect (Bonaventure 2012). For instance, spider mite (*Tetranychus urticae*) infestation induces jasmonic acid (JA) and salicylic acid (SA) signaling as well as the synthesis of terpenoids and flavonoids in pepper (Zhang et al. 2020). In cassava, the phenylpropanoid super pathway encodes the production of monolignol, flavonoid, and lignan, which reduce the performance of whiteflies (Perez-Fons et al. 2019). Multiple metabolic pathways and biomarkers like galactaric acid, hydroxycinnamic acids, and quinic acid promote resistance to whitefly-mediated tomato curly stunt virus (ToCSV) (Rossouw et al. 2019).

Plant responses result in morphological or metabolic changes that influence indirect interactions with other community members (Han et al. 2020). In cucumber, spider mite infestation leads to changes in terpene, green-leaf volatiles, and cucurbitacin biosynthesis that are potentially involved in the regulation of induced direct and indirect defenses (He et al. 2020). Secondary metabolites have been studied extensively in the context of plant–insect interactions and may have an impact on insect establishment. An initial herbivore attack can strengthen the plant's defense profile (Poelman and Dicke 2018). For example, *Phthorimaea absoluta* (*Tuta absoluta*) infestation induces various secondary metabolites and volatile organic compounds (VOCs), which enhance the resistance of tomato plants (Chen et al. 2021b; Roumani et al. 2022). Signaling genes from PR1b1, NPR1, NPR3, MAPKs, and ANP1 families associated with salicylic acid in eggplant mediate plant immunity against *T. absoluta* (Chen et al. 2021a).

The polyphenol oxidase (PPO) and protease inhibitors (PIs) in plant tissues may also be impacted by *T. absoluta* attack, which would hinder larval development (D'Esposito et al. 2021). Similarly, *Spodoptera litura* herbivory in pepper-induced toxic phenolic compounds like vanillic acid and syringic acid. The metabolite profiles of pepper containing capsianosides are associated with western flower thrips

Table 9.2 Herbivore-induced plant metabolites/volatiles and their defense function in vegetable crops

Crop	Insect interaction	Induced metabolite/ volatile	Defense function	Reference
Tomato	*Phthorimaea absoluta* (*Tuta absoluta*)	Accumulation of phenolamides, spermine, dihydrocinnamic acid derivatives and caffeoylputrescine	Antibiosis	Roumani et al. (2022)
	T. absoluta	Aldehydes, alcohols, sugars, aromatics, amines, terpenoids, ketones, phenolics and olefins	Antibiosis	Chen et al. (2021b)
	T. absoluta	Monoterpenes	Attract predator *Nesidiocoris tenuis*	Ayelo et al. (2021)
	T. absoluta and *Bemisia tabaci*	Chorismate-derived compounds, C_{18}-fatty acids and cyclic sesquiterpenes	Attract natural enemies	Silva et al. (2017)
	T. absoluta and *Tetranychus urticae*	(*Z*)-3-hexenyl propanoate [(*Z*)-3-HP]	Host plant resistance	Pérez-Hedo et al. (2021)
	B. tabaci	Increased levels of galactaric acid, hydroxycinnamic acids and quinic acid	Antibiosis	Rossouw et al. (2019)
	B. tabaci	Flavonoids	Reduce the ability of *Bemisia tabaci* to land, settle, probe, and phloem-feeding	Yao et al. (2019)
	B. tabaci	7-Epizingiberene	Repellent	Rosen et al. (2015)
	Trialeurodes vaporariorum	Methyl salicylate (MeSA)	Intracellular defense signaling	Conboy et al. (2020)
	Macrosiphum euphorbiae	Isoprenoids	Attract the parasitoid *Aphidius ervi*	Coppola et al. (2019)
	Frankliniella occidentalis	α-Tomatine and phenolic compound	Defensive compounds	Bac-Molenaar et al. (2019)
	Thrips, whiteflies, aphids and	Acylsugars and myricetin	Inhibit oviposition and antibiosis	Leckie et al. (2016)

(continued)

Table 9.2 (continued)

Crop	Insect interaction	Induced metabolite/ volatile	Defense function	Reference
	Spodoptera exigua			Vosman et al. (2018)
	S. litura	Chlorogenic acid and catechin	Redistribution of primary and secondary metabolites in local and systemic leaves	Kundu et al. (2018)
	S. exigua	Physostigmine, 4-oxododecanedioic acid, and azelaic acid	Antibiosis	Rivero et al. (2021)
	S. litura	(*Z*)-3-hexenol and glycoside	Feeding inhibition	Sugimoto et al. (2014)
Potato	*P. operculella*	Jasmonic acid (JA) and abscisic acid (ABA)	Activation of early defense response	Mao et al. (2022)
	P. operculella	α-Chaconine and glycoalkaloids	Larval feeding inhibition	Wang et al. (2020)
	Tecia solanivora *S. exigua* *S. frugiperda*	Chlorogenic acid, α-solanine and α-chaconine	Antibiosis	Kumar et al. (2016)
	Macrosiphum euphorbiae	Cis-jasmone (CJ)	Affect settling and performance	Sobhy et al. (2017) Sobhy et al. (2020)
	Myzus persicae	β-Bisabolene, (*E*)-β-farnesene, trans-α-bergamotene,	Attract the parasitoid, *Diaeretiella rapae*	Ali et al. (2022a)
Eggplant	*T. absoluta*	Signaling genes associated with salicylic acid	Plant immunity	Chen et al. (2021a)
	F. occidentalis	Quinic acid	Host plant resistance	Liu et al. (2022)
Pepper	*T. urticae*	Terpenoids and flavonoids	Jasmonic acid (JA) and salicylic acid (SA) signaling	Zhang et al. (2020)
	S. litura	Vanillic acid and syringic acid	Induced resistance	Movva and Pathipati (2017)
	F. occidentalis	Capsianosides	Host plant resistance	Macel et al. (2019)

(continued)

Table 9.2 (continued)

Crop	Insect interaction	Induced metabolite/ volatile	Defense function	Reference
Pepper and cabbage	*M. persicae*	α-Pinene, decanal phthalic acid, and isophorone	Attracts the endoparasitoid *Aphelinus varipes*	Ali et al. (2022b)
Cucumber	*T. urticae*	Terpene, green-leaf volatiles and cucurbitacin	Induced direct and indirect defenses	He et al. (2020)
Common bean	*Liriomyza huidobrensis*	Methyl salicylate and (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT)	Attracts its parasite *Opius* sp.	Yang et al. (2021)

(*Frankliniella occidentalis*) resistance (Movva and Pathipati 2017; Macel et al. 2019). Bac-Molenaar et al. (2019) identified α-tomatine and a phenolic compound as potential defensive compounds against western flower thrips in tomato. The higher amounts of quinic acid in thrips-resistant eggplant improved the resistance of susceptible eggplant to western flower thrips on external application (Liu et al. 2022).

Following herbivory, induced defenses cause localized and systemic elevations of toxic secondary compounds above constitutive levels, which affect herbivore preference, performance, and feeding activity (Perkins et al. 2013; Zalucki et al. 2017) (Fig. 9.1). *S. litura* herbivory in tomato redistributes primary and secondary metabolites in local and systemic leaves, which substantially slow down larval growth (Kundu et al. 2018). Tomato plants exhibit higher levels of resistance following herbivore attack, as evidenced by the decrease in larval development of insects that feed on damaged leaves (Escobar-Bravo et al. 2017; Hamza et al. 2018). Metabolites can also affect the insect behavior and interrupt their host choice; for instance, tomato flavonoids reduce the ability of *Bemisia tabaci* to land, settle, probe, and phloem-feeding efficiency and prevent the spread of the tomato yellow leaf curl virus (TYLCV) (Yao et al. 2019). Plants mediate interactions between aboveground and belowground herbivores via plant secondary metabolites. Aboveground herbivory by *Phthorimaea operculella* in potato increased α-chaconine and glycoalkaloids in tubers and negatively affected larvae feeding on tubers (Wang et al. 2020). On the other hand, localized tuber damage by Guatemalan tuber moth (*Tecia solanivora*) induces aboveground resistance against *Spodoptera exigua* and *S. frugiperda* by increased foliar abundance of chlorogenic acid, α-solanine, and α-chaconine (Kumar et al. 2016).

The acyl sugars, sesquiterpenes, and methyl ketones are the three main allelochemicals present in tomato. Acylglycosis and acylsucrose are important acylsugars in the leaf trichomes of wild tomato species (Da Silva et al. 2016). Acylsugars and myricetin from *Solanum pennellii* and *S. galapagense* demonstrate resistance against thrips, whiteflies, aphids, and *S. exigua* (Leckie et al. 2016; Vosman et al. 2018). Similarly, *S. pennellii* and *S. habrochaites* lines predominated by acyl sugars are linked to whitefly resistance (Marchant et al. 2020; Kortbeek et al.

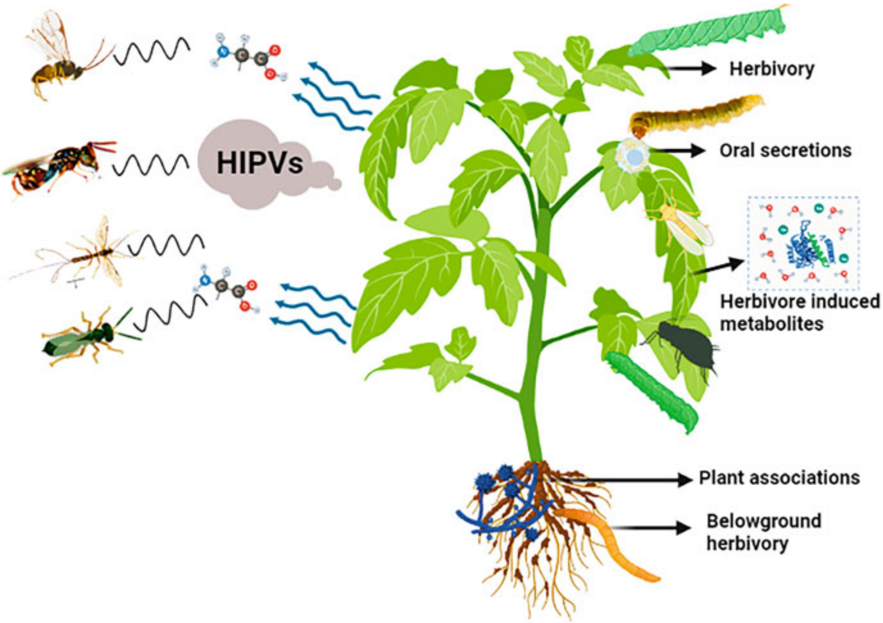

Fig. 9.1 Plant–insect interactions in vegetable plants involving defense elicitors such as herbivory, oral secretions, plant associations, and belowground herbivory, as well as induced defense responses of plants against herbivores that include herbivore-induced metabolites and herbivore-induced plant volatiles (HIPVs) attracting natural enemies

2021). Tolerant tomato genotypes display high levels of acyl sugars and other metabolites after *T. absoluta* infestation (De Falco et al. 2019).

Plants must be able to recognize the difference between physical injury and insect feeding in order to launch an insect-specific defense. The saliva of chewing and phloem-feeding insects contains chemical compounds and particular proteins that have been linked to herbivore manipulation of plant defenses (Villarroel et al. 2016). Various elicitors in insect saliv/oviposition fluid modulate plant's defense. These elicitors are recognized by plants and play a crucial role in downstream signaling cascades linked to defense (Bonaventure 2018) (Fig. 9.1). Based on their molecular makeup and structure, elicitors are categorized into six groups: enzymes, fatty acid amino acid conjugates (FACs), fatty acids, peptides, esters, and benzyl cyanide (Zunjarrao et al. 2020). In oral secretions, enzymes, fatty acids, and peptides are produced; however, during egg laying, esters and benzyl cyanide are released in oviposition fluids (Aljbory and Chen 2018; Bonaventure 2018).The microbes in the oral secretions of *P. operculella* regulate jasmonic acid (JA) and abscisic acid (ABA) during herbivory, which activate early defense response in potato (Mao et al. 2022).

Plant associations with other organisms help them to withstand various stresses and have an impact on the expression of defenses. For instance, tomato plants primed with *Trichoderma harzianum* and arbuscular mycorrhizal fungi (AMF) enhance the defense against aphids and *S. exigua* by increased accumulation of isoprenoids, physostigmine, 4-oxododecanedioic acid, and azelaic acid (Coppola et al. 2019; Rivero et al. 2021). In some cases, insect herbivory can increase plant susceptibility and make the host more alluring to the pest. For example, Cucurbit chlorotic yellows virus (CCYV) infection in cucumber attracts whiteflies by reducing protective flavonoids and terpenoids (Zhang et al. 2022b). Similarly, *B. tabaci* infestation decreases the production of repellent flavonoids and monoterpenes (-α-phellandrene and α-terpinene), which enhanced the oviposition of whiteflies on tomato (Su et al. 2018).

9.3.3 Herbivore-Induced Plant Volatiles (HIPVs)

Upon herbivore attack, plants emit blends of volatile organic compounds (VOCs) that differ from those that are constitutively emitted. Herbivore-induced plant volatiles (HIPVs) are a class of small-molecule volatile substances that are produced by plants (Pérez-Hedo et al. 2021). These include terpenoids, volatile fatty acid derivatives, phenylpropanoids, volatile amino acid derivatives, glucosinolates, benzoxazinoids, and aromatic compounds (Bouwmeester et al. 2019). HIPVs form an indirect defense strategy as they are used as cues by natural enemies of plant-feeding insects to locate their prey or hosts, and also they are used to activate pre-infestation defense mechanisms by adjacent healthy plants (Pérez-Hedo et al. 2017; Silva et al. 2017) (Fig. 9.1). HIPVs may differ quantitatively and qualitatively upon damage by different species, for example, tomato volatiles were dominated by chorismate-derived compounds and C_{18}-fatty acids when infested with *T. absoluta*, whereas *B. tabaci* herbivory induced cyclic sesquiterpenes; these volatiles attract species-specific natural enemies (Silva et al. 2017). Plant volatiles are useful indicators of ongoing herbivore attack because they are released during insect feeding. Such signals are detected by plants, which are then used to intensify their innate or induced defense mechanisms. For instance, exogenously applied green leaf volatile ((*Z*)-3-hexenol) can prime the production of defense signaling molecule jasmonic acid in tomato (Su et al. 2020). Utilization of such HIPVs might be a more environmentally sound choice. In order to effectively manage begomovirus diseases, volatile terpenes, such as 7-epizingiberene from *S. habrochaites*, can be used as repellents against *B. tabaci* (Rosen et al. 2015).

Some green leaf volatiles can be transformed into toxic compounds or have defensive qualities of their own when perceived by plants. For instance, in tomato uptake of (*Z*)-3-hexenol, conversion of it into a glycoside inhibits the ability of *S. litura* to feed on recipient plants (Sugimoto et al. 2014). Similarly, tomato plants artificially induced with (*Z*)-3-hexenyl propanoate [(*Z*)-3-HP] were less susceptible to the attack of *T. absoluta* and *T. urticae* (Pérez-Hedo et al. 2021). Application of elicitor, methyl salicylate (MeSA) triggers intracellular defense signaling on un-infested tomato plants, which reduced the greenhouse whitefly (*Trialeurodes vaporariorum*) population (Conboy et al. 2020).

Herbivore-damaged plants emit volatile organic compounds (VOCs) that can alert neighbors and boost their resistance. VOCs released by herbivore-induced potato plants boosted resistance in receiver plants against *S. exigua* (Vázquez-González et al. 2023). Sweet potato weevil (*Cylas formicarius*) feeding induced volatiles, (*Z*)-3-hexenyl acetate (z3HAC) and allo-ocimene, which prime neighboring plants to defend themselves against sweet potato weevil (Xiao et al. 2023). Similarly, potato plants primed with defense activator cis-jasmone (CJ) significantly result in elevated emission of aphid defense-related volatiles, which negatively affect aphid (*Macrosiphum euphorbiae*) settling and performance (Sobhy et al. 2017, 2020). HIPVs not only draw in natural enemies but also influence the movement of conspecific herbivores. For example, tomato and eggplant volatiles ((*Z*)-3-hexen-1-ol and terpenoids) mediate the preference of greenhouse whitefly to its hosts (Darshanee et al. 2017). Similarly, Zhang et al. (2019b) showed that HIPVs from tomato plants infested with whiteflies can make nearby plants more susceptible by inhibiting JA-dependent defenses.

9.3.4 Tri-trophic Interactions

The increased release of volatiles from a plant following an insect attack is thought to be an induced indirect defense. Tri-trophic interactions are reliant on communicating the location of herbivores on infested plants to parasitoids and predators of the herbivores (Turlings and Erb 2018) (Fig. 9.1). Understanding the evolution of plant-natural enemy relationships requires knowledge of these mechanisms (Stahl et al. 2018). HIPVs can induce plants to repel herbivores or draw pest's natural enemies (Ayelo et al. 2021; Naselli et al. 2016; Pérez-Hedo et al. 2015a). For instance, aphid (*Myzus persicae*) induces α-pinene, decanal phthalic acid, and isophorone in pepper and cabbage, which attract its endoparasitoid *Aphelinus varipes* (Ali et al. 2022b). Similarly, aphid (*M. euphorbiae*) infestation on tomato plants treated with *Trichoderma harzianum* induced aphid mortality and attracted the aphid parasitoid *Aphidius ervi* (Coppola et al. 2019). *T. absoluta*-induced monoterpenes attract its predator *Nesidiocoris tenuis* in tomato (Ayelo et al. 2021). Pea leafminer (*Liriomyza huidobrensis*) induced methyl salicylate, and (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) in bean leaf attracts its parasite *Opius* sp. (Yang et al. 2021). In response to herbivory, plants synthesize and release variable mixtures of herbivore-induced plant volatiles (HIPVs) as indirect defense traits that attract enemies of the herbivores. For example, HIPVs emitted by insect-infested cucumber and potato were used as cues by the predatory ant *Formica pratensis* to locate its prey (Schettino et al. 2017). Volatiles from wild potato (*Solanum stoloniferum*) accessions significantly attracted the parasitoid, *Diaeretiella rapae* against *M. persicae* (Ali et al. 2022a).

Apart from herbivores, the predator activity on host plants can also prime defense against insects. For instance, green lacewing larvae (*Chrysoperla carnea*) activity in tomato induces myrcene and α-terpinene, which aid in plant defense (Errard et al. 2016). Zoophytophagous insect, *N. tenuis* feeding punctures on tomato stimulate the jasmonic and abscisic acid (ABA) pathways, making the plants less attractive to *T. absoluta* and *B. tabaci* but more attractive to the whitefly parasitoid *Encarsia formosa* (Pérez-Hedo et al. 2015b). In tomato plants, defenses are primed both locally and systemically in response to attacks from predators (*Macrolophus pygmaeus* and *tenuis*), (*Z*)-3-hexenyl propanoate induced by *N. tenuis* damage can indirectly prime the defenses of healthy plants (Pappas et al. 2015; Pérez-Hedo et al. 2018, 2021).

9.4 Transgenics and Genome Editing

Insect pests are the primary biotic stressors that cause significant crop losses worldwide by directly feeding on and transferring plant diseases (Douglas 2018). Biotechnological interventions in insect pest management to protect crop output have received increased focus, ranging from insect resistance breeding through transgenic introgression of novel genes to the genome editing (Doudna and Charpentier 2014). Some biotechnological approaches include gene transformation, genome editing, RNA interference, marker-assisted selection, anther culture, embryo culture, protoplast fusion, somaclonal variations etc. (Talakayala et al. 2020). Introducing a specific DNA segment or gene into crop plants to provide resistance against insect pests is known as gene transformation or genetic engineering of crops for insect resistance (Gatehouse 2013). The DNA segment that is inserted normally encodes an insecticidal protein. Plants obtain resistance to specific insect pests by expressing an insecticidal protein found in the inserted DNA segment (Birkett and Pickett 2014).

9.4.1 Cry Genes

Insecticidal activity in insect-resistant Bacillus thuringiensis (Bt) crops is expressed by the genes coding for parasporal crystal protoxins (Panwar et al. 2018). Insecticidal crystal protoxins produced by transgenic plants have significantly impacted the successful evolution of insect resistance (Paul and Das 2021). The crystal involves a protoxin protein, which gets solubilized in the larval midgut due to alkaline pH to produce more toxic protein that leads to gut paralysis, cessation of feeding and mortality within 2/3 days (Rajadurai et al. 2018). Soliman et al. (2021) reported that tomato leaf miner, *T. absoluta*, was susceptible to a synthetic Cry1Ab gene inserted into tomato, with 100% insect mortality in T_0 generation within 4–5 days. Similarly, Cry1Aa gene expression in sweet potatoes conferred resistance to *Spodoptera litura* (Zhong et al. 2019).

9.4.2 Lectins

Plant lectins are proteins that bind to carbohydrates and have an increased affinity for certain sugars found in glycoproteins and glycolipids in the cell membrane. Lepidoptera, Coleoptera, and Hemiptera insects of various orders have been demonstrated to perform worse when exposed to lectins in fake diets and their production in transgenic plants (Camaroti et al. 2018). Fitches et al. (2004) found increased toxicity of GNA-spider-venom toxin I (SFI1) fusion protein to larvae of the tomato moth (*L. oleracea*) and the peach potato aphid (*M. persicae*).

9.4.3 Fusion Proteins

Two recent techniques to address potential limits in conventional transgenic insect pest control are the stacking or pyramiding of numerous transgenes in the same transgenic plant and the use of hybrid toxins against insect pests (Fig. 9.2) (Boddupally et al. 2018; Talakayala et al. 2020). The feeding and growth of the tomato moth were found to be inhibited by a GNA-neuropeptide-allatostatin fusion protein (*L. oleracea*) (Fitches et al. 2004). A fusion protein from the South Indian red scorpion (*Mesobuthus tamulus*) that contains a GNA-lepidopteran-specific toxin (ButalT) was found to be more harmful to tomato moth larvae (Trung et al. 2006).

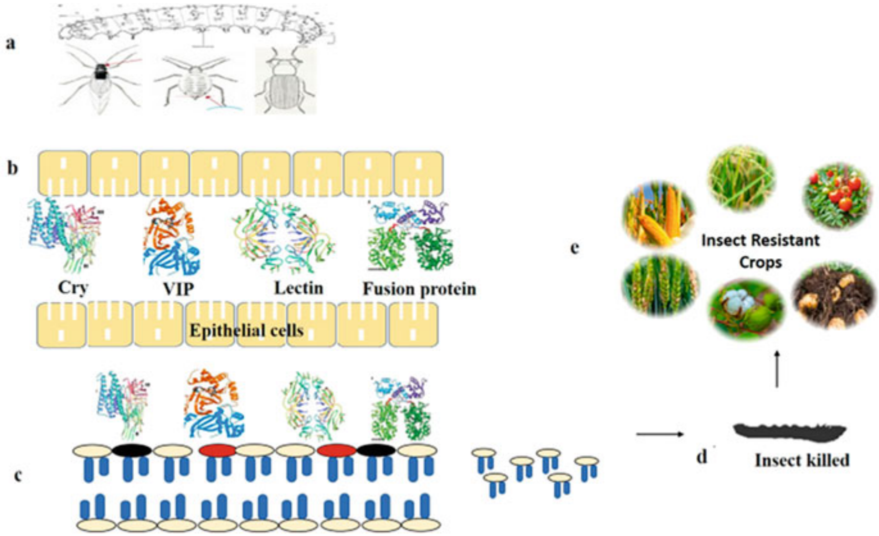

Fig. 9.2 Schematic representation of the mode of action of insecticidal proteins like Cry proteins, VIP proteins, lectins, and other fusion proteins in the gut of lepidopterans, aphids, and other insects. (**a**) Different insects that feeds on major crops (**b**) mode of action of different proteins in the gut epithelial cells (**c**) cell lysis by ICP on epithelial cells (**d**) death of the insect (**e**) insect-resistant crops (Source: Talakayala et al. 2020)

9.4.4 RNAi for Plant Resistance to Insect

RNAi, referred to as co-concealment, post-transcriptional gene silencing (PTGS), and suppressing, is a technique for reducing gene expression by reducing particular regions (Kamthan et al. 2015). Planning the (distribution) strategy and deciding whether a transformative or non-transformative RNAi-plant protection technique might be preferable requires knowledge about the target insect's eating patterns. For chewing insects, dsRNA can be supplied through a foliar spray, such as a typical plant protection chemical, and picked up straight from leaves. Products based on RNAi that can be sprayed are currently being developed and will soon hit the market. However, the spraying strategy would not affect the piercing-sucking bugs that consumed phloem sap, insects that fed on the root system, or stem borer pests that consumed plant stems (Fig. 9.3). The delivery of dsRNA through the phloem sap is necessary for sap-sucking insects, and this can be done by irrigation water, trunk injection for perennial trees, in planta dsRNA creation (transgenic or transplastomic plants), or recombinant plant viruses (Joga et al. 2016). In order to develop insect resistance in tobacco and tomatoes, the chitinase gene (HaCHI) in *H. armigera* was silenced using HI-RNAi. This resulted in the downregulation of the target gene

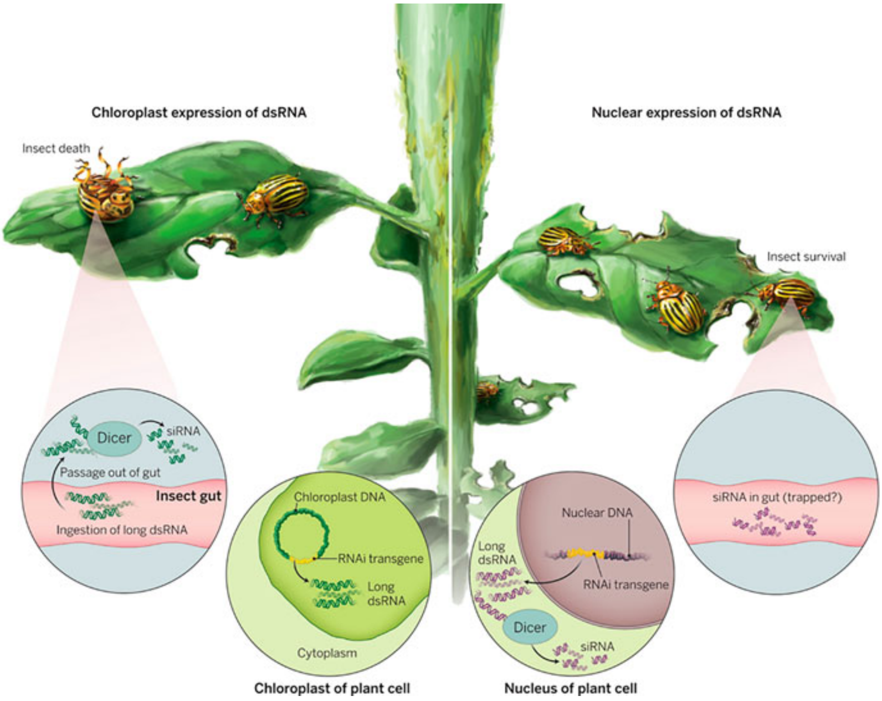

Fig. 9.3 The transgenic potato plants producing dsRNA in the plant cell cytoplasm do not kill potato beetles, whereas the plants bred to express insect-specific long dsRNA in chloroplasts do. (Source: Zhang et al. 2015)

transcripts, which led to mortality and developmental deformities at the larval, pupal, and adult stages (Mamta and Rajam 2017). The tobacco whitefly, *Bemisia tabaci*, has recently been identified as having no impact on tomato plants using a dsRNA that targeted a gene expressing a phenolic glucoside malonyltransferase, detoxifying phenolic glycosides (Xia et al. 2021). These results indicate that RNAi is one of the most efficient ways to produce insect-resistant plants. Although the technology is still in its infancy, its current drawbacks make it less practical to manage insect pests (Scott et al. 2013).

9.4.5 Genome Editing

The process of "genome editing," also known as "gene editing," includes adding, removing, or replacing DNA bases in a target DNA sequence of the genome in order to successfully change a gene's function through the cell's inherent mechanisms (Bortesi and Fischer 2015; Asokan et al. 2022; Ashok et al. 2023). The most recent and technically straightforward tool for creating insect pest resistant cultivars is CRISPR/Cas9 (Fig. 9.4). It has been successfully employed by eliminating the gene or causing missense mutations in the target gene to stop the accumulation of specific gene products in various crops (Gao 2021). In the wild tomato *S. pimpinellifolium*, CRISPR/Cas9 was utilized to target six loci related to tomato yield and efficiency (Zsögön et al. 2018). *Plutella xylostella* had increased levels of resistance to cry1Ac protoxin following the CRISPR/Cas9 tool's knockout of two ABC transporters, PxABCC2 and PxABCC3 (Guo et al. 2019). To identify host plants, the majority of polyphagous insects rely on the plant's own volatiles, gustatory cues, outward appearance, oviposition sites, and interactions (Larsson et al. 2004). Genome editing can change plant volatile mixtures, which could be an alternative pest management strategy in future.

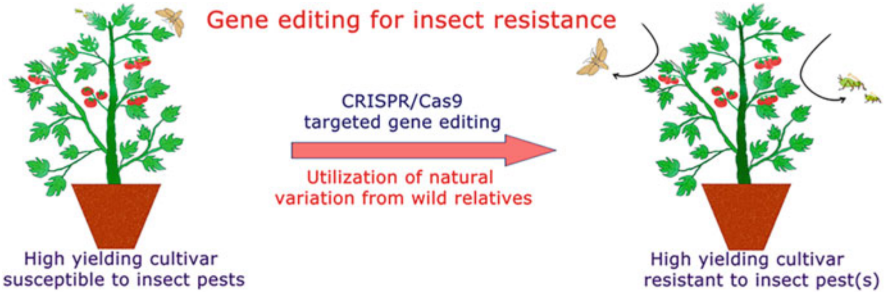

Fig. 9.4 Gene editing for insect resistance: utilization of natural variation for improvement of susceptible cultivars for resistance against insect pest(s) through CRISPR. (Source: Tyagi et al. 2020)

9.5 Critical Gaps, Challenges, and Priorities

The dynamic interplay of molecular and physiological responses that probably develop between plants and insects throughout time is not well captured by many current techniques. There are now more options for pest control, thanks to the modern biotechnological techniques, which offer excellent chances to build a long-lasting, multi-mechanistic resistance to insect pests. Although current technology is used in crops to help them become resistant to a range of insect pests, some agricultural pests regularly acquire a resistance to insecticidal toxins, which has a disastrous effect on crop yield. The research teams should focus on the challenges to understanding the plant–insect interactions.

Plant–insect interaction research has historically taken a stance, approaching issues from either an insect- or a plant-centric standpoint. Particularly with regard to molecular reactions, both partners are rarely taken into account at once (e.g., tomato against hornworm, Havko et al. 2020). Most studies frame concerns about defensive systems from the viewpoint of plants, with insects being portrayed as having countermeasures or adaptations to their hosts (Heidel-Fischer and Vogel 2015; Wouters et al. 2016; War et al. 2018). As a result, our understanding of host plant defenses and the molecular mechanisms behind insect virulence is far from perfection (Bansal and Michel 2015; Yates-Stewart et al. 2020).

Although numerous genes or pathways are likely involved in HPR in reality, quantitative approaches are required, much as those that are gaining popularity for creating pathogen resistance (Pilet-Nayel et al. 2017). The emergence of various biotechnology-based technologies, including marker-assisted selection, somaclonal variation, anther culture, embryo culture, genetic transformation, and protoplast fusion, may hasten the development of insect-resistant crops in the present and in the future. Future HPR breeding efforts will depend mainly on the ability to reliably identify fresh sources of resistance and conduct large-scale screening for that resistance. Resistance cannot be introduced into the pipeline for cultivar development if it cannot be discovered or screened for.

9.5.1 Phenomics

The measurement of groups of phenotypes, frequently physical or biochemical properties, is known as phenomics. Phenomics is rapidly being included into commercial HPR breeding projects because of its enormous potential to reduce the high cost of field phenotyping of plant resistance responses. One of the main benefits of phenomics is that the classification of resistance reactions is often noninvasive and standardized across fields, reducing human error (Mahlein et al. 2019). However, applicability across crops and diseases/pests remains a challenge (Varshney et al. 2021).

9.5.2 Genome Editing for Insect Resistance

This fascinating tool has emerged as an imperative contribution that allows modifications in the genome by adding/editing/deleting particular stretch of DNA sequences, thereby providing opportunities for utility in plants, animals, and humans. In the present scenario of constricted agricultural fields and increased load of insect pests on crop plants, genome editing will serve as a potential tool to combat insect pests. The latest revolutionary technology for genome editing is based on the RNA-guided engineered nucleases called CRISPR (clustered regularly interspaced short palindromic repeats)/Cas9, which hold great promise because of their specificity, simplicity, efficiency, and versatility by addressing key challenges posed by other genome editing tools (Tyagi et al. 2020). Genome editing in insect pest management for diamondback moth in cabbage for body segmentation trait with target gene (*abdominal-A* gene knockout) was done (Sun et al. 2017). Despite success in economically important crops to combat pathogens, their use in insect management has not been exploited to the fullest.

Though editing insects is an intriguing option, it requires caution in the selection of traits that need to be environmentally friendly so that the food chain is not affected. The major setback has been the lack of availability of target genes in contrast to other stresses. Therefore, emphasis needs to be given by scientists globally to the identification of resistance sources that can form a platform for insect management.

9.5.3 Volatilomics (Volatile Organic Compounds-VOCs)

Comparing the volatilomics of plants helps us to find out how they respond to different kinds of herbivory. The plants are also known to communicate with each other and share information among them. Volatilomics deals with the studies on how biological systems emit volatile organic compounds. To date, VOCs are applied in agriculture solely for the “push-pull strategy,” where the crop of interest is both intercropped with plant species that emit VOCs able to repel (“push”) herbivores, and surrounded with plants emitting VOCs that simultaneously attract (“pull”) herbivores away from the field (Stenberg et al. 2015; Picket and Khan 2016). VOCs are not more intensively used in the host plant resistance as the experiments on the efficacy in the laboratory cannot be simulated and correlated with the open field for conferring the resistance. There is a need to generate baseline information on the inheritance of resistance to insect pests and the host plant–insect–environment interactions to understand the genetic control of different mechanisms of resistance for the development of suitable strategies to increase the levels and diversify the bases of resistance. There is a necessity to break the linkage between the parameters conferring resistance to the target insect pests and the low-yield trait that results in susceptibility and at the same time does not have a negative effect on the quality of the product (Sharma et al. 2017).

9.6 Conclusion

Vegetable crops are influenced by interactions with their environment and insects in terms of quality, nutrients, and yield. In natural ecosystems, it is very likely that numerous herbivores would attack plants sequentially or simultaneously. The primary chemical components of cells that directly or indirectly affect the interactions between plants and insects in vegetables are metabolites and volatiles. These chemical cues mediate tri-trophic interactions influencing plant resistance specificity and local adaptation to natural enemies. Therefore, it is necessary to investigate the metabolites and volatiles that are involved in the resistance mechanism in order to enhance the innate potential of vegetable crops to withstand insect damage. The sustainable management of vegetable plant health can be achieved by understanding constitutive and induced candidate metabolites and/or volatiles that function as phytohormones, signaling molecules, communication agents, elicitors, inhibitors, repellents, and antimicrobials involving numerous biosynthetic pathways.

It has been discovered that plant metabolites and HIPVs are an efficient and environmentally friendly way to manage insects with the potential to lead to the development of new pest management technologies. Vegetable plant associations with beneficial microbes influence metabolic changes that govern plant resistance and attract natural enemies of herbivores. Developing insect-resistant cultivars reduces the number of pests in a stable and cumulative manner while having no negative environmental effects. There has been a substantial advancement in the identification of insect resistant sources in different crops. Unfortunately, because of the entanglement of quantitative features at numerous loci, the production of insect-resistant crop varieties using standard approaches is slow and challenging to achieve. Developing a global database and incorporating it into molecular breeding programs for improved resistance and crop health could be aided by identifying the metabolites involved in plant–insect interactions in various vegetable systems and validating them with insects with different modes of feeding. Development of a long-lasting, multi-mechanistic resistance to insect pests has been possible because of new prospects presented by more advanced biotechnological techniques. This is a new and promising approach to future sustainable, environmentally friendly vegetable production.

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Role of Induced Resistance in Insect-Pest Management

10

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Abstract

Induced resistance is a process by which plants increase their resistance against pathogens and herbivores through the activation of their own defence mechanisms. This phenomenon has been extensively studied in the context of plant–pest interactions and has proven to be an effective strategy for pest management. Induced resistance can be triggered by various stimuli, including insect feeding, application of plant growth regulators or phytohormones, and exposure to certain chemicals. Once induced, plants can produce a range of defence compounds, such as alkaloids, terpenoids, and phenolics, which can deter or kill herbivores and pathogens. The use of induced resistance as a pest management strategy has several advantages over traditional chemical pesticides. Firstly, it is an environmentally friendly approach that does not harm non-target organisms or pollute the environment. Secondly, induced resistance is a long-term solution as it strengthens the plant's natural defence mechanisms, making it more resistant to future pest attacks. Finally, induced resistance can be integrated with other pest management strategies such as biological control, cultural control,

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and physical control. However, there are some challenges associated with the use of induced resistance. The effectiveness of induced resistance can vary depending on the plant species, the type of pest, and the environmental conditions. Additionally, the cost and time involved in inducing resistance can be higher than those of conventional pest control methods.

In conclusion, induced resistance is a promising strategy for pest management that can be used in combination with other pest control methods. Further research is needed to better understand the mechanisms underlying induced resistance and to optimize its application in agriculture.

Keywords

Biotic stress · Defence · Herbivore · Pest management · Plant secondary metabolites

10.1 Introduction

Plants and insects are highly diverse groups due to their ability to exploit a wide range of niches, from deserts to arctic zone. Since the Devonian Era, plants and insects have co-existed (Labandeira 2007). In the course of evolution, numerous interactions between insects and plants have evolved, including antagonistic interactions with insect herbivores and symbiotic interactions with insect carnivores (natural enemies) and pollinators (Dicke 2001). Both plants and insect herbivores have developed a variety of defence systems to combat one another throughout the course of these lengthy interactions and coevolution. Evidently, plants are able to survive and thrive despite significant tissue damage and occasionally full defoliation. Plants respond to insect herbivory through an intricate and dynamic defence system, which is mediated physiologically and biochemically. Host plant defence against herbivores is a complex array of structural, chemical, and physiological traits intended to perceive the attacking organisms and restrain them before they are able to cause extensive damage (Howe and Jander 2008; Sharma 2009; War et al. 2011a; Hanley et al. 2007; Karban 2011). To combat herbivore attack, plants react to them through a variety of morphological, biochemical, and molecular processes (War and Sharma 2014). Direct and indirect defence systems may both be present naturally or may be produced as a result of insect attack. Constitutive defence occurs in plants irrespective of the external stimuli such as insect damage and/or elicitor application, often providing a first line of defence. Induced defences are a second line of defence and are activated in plants in response to the external stimuli such as insect damage, pathogen infestation, abiotic stress, and/or elicitor application (Bown et al. 2002). Induced defence is key element of plant defensive strategy and has gained increased focus in insect control programmes (Sharma 2009; War et al. 2011b; Karban 2011). Induced defences make the plants phenotypically pliable and thus, less vulnerable to insect attack. However, the timing of induced resistance is crucial; the earlier the response, the greater the benefit to the plant and the lower the risk of subsequent herbivore and pathogen attack, in addition to improvement in overall plant fitness (Cipollini et al. 2004; War et al. 2011a). Application of induced resistance in pest management has the potential to reduce pesticide use on crops. By thorough understanding of the mechanism of induced resistance, we can forecast about its effect on the target species. Crop plants can be sprayed with elicitors of induced responses to strengthen their natural defences against herbivore harm. The genetically modified induced responses allow producing the defence chemicals naturally in plants after herbivory. Therefore, a thorough understanding of insect–plant interactions and defence mechanisms of plants will provide opportunities to develop new strategies, such as development of resistant crops or pest management strategies. This in turn will help reduce pesticide load on a crop and promote safer crop production. This chapter focuses on various aspects of induced direct and indirect defence strategies exhibited by plants against insect herbivores. Besides this, the role of phytohormones in defence mechanism, their cross talk, and plant defence priming, a chemical-free technique and its role in protecting the plants and boosting the sustainable agricultural production have been discussed.

10.2 Early Signalling Events at the Plant–Insect Interface

Successful implementation of an induced defence response requires quick and accurate plant response to herbivory. Early signalling events at the plant–insect interface, which occur well before changes in host plant gene expression and defence-related metabolism, are critical for the process of herbivore recognition (Maffei et al. 2007b). The presence of dislocated plant molecules and fragments of macromolecules from disrupted cells allows plants to recognize damage (Duran-Flores and Heil 2016). These so-called DAMPs (damage-associated molecular patterns) are sufficient in many systems to cause induced resistance following mechanical wounding. Plants also respond to molecules specifically from herbivores (herbivore-associated molecular patterns, or HAMPs) that the plants encounter during herbivore feeding or other activities (Acevedo et al. 2015). For example, legumes recognize inceptin, a catabolic plant product that is broken down by enzymes from a feeding caterpillar (Schmelz et al. 2006).

Plants most commonly respond to cues that are released by their own damaged tissues, as opposed to those of other individuals (Karban et al. 2006; Frost et al. 2007; Heil and Bueno 2007). These cues may travel from cell to cell, through the vascular system of the plant, or through the gaseous headspace that connects plant tissues. Volatile cues that are emitted during damage allow nearby individuals to eavesdrop on neighbours and adjust their defences (Karban et al. 2014).

10.3 Induced Responses to Herbivory

Damage from herbivores causes a variety of changes in plants, and some of these “induced responses” offer “induced resistance” to further animal exploitation. (Karban and Myers 1989). While induced resistance has been proven to be ubiquitous, "induced defences," which boost plant fitness under conditions of high risk of herbivory, have only been demonstrated infrequently. The connection between reductions in the performance of herbivores and benefits to plants has often been implicit (Hare 2011; Erb 2018) although a limited number of studies have found compelling evidence for this link, e.g. for direct defences (Agrawal 1998) and indirect defences that involve predators of herbivores (Schuman et al. 2012).

Herbivory causes large-scale changes in gene expression. For example, in hybrid poplar *Populus trichocarpa* × *deltoides*, it is estimated that 11% of the transcriptome is modified by forest tent caterpillar (Ralph et al. 2006). A common aspect of insect feeding (unlike pathogen attack) is some degree of mechanical damage, and many studies have focused on the regulatory signals generated as a result of artificial wounding. Plants may discriminate insect herbivory from experimental wounding by the different temporal and spatial patterns of natural and artificial injuries (Mithofer et al. 2005). Moreover, the type of feeding (e.g. chewing vs sucking) and blend of oral secretions (saliva or regurgitant of the attacker) may determine the specific response signature of the host plant. In particular, insect-derived elicitors produced during feeding have been shown to trigger direct and indirect defence responses, as detected by changes in gene and protein expression, and production of VOCs and other secondary metabolites (Felton 2008) (Fig. 10.1).

10.3.1 Direct Defences

There are many different herbivore resistance mechanisms in plants, which are typically divided into two main categories: tolerance and avoidance (Rosenthal and Kotanen 1994; Boege and Marquis 2005) that draw a distinction between a plant's tolerance of herbivore attack and its ability to avoid herbivory through

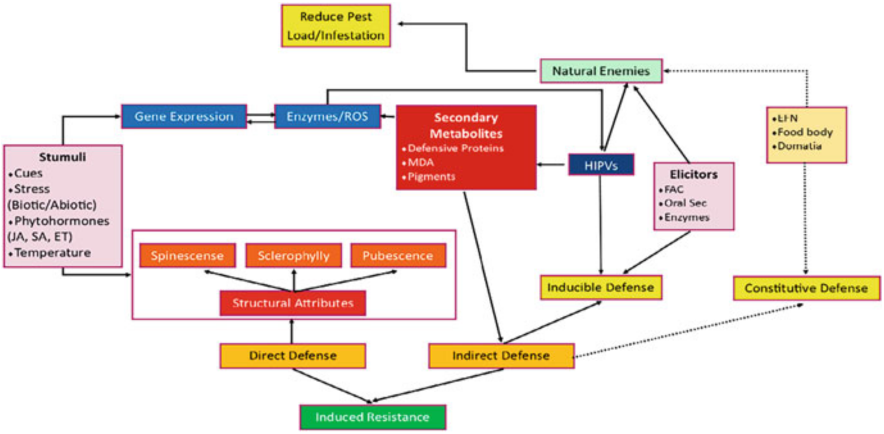

Fig. 10.1 Direct and indirect defence mechanism in induced resistance

defence. Some authors (Strauss and Agrawal 1999; Stowe et al. 2000) view "defence" as an umbrella term covering both avoidance and tolerance. Avoidance involves structural defence (leaves surrounded by thorns—Gowda 1996). In order to prevent herbivores from continuing to feed after taking a bite, plants produce chemicals called phenolics (Hanley and Lamont 2001). Phenological defences, such as quick turnover of vulnerable parts or timing of the life cycle, are also used to prevent herbivores from feeding (Saltz and Ward 2000). Structural defences are avoidance strategies based on structural traits, whether these be obtrusive substances kept by the plant or minute changes to cell wall thickness. Consequently, a good definition of structural defence may be any morphological or anatomical feature that gives the plant a fitness advantage by actively deterring herbivores from feeding on it (consistent with Rosenthal and Kotanen 1994; Boege and Marquis 2005). The initial physical defence against insect eating is provided by plant structural features like waxy leaf surfaces, trichomes, thick cell walls, and lignification. The second line of defence is provided by secondary metabolites that serve as poisons and inhibit growth, development, and digestibility. Furthermore, the defence mechanism of plants against insect invaders is strengthened by the synergistic effects of many defensive components. Trypsin proteinase inhibitors and nicotine expression worked together to strengthen wild tobacco plant (*Nicotiana attenuata*) defences against beet armyworm (*Spodoptera exigua*) (War et al. 2012).

10.3.1.1 Structural Defence

The first line of defence against insect pests is a plant's structure, which also contributes significantly to the host plant's insect resistance. The construction of a physical barrier, such as a waxy cuticle or the growth of spines, setae, and trichomes, is a plant's first line of defence against insect pests. Anatomical and morphological traits known as structural defences give a plant a fitness benefit by directly deterring insects or herbivores from feeding on it. These characteristics can range from conspicuous features on a plant to minute adjustments in cell wall thickness brought on by lignification and suberization. It is well known that induced lignification and suberization of cell walls strengthen cell walls and create a region of water-impervious tissue that isolates the wound from nearby healthy cells. (Eyles et al. 2003).

Plants are primarily protected against insect pests by structural characteristics like spines and thorns (spinescence), pubescence, toughened or hardened leaves (sclerophylly), incorporation of granular minerals into plant tissues, and divaricated branching (shoots with wiry stems produced at wide axillary angles).

10.3.1.1.1 Spinescence

The aggregate term "spinescence" is used to describe the plant parts with spines, thorns, and prickles. A spine is a woody, sharp-pointed branch, a thorn is a sharp-pointed branch, and a prickle is any sharp-pointed protrusion from the cortex or epidermis of an organ (Grubb 1992; Gutschick 1999). According to reports, spinescence protects plants from a variety of insects particularly vertebrates as compared to invertebrates, due to the size relations of the plant–herbivore interactions (Cooper and Owen-Smith 1986). Obeso (1997) demonstrated that holly shrubs with very spiny leaves were far less likely to suffer herbivory by large ungulates than nearby less spiny plants. The European holly (*Ilex aquifolium*) demonstrates great diversity in leaf spinescence.

10.3.1.1.2 Pubescence

The layer of hairs (trichomes) found on stems, leaves, and even fruits is referred to as pubescence. Trichomes are hair-like appendages that protrude from the epidermis of aerial tissues. They might be straight, spiral, stellate, hooked, or glandular (Levin 1973). According to Haberlandt (1914), leaf hairs play a part in herbivore defence as well. Trichomes can limit insect oviposition in addition to hindering herbivore mobility by changing how firmly the eggs are adhered to leaves (Haddad and Hicks 2000; Handley et al. 2005). For example, hooked trichomes can entrap or even puncture some insects, including the primary predator of Mentzelia, the beetle *Hippodamia convergens* (Quiring et al. 1992; Eisner et al. 1998).

10.3.1.1.3 Sclerophylly

Schimper (1903) coined the term “sclerophylly,” which literally translates to “hard-leaved.” Through longer leaf life, hard leaves may also boost total (but not immediate) absorption efficiency and defence compound buildup (Wright et al. 2004). Scleromorphic leaves and shoots make plant material less palatable and digestible (Grubb 1986; Robbins 1993), which eventually reduces herbivore fitness (Perez-Barberia and Gordon 1998). For instance, Bjorkman and Anderson (1990) demonstrated how butterfly larvae typically steer clear of feeding on the blackberry’s (*Rubus bogotensis*) hardened leaves in South America.

10.3.1.2 Inducible Anatomical Defences

A well-recognized form of anatomical modification is the formation of traumatic resin ducts (TRDs) in the xylem and/or phloem of many conifer species. TRDs are associated with induction of terpene biosynthesis and increased resin flow within 2–3 weeks after attack (Luchi et al., 2005). The formation of the wound (necrophylactic) periderm, particularly its rate of formation, is considered to be a critical resistance mechanism to phloem-feeding borers (e.g. Buprestid beetles) and phloem-invading microorganisms (e.g. stem cankers; Eyles et al. 2003).

10.3.1.3 Secondary Metabolites for Chemical Defence of Plants

Plants produce a large and diverse array of organic compounds that appear to have no direct functions in growth and development but play a significant role in direct defence, impair herbivore performance by one of two general mechanisms: these chemicals may reduce the nutritional value of plant food, or they may act as feeding deterrents or toxins (Berenbaum 1995). In response to an insect or microbe attack, the defensive (secondary) metabolites may be either induced or constitutively stored in inactive forms. Both are referred to as phytoalexins and phytoanticipins, respectively (antimicrobial compounds synthesized by plants that accumulate rapidly at areas of pathogen infection). During herbivory, −glucosidase primarily activates the

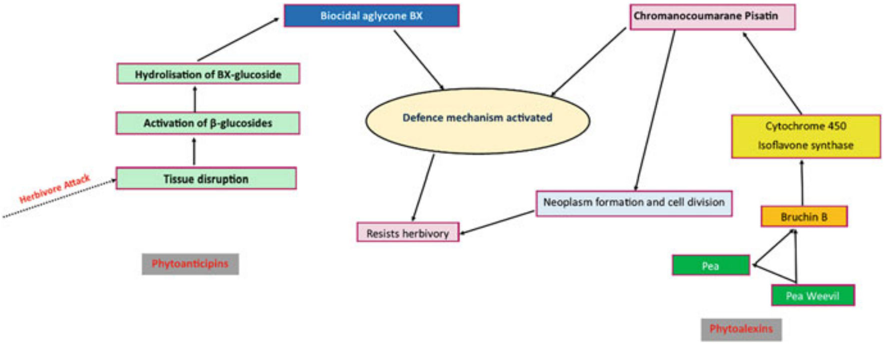

Fig. 10.2 Secondary metabolites as chemical defence in plants. (**a**) Phytoanticpins-Hydrolysation of BX-glucosides (Benzoxinoid) by plastid-targeted β-glucosidases during tissue damage leads to the production of biocidal aglycone BXs, which play an important role in plant defence against insects. (**b**) Phytoalexins-insect inducibility in peas, where the elicitor Bruchin B from the pea weevil was shown to induce a cytochrome P450 isoflavone synthase, resulting in successive accumulation of the chromanocoumaranepisatin, which stimulates the cell division and neoplasm formation and activates other plant defence responses

phytoanticipins, which then mediate the release of different biocidal aglycone metabolites. Glucosinolates, which are degraded by myrosinases (endogenous-thioglucoside glucohydrolases) during tissue rupture, are the standard illustrations of phytoanticipins. Benzoxazinoids (BXs), which are extensively dispersed throughout Gramineae, are among the other phytoanticipins. Isoflavonoids, terpenoids, alkaloids, and other phytoalexins affect how well and how long insects can survive (Fig. 10.2). The plants' secondary metabolites not only protect them from various challenges but also improve their fitness. According to reports, the presence of the secondary metabolites C-glycosyl flavone maysin and the phenylpropanoid derivative, chlorogenic acid, contributes significantly to maize's susceptibility to the corn earworm, *Helicoverpa zea*. Shoot fly resistance in sorghum has been linked to the compound 4,4-dimethyl cyclooctene (Chamarthi et al. 2011).

10.3.1.3.1 Plant Phenolic Compounds

Plant phenols are one of the most prevalent and extensive classes of defensive chemicals among secondary metabolites, and they play a significant role in the host plant's ability to resist insects. Phenols serve as a defence strategy for plants not just against insects but also against competitive plants and microbes.

A key component of plant defence against pests and pathogens is lignin, a phenolic heteropolymer. It restricts the entry of diseases by physically obstructing them or making the leaf tougher, which inhibits insect feeding and lowers the leaf's nutritional value. It has been discovered that insect or pathogen attack induces lignin synthesis, and that its fast deposition inhibits further disease or insect fecundity growth.

10.3.1.3.2 Plant Lectins

Lectins are proteins that bind to carbohydrates and serve as a barrier against a variety of pests. Different plant lectins have been used as naturally occurring pesticides against insect pests because of their insecticidal properties. The ability of lectins to survive in insects' digestive system, which gives them a significant insecticidal potential, is one of their most crucial characteristics. By attaching to the membrane glycosyl groups lining the digestive tract, they function as antinutritive and/or poisonous chemicals and cause a variety of systemic adverse effects. The damage to the luminal epithelial membranes caused by lectins, which are stable across a wide pH range, prevents the digestion and absorption of nutrients.

10.3.1.3.3 Proteinase Inhibitors

One of the most prevalent kinds of protective proteins in plants is known as a proteinase inhibitor (PI). One to ten per cent of the total proteins in storage organs like seeds and tubers contain PIs, which inhibit a variety of enzymes and are crucial for plant defence against insects. PIs may be found even in higher concentrations in these organs. Insects are starved or slowed down in their development as a result of the lack of amino acids caused by PIs' binding to the digestive enzymes in their stomach and inhibiting their action. Many PIs have been researched for their defensive properties against lepidopteran and hemipteran insects, either directly or by expression in transgenic plants to increase plant resistance to insects. The success of transgenic crops in expressing PIs against insect pests has accentuated the need to understand the mechanisms, interactions of multiple PIs with other defences, and the adaptive responses of the insects.

10.3.1.3.4 Enzymes

Enzymes have a significant role in the disruption of insect nutrition and are one of the key components of host plant resistance to insects. Peroxidases, polyphenol oxidases, ascorbate peroxidases, and other peroxidases all prevent insects from absorbing nutrients by creating electrophiles when they oxidize mono- or dihydroxyphenols. PPOs, in particular, appear to reduce the absorption of amino acids by oxidizing orthodiphenolic chemicals to quinones, which cross-link proteins in the stomach of insects and render them indigestible (Felton et al. 1992).

10.3.2 Indirect Defence Methods

A crucial part of defending plants from insect attack is the defensive response in plants that attracts natural enemies of insects. As a result of the combined impact of mechanical damage and elicitors from the attacking herbivore, indirect defences may be constitutive or induced. Plants interact with natural enemies of insect pests (i.e. parasitoids or predators) through the production of volatiles and the secretion of additional floral nectar, which actively lowers the quantity of feeding herbivores. Induced indirect defences have been examined at the genetic, biochemical, physiological, and ecological levels in recent years (Furlong et al. 2018).

10.3.2.1 Herbivore-Induced Plant Volatiles (HIPVs)

Plants emit a mixture of volatile and non-volatile chemicals to covertly protect themselves from insect feeding. Insect-induced plant volatiles (HIPVs) are essential for plant defence because they either draw an insect's natural predators or prevent an insect from laying eggs. In reaction to an insect attack, plants emit HIPVs, which are lipophilic chemicals with a higher vapour pressure, into the atmosphere through their leaves, flowers, and fruits as well as into the soil through their roots.

10.3.2.1.1 Biosynthesis of HIPVs

Different metabolic routes, including terpenoids, fatty acid derivatives, and phenylpropanoids or benzenoids, are used to synthesize HIPVs (Mumm and Dicke 2010).

Terpenoids

Monoterpenes (C10), sesquiterpenes (C15), and homoterpenes (C11 or C16) are the main terpenoid volatiles, and they all considerably contribute to any mixture of volatiles obtained from plants. The cytosolic mevalonate (MVA) and the methylerythritol 4-phosphate (MEP) pathways are the two pathways used to produce all terpenoids (Chappell 1995; Aharoni et al. 2005; Cheng et al. 2007). It has been suggested that JA, SA, and ET signalling pathways interact antagonistically or synergistically to govern the distinctive mixture of terpenoids in response to herbivory (Ozawa et al. 2000; Engelberth et al. 2001; Horiuchi et al. 2001; Schmelz et al. 2003). Terpenoids have also been proven to have the ability to attract natural enemies by themselves or in conjunction with other plant volatiles or herbivore pheromones (Dicke et al. 1990; Erbilgin and Raffa 2001; Pettersson 2001; De Boer et al. 2004; Mumm and Hilker 2005).

Volatile Fatty Acid Derivatives

Green leaf volatiles (GLVs), also known as volatile fatty acid derivatives, are frequently linked to the green leaf odour released following tissue damage. GLVs originate from C18 unsaturated fatty acids, such as linoleic acid and linolenic acid involving deoxygenation catalysed by lipoxygenases (Feussner and Wasternack 2002), and are synthesized via the octadecanoid pathway, which is also used to make the phytohormone JA. They assist in systemic induction or priming of changes in plant phenotype or serve as attractants for herbivores' natural enemies in indirect plant defence (Reddy 2002; Shiojiri et al. 2006; Frost et al. 2007; Heil and Bueno 2007; Van Wijk et al. 2008; Wei and Kang 2011).

Phenypropanoids/benzenoids

A sizable class of HIPVs known as phenypropanoids and benzenoids play a significant role in plant defence against herbivores. They are produced from L-phenylalanine, which is transformed into trans-cinnamic acid by L-phenylalanine ammonia-lyase. Then, methylation and hydroxylation are used to transform hydroxyl cinnamic acid into a range of hydroxycinnamic acids, aldehydes, and alcohols (Humphreys and Chapple 2002). Volatiles are released from some of these intermediary molecules. *Trans*-cinnamic acid can also be used to synthesize benzenoids. However, a C2 unit is added to the *trans*-cinnamic acid during their production. The CoA-dependent non-oxidative process, the CoA-independent non-oxidative pathway, and a combination of these two mechanisms have all been postulated as possible pathways for chain shortening (Boatright et al. 2004). The benzenoid ester methyl salicylate (MeSA), which is regularly released by plants with herbivore infestations and serves as a plant indirect defence, is the most researched of this class of substances (Dicke et al. 1990; Van Poecke and Dicke 2002; James 2003; Ament et al. 2004; De Boer et al. 2004).

10.3.2.1.2 Role of HIPVs in Plant Defence Against Herbivores

As long as the generation of volatiles continues, parasitoids will use these volatiles as cues to hunt their prey and will give the emitting plants an adaptive edge. These interactions are particular to an interaction between an insect and a plant. For example, *Zea mays* TPS10 is a herbivore-induced terpene synthase that forms (E)-β-farnesene, (E)-α-bergamotene, and other sesquiterpenes in *Arabidopsis thaliana*, which does not produce significant amounts of volatile terpenes, suggesting that a single herbivore-induced gene from *Z. mays* is sufficient to elicit this indirect defence (Schnee et al. 2006). Damage from the larvae of the corn rootworm *Diabrotica virgifera* causes the release of (E)-caryophyllene, which draws the nematode *Heterorhabditis megidis*, which feeds on the larvae of *D. virgifera* (Rasmann et al. 2005).

Due to increased volatile emissions from HIPV-exposed leaves, *Lymantria dispar* larval weight was reduced by 70% on branches exposed to HIPVs (Fig. 10.3). Many caterpillars are repulsed by many volatiles produced by Gipsy moth in *Vaccinium corymbosum*, including linalool and farnesenes (Rodriguez-Saona et al. 2009; Markovic et al. 1996).

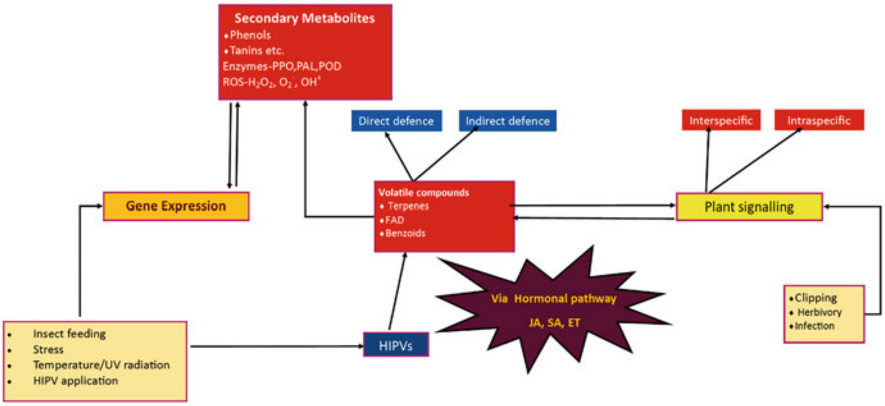

Fig. 10.3 Role of HIPVs in plant defence

10.3.2.2 Defence Elicitors (Insect Oral Secretion)

In response to physical and chemical signals caused by herbivores, such as chemicals found in oviposition fluids and oral secretions of insects, plants experience a dynamic alteration in their transcriptomes, proteomes, and metabolomes. The widespread consensus is that herbivore oral secretions and regurgitates mediate insect-induced plant responses. Depending on the type of elicitor and the biological processes involved, different elicitors produce different defences. The enzyme-glucosidase has been identified as a potential elicitor of herbivore-induced plant volatiles from the regurgitation of *Pieris brassicae* L. larvae. This enzyme causes mechanically injured cabbage leaves to emit a volatile mixture that attracts the parasitic wasp *Cotesia glomerata* (L.) (Steppuhn and Baldwin 2007).

10.3.2.3 Inducible Constitutive Traits in Indirect Plant Defence

Numerous plant features are expressed constitutively, but they can also be induced under specific circumstances. These inducible constitutive features frequently serve many purposes. Extrafloral nectar, food bodies, and domatia are a few instances of these inducible constitutive features. (Turlings and Wackers 2004).

10.3.2.3.1 Extrafloral Nectar

Extrafloral nectary organs secrete extrafloral nectar, an aqueous solution with sugars and amino acids (Koptur 1992). More than a thousand different plant species' shoots, leaves, and inflorescences have been seen to contain extrafloral nectar (Koptur 1992; Wackers et al. 2001; Turlings and Wackers 2004). Extrafloral nectar draws parasitoids and predators alike (Heil and McKey 2003). Regardless of whether there are herbivores present, most plants still exude some extrafloral nectar (Turlings and Wackers 2004). This constitutive nectar's baseline secretion enables plants to host and feed some natural enemies (Wackers et al. 2001). However, in the presence of herbivores, extrafloral nectar can be stimulated to a much higher level (Heil et al. 2001; Wackers et al. 2001; Huntzinger et al. 2004; Gonzalez-Teuber and Heil 2009), in response to mechanical damage, and by exogenous JA application (Heil et al. 2001; Heil et al. 2004; Kost and Heil 2005, 2008). Extrafloral nectar-fed parasites have an increased rate of reproduction and a much longer life span (Rose et al. 2006).

Extrafloral nectars are frequently combined with other defensive strategies (Arimura et al. 2005). When plants are exposed to exogenous application of JA, both volatile emission and extrafloral nectars secretion increase in the lima bean (Heil 2004). Lima bean plants treated with volatiles emit higher quantities of extrafloral nectars, such as (Z)-3-hexenyl acetate, (E)-3-hexenyl acetate, (E)-2-hexenyl acetate, 5-hexenyl acetate, (Z)-3-hexenyl isovalerate, and (Z)-3-hexenyl butyrate. (Kost and Heil 2008). Other plants from a variety of plant taxa frequently activate both extrafloral nectar release and volatile emission after herbivore attack (Kost and Heil 2006; Choh et al. 2006).

10.3.2.3.2 Food Body (Pearl Body)

Although the components of nutrients found in food bodies on various plants vary, polysaccharides, lipids, and proteins are frequently present (O'Dowd 1982; Silva and Machado 1999; Heil et al. 2004; Webber et al. 2007; Paiva et al. 2009). Similar to extrafloral nectar, food bodies can draw in and feed ants and other herbivores' natural enemies (Turlings and Wackers 2004).

10.3.2.3.3 Domatia

Small morphogenetic hollow structures called "domatia" can be seen on plants and act as homes for mites and other arthropods (Norton et al. 2000; Heil and McKey 2003; Romero and Benson 2004, 2005). In exchange, mites and other arthropods residing in domatia serve the plants by removing pathogenic fungus spores and hyphae as well as by consuming phytophagous mites and other undesirable arthropods (O'Dowd and Willson 1997; Norton et al. 2000; Romero and Benson 2004, 2005; Duso et al. 2005; Zemek 2005; English-Loeb et al. 2005; Monks et al. 2007; Pozzebon et al. 2009; O'Connell et al. 2015; Tempfli et al. 2015). Even though other arthropod species, including thrips, may also benefit from the protection provided by this structure, the majority of arthropod species found in domatia are mites and ants (Monks et al. 2007; O'Dowd and Willson 1997).

10.3.2.3.4 Inducible Civilian Defences

Plants can minimize the negative fitness consequences of tissue lost to herbivory by activating physiological processes that allow the plant to compensate for the reduction in total photosynthetic capacity. These are termed "civilian" defences. Unlike host resistance, civilian defences do not directly affect the biotic agent's performance. For example, in insect–host interactions, host tolerance allows plants to support herbivore populations similar to a susceptible host without a concomitant reduction in plant fitness (Karban and Baldwin 1997; Haukioja and Koricheva 2000). Mechanisms of tolerance appear common in cases of attack by both leaf-feeding herbivores and foliar pathogens. These include up-regulation of photosynthetic rates in remaining uninfected/undamaged leaves (Quentin et al. 2010), alteration in growth patterns to favour development of leaf area (Frost and Hunter 2008) and shifts in resource allocation patterns within and between the above- and below-ground organs of a tree. The latter can be achieved by remobilization of reserves from storage tissues or by mobilization of resources to temporary storage in organs that are less susceptible to damage (e.g. the root system) (Babst et al. 2008; Frost and Hunter 2008). Collectively, these changes enhance the plant's ability to tolerate subsequent pathogen and herbivore attack.

10.3.2.4 Role of Phytohormones in Induced Resistance in Plants

Numerous signal transduction pathways that are mediated by a network of phytohormones are involved in plant defence against insect attack. Plant hormones are essential for controlling a plant's development, growth, and defence systems. In plants harmed by insects, a number of plant hormones have been linked to intra- and inter-plant communication. Jasmonic acid, salicylic acid, and ethylene-mediated signal transduction pathways are responsible for activating the majority of plant defence responses against insects. These pathways during injury or insect feeding activate particular sets of defence-related genes. Depending on the attacker, these hormones may operate alone, synergistically, or antagonistically.

10.3.2.4.1 Jasmonic Acid in Plant Defence

Upon insect feeding, jasmonic acid (JA) synthesis is rapidly triggered, inducing massive defence-related genes, the production of diverse secondary metabolites (terpenoids, phenolics, as well as nitrogenous and sulphur-containing compounds), specific defence proteins (protease inhibitors, polyphenol oxidases, leucine aminopeptidase, lectins, and chitinases), and the formation of a physical barrier (e.g. trichomes) to suppress or prevent the feeding (Boter et al. 2004; Falk et al. 2014). JA is changed in plants into a variety of functional forms, including as JA-Ile, methyl jasmonate (MeJA), and the JA precursor 12-oxophytodienoic acid (OPDA) (Staswick and Tiryaki 2004; Wang and Jiang 2007; Woldemariam et al. 2012). Plants respond to MeJA by launching a number of JA-mediated defence mechanisms, increasing their resistance to herbivores (Farmer and Ryan 1992; Grimes et al. 1992; Melan et al. 1993; Kahl et al. 2000; Truitt et al. 2004). Comparable to plants aroused with herbivore elicitors, the MeJA-treated plants enhance volatile emissions and draw predators and parasitoids (Dicke et al. 1999; Thaler 1999; Meiners and Hilker 2000; Kessler and Baldwin 2001; Mumm et al. 2003; Heil 2004; Bruinsma et al. 2009).

Arabidopsis plants deficient in JA biosynthesis and signalling typically suffer more damage from molluscan herbivores (Falk et al. 2014). MeJA treatment induced the expression of glucosinolate (GS) synthesis genes, as well as GS accumulation (Mikkelsen et al. 2003; Reymond et al. 2004). MYC2/3/4 directly binds to the promoters of GS biosynthetic genes and interacts with GS-related MYBs, thereby promoting the JA-mediated synthesis of secondary metabolites and defence against external assaults (Schweizer et al. 2013). Consistent with this, the Arabidopsis myc2/3/4 triple mutant is completely devoid of GS and is extremely susceptible to the generalist herbivore *Spodoptera littoralis* (Schweizer et al. 2013) and spider mite herbivory (Zhurov et al. 2013). In rice, the concentrations of JAs were dramatically increased after a brown planthopper (BPH) attack, along with an increase in H_2O_2 level (Qi et al. 2015). BPH performed better on JA-deficient lines (AOC and MYC2 knockout) than on wild-type (WT) plants due to the attenuation of defensive secondary metabolites accumulation (Xu et al. 2021). Additionally, rice COI1 RNAi lines increase susceptibility to chewing insect *Cnaphalocrocis medinalis* as a result of impairing inducible defence by induction of trypsin protease inhibitor (TrypPI), peroxidase (POD), and polyphenol oxidase (PPO) (Fonseca et al. 2014). Tomato plants treated with JA showed reduced numbers of *Frankliniella occidentalis* (thrips), *Helicoverpa armigera*, flea beetles, and aphids due to an increase in the activities of PIs and polyphenol oxidase (Thaler et al. 2001). Furthermore, the development of glandular trichomes in tomato leaves is controlled, in part, by the JA pathway (Peiffer et al. 2009), providing an important anti-insect defence layer (Kang et al. 2014) (Fig. 10.4).

Fig. 10.4 Multiple roles of Jasmonic acid in plant immunity to insects. (**a**) Promotes resistance to a wide range of arthropod herbivores, including caterpillars (Lepidoptera), beetles (Coleoptera), thrips (Thysanoptera), leafhoppers (Homoptera), spider mites (Acari), fungal gnats (Diptera), (**b**) regulation of global changes in gene expression in response to both mechanical wounding and herbivory, (**c**) regulation of tritrophic interactions, (**d**) host plant resistance to phloem-feeding insects, (**e**) trichome-based defences (**f**) priming of direct and indirect defences, (**g**) systemic transmission of defence signals, (**h**) plant development

10.3.2.4.2 Salicylic Acid in Plant Defence

The monohydroxybenzoic acid salicylic acid (SA) is formed from cinnamate, which is created from phenylalanine by the action of phenylalanine ammonia lyases (Chen et al. 2009). SA has important role in controlling plant growth and development, just like other plant hormones (Rivas-San Vicente and Plasencia 2011), and is involved in plant defence against herbivores (Ryals et al. 1996; Potlakayala et al. 2007; Benedetti et al. 2015; Khan et al. 2015). More and more evidence points to the involvement of SA-related signalling pathways in indirect defence through the induction of volatile emission (Ozawa et al. 2000; Kessler and Baldwin 2002; de

Boer et al. 2004; Maffei et al. 2007a; Diezel et al. 2009). First, the bioactive SA derivative MeSA can be directly derived from SA. After spider mite infestation, lima bean and tomato plants showed elevated levels of MeSA and a strong attraction to natural herbivore foes (Dicke et al. 1990; Dicke et al. 1998; Ozawa et al. 2000), pear plants upon spider mite attack (de Boer et al. 2004); pear plants in responding to psyllid infestation (Scutareanu et al. 1997); and potato plants in responding to Colorado potato beetle infestation (Bolter et al. 1997). MeSA-treated poplar tree leaves show elevated expression of defence genes and increased volatile chemical emission (Arimura et al. 2004). The MeSA-treated lima bean plants also emit more of two homoterpenes, which can draw predatory mites that are out foraging (Dicke et al. 1999; Ozawa et al. 2000). These findings imply that MeSA can both directly attract natural predators of insect herbivores and indirectly boost indirect defence by inducing the emission of other volatiles.

However, not all insect species have the ability to cause MeSA to develop. Caterpillar injury increases levels of SA and activates genes that are SA-inducible, but it does not cause the emission of MeSA. (Turlings et al. 1993; Bi et al. 1997; Ozawa et al. 2000; Diezel et al. 2009). Similarly, not every plant species responds to MeSA treatments. Wild tobacco plants treated with MeSA are not attractive to predatory foragers (Kessler and Baldwin 2001). Arabidopsis plants treated with SA are not attractive to the parasitoid *Cotesia rubecula*, a parasite of caterpillar *P. rapae*, (van Poecke et al. 2001). These findings imply that while SA increases defence against piercing and sucking insects, JA is primarily engaged in defence against leaf-chewing herbivores (Walling 2000; van Poecke and Dicke 2004; Zhao et al. 2009).

10.3.2.4.3 Ethylene in Plant Defence

Ethylene (ET) plays a critical role in the activation of plant defences against different biotic stresses through its participation in a complex signalling network that includes jasmonic acid (JA), salicylic acid (SA), and abscisic acid (ABA). Pathogen attack, wounding, and herbivory trigger asymmetric activation of this defence signalling network, thereby affecting the final balance of interactions between its components and establishing a targeted response to the initial threat. Ethylene's contribution to the modulation of this defence network relies on the complexity of the regulation of multigene families involved in ET biosynthesis, signal transduction, and cross talk and enables the plant to fine-tune its response. It is generally accepted that ET cooperates with JA in the activation of defences against necrotrophic pathogens and antagonizes SA-dependent resistance against biotrophic pathogens (Adie et al. 2007).

Fine-tuning of local versus systemic defence responses by ET has been highlighted in *Nicotiana attenuata* by Kahl et al. (2000). They found that ET locally decreased nicotine accumulation in leaves following herbivory by larvae of the nicotine intolerant *Manduca sexta*. However, local volatile terpenoids and endogenous JA pools remained unaffected. It was hypothesized that this adaptive tailoring of defences would reduce nicotine uptake by the larvae, thereby making them more susceptible to their nicotine-sensitive parasitoids.

10.3.2.5 Hormone Cross Talk in Plant Defence

Cross talk between several hormones is how plant hormones control the regulation of plant growth, development, and differentiation (Dicke and van Poecke 2002; Kessler and Baldwin 2002; van Poecke and Dicke 2004; Felton and Tumlinson 2008; Wu and Baldwin 2010; Erb et al. 2012). A phenomenon called hormone cross talk occurs when various hormone signalling pathways interact either antagonistically or synergistically, offering a significant regulatory potential to nimbly adjust the plant's adaptive response to a variety of environmental inputs. As a key regulatory mechanism of plant immunity, cross talk between the SA, JA, and ET signalling pathways has developed (Spoel and Dong 2008; Grant and Jones 2009; Pieterse et al., 2009). SA-mediated defences are predominantly effective against biotrophic pathogens, such as *P. syringae*, whereas JA-mediated defences are primarily effective against herbivorous insects and necrotrophic pathogens. Numerous investigations have shown that endogenous SA accumulation counteracts JA-dependent defences, favouring SA-dependent resistance over JA-dependent defence (Koornneef and Pieterse 2008). ET frequently modulates this in this way (Leon-Reyes et al. 2009; Zander et al. 2009). However, JA can also obstruct the SA pathway, depending on the plant type and the attacker's scheme of attack. For instance, it has been shown that in wild tobacco (*Nicotiana attenuata*), JA and ET bursts caused by elicitors originating from herbivores block the SA burst, causing tuning of the SA-JA signal interaction and, consequently, the defence responses of the plant to herbivory (Diezel et al. 2009). Auxins, gibberellins, brassinosteroids, and abscisic acid (ABA) have all recently become powerful players on the battlefield. These hormones frequently have interactions with the SA-JA-ET core of the plant immune signalling network that are antagonistic or synergistic, which guide the output of the defence mechanism (Wang et al. 2007; Navarro et al. 2008; Yasuda et al. 2008; Campos et al. 2009; De Torres-Zabala et al. 2009; Ton et al. 2009; De Vleesschauwer et al. 2010; Jiang et al. 2010).

10.3.2.6 Plant Defence Priming

Plant defence priming is a strategy for crop protection which is operated by the exploitation of the immune capacity of the plant. Priming protects the plants by boosting their responsiveness to attackers based on prior experience. Plant defence priming is a new tool for sustainable crop improvement. This strategy could also be called green vaccination. As we know, in the case of humans, in vaccination, mild doses of inactivated or heat killed germs are introduced into the body to develop antibodies against that particular organism. In the same way, plants can be vaccinated by intentionally exposing them to a mild level of stress (biotic or abiotic) as a primary stimulus and letting the plants know about their immune capability (Tiwari and Singh 2021) In priming, the plant is challenged intentionally with a mild level of any biotic (pathogens, beneficial microbes, insects, chemical elicitors), or abiotic stress (primary stimulus) which brings the plant into a vigilant or alarmed state. This alarmed state is called the primed state (Tiwari and Singh 2021), which is marked by accumulation of calcium, tricarboxylic acids, reactive oxygen species, hormone conjugates, amino acids, sugars, and post-transcriptional modifications and activation of defence-related genes (Beneloujaephajri et al. 2013, Chassot et al. 2008). In the priming phase, the plant remains only in an alert or vigilant state but does not exhibit any defence response. Upon subsequent attack by attackers (secondary stimulus), the plant exhibits enhanced perception towards attackers and faster and stronger defence response against attackers, which is called the post challenge priming phase, which is marked by accumulation of glucosinolates, phytoalexins, callose, phenolics, hormones such as SA and JA, pathogenesis-related (PR) proteins, and histone modifications (Mauch-Mani et al. 2017). Seedlings of *Vigna radiata* primed with sodium nitroprusside showed defence response against salinity through enhancement in the level of protective metabolites, alteration in the level of antioxidative enzymes, and reduction in the extent of cell wall damage and chlorophyll loss (Roychoudhury et al. 2021). The priming with silicon dioxide nanoparticles enhanced the ability of wheat plants to cope with drought conditions and also improved the rate of seed germination and biomass production (Rai-Kalal et al. 2021).

10.3.2.6.1 Synthetic Chemical Inducers as Priming Agents

Synthetic chemical inducers, also known as plant strengtheners, are structurally different from the natural plant defence elicitors. They may activate or prime plant immunity by simply mimicking the structures of natural immune inducers. Alternatively, they can also be structurally unrelated to natural elicitors and target a subset of defence signalling components, and little is known about other mechanisms by which they may increase plant resistance (Wang et al. 2020). The exploitation of induced plant defences for pest control is a promising strategy to reduce the use of pesticides in agriculture.

JA Analogue

The phytotoxin, coronatine, is a natural structural and functional mimic of JA-Ile (Weiler et al. 1994; Fonseca et al. 2009). Coronatine can elicit similar responses as JA. In an effort to identify more potent mimics of coronatine, the synthetic JA mimic coronalon was synthesized (Schuler et al. 2001). Later research revealed that the coronon mediates stress responses in a variety of plant species (Schuler et al. 2004). It can activate defence proteins known to be activated by MeJA as well as MeJA-responsive genes (Pluskota et al. 2007). Several artificial JA mimics, including coronalon, have been investigated and demonstrated to trigger JA signalling and defence responses in lima bean, soybean, and coyote tobacco (Krumm et al. 1995; Fliegmann et al. 2003; Pluskota et al. 2007). Based on the co-receptor structure, a coronatine derivative, coronatine-O-methyloxime (COR-MO), was synthesized through direct chemical derivation and identified as a potent competitive antagonist of jasmonate perception (Monte et al. 2014).

10.3.2.6.2 β-Aminobutyric Acid (BABA)

BABA is a non-protein amino acid that has been known to induce plant resistance since 1963 (Papavizas and Davey 1963). It has been shown to protect about 40 different plant species against a diverse range of pathogen and pests including viruses, bacteria, oomycetes, fungi, nematodes, and arthropods (Cohen et al. 2016). BABA primes multiple defence mechanisms regulated by SA-dependent and SA-independent pathways (Zimmerli et al. 2000; Ton et al. 2005). The priming effects elicited by BABA can be maintained to the next generation, making BABA the first plant immune inducer with transgenerational efficacy (Slaughter et al. 2012). BABA is sensed by an aspartyl-tRNA synthetase, IBI1 (Luna et al. 2014). Binding of BABA to IBI1 primes it for alternative defence activity. However, the inhibition of BABA on the aspartyl-tRNA synthetase activity leads to toxicity in plants, which makes BABA unsuitable for agricultural use. While BABA has long been considered as a synthetic plant immune priming agent, a recent study has unequivocally identified BABA as an endogenous metabolite synthesized by various plant species including Arabidopsis, Chinese cabbage, maize, teosinte, and wheat (Thevenet et al. 2017).

10.3.2.6.3 Induction of Defence in Cereals by 4-Fluorophenoxyacetic Acid Suppresses Insect Pest Populations

Exogenous application of 4-fluorophenoxyacetic acid (4-FPA) protects cereals from piercing-sucking insects and thereby increases rice yield in the field. 4-FPA does not stimulate hormonal signalling, but modulates the production of peroxidases, H_2O_2, and flavonoids and directly triggers the formation of flavonoid polymers. The increased deposition of phenolic polymers in rice parenchyma cells of 4-FPA-treated plants is associated with a decreased capacity of the white-backed planthopper (WBPH) *Sogatella furcifera* to reach the plant phloem. Thus, the application of 4-PFA in the field enhances rice yield by reducing the abundance of, and damage caused by, insect pests. 4-FPA also increases the resistance of other major cereals such as wheat and barley to piercing-sucking insect pests (Wang et al. 2020).

10.4 Outlook and Future Challenges

In all natural habitats, plants are surrounded by an enormous number of potential enemies (biotic) and various kinds of abiotic environmental stresses. Nearly all ecosystems contain a wide variety of bacteria, viruses, fungi, nematodes, mites, insects, mammals, and other herbivorous animals, greatly responsible for heavy reduction in crop productivity. By their nature, plants protect themselves directly by developing different morphological structures and by producing some compounds called as secondary metabolites. Plant mechanical defences act negatively on herbivorous insects, affecting their larval and adult performance.

The ecological interactions between plants and herbivores can be understood through an understanding of induced resistance in plants, which can also be used to manage pests in crops. The elicitors of these pathways could be employed as inducers in various crops because the metabolic pathways that result in induced resistance are highly conserved among plants. The next task will be to identify the genes that encode proteins that are up- or down-regulated during a plant's reaction to a herbivore attack. These genes can then be used to genetically modify plants so that they can confer resistance to herbivores. However, its crucial to understand the chemical changes that elicitors cause in plants, how they affect herbivores, particularly in the field, and whether there have been any changes to plant development and yield before applying them effectively in agricultural systems. The Ecogenomic technique, which combines association and correlation studies, mapping of natural selection, and population genomics, allows for the assessment of variable selection at loci and distinguishes it from processes that act on the entire genome, such as migration and genetic drift.

From a biotechnological, food-developmental, and breeding point of view, understanding the defence systems of plants and learning how to apply the knowledge are of course of huge interest. For instance, modifications of the jasmonic acid pathway have been proposed (Grant et al. 2013). However, due to the extensive cross talk with other hormone signalling pathways, increased resistance against one certain insect herbivore might result in susceptibility towards another. Furthermore, some defence responses might have negative effects on the environment and humans as well, as they involve toxic bioactive natural products and proteins reducing digestibility of plant material. Still, reducing the need for synthetic insecticides, by developing crop plants resistant to insect herbivores, would be of significant gain for the food and production industry, both at an economical and environmental level.

Defence priming is very effective strategy to protect plants and enhance agricultural productivity to achieve the aim of sustainable global food security. Priming is a big solution to the problem of global hunger and application of chemicals in our food. There is urgent need of the chemical-free technique of plant protection. Priming can provide increased resistance to a wide range of biotic and abiotic stresses. This mechanism helps to avoid the unnecessary wastage of valuable resources in expression of defence during absence of challenge. This approach can brighten the future of agriculture because it has the potential to protect the crop without incurring yield penalty. Transgenerational potential of priming makes it more sustainable by increasing the profitability of farming.

In agriculture, the discovery of natural and synthetic inducers that mimic the action of the natural signals prompted a strong interest in IR as a strategy for crop protection (Vallad and Goodman 2004; Goellner and Conrath 2008). The great expansion of synthetic immune inducers has also provided opportunities to dissect the signalling networks of plant immune system that is not accessible to genetic screens due to the lethality and gene redundancy. With the discovery of the hidden drug-able targets in plant immune system, new synthetic immune inducers may be developed to target these hidden points. These new inducers can again enhance our ability to dissect plant immune system and keep this discovery cycle going on.

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11 Different Generations of Genetically Modified Crops for Insect Resistance

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Abstract

Crops are exposed to a variety of insect pests throughout their lifetime. Insect pests cause significant damage to crop plants by feeding on their tissues or sap. Besides the conventional methods which are based on using chemicals, the genetic transformation of plants with insecticidal toxin genes such as *Bt* has been widely applied to control insect pests. In addition to *Bt* genes, other toxin genes from different sources were also transferred to plants. Transgenic plants have been on the market for over two decades and have had remarkable achievements so far. However, current restrictions on these products, as well as public concern make scientists explore new approaches. The advent of RNA interference technology and later the CRISPR/Cas genome editing tool has opened up a promising new avenue in the development of next-generation biotech crops. These new approaches allow scientists to introduce new plant genotypes resistant to pests and diseases without transferring toxin genes, and all it takes is to edit target regions in the genome or apply modifications to the host transcriptome content. In this chapter, we will review different generations of biotech crops developed for insect resistance.

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Bt crops · CRISPR/Cas system · Insect resistance · RNA interference · Transgenic crops

11.1 Introduction

Sustainable crop production is one of the biggest challenges we face to ensure the availability of adequate nutrition for the world's growing population. According to the United Nations report, the world population which is currently around 8 billion in 2023, will reach 9.7 billion in 2050. The increase in food demand by 59–98% during this time renders traditional agricultural practices insufficient to secure the food supply (Valin et al. 2014). In addition, unfortunately, global climate change, biotic and abiotic stress factors cause serious problems in agricultural production. According to a research report, global crop losses caused by pests and diseases have been calculated as up to 37%, with 13% of losses due to insects (Gatehouse et al. 1992). Insect pests damage different parts of plants including roots, stems, leaves, and fruits either by chewing these parts or sucking the plant sap. Moreover, these pests may cause indirect damage to the host plant as a vector for viral, bacterial, and fungal pathogens (Mahmood-ur-Rahman et al. 2021). In order to protect the crops against biotic factors, farmers traditionally adopt a variety of synthetic insecticides, however, the increasing use of chemicals has been proven to be harmful to the environment and public health (Curry et al. 2002). The advent of recombinant DNA technology has opened up a horizon of promise to reduce chemical use concerns. The successful transformation of tobacco plants with *Cry* gene from *Bacillus thuringiensis* (Vaeck et al. 1987) made the genetic modification of crops a novel approach to reducing insecticide use. Together with tobacco, transgenic cotton plant was also produced in 1987 (Umbeck et al. 1987). Since the introduction of the first biotech crop to the market in 1996, the production ratio of these crops has increased more than 100-fold, with 190.4 million hectares grown in 29 countries in 2019 (ISAAA 2019).

So far, numerous plant transformation studies with *Bt* genes have taken important steps forward. However, based on laboratory selection and data collected from the field, the resistance conferred by *Bt* genes proved fragile as some species developed resistance to Cry toxins (Tabashnik 1994; Ferré et al. 1995). Moreover, the genetic modification of crops has been questioned and criticized by the public and scientists (Godfrey 2000). Thus, despite the successes achieved by Bt crops, they turned out to be insufficient on their own to be considered as a guaranteed long-term alternative approach to agricultural production. Using resistance genes isolated from plants such as agglutinin lectin genes (*GNA*, *ASAL*, *ACA, WGA*), Potato inhibitor II genes, and the gene stacking strategy was then carried out to improve the utility of these crops (Bakhsh et al. 2015). Besides, the employment of genetic modification technologies such as RNAi and CRISPR/Cas system pave the way to novel insect pest management studies. This chapter reviewsdifferent generations of genetically modified crops including Bt-, RNAi- and CRISPR/Cas-based developed crops resistant to insect pests.

11.2 Transformation of Crop Plants with Resistance Genes

11.2.1 Bt Crops

The genetic transformation of plants with insecticidal toxin genes such as Cry toxins has been widely used to control insect pests. *Bacillus thuringiensis* is the source of different insecticidal agents, including *Cry* toxins, and has been deployed in pest management strategies. *B.thuringiensis* is a gram-positive soil-dwelling spore-producing bacterium that has been used as a biological control agent for nearly a century. *B. thuringiensis* is safe for humans and is the most environmentally compatible microbial insecticide worldwide (Ibrahim et al. 2010). This unique bacterium is the source of insecticidal toxin genes, mainly *Vip*, *Sip*, *Cry* (Crystal), and *Cyt* (Cytolytic) genes, which are produced throughout the bacterium's life cycle (Santos et al. 2022). *B. thuringiensis* can colonize inside the insect gut, therefore, it is an appropriate insecticidal agent for pest management strategies (Deist et al. 2014).

According to the classification by Crickmore et al. (1998), *Cry* genes are divided into 51 groups and subgroups, and Cry toxins based on the insect host specifications are classified into six main groups including group 1 lepidoptera (*Cry1*, *Cry9* and *Cry15*); group 2 lepidoptera and diptera (*Cry2*); group 3coleoptera (*Cry3*, *Cry7* and *Cry8*); group 4 diptera (*Cry4*, *Cry10*, *Cry11*, *Cry16*, *Cry17*, *Cry19* and *Cry20*); group 5 lepidoptera and coleoptera (*Cry1I*); and group 6 nematodes (*Cry6*) (reviewed in Ibrahim et al. 2010).

Using the advantage of recombinant DNA technology in the late 1980s, the first *Bt* gene was transferred to tobacco and cotton plants (Vaeck et al. 1987; Umbeck et al. 1987) and commercialization of transgenic crops expressing the *Bt* gene started in the mid-1990s and by 1999 different transgenic Bt crops such as potato, cotton, and corn were also introduced (Tabashnik et al. 2013). To date, different *Cry* genes have been transferred to agricultural crops to confer resistance to different pest species of lepidoptera, coleoptera, diptera (reviewed in Bakhsh et al. 2015). The introduction of Bt crops has reduced the use of chemical pesticides in the fields and their subsequent harmful side effects. Most Bt strains are harmful to lepidopterans; however, some are also lethal to coleopterans (McPherson et al. 1988) or dipterans (Yamamoto and McLaughlin 1981). It has been determined that Bt proteins do not show any toxicity to beneficial insects, other animals, or humans (Klausner 1984). Modification of *Bt* genes for improved expression in plants was a critical step toward achieving insect resistance in plants (Perlak et al. 1991). Codon-optimized genes conferring protection against insects of coleoptera and lepidoptera were respectively transferred to potato and cotton at first (Perlak et al. 1991). After the first reports of insect resistance, many successful studies were carried out to confer resistance against insect pests (Table 11.1).

Table 11.1 List of the toxin genes transferred to some of the crop plants

Crop	Toxin genes	Targeted insect order	Reference
Alfalfa	*Cry3a*	Coleoptera	Tohidfar et al. (2013)
Canola	*Cry1Ac*	Lepidoptera	Tabashnik et al. (1993) Stewart Jr et al. (1996) Ramachandran et al. (1998) Halfhill et al. (2001) Wang et al. (2014a, b) Rahnama and Sheykhhasan (2016)
Chickpea	*Cry1A (c)* *Cry2Aa* *Cry1Ac + Cry1Ab* *ASAL* *Vip3Aa*	Lepidoptera Hemiptera	Sanyal et al. (2005) Indurker et al. 2010 Chakraborti et al. (2009) Acharjee et al. (2010) Mehrotra et al. (2011) Singh et al. (2022)
Cotton	*Cry1Aa* *Cry1Ab* *Cry1Ac* *Cry2A* *Cry1EC* *Cry2Ab* *Cry3Bb1* *Cry3* *Cry11* *Cry1h* *Cry1Ia12* *potato proteinase inhibitor* *GNA* *ACA* *ASAL*	Lepidoptera Hemiptera	Perlak et al. (1990) Majeed (2005) Wu et al. (2006) Tohidfar et al. (2008) Khan et al. (2011) Pushpa et al. (2013) Vajhala et al. (2013) Anayol et al. (2016) Bakhsh et al. (2016) Khabbazi et al. (2018) Siddiqui et al. (2019) Zafar et al. (2022) Razzaq et al. (2023) Tariq et al. (2022)
Maize	*Cry3Bb1* *Cry1Ab* *Cry1Ab* (MON810) *Cry19c* *GNA*	Lepidoptera Hemiptera	Koziel et al. (1993) Vaughn et al. (2005) Wang et al. (2005) Gassmann et al. (2011)
Potato/sweet potato	*Cry3A* *Cry3Aa* *Cry1Ac* *Cry1Ab* Cowpea trypsin inhibitor *Cry1Ba1* *Cry1Ca5* *Cry9Aa2* *GNA* *ConA*	Coleoptera Lepidoptera Hemiptera	Peferoen et al. (1990) Cheng et al. (1992) Adang et al. (1993) Perlak et al. (1993) Newell et al. (1995) Morán et al. (1998) Gatehouse et al. (1999) Meiyalaghan et al. (2006) Jacobs et al. (2009) Mi et al. (2015) Salehian et al. (2021)
Rice	*Cry1A(b)* *Cry1A(c)*	Lepidoptera Hemiptera	Fujimoto et al. (1993) Wünn et al. (1996)

(continued)

Table 11.1 (continued)

Crop	Toxin genes	Targeted insect order	Reference
	PinII *Cry1C* *Cry2AX1* SBK + SCK *GNA* *ASAL* *DB1/ G95A-mALS*		Cheng et al. (1998) Bashir et al. (2005) Tang et al. (2006) Zhang et al. (2013) Ramesh et al. (2004) Yoshimura et al. (2012) Chandrasekhar et al. (2014) Chakraborty et al. (2016) Boddupally et al. (2018) Liu et al. (2022)
Soybean	*Cry1Ab* *Cry1Ac* *Cry8-like* *eCry1Gb.1Ig*	Lepidoptera	Parrott et al. (1994) Dufourmantel et al. (2005) Dang and Wei (2007) Qin et al. (2019) Je et al. (2022) Chae et al. (2022)
Tomato	*Cry1Ac* *Cry1Ab*	Lepidoptera	Mandaokar et al. (2000) Kumar and Kumar (2004) Koul et al. (2014)

Most of the transgenic crops are harboring constitutive promoters in particular the 35S CaMV promoter driving the foreign genes which providethe strong production of toxin protein in whole plant tissues and organs including root, stem, flowers, pollens, etc. Hence to restrict the unnecessary production of toxins in plants, foreign genes can be expressed by inducible promoters. For instance, to restrict the production of Crytoxin to insect-biting sites in plants toxin genes were expressed under the control of the wound-inducible promoter (AoPR1) isolated from *Asparagus officinalis* (Özcan et al. 1993; Bakhsh et al. 2016; Anayol et al. 2016; Khabbazi et al. 2018). The use of AoPR1 promoter confines the accumulation of Bt toxin to the wounding part of the plant, therefore, it is a valuable approach in insect pest management considering the public concerns regarding transgenic Bt crops.

11.2.2 Transgenics Harboring Plant-Derived Insect Resistance Genes

Cultivation of Bt crops increased crop production and reduced the use of chemical insecticides in the field (Toenniessen et al. 2003). Therefore, it has had an important contribution to global food security and poverty reduction. Reports indicate that this technology is beneficial for farming communities and consumers (Qaim 2009). To date, many *Cry* resistance genes have been transferred to crops to cope with damaging insects. While most of these have had a satisfactory outcome at first, the efficacy of resistance genes has been compromised by the widespread cultivation of transgenic crops. Based on reports some of the pest species have evolved resistance against Cry proteins which indicates that the toxic effect of these genes has diminished (Calles-Torrez et al. 2019; Smith et al. 2019; Tabashnik and Carrière 2019). For example, the excessive use of *Cry1Ac* has led to the development of resistance in insect pests. This resistance is due to mutations occurring in the midgut receptors like cadherin. Development of crops harboring the codon-optimized *Bt* genes is an efficient method to combat the field-evolved resistance to Bt toxins (Tabashnik and Carrière 2017; Benowitz et al. 2022; Siddiqui et al. 2023). In addition, the investigation of new insecticidal genes and approaches is a necessity for sustainable pest management strategies. Using plant-derived toxin genes alone or in combination with *Cry* genes could be another approach to this goal (Khabbazi et al. 2018; Boddupally et al. 2018). Different lectin genes are toxic to members of coleoptera, lepidoptera (Czapla and Lang 1990), and diptera (Eisemann et al. 1994). Lectins stimulate endocytosis and possibly other toxic metabolites in the midgut, resulting in the inhibition of nutrient absorption or disruption of midgut cells (Czapla and Lang 1990). Plant lectin genes are toxic to sap-sucking insects of hemiptera and have an inhibitory effect on their growth and fecundity (Wang et al. 2005; Chakraborti et al. 2009; Khabbazi et al. 2018).

Transformation of crops with *Galanthus nivalis* agglutinin lectin gene (*GNA*) isolated from the snowdrop plant confers resistance to *Aphis gossypii, Rhopalosiphum maidis, Sitobion avenae* and other sap-sucking members of hemiptera (Khabbazi et al. 2018; Wang et al. 2005; Stoger et al. 1999). This gene as well as other agglutinin lectin genes derived from garlic (*ASAL*), onion (*ACA*), wheat (*WGA*) etc. has no harmful effect on the mammalian oral system (Peumans and van Damme 1996; Khabbazi et al. 2016) and have been transferred to some of the important crops such as cotton, maize, chickpea and rice (Table 11.1) and resulted in increased resistance to different sap-sucking insects including aphids, jassids, planthoppers and whiteflies (Bakhsh et al. 2015). Along with the transformation of plants with resistance genes, RNAi and CRISPR/Cas-based methods are other relatively new approaches contributing to sustainable pest management strategies in agriculture.

11.3 RNA Interference-Mediated Modifications in Plants

11.3.1 What Is RNAi and How Does It Work?

RNA silencing is a process that causes the downregulation of a target gene expression.This technology is a worthy reverse genetics tool to study gene function (Harmon et al. 2000). It is divided into transcriptional gene silencing (TGS) and post-transcriptional gene silencing (PTGS). PTGS also known as RNA interference (RNAi) is a highly specific homology-based gene silencing tool that is frequently used to downregulate the expression of target genes via mRNA degradation and hence is also called a knockdown process (Small 2007; Tang and Galili 2004). RNAi is triggered by the introduction of double-stranded RNA (dsRNA) molecules microRNAs (miRNAs) and small interfering RNAs (siRNAs) are the two main

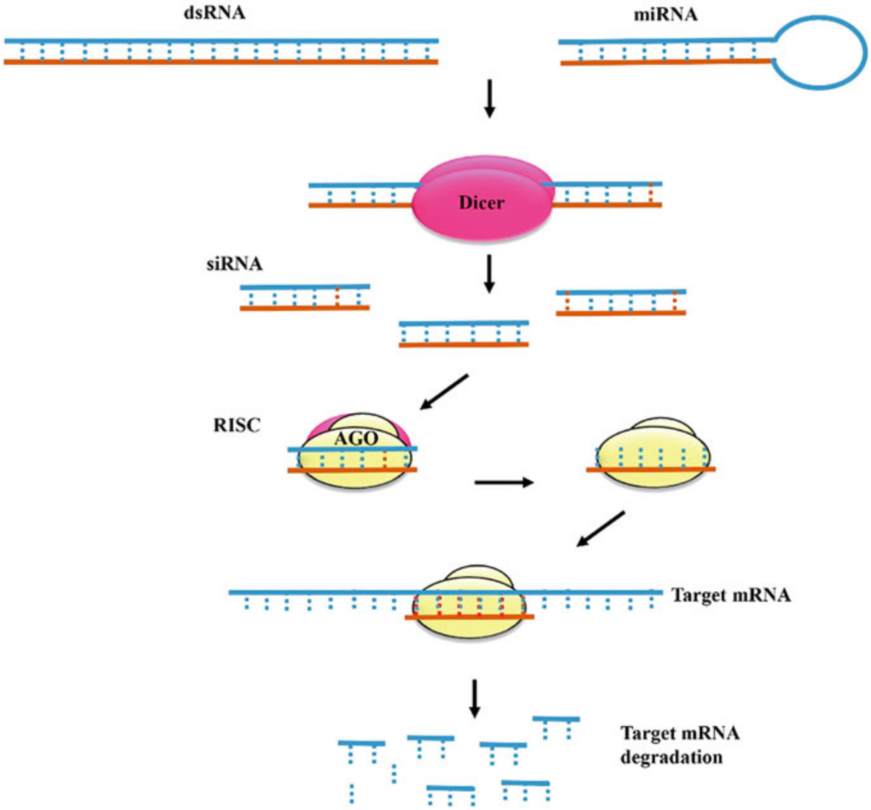

Fig. 11.1 Mechanism of the RNAi pathway. Long dsRNA or miRNA molecules are cleaved by the Dicer enzyme into short duplexes of 21–25 nucleotide RNAs. Small RNAs bind to the RISC complex and single-stranded short RNAs are produced and directed to the target mRNA, causing degradation of the mRNA

classes of small non-coding RNAs that initiate gene silencing in plants (Axtell 2013). Small interfering RNA constructs are short duplexes of 21 to 25 nucleotides produced after long dsRNA precursors are cleaved by the ribonuclease III Dicer-like (DCL) enzyme (Zamore et al. 2000; Bernstein et al. 2001). Afterward, miRNAs or siRNAs incorporated into RNA-induced silencing complex (RISC), argonaute, and other effector proteins bind to complementary mRNA molecules and subsequently degrade the mRNA and causing downregulation of the target gene (Fig. 11.1) (Bosher and Labouesse 2000; Kim and Rossi 2007; Mittal et al. 2011).

11.3.2 RNAi-Based Gene Regulation for Insect Resistance in Plants

The RNAi process is conserved in higher eukaryotes and naturally protects the host from viruses in plants, but is currently used in a variety of ways for different purposes, including insect-plant interaction studies (Khabbazi et al. 2020). RNAi has opened a new avenue in insect pest management strategies. This technology is particularly effective in controlling insects of the order coleoptera, whereas insects of lepidoptera and hemiptera are recalcitrant in response to RNAi which may be due to the biological barriers limiting the use of RNAi in these species (Terenius et al. 2011; Baum and Roberts 2014).

dsRNAs are either expressed by host plants or applied by methods like microinjection, feeding and spraying to control the insect pest damage on plants. Host-induced gene silencing (HIGS)-mediated RNAi has been successfully used in a variety of crop species to manage different agricultural insect pests including sap-sucking and chewing species (Table 11.1). In this approach, plant genetic background is engineered to produce dsRNAs targeting the essential genes in insect pests. After insects are fed with transgenic plants, dsRNAs are transported to the insect salivary glands or gut, and adsorbing cells subsequently activate the insect RNAi machinery and silence the targeted genes that interfere with insect vital metabolism. The utilization of plant-mediated RNAi provides a promising tool in crop protection without the use of chemicals and has the potential to target an unlimited number of genes in insects (Zhang et al. 2017).

Aphids are the members of the order hemiptera that damage crop plants by phloem-feeding and transmitting viral diseases. In HIGS-mediated RNAi studies in aphids, the focus has been on studying the management of *Myzus persicae* and *Sitobion avenae* aphid species in transgenic host plants including *Arabidopsis thaliana*, *Nicotiana tabacum*, *N. benthamiana*, and *Solanum lycopersicum* and *Triticum aestivum* (reviewed in Zhang et al. 2022). RNAi-mediated knocking down of the salivary effectors (MpC002, MpPIntO1, MpPIntO2, Mp55), Receptor of Activated Kinase C (Rack1), CuticularproteinMyCP, Acetylcholinesterase 1 (Ace1), Dynein heavy chain 64C (MpDhc64C), Chitin synthase 1(CHS1), Zinc finger protein (SaZFP), Carboxylesterase(CbE E4) and Lipase maturation factor 2-like gene adversely affected aphid fecundity and survival.

dsRNA-mediated downregulation of the *Sucrose non-fermenting 7* (*DvSnf7*) gene coding for an essential protein in vacuolar sorting in transgenic maize plant (*Zea mays*) conferred resistance to the western corn rootworm, *Diabrotica virgifera* (Coleoptera: Chrysomelidae) (Baum et al. 2007). *Snf7* dsRNA alone takes a long time to kill WCR larvae, so the RNAi pathway is accompanied by *Cry* genes from *B. thuringiensis* to accelerate the killing action. Further, combining the *Bt* and RNAi mechanisms reduces the occurrence of insect resistance to Bt crops. Maize plant expressing three different *Cry* genes plus dsRNA constructs for the *DvSnf7* gene, event MON87411, was approved for commercialization and release by The Canadian Food Inspection Agency (CFIA) in 2016 (Head et al. 2017). Later, in 2017, The United States Environmental Protection Agency (US-EPA) also granted permission for the commercial planting of MON87411 (Zotti et al. 2018).

Cotton bollworm, *Helicoverpa armigera*, is another devastating agricultural insect pest belonging to the order Lepidoptera. This pest has a wide host range and causes millions of dollars in losses each year (Sharma 2001). Cotton contains a polyphenolic compound called gossypol to protect itself from herbivorous insects, however, *H. armigera* can tolerate its moderate concentrations owing to the P450 monooxygenase gene, *CYP6AE14,* as this enzyme detoxifies the gossypol content. Feeding *H. armigera* larvae on leaves of transgenic Arabidopsis, tobacco, and cotton plants expressing dsRNA for *CYP6AE14*, resulted in suppression of the P450 monooxygenase gene in *H. armigera* and retarded larvae growth and enhanced host resistance to cotton bollworms (Mao et al. 2007, 2011).

Later Kumar et al. (2014) described how *Manduca sexta* larvae feeding on native *Nicotiana attenuata* can tolerate high concentrations of nicotine, a neurotoxin produced by tobacco species. Wolf spiders (*Camptocosa parallela*) avoid nicotine-fed larvae, therefore, *M. sexta* larvae deter its predator by exhaling nicotine through the spiracles as an anti-spider signal. Transformation of *N. attenuata* with constructs producing dsRNA to target the *M. sexta CYP6B46* gene and feeding the larvae with transgenic plants silenced the *CYP6B46* gene. Subsequently, insect vulnerability to spider predation was increased because of the less nicotine exhaled.

Another approach to managing insect pest damage is to interfere with chitin metabolism. Chitinase hydrolyzes chitin and, therefore, its function is vital for insect molting andmetamorphosis (Agrawal et al. 2013). Transgenic tobacco and tomato plants expressing RNAi constructs for the chitinase (*HaCHI*) gene significantly reduced chitinase production and adversely affected the overall growth and survival of *H. armigera* after continuous feeding with leaves of transgenic HaCHI-RNAi lines (Mamta and Rajam 2016).

In another study, tobacco plants were transformed to produce dsRNA targeting the *Sl102* gene in *Spodoptera littoralis*. *Sl102* is a gene involved in the immune cellular responses of *S.littoralis*, which was knocked down to increase the susceptibility of the insect pest against the pathogenicity of *B. thuringiensis*-based insecticides. Experimental larvae reared on transgenic leaves showed low transcript levels for the *Sl102* genewhich was positively associated with food consumption in the larvae (Di Lelio et al. 2022).

11.4 CRISPR/Cas System

11.4.1 Origin, Classification, and Efficiency

Genome editing of plants has achieved remarkable success since the advent of sequence-specific nucleases (Shelake et al. 2019). Zinc finger nucleases (ZNFs) and transcription activator-like effector nucleases (TALENs) were the pioneer editing tools. However, these tools are technically complex and cumbersome, with low efficiency, and therefore are not used any further (Kumar et al. 2018). In contrast, the discovery of the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/Cas system paved the way for a simple and precise method to

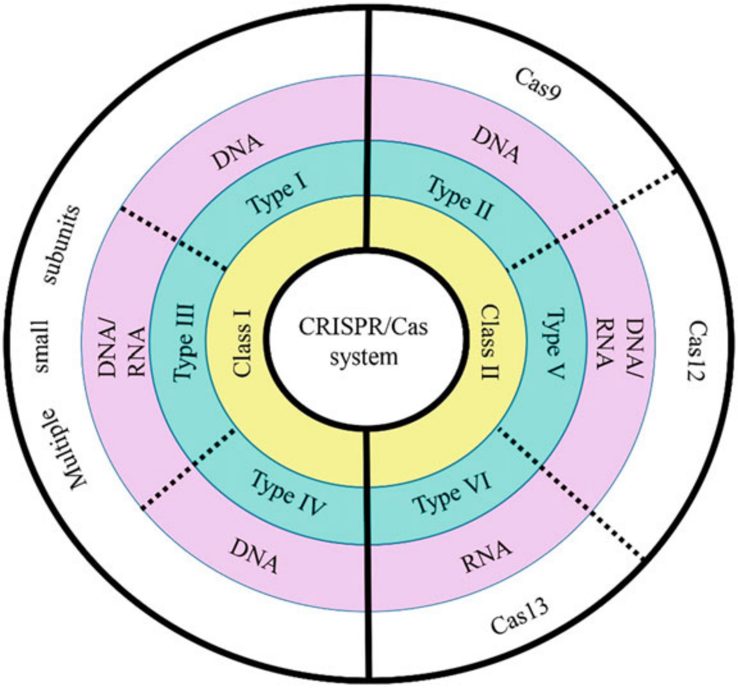

Fig. 11.2 The conventional classification of CRISPR/Cas system

modify several targets in the genome at the same time. CRISPR/Cas system was first discovered in the sequences of DNA from *Escherichia coli* (Ishino et al. 1987). Archaea and bacteria naturally use this system to protect themselves against viral invasions (Bhaya et al. 2011). After genetic elements such as phages invade the host cell, small nucleic acid fragments of invading pathogens are inserted into the host's CRISPR loci (spacers) and stored there for later encounters (Amitai and Sorek 2016). When the host cell faces a new invasion, spacer sequences are transcribed, and individual CRISPR RNAs (crRNAs) lead the Cas nuclease to the cognate nucleic acid sequences of the pathogen and cleave them (Barrangou et al. 2007). Depending on the nature of the interfering molecules, CRISPR/Cas system is divided into two classes (Fig. 11.2). Class 1 includes types I, III, and IV multiprotein effector modules that target DNA, DNA/RNA, and DNA molecules, respectively. Class 2 includes types II, V, and VI effector modules that associate with DNA, DNA/RNA, and RNA molecules, respectively. Unlike class 1, members of class 2 are single protein effector modules and the most notable examples of this class are Cas9, Cas12, and Cas13 (reviewed in Gostimskaya 2022). Type II CRISPR/Cas9 has been isolated from *Streptococcus pyogenes* and is based on RNA-guided interference with DNA and has the most contribution to genome editing studies in plants (Khabbazi et al. 2021). This system consists of a Cas9 nuclease and a single guide RNA (sgRNA) molecule. A twenty-nucleotide at the 5'end of the sgRNA

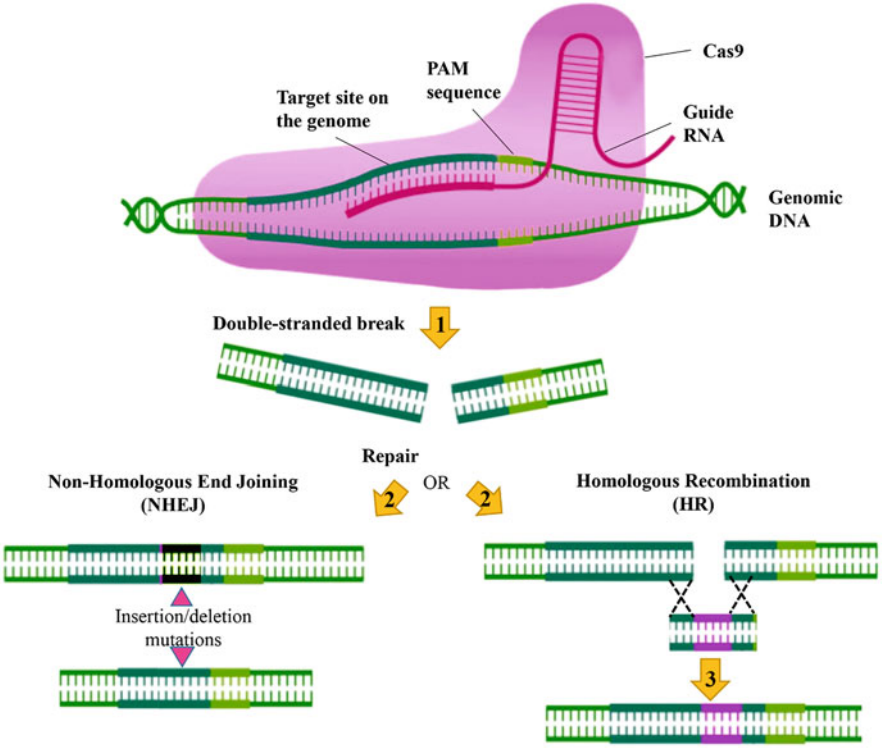

Fig. 11.3 The mechanism of CRISPR/Cas9 genome editing. Guide RNA molecule directs the Cas9 nuclease to the target site in the genome. The presence of PAM near the matching sequence in the genome is critical in finding the target site.After double-strand breaks are made, the broken ends are repaired via the NHEJ or HR processes

directs the CRISPR/Cas9 complex to the complementary sequence in the genome. The presence of conserved protospacer-adjacent motifs (PAM) near target sites in the genome plays a critical role in the in-target function of this complex. Following double-stranded DNA breaks by the Cas9 enzyme, it is subjected to cell repair machinery, which can be error-prone non-homologous end joining (NHEJ) repair or precise homology-directed repair (HDR) (Fig. 11.3). The targeted insertion or modification of desired sequences into the genome makes the HDR approach an outstanding tool for the genetic engineering of plants (Voytas and Gao 2014).

The importance of the breakthrough CRISPR/Cas technology is particularly emphasized as it causes heritable targeted modifications and also contributes to the development of transgene-free plants (Wang et al. 2014a, b; Pan et al. 2016). The first genome editing study in plants was reported by Feng et al. (2013), however, the same year there were other works that reported the successful use of the CRISPR system in genome modification of plants such as Arabidopsis, tobacco, wheat, and rice (Upadhyay et al. 2013; Jiang et al. 2013; Feng et al. 2013). Afterward, numerous studies have been conducted to apply desired modifications to a variety of plants including maize, soybean, potato, cotton, grapes, tomato, cucumber, Cacao tree, sweet orange, Grapefruit, apple, etc. (Khabbazi et al. 2021).

11.4.2 CRISPR/Cas-Based Genome Editing of Plants for Insect Resistance

Insects can damage crops by directly feeding on plant tissues or indirectly transmitting various diseases, thereby significantly reducing crop production and yield. The application of extensive chemicals has caused serious harm to human and animal health as well as the environment. After the successful contribution of transgenic crops for example Bt crops in reducing the usage of chemicals yet the existence of political, ethical, and societal resistance to these crops is a serious issue in many countries. The possibility of employing CRISPR/Cas technology in genome editing of plants towards insect resistance has already been discussed (Douglas 2018). Employing the CRISPR tool provides the opportunity to tackle the concerns in two ways; creating de novo resistance in case there is no convenient R-gene available, and controlling the insect pest population dynamics by breaking insecticide resistance, killing or causing sterility in insects. In such situations, CRISPR technology has the potential to develop designer plants for generating superior traits or to initiate a gene drive to selectively propagate mutations that lead to reduced fecundity or female death in the target insect population (Bisht et al. 2019).

Elucidation of molecular mechanisms of plant defense systems is a prerequisite for developing a new strategy to generate insect-resistant crops. Plants have developed a complex defense mechanism under millions of years of selection pressure from insects (Erb and Reymond 2019). Species of different orders show a strong spatio temporal variation in the expression of metabolites involved in defense against insects (Barton and Boege 2017). The expression level of immunity-associated genes in Arabidopsis plants is correlated with the duration of the vegetative stage (Davila Olivas et al. 2017; Glander et al. 2018), illustrating the relationship between flowering and resistance to insects.

Plant Calcium ion (Ca^{2+}) signals are involved in a wide variety of signaling pathways in the cell. Ca^{2+}enacts an important role in the circadian regulation of photoperiod-controlled flowering in the common morning glory (*Ipomoea purpurea*) (Dodd et al. 2010). Calcium-dependent protein kinase (*CDPK*) is one of the main receptors in the calcium signaling pathway and transduces the signal by phosphorylation (Harmon et al. 2000). In Arabidopsis, the loss of function of the *CPK33* causes late flowering (Kawamoto et al. 2015). $Ca^{2+}$is also involved in early defense signaling in plants (Yan et al. 2018), after insect feeding, there is a striking Ca^{2+}influx limited to a few cell layers lining the injured site (Maffei et al. 2007). In Arabidopsis plants, *CPK3* and *CPK13* activate the herbivore-induced network by increasing the transcription levels of plant defensin gene *PDF1.2* (Kanchiswamy et al. 2010). In another study, the knockdown of *NaCDPK4* and *NaCDPK5* genes in Coyote Tobacco (*Nicotiana attenuata*) up-regulated jasmonic acid accumulation and increased resistance to *Manduca sexta* (Yang et al. 2012).

CRISPR/Cas9 mediated knockout of *CPK* gene (*GmCDPK38*) in soybean resulted in late flowering time in *gmcdpk38* mutants regardless of the photoperiodic conditions. In addition to delayed flowering time, *gmcdpk38* mutants also exhibited enhanced resistance to *Spodoptera litura* (Li et al. 2022). This revealed the dual role of *GmCDPK38* in regulating photoperiod-induced flowering in soybean and resistance to *Spodoptera litura*, suggesting a possible link between flowering and insect resistance.

Resistance to insects is multifaceted with highly complex regulation in both insects and the host plant itself. Phytohormones such as jasmonic acid (JA), salicylic acid (SA), abscisic acid (ABA) and ethylene can affect plant response to insect pests. Deficiency of ABA in plants increases their susceptibility to insect pests (Thaler and Bostock 2004; Dinh et al. 2013) whereas exogenous application of ABA can increase plant resistance to brown planthopper (BPH) by promoting callose formation (Liu et al. 2017). In a recent study, overexpression of the 9-cis-epoxycarotenoid dioxygenase-3 (NCED3) enzyme in rice plants increased ABA biosynthesis and subsequent resistance to BPH (Sun et al. 2022).

Responses of plants to insect pests are also correlated with the feeding manner and the degree of damage at the feeding site. Therefore, the molecular response of plants induced by sap-sucking insects is different from chewing pests. One study demonstrated the role of serotonin regulation as part of the defense mechanism against insect pests in plants (Lu et al. 2018). In rice plants, the cytochrome P450 gene *CYP71A1* encodes tryptamine 5-hydroxylase, which catalyzes the conversion of tryptamine to serotonin (Fujiwara et al. 2010). Sap-sucking insects cause only a little damage to plant tissue therefore salicylic acid (SA) signaling pathway has the main role in insect infestation (Li et al. 2017). Serotonin biosynthesis is induced by insect infestation in rice, and its suppression confers resistance to BPH and striped stem borers (SSB). CRISPR-mediated *CYP71A1* gene knockout inhibits serotonin production resulting in higher salicylic acid levels and thus resistance to BPH and SSB in rice (Lu et al. 2018). However, *cyp71a1* mutant individuals showed increased resistance to rice blast, *Magnaporthe grisea* (Ueno et al. 2008) and susceptibility to rice brown spot disease *Bipolaris oryzae* (Ishihara et al. 2008).

11.5 Conclusion

Until the beginning of the current century, different approaches such as classical plant breeding methods and the application of chemicals in the field contributed to enhancing crop yield and production. The requirement of sufficient agricultural production for the increasing world population and ensuring global food security have led plant scientists to explore more efficient strategies, especially in terms of pest management. Existing criticism of traditional pest control approaches, such as environmental and health concerns and the development of resistance to insecticides, has rendered these methods inadequate on their own. The advent of recombinant DNA technology and the introduction of genetically modified crops expressing the *Bt* toxin gene was a new era in agriculture. Later advances in molecular biology discoveries such as RNAi and CRISPR/Cas technologies soon opened up a new avenue in the production of biotech crops. The next generation of GM crops has the potential to address concerns about transgenic crops and is of great importance for developing sustainable and environmentally friendly methods for crop improvements.

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High-Throughput Phenotyping and Its Importance in Host Plant Resistance

12

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Abstract

Plant phenotyping has been the topic of research for several decades across the globe, which has made significant contributions to the advancements in plant cultivation and breeding. However, the implication of high-throughput phenotyping (HTP) in evaluating the study made in the field of plant-insect interaction is in its infancy. Here, we take the opportunity to revisit and highlight the different scopes of employing HTP for large-scale analysis of the insect damage signatures across different plant parts and the respective insect behavior. Screening for insect-resistant host plants and breeding for insect-resistant varieties require phenotyping data to identify and ensure the level of resistance in plants. HTP allows a nondestructive way of quantifying plant damage, insect feeding behavior, choice, and no-choice assays and generates a tremendous amount of data through image capturing, image processing, and video recordings. Different automated image capturing platforms are available to determine the plant traits and insect behavior, and by utilizing the HTP, a large number of plant accessions can be screened in a shorter time while maintaining the data accuracy and sensitivity. This chapter, thus, highlights the various mechanisms to employ HTP in large-scale plant-herbivore interaction studies to make the future better for the scientists of tomorrow.

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High-throughput phenotyping · Plant imaging · Plant-insect interactions · Insect behavior · Feeding guilds · Machine learning · Automation

12.1 Introduction

Plant pests can cause 20–40% crop yield losses globally with an annual loss of USD $290 billion (Kundu and Vadassery 2021). Insects can account for 23% of crop losses among all pests (https://www.agrivi.com/blog/yield-losses-due-to-pests/). It is believed that plants and insects have been coevolving for 400 million years (Labandeira 2013). In this coevolutionary process, plants have developed sophisticated defense mechanisms to protect against insect attacks and vice versa (War et al. 2012). Understanding the plant defense mechanisms and development of insect pest-resistant/tolerant varieties is a very promising, effective, and sustainable way of pest management (Panda and Khush 1995; Sharma and Ortiz 2002).

Host plant resistance to insects encompasses plant traits via three categories—antixenosis, antibiosis, and tolerance (Panda and Khush 1995; Stout 2014). First, antixenosis/non-preference refers to the morphological characteristics of plants that deter/repel insects to feed, reproduce, and/or grow. Second, antibiosis refers to the chemical characteristics of plants that can adversely affect insect growth and reproduction. Third, tolerance is the most durable plant resistance category that does not affect insect fitness but recovers/compensates for plant growth losses caused by insect feeding via enhanced plant physiological processes; hence, it does not allow faster development of insect biotypes (Peterson et al. 2017). Conventional plant breeding methods for insect resistance require extensive plant phenotyping in heterogeneous plant populations to understand the genetic basis of insect resistance. Furthermore, modern genomic approaches also require plant phenotyping to evaluate insect feeding-based plant damage and other agronomic growth drifts because of foreign gene incorporation. Looking at the farmers' interest/ideal scenario, insect-resistant plants should not compensate for plant yield. For instance, genetic engineering for insect resistance in plants could lead to off-types or yield drift, or any other undesirable characteristics. Therefore, plant phenotyping plays a crucial role in screening insect-resistant and -tolerant crop varieties (Goggin et al. 2015).

Several insect species, among lepidopterans, dipterans, homopterans, heteropterans, orthopterans, and coleopterans, chew leaves or burrow through fruits, stems, or roots during their larvae and/or adult stages of the life cycle (Satpathy et al. 2020; Fuentes-Jacques et al. 2021; Bhuvaneswari et al. 2022). Insects belonging to different feeding guilds can cause different types of damage such as defoliation, chlorosis, leaf mining, stunted plant growth, and development of galls. Insects with chewing type of mouthparts could result in visible feeding scars, whereas piercing-sucking-type insects keep the plant cell alive for their nourishment and result in chlorophyll loss (van Emden and Harrington 2017). Attack of insects on plants is a multistep process such as host finding, host selection, host acceptance, sustained feeding, and oviposition (Powell et al. 2006; Follett 2017; Finch and Collier 2000). Plants with different defense traits could impact different steps of the abovementioned process. The insect damage phenotyping usually directly relies on visual parameters such as percent insect-fed areas, chlorosis, or damage rating. Especially, the damage rating could be very subjective and not a very accurate measure. Inconsistencies and inaccuracies for insect damage ratings could hinder the process of identifying the genetic loci responsible for insect resistance. Furthermore, conventional phenotyping does not capture the physiological and biochemical phenotypes of plants. Detailed plant phenotyping beyond measuring direct yield can help to distinguish different host plant resistance mechanisms and plays a crucial role in genome-wide association, nested association mapping, and other genetic studies (Kloth et al. 2012; Araus et al. 2018).

The interaction between environment and genotype leads to phenotype. Evaluating different genotypes in different environmental conditions ends up in a very high number of combinations to be tested. Crop phenotyping involves the use of specific protocols and methodologies to measure plant morphological/structural traits, physiological traits, and component content traits of different parts of the plants (Dhondt et al. 2013). These methodologies are very time-consuming, resource-heavy, and labor-intensive. Despite considerable progress in plant genotyping and molecular breeding core facilities, plant phenotyping still remains a bottleneck in breeding efforts (Dhondt et al. 2013; Goggin et al. 2015; Walter et al. 2015; Ubbens and Stavness 2017).

To accelerate the development of insect-proof plants, it becomes imperative to overcome the plant phenotyping bottleneck by identifying the plant traits which are good measures of insect resistance and tolerance. For instance, SPAD meters have been used to measure chlorophyll loss in response to aphid attacks in a nondestructive way (Lage et al. 2003). Using the metabolomics approach, the abundance of secondary metabolites can be estimated to know the plant resistance status (Zogli et al. 2020; Grover et al. 2022a). Furthermore, methods like ELISA can be used to test for the presence of viruses in plants (Mondal et al. 2016). The phenotypic traits such as root and shoot biomass, fruit and/or seed yield, plant height, number of leaves, leaf area, and photosynthetic efficiency are heavily impacted by insect attack (Kessler and Baldwin 2002). The precise and accurate assessment of these phenotypic parameters is crucial to unravel and quantify the potential of different plant genotypes in the insect control space. High-throughput phenotyping strategies are gaining enormous attention these days in plant science studies due to (1) precise, accurate, and objective measurement of phenotypic variables in automated and nondestructive way; (2) time series assessment of plant performance under insect attack at high resolution; and (3) reduction in time, labor, and several other human resources through automation and digitization of data analyses (Dhondt et al. 2013; Goggin et al. 2015; Ubbens and Stavness 2017).

12.2 High-Throughput Phenotyping (HTP) for Plants

Phenome refers to a set of physical and biochemical traits that develop in an organism in response to varied environmental stimuli, and a measurement of these phenotypes is referred to as phenomics. The study of plant phenomics, thus, plays a crucial role in the detection of the first emergence of insects in millions of hectares of agro-economically important crop fields, thereby rendering us with a wide range of downstream datasets that give insight into future directions. HTP, thus, results in the production of huge datasets that leads to successful curation by the application of deep learning, which is one of the budding fields of research in plant phenomics (Arya et al. 2022). Despite modern digital techniques such as imaging, there are few non-imaging-based HTP methods available. For example, Xing et al. (2017) developed a dynamic and efficient HTP method for the evaluation of antixenosis against common cutworms in soybeans. Though this method shortened evaluation time to 4X and increased efficiency to 12X, these methods highly depend on the type of insects and crops. Therefore, digital imaging techniques could fill those gaps for plant HTP to insect attack. An improved high-throughput phenotyping method was recently developed to screen rice germplasm resistance against rice gall midge (*Orseolia oryzae*), which allowed to screen 60 lines/varieties of rice (Cheng et al. 2021).

12.2.1 Different Feeding Patterns of Insects

Pests employ diverse feeding strategies to obtain nutrition from their host plants. Insects of major feeding guilds include leaf-chewing insects, plant sap feeders, and root feeders (Carvalho et al. 2014). Chewing insects are voracious leaf eaters that completely vanish the whole aboveground part of the plants leaving the midveins and the vascular regions untouched (Meena et al. 2019). Piercing-sucking insects, however, directly inject their salivary components into the vascular tissues, thereby suppressing plant defense and slowly sucking the nutrients from the plant sap. Moreover, insect species from the hemipteran order indirectly affect crops and vegetables by transmitting bacterial, viral, or fungal diseases from plant to plant (Yi 2020). A wide range of root feeders feed on plant roots dwelling in the soil, thereby causing hydraulic changes to the entire plant body. As feeding patterns differ, the phenotypic characteristics of the damage caused by these wide range of insects also differ considerably (Fig. 12.1). The aboveground visible effects include leaf mining, defoliation, oviposition scars, cell content feeding, and stem boring. Herbivores also cause chlorophyll loss, discoloration of leaves with premature senescence, reduced water content, and developmental growth retardation (Campbell et al. 2018).

The acceleration in the utilization of plant phenotyping is highly based on the availability of different imaging systems, and the foundation for these imaging systems relies on the insect damage types, which could affect different plant characteristics like absorption, transmission, or reflectance of light. Measurement

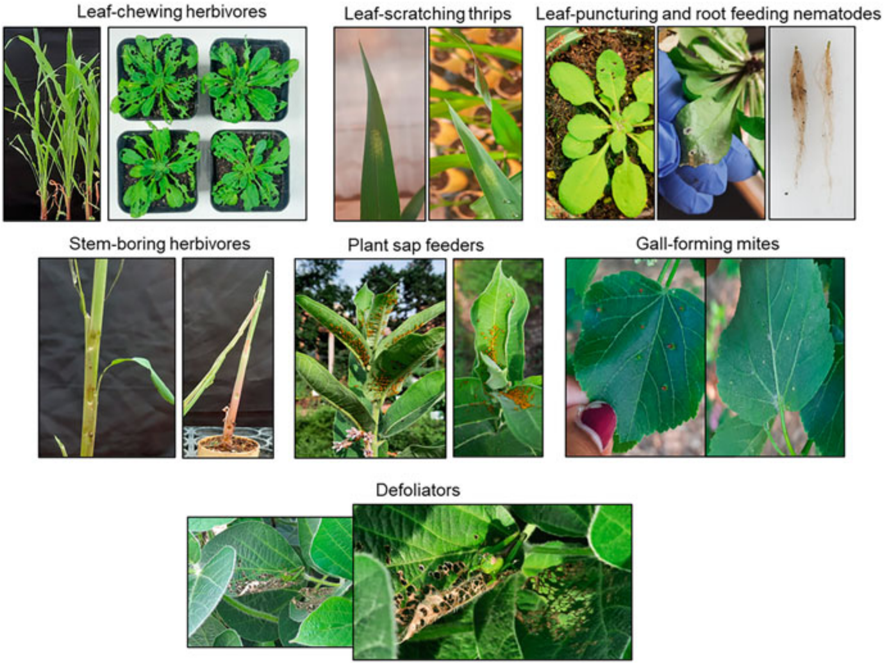

Fig. 12.1 Insects of different feeding guilds incur diverse plant damage phenotypes

of variation in plant reflectance can be employed to study pest attacks and the inflicted damage by using high-throughput cameras.

12.2.2 Imaging Techniques for Insect Damage Plant Phenotyping

Eastman Kodak's invention of the digital camera in 1975 led to a huge implication of visible light imaging technology that was employed to analyze the shoot biomass, leaf area index (LAI), yield-related traits, panicle traits, and architecture traits of plant roots (Kundu et al. 2022; Kundu and Sahu 2021; Yang et al. 2013). The present-day imaging technologies have developed from red-green-blue:visible (RGB), infrared, hyperspectral, and thermal to fluorescence including 3D laser scanning and tomographic imaging by employing magnetic resonance imaging (MRI) or X-ray computed tomography (CT) (Song et al. 2021).

Though there are several commonalities among plant traits in response to biotic and abiotic stresses, HTP methods for screening plants against insects are limited. Recently, digital imaging has been shown to detect differences in the yellowing of rice leaves in response to brown plant hopper and white-backed plant hopper feeding using the differences in red and blue reflectance (Horgan et al. 2020). Whereas visible imaging (red-green-blue; RGB) is primarily used to capture the morphological traits of plants, several recent techniques incorporate the characteristic infrared radiation released from the molecules that can be screened using the near-infrared (NIR) and far-infrared (far-IR) imaging devices. Infrared thermography has recently been reported to be highly applicable for detecting the time and abundance of the emergence of spotted lanternfly, an invasive plant pest in the fields of North America (Liu et al. 2021). Visible/near-infrared hyperspectral imaging was used to find the early infestation of striped stem borer in rice and the degrees of pest infestation (Fan et al. 2017). Another recent study demonstrates that robotic technology facilitated precision agriculture to automatize the selection of 18 different traits from the aboveground parts of the plant, flower, and fruit traits relevant for strawberry breeding programs (James et al. 2022). Similar methodologies could be used in understanding the various aspects of insect-resistant crop breeding.

Another growing area of imaging, hyperspectral imaging, further divides images into a huge portion of electromagnetic spectrums that are used to understand plant growth and insect-mediated damage characteristics. This technique also provides the opportunity to discriminate between the healthy kernels from the insect-damaged ones of wheat or other important crops (Singh et al. 2010) and to detect the soil nematode, *Heterodera schachtii*, in the sugar beet field (Hillnhütter et al. 2011). Similarly, the potential of hyperspectral imaging was also used to accurately detect the attack of the aphid, *Myzus persicae* on Chinese cabbage and *Pieris rapae* caterpillar on cabbage plants (Wu et al. 2016; Zhao et al. 2017). The use of hyperspectral cameras helped to distinguish soybean plants infested with stink bugs and caterpillars where the caterpillar-infested plants displayed varied amounts of reflectance as compared to noninfested plants (Filho 2022).

Fluorescence imaging measures the physiological changes in the plants like photosynthetic efficiency, plant respiration, and chlorophyll loss during biotic or abiotic stresses (Pérez-Bueno et al. 2019). It allows the screening of plants with normal and impaired metabolism, and the degree of changes in metabolism in response to herbivory can potentially help to distinguish the insect-resistant and -susceptible plants. Moustaka et al. (2021) used chlorophyll fluorescence to measure the photosynthetic efficiency of *Spodoptera exigua*-fed tomato plants. Similarly, the chlorophyll fluorescence technique revealed that photosynthesis was inhibited in tobacco plants upon *Manduca sexta* feeding due to jasmonic acid signaling (Nabity et al. 2013). Active IR operates at the lower wavelengths; however, thermal imaging functions in the mid- to longer IR wavelength energies, which are passive and sense the difference in heat energy. These sensors then convert the invisible radiation pattern (temperature) of any object into a visible image that allows to record the surface temperature of any object at a high resolution in two dimensions: black for cold and white for hot. These thermal data can then be used directly or indirectly in multiple ways (Ali et al. 2022; Mahanti et al. 2022). For example, infrared thermal screening has been deployed since several decades to detect infestation by six different developmental stages of the rusty grain beetle, *Cryptolestes ferrugineus*, under the seed coat on the germ layer of the wheat kernels by undergoing temperature screening (Manickavasagan et al. 2008). Insect herbivory has been shown to elevate leaf temperature (Havko et al. 2020; Zavala et al. 2013). Thermal imaging can help in monitoring the pest attack by measuring the leaf temperature and examining the stomatal opening and transpiration. Occasionally, stress conditions result in the closing of stomata followed by a decrease in transpiration and changes in the temperature of plants (Zhang and Zhang 2018). A great advantage for thermal imaging sensors being on the longer wavelengths is that the sensors do not absorb the reflected light and thus remain unaffected by dust, smoke, headlights, and other foreign objects.

12.2.3 Advancements in Plant Phenotyping Through Machine Learning to Develop HTP Platforms and Commercial Products

Though HTP can help screen hundreds of plant genotypes, the data generated with HTP is another bottleneck in handling enormous datasets and downstream data analysis pipelines. Machine learning provides us with tools to develop imaging and video-based products for plant phenotyping. Machine learning has been developed over the years to provide us with a wide range of pest screening techniques that help us to not only detect their presence but also in several instances provide information about the stage of the infesting insects. Support vector machine (SVM) is another such powerful method that is widely employed for pattern recognition (Banerjee and Madhumathy 2022). For the ease of farmers, the health conditions of crops can be analyzed easily by image processing and SVM, which is further incorporated into the Internet of Things (IoT) and sensor networks. SVM has been employed for the detection of leaf damage types in cotton (fungal/bacterial/pests), which shows up to 94% accuracy. SVM has also been incorporated to analyze and confirm the damage degrees caused by the leaf miners by recording the spectral reflectance at several sensitive wavelengths (Dake and Chengwei 2006). The leaf near-infrared spectral reflectance is generally measured by the UV-VIS-NIR spectrophotometer by the Shimadzu Corp. LiDAR is another actively used sensor technique that employs the visible to NIR wavelengths to measure the LAI, alongside the canopy temperature, aboveground biomass, and plant heights (Araus et al. 2018; Campbell et al. 2018; Singh et al. 2016a, 2016b). LiDAR sensors with 360° scanning facility have been used for the detection of flying insects in the range of 50 m. However, the identification of the detected insect/object is not possible for such poor resolution. Scientists are thus working on developing a convolutional neural network (CNN)-based grayscale image detection that would further facilitate identifying the type of object and with the help of a camera recording the image post-detection (Hosseini et al. 2020). Recent advances in the implication of the high-throughput imaging system for the detailed analysis of the type of damage caused by insects include a remote pheromone trap system that continuously monitors the arrival of bugs in large fields using wireless sensor networks (Song et al. 2021).

Insects of any feeding guilds upon entry into the plant cell alter several parameters in the host that includes leaf surface temperature, photosynthetic efficiency, CO_2 gas exchange, stress-induced pigmentation, and other physiological features that are reflected upon spectral imaging. Scientists are thus proposing the launch of a UAV phenotyping platform as the best choice for monitoring insect-mediated plant damage in large fields (Kloth et al. 2012).

12.2.4 Plant Phenotyping for Photosynthetic Gas Exchange Parameters

Insect pests have been reported to affect plant photosynthesis, growth, and yield negatively (Rossato Jr et al. 2019). For instance, aphid infestation can heavily impact the photosynthesis, growth, and yield of Brassicaceae and wheat cultivars (Hussain et al. 2015; Shahzad et al. 2019). Chlorophyll fluorescence imaging has been immensely employed for evaluating the photosynthetic efficiency upon stress in plants. Furthermore, a handheld spectrophotometer (SPAD meter) has been employed for large-scale screening of sorghum plants against greenbugs that measures the levels of chlorosis in infested leaves as compared to the control ones (Girma et al. 1998; Nagaraj et al. 2002). In plant biology, there was an immense need of advanced instruments, which could measure photosynthetic parameters in a nondestructive way.

An advanced high-throughput phenotyping platform has been developed by LI-COR Biosciences that serves the research community by providing cutting-edge scientific instruments to collect and analyze large-scale scientific data with maximum accuracy and ease. Poljaković-Pajnik et al. (2016) determined the aphid feeding effects on multiple poplar cultivars by measuring some of the key physiological parameters such as stomatal conductance and relative chlorophyll concentration using LI-600. LI-600 enables researchers to integrate additional data such as GPS location and the angle of the leaf relative to sunlight. They reported a significant decrease in photosynthesis rate up to 25–75% and an increased respiration rate ranging from 15 to 56.77%. They concluded that aphid colonization reduced stomatal conductance that adversely affects other physiological processes. Similarly, determining leaf area index (LAI) of fruit canopy plays an important role in pest management such as amount of pesticide to be applied per unit area, developing efficient spraying strategies, improved pesticide delivery, and cost reduction (Zhai et al. 2018; Wu et al. 2017; Wu 2007; Verrelst et al. 2015). Liu et al. (2021) took the advantage of LAI-2200C plant canopy analyzer to nondestructively measure LAI with maximum accuracy and ease in parallel with multispectral data acquisition by an unmanned aerial vehicle to propose machine learning models to enable efficient management of large-scale apple orchards.

Similarly, Chen et al. (2017) measured the net photosynthesis rate (PN) broadleaf evergreen canopy, *Schima superb*, in response to the attack of the moth, *Thalassodes quadraria*, using Li-6400XT portable photosynthesis system and concluded that insect outbreaks negatively impact *S. superba* by retarding the radial growth. Furthermore, rice tungro bacilliform virus (RTBV) and rice tungro spherical virus (RTSV) cause a complex disease in rice named tungro that affects photosynthetic machinery, chlorophyll biosynthesis, Fe/Zn homeostasis, and gene regulation associated with this biological process (Hull 1996; Sailaja et al. 2013; Mangrauthia et al. 2012; Srilatha et al. 2019). Symptoms include stunting, twisting of leaf tips, leaf discoloration, and reduction in ear-bearing rice tillers (Azzam and Chancellor 2002; Hull 1996). Insect vector green leafhopper facilitates the disease transfer (Azzam and Chancellor 2002; Hibino et al. 1978). Srilatha et al. (2019) analyzed the effect of disease on rice plant photosynthesis, biosynthesis of chlorophyll, and ion homeostasis. In this study, they used a high-throughput platform, Li-Cor 6400 to determine stomatal conductance (gs), net photosynthetic rate (PN), intercellular CO_2 concentration (Ci), and transpiration rate (E). Their finding suggests the involvement of RTBV ORF1 protein in regulating host cell photosynthesis and symptom development. Though there are several reports available on the effects of insect infestation on plant photosynthesis, the exact underlying mechanisms are largely unknown. Recently, a breakthrough study revealed that thrips can ingest chloroplasts, which are the core of plant photosynthesis (Wu et al. 2022). These mechanisms would help us to understand the commonalities between biotic and abiotic stress responses and, consequently, help to develop common HTP platforms for multiple stress agents.

12.2.5 Connecting the Effects of Biotic and Abiotic Stresses on Plant Gas Exchange Parameters

Plant responses to biotic and abiotic stress agents may complement/antagonize to each other. It has been reported that plant defenses to insects may get enhanced/suppressed in interaction with abiotic stress conditions (Table 12.1). For instance, in a study conducted by Xu et al. (2018), authors used LI-190R equipped with an LI-1500 radiation illuminance measuring instrument from LI-COR biosciences to measure PAR data to study maize diurnal responses to different water stresses at the canopy scale and concluded that both leaf folding and physiological changes are deployed by maize to cope with water stress. Similarly, Gago et al. (2017) used Li-Cor 6400 to measure leaf gas exchange, photosynthesis, and stomatal conductance to study metabolic components of water stress within a vineyard. From this study, they proposed an integrative methodology that combines UAV-based remote sensing, metabolomics, and organ-level physiology of the vineyard canopy responses to water stress. Liu et al. (2022) took advantage of a fast-response infrared gas analyzer (LI-500A), leaf area index analyzer (LAI-2200C), and canopy surface transpiration analyzer (LI-6400XT) from Li-Cor Inc. to measure the water stress index for monitoring water status in an oak plantation. Above-cited examples suggest the efficacy of the Li-Cor platform to assess water-related stress by measuring related physiological parameters in a high-throughput manner. In a recent study, Kansman et al. (2022) reported that plant water stress negatively impacts aphid performance. They correlated poor aphid performance with water stress-induced plant defense and reduced nutritional quality. Drought stress promotes resistance to herbivory by induction of phytohormone-mediated defense response (Nguyen et al. 2016; Blundell et al. 2020; Lin et al. 2021). Similarly, drought stress also induces the level of sucrose in plant phloem (Marček et al. 2019). Previously, it has been reported that high concentrations of some sugars such as trehalose, fructose, and

Table 12.1 High-throughput phenotyping used in different plant-insect study systems

Crop(s)	Insect(s)	Tool(s)/technique (s) used	Parameter(s) recorded	Conclusions	References
Arabidopsis (*Arabidopsis thaliana*) and lettuce (*Lactuca sativa*)	Aphid (*Myzus persicae*)	Video tracking	Aphid behavior	Video tracking can be used to screen large plant populations for resistance to aphids	Kloth et al. (2015)
Soybean (*Glycine max*)	Stink bugs (*Nezara viridula* and *Piezodorus guildinii*)	LI-COR	Levels of photosynthetically active radiation	Isoflavonoid induction by UV-B radiation provides resistance to stink bugs in soybean	Zavala et al. (2015)
Tomato (*Solanum lycopersicum*)	Whitefly (*Bemisia tabaci*)	LI-COR	Net photosynthetic rate	Elevated CO_2 conditions increased plant photosynthetic rate and confer resistance to whitefly	Guo et al. (2016)
Tomato (*Solanum lycopersicum*)	Tomato leaf miner (*Tuta absoluta*) and silverleaf whitefly (*Bemisia tabaci*)	LI-COR	Photosynthetic rate, transpiration rate, and stomatal conductance	Plants under nitrogen or water-limited conditions significantly affected *T. absoluta* survival and development, while survival of *B. tabaci* was affected only by nitrogen limitation	Han et al. (2016)
Arabidopsis (*Arabidopsis thaliana*)	Green peach aphids (*Myzus persicae*)	Video tracking/ EthoVision	Aphid behavior	Feeding behavior on knockout mutants and overexpression lines showed that *WRKY22* increases susceptibility to aphids	Kloth et al. (2016)

Tomato (*Solanum lycopersicum*)	Glasshouse whitefly (*Trialeurodes vaporariorum*)	EPG	Feeding behavior	In wild tomato species, whiteflies exhibited a shorter duration of second feeding bout, reduced pathway phase probing, longer salivation in phloem, and more non-probing activities in the early stages of the EPG compared to the commercial tomato. It confirms resistance factors' presence in wild tomato	McDaniel et al. (2016)
Soybean (*Glycine max*)	Soybean looper (*Chrysodeixis includens*), corn earworm (*Helicoverpa zea*), fall armyworm (*Spodoptera frugiperda*), and velvet bean caterpillar (*Anticarsia gemmatalis*)	ImageJ	Defoliation	Soybean resistance to insects was enhanced by QTL-M and QTL-E. Pyramiding these QTLs with cry1Ac increases protection against Bt-tolerant pests	Ortega et al. (2016)
Maize (*Zea mays*)	Western corn rootworm (WCR; *Diabrotica virgifera virgifera*)	Positron-emission tomography, root autoradiography, and radiometabolite flux analysis	Maize tolerance to WCR by auxin biosynthesis	WCR feeding induces local changes in roots, which leads to increased auxin biosynthesis flux and provides tolerance to WCR	Qu et al. (2016)
Arabidopsis (*Arabidopsis thaliana*)	Western flower thrips (*Frankliniella occidentalis*)	Video tracking	Thrip behavior	Video tracking is a promising phenotyping tool to assess host-plant resistance to thrips in large plant populations	Thoen et al. (2016)

(continued)

Table 12.1 (continued)

Crop(s)	Insect(s)	Tool(s)/technique (s) used	Parameter(s) recorded	Conclusions	References
Tomato (*Solanum lycopersicum*)	Whitefly (*Bemisia tabaci*)	EPG	Stylet penetration activities and inoculation of tomato chlorosis virus (ToCV) in tomato	ToCV inoculation is mainly associated with stylet activities in phloem sieve elements	Prado Maluta et al. (2017)
Wheat, *Triticum aestivum* (L.), and *T. monococcum* lines	English grain aphid (*Sitobion avenae*)	EPG	Feeding behavior	Mycorrhizal colonization increased aphid phloem feeding on wheat varieties	Simon et al. (2017)
Chinese cabbage (*Brassica rapa*)	Fungal pathogen *Pandora neoaphidis*-infected and uninfected green peach aphid (*Myzus persicae*)	EPG	Feeding behavior	Fungal infection has an effect on the feeding behavior of aphids, which potentially decreases the feeding capacity	Chen et al. (2018)
Olive (*Olea europaea*)	Meadow spittlebug (*Philaenus spumarius*)	EPG, video recordings, microcomputer tomography (micro-CT)	Feeding behavior	Correlation was observed between EPG waveforms and specific biological behaviors of *P. spumarius* captured by video recordings	Cornara et al. (2018)
Cabbage (*Brassica oleracea* L.)	Diamondback moth (*Plutella xylostella*) and aphids (*Myzus persicae*)	ImageJ	Photosynthetic area of leaves	Seed coating with jasmonic acid and chitosan leads to long-term defense priming in chewing and sap-feeding insects	Haas et al. (2018)
Maize (*Zea mays* L.)	Green belly stink bugs (*Dichelops melacanthus*)	Hyperspectral imaging	Leaf phytocompound levels	Hyperspectral imaging may be considered as a powerful tool to increase our understanding on plant communication after herbivory	do Prado Ribeiro et al. (2018)

Arabidopsis (*Arabidopsis thaliana*)	Western flower thrips (*Frankliniella occidentalis*)	Video tracking/ EthoVision	Thrip behavior	The analysis using software resulted in much larger contrasts in behavior traits of thrips than previously reported	Jongsma et al. (2019)
Cassava (*Manihot esculenta*), sweet potato (*Ipomoea batatas*), tomato (*Solanum lycopersicum*), and cotton (*Gossypium hirsutum*)	Whitefly (*Bemisia tabaci*)	EPG	Feeding behavior	Preference of host species was recorded, and host-specific whiteflies' feeding was not restricted to its host	Milenovic et al. (2019)
Five capsicum species (*Capsicum annuum*., *C. chinense*, *C. baccatum*, *C. pubescens*, and *C. eximium*)	Thrips (*Frankliniella occidentalis*)	ilastik and ImageJ	Quantification of feeding damage	In capsicum, leaf position and ontogeny are important determinants of resistance against thrips	Visschers et al. (2019)
Cotton (*Gossypium hirsutum*)	Cotton bollworm (*Helicoverpa armigera*) and cotton leafworm (*Spodoptera litura*)	ImageJ	Trichome and stomatal densities and length	Tolerant cotton variety had longer trichome and high stomatal density compared to susceptible variety	Diaz-Montano et al. (2006)
Arabidopsis (*Arabidopsis thaliana*)	Shield bug (*Eurydema oleracea*)	ImageJ	Leaf damage	*E. oleracea* suppresses plant defense by manipulating hormone signaling components in plants	Grover et al. (2020)
Sorghum (*Sorghum bicolor*)	Sugarcane aphid, (*Melanaphis sacchari*)	LI-COR and metabolomics	Photosynthesis parameters	Sorghum-tolerant line has robust photosynthetic machinery along with higher levels of OPDA	Grover et al. (2020)

(continued)

Table 12.1 (continued)

Crop(s)	Insect(s)	Tool(s)/technique (s) used	Parameter(s) recorded	Conclusions	References
Grass species (*Brachypodium distachyon*)	Cotton bollworm (*Helicoverpa armigera*) and house cricket (*Acheta domesticus*)	ImageJ	Leaf surface morphology	Silicon changes the morphology of defense structures on leaves and acts as a direct defense against leaf-chewing insects	Hall et al. (2020)
Potato (*Solanum tuberosum*)	Aphid (*Myzus persicae*)	LI-COR	Stomatal conductance	With drought stress and aphid infestation, stomatal conductance was not affected	Quandahor et al. (2020)
Kidney bean (*Phaseolus vulgaris*)	Western flower thrips (*Frankliniella occidentalis*)	LI-COR	Leaf area	Kidney bean leaf damage caused by thrips was significantly affected by CO_2 level and wounding time	Qian et al. (2021)
Apple (*Malus domestica*)	Woolly apple aphid (*Eriosoma lanigerum*)	EPG	Feeding behavior	Aphids prefer to feed on shoots of plant compared to other tree parts	Zhou et al. (2021b)
Tomato (*Solanum lycopersicum*)	Mirid bug (*Tupiocoris cucurbitaceus*)	EthoVision	Prey-searching behavior	Mirid bug preferred to prey on eggs of leaf miner (*Tuta absoluta*)	Cáceres et al. (2022)
Grapevine (*Vitis vinifera*)	Two spittlebugs [meadow spittlebug (*Philaenus spumarius*) and spittlebug (*Neophilaenus campestris*)]. Two sharpshooter leafhoppers	DC-EPG	Feeding behavior	Sharpshooters tended to perform significantly more probes than spittlebugs	Markheiser et al. (2022)

	[rhododendron leafhopper (*Graphocephala fennahi*) and green leafhopper (*Cicadella viridis*)				
Cotton genotypes	Different sucking pests	Leaf area meter	Leaf area	Leaf area was significantly declined with increasing sucking insect pest infestation levels	Singh et al. (2022)

sucrose negatively affect aphid performance (Douglas 2006; Grover et al. 2022b). Drought stress also contributes to the production of plant defensive compounds such as peroxidases, phenolics, glucosinolates, and physical structures such as callose, which deters insect pest infestation (Kansman et al. 2022). Hence, measuring physiological parameters pertaining to water stress may be recommended as a key component of HTP of insect performance on crops.

12.2.6 Development of Software Packages to Analyze Image Data

Several imaging platforms such as fluorescence imaging, multispectral imaging, hyperspectral imaging, thermal imaging, 3D imaging, and visible imaging have enabled high-throughput phenotyping in detecting and controlling crop losses to disease and pests (Singh et al. 2020). In their review, Minervini et al. (2015) describe that the speed of phenotype extraction through image analysis (the software) is not matching the speed of genotyping and remains a bottleneck in modern-day sustainable agricultural practices. However, in recent years, a cascade of publicly available software has been developed to analyze high-throughput plant phenotyping data. For chewing insects, digital imaging has been employed with the help of scanners and public domains to feed the software with the entire and fed portions of leaves, thus largely cutting the time for large-scale plant phenotyping (O'Neal et al. 2002). Maize-IAS, an easy-to-use image analysis software, uses artificial intelligence and deep learning for high-throughput maize phenotyping (Zhou et al. 2021a). Maize-IAS offers a plethora of functions for the processing of large datasets and enables automation, which greatly minimizes human error in performing quantitative analysis. Similarly, HSI-PP, a stand-alone open-source software that combines advanced image processing with the extraction of meaningful information from hyperspectral images, enables decision-making in agricultural research (ElManawy et al. 2022). HSI-PP delivers by preparing images for deep leaning analysis and by enabling the machine learning model for classification and regression. HSI-PP is expected to be revolutionary in improving the efficiency of high-throughput phenotyping in agricultural management, plant physiology, breeding programs, and functional genomics. Gehan et al. (2017) developed and rewritten Plant CV v2, an improved version of Plant CV v1.0, on the Python platform to add novel functionality in image analysis to support high-throughput phenotyping. Plant CV v2 offers new functionalities such as white balancing, size marker normalization, auto-thresholding, multiplant detection, watershed segmentation, combined image processing, improved image segmentation, and landmarking. Gehan et al. (2017) explicitly elaborate the way each of these applications substantially improves image analysis in a user-convenient way.

12.3 High-Throughput Phenotyping for Insects

In addition to studying plant traits, insect parameters (behavior, growth, and reproduction) are other important aspects that can be studied for screening plants for insect resistance. Unlike plant parameters, insect parameters are quicker to study and record. For instance, insect growth differences can be measured in a few days compared to the effects of insect attacks on plants that can last for several days. Studying insect-feeding behavior on varied plant varieties deduces the status of resistant and susceptible plants. Moreover, insect behavior studies usually range from a few minutes to hours. Robust phenotyping systems can fasten the process of selecting resistant plant types with a high level of accuracy. The basis for designing HTP to understand insect behavior depends on parameters like feeding behavior, damage caused to crops, and growth stages of the insects. In this section, we have discussed the currently available tools for identifying resistant plants by studying insect behavior.

12.3.1 Video Tracking/EthoVision

Plant images can provide a greater amount of information about plant traits, feeding damage, and physiological changes in plants in response to insect feeding. However, tracking the behavior and movement of insects on plants can help to analyze the acceptance or rejection of plant material. An automated video tracking software called EthoVision was developed, which has been developed over the years that showed high potential for screening a large number of host plants for insect resistance, tracking the movement of insects, and recording their behavior pattern (Noldus et al. 2002; Kloth et al. 2015). Additionally, video tracking can also reduce resource use, such as using leaf discs instead of the whole plant. For aphids, automated video tracking was employed to track the movement, stylet penetrations, and feeding patterns on leaf discs of *Arabidopsis* and lettuce to identify the level of resistance. The analyses were performed in EthoVisionXT software to record the duration of aphid penetration and detailed movements over the leaf disc (Kloth et al. 2015). This study also offers unique opportunities to employ video tracking system for other piercing and sucking-type and/or rasping-sucking-type insects like thrips. Recently, a choice assay setup for western flower thrips (WFT, *Frankliniella occidentalis*) was developed, and an automated video tracking system was used to track the choice made by thrips on *Arabidopsis* plant accessions for resistance (Thoen et al. 2016). Further T-maze system was developed for insect choice assay (WFT) automation and analysis of the tracking of insect movement simultaneously. The integrated approach was named EntoLabs (Jongsma et al. 2019). Recently, a Trax software was developed to track the movement of color-tagged insects in video recording (Gal et al. 2020). Collectively, EthoVision has been extensively used in plant-insect interactions in a wide range of systems such as clover seed weevils on white and red clovers (Nyabuga et al. 2015), corn root worm on maize (Bernklau and Bjostad 2009), whitefly on eggplants (Moreno-Delafuente et al. 2013), tobacco hornworm on corn pericarp (Tayal et al. 2020), aphid on lettuce (Booij et al. 2013), green rice leafhoppers on rice plants (Chang et al. 2021), and *Eucalyptus* weevils on *Eucalyptus* (Branco et al. 2019). Further automation in assay setups, data recordings, and analyses would immensely enhance the use of video tracking in plant-insect interaction studies.

12.3.2 Electrical Penetration Graph (EPG) Technique for Sap-Sucking Insects

Electrical penetration graph (EPG) technique is a powerful tool to precisely measure the feeding behavior of piercing and sucking type of insects (Tjallingii 1985). This technique is widely used to understand plant-insect interactions, characterize plant resistance to insects, and understand insecticide resistance in insects and virus transmission (Moreno et al. 2012; Garzo et al. 2016; Grover et al. 2019). Hemipteran insects use their stylets to pierce the cell wall and penetrate inside to ingest the cell sap and derive away the nutrients from plants causing minimal visible injury to plants. Therefore, EPG system allows to track the movement of hemipteran insects' stylets and to study the probing behavior of insects (Backus and Shih 2020). It can precisely tell where the insect is exactly feeding on the plant part in a nondestructive manner. On the contrary, stylectomy is a destructive technique where aphid stylet fed on phloem tissue is severed to quantify the proteins present in phloem sap, which could potentially be involved in plant defenses, hence not preferred over EPG. A wide adaptability of EPG in all crops such as sorghum, corn, soybean, tea, wheat, cotton, tomato, tobacco, beans, potato, and *Arabidopsis*, to study the feeding behavior of hemipterans, has significantly contributed to enormous improvements over the last three decades (Pegadaraju et al. 2007; Trębicki et al. 2012; Civolani et al. 2014; Pearson et al. 2014; Cervantes et al. 2016; Garzo et al. 2016; Grover et al. 2019, 2022b; Souza and Davis 2021; Jhou et al. 2021; Rech et al. 2021; Salsabillah et al. 2021).

EPG system consists of two electrodes, namely the plant electrode and the insect electrode (Van Helden and Tjallingii 2000). When an insect stylet pierces through plant tissues, it completes the circuit leading to the flow of current. Before sustained feeding starts on plants, insects insert their stylet intracellularly or intercellularly to sample the cell contents. EPG generates distinct waveforms associated with different activities performed by insects. The waveforms are mainly categorized into three phases: (1) pathway phase where an insect is looking for potential feeding sites, inserts the stylet into plant tissue, samples the cell content, and accepts or rejects the plant; (2) phloem phase where the insect salivates and aggressively ingests the feeds on the phloem tissue or sieve elements for longer periods; and (3) xylem phase where it feeds on water (Nalam et al. 2018). In non-probing phase, insects generally do not perform any feeding behavior other than walking or relaxing on the plant (Nalam et al. 2018). EPG has revolutionized the plant-insect interaction area of study due to its ability to screen insect-resistant host plants faster and understand host resistance barriers to insects precisely. This technique can collectively demonstrate host resistance based on antibiosis or antixenosis (Diaz-Montano et al. 2006). Phloem-based host resistance is usually attributed to the presence of antibiotic factors in phloem, which negatively affects insect physiology. Although EPG provides accurate data, it is a sensitive system and requires high human precision while handling insects and can generate data only from a limited number of plants at a time. Over time, advancements have been made in automating the EPG analysis of different waveforms as manually calculating each waveform is very tedious and time-consuming. Software like MacStylet, Aphid-AutoEPG, EPF-Calc, and A2EPG (Febvay et al. 1996, Giordanengo 2014, Adasme-Carreño et al. 2015, Prufer et al. 2014) have been developed to bring automation in EPG analysis.

12.4 Functional Phenomics

Functional phenomics refers to the interdisciplinary emerging approach integrating high-throughput phenotyping, plant physiology, bioinformatics, and "*omic*" approaches (York 2019; Jammer et al. 2022). The overall goal of functional phenomics is to understand and connect plant phenotypes with plant functions. The use of various phenotyping methods for understanding plant phenotypes and insect behavior has significantly advanced the knowledge in the area of plant-insect interactions (Table 1). Despite these significant outcomes, understanding and establishing the relationship between plant phenotypes and plant function have been a bottleneck for breeding superior and resilient cultivars despite the enormous progress in knowledge available in genetics. For instance, it has been shown that the root crown architectural phenes are correlated to rooting depth, yield, and senescence phenology (Slack et al. 2018). This information would be immensely helpful in breeding cultivars with desired traits. Functional phenomics in the area of plant-insect interactions has not been explored much. For example, a recent study from Australian *Vitis* sp. in abiotic stress reports the use of RGB-based digital imaging and *LI-COR* measurements to correlate the high temperature-mediated accumulation of Cl^{-1} ions in the lamina of the *Vitis* leaves (Dunlevy et al. 2022). This technique could be further extrapolated for its employment in herbivory, where leaf-chewing caterpillars lead to a significant accumulation of Ca^{2+} ions in the plant cell within seconds. Moreover, plant morphological characteristics such as the presence of trichomes, leaf thickness, lamina type, and stem thickness can also impact the plant's resistance to herbivory (Heinze 2020; War et al. 2012). Functional phenomics has the potential to identify biomarkers/biosignatures directly related to plant resistance, possibly by combining HTP and "*omic*" approaches (Fig. 12.2). Going forward, this emerging approach offers unique opportunities to combat global challenges by accelerating the process of developing pest-resistant genotypes.

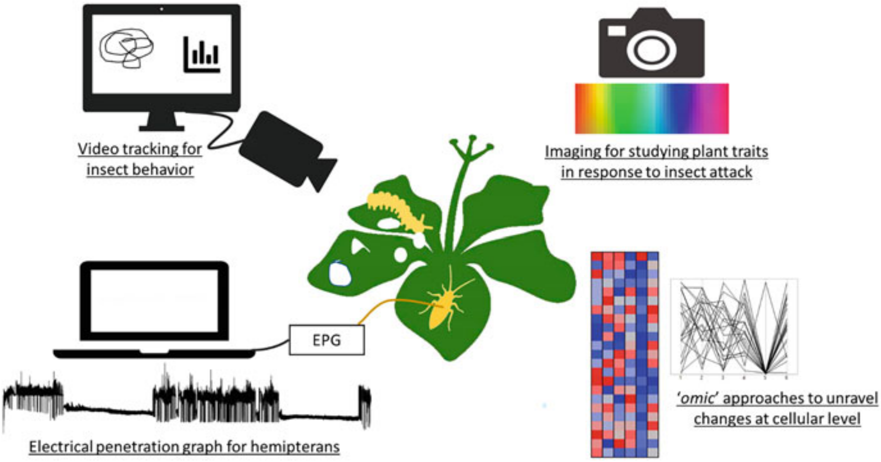

Fig. 12.2 A holistic representation of functional phenomics approach to understand plant-insect interactions using multiple methods and linking cellular and physiological phenotypes to insect phenotype

12.5 Bottlenecks in the Advancement of HTP in Plant-Insect Interactions

Despite the progress of HTP in plant sciences, it is still not being largely used for the screening of insect-resistant plants. The cost of HTP in plants is still very high, and scientists with limited funding for research cannot afford to set up this system in individual labs and departments. For such a kind of initiative, scientists need to collaborate within and beyond the area of entomology. Though working on different plant-insect systems, entomologists can still use common tools to address specific research questions. Furthermore, interdisciplinary collaborations are highly required with plant scientists, engineers, data scientists, and statisticians. Entomologists are primary participants in the area of host plant resistance to insects (Peterson et al. 2017). There are a handful of scientists with interdisciplinary expertise in plant physiology, biochemistry, metabolism, plant anatomy, and water relations. The lack of interdisciplinary training to entomologists is still an obstacle to the development of novel and innovative tools to move the discipline forward. Additionally, to streamline the phenotyping process globally, several organizations like European Plant Phenotyping Network (EPPN) and International Plant Phenotyping Network (IPPN) have been working on setting the standards for the quantification of the phenotypic data to be used worldwide (Williams et al. 2018).

12.6 Conclusions and Future Directions

Food security is a common challenge where all agricultural scientists are working towards using different paths and trajectories. To meet the global food security challenges of the future in a sustainable manner, research on plant-insect interactions is one of the top-most priorities where the natural potential of plants to fight against insects can be unlocked. Considering the ill effects of chemicals on the environment, the public perception of GMOs, and the increasing cost of seeds for transgenic plants, research on plant-insect interactions can accelerate the development of insect-resistant plants. To meet the pace of food security challenges, sustainable agricultural products have to be developed sooner than later. HTP in plants for insect resistance needs to be utilized to match the pace of molecular breeding and genomic studies. In order to achieve this goal, we need to foster interdisciplinary teams of scientists' workforce. Consequently, it is crucial that entomologists, plant scientists, statisticians, data scientists, and engineers work collaboratively to develop and utilize HTP capabilities for accelerating the development of sustainable insect control products. HTP would enormously increase the capacity to screen plant populations against insect infestations. This would ultimately assist basic and applied studies in the area of plant-insect interactions to understand the genetic basis of insect resistance.

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