Ramesh Arora · Surinder Sandhu
Editors

Breeding Insect Resistant Crops for Sustainable Agriculture

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Ramesh Arora
Department of Entomology & Zoology
Eternal University
Baru Sahib, Himachal Pradesh, India

Surinder Sandhu
Department of Plant Breeding and Genetics
Punjab Agricultural University
Ludhiana, Punjab, India

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Preface

The world population has been galloping upward at an unprecedented rate in the recent past and has jumped from 3.5 billion to more than 7.4 billion during the last 50 years. So far, modern agricultural technologies have enabled us to meet the rising demand for food, feed, and fiber for the increasing human population through improved productively of major crops. But modern crop protection practices, based largely on the intensive use of pesticides, have failed to reduce crop losses by insect-pests, which still destroy an estimated one-fifth of the global agricultural production of important crops. Rather, pesticidal interventions in the agroecosystem have created human health hazards, lowered environmental quality, and disrupted natural control of pests. Therefore, there is an urgent need to strengthen non-chemical approaches for reducing pest damage, which should be safe, economical, and durable.

Pest-resistant cultivars represent one of the most environmentally benign, economically viable, and ecologically sustainable options for utilization in pest management programs. Beginning in the 1920s, modern work on plant resistance to insects was pioneered by Professor R. H. Painter and colleagues at Kansas State University, USA. This paved the way for notable successes in developing pest- and disease-resistant cultivars. Hundreds of insect-resistant cultivars of rice, wheat, maize, sorghum, cotton, sugarcane, and other crops have been developed worldwide and are grown extensively for increasing and stabilizing crop productivity. Remarkable success was achieved in developing multiple pest- and disease-resistant rice cultivars especially IR-36, IR-64, IR-72, and IR-74 by Professor G. S. Khush and colleagues at the International Rice Research Institute, Los Banos, Philippines. The wide adoption of these cultivars led to a quantum jump in rice production in tropical Asia. Similar but less spectacular successes were also achieved in several other important crops. As per recent estimates, the annual economic value of arthropod resistance genes deployed in global agriculture is greater than US$2 billion.

Despite spectacular achievements and even greater potential for contributing to sustainable agriculture, only a handful of books have been published on the topic of host-plant resistance to insects. Professor R. H. Painter published his monumental book *Insect Resistance in Crop Plants* (MacMillan) way back in 1951 and laid the foundations of HPR to insects as a sub-discipline in agricultural entomology and crop protection. Other major works include *Plant Resistance to Insects: A Fundamental Approach* (Wiley) by C. Michael Smith (1989), *Host Plant Resistance to Insects* (CABI) by N. Panda and G. S. Khush (1995), and *Plant Resistance to*

Arthropods: Molecular and Conventional Approaches (Springer) by C. Michael Smith (2005).

The advent of molecular biology tools has enabled us to overcome some of the major limitations of conventional breeding approaches. The new book *Breeding Insect Resistant Crops for Sustainable Agriculture* emphasizes the recent advances in host-plant resistance to insects, which have enhanced our capability and speed to develop insect-resistant cultivars for improving productivity as well as for bringing stability in agricultural production.

The introductory chapter by the two editors gives an overview of the fascinating science of insect-plant interrelationships, which provides the bases for development of insect-resistant crop plants. The second chapter provides a concise account of the extent of losses caused by insect-pests in important crops. The commercial cultivation of insect-resistant cultivars can help in minimizing these losses in an environmentally benign manner. The breeding methods for developing insect resistance in self- and cross-pollinated crops have been elaborated in Chap. 3. The new insights on structural and functional aspects of insect resistance conferring R-genes have been emphasized for their better utilization by researchers.

Leaf hoppers and plant hoppers are major biotic constraints in rice production, and consistent research efforts on HPR to hoppers have resulted in identification of more than 70 genes for resistance to hoppers. Several hopper-resistant rice cultivars are being grown commercially around the world, and their development, status, and prospects are reviewed in Chap. 4. Several species of insect-pests limit the production and productivity of grain legumes, which are major dietary sources of proteins for the humans. The success, limitations, and prospects of development of insect-pest-resistant genotypes of grain legumes have been reviewed in Chap. 5. The productivity of oilseed brassicas is severely affected by aphid pests, but not much progress has been made in breeding for resistance in brassicas against aphids primarily due to nonavailability of resistance source within the crossable germplasm as well as lack of knowledge on its trait genetics. The problems and prospects for development of aphid resistance in brassicas are enumerated in Chap. 6.

Maize, being a leading contributor to the world cereal basket, has undergone various improvements through diverse breeding tools to minimize the losses due to insect-pests. Chapter 7 provides an overview of these efforts including the application of novel breeding methods for development of insect-resistant cultivars of maize. Sorghum and millets are crucial to the food and nutritional security in arid and semiarid regions of the world. Considerable success has been achieved in developing sorghum and millets genotypes resistant to shoot fly and to a lesser extent to stem borer and other pests. The progress, problems, and prospects for incorporating insect-pest resistance in sorghum and millets are outlined in Chap. 8. Cotton crop suffers from ravages by a wide range of insect-pests and has received a lot of attention for nearly a century for incorporating resistance to sucking pests as well as bollworms using conventional and molecular techniques. The development of insect resistance in cotton is described in Chap. 9.

The development of insect-resistant cultivars of fruit plants provides a durable alternative to the use of insecticides for management of insect-pests. The classical breeding

approaches have been complimented with innovative biotechnological tools to achieve the desired results as discussed in Chap. 10. The status of development of rice genotypes resistant to stem borers and gall midge presents two contrasting scenarios as illustrated in Chap. 11. The sources for gall midge resistance available in crossable gene pool have been exploited to produce gall midge-resistant cultivars, which have been released for commercial cultivation. But, due to a lack of sources of resistance against stem borers, the alternate approaches like Bt-transgenics and RNAi are being pursued for development of borer-resistant rice.

Chapter 12 outlines the sources of resistance available for major insect-pests of mung bean and urd bean, mechanism of resistance, and current status as well as prospects for development of insect-resistant cultivars in these crops. Insects being versatile organisms can overcome plant resistance by developing new biotypes, which adversely affect the sustainability and durability of insect-resistant cultivars. The evolution of insect biotypes and strategies for their management are outlined in the concluding chapter.

We are thankful to all the contributors for the meticulous job they have done in preparing their respective chapters. Special thanks are due to Professor M. S. Kang, formerly vice-chancellor at Punjab Agricultural University, Ludhiana, for guiding us throughout the preparation of this manuscript. It is hoped that the book will fill the wide gap in literature on breeding for insect resistance in crops. It is intended for plant breeders, entomologists, plant biotechnologists, and IPM experts, as well as those working on sustainable agriculture and food security.

Baru Sahib, Himachal Pradesh, India — Ramesh Arora
Ludhiana, Punjab, India — Surinder Sandhu

Contents

Contributors

P.K. Arora Regional Research Station, Punjab Agricultural University, Abohar, India

Ramesh Arora Department of Entomology & Zoology, Eternal University, Baru Sahib, Himachal Pradesh, India

Department of Entomology, Punjab Agricultural university, Ludhiana, India

S.S. Banga Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India

J.S. Bentur Directorate of Rice Research, Hyderabad, India

Vitthal R. Bhagwat ICAR-Indian Institute of Millets Research, Hyderabad, India

Dharminder Bhatia Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India

D.S. Brar School of Agricultural biotechnology, Punjab Agricultural University, Ludhiana, India

Plant Breeding, Genetics, and Biotechnology Division, International Rice Research Institute, Los Baños, Philippines

Harpreet Kaur Cheema Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India

M.I.S. Gill Department of Fruit Science, Punjab Agricultural University, Ludhiana, India

Jagdish Jaba International Crop Research Institute for Semi-Arid Tropics (ICRISAT), Patancheru, India

Manjit S. Kang Department of Plant Pathology (Geneticist), Kansas State University, Manhattan, KS, USA

Punjab Agricultural University, Ludhiana, India

Chikkappa G. Karjagi Indian Institute of Maize Research, New Delhi, India

Sanjeev Kumar Kataria Punjab Agricultural University, Bathinda, India

Jaswinder Kaur Indian Institute of Maize Research, New Delhi, India

Rubaljot Kooner Department of Entomology, Punjab Agricultural University, Ludhiana, India

Krishan Kumar Regional Research Station, Punjab Agriculture University, Abohar, India

Pradyumn Kumar Indian Institute of Maize Research, New Delhi, India

Sarwan Kumar Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India

Soujanya P. Lakshmi Indian Institute of Maize Research, New Delhi, India

Gurpreet Singh Makkar Department of Plant Breeding & Genetics, Punjab Agricultural University, Ludhiana, Punjab, India

M.G. Mallikarjuna Indian Institute of Maize Research, Pusa Campus, New Delhi, India

Division of Genetics, Indian Agricultural Research Institute, New Delhi, India

Aditya Pratap ICAR-Indian Institute of Pulses Research, Kanpur, India

P. Sanjana Reddy ICAR-Indian Institute of Millets Research, Hyderabad, India

Surinder Sandhu Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, Punjab, India

P.S. Sarao Department of Plant Breeding & Genetics, Punjab Agricultural University, Ludhiana, India

J.C. Sekhar Indian Institute of Maize Research, New Delhi, India

H.C. Sharma Dr. Y. S. Parmar University of Horticulture and Forestry, Nauni, India

International Crop Research Institute for Semi-Arid Tropics (ICRISAT), Patancheru, India

Smriti Sharma Department of Entomology, Punjab Agricultural University, Ludhiana, India

G. Shyam Prasad ICAR-Indian Institute of Millets Research, Hyderabad, India

Paramjit Singh Punjab Agricultural University, Bathinda, India

S.B. Suby Indian Institute of Maize Research, New Delhi, India

G.K. Sujayanand ICAR-Indian Institute of Pulses Research, Kanpur, India

Gaurav K. Taggar Department of Plant Breeding & Genetics, Punjab Agricultural University, Ludhiana, India

Vilas A. Tonapi ICAR-Indian Institute of Millets Research, Hyderabad, India

Sumit Vashisth International Crop Research Institute for Semi-Arid Tropics (ICRISAT), Patancheru, India

About the Editors

Dr. Ramesh Arora is professor of entomology at Eternal University, Baru Sahib, HP, India, and holds a Ph.D. in entomology (1990) from Punjab Agricultural University (PAU), Ludhiana, Punjab, India. He served at PAU for more than 37 years as a researcher in various capacities. His research interests include development and dissemination of IPM in cotton, vegetables, oilseeds, and forage crops and climate-resilient pest management. Dr. Arora has nearly 300 publications, including 90 research articles in refereed national and international journals and 100 conference/symposia presentations. He has also authored/edited 14 books on entomology, pest management, and sustainable agriculture and contributed 42 book chapters in edited books published by leading publishers. He has been involved in designing course curricula and teaching UG and PG courses in entomology. He has guided the research work of more than 30 PG students in entomology, plant pathology, zoology, microbiology, biochemistry, agricultural biotechnology, and extension education. Dr. Arora is associated with several professional societies as vice president/general secretary/editor in chief/EC member and has served as organizing secretary/co-organizing secretary/member of the organizing committee of more than a dozen international and national conferences/seminars/symposia.

Dr. Surinder Sandhu is professor of plant breeding at Punjab Agricultural University (PAU), Ludhiana, Punjab. She received her Ph.D. in genetics (minor in plant breeding) from PAU, Ludhiana, in 1995 and won the prestigious J. L. Nehru Award for outstanding Post Graduate Research in Agriculture from ICAR, New Delhi. She started her research career as scientist (crop improvement) (1995–2002) at the ICAR-Central Potato Research Institute's Regional Station, Jalandhar. Later, she became a sugarcane breeder (2002–2010) at PAU, Ludhiana. She served as a research scholar at the University of Florida, Gainesville, USA, from December 2007 to June 2008. She received the Best Teacher Award (ICAR) for the year 2010–2011 and was granted the Australian Endeavour Research Fellowship Award in 2010. Dr. Sandhu has been instrumental in the development of four sugarcane varieties, which were released in the state, two of which were recommended at zonal level. She has published 24 research papers in refereed international and national journals and written three manuals and four book chapters. She was promoted to the position of professor of plant breeding in 2011 and presently working on varietal develoment in oilseed crops.

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Insect-Plant Interrelationships

1

Ramesh Arora and Surinder Sandhu

Abstract

The green plants and insects represent the two dominant groups of living organisms on Earth. The green plants occupy the most capacious segment among all biological organisms, whereas the insects are the most specious group. These two 'empires' are interconnected as well as interdependent. Green plants are the primary producers of food, and all animals being heterotrophs depend directly or indirectly on plant-produced food. In turn, nearly three fourths of all angiosperms require the services of insect pollinators. The entomophilic flowering plants and their insect pollinators thus represent the most evident and widely applicable example of mutualism among living organisms. But a wide variety of phytophagous insects also flourishes, diversifies and sustains on these plants. Consequently, the plants have evolved a dizzying array of morphological and biochemical (constitutive as well as induced) barriers for protection against insects and other herbivores. Evolutionary interactions between plants and insects may have contributed to the increased biodiversity and success of both these groups. The study of these interrelationships, as outlined in this chapter, is of great practical significance for the future agricultural production. The development of pest-resistant cultivars of crop plants and progress in integrated pest management both require an intricate understanding of insect-plant relationships.

R. Arora (✉)
Department of Entomology & Zoology, Eternal University,
Baru Sahib, Himachal Pradesh 173101, India
e-mail: arorarame@gmail.com

S. Sandhu
Department of Plant Breeding and Genetics, Punjab Agricultural University,
Ludhiana, Punjab 141 004, India
e-mail: surindersandhu@pau.edu

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State-of-the-art techniques such as mutant analysis, metabolomics, RNAi and proteomics developed during the last three decades have been instrumental in providing improved insight into these interrelationships.

Keywords
Coevolution • Pollinators • Insect pests • Flowering plants • Mutualism • Plant defences

1.1 Introduction

The 'plant kingdom' and the 'class Insecta' represent the two dominant groups of living organisms, in terms of the abundance of species as well as in the amount of biomass. Green plants are the primary producers of food, and all animals being heterotrophs depend directly or indirectly on plant-produced food (Schoonhoven et al. 2005). In turn, a majority of the 300,000 plant species require the services of insect pollinators for reproduction. Colourful, scented flowers and floral nectarines were in all probability developed by plants for attracting insect pollinators. Flower anatomy ensured that while feeding, the insects also picked up the pollen (Kearns et al. 1998). Consequently, to prevent over-exploitation, the plants have also evolved a dizzying array of structural and biochemical barriers for protection against insects and other herbivores. While some of these barriers are synthesized by plants regardless of the presence of herbivores (constitutive defences), many others are produced only in response to herbivory (induced defences). Only those insect species, which are able to overcome these barriers in one or more plant species by avoidance, detoxification, etc., can access that plant species as food. The insects which damage the economically important plants have been termed as 'insect pests' by humans. The important mutualistic and antagonistic interactions between plants and insects are introduced hereunder.

1.2 Mutualistic Interactions: Flowering Plants-Insect Pollinators

The most evident and widely applicable example of mutualism is that between insect-pollinated flowering plants and their insect pollinators. Nearly 80% of all flowering plants are bisexual and bear flowers with stamen and pistils in the same flower. This promotes self-fertilization and consequently inbreeding. The plants avoid self-fertilization either by separating the sexes in time and space (differences in the timing of maturation) or by self-incompatibility. Both mechanisms promote cross-pollination, which is assisted by various agencies e.g. wind, water, and animals, etc. More than three fourths of all flowering plants are wholly or partially

insect-pollinated (Faegri and Pijl 1971). The economic value of insect pollinators is enormous. Most of the important oilseeds, pulses, fruits, vegetables, nuts, spices and ornamentals (Hill 1997; Atwal 2000) show improved yields with animal pollination (Klein et al. 2007). It has been estimated that animal pollination has an economic value of €153 billion annually, which is nearly one tenth of global agricultural production (Galai et al. 2009).

Some of the widely accepted estimates of the number of angiosperms pollinated by animals vary from 67% to 96% of all angiosperm species (Axelrod 1960; Nabhan and Buchmann 1997). Ollerton et al. (2011) observed that these estimates are not based on firm data. They compiled data on published and unpublished community level surveys of plant-pollinator interactions and concluded that proportion of animal-pollinated species was 78% in temperate-zone communities and 94% in tropical communities, with a global mean of 87.5% of all flowering plants. The pollinators benefit from rewards in the form of nectar and pollen. Both are nutrient-rich foods with nectar containing 50% sugars and pollen 15–60% proteins and other essential elements (Proctor et al. 1996; Roulston et al. 2000). Together, they provide nourishment for the bees, which are the most important among insect pollinators (Schoonhoven et al. 2005).

The entomophilous flowering plants and the pollinating insects constitute an example par excellence of mutualism. However, the degree of mutualism varies among various plant-pollinator combinations (Schoonhoven et al. 2005). In some cases, there is obligate mutualism, and a species of plant can only be pollinated by a single species of pollinator, which depends on it for food. For instance, figs (*Ficus* spp., Moraceae) are dependent upon fig wasps (Agaonidae, Chalcidoidea) for pollination (Wiebes 1979). Every species of fig is pollinated by a specific wasp species, e.g. the pollination in *Ficus carica* Linnaeus is carried out by the fig wasp, *Blastophaga psenes* (Linnaeus) (Ramirez 1970). Another example of obligate mutualism is observed between yucca moths (Prodoxidae) and yucca plants (Agavaceae). The yucca moths are the sole pollinators for yucca flowers and deposit their eggs in the locule of the ovary of flowers so that the young caterpillars can feed on the developing seeds (Pellmyr and Krenn 2002).

Another interesting example is based on the great naturalist Charles Darwin's prediction. In 1862, while doing research on orchids, Darwin found that the astounding Christmas orchid, *Angraecum sesquipedale* Thouars, had nearly a foot-long green nectary. As this group of orchids was moth pollinated, Darwin predicted that there must be a gigantic moth species with extended proboscis capable of feeding on the long nectary. More than four decades later, Rothshild and Jordan in 1903 described the Morgan's sphinx moth, *Xanthopan morganii* Walker with an extended proboscis length of >12 in., as the only known pollinator of *A. sesquipedale*, which is endemic to Madagascar (Kritsky 2001). However, such reciprocal evolution in plant-pollinator relationships is not widespread. Burkle and Alarcon (2011) observed that most plant-pollinator relationships have a fairly broad range with a high degree of annual turnover of pollinator species, and the relative importance

of a pollinator species may vary in different years for pollination of the same plant species.

Insect pollination has undoubtedly contributed to the evolutionary success of angiosperms. The fossil records show that pollination originated around 250 Myr ago (Labandeira 2013). The early angiosperms were probably pollenized both by the wind and animals. In view of the advantages conferred by entomophily, its importance increased over evolutionary time (Cox 1991; Crepet et al. 1991). Entomophilic angiosperms display a diversity of flower size, shape, colour and fragrance which may have been determined by the requirements of the pollinators. The pollen in flowers of such plants may have a sculptured structure and/or is covered with sticky substances which help it to easily adhere to the insect body. The hairs on the insect legs and other body parts also aid in pollen transfer. The bumble bee pollinated flowers in foxglove, *Digitalis purpurea* Linnaeus are bell shaped, while the butterfly pollinated flowers of *Calopheria* spp. have tubular corolla, which is an adaptation to the long probocis (Schoonhoven et al. 2005). In addition, the latter contain higher levels of amino acids than flowers fed on by flies (Baker and Baker 1986). In order to attract pollinators, some plant species produce sterile 'reward anthers' which are brightly coloured (Nepi et al. 2003). Flowers of the orchid Mirror of Venus, *Ophrys speculum* Link, imitate the virgin female wasps of their pollinator, *Dasyscolia ciliata* (Fabricius), by releasing the female sex pheromone to entice the male wasps. The attracted male wasps try to mate with the flowers and in doing so act as pollination vectors (Ayasse et al. 2003).

Hymenopterans, especially the Apoidea, are the most important group involved in flower pollination at present, but other groups have been equally important in the past. Basal angiosperms are even now primarily pollenized by the beetles and flies (Thien et al. 2000). Bees are closely adapted to a floral diet (Atwal 2000) and are able to assimilate pollen grains despite the presence of an almost impermeable cuticle (Velthius 1992). Individual honeybees often exhibit flower constancy by preferably visiting flowers of a single species. It improves pollinator efficiency and also helps in reproductive isolation of plant species. The insects' ability to remember combinations of flower odours and colours plays a central role in flower constancy. Honeybees have been reported to have the capacity to distinguish at least 700 different floral aromas (Schoonhoven et al. 2005).

1.3 Antagonistic Interactions: Herbivorous Insects-Green Plants

Insects are the most diverse and a tremendously successful group of organisms on Earth. The members of a number of insect orders infest plants and obtain food from them. Species in some of the insect orders are almost exclusively (Lepidoptera, Orthoptera, Phasmida) or predominantly (Hemiptera, Thysanoptera) herbivorous. But Coleoptera, Hymenoptera and Diptera are only partly herbivorous and also include numerous carnivorous species (Schoonhoven et al. 2005). Every vascular

plant species usually harbours several insect species. There are insect species feeding on all parts of the plant including the roots, stem, bark, shoots, leaves, flowers and fruits. While solid feeders chew plant tissues externally (defoliators) or internally (borers), others suck the sap (aphids, jassids), reduce plant vigour and even act as vectors of plant pathogens, e.g. whitefly.

Most insects usually exhibit a high degree of specialization in their choice of food plants. The monophagous insects feed on only a single or a few closely related species of plants, while oligophagous ones feed on a number of plant species, all of which belong to the same family. In contrast, the polyphagous insects use a wide range of plants from different plant families as food (Panda and Khush 1995). But most insects exhibit some degree of specialization in their host plant choice. Investigation on herbivorous insects has revealed that only around one tenth of these insects have the ability to feed on plants of more than three plant families. The host range of each insect species is constrained by several structural, biochemical and ecological factors. As a generalization, it may be stated that, except for Orthoptera, all other orders of herbivorous insects are largely composed of species specialized to feed on particular plant species (Schoonhoven et al. 2005). According to Bruce (2015), the herbivores have evolved over time to become specialized feeders, even though some of polyphages continue to be important agricultural pests. Insects have the ability to recognize and respond to host cues for feeding and oviposition.

Despite the antagonistic relationships between plants and phytophagous insects presumed to operate in all cases, herbivory has been observed to increase plant growth and fitness in some cases (Owen 1980; Vail 1994; Sadras and Felton 2010). Yield decreases due to arthropod feeding are quite common, but there are examples of increased yield recorded in insect-damaged as compared to undamaged plants (Harris 1974). The compensatory responses to herbivore damage may in some cases more than offset the damage caused. It basically depends on how plants respond to attack by insects or other herbivores.

1.3.1 Plant Defences Against Herbivores

Plants are immobile organisms and have to defend themselves against insects and other herbivores. Most plants in natural ecosystems show little or no obvious damage in spite of the presence of wide variety of phytophagous insects in large numbers. Complete defoliation by phytophagous insects is an exception rather than a rule. It has been estimated that on an average, insects consume only around 10% of all annually produced plant biomass (Barbosa and Schulz 1987). This is primarily due to the fact that plants have evolved a diverse range of structural and biochemical characteristics to protect themselves from herbivores. In contrast, insect pest's damage is usually higher in agroecosystem as many of these characteristics have been lost while breeding plants more palatable to human taste and/or outyielding the traditional plant genotypes. There is a need to study these plant defences to exploit them optimally in commercial agriculture.

1.3.1.1 Structural Defences

1.3.1.1.1 Surface Wax Layer(s)

Surface waxes over the epicuticle protect the plant against desiccation, herbivore feeding and pathogen invasion. Wax layers are variable in thickness and structure, and their amount may reach up to several percent of the dry weight of a plant. Wax crystals often act as structural barriers to insect feeding (Jeffree 1986). Further, the mechano- and chemoreceptors on the insect tarsi and mouth parts receive negative tactile and chemical stimuli from the plant surface covered with a wax layer. For instance, leaf epicuticular wax in Brassicaceae results in non-preference for feeding by the flea beetle, *Phyllotreta cruciferae* (Goeze) in (Bodnaryk 1992).

But wax layer may also have the opposite effect by favouring some insects. In several instances, plants with glossy leaf surfaces (reduced wax layer) have also been shown to be less susceptible to insect pests (Eigenbrode and Espelie 1995). As an indirect effect, wax crystals and wax blooms may also impair the adhesion, mobility and effectiveness of predatory insects resulting in an increase of herbivore populations (Eigenbrode et al. 1999).

1.3.1.1.2 Trichomes

The epidermal surface in plant is usually covered with hair-like structures, which are variable in shape, size, location and function (Werker 2000). The hairs present on the aerial parts of a plant are commonly referred to as trichomes, while the term pubescence refers to the collective trichome cover of a plant surface. The trichomes range in size from a few microns to several centimetres, and the shape varies greatly in different species. The trichomes are of two types: non-glandular and glandular (Payne 1978). Non-glandular trichomes may act as physical barriers against the movements of insects over the plant surface or prevent the herbivores' mouth parts from accessing the feeding tissues of the plant (Ram et al. 2004). Glandular trichomes are specialized to secrete a variety of chemicals (Fahn 2000), which act as important chemical barriers against pests and pathogens (Glas et al. 2012). Hooked trichomes of black bean, *Phaseolus vulgaris* Linnaeus, were found to impale the aphid, *Aphis craccivora* Koch (Johanson 1953), and the leafhopper, *Empoasca fabae* (Harris), leading to wounding and death (Pillemer and Tingey 1978). Interestingly, in some cases, trichome density has been observed to be induced in response to insect feeding. Feeding by the cabbage-white butterfly, *Pieris rapae* (Linnaeus), and the cabbage looper, *Trichoplusia ni* (Hubner), on young black mustard, *Brassica nigra* (Linnaeus) W. D. J. Koch, plants resulted in increased trichome density on newly expanded leaves (Traw and Dawson 2002). Some insect pests have also been reported to have developed morphological or biochemical adaptations to neutralize the effect of trichomes. Trichomes may also have indirect effects on plant resistance by limiting the searching capacity of natural enemies of herbivores. The parasitic wasp, *Encarsia formosa* Gahan, is considerably more efficient in finding its host – whitefly nymphs – on glabrous cultivars than on hairy leaves (van Lenteren et al. 1995).

1.3.1.1.3 Plant Toughness

Coley (1983) observed that leaf toughness was the best predictor of interspecific variation in herbivory rates, in a lowland tropical forest. Plant cell walls strengthened by deposition of macromolecules such as cellulose, lignin, suberin and callose together with sclerenchymatous fibres make a plant resistant to penetration by mouth parts (piercing sucking) and ovipositors (adult females) of insects as well as tearing action of mandibles of chewing insects. In wheat, solid-stemmed cultivars were resistant to stem sawfly, *Cephus cinctus* Norton (Platt and Farstad 1946). In sugarcane, rind hardness was an important factor in reducing internode borer *Diatraea saccharalis* (Fabricius) damage (Martin et al. 1975). Seed damage due to the seed chalcid *Bruchophagus roddi* (Gussakovsky) in alfalfa was less in genotypes with highly lignified pod walls (Springer et al. 1990).

1.3.1.1.4 Plant Architecture

The suitability of a plant to serve as a host for phytophagous insects may vary with plant size and architecture. Plant characteristics such as canopy spacing; stem, leaf and bud shapes and dimensions; and branching angles may affect insect preferences and survival. The increasing size and architectural complexity of plants from monocots through herbs, to bushes and trees, is correlated with an increase in the diversity of the associated insect fauna (Lawton 1983). Indirect effects of plant architecture on herbivores are also mediated through their influence on the natural enemies. In cotton, okra-leaved cultivars suffer less damage by a number of insect pests including bollworms, whitefly and boll weevil as compared to normal-leaved cultivars (Ram et al. 2004). In soybean, cultivars with smaller cotyledons and unifoliate leaves were resistant to the legume seedling fly, *Ophiomyia phaseoli* (Tryon), and these are the parts where the insect lays eggs (Talekar and Tengkano 1993).

1.3.1.2 Biochemical Defences

Plants have evolved a plethora of chemical structures to prevent colonization by insects and other herbivores. While a limited number of chemicals are involved in primary metabolism, many other compounds have been found to repel, deter, kill or prevent insects and other herbivores from utilizing these plants as food sources (Chapman 1974; Harborne 1993; Mithofer and Boland 2012). As phytophagous insects have developed the ability to exploit their hosts, the plants have responded by evolving defensive biochemicals to counteract herbivore attack (Johnson 2011). The chemicals produced by plants, thus, fall into two broad categories: nutrients and allelochemicals.

1.3.1.2.1 Nutrients

The suitability of a plant as a host for one or more insect species is dependent on its ability to supply holistic nutrients for development and multiplication of these insects. From an insect's perspective, the plants usually supply a mixture of nutrients at suboptimal concentrations, which are combined with indigestible structural compounds, such as cellulose and lignin, and a variety of allelochemicals (Schoonhoven et al. 2005). The latter may exert a wide range of behavioural,

physiological and growth-inhibiting effects, some of which may even lead to insect mortality.

Most insects have qualitatively similar nutritional requirements, consisting of carbohydrates, amino acids, fatty acids, sterols and a number of micronutrients. Host plants are often nutritionally suboptimal per se. The main groups of primary plant metabolites – amino acids, carbohydrates and lipids involved in fundamental plant physiological processes – serve as essential nutrients for herbivores. Therefore, changes in primary plant metabolites and nutrients greatly affect the survival and multiplication of phytophagous insects (Berenbaum 1995).

Nitrogen is especially important as insects are unable to exploit inorganic nitrogen, and organic nitrogen content of plants is suboptimal for the insects (Schoonhoven et al. 2005). This may constitute a major barrier to successful exploitation of plants by a majority of insect taxa (orders). Interestingly, the herbivorous taxa include nearly half of the total arthropod fauna in less than one-third of insect orders, indicating that once the nitrogen deficiency barrier is breached, these organisms are able to access an abundant supply of food (Strong et al. 1984).

1.3.1.2.2 Selected Examples of Nutritional Factors in Plant Defence Against Insects

The host plant, which is deficient in one or more essential nutrients required by the insect, may prove insect resistant by causing antibiotic and antixenotic effects on the insect. Such effects could also result from an imbalance of available nutrients (Arora and Dhaliwal 2004).

Cotton Cotton genotypes with inbuilt defence based on nutritional factors have been evolved for insects such as the leafhopper, *Amrasca biguttula* (Ishida); whitefly, *Bemisia tabac*i (Gennadius); stem weevil, *Pempherulus affinis* (Faust); and the thrips complex (Uthamasamy 1996). The whitefly *B. tabaci*-resistant genotypes showed higher contents of K, P and Mg and lower of N and Fe as compared to susceptible ones. But the other parameters like sugars, proteins, Ca and Cu did not show significant relationship with whitefly buildup. In another study, it was reported that total sugar content of cotton cultivars was positively correlated with whitefly incidence during the vegetative phase but negatively correlated with it after flowering of the crop (Rao et al. 1990). In the case of leafhopper, *A. biguttula*, highly susceptible genotype Acala 4–42 had higher amount of reducing sugars (2.55%), proteins (18.49%) and free amino acids (10.15 mg/g) as compared to highly resistant BJR 741 containing 1.63% reducing sugar, 13.45% proteins and 6 mg/g free amino acids (Singh and Agarwal 1988).

Rice The thrips, *Stenchaetothrips biformis* (Bagnall)-resistant rice genotypes possessed significantly less reducing sugars and free amino acids in comparison with the susceptible genotypes (Thayumanavan et al. 1990). The occurrence of asparagine in minute quantities in rice variety ‘Mudgo’ was considered to be the primary cause of resistance to brown plant hopper, *Nilaparvata lugens* (Stal). Young females of brown plant hopper caged on variety Mudgo had underdeveloped ovaries con-

taining few eggs, while those caged on susceptible varieties had normal ovaries full of eggs (Sogawa and Pathak 1970). The gall midge *Orseolia oryzae* (Wood-Mason)-resistant varieties PTB 18, PTB 21 and Leuang 152 had higher content of free amino acids and less sugar in their shoot apices than susceptible varieties Jaya and IR8. In the case of stem borer, *Scirpophaga incertulas* (Walker), stems of both the resistant (TKM6) and moderately resistant (Ratna) genotypes had less amino acids and sugars than susceptible genotype (IR8) (Vidyachandra et al. 1981).

Legumes The importance of amino acid concentration in the pea plant on susceptibility to aphid, *Acyrthosiphon pisum* (Harris), was revealed by Auclair (1963). He observed that the concentrations of amino acids in the sap of susceptible genotypes were significantly higher than those in the resistant genotypes. It has been reported that high percentage of non-reducing sugars and low percentage of starch in the seeds of chickpea genotype GL 645 might be responsible for the low incidence of the pod borer *H. armigera* in the test cultivar as compared to the infestor (Chhabra et al. 1990).

Low amino acid, protein and sugar contents and high phenol content induced resistance in pigeon pea cultivars against pod borers. Sugar content was high both in seeds (3.64–4.82%) and in the pod coat (3.66–4.92%) of susceptible cultivars (ICPLI, ICPLS7 and UP AS20). In the resistant cultivars, the total sugar content ranged between 2.86 (ICPLS3024) and 3.51% (HS9–2) in the seeds and 2.91 (ICPLS3024) and 3.44% (HS9–2) in the pod coat. The amino acid content was low in the pod coat (1.40–1.52 mg/g) and seed (1.39–1.55 mg/g) of resistant pigeon pea cultivars tested as compared to the susceptible cultivars (1.89–2.57 mg/g in pod coat; 2.04–2.62 mg/g in seed). Highly significant positive correlation observed between amino acid content and incidence of individual borer species supported the possible role of amino acids in offering resistance to the pod borers (Sahoo and Patnaik 2003).

1.3.1.2.3 Allelochemicals

The plant-produced allelochemicals are mainly secondary metabolites which do not play major role in primary metabolic pathways of plants. While the primary metabolic pathways are common in almost all flowering plants, these secondary substances vary widely in different plant species (Schoonhoven et al. 2005). It was Fraenkel (1959) who first postulated that these substances act to deter insects and other herbivores. It has been observed that the plant produce a dazzling variety of secondary metabolites, and more than 200,000 of these have been identified (Dixon and Strack 2003).

The allelochemicals have been functionally classified into two categories: *allomones* which benefit the producing organism, i.e. the host plant, and *kairomones* – which benefit the organism perceiving it, i.e. the phytophagous insect. The involvement of allelochemicals in various types of insect-plant relationships can determine the status of a plant either as a host (presence of kairomone) and non-host (absence of kairomone) or as resistant (presence of allomone) and susceptible (absence of allomone) (Panda and Khush 1995). Allomones are considered a major

Table 1.1 Major groups of phytochemicals utilized in plant defences

Phytochemical group	Example	Typical plant source	Approximate number of compounds known
Terpenoids	(E)-β-Farnesene cucurbitacins	Ubiquitous	>30,000
Steroids	Phytoecdysteroids	Ranunculaceae	~200
Cardenolides	Digoxigenin	Plantaginaceae	~200
Alkaloids	Nicotine	Solanaceae	>12,000
Fatty acid derivatives	(3Z)-Hexenylacetate	Ubiquitous	Not available
Glucosinolates	Sinigrin	Capparales	~150
Cyanogenic glucosides	Dhurrin	Rosaceae, Fabaceae	~60
Phenolics	Simple phenols, coumarins, lignin, tannin	Ubiquitous	>9000
Polypeptides	Trypsin inhibitor	Ubiquitous	Not available
Nonprotein amino acids	γ-Aminobutyric acid	Fabaceae	>200
Silica	SiO_2	Poaceae	1
Latex	Undefined emulsion	Euphorbiaceae	Not available

Modified from Mithofer and Boland (2012)

factor responsible for plant defence against insects, and these have been exploited to increase levels of resistance in several agricultural crops (Green and Hedin 1986). The various groups of secondary plant metabolites implicated in plant defence against insects (Table 1.1) are briefly discussed here (Rosenthal and Berenbaum 1991; Arora and Dhaliwal 2004; Schoonhoven et al. 2005; Iason et al. 2012).

Nonprotein Amino Acids The nonprotein or unusual amino acids are common in a number of unrelated families of higher plants as well as in some lower plants. At least 600 such amino acids have been elucidated from various plants especially legumes. Nonprotein amino acids may afford protection against predators and pathogens due to their structural analogy to the common nutritionally important amino acids. The biological effects on insects are partly due to the fact that the analogue molecule gets misincorporated into protein synthesis of the insect or through inhibition of biosynthetic pathways (Rosenthal 1991; Huang et al. 2011; Yan et al. 2015). Among these, canavanine, azetidine-2-carboxylic acid, 2,4-diaminobutyric acid, mimosine, 3-hydroxyproline, 5-hydroxynorvaline, β-cyanoalanine and pipecolic acid are significant in causing insect growth disruption (Parmar and Walia 2001, Yan et al. 2015).

Terpenoids Terpenoids are the largest and most diverse class of organic compounds found in plants. They exhibit enormous chemical variety and complexity, but all are formed by fusion of five-carbon isopentane units, and most of them are lipophilic substances (Ruzicka 1953). Terpenoids achieve their greatest structural

and functional diversity in the plant kingdom. Nearly 30,000 terpenoids are known in plants, and a majority of them serve as defences against herbivores and pathogens or as attractants for pollinators and fruit-dispersing animals. The terpenoids are constituted of two or more five-carbon units in their structures: monoterpenoids ($2xC_5$), sesquiterpenoids ($3xC_5$) diterpenoids ($4x\ C_5$), triterpenoids ($6xC_5$), tetraterpenoids ($8xC_5$) and polyterpenoids [(C_5) n where n>8] (Gershenzon and Croteau 1991).

Monoterpenoids have been demonstrated to work as toxins and as feeding/oviposition deterrents against a large number of insects. The best known insect toxin among monoterperoids is the botanical insecticide pyrethrum, found in the flowers and leaves of certain *Chrysanthemum* species. The active ingredient in pyrethrum is a mixture of monoterpene esters collectively known as pyrethroids (Casida 1973).

Cotton and related malvaceous plants possess spherical pigment glands in leaves, flowers and most other parts of the plants. In addition to anthocyanin pigments, these pigment glands contain high concentrations of a variety of mono- and sesquiterpenoids especially gossypol. Gossypol is a phenolic, sesquiterpene dimer with two aldehyde residues. Gossypol is toxic to a variety of herbivorous insects, causing significant decrease in the survival, growth and development of a number of important lepidopterous and coleopterous pests. The toxicity of gossypol to herbivores is supposed to result from its binding to proteins in the gastrointestinal tract, causing a reduction in the rate of protein digestion. The proteins in the gastrointestinal tract may be the ingested dietary proteins or the digestive enzymes produced by the insect (Meisner et al. 1977). The sesquiterpene lactone, *beta*-D-glucopyranosyl ester (TA-G), a major secondary metabolite of the common dandelion, *Taraxacum officinale* G. H. Weber ex Wiggers, protects the plant against its major native root herbivore, the common European cockchafer, *Melolontha melolontha* Linnaeus, by deterring larval feeding (Huber et al. 2016).

Triterpenoids (C_{30}) with six-C_5 isoprene units are the largest of terpenoid compounds. The three major groups of triterpenes which have significant roles in plant-herbivore interactions are the cucurbitacins, limonoids and saponins. Cucurbitacins are a group of about 20 extremely bitter and toxic tetracyclic triterpenes, confined mainly to plants in the Cucurbitaceae family. These compounds serve as toxicants and feeding deterrents against a wide range of phytophagous insects (Tallamy et al. 1997). Some specialist insects feeding on cucurbits are, however, able to metabolize or avoid these toxic compounds and even use cucurbitacins as host recognition cues (Abe and Matsuda 2000).

The limonoids are a large group of highly oxygenated substances with a basic skeleton of 26 carbon atoms. Limonoids are found in three closely related families, the Rutaceae, Meliaceae and Cneoraceae. Limonoids are powerful feeding deterrents against insects. Over 100 triterpenoids have been isolated from the neem *(Azadirachta indica* A. Juss.) seeds, and a number of these are active as insect feeding deterrents and antifeedants. Most important of these is the azadirachtin, which is effective at dosages as low as 50 parts per billion. More than 400 species of insects have been reported to be susceptible to neem preparations at various concentrations. In addition to antifeedant effects, neem is reported to affect the survival,

growth, development, vigour and fecundity of insects (Schumutterer 1995; Dhaliwal and Arora 2001).

Saponins are common constituents of a large number of plant species and consist of a sugar moiety (glycoside) linked to a hydrophobic aglycone, which may be a triterpene or a steroid, both of which originate from the C_{30} precursor, squalene. Triterpenoid saponins have been detected in common legumes such as soybeans, beans, peas, tea, spinach, sugar beet and quinoa. Steroidal saponins are found in oats, capsicum, peppers, aubergine, tomato seed, allium and asparagus (Francis et al. 2002). Saponins exert a strong insecticidal action against several orders and cause increased mortality, lowered food intake, weight reduction, growth retardation and moulting defects (Geyter et al. 2007).

Alkaloids The alkaloids are a heterogeneous class of natural products that occur in all classes of living organisms but are most common in plants. Alkaloids generally include basic substances that contain one or more nitrogen atoms, usually in combination as part of a cyclic system. Most of them are derivatives of common amino acids, such as lysine, tyrosine, tryptophan, histidine and ornithine (Facchini 2001). Alkaloids are found in some 20% of the species of flowering plants. Generally, each alkaloid-bearing species displays its own unique, genetically defined alkaloid pattern. Numerous alkaloids have been reported to be toxic or deterrent to insects. Because of their nitrogenous nature, many alkaloids interfere with the key components of acetylcholine transmission in the nervous system. Nicotine and nornicotine derived from tobacco plant were popular as botanical insecticides before the advent of synthetic organic insecticides (Dhaliwal and Arora 2001). Several groups of structurally unrelated alkaloids such as pyrrolizidines, quinolizidines, indole alkaloids, benzylisoquinolines, steroid alkaloids and methylxanthines are feeding deterrents to many insects and other herbivores at dietary concentrations over 0.1% (Schoonhoven et al. 2005).

Glucosinolates Glucosinolates form a small group of about 100 sulphur- or nitrogen-containing distinctive secondary compounds, which act as precursors of mustard oils. Glucosinolates occur commonly in the order Brassicales, including the commercially important family Brassicaceae. Glucosinolates appear to contribute to effective chemical defences against a majority of non-adapted phytophagous insects (Fahey et al. 2001). In the thale cress *Arabidopsis thaliana* (Linnaeus) Heynhold genome, at least 52 genes are involved in glucosinolate biosynthesis (Arabidopsis Genome initiative 2000, Halkier and Gershenzon 2006). When herbivores attack plant tissues, glucosinolates are hydrolysed by the enzyme myrosinase into several herbivore-deterring metabolites (Hopkins et al. 2009). On the other hand, a small minority of adapted (Brassica-feeding) insects are able to utilize glucosinolates in host seeking and host recognition behaviour. Glucosinolates and their volatile hydrolysis products are also used as cues by natural enemies of Brassica-feeding insects (Louda and Mole 1991).

Insect Hormone Mimics and Antagonists The endocrine system is critical for the development, growth, survival and multiplication of insects. Although many insect hormones are known, two powerful hormones, the juvenile hormone (JH) and the ecdysone or moulting hormone (MH), are recognized to play a major role in these processes. The analogues of these hormones are called juvenoids and ecdysteroids, respectively. It is presumed that plants may have developed juvenoids and ecdysteroids as subtle defences against insect pests. Plant species having high ecdysteroid content (> 1000 ppm) are avoided by insects. Farnesol, sesamin, juvabione, sterculic acid, bakuchiol and thujic acid are some of the important juvenoids isolated from plants and are known to disrupt metamorphosis, moulting and reproduction in insects (Bowers 1991).

Proteinase Inhibitors Protease inhibitors (PIs) constitute an abundant and important group of compounds in plants, which have a defensive function against herbivores, especially insect pests (Dunaevsky et al. 2005). Recent studies using microarrays and proteomic approaches have revealed that the protein-based plant defences play a more important role against herbivores then previously realized (Felton 2005; Zhu-Salzman et al. 2008). Defence-related proteins such as arginases, polyphenol oxidases and peroxidases may have antimicrobial properties; others such as chitinases, cysteine proteases, lectins and leucine amino peptidases may be toxic (Zhu-Salzman et al. 2008). However, the anti-insect action of plant proteins is easily inactivated by proteases. These proteolysis-susceptible proteins can be protected with PIs (Mithofer and Boland 2012).

The PIs inhibit the activities of various enzymes in insects especially insect peptidases including serine, cysteine and aspartate proteinases and metallocarboxypeptidases, which are involved in insect growth and development. The PIs also reduce the digestive ability of the insect pests, thus leading to the shortage of important food constituents such as amino acids resulting in slow development and/or starvation. A large number of PIs have been reported in plants (De Leo et al. 2002), which are effective against many lepidopteran and hemipteran insect pests (War and Sharma 2014). For instance, in tomato plants, PIs were positively tested for their trypsin- and *H. armigera* gut proteinase-inhibitory activity in different parts of the plant (Damle et al. 2005).

Lectins Lectins or phytohaemagglutinins are proteins with a capacity to reversibly bind to the carbohydrate moieties of complex carbohydrates without altering the covalent structure of any of the recognized glycosyl legends. Lectins are distributed universally throughout the plant kingdom, where they constitute 6–11% of the total plant proteins. The cotyledons of the seeds of legumes are especially rich in lectins. Lectins are associated with the defence of plants against insects and phytopathogens (Liener 1991). *Arisaema helleborifolium* Schott lectin exhibited anti-insect activity towards the second instar larvae of melon fruit fly, *Bactrocera cucurbitae* (Coquillett) (Kaur et al. 2006).

Phenolics Phenolics are aromatic compounds with one or more hydroxyl groups and are ubiquitous in plants (Harborne 1994). Examples of relatively simple phenolics include hydroxybenzoic acids like vanillic acid, the hydroxycinnamic acids like caffeic acid and the coumarins (Schoonhoven et al. 2005). Coumarins possess a 5,6-benz-2-pyrone skeleton and may be variously hydroxylated, alkylated, alkoxylated or acylated. Coumarins can deter feeding as well as interfere with development of insects. The simple coumarin, bergamottin, is ovicidal to the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), while mammein is toxic to the mustard beetles. Coumarins appear to act as kairomones for certain insects that are specialized for feeding on coumarin-containing plants (Berenbaum 1991b).

Among the phenolics, flavonoids are found in nearly all higher plants, and most plants show their own distinctive flavonoid profile. The flavonoids share a basic C_6-C_3-C_6 structure, which is linked to a sugar moiety to form a water soluble glycoside. Common examples of flavonoids isolated from plants are catechin, botanical insecticide rotenone and phaseolin, all of which act as feeding deterrents against insects (Schoonhoven et al. 2005).

Tannins are polyphenolic compounds commonly found in higher plants. The phenolic hydroxyl groups of tannins bind to almost all soluble proteins, producing insoluble copolymers. Proteins bound to tannins are indigestible and thus decrease the nutritional value of plant tissues (Schoonhoven et al. 2005).

Latex Latex is present in specialized cells called laticifers and consists of chemically undefined milky suspensions or emulsions of particles in an aqueous fluid (Agrawal and Konno 2009). Laticifers have a defensive function. Small insects may be physically trapped in latex or their mouthparts may get glued together, and chemical constituents in latex including proteins and toxins affect insect development (Dussourd 1995). Wounding of laticifers by insects results in leakage at wound site (Mithofer and Boland 2012). In the milkweed, *Hoodia gordonii* (Masson) Sweet ex Decne, both larval feeding and adult oviposition by *T. ni* was deterred when latex was added to artificial diet or painted on the leaves of the host plant (Chow et al. 2005).

1.3.1.2.4 Selected Examples of Allelochemicals in Plant Defence Against Insects

Maize Maize, the world's most productive grain crop, is attacked by a diverse range of insect pests. Well-studied anti-herbivore defences in maize include small molecules such as benzoxazinoids (Frey et al. 2009), chlorogenic acid (Cortes-Cruz et al. 2003) and maysin (Rector et al. 2003) in addition to defence-related proteins (Chuang et al. 2014). Xie et al. (1992) analysed several maize lines resistant to western corn rootworm, *Diabrotica virgifera* Le Conte, for hydroxamic acid levels. All the root extracts were found to contain four major hydroxamic acids: 2,4-dihydroxy-7methoxy-l,4-benzoxazin-3-(4H)-one (DIMBOA), 2,4-dihydroxy-7,8dimethoxy-l,4-benzoxazin-3(4H)-one (DIM2BOA), 2-hydroxy,7-methoxy,1,4-benzoxazin-3(4H)-one (HMBOA) and 6-methoxy-benzoxazolinone (MBOA). These chemicals adversely affected the survival development, weight and head

capsule width of rootworm larvae. Wiseman et al. (1992) reported a highly significant negative relationship between weights of corn earworm, *Helicoverpa zea* (Boddie), as well as the fall armyworm, *Spodoptera frugiperda* J. E. Smith, larvae and maysin concentration in the silks of a large number of corn entries.

Cotton The allelochemical compounds known to exert adverse effects on insect pests in cotton include gossypol, gossypurin, heliocides, hemigossypolone, tannins, anthocyanins, flavonoids and phenolics. Gossypol was first reported to confer resistance to cotton bollworm *Heliothis zea* by Bottger et al. (1964). Most commercial cotton cultivars have a gossypol content of about 0.5% in squares. Vilkova et al. (1988) reported that high gossypol cotton cultivars (No.1 6482, 6501 and Termez-14) had detrimental effects on insect development, viz. increasing incubation period, causing greater mortality among young larvae and lowering larval weight compared with low gossypol cultivars. They further stated that antibiotic effect of high gossypol reduced the fecundity of *H. armigera* by more than 50%. Gossypol is known to adversely affect the nutritional quality of bolls by forming complexes with amino acids, proteins and enzymes. The tree cotton *Gossypium arboreum* Linnaeus genotypes with high gossypol-gland density on ovary surface suffered lower incidence of bollworm complex including *H. armigera*, *Earias vittella* (Fabricius) and *Pectinophora gossypiella* (Saunders) (Mohan et al. 1994).

In the case of cotton stem weevil, *P. affinis*, when the healthy test plants were assayed, the concentration of tannins was low in susceptible MCU5 and high in the resistant accessions. The concentration increased in the gall region when the plants were infested, and the increase was more in resistant accessions compared to the susceptible MCU5. There was no variation in the total phenolic content in the healthy stem of resistant and susceptible accessions. However, when infested, the concentration of total phenolics increased in the gall regions significantly, the increase being more in resistant accessions. It could thus be inferred that increased tannin and phenolic concentrations might provide a protective mechanism against the stem weevil (Uthamasamy 1996).

Vegetables Potato glycoalkaloids are known to act as natural resistance factors in *Solanum* species against the Colorado potato beetle (CPB), *L. decemlineata*, and the potato leafhopper, *E. fabae*. Several wild *Solanum* species have shown a positive correlation between total leaf glycoalkaloid content and resistance to species of *Leptinotarsa.* Leptine is a very effective feeding deterrent totally inhibiting feeding, while tomatine and demissine are intermediate in activity, followed by solanine and chaconine (Tingey 1984). The field resistance of tetraploid potato *(Solanum tuberosum* L.) selection ND 2858-1 and its backcross progeny against the Colorado potato beetle is caused by antibiosis. Neonates of CPB developed slowly in detached-leaf assays on resistant genotypes, and larval weight gain after 4 days was inhibited by 75% relative to larval development and weight gain on susceptible genotypes. Foliar glycoalkaloids of resistant genotypes included low levels of leptines I and II (Lorenzen et al. 2001).

The wild species of tomato, *Lycopersicon hirsutum* and *L. hirsutum* f. *glabratum*, showed antibiosis against the tomato fruit borer *H. zea*. The chemicals responsible for antibiosis were identified as L-tomatine, 2-tridecanone, phenolics and iron and zinc (Ferry and Cuthbert 1975; Dimock and Kennedy 1983; Kashyap 1983). The allelochemic 2-tridecanone was acutely toxic to *H. zea, Manduca sexta* Linnaeus and *L. decemlineata.* High phenolic content has also been reported to confer resistance to the related species, *H. armigera* (Banerjee and Kalloo 1989), while high tomatine content is inimical to the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood) (Steehius and van Gelder 1985).

The protease inhibitor and chlorogenic acid were responsible for aphid resistance in tomato (Felton et al. 1989). The sesquiterpene carboxylic acids (SCA), (+) E-α-santalen-12-oic, (−)-E-endo-α-bergamoten-12-oic and (+)-E endo-β-berqamoten-12-ion acids were produced in glandular trichomes of *Lycopersicon hirsutum* f. *typicum* accession (LA) 1777, which is highly resistant to pests commonly damaging commercial tomato, *L. esculentum.* Both the tomato fruitworm, *H. zea*, and the beet armyworm, *Spodoptera exigua* (Hubner), larvae exhibited reduced feeding, slow development rates and low survival in presence of these compounds. Sublethal effects were observed at concentrations as low as 2 mg SCA/g of diet, and a concentration of 60 mg SCA/g in diet proved lethal to the larvae (Frelichowski and Juvik 2001).

1.3.1.3 Types of Plant Defences

The plant defences may be classified into: *constitutive*, which are always present in the host plant irrespective of the presence of insect or noninsect pests, and *induced*, which are produced in response to various abiotic and biotic stressors.

1.3.1.3.1 Constitutive Defences

Plants have evolved a plethora of structural and chemical defences that are incorporated into their tissues irrespective of the presence or absence of herbivores. These constitutive defences can deter, repel, intoxicate or disrupt the feeding, development or multiplication of insects (Arora and Dhaliwal 2004; Ram et al. 2004; Mithofer and Boland 2012). These defences include the texture and composition of the plant surface (Johnson 1975); the presence of anatomical structures such as thin veins, thorns, silica, trichomes or resin ducts (Hanover 1975); the absence of essential nutrients (House 1961); the presence of hormone-like substances that disrupt insect development (Williams 1970); unsuitable pH or osmotic pressure (Beck 1965); or the accumulation of secondary metabolites (Chapman 1974). The secondary metabolites are diverse, ranging from amino acids to alkaloids, terpenes, phenolics, steroidal, cyanogenic and mustard oil glycosides (Mithofer and Boland 2012). In addition plants may also convert nitrogen to compounds which are not available to insects (White 1978). The advantage of such constitutive defences to insects is that these are produced during high metabolic periods and can be utilized over an extended period of time. Such defences work well against a diverse group generalist herbivores, but continuous exposure to these chemicals exerts strong selective pressure

on the phytophagous insects, which may result in evolution of specialist feeders. Thus, even the best defended species are attacked by a few specialist herbivores.

1.3.1.3.2 Induced Defences

Induced defence is activated in presence of herbivores and enables the plant to resist pest feeding and colonization (Sadras and Felton 2010). Initiation of insect feeding activates several defence signals, leading to suitable defence responses (Wu and Baldwin 2010; Hogenhout and Bos 2011; Bruce 2015). The plants have also been reported to respond to insect oviposition in a similar fashion (Hilker and Meiners 2006). Plant-released volatile organic chemicals (VOCs) have been found to attract natural enemies of pests (Tamiru et al. 2011; Fatouros et al. 2012) or induce direct defences so that insect growth rates are reduced on plants harbouring eggs (Gieselhardt et al. 2013).

Plants respond to elicitors derived from oral secretion of insect herbivores, mechanical damage and/or the exogenous application of inducers. Insect oral secretion/regurgitant contains a number of elicitors of plant defence, the important ones being fatty acid conjugates (FACs). The FACs are composed of two moieties: a fatty acid and an amino acid. It has been observed that the fatty acid and amino acid originate from the plant and the insect, respectively, and are synthesized in the insects' midgut. Expressing the unique insect-plant interaction, the FACs not only serve as important elicitors for plants to perceive insect attack but are also involved in insect nitrogen metabolism. The first FAC isolated from oral secretion of the beet armyworm *S. exigua* larvae was N-(17-hydroxylinolenoyl)-L-glutamine (volicitin), and it stimulates maize plants to produce volatiles, which attract natural enemies of the pest (Alborn et al. 1997). Similarly, regurgitant of the tobacco hornworm, *M. sexta*, contains N-linolenoyl-glu, a potential elicitor of volatile emissions in tobacco plants. In addition, some FACs activate mitogen-activated protein kinase (MAPK) pathway, producing a number of plant defensive compounds having a role in signalling transduction in response to various stresses including drought, pathogen and insect attacks. MAPK signalling is a well-conserved pathway in eukaryotes, and its critical role in plant signalling especially for pathogen stresses is well established. The central role of MAPK in regulating plant transcriptomes has been demonstrated (Wu and Baldwin 2010). Some FACs induce accumulation of 7-epi-jasmonic acid, which activates herbivore-defence genes in tobacco plants. Furthermore, FACs also induce nicotine and proteinase inhibitors (PI) in the coyote tobacco, *Nicotiana attenuata* (Torr. ex S. Watson) (Wu and Baldwin 2010; War and Sharma 2014).

The plant plasma membrane is exposed to the environment and initiates a cascade of events following recognition of pest attack. The changes in cell membrane potential (Vm) induced by herbivory are followed by fast electrical signals, which are systematic in nature. Calcium ions ($Ca+^{2}$) function as a second messenger in several plant signalling pathways. The signal may appear a few seconds after herbivore attack as a single transient oscillation or repeated spikes with specific subcellular localisation lag time, amplitude and frequency. The $Ca+^{2}$ signals activate calmodulin and other calcium-sensing proteins. This promotes a cascade of

downstream effects, like altered protein phosphorylation and gene expression patterns (Furstenberg-Hagg et al. 2013).

Herbivory leads to the accumulation of phytohormones in plants, the important ones being salicylic acid (SA), jasmonic acid (JA) and ethylene. The phytohormones mediate various signal transduction pathways involved in plant defence against various biotic and abiotic stresses. The main transduction pathways involved in plant defence against herbivorous insects are phenylpropanoid and octadecanoid pathways mediated by SA and JA, respectively. These pathways lead to synthesis and accumulation of toxins at the feeding site or in other parts, which are then transported to the feeding site. In addition, antioxidative enzymes involved in plant defence accumulate in plant tissues on account of insect damage (Wu and Baldwin 2010). Yan et al. (2015) reported accumulation of nonprotein amino acid 5-hydroxynorvaline in leaves of maize inbred line B73 following herbivory by the corn leaf aphid *Rhopalosiphum maidis* (Fitch) and the beet armyworm *S. exigua*, as well as in response to treatment with methyl jasmonate, salicylic acid and abscisic acid.

Both constitutive and induced defences can be either direct or indirect. Direct defences target the herbivores, while indirect defences act via recruitment of natural enemies of insect pests in the aid of plants. Certain volatile organic compounds (VOCs), containing terpenoids, fatty acid derivatives and a few aromatic compounds, serve to attract natural enemies of phytophagous insects (Mithofer and Boland 2012).

1.3.2 Counter-Defences of Insects to Plant Defences

Plants defend themselves from herbivore damage through a plethora of structural and chemical defences. These defences may have exerted enormous selection pressure on the insects resulting in evolution of counter-defences (adaptations) in herbivorous insects. The insect adaptations to plant defences can be physical, behavioural or biochemical and comprise of various mechanisms such as penetration barriers, special excretions, sequestrations, temporary binding with carrier proteins and storage of toxins in adipose tissue, enzymatic detoxifications and target-site mutation. It is important to gain an understanding of these insect adaptations to plant defence to minimize their effects on stability of resistance in plants to insects. The important counter-defence strategies of insects to plant defences are briefly introduced hereunder (War and Sharma 2014; Bruce 2015).

1.3.2.1 Adaptations to Physical and Structural Defences

The slippery wax layer presents a serious obstacle to the movement of insects on plants, and many insects have developed special devices to overcome the problem. For instance, the minute setae on tarsal pulvilli of some chrysomelids excrete an adhesive material for good attachment (Gorb and Gorb 2002). Leafhoppers of *Empoasca* species can use their tarsal pulvilli as suction cups (Lee et al. 1986), while many lepidopteran caterpillars glue a silk thread ‘rope ladder’ to the plant

surface to serve as a 'foot hold' (Eigenbrode 2004). To overcome the problem of trichomes on the plant surface, the aphid *Myzocallis schreiberi* Hille Ris Lambers & Stroyan has specialized structure in the form of claws and flexible empodia that serve to get a good grip on the short woolly trichomes on the leaves of its host, the Holm oak, *Quercus ilex* Linnaeus (Kennedy 1986).

Leaf toughness has been found to reduce herbivory. As an adaptation to food hardness, in caterpillars of *Pseudaletia unipuncta* Haworth, the head and chewing musculature are twice as large when fed on hard grass as on soft artificial food, even though body mass is similar (Bernays 1986). Water lily beetles *Galerucella nymphaeae* (Linnaeus) feeding on the 'hard' water lily have disproportionally bigger mandibles than conspecifics feeding on the great water dock grin, *Rumex hydrolapathum* Huds., another host plant with softer leaf tissues (Pappers et al. 2001).

1.3.2.2 Adaptations to Protease Inhibitors

Production of protease inhibitors is induced in some plants in response to insect damage. Herbivore attack on *N. attenuata* rapidly increases the production and accumulation of trypsin PIs; *M. sexta* and *S. exigua* larvae performed better on Trypsin PI-deficient plants as compared to similar plants producing PIs (Zavala et al. 2004; Steppuhn and Baldwin 2007). However, many insect pests have adapted to plant PIs, which increases damage to the host plants. This counter-defence of PIs by insect pests is a major barrier to the manipulation and utilization of PIs for a stable plant defence and thus warrants an understanding of the mechanisms by which insects counteract the PI-based plant defence. Two types of resistance or adaptation to protease inhibitors have been observed in insect pests. One of these depends on having the alternative proteases that are resistant to PIs (Parde et al. 2010). These insensitive proteases can occur constitutively in the plant and/or are induced when the other proteases are inhibited to compensate their loss (Jongsma et al. 1995; Parde et al. 2012). *S. exigua* has been reported to adapt to potato proteinase inhibitor II by induced gut proteinase activity, which is not inhabited by the PIs. Further, when fed on the soybean proteinase inhibitor (SPI)-containing diet, larval proteases showed insensitivity to the inhibitor (Brioschi et al. 2007). Trypsins insensitive to plant PIs have been characterized from *Agrotis ipsilon* (Hufnagel), *T. ni* and *H. zea* (Volpicella et al. 2003).

The second mechanism of resistance to PIs in insects involves the synthesis of specific proteases, which are able to degrade the protease inhibitors so as to reduce their inhibitory activity. Proteolytic inactivation is an important adaptation developed by insects to withstand the proteolytic inhibition by PIs. A new trypsin-like enzyme is produced by S. *frugiperda* (J.E. Smith) larvae when fed on artificial diet with soybean PIs (Brioschi et al. 2007). The diamondback moth, *Plutella xylostella* Linnaeus, larvae have been found to be insensitive to mustard trypsin inhibitor 2 (MTI2). This insensitivity has been attributed to degradation of MTI2 by the pest, thus avoiding the effect of the PI (Yang et al. 2009).

1.3.2.3 Adaptations to the Glucosinolate-Myrosinase System

The glucosinolate-myrosinase system, also known as the 'mustard oil bomb', present in Brassicales (Brassicaceae, Capparidaceae, Tropaeolaceae) constitutes the most effective and well-studied defence system in these plants against insect pests. Under normal conditions, glucosinolates are compartmentalized and thus protected from their hydrolysing enzyme – a thioglucosidase – myrosinase. While the glucosinolates are distributed in many plant tissues, the myrosinase is localized in scattered cells only. Upon tissue damage, the myrosinase and glucosinolate come into contact producing the unstable aglycones, which spontaneously rearrange into various active compounds, mainly nitriles and isothiocyanates (Li et al. 2000; Hopkins et al. 2009).

It has been revealed that high glucosinolate- and myrosinase-containing lines of *Brassica juncea* (Linnaeus) Czern. are more defensive against *Spodoptera eridania* (Cramer) larvae than the ones with lower content of these two chemicals (Li et al. 2000). The larvae of *T. ni*, a lepidopteran generalist, avoided *A. thaliana* ecotypes that produced isothiocyanates upon glucosinolate hydrolysis and, instead, fed on ecotypes that produced nitriles (Lambrix et al. 2001). Further, certain parasitoids use glucosinolates that are released by feeding herbivores to detect their host insects. In such cases, glucosinolates have a dual function for the attacked host plant, in direct as well as in indirect defence (Hopkins et al. 2009).

Some insect pests even use glucosinolates for their own defence. *Myzus persicae* (Sulzer), *Athalia rosae* (Linnaeus) and *P. rapae* sequester glucosinolates into their hemolymph and body tissues (Muller and Brakefield 2003; Kazana et al. 2007; Bridges et al. 2002). When a predator attacks, the haemolymph oozes out glucosinolates that deter the predators such as ants and predatory wasps (Muller and Brakefield 2003). Some aphids especially *Brevicoryne brassicae* (Linnaeus) and *Lipaphis erysimi* (Kaltenbach) sequester glucosinolates from the phloem sap (Kazana et al. 2007, Bridges et al. 2002). Furthermore, Pierinae caterpillars such as *P. rapae* detoxify the glucosinolates from their host plants by converting these otherwise toxic breakdown products to inert metabolites through a nitrile-specifier protein (NSP). The NSP activity in the gut of *P. rapae* modulates the hydrolysis of glucosinolates and leads to the formation of nitriles instead of toxic isothiocyanates (Wittstock et al. 2004).

1.3.2.4 Adaptations to Tannins

Tannins are the polyphenolic compounds that strongly bind to proteins or to digestive enzymes in the gut, thereby reducing their digestibility by insect pests and thus affecting insect growth and development. In addition, tannins also act as feeding deterrents to many insects because of their astringent (mouth puckering) nature (Barbehenn and Constabel 2011). Tannins form hydrogen or covalent bonds with the protein amino groups, which leads to precipitation of proteins and the digestive enzymes of herbivores. Furthermore, chelation of metal ions in insects by tannins reduces their availability to the insect pests, thus affecting growth and development. Tannins have also been reported to inhibit feeding and cause midgut lesions and pharmacological toxicity (Bernays and Chamberlain 1980). However, insects have

developed several adaptive mechanisms to avoid the toxicity of tannins. The potential mechanisms insects use to avoid toxicity of tannins include alkaline gut pH, tannin absorption through peritrophic membrane, polymerization and excretion of the polyphenols after concentration (War and Sharma 2014). The surfactants formed as products of lipid digestion in the gut lumen prevent precipitation of proteins (Martin et al. 1987). Oxygen levels in foregut also play an important role in toxicity of tannins. At higher pH, oxygen levels are low and reduce autoxidation of tannins, thereby lowering their toxicity. The antioxidative system of insects also plays an important role in reducing the tannin toxicity. For example, ascorbate reduces the oxidation of tannins and formation of reactive oxygen species (ROS) in insect gut (Krishnan and Sehnal 2006). The grasshoppers possess a strong midgut antioxidative defence, which enables them to withstand tannins. This antioxidative defence mainly comprises of glutathione, α-tocopherol and ascorbate. The tolerance to tannins, and its association with peritrophic membrane in *S. gregaria*, has been attributed to the ultrafiltration of tannins. In some species including *Melanoplus sanguinipes* (Fabricius), tannic acid does not bind to the peritrophic membrane. In addition, peritrophic membrane protects the insect epithelium against lesions and damage by ROS by adsorbing highly reactive ferrous ions (Barbehenn 2003).

1.3.2.5 Detoxification of Plant Metabolites

Enzymatic detoxification of toxic chemicals mediates the adaptation of insects to plant allelochemicals and thus helps the herbivores to overcome plant chemical defences. Insects react strongly to the toxic allelochemicals, when provided with the natural host plant diet or incorporated in the artificial diet, by increasing the metabolic mechanisms that result in the production of detoxifying enzymes, such as monooxygenases and glutathione-S-transferases (GST) (Nitao 1989, Wadleigh and Yu Wadleigh and Yu 1988). The mechanisms of detoxification that operate in insects depend on the host plant chemistry, and its levels are generally influenced by concentration of the allelochemicals in the plant (War and Sharma 2014). Insects deploy various enzymes for detoxification of pesticides and plant allelochemicals, and some systems are thought to be ubiquitous (Francis et al. 2005; Scott et al. 2010). The best known is the system of polysubstrate monooxygenases (also called mixed-function oxidases). The terminal component of this system is cytochrome P-450, so called because it absorbs light maximally at around 450 nm when complexed with carbon monoxide. Cytochrome P-450 combines with the substrate (which may be a toxin) and with molecular oxygen, catalysing the oxidation of the substrate. Cytochrome can combine with many different lipophilic substrates and exists as several isozymes that vary in their substrate specificity (Feyereisen 2006).

The P450s are regarded as one of the important players in insect-plant coevolution, since these are used by the plants to produce toxins and by the insects for detoxification of phytochemicals (Schuler 1996). The desert dwelling species of *Drosophila mettleri* Heed feeding on cactus containing toxic allelochemicals possess inducible amounts of P450 involved in the metabolism of these toxins (Danielson et al. 1997). The metabolism of isothiocyanates such as 2-phyenylethylisothiocyanate, indole-3-carbinol and indole-3-acetonitrile in

S. frugiperda midgut microsomes is Cyt P450 dependent (Yu 2000). Adaptation of lepidopteran insects to plant secondary metabolites such as furanocoumarins has been attributed to P450s. Black swallowtail, *Papilio polyxenes* Fabricius, feeding on plants containing furanocoumarins tolerates up to 0.1% xanthotoxin in diet (Berenbaum 1991a), which is detoxified by P450 monooxygenases (Bull et al. 1986). A clearer picture of involvement of P450 in detoxification of plant allelochemicals came after the sequencing of *CYP6B1* from *P. polyxenes*, which codes for P450s. Expression of *CYP6B161* and *CYP6B162* coding for P450s is induced in lepidopteran cell lines, indicating the involvement of P450s in metabolism of linear furanocoumarins, such as xanthotoxin and bergapten (Ma et al. 1994). A number of P450s involved in detoxification of phytochemicals have been isolated from herbivores, for instance, from parsnip webworm, *Depressaria pastinacella* Duponchel (Cianfrogna et al. 2002), *M. sexta* (Stevens et al. 2000) and *Helicoverpa* species. Furthermore, the conversion of dihydrocamalexic acid to camalexin, which are the major *Arabidopsis* phytoalexins, is catalysed by cytochrome P450 PAD3 (Schuhegger et al. 2006). Aphid resistance to glucosinolates is attributed to the CYP81F2, which is a downstream part of the indolic glucosinolate pathway (Pfalz et al. 2009).

P450s have also been characterized from many other insects where they serve to metabolize the host chemicals. For example, in *Musca domestica* Linnaeus, CYP6A1 metabolizes the terpenoids (Andersen et al. 1997); in *H. armigera*, P450 monooxygenase CYP6AE14 detoxifies gossypol (Mao et al. 2007); in *Anopheles gambiae* Giles, CYP6Z1 metabolizes xanthotoxin and bergapten (furanocoumarins), furanochromones and natural myristicin, safrole and isosafrole (Chiu et al. 2008), while CYP6Z2 metabolizes xanthotoxin, lignin, piceatannol and resveratrol (McLaughlin et al. 2008); and in *Diploptera punctata* Eschscholtz, CYP4C7 hydroxylates sesquiterpenoids (Sutherland et al. 1998). Bark beetles such as *Ips pini* Wood & Bright and *Ips paraconfusus* Lanier detoxify the monoterpenes, sesquiterpenes and diterpenoid resin acids by P450s (Seybold et al. 2006).

The glutathione-S-transferase (GST) is another enzyme system involved in insect resistance to host plant defence by detoxification of xenobiotics and catalysation of the conjugation of electrophilic molecules with the thiol group of reduced glutathione, which results in their rapid excretion and degradation (Francis et al. 2005). This family of enzymes has been implicated in neutralizing the toxic effects of insecticides that are neurotoxic and/or affect insect growth and development. These include spinosad, diazinon, DDT, nitenpyram, lufenuron and dicyclanil (Sintim et al. 2009). Several studies have advocated the role of GST in insect adaptation to plant glucosinolates or other plant secondary metabolites incorporated into the artificial diet in *S. frugiperda*, *S. litura, T. ni, M. persicae*, *Aulacorthum solani* (Kaltenbach) and *A. pisum* (Enayati et al. 2005). The overproduction of GST in *M. persicae* has been attributed to insect adaptation to glucosinolates and isothiocyanates in members of Brasicaceae, although there is no direct confrontation of isothiocyanates, because aphids directly insert their stylets into the phloem (Francis et al. 2005; Kim et al. 2008).

1.3.2.6 Insect Gut Symbionts in Counter-Defence

The induction of plant defences in response to herbivore attack has been observed to be modulated by crosstalk between jasmonic acid (JA)- and salicylic acid (SA)-signalling pathways. Herbivores possess diverse microbes in their digestive tracts, and these symbionts can modify plant-insect interactions (Hogenout et al. 2009). Chung et al. (2013) reported that Colorado potato beetle, the *L. decemlineata*, grubs exploited gut bacteria in their oral secretions to overcome anti-herbivore defences in tomato. The antibiotic-untreated larvae decreased the production of JA and JA-responsive anti-herbivore defences but increased SA accumulation and SA-responsive gene expression. The downregulation or plant defences resulted in enhanced larval growth. The gut bacteria belonging to three genera (*Stenotrophomonas, Pseudomonas* and *Enterobacter*) were implicated for defence suppression in this study.

Hammer and Bowers (2015) recently proposed the 'gut microbial facilitation hypothesis', which proposes that variation among herbivores in their ability to consume chemically defended plants can be due, in part, to variation in their associated microbial communities. These hypotheses have drawn support from molecular studies on gut bacteria. The gut bacteria in Japanese common stink bug, *Megacopta punctatissima* (Montandon), is capable of decarboxylating oxalate, a common plant secondary metabolite (Nikoh et al. 2011). The mountain pine beetles harbour gut bacteria associated with terpene detoxification (Adams et al. 2013) and are capable of metabolizing terpenes in vitro (Boone et al. 2013). The *Acinetobacter* species from the midguts of gypsy moth larvae are capable of metabolizing dietary phenolic glycosides (Mason et al. 2014). Given the widespread occurrence of gut bacteria in oral secretions of insects, these may be associated with hijacking of plant defence responses in other cases of insect-plant interactions as well.

1.4 Human-Induced Plant Defences and Insect Counter-Defences: Case Study of Hessian Fly-wheat Interactions

The Hessian fly (HF), *Mayetiola destructor* (Say) (Cecidomyiidae: Diptera), is a serious pest of wheat with a long history of pestilence in the USA. The HF is distributed in North Africa, Europe, West and Central Asia, North America and New Zealand (Buntin and Chapin 1990). The pest has been successfully managed through release of a series of insect-resistant cultivars carrying HF-specific R-gene(s). However virulent biotypes of HF are capable of overcoming resistance in about 6–8 years (Chen et al. 2009; Stuart et al. 2012). Following egg hatch, the neonate HF larva on the upper surface of leaf crawls to the base of the seedling, wherein it establishes a sustained feeding site in susceptible genotypes but fails to do so in resistant ones. Virulent HF biotypes on a susceptible cultivar result in a compatible interaction favouring pest establishment, while a virulent biotype on the resistant cultivar results in incompatible interactions and pest mortality in 3–5 days (Subramanyam et al. 2015) (Table 1.2).

Table 1.2 Variations in responses of wheat and Hessian fly during compatible and incompatible interactions

Compatible interaction	Incompatible interaction
Larval growth completed in 10–12 days	Larvae die within 5 days of attack
	No larval growth
	Gut shows signs of toxin exposure
Seedling apical shoot meristem death	Seedling survival
Shorter plants, fewer heads, fewer seeds	
Increased cell permeability at attack sites	Localized cell death
	Accumulation of reactive oxygen species
Creation of nutritive cells	Adjacent living cells fortified
Cell wall breakdown	Transient increase in permeability
	Epicuticular waxes accumulate
Membrane permeability increases	Toxin production increases
Stress-related proteins increase	Class III peroxidases increases
C/N ratio shift favours N (52% change)	Phenylpropanoid metabolism increases
Nutrient metabolism and transport increases	
Cell wall metabolism decreases	Cell wall and lipid metabolism increases. Nutrient metabolism and transport suppressed
Basal defence response suppressed	Fatty acid degradation suppressed
Phenylpropanoid metabolism suppressed	Phospholipid metabolism suppressed
Histones and structural proteins decrease	Stress-related protein decrease

Modified from Stuart et al. (2012)

As many as 35 distinct resistance genes (*H1-H3*, *h4, H5-H34* and *Hdic*) from wheat and related plants have been characterized and incorporated in commercial wheat cultivars (Chen et al. 2006; Stuart et al. 2012). The HF-wheat system is considered a model system for study of gene-for-gene (GNG) interaction between host plants and insect pests (Hatchett and Gallun 1970; Subramanyam et al. 2015). In the case of resistant cultivars carrying R genes, the plants respond to attack of HF larvae by accumulation of reactive oxygen species (Liu et al. 2010) and production of enzyme inhibitors (Wu et al. 2008), lectins (Williams et al. 2002; Subramanyam et al. 2008) and secondary substances (Liu et al. 2007). On the other hand, the compatible interactions are characterized by increased nutrient availability at the site of attack along with an accumulation of nitrogen-rich molecules (Liu et al. 2007; Williams et al. 2011). It has been revealed that the HF is able to overcome resistance through recessive mutations in corresponding avirulence (HF*Avr*) genes (Aggrawal et al. 2014). The HF*Avr* genes code for proteins (called effectors) that are injected with the saliva in to the plant tissue during feeding (Hogenhout et al. 2009). The plants carrying R genes are able to recognize these secretions and stimulate the defence pathways (Chisholm et al. 2006). In virulent HF biotypes, the Avr proteins are modified to avoid either detection by the plant or a failure to trigger the defence pathway (Chen et al. 2016).

1.5 Theories on Evolution of Insect-Plant Interrelationships and Their Role in Diversification

As early as 1859, Darwin in his magnum opus *On the Origin of Species* wrote of 'Coadaptations of organic beings to each other…'. Every living organism interacts with others of the same as well as another kind. Coevolution refers to genetic change in two interacting species. In other words, coevolution is reciprocal evolutionary change in interacting species. The term was originally used by C.J. Mode in 1958 for the coevolution of obligate parasites and their hosts. Ehrlich and Raven (1964) were the first to extend its relevance to insect-host plant coevolution based on their study of Monarch butterfly-milkweed (host plant) interactions.

A plant is neither susceptible to all the phytophagous insects nor any insect species is a pest on all the species of plants it encounters in nature. Further, less than one third of all insect orders contain exclusively (Lepidoptera, Orthoptera, Phasmida), predominantly (Hemiptera, Thysanoptera) or partially (Coleoptera, Diptera, Hymenoptera) phytophagous species. But such species comprise nearly half of all insect species. This is attributed to the fact that all plants have developed a dazzling array of structural and biochemical defences (constitutive as well as induced) against herbivores. Only those species which are able to breach these defences in one or more plant species can access such plants for food (Arora 2012). The insects thus keep on developing strategies for detoxifying or otherwise overcoming these defensive mechanisms.

The extant phytophages and their host plants are the result of a coevolutionary process that has been ongoing for nearly 400 Myr (Labandeira 2013). Insects have acquired a sensitive system for perceiving their external environment, analysing the sensory input and responding to it suitably (Martin et al. 2011). Successful host finding and acceptance are primarily controlled by chemical cues. The insect responses are dependent on a combination of host and environmental cues (Riffell et al. 2009; Webster et al. 2010). Concomitantly, the plants have also evolved numerous structural and chemical defences for protection against insects and other herbivores. The insects in turn have evolved to avoid or overcome these defences. A number of theories have been propounded to explain this evolutionary arms race between these two interdependent groups of organisms.

1.5.1 Theory of Coevolution

This theory was elaborated by Ehrlich and Raven (1964) and later supported by Berenbaum (1983). According to this theory, many plant taxa manufacture a prototypical phytochemical that is mildly noxious to phytophages and that may have an autecological or physiological function in the plant. Some insect taxa feed upon plants with only this and other, similarly mild, phytochemicals, thus reducing plant fitness. Plant mutation and recombination cause novel, more noxious phytochemicals to appear in the plants. The same chemical can appear independently in distantly related plant groups. Insect feeding is reduced because of toxic or repellent

properties of the novel phytochemical; thus plants with more and more potent defences are preferred by the pressure of insect herbivory. In response, the insects have evolved the capacity to avoid or neutralize the effective chemical and even utilize the same compound as well as the plant producing it for their own benefit. An insect can specialize in feeding upon plants with the novel compound. Here it would be free to diversify due to a lack of competition from non-adopted herbivores. The cycle may be repeated, resulting in more phytochemicals and further specialization of insects.

Some supporting evidence for the theory is available from species-level studies on taxa of selected insects and their host plants. Closely related *Phyllobrotica* species feed monogamously on closely related *Scutellaria* species as revealed by the cladograms of the two groups (Farrell and Mitter 1990). Evidence is also available at the level of populations. An analysis of different populations of wild parsnip, *Pastinaca sativa* Linnaeus, and its specialist herbivore pest the parsnip webworm, *Depressaria pastinacella* Duponchel, revealed trait matching between furanocoumarin-based chemical defences in the plants and cytochrome P450 monooxygenase-based insects' detoxification profiles (Berenbaum and Zangerl 1998, Zangerl and Berenbaum 2003).

An interesting example of coevolution is that involving the brassicaceous plants and the pierid butterflies. The glucosinolate-myrosinase system evolved by Brassicales (Sect. 1.3.2.3) around 90 Myr represents a key step in anti-herbivore defences by plants. But shortly thereafter, the Pierinae butterflies which utilized Fabales as host plants came up with a detoxifying system in the form of nitrile-specific protein (NSP) and started colonizing the Brassicales. This resulted in increasing the species diversification rates in Pierinae as compared with that of their sister clade Coliadinae, whose members did not colonize Brassicales, thus lending strong support to the coevolutionary theory (Wheat et al. 2007; Edger et al. 2015).

1.5.2 Theory of Sequential Evolution

The theory of sequential evolution (Jermy 1976, 1984) proposes that evolution of herbivorous insects follows the evolution of plants, without however significantly affecting plant evolution. According to this theory, reciprocal selective interactions between plants and herbivorous insects have not been proved so far. Plants undeniably cause evolutionary changes in phytophagous insects, whereas the latter exert selective pressure on the plants only in rare cases and even in these only weakly. The insects choose their host plants largely based on perception of chemical cues. Therefore, any changes in chemical composition of host plants or their chemosensory perception by insects may lead to emergence of new insect-host plant relationships. However, contradictory paleontological evidence in the form of insect familial diversification preceding the major diversification of angiosperms contradicts this theory. As a consequence, speciation in herbivorous insects may be mediated by plants, but speciation in plants has not been proved to occur as a consequence of interaction with herbivorous insects.

Further evidence in support of the theory was presented by Labandeira (1998) and Janz et al. (2006), who showed that species richness in butterfly family Nymphalidae was strongly correlated with diversity of host use.

1.5.3 Theory of Diffuse Coevolution or Community Coevolution

The theory of diffuse coevolution proposes that, instead of the pairwise reciprocal evolutionary interactions, coevolution must be considered in a community context and not simply as a reciprocal two-species interaction. Every plant may be affected by a diversity of herbivores, plant pathogens, competing conspecifics, plants of other species including alternate host plants of insect pests and organisms at higher tropic levels (Fox 1988). This theory is thus only an extension of the coevolutionary theory.

1.5.4 The Geographic Mosaic Theory of Coevolution

This theory states that the coevolutionary process operates at the level of populations rather than at species level. Thompson (1994, 1999, 2005) propounded that interspecific interactions commonly differ in outcome among populations. These differences result from the combined effects of differences in the physical environment, the local genetic and demographic structure of populations and the community context in which the interaction occurs. As a result of these differences in outcomes, an interaction may coevolve some populations (coevolutionary hot spot), affect the evolution of only one of the participants in other populations (coevolutionary cold spot) and have no effect on evolution in yet another local population (again coevolutionary cold spot). In addition, populations differ in the extent to which they show extreme specialization to one or more species. Some populations may specialize on and sometimes coevolve locally with only one other species, other populations may specialize on and perhaps coevolve with different species and yet others may coevolve simultaneously with multiple species. These interpopulational differences in outcome and specialization create a geographic mosaic in interactions. Gene flow among populations, random genetic drift, selection for novel traits and extinction of some demes reshape the geographic mosaic of coevolution as the adaptations and patterns of specialization developed locally spread to other population or are lost. The result is a dynamic geographic pattern of coevolution between any two or more species.

The coevolutionary relationship between the obligate seed predator, the camellia weevil, *Camellia japonica* Linnaeus, and its host plant, the Japanese camellia, *Camellia japonica* Linnaeus, represents an interesting example of geographic mosaic across the Japanese islands (Toju and Sota 2006, Toju et al. 2011). The thickness of camellia pericarp through which the female weevils bored to lay eggs into seeds correlated with the length of rostrum in females. Further, the pericarp was significantly thicker on islands with weevils than on islands devoid of weevils, and the trait was heritable.

1.6 Practical Applications of Insect-Plant Interrelationships Research

An intricate understanding of insect-plant relationships has immense practical significance for future agricultural production. As consumers of plant products, humans wish to minimize crop losses caused by all other organisms including insect pests and maximize crop productivity. The mechanisms underlying insect-plant interactions are the key to achieve these objectives in the following ways.

1.6.1 Breeding Insect-Pest-Resistant Crops

Insect-resistant cultivars represent one of the most environmentally benign, economically feasible and ecologically sustainable options for management of insect pests. The breeding of arthropod-resistant plants has been undertaken for more than a century and blossomed as a field of research in the first half of the twentieth century with the work of Prof R H Painter at Kansas State University, Manhattan, Kansas, USA (Painter 1951). An outstanding early success in utilizing host plant resistance in pest management was the control of the grape phylloxera *Daktulosphaira vitifoliae* (Fitch) in France by grafting European grapevines onto resistant North American rootstocks (Painter 1951). In India, the early work of Hussain and Lal (1940) led to hairy cotton varieties resistant to jassid, and by 1943 resistant varieties such as Punjab 4F, LSS and 289 F/43 covered extensive areas, where jassid had posed a serious threat. Over the past 70 years, breeding stress-resistant crops has gained increased importance with the involvement of national and international agricultural research centres as well as private sector seed producers. Hundreds of insect-resistant crop cultivars have been developed worldwide and are grown extensively for increasing and stabilizing the crop productivity (Panda and Khush 1995). In economic terms, the arthropod resistance genes deployed in global agriculture currently save us more than US$2 billion annually (Smith and Clement 2012).

Identification of the mechanism of resistance to insect pests followed by isolation and cloning of gene(s) responsible for production of the desired chemical/characteristic is likely to fast-track the production of insect-resistant cultivars. An improved understanding of plant defence responses to herbivory is also essential for further exploitation of induced resistance and plant-released volatiles for development of insect-resistant genotypes (Sandhu and Arora 2013). Exploitation of insect-resistant genes from unrelated organisms (mainly microbes) and their incorporation into elite germplasm is another fruitful approach which has found widespread application. A total of 20 Bt genes from the soil bacterium, *Bacillus thuringiensis*, imparting resistance to lepidopteran and coleopteran pests have been incorporated into cotton, corn, soybean, potato and other crop plants (Shera and Arora 2015).

1.6.2 Cultural Control of Insect Pests

The manipulation of crop production and management techniques for reducing or avoiding pest damage is known as cultural control. An understanding of crop plant-insect pest relationship is useful to modify the crop environment against the pest or in favour of the natural enemies. For instance, early sowing/planting has been found to reduce gall midge and leaf folder damage in rice, shoot fly and headbug damage in sorghum and millets, white grubs' damage in groundnut and aphid damage in crucifers in Northern India (Dhaliwal and Arora 2006).

Increasing intra-field diversity through intercropping, trap cropping or planting of hedge rows results in reduced damage by several species. Tomato intercropped with cabbage has been reported to reduce incidence of diamondback moth. Trap crop of African marigold lowers the incidence of fruit borer *H. armigera* in tomato (Srinivasan 1994). Napier grass and Napier millet serve as trap crops for lowering the incidence of stem borer *C. partellus* in maize and sorghum (Khan 1999; Dhaliwal and Arora 2006).

The parasitoids and predators of insect pests may attain higher population densities in polycultures than in monocultures, because polycultures often offer additional food sources, such as honeydew, nectar and pollen, and more refuges where insects can shelter in the shade (Coll 1998). More than half among the 130 natural enemy species surveyed reached higher population densities in polycultures, than in monocultures, whereas in less than 10% of the cases, lower population densities were observed (Andow 1991).

1.6.3 Botanical Insecticides

Plants have developed pathways to a diverse array of chemicals to prevent their exploitation by insects and other herbivores over millions of years. These chemicals exert behavioural, physiological and biochemical effects on insects, and some of these may even cause mortality in susceptible insects. Botanicals insecticides, as these plant-derived products are known, have been utilized by humans since ancient times. Neem, pyrethrum, *Tephrosia*, tobacco, derris, *Ryania*, sabadilla and many other plants have been used to protect agricultural crops, grains and other commodities from the ravages of insects and noninsect pests in different parts of the world for centuries (Dhaliwal and Arora 2001).

Phytochemicals have also served as prototypes for synthesis and development of novel groups of insecticides. For instance, pyrethrum, derived from the dried flowers of *Chrysanthemum cinerariaefolium* Linnaeus, has been used as an insecticide since ancient times. It is a potent toxicant against insects and comparatively safe to mammals. But it is highly photolabile (Casida 1973). Therefore, the chemical structure of pyrethrum was elucidated to develop synthetic analogues with improved photostability. Many of these chemicals like fenvalerate, deltamethrin, fluvalinate

and cyfluthrin became popular insecticides during the 1980s (Dhaliwal and Arora 2006). Similarly synthetic analogues of nicotine, another popular botanical insecticide obtained from tobacco, called neonicotinoids are currently widely used against a broad range of sucking insect and mite pests (Simon-Delso et al. 2015). Thus, botanical insecticides have not only proved useful directly in pest control but have also served as models for generation of new classes of synthetic insecticides. Since plants contain tens of thousands of such chemicals, the scope of their utilization in insect pest management is almost endless.

1.6.4 Biological Control of Insect Pests

The importance of studies on tritrophic and multi-trophic interactions for enhancing the efficiency of natural biological control and integrated pest management can hardly be over-emphasized. Plant-produced volatiles are known to attract natural enemies of insect pests (Weseloh 1981). Ramachandran et al. (1991) reported that the parasitoid *Microplitis demolitor* Wilkinson was attracted by the volatile 3-octanone released by the soybean plant which hosts the soybean looper, *P. includens*. The parasitoid was markedly more arrested by the volatile guaiacol, which was found only in its hosts' frass. But all such interactions may not favour the natural enemies. Hare (1992) found the spectrum of interactions between natural enemies and crop resistance to range from synergistic, to additive, to none apparent, through to disruptive or antagonistic. Dhaliwal et al. (2004) conducted a meta-analysis of 27 studies on interaction of resistant crop cultivars and biocontrol of insect pests. Antagonism was recorded in 29.6%, synergism in 25.9% and additive relationship in 33.3% of cases. In the remaining three cases, the form of relationship varied with resistant level of the cultivars employed. As knowledge of these multi-trophic interactions expands, researchers and IPM practitioners need to exploit it for management of insect pests (Verkerk 2004).

1.6.5 Behavioural Manipulation in Insect Pest Management

Insect behaviour is elicited in response to olfactory, visual, tactile, acoustic and gustatory-sensory information from the host plant as well as the surrounding environment. An improved understanding of cues utilized by insects for feeding and oviposition preference on host plants can help in manipulation of such behaviour, leading to reduced crop damage (Foster and Harris 1997).

The attract and kill method is by far the most popular behavioural manipulation utilized in pest management. The Japanese beetle *Popillia japonica* Newman is successfully managed by a combination of the female sex pheromone, with a food lure (a mixture of phenethyl propionate, eugenol and geraniol) (Ladd et al. 1981). Foods baits have also been found useful for monitoring and controlling tephritids. Protein-hydrolysate-baited traps containing insecticides have been successful against the Mediterranean fruit fly, *Ceratitis capitata* Wiedemann, in the USA

(Chambers 1978). An innovation of the 'attract-annihilate method' has worked against the apple maggot fly, *Rhagoletis pomonella* (Walsh). The female flies locate host trees and suitable oviposition sites on apple through olfactory and visual stimuli. Wooden spheres in red colour and covered with a sticky substance at one trap tree^{-1} afforded good protection of fruits from *R. pomonella* (Aluja and Prokopy 1993; Foster and Harris 1997).

1.6.6 Push-Pull Strategy for Management of Insect Pests

An innovative manipulation of the behavioural approaches is the push-pull IPM or stimulo-deterrent approach in pest management. It involves utilization of attracting (pull) and repelling (push) components in tandem to divert the pest away from the main crop and towards the trap crop, from where these may be subsequently removed (Khan et al. 1997; Cook et al. 2007). The technology has been successfully applied for management of several species of stem borers (*C. partellus, Eldana saccharina* Walker, *Busseola fusca* Fuller, *Sesamia inferens* Hampson) infesting maize and sorghum in Eastern and Southern Africa. The ovipositing female moths of borers are repelled from the main crop by repellent non-host intercrops, particularly molasses grass, silverleaf desmodium or greenleaf desmodium (push), and prefer to oviposit on attractive trap plants, primarily Napier grass or Sudan grass (pull). Intercropping of molasses grass with maize increased parasitization by *Cotesia sesamiae* Cameron in addition to lowering the incidence of stem borer (Khan et al. 2011). Push-pull strategies have also been effectively demonstrated against *Helicoverpa* in cotton, *L. decemlineata* in potato, striped pea leaf weevil *Sitona lineatus* (Linnaeus) in beans, rapeseed pollen beetle *Brassicogethes aeneus* (Fabricius) in oilseed rape, onion maggot *Anthomyia antiqua* (Meigen) in onions, western flower thrips, *Frankliniella occidentalis* (Pergande) in chrysanthemum and bark beetles (Scolitidae) in conifers, in addition to several veterinary and medical pests (Cook et al. 2007).

1.6.7 Managing Insect Biotypes

The continuous growing of insect-resistant cultivars exerts selection pressure on the targeted pest, which responds by developing new physiological and behavioural mechanisms to enable feeding and development on the resistant cultivars. Insect biotypes refer to populations within an insect species that can survive on and destroy varieties that have genes for resistance (Heinrichs et al. 1985). Biotype selection is one of the major constraints encountered in breeding programmes for varietal resistance. The concept of biotypes involves gene-for-gene relationship between the gene for resistance in the host plant and the gene for virulence in the insect pest. Aphids comprise 18 of the 39 insect species in which 2 or more biotypes have been reported (Sandhu and Arora 2013). Brown plant hopper, *Nilaparvata lugens* Stal, on rice (Brar et al. 2015) and Hessian fly, *M. destructor* on wheat are the major pests in

which biotype development has led to breakdown of resistance in the field (Aggrawal et al. 2014; Subramanyam et al. 2015). The durability of insect resistance can be increased by sequential release of cultivars, gene pyramiding/stacking and gene rotation (Sandhu and Arora 2013). An improved understanding of insect-plant interactions is crucial for efficient management of insect biotypes resulting in greater stability of resistant genotypes.

1.6.8 Biological Control of Weeds

The losses caused by weeds are estimated to be higher than those caused by insect pests to agricultural crops and the global use of herbicides exceeds that of insecticides in crop protection (Oerke 2006). In view of the widespread problems caused by extensive use of herbicides, there is an urgent need to strengthen biological control of weeds. Exotic weeds may be successfully managed by introducing monophagous or oligophagous insect species from the plants' place of origin. Important successful examples include management of shellmound prickly pear, *Opuntia stricta* (Haworth) Haworth, in Australia through releases of the small Argentinian moth, *Cactoblastis cactorum* Berg (Dodd 1940), and of giant salvinia, *Salvinia molesta* D. S. Mitchell, in Papua New Guinea by releasing the weevil *Cyrtobagous salviniae* Calder & Sands imported from Brazil (Room 1990). In Hawaii extensive programmes on biological control of weeds through releases of herbivorous insects as well as pathogens have been undertaken, resulting in complete control of 7 out of 21 target weed species and significant partial control of another 3 species (Gardner et al. 1995; McFadyen 2003).

In some cases, the native insects have also been artificially multiplied and released or otherwise manipulated for the control of native weeds. Native coccids, *Austrotachardia* sp. and *Tachardia* sp., are used for the control of *Cassinia* sp., native woody shrubs in Australia (Holtkamp and Campbell 1995). Conservation/augmentation of the stem-boring agromyzid, *Phytomyza orobanchia* Kaltenbach, has been utilized for managing the parasitic weeds, *Orobanche* spp. in the southern USSR (Kroschel and Klein 1999).

1.6.9 Pollinator Conservation for Improving Crop Productivity

Insect pollinators are essential for successful pollination and reproduction by a vast majority of terrestrial flowering plants. Even self-pollinating crop species may show yield enhancement in vicinity of a good pollinator habitat. Coffee shrubs, for instance, show significant yield increases in regions with stable native or introduced bee populations (Roubik 2002). Most studies on plant-pollinator systems have focused on a single plant species and usually one or a few closely associated visitor taxa. But recent studies have revealed that pollinator complexes are relatively generalized, due to spatiotemporal variation in pollinator visits (Herrera 1996; Waser 1998; Burkle and Alarcon 2011). It is important to understand the bases of spatial

and temporal variation in plant-pollinator interactions to answer questions in community structure and function. It will also help in formulating optimal conservation strategies (Burkle and Alarcon 2011). Climate change may disrupt the synchrony between the flower production season of plants and the activity period of pollinating insects. A shortage of nectar and pollen during critical periods may also lead to a decline in population of pollinators (Hoover et al. 2012; Sharma et al. 2014). A precise understanding of the flowering plant-pollinator interactions may help in arresting pollinator decline and maintaining agricultural productivity.

1.7 Conclusions

Insects and green plants, the two dominant life forms in the terrestrial ecosystem, are bound together by intricate relationships. A majority of the angiosperms require the services of pollinating insects for successful reproduction. The shape, size, colour and scent of flowers all serve to attract pollinators, which mostly feed on nectar and pollen produced by these plants. Further, nearly half of all insect species are herbivorous and depend on plants for food, shelter (at least for a part of life cycle) and oviposition sites. Consequently, the plants have evolved a staggering variety of structural and biochemical barriers to protect themselves from insects and other herbivores, as well as pathogens. The insects which are able to overcome these barriers (through avoidance, detoxification, sequestration, etc.) can gain an abundant supply of food with very little competition from other herbivores. Reciprocal adaptation and counter-adaptation between plants and insects have, thus, been an important mechanism driving a steady increase in biodiversity of both these groups of organisms over the last more than 400 million years.

The study of these interrelationships between insects and flowering plants is of great practical importance for future agricultural production. We are only just beginning to understand the intricacies of these relationships. The new techniques of molecular biology including genomics, proteomics and RNAi offer exciting opportunities for further exploration and precise understanding of insect-plant interactions, which is essential for conserving ecosystem biodiversity and developing insect-resistant crop plants, as well as for sustainable management of insect pests and weeds.

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Insect Pests and Crop Losses

2

Smriti Sharma, Rubaljot Kooner, and Ramesh Arora

Abstract

The world population has been galloping upwards at an unprecedented rate during the last 50 years. So far, the modern agricultural technology has enabled us to largely keep pace with the increasing human population through increased productivity of major crops. But in addition to causing environmental deterioration, it has also resulted in increasing losses by pests, pathogens and weeds. There is however a paucity of reliable data on the extent of food losses caused by these biotic agents, especially in the developing countries. The limited data available indicate that arthropods may be destroying an estimated 18–20% of the annual crop production worldwide estimated at a value of more than US$470 billion. Further, the losses are considerably higher in the developing tropics of Asia and Africa, where most of the future increase in world population is expected during the next 50 years. There is an urgent need to precisely estimate the extent of food loss and waste at different stages from the agricultural fields to human consumption with emphasis on the developing countries. This is the necessary first step towards development of safe, economical and sustainable methods of pest management, as well as food security, for the future.

Keywords

Crop losses • Insect pests • Global losses • Food security • Potential food loss

S. Sharma (✉) • R. Kooner
Department of Entomology, Punjab Agricultural University, Ludhiana 141004, India
e-mail: smritisharma80@pau.edu; rubalsidhu05@pau.edu

R. Arora
Department of Entomology & Zoology, Eternal University, Baru Sahib,
Himachal Pradesh 173101, India
e-mail: arorarame@gmail.com

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2.1 Introduction

In natural ecosystems, phytophagous insects coexist in a complex relationship with plant communities. Different species of plant-feeding insects must search out their host plants from the mixed vegetation. In this search, they face the dangers of annihilation by various abiotic and biotic agents. Therefore, the damage caused by insects is quite limited in the natural ecosystems. In contrast, the natural regulating factors play only a limited role in agroecosystem, and insect pest outbreaks are quite frequent. Further, rapidly increasing human population during the last century has necessitated intensification of agriculture, which has resulted in aggravation of pest problems and increasing pest-associated losses (Pimental 1977; Bramble 1989; Arora and Dhaliwal 1996; Dhaliwal and Arora 2006).

Despite great advances in agricultural productivity and economic well-being in much of the world over the past 50 years, food insecurity continues to be a serious issue for large sections of the human population. The world population has been galloping upwards rather rapidly in the recent past. While it took more than a million years for humans to reach the first billion mark in 1804, it reached a level of 7 billion in another 207 years by 2011 (Anonymous 2011). During the last 50 years, the human population has jumped from 3.5 billion to more than 7.4 billion. There has thus been more growth in human population in the last 50 years than during the entire period of more than a million years that humans have inhabited the Earth. Interestingly, the greatest episode of population growth in human history was accompanied by an increase in the per capita food supply, especially during the first half of this period. This was made possible by the 'green revolution', which resulted in a quantum jump in the productivity of major cereal crops in Asia and to a lesser extent other parts of the world from the late 1960s onwards. It thus helped to avert mass famines but may also have contributed to the population explosion.

During the last five decades, intensive agriculture utilizing green revolution technologies has caused tremendous damage to the natural resources that sustain it. Fresh water, quality soil, energy and biodiversity are all being depleted, degraded and/or polluted (International Food Policy Research Institute 2016). The rate of increase in productivity of major cereal crops has also declined significantly. Consequently, the per capita availability of food grains has been declining of late. Thus, intensive high-input technologies may not be able to meet the human needs for food, feed and fibre in future.

As per various estimates, around 1 billion people in the world are undernourished and/or living without adequate energy. Further, the human population continues to grow at a rapid rate and is likely to reach 9.1 billion by 2050. Even more alarming is the fact that future increases in population will be largely concentrated in the developing countries of Asia and Africa, many of which are already battling severe food shortages. It has been estimated that world food production will need to rise by 70%, and production in developing countries will need to double to meet the food needs of the world by 2050 (Anonymous 2015a). This must be achieved in the face of energy shortages, growing depletion of underground aquifers, continuing

loss of farmland to urbanization and increased drought and flooding due to climate change (Schuster and Torero 2016).

In the face of increasing demand for food, it is ironic that at least one-third of the potential agricultural production is lost due to damage by animal pests and diseases (Oerke et al. 1994). Reduction in pre-harvest pest-associated losses is one of the important means of increasing agricultural production. Minimizing pest-associated losses will take us a step closer to achieving the recently adopted global Sustainable Development Goals (SDGs) of ending poverty, hunger and all forms of malnutrition (Anonymous 2016). However, precise estimates of the extent of losses caused by insect and non-insect pests in important crops are not available for most of the developing countries (Culliney 2014). The losses have been reported to vary widely in different crops as well as across different regions of the world (Oerke et al. 1994; Oerke 2006). This chapter attempts a brief overview of the extent of field losses caused by insect pests in important crops.

2.2 Types of Crop Losses

Insects are the most ubiquitous, diverse and abundant group of animals on planet Earth. These tiny but versatile creatures are the major competitors with humans for the resources generated by agriculture (Oerke and Dehne 2004). The damage caused by these organisms is one of the most important factors in the reduced productivity of any crop plant species (Metcalf 1996; Pimentel 1976). FAO/WHO (2014) have defined pest as 'any species, strain or biotype of plant, animal or pathogenic agent injurious to plants and plant products, materials or environments and includes vectors of parasites or pathogens of humans and animal disease and animals causing public health nuisance'.

Crop losses are usually defined as the reduction in either quantity or quality of yield (Zadoks and Schein 1979), and these may be caused by abiotic and biotic factors, leading to the reduction in crop productivity and lower actual yield than the attainable yield of crops. Losses can occur at any stage of crop production in the field (preharvest) or even during storage (postharvest) (Oerke 2006). Direct yield losses caused by pathogens, animals and weeds are altogether responsible for 20–40% loss of global agricultural productivity (Teng 1987; Oerke et al. 1994; Oerke 2006). Although crop protection aims to avoid or prevent crop losses or to reduce them to an economically acceptable level, the availability of quantitative data on damage caused by these pests is limited (Oerke 2006).

The ultimate effect of the attack by pest organisms on a crop is commonly expressed as the effect on yield, the quantity of harvestable economic product which is typically given as weight of product per unit area, such as kilograms or tonnes per hectare. Still, several ways of categorizing yield have been proposed (Nutter et al. 1993). The theoretical yield potential is the yield obtained, when crops are grown under optimal environmental conditions using all available production and pest control technologies to maximize the yield. The attainable yield is defined as the site-specific technical maximum, depending on abiotic growth conditions, which in

general is well below the yield potential. This is a theoretical yield level that cannot be realized under practical growth conditions. The actual yield is the site-specific yield obtained, when crops are grown using practical cultivation and plant protection practices at the farm level (Oerke et al. 1994).

Crop losses may also be expressed in absolute terms (kg/ha, financial loss/ha) or in relative terms (per cent loss). Quantitative losses are expressed as loss in productivity leading to a smaller yield per unit area, while qualitative losses are defined as loss in content of important ingredients or reduced market quality. Two loss rates must be differentiated: the potential loss and the actual loss. The potential loss from pests includes the losses without physical, biological and chemical crop protection compared with yields with similar intensity of crop production in a no-loss scenario. Actual losses comprise the crop losses sustained despite the crop protection practices employed, and under such conditions, the efficacy of crop protection practices is calculated as the percentage of potential loss prevented (Oerke 2006). The loss rate may be expressed as the proportion of attainable yield, but sometimes the proportion of the actual yield is calculated. The economic relevance of crop losses may be assessed by comparing the costs of control options with the potential income from the crop losses prevented due to pest control. The recent Global Food Policy Report from the International Food Policy Research Institute (IFPRI), Washington, DC, introduces a new term 'potential food loss and waste' (PFLC) covering loss and waste along all stages of the value chain, from pre-harvest to table waste. As per the report, a standard definition and terminology for food loss and waste are crucial. The report emphasized that the methodology used to measure food loss and waste must capture both quantitative and qualitative food loss along the value chain as well as discretionary food waste in processing, distribution and retail sectors (Schuster and Torero 2016). But this does not include the field losses from sowing to the pre-harvest stage.

2.3 Trends in Crop Losses Due to Insect Pests

There have been many reports worldwide on estimates of crop losses, e.g. in the USA, Marlatt (1904) estimated pre-harvest losses caused by insect pests to be nearly 10%. As per German authorities, in 1929 animal pests and fungal pathogens each caused a 10% loss of cereal yield, while, in potato, pathogens and animal pests reduced production by 25 and 5%, respectively, and in sugar-beet, production was reduced by 5 and 10% due to pathogens and animal pests, respectively (Morstatt 1929). Production losses in various field crops, fruits and vegetables in Great Britain were assessed by Ordish (1952). The first systematic attempt to estimate crop losses due to various pests globally was made by Cramer (1967), who estimated overall annual losses in major crops (including cereals, potato, vegetables, fruits, oil crops, fibre crops and natural rubber) to be about 34%. An analysis of crop losses in different regions showed that production losses in Europe (28.2 %), North America (31.2 %) and Oceania (36.2%) were below average, whereas in Africa and Asia reached almost 50% (Table 2.1). The losses due to animal pests in Asia (18.7%) were nearly double than those in developed countries, and losses from weed competition in Africa and Asia were approximately double than the same in Europe (Oerke et al. 1994).

Table 2.1 Crop losses in different continents

Continent	Crop loss (%)			
	Animal pests	Pathogens	Weeds	Total
Africa	16.7	15.6	16.6	48.9
N. America	10.2	9.6	11.4	31.2
Latin America	14.4	13.5	13.4	41.3
Asia	18.7	14.2	14.2	47.1
Europe	10.2	9.8	8.3	28.2
USSR	12.9	15.1	12.9	40.9
Oceania	10.7	15.2	10.3	36.2
Mean	15.6	13.3	13.2	42.1

Modified from Oerke et al. (1994)

The crop losses due to insect pests were less in the pre-green revolution period as compared to those in the post-green revolution period and beyond, throughout the world in almost all the crops except cotton and rice. While decrease in crop losses to the tune of 6.8% was observed in rice, it contrasted with an increase of 1.5 and 4.2% in maize and wheat, respectively, in a comparison of traditional and modern agriculture (Benedict 2003). Oerke et al. (1994) estimated that the total crop losses caused by all groups of pests varied from 32.4% in soybean to 51.4% in rice, while those by animal pests ranged from 8.8% in barley to 20.7% in rice. In comparison with these studies, Oerke and Dehne (2004) reported that pests caused substantial losses in most of the crops grown worldwide, and these accounted to be as much as 50% in rice, 41% in potato, 40% in coffee, 39% in maize, 38% in cotton, 34% in wheat, 32% in soybean, 30% in barley and 26% in sugar beet. Further, it was reported that the total global potential loss due to pests varied from about 50% in wheat to more than 80% in cotton production. After the green revolution, the losses were estimated to be 26–29% for soybean, wheat and cotton, and 31, 37 and 40% for maize, rice and potatoes, respectively (Oerke 2006). It was further stated that around one-third of the total production in major crops was damaged due to animals (mostly insects), diseases, viruses and weeds at the global level (Oerke 2006). According to the Food and Agriculture Organization of the United Nations (FAO), global cereal losses are estimated at 19–30%, root and tuber losses at 33–60% and fruit and vegetable losses at 37–55% (FAO 2011). Since, crop yield is affected by a multitude of variables and their interactions (Culliney 2014); hence the studies on these combined effects on crop yields are essential.

Over the decades, the losses inflicted by insect pests globally have shown a variable trend in different crops as per various estimates, which are summarized in Table 2.2. The first comprehensive attempt to estimate crop losses due to various pests by Cramer (1967) revealed a loss of 5.1, 27.5, 13, 5.9, 4.4, 16 and 3.9% in wheat, rice, maize, potato, soybean, cotton and barley, respectively. The estimated losses in wheat crop increased from 5.1% in 1967 to 9.3% in 1994 (Oerke et al. 1994). After another decade, Oerke and Dehne (2004) stated that the losses in wheat crop declined slightly to 9% and further to 7.9% in a succeeding estimate (Oerke 2006). The losses in rice crop showed a variable trend in different estimates by

Table 2.2 Global estimates of crop losses due to insect pests/animal pests

Crop	Cramer (1967)	Oerke et al. (1994)	Oerke and Dehne (2004)	Oerke (2006)
Wheat	5.1	9.3	9	7.9
Rice	27.5	20.7	24	15.1
Maize	13.0	14.5	15	9.6
Potatoes	5.9	16.1	18	10.9
Soybean	4.4	10.4	11	8.8
Cotton	16.0	15.4	37	12.3
Barley	3.9	8.8	7	–
Sugar beet	–	–	6	–
Coffee	–	14.9	–	–

various workers over the years. The losses were estimated to be 27.5% by Cramer (1967), 20.7% by Oerke et al. (1994), 24% by Oerke and Dehne (2004) and 15.1% by Oerke (2006). In case of maize, soybean and potato, the highest losses of 15, 11 and 18%, respectively, were reported by Oerke and Dehne (2004). In cotton, the losses caused by insect pests were reported to be 16% by Cramer (1967), 15.4% by Oerke et al. (1994) and 37% by Oerke and Dehne (2004). However, the introduction of *Bt* cotton led to a precipitous decline in yield losses with only 12.3% loss reported by Oerke (2006) (Table 2.2).

Globally arthropods destroy an estimated 18–20% of annual crop production worldwide, at a value of more than US$ 470 billion. The greater proportion of these losses (13–16%) occurs in the fields, before harvest, and losses have been heaviest in developing countries. An overview of recent studies on global food loss and waste magnitudes shows a range from 27 to 32% of all food produced in the world (Schuster and Torero 2016). But this estimate did not include the field losses during production.

Losses due to insect pests in Indian agriculture have also been estimated from time to time (Pradhan 1964; Krishnamurthy Rao and Murthy 1983; Atwal 1986; Jayaraj 1993; Lal 1996; Dhaliwal and Arora 1996, 2002; Dhaliwal et al. 2003, 2004), and the increase in crop losses after green revolution was quite large as compared to that recorded at the world level (Pradhan 1964; Dhaliwal et al. 2004). As per estimates by Dhaliwal et al. (2007), the crop losses increased from 7.2% in the early 1960s to 23.3% in the early 2000s, but later on, these losses declined to 17.5% during the twenty-first century (Dhaliwal et al. 2010). In an estimate of losses caused by the insect pests, it was reported that during the pre-green revolution era, losses ranged from 3.5% in sorghum and millets to 16% in cotton. During the post-green revolution era, it showed an increase in soybean (4.4–10.4 %), potato (5.9–16.1 %), groundnut and pulses (5.0–15.0 %), sugarcane (10.0–20.0 %) and sorghum and millets (3.5–30.0 %) with a minor decrease in cotton (16–15.4 %) (Oerke et al. 1994; Dhaliwal et al. 2007). Preharvest crop losses of about 40% have been unavoidable in addition to harvest and postharvest losses, which have been estimated to be 10–30% of production (Swaminathan 1983). As per Dhaliwal et al. (2010), the crop losses declined from 23.3% during the 1990s to 17.5% in 2010 and further to 15.7% recently (Dhaliwal et al. 2015). These changes in crop losses could be attributed to

Table 2.3 Estimates of crop losses due to insect pests (%) in India

Crop	Pradhan (1964)	Pradhan (1983)	Dhaliwal and Arora (1996)	Lal (1996)	Dhaliwal et al. (2007)	Puri and Ramamurthy (2009)	Dhaliwal et al. (2010)	Dhaliwal et al. (2015)
Cotton	18	18	50	22	50	50	30	30
Rice	10	10	25	18.6	25	25	25	25
Oilseeds	5	5	35	25	25	25	15	20
Pulses	5	5	30	7	15	15	15	15
Groundnut	5	–	15	–	15	15	15	15
Wheat	3	–	5-10	11.4	5	5	5	5
Maize	5	–	25	–	25	25	20	18
Sorghum and millets	3.5	–	35	10	30	30	10	8
Sugarcane	10	–	20	15	20	20	20	20

paradigm shifts in the crop management and cultivation scenario of agriculture since the beginning of this century. Moreover, concerted efforts were made to implement integrated pest management programmes in principal food and cash crops.

Over the decades, from pre-green revolution to post-green revolution era, the crop losses due to insect pests in India are summarized in Table 2.3. Before the green revolution, Pradhan (1964) reported losses of 3–18% in different crops. Later, Pradhan (1983) reported a loss of 18, 10, 5 and 5% in cotton, rice, oilseeds and pulses, respectively. In case of cotton, the losses caused by insect pest complex ranged from 18% in the 1960s and 1980s (Pradhan 1964, 1983) to 22–50% in the 1990s (Lal 1996; Dhaliwal and Arora 1996). These losses rose to an alarming figure of 50% or more at the turn of the century (Dhaliwal et al. 2007; Puri and Ramamurthy 2009). Even after the introduction of bollworm-resistant *Bt* cotton, which now covers more than 95% of area under cotton, losses caused by insect pests have been estimated at a whopping 30% (Dhaliwal et al. 2010, 2015). In rice crop, the insect pest-inflicted losses were estimated at 10% in 1964 (Pradhan 1964, 1983) and 25% in later studies (Dhaliwal and Arora 1996; Dhaliwal et al. 2007, 2010, 2015). The yield losses due to insect pests in oilseeds varied from 5% (Pradhan 1964, 1983) to up to 35% (Dhaliwal and Arora 1996). A similar trend was recorded in case of pulses as insect pest-inflicted crop losses were estimated to be 5% by Pradhan (1964), 30% by Dhaliwal and Arora (1996) and later stabilized at around 15% (Dhaliwal et al. 2007, 2010, 2015; Puri and Ramamurthy 2009). Wheat crop witnessed lower damage rates by insect pests as traditionally diseases have been the major biotic stress limiting its production. The yield losses due to insect pests in wheat were reported to be 3% by Pradhan (1964), 11.4% by Lal (1996) and 5% by Dhaliwal et al. (2007). The sugarcane crop is ravaged by many insect pests, and insect pest-inflicted losses to the tune of 10 (Pradhan 1964) to 20% have been estimated by various workers (Dhaliwal and Arora 1996; Dhaliwal et al. 2007, 2010, 2015; Puri and Ramamurthy 2009) (Table 2.3).

2.4 Extent of Losses Caused by Insect Pests in Important Crops

2.4.1 Rice

Rice is the staple food for around half of the world's population. Rice production is largely concentrated in Asia, where it is the major food source, and weeds, animal pests and pathogens are regularly of economic importance despite regional differences. Over 800 insect species have been identified damaging either standing or stored rice (Grist and Lever 1969). Oerke and Dehne (2004) reported an actual loss of nearly 40% due to insect pests in rice worldwide, whereas the total potential loss was estimated to be 65–80% of attainable yields. The actual losses ranged from 22% in Oceania to 51% in Central Africa indicating significant differences in the efficacy of crop protection practices (Oerke 2006). In India, the overall yield losses in rice due to insect pests were estimated to vary from 21 to 51% (Singh and Dhaliwal 1994).

Amongst the damaging insect pests, brown plant hopper, *Nilaparvata lugens* (Stal), appeared as a sporadic pest in India during 1958 and 1962, while its first serious epidemic occurred in 1973 in Kerala resulting in 10–70% loss in grain yield (Puri and Mote 2003), followed by a series of outbreaks in different rice-growing regions of the country. It was estimated that this pest reduces yield by 40–57% (Kataki et al. 2001). The white-backed plant hopper *Sogatella furcifera* (Horwath) appeared on rice in Punjab, India, during 1966, and outbreaks of the pest were reported from several parts of the country during the 1970s and 1980s (Subramanian et al. 1992). Outbreaks of the pest were also reported from Bangladesh, Korea, Pakistan and Sri Lanka (Dhaliwal and Arora 2006). The leaf folder, *Cnaphalocrocis medinalis* Guenee, is another pest, which has been causing increasing damage to rice crop. The pest reduces yield by 40–57% (Uthamasamy 1985). There have been alarming reports of damage by new biotypes of gall midge, *Orseolia oryzae* (Wood-Mason), which are causing estimated losses ranging from 15 to 60% (Puri and Mote 2003). In case of other pests, the widespread epidemics of rice hispa, *Dicladispa armigera* (Olivier), were reported during the 1960s and 1970s, and there were reports of yellow stem borer, *Scirpophaga incertulas* (Walker), causing losses of 25–30% (Puri and Mote 2003).

2.4.2 Wheat

Wheat is one of the major cereal crops with its cultivation starting about 10,000 years ago, when a transition from the hunter-gatherer phase to a settled agriculture took place (Kamran et al. 2013). Traditionally, the only serious insect pests damaging wheat were the termites, *Microtermes* spp. and *Odontotermes* spp., and the weevil, *Tanymecus indicus* Faust. However, the pest problems multiplied rapidly after the introduction of high yielding, semi-dwarf varieties accompanied by increased irrigation facilities and intensive use of agrochemicals. By the end of the 1980s, more

than 100 species of insects were reported damaging the crop in India alone (Deol 1990; Arora and Dhaliwal 1996). Further, due to increasing night temperatures in winter, several species of cereal aphids including *Sitobion avenae* (Fabricius), *Schizaphis graminum* (Rondani), *Rhopalosiphum maidis* (Fitch), *R. padi* (Linnaeus) and *Macrosiphum miscanthi* (Takahashi) are appearing earlier on the wheat crop and require timely control measures (Arora and Dhawan 2013). The other pests increasing in importance include the plant bugs *Eurygaster* sp. (Oerke et al. 1994), pink stem borer *Sesamia inferens* Walker, root aphid *Rhopalosiphum rufiabdominalis* (Sasaki) (Singh 2011) and the armyworms *Mythimna* spp. (Arora and Dhaliwal 1996). Estimates of potential loss by animal pests in wheat were 9%, as compared to 16, 3 and 23% in case of pathogens, viruses and weeds, respectively (Oerke 2006). The worldwide crop loss due to insect pests showed an increase to 9.3% in the post-green revolution era from 5.1% in pre-green revolution era (Benedict 2003). Oerke and Dehne (2004) reported actual losses of more than 26–30% due to insect pests in wheat crop at the world level. These varied considerably from 14% in Northwest Europe to 35% and above in Central Africa, Southeast Asia and Oceania. In India, yield losses of 43–91% were reported due to infestation by the two termite species, viz. *Odontotermes obesus* (Rambur) and *Microtermes obesi* (Holm) (Kakde et al. 2006; Chhillar et al. 2006). The losses caused by aphids have been reported to be up to 35–40% (Aslam et al. 2005).

2.4.3 Maize and Sorghum

Maize or corn is one of the world's most important food, feed, fodder and biofuel crops. Maize dominates over other crops because of its high yielding ability, fast growing habit and wide adaptation to adverse environments. Sarup et al. (1987) listed 130 insect species damaging maize, while Mathur (1991) reported that more than 250 species of insect and mite pests attacking maize. Of the various insect species, around a dozen species cause serious damage (Mathur 1994). Sorghum is the fifth most important cereal crop in the world after wheat, rice, maize and barley. It is grown in the arid and semiarid parts of the world. About 150 insect species have been reported as pests on sorghum (Sharma et al. 2005). The shoot fly, *Atherigona* spp., and stem borer, *Chilo partellus* (Swinhoe), are major constraints in achieving high yield of maize and sorghum.

The maize stem borer, *C. partellus*, is a traditional destructive pest of maize and sorghum causing 29–72% loss in yield under varied agroclimatic conditions, while pink borer, *Sesamia inferens* (Walker), caused a loss of 25–35% in maize (Puri and Mote 2003). It has been estimated that shoot fly (*Atherigona soccata* Rondani) caused maximum yield losses of 75.6% in grain and 68.6% in fodder crop of sorghum (Pawar et al. 1984). On a global basis, annual yield losses due to insect pests in sorghum have been estimated to be over $1079 billion, out of which stem borer and shoot fly are known to cause losses of about $ 334 million and 274 million, respectively (Sharma 2006).

2.4.4 Oilseeds

Asia is one of the largest oilseed-producing regions of the world with groundnut and rapeseed-mustard as the principal annual oilseed crops. Nearly two-thirds of all groundnuts are produced in the semiarid tropics. Groundnuts are attacked by nearly 500 species of arthropods with around 15 species causing major damage (Natural Resources Institute 1996). More than 90 species of insects and mites have been reported to feed on the groundnut in India (Reddy and Ghewande 1986). There has been increasing damage by the white grubs *Holotrichia* spp., jassid *Empoasca kerri* Pruthi, aphid *Aphis craccivora* Koch, thrips *Frankliniella schultzei* (Trybom), leaf miner *Aproaerema modicella* Dev, tobacco caterpillar *Spodoptera litura* Fabricius and gram pod borer *Helicoverpa armigera* (Hubner) (Dhaliwal and Arora 1993). Jena and Kuila (1997) observed 6.31 q/ha loss in pod yields due to infestation by the leaf miner, while Amin (1987) reported that the pest may reduce yield by 24–92%.

The insect pest problems in rapeseed-mustard have been increasing in intensity due to increase in area under these crops and introduction of nontraditional crops like *Brassica napus* and *B. carinata*. Many new pests have been reported feeding on rapeseed-mustard crops. But the mustard aphid, *Lipaphis erysimi* (Kaltenbach), continues to be the key pest damaging oilseed brassicas (Arora 1999). Yield losses attributed to mustard aphid in *Brassica* oilseeds varied from 4 to 81% during different years at various locations in the country. The mean yield losses in rapeseed-mustard in India were estimated to be 35–73% (Arora 1999). In addition, there was a 6–10% reduction in oil content. Higher losses were reported in *B. campestris* and *B. napus*, while losses were lower in *B. carinata*. In *B. juncea*, the losses were highly variable. Rohilla and Singh (1992) recorded reduction in grain yield and oil content to the level of 63.93 and 11.96%, respectively, due to damage by the leaf roller, *Antigastra catalaunalis* Duponchel, in sesamum. The tobacco caterpillar, *S. litura*, could cause more than 90% defoliation in sunflower (Sujatha and Lakshminarayana 2007). Bud fly, *Dasineura lini* (Barnes), and semilooper, *Achaea janata* (Linnaeus), resulted in losses of 48 and 30% in linseed and castor crops, respectively (Puri et al. 2000). Ghule et al. (1986) observed yield losses in the range of 19.9–23.9% by the aphid, *Uroleucon carthami* (Hille Ris Lambers), in safflower.

2.4.5 Legumes

Legumes are capable of growth under conditions of low moisture and poor nutrient availability. They help to maintain soil fertility, through biological nitrogen fixation, and contribute to sustainability in the agroecosystem. Legumes are grown for grains (pulses), fodder and vegetables and are a major dietary source of protein for humans as well as domesticated animals. Being protein rich, leguminous crops are attacked by a wide variety of arthropod pests, which causes substantial yield losses.

Chickpea and pigeon pea are highly vulnerable to several pathogens, insect pests and nematodes (Nene and Sharma 1996; Reed et al. 1989; Chhabra et al. 1992),

which damage these crops right from seedling to maturity and in storage. Patel (1979) reported a loss of 10–60% in yield of chickpea due to damage by the pod borer, *H. armigera.* Lal (1996) estimated losses to the tune of 75–90% due to attack of insect pests in pulses. Pod damage of 20.8 and 36.4% in pigeon pea was caused by the pod fly, *Melanagromyza obtusa* (Malloch), and pod borer, *H. armigera*, respectively (Sachan 1990). Pod damage of 7.8 and 17–20% has been reported to be caused by *H. armigera* in chickpea and Indian bean, respectively (Reed et al. 1989; Rekha and Mallapur 2007). Yield losses up to 80% have also been reported in various vegetables and grain legumes due to legume pod borer, *Maruca vitrata* (Fabricius), damage in Asia and Africa (Ulrichs and Mewis 2004). Bhoyar et al. (2004) reported that the peak incidence of *Tur* plume moth, *Exelastis atomosa* (Walsh) caused pod damage from 9.95 to 10.9% in pigeon pea. Amongst the forage legumes, the pod borer, *H. armigera*, caused avoidable seed yield losses of 70, 43 and 27% in Egyptian clover (berseem), alfalfa and Persian clover, respectively. In the popular berseem late-maturing cultivar BL 10, seed yield losses as high as 75% were recorded (Arora et al. 2011).

2.4.6 Cotton

Historically, cotton crop has received the largest amounts of insecticides among all agricultural crops in the world (Fitt 2008), a trend largely driven by the presence of numerous insect pest species belonging to orders Lepidoptera, Hemiptera, Coleoptera and Thysanoptera. Global losses to the tune of 16% were reported in cotton crop by Cramer (1967). A survey by the International Cotton Advisory Committee (1992) showed that about 15% of the total crop of producing raw cotton was utilized for pest control. In Sudan, the use of insecticides alone constituted about 42% of the total expenditure (International Cotton Advisory Committee 1994). In Punjab, India, the cost of insecticides as percentage of cost of cultivation increased from 2.1% in 1974–1975 to 13% in 1994–1995 (Dhaliwal and Arora 2006). It is estimated that cotton accounts for about 22.5% of the total insecticide use worldwide (Anonymous 1995). Insect pests thus constitute a major constraint in cotton cultivation all over the world. Oerke et al. (1994) reported losses to the tune of 8–49, 18–69, 5 and 55–82% due to the attack of whitefly, *Bemisia tabaci* (Gennadius); bollworms [american bollworm *H. armigera*, pink bollworm *Pectinophora gossypiella* (Saunders), spotted bollworm *Earias insulana* (Boisduval), *E. vittella* (Fabricius)]; aphids, *Aphis gossypii* Glover; and a complex of sucking pests, respectively. Oerke and Dehne (2004) reported potential loss of more than 80% and an actual loss to the tune of 26–30% due to insect pests.

In India, cotton crop occupying only 5% of the cultivated area consumed 53% of the total insecticides used in the country. Bollworms alone were estimated to cause 49% losses in yield (Basu 1995). As per Dhawan et al. (1986), still higher yield losses to the extent of 66 and 95% were incurred due to bollworms in *arboreum* and *hirsutum* cotton, respectively. Kranthi et al. (2009) reported that for nearly two decades after 1985, bollworms caused yield losses of 30–80%. Yield loss estimates

Table 2.4 Extent of losses in sugarcane due to different insect pests in India (Anonymous 2015b)

Name of pest	% Reduction in cane yield	% Reduction in sugar recovery
Early shoot borer	22–33	2
Internode borer	34.88	1.7–3.07
Top shoot borer	21–37	0.2–4.1
Stalk borer	33	1.7–3.07
Gurdaspur borer	5–15	0.1–0.8
Root borer	35.00	0.3–2.90
Scale insect	32.60	1.5–2.5
Black bug	35	0.1–2.8
Pyrilla	31.60	2.0–3.0
Whitefly	86.00	1.4–1.8
White grub	80–100	5.0–6.0
Termite	33	4.5

in cotton due to insect pests and diseases in the Philippines ranged from 41 to 47% (Cotton Research and Development Institute 1994). In contrast to these countries, damage by insect pests to cotton in the USA is quite moderate as the efficiency of crop protection is high. Total damage by all pests in US cotton averaged 7.4% from 1986 to 2009 (Naranjo 2011). There has been a significant decline in losses caused by insect pests especially bollworms in all the countries where Bt cotton has been introduced (Brookes and Barfoot 2015).

2.4.7 Sugarcane

Sugarcane is infested by about 288 species of insects, of which more than a dozen causes heavy losses in yield as well as quality of the crop. Severe whitefly, *Aleurolobus barodensis* Mask, infestation was reported to cause reduction in cane yield up to 24–86% and loss in sugar up to 2.9–100% (Khanna 1948). Aheer et al. (1994) reported 36.51% losses in sugarcane by top borer, *Scirpophaga nivella* (Fabricius). Sardana and Das (2001), Madan and Singh (2001) and Singh et al. (2005) recorded 20–40, 24.2 and 100% loss in cane yield due to top borer, *S. nivella*. The borer complex resulted in more than 25% reduction in cane yield, sugar content and quality of juice (Gupta and Singh 1997). It has been reported that early shoot borer, *Chilo infuscatellus* (Snell); top borer, *S. nivella*; stalk borer, *Chilo auricilius* Dudgeon; and internode borer, *Chilo sacchariphagus indicus* (Kapur), can cause losses to the tune of 33, 37, 33 and 34%, respectively, in cane yield (Anonymous 2015b) (Table 2.4). In contrast, Shah and Singh (2007) reported 20% reduction in cane yield caused by insect pests including 2, 4, 6, 8 and 10% by internode borer, root borer, *Emmalocera depressella* (Swinhoe), top borer and termite *O. obesus* and *Microtermes obesi* Holmgr, respectively. A reduction of 20% in cane yield and 30% in sucrose content due to sugarcane mealybug, *Saccharicoccus sacchari* (Cockerell), was observed by Rao et al. (2008). Sharanabasappa et al. (2009) reported 7–39 and 1.2–3.43% reduction in cane yield and sugar recovery due to damage by woolly

Table 2.5 Yield losses due to major insect pests in vegetable crops in India

Crop	Pest	Yield loss (%)
Tomato	Fruit borer (*H. armigera*)	24–73
Brinjal	Fruit and shoot borer (*L. orbonalis*)	11–93
Chilli	Thrips (*S. dorsalis*)	12–90
	Mites (*Polyphagotarsonemus latus* (Banks))	34
Okra	Fruit borer (*H. armigera*)	22
	Leafhopper (*A. biguttula biguttula*)	54–66
	Whitefly (*B. tabaci*)	54
	Shoot and fruit borer (*E. vittella*)	23–54
Cabbage	Diamondback moth (*P. xylostella*)	17–99
	Cabbage caterpillar (*P. brassicae*)	69
	Cabbage leaf webber (*Crocidolomia binotalis* Zeller)	28–51
	Cabbage borer (*H. undalis*)	30–58
Cucurbits	Fruit fly (*B. cucurbitae*)	20–100
Potato	Aphid (*Myzus persicae* (Sulzer))	3–6
	Tobacco caterpillar (*S. litura*)	4–8
	Potato tuber moth (*Phthorimaea operculella* (Zeller))	6–9
	Mite (*P. latus*)	4–27

Modified from Rai et al. (2014)

aphid, *Ceratovacuna lanigera* Zehnt. Termite infestation has been reported to cause 10% yield loss in sugarcane (Shah and Singh 2007), while the scale insect caused 6.5–47% reduction in sucrose and 8–54% losses in yield (Rao et al. 2008).

2.4.8 Vegetable Crops

Vegetable crops occupy an important status in the agricultural economy and form an essential component of the human diet. Potato being a vegetatively propagated crop is damaged by all pest groups which assume economic status in this crop. Oerke and Dehne (2004) reported an actual loss of 39% due to insect pests in potato worldwide, and without crop protection about 71% of attainable potato production may be lost to pests. Actual total losses were estimated to vary from 24% in Europe to more than 50% in Africa (Oerke 2006).

In India, the crop losses to the tune of 30–40% have been reported in vegetable crops in India (Rai et al. 2014). Fruit borer, *H. armigera*, can cause yield loss of 73% in tomato. It has also been reported that severe incidence of diamondback moth, *Plutella xylostella* (Linnaeus), in Cole crops and fruit fly in cucurbits, *Dacus dorsalis* (Hendel), can result in crop failure (Table 2.5). Kartosuwondo and Sunjaya (1991) mentioned *P. xylostella* as one of the most important pests of cruciferous crops throughout the world, and in India, an outbreak of *P. xylostella* on cauliflower was reported in Uttar Pradesh, which led to 100% loss of the crop (Ahmed et al. 2009). On cruciferous vegetables, losses to the tune of 30–99% have been reported

to be caused by different insect pests by various authors. Ram et al. (1987) estimated a loss of 36.5% by the cabbage aphid, *Brevicoryne brassicae* (Linnaeus), and sawfly, *Athalia rosae* (Linnaeus). Thakur (1996) and Sharma (2011) reported a loss of 68.5 and 40% on cruciferous vegetables by the cabbage butterfly, *Pieris brassicae* (Linnaeus). In another study cabbage butterfly, diamondback moth, sawfly, aphid and cabbage borer, *Hellula undalis* Fabricius, accounted for a loss in yield by 68.5, 16.9–98.8, 36.5, 36.5 and 30–58,%, respectively (Dhandapani et al. 2003).

Fruit borer in brinjal can cause enormous losses in yield. Naresh et al. (1986) reported 95% yield loss on brinjal by the shoot and fruit borer, *Leucinodes orbonalis* Guenee, while many workers have reported variable losses ranging from 20 to 92% due to this pest on brinjal (Mall et al. 1992; Reddy and Srinivasa 2005; Ghosh and Senapti 2009; Singh and Nath 2007). Many workers have reported losses ranging from 40 to 88% due to leafhoppers on okra, *Amrasca biguttula biguttula* (Ishida) (Krishnaiah 1980; Sharma and Sharma 2001; Dhandapani et al. 2003; Satpathy et al. 2005), and 22–91.6% losses due to the attack of fruit borer *E. vittella* (Hafeez and Rizvi 1994; Pareek and Bhargava 2003; Satpathy et al. 2005; Kanwar and Ameta 2007). Further, a loss of 54.04% has been reported by Dhandapani et al. (2003) in case of whitefly, *B. tabaci*, infestation on okra. On chilli crop the yield loss due to thrips, *Scirtothrips dorsalis* Hood, has been estimated by different workers ranging from 11.8 (Borah and Langthasa 1995; Nelson and Natarajan 1994) to more than 90% (Dhandapani et al. 2003).

Important insect pests inflicting damage on cucurbitaceous crops were reported to be melon fruit fly and red pumpkin beetle. The extent of losses caused by melon fruit fly *Bactrocera cucurbitae* (Coquillett) were reported to vary from 30 to 100% depending on the cucurbit species and season (Dhillon et al. 2005). Red pumpkin beetle, *Aulacophora foveicollis* Lucas, has been reported to inflict 30–100% yield loss (Gupta and Verma 1992; Dhillon et al. 2005). Many workers have reported losses ranging from 20 to 83 and 60 to 80%, respectively, on cucumber and bitter gourd due to melon fruit fly (Dhandapani et al. 2003; Satpathy et al. 2005; Gupta et al. 1992). Further, losses of 50, 63 and 76–100% have been reported due to this pest on sponge gourd (Gupta et al. 1992), snake gourd (Borah and Dutta 1997) and muskmelon (Satpathy et al. 2005), respectively.

2.4.9 Fruit Crops

Fruits are known as protective foods because of their richness in vitamins, minerals and antioxidants, and their daily consumption protects mankind from various kinds of diseases. The current global fruit production is 599.3 million metric tonnes from an area of 55.08 million hectares. China, India and Brazil are the three leading fruit-growing countries in terms of area and production (Anonymous 2012). In the category of biotic stresses, apart from diseases, insect pests cause heavy yield losses. As per 1996 estimates, insects cause 6% fruit crop losses despite the use of insecticides, and in absence of insecticide protection, these losses reach 23% (Krattiger 1997). The insects besides causing direct reduction in the yield of fruit crops (by causing a

Table 2.6 Losses caused by insect pests in fruit crops

Crop	Insect pest	Loss (%)	Reference
Fruit crops			
Mango	Hopper	20–100	Sohi and Sohi (1990)
	Fruit fly	10–80	Anonymous (2013)
	Mealybug	50–90	Moore (2004)
		50	Atwal (1963)
		100	Olufemi et al. (2000)
Citrus	Fruit-sucking moth	10–15	Kumar and Lal (1983)
		20–30	Cai and Geng (1997)
		10–55	Dadmal and Pawar (2001)
		95	Waterhouse and Norris (1987)
Guava	Fruit fly, bark borer and fruit borer	3–38	Haseeb and Sharma (2007)
Papaya	Mealybug	8–33	Tanwar et al. (2007)

loss to different parts of the fruit trees, viz. foliage, twigs, flowers and fruits) also serve as vectors of various disease-causing pathogens.

It has been reported that mango hopper, *Idioscopus nitidulus* (Walker); fruit fly, *Ceratitis cosyra* (Walker); and mealybug, *Drosicha mangiferae* Stebbins, cause damage up to 100, 80 and 100% on mango, respectively. Similarly, fruit-sucking moth, *Eudocima materna* (Linnaeus), and fruit fly *Bactrocera dorsalis (*Hendel) could result in loss of 95 and 80% on citrus and kinnow, respectively (Table 2.6). Sapota seed borer, *Trymalitis marginatus* Meyrick, was an introduced pest in Konkan region of Maharashtra (Puri and Mote 2003), and the crop suffered to the extent of 40–90% (Sharma and Singh 2012).

2.5 Conclusions

The global human population growth has wiped out the impressive food production increases in large parts of the world brought about by the green revolution, leading to a decline in per capita availability of food grains for the last 15 years. Even more alarming is the fact that future increases in population will be largely concentrated in the developing countries of Asia and Africa many of which are already battling severe food shortages. Since, nearly all the cultivable land is already under cultivation, future increases in food, feed and fibre production must be achieved with increased productivity and improved crop protection in the face of reduced availability of natural resources and arresting the decline in environment quality. Ironically, at least one-third to half of the global agricultural production or potential production is lost due to animal pests, diseases and weeds or is wasted. Reduction of potential food loss or waste will result in a significant increase in availability of food for consumption. Arthropod pests destroy an estimated 18–20% of annual production worldwide, which is valued at more than US $470 billion. Indian agriculture suffers an annual loss of about 15.7% due to ravages by these insect pests which

accounts for US$ 36 billion. But there is a paucity of accurate data on pest-associated losses in various crops, and all estimates have been obtained by extrapolation from the few estimates available in a limited number of crops. An accurate assessment of these losses is the essential first step in minimizing these losses.

It is, however, universally recognized that crop losses due to various biotic and abiotic stresses are rising in the face of increasing intensity of cultivation, reduced agroecosystem diversity, narrow genetic base of modern crop cultivars, intensive use of agrochemicals and the rapid changes in climate. Therefore, there is a pressing need for development of suitable pest management technologies which are profitable, safe and durable at the same time. The use of pest-resistant cultivars offers all these advantages and may form the core around which sustainable agricultural systems are developed.

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Advances in Breeding for Resistance to Insects

3

Surinder Sandhu and Manjit S. Kang

Abstract

Traditionally, researcher has put more focus on disease resistance than on insect resistance, but the adverse effects of excessive use of pesticides on human health, environment, phyto-sanitation, market access, and global trade have led to renewed interest in breeding for resistance to insects. The development of insect-resistant crops is a sustainable way to manage pests. In this chapter, historical impact of resistance to insects in ensuring food security has been cited. The identification of new sources of resistance to insects and better understanding of resistance mechanisms have opened new avenues in the field of host-plant resistance (HPR). New insights into structural and functional aspects of genes conferring resistance to insects (R-genes) during the past two-three decades and their proper utilization, by researchers, have been discussed. The breeding methods for developing resistance to insects in self- and cross-pollinated crops have been elaborated. The findings on complex host-pest interactions and overlapping of controlling genes or quantitative trait loci (QTL) for resistance to biotic and abiotic stresses emphasizes the adoption of holistic approaches to develop insect-resistant crops.

S. Sandhu (✉)
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, Punjab 141 004, India
e-mail: surindersandhu@pau.edu

M.S. Kang
Department of Plant Pathology (Geneticist), Kansas State University, Manhattan, KS 66506-5502, USA
e-mail: manjit5264@yahoo.com

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Insects make up one of the most diverse and abundant groups of plant consumers (Zheng and Dicke 2008). Interactions between plants and their arthropod herbivores dominate the terrestrial ecology of our planet (Jander and Howe 2008). Forty-five percent of the approximately one million described insect species feed on plants (Schoonhoven et al. 2005). The survival of an estimated one million or more phytophagous (plant-eating) insect species depends on plants as a source of food (Jander and Howe 2008). Despite the annual cost of US$ 40 billion for the use of three million metric tons of pesticides, in addition to the use of various biological and other nonchemical plant protection measures worldwide, global crop losses remain a matter of concern (Pimentel and Peshin 2014). Crop losses due to arthropod pests have been estimated at 18–26% of the annual crop production worldwide (Culliney 2014). In another recent estimate, the authors concluded that during the post-green-revolution era, crop losses attributable to insect pests may have declined. But such losses were still pegged at 10.8% at the global level and at 15.7% in India (Dhaliwal et al. 2015).

Plants have evolved with diverse attributes for their survival and continuance. Per Mack et al. (2002), when their population size is small, plants generally exhibit asexual and self-fertilization modes of propagation and outcross when population size increases to harness the gains of genetic diversity. They credit nature with evolution of plant species with prolonged flowering and fruiting span for enhanced chance of pollination, profuse seed production, means of efficient seed dispersal, short vegetative phase, and better photosynthetic efficiency to improve their chances of survival.

Plants continuously encounter biotic stresses, for example, attacks by a diverse range of organisms. Unfortunately, plants cannot move to escape damage. Insects cause injury to plants either directly or indirectly to secure food, and almost all parts of the plants, viz., roots, stem, bark, shoots, leaves, buds, flowers, and fruits, can be attacked and damaged by insects (Atwal and Dhaliwal 2015). During a long "arms race," plants have evolved effective defense mechanisms by which they perceive insect attacks and translate that perception into adaptive responses to prevent or limit the damage (Dangle and Jones 2001). Insect-resistant cultivars have been utilized for more than a century to minimize insect pest damage to crops. However, the emergence of synthetic insecticides in the mid-twentieth century, which initially provided remarkable control of harmful pests, served to dilute the focus on host-plant resistance and other ecologically benign methods of pest management. Extensive pesticide application results in increased cost of crop production, reduces populations of natural enemies of insect pests, leads to the development of pesticide-resistant races of insects, and pollutes the environment (Kavitha and Reddy 2012). Consequently, exploration of nonchemical strategies for pest control in crop plants began to receive impetus.

Periodic reviews of issues related to important topics, such as resistance to insects, are needed. Therefore, the major aims of the present chapter on "Advances in Breeding for Resistance to Insects" are to discuss the need to breed for resistance to insects, resistance mechanisms, types of resistance, role of resistance (R) genes, gene-for-gene hypothesis, sources of resistance/tolerance, inheritance of resistance, and current breeding methodologies used for developing insect-resistant cultivars. Some of the major advances that have taken place in the past few years are highlighted in this article. In this chapter, we make a distinction between "resistance to insects" and "insect resistance." The former term refers to plants or crops possessing resistance to insects, whereas the latter term refers to insects developing resistance to chemicals/insecticides.

To sustain agricultural production and to minimize crop losses, genes for resistance to biotic stresses can rightfully be considered one of the most important natural resources (Mundt 1994). Breeding for resistance to insects presents some difficulties; for example, under threats to their survival, insects can evolve new biotypes to adapt to new situations (Roush and McKenzie 1987). The dynamic nature of host-insect interaction, loss of effectiveness of chemicals, breakdown of natural or artificial plant resistance, and complexities in screening and selection of the resistant material under uniform insect infestation across environments make breeding for resistance to insects a greater challenge (Roush and McKenzie 1987).

Crow (1957) opined that following several generations of insecticide application, insects could become resistant to insecticides. This phenomenon was considered an example of rapid evolution and an economic issue (Crow 1957). Melander (1914) recognized heritable insect resistance when he posed this question: Can insects become resistant to sprays? In his book, *Genetics and the Origin of Species*, Dobzhansky (1951) pointed out that the process of evolution was ordinarily very slow, and as such, the changes happening in wild species cannot be observed within a human lifetime. However, he cited a conspicuous and important exception, i.e., the citrus pest "California red scale" (*Aonidiella aurantii*) developing resistance to cyanide sprays. This confirmed that the spread of resistant strains constituted a proof of the effectiveness of natural selection.

3.1 Host-Plant Resistance (HPR)

Host-plant resistance (HPR) is considered a highly desirable pest-control mechanism, as it has no negative impact on environment, economics, and society. Snelling (1941) defined host-plant resistance as those characteristics which enable a plant to avoid, tolerate, or recover from the attacks of insects under conditions that would cause greater injury to other plants of the same species. Painter (1951) defined plant resistance as the relative amount of heritable qualities possessed by a plant which influence the ultimate degree of damage done by the insect. Smith (2005) described host-plant resistance as sum of the constitutive, genetically inherited qualities that result in a plant of one cultivar or species being less damaged than a susceptible plant lacking these qualities. Practically, host-plant resistance refers to the ability of

a genotype/variety (resistant) to produce larger yield of good quality than an ordinary genotype/variety (susceptible) at the same level of herbivore damage.

The effects of resistance to insects are cumulative across time, and the longer the resistance is employed and effective, the greater the benefits. Per Panda and Khush (1995), resistance has the following four characteristics:

1. Resistance is *heritable* and controlled by one or more genes.
2. Resistance is *relative* and can be measured only by comparison with a susceptible cultivar of the same plant species.
3. Resistance is *measurable by* standard scoring systems.
4. Resistance is *variable* and is likely to be modified by the biotic and abiotic environments.

Host-plant resistance has played a pivotal role in pest management in important food crops. In several cereal and forage crops, HPR relative to insects has been an extremely successful method of suppressing pest populations or minimizing pest damage. Panda (1979) demonstrated an average of 12-fold population reduction among 25 different insect pests of 10 food and fiber crops. Waibel (1986) determined that 10-year average yield losses of insect-resistant rice varieties were approximately one half (14%) of the losses suffered by susceptible rice varieties (26%). Cartwright and Wiebe (1936), for the very first time, characterized resistance based on genetic factors. Maxwell et al. (1972) reported that more than four million ha in 34 states in the USA were planted to 23 Hessian fly-resistant cultivars of wheat, and the annual value of increased yield resulting from the resistant cultivars was estimated at $238 million. Genetic resistance to jassid [*Amrasca biguttula biguttulla* (Ishida)] – a pest of cotton, initially developed more than 90 years ago in South Africa, was the first case of success in using resistant cultivars to control a crop pest (Parnell 1925). Another well-known example of HPR is that of phylloxera or wine louse [*Daktulosphaira vitifoliae* (Fitch)] in grapes. About 100 years ago, phylloxera-resistant stocks were exported from the USA to France to combat wine louse, and those vines still form an important means of control of this insect in France. Beginning around 1960, increased emphasis had begun to be placed on research on HPR to insects in cotton because cotton boll weevil (*Anthonomus grandis* Boheman) had developed resistance to chlorinated hydrocarbon insecticides and the cost to control cotton insects by use of chemicals was enormous (Jenkins 1981).

Several morphological and biochemical characteristics of cotton plant are associated with resistance to insect pests. Pubescent varieties of cotton were found to be resistant to leafhoppers (Khan and Agarwal 1984), but the same were preferred for oviposition by the whitefly (Bindra 1985) and spotted bollworm (Sharma and Agarwal 1983). In contrast, pubescence adversely affected the mobility and survival of young tobacco budworm (*Heliothis virescens*) larvae (Ramalho et al. 1984). High gossypol genotypes restricted the development of pink bollworm (*Pectinophora gossypiella* Saunders) larvae, causing increased mortality and reducing both larval weight and adult fecundity (Agarwal et al. 1976). A similar effect was recorded for cotton bollworm (*Helicoverpa armigera* Hübner) (Vilkova et al. 1988). These plant

traits started to receive increased attention in developing HPR in cotton. In 1985, the USDA and Mississippi Agricultural and Forestry Experiment Station jointly registered and released two cotton germplasm lines (MWR-1 and MWR-2) that carried resistance to boll weevil (McCarty et al. 1987). A major achievement in developing bollworm-resistant cotton was the development and commercialization of Bt-transgenic cotton during the 1990s. The Bt cotton has been fortified with a gene from the soil-inhabiting entomopathogen, *Bacillus thuringiensis* (Peferoen 1997). The *Bt* gene provides effective resistance against several species of bollworms and budworms (International Cotton Advisory Committee 1997), and Bt cotton covers large areas in the USA, India, China, Australia, and other cotton-growing regions of the world (James 2015).

3.2 Resistance Mechanisms

Painter (1951) advanced three "mechanisms" or "bases" of host-plant resistance, viz., antibiosis, non-preference, and tolerance. He used the term "antibiosis" to describe adverse effects of resistant plants on insect physiology and life history, e.g., survival, reduced growth, and fecundity. The term "non-preference" referred to the situation where herbivore (insect) behavior was affected by certain plant traits, which led to reduced colonization or acceptance of a plant as a host. "Tolerance" referred to the ability of a host plant to resist or tolerate insect damage, such that, under equivalent insect injury, economic traits (agronomic yield or quality) of tolerant plants were affected to a lesser extent than of plants lacking the ability to tolerate damage.

Antibiosis is a most striking resistance mechanism. High levels of antibiosis usually place great selection pressure on the insect for developing new biotypes, especially if the insect is a primary or obligate feeder on one crop. An excellent example of antibiosis is C-glycosyl flavones (e.g., maysin) in maize silks that confer resistance (i.e., antibiosis) to corn earworm (*Helicoverpa zea* [Boddie]) larvae (Lee et al. 1998). Antibiosis resistance often results in increased mortality or reduced longevity and reproduction of the insect (https://ipmworld.umn.edu/teetes). In non-preference, later referred to as antixenosis (Kogan and Ortman 1978), the crop plant being a poor host, the insect pest selects an alternate host. This type of resistance to insects is also known as "nonacceptance." It refers to various features of host plant that make it undesirable or unattractive to insects for food, shelter, or reproduction. Smith and Clement (2012) defined antixenosis as adverse effects on insect behavior, which lead to delayed acceptance and possible outright rejection of a host plant, whereas Emden (2002) defined antixenosis as the first stage in the encounter between the pest and plant. Leaf-feeding resistance to European corn borer [*Ostrinia nubilalis* (Hübner)] in maize has been primarily attributed to the chemical 2,4-dihy droxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) (Klun and Brindley 1966), which has strong antixenotic and antibiotic properties (Robison et al. 1982). The products,6-methoxybenzoxalinone (MBOA) and DIMBOA, isolated from leaves of resistant maize plants, were found to inhibit the growth of young larvae (Abel

1998). Morphological (color, light penetration, hairiness, leaf angle) and/or biochemical (odor, taste) plant characters may be associated with non-preference. For instance, red plant body, smooth leaves, okra leaf, long pedicel, open canopy, frego bract, nectarilessness, and thickness and hardness of boll rind make cotton plant a non-preferred host to bollworms, whereas hairiness of leaf and stem makes it non-preferable to jassids. Pea aphid prefers blue-green pea genotypes over yellow-green ones (Din et al. 2016). Type VI glandular trichomes in tomato leaves produce a "natural insecticide" (2-tridecanone), which renders it a non-preferred host for oviposition by whitefly (Williams et al. 1980). An association between density of this type of trichomes and resistance to the whitefly was verified by Channarayappa et al. (1992). Bergau et al. (2015) found type VI glandular trichomes to be the most abundant trichome type on leaves and stems of cultivated tomato plants, which significantly contributed to resistance to herbivore, particularly in a related wild species of tomato (*Solanum habrochaites*). Similarly, various plant features in maize serve as morphological defenses and restrict feeding and oviposition by insects. For instance, tight-husked ears resist the corn earworm attack (Wiseman and Widstorm 1992). Reduced trichome density and delayed development of pubescence make maize genotypes less preferred for oviposition by the corn earworm and resistant to larval feeding (Chatzigeorgiou et al. 2010). Similar effect of trichome density on oviposition behavior of pink bollworm (*Pectinophora gossypiella*) of cotton was observed during early phase of cotton season, as overwintering females oviposit on vegetative parts during this phase (Chatzigeorgiou et al. 2010). High trichome density is preferred by female moths as hairy substrate allows them to maintain proper footing during oviposition and offers improved surfaces to retain eggs as compared with smooth surfaces (Renwick and Chew 1994). Some biochemical attributes also affect herbivore behavior, e.g., increased leaf and stem silica content contributes to European corn borer resistance (Rojanaaridpiched et al. 1984); and brown plant hopper (BPH) exhibits its preference for amino acid asparagine in rice; varieties resistant to BPH attack were found to contain a negligible amount of asparagine (Mahabal 2014). The information on morphological and biochemical traits associated with host resistance could be very useful in initial screening of genotypes from diverse germplasm, and the genotypes harboring many of these traits could serve as donors to breed for resistance to insects. At the same time, extensive information on feeding behavior and preferences of all important insect pests is required, as one plant trait may serve as a deterrent for one insect species but be preferred by another one. For instance, as mentioned above, hairy leaves are non-preferred by some species of bollworms but highly preferred by jassids in cotton.

Plant tolerance is the inherent genetic capability of resistant plants to withstand herbivore damage. The basic difference between tolerance and the other two forms of resistance mechanisms is that tolerance stems from plants' response to insect attack, whereas the other two (antibiosis and non-preference) relate to the insect pest's reaction to certain specific host-plant characteristics. Tolerance is of immense value in HPR. Tolerant cultivars are often highly stable, as they put little or no selection pressure on pest populations to evolve virulence (Heinrichs 1986). Virulent Russian wheat aphid (*Diuraphis noxia*) overcame the antibiosis component of

resistance conferred by several different wheat resistance genes but was not able to overcome tolerance (Basky 2003). A tolerant plant can harbor large numbers of herbivores without interfering in insect's physiology or behavior (Koch et al. 2016). According to Horber (1980), Painter's trichotomy of "functional categories" represented a "workable compromise" between "mere categorization of phenomena" and basic study of causative factors or processes, as not all forms of resistance can be assigned to one of the three categories. An insect confined to a resistant plant may fail to gain weight at the rate it normally does on a susceptible plant, presumably because of the presence of antibiotic compounds in the resistant plant. However, reduced weight gain may also be attributed to the presence of an antixenotic physical or chemical feeding deterrent that causes aberrant behavior in the insect, weakening it physiologically. Additional mechanisms of resistance have been proposed, which are not entirely consistent with the original concepts of antibiosis, antixenosis, or tolerance advanced by Painter (Wu and Baldwin 2010). One of the important examples is indirect defense, wherein, upon being attacked by insect, plant expresses certain traits that facilitate the actions of predators and parasitoids of insect herbivores and reduce the damage by controlling insect populations without any direct effect on insect behavior or preference. So, this mechanism does not affect herbivore fitness directly, but effects on herbivores are mediated by and contingent upon the actions of the third trophic level in the food chain, i.e., natural enemies of herbivores (Chen 2008; Zheng and Dicke 2008).

3.3 Types of Resistance

Stout (2013) reviewed the conceptual framework for applied research on HPR and argued that the trichotomous framework, proposed by Painter (1951), did not encompass all known mechanisms of resistance and that the antixenosis and antibiosis categories were ambiguous and inseparable in practice. Stout (2013) proposed a dichotomous scheme to replace Painter's trichotomous scheme, with a major division between resistance and tolerance, and the resistance was further subcategorized as constitutive/inducible and direct/indirect defense.

Plants either express constitutive resistance, which is displayed irrespective of any external stimulator-induced resistance, which is in response to insect injury caused to the host (Schoonhoven et al. 2005). In the constitutive resistance, also referred to as direct defense, various physical and/or chemical plant attributes, for instance, trichome density, cell wall lignification, and silica deposition, serve as defense arsenal of the host plant (Kaplan et al. 2009). In addition, specific secondary metabolites may be involved, which serve as natural repellants, deterrents, antinutrients, and antidigestive compounds that deter insects from settling, penetrating, and colonizing (Wu et al. 2008; Sharma et al. 2009). There are more than 500,000 secondary metabolites synthesized by plants (Mendelsohn and Balick 1995), which include glucosinolates, cyanogenic glucosides, alkaloids, phenolics, and proteinase inhibitors (PIs) and play an effective role in constitutive defense, which is also called "passive defense." In induced resistance, also referred to as

"indirect defense," in response to insect attack, host plant responds by synthesizing certain compounds, viz., antifeeding proteins, insecticidal secondary metabolites, extrafloral nectars, and/or volatile organic compounds to attract natural enemies of insects, such as parasitoids, to control insect population (Stotz et al. 1999; Karban et al. 2000). Plants have evolved these powerful defenses during the long "arms race" to protect themselves against herbivore damage and, hence, to survive (Kessler and Baldwin 2002). To counter the defense arsenal of plants, insects have also evolved to efficiently seize toxic metabolites generated by plants. Aphids and whiteflies take advantage of their adept feeding strategies and overcome many plant defenses. These insects deceive their hosts and natural enemies by using their stylets to deliver salivary chemicals and/or proteins into the plant to interfere with wound healing and defense-signaling pathways. Such strategies are also used by phytopathogenic microbes to avoid recognition and resist plant defenses (da Cunha et al. 2007). To combat plant defenses, pathogens also tend to manipulate host's metabolic pathways by introducing effectors into plants cells. These effectors influence all stages of plant-biotroph interactions, viz., pre-entry, entry, and colonization, which constitute the framework for adaptations and evasive strategies used by phloem-feeding insects (Walling 2008).

Herbivore-induced plant volatiles (HIPV) act as cues in indirect defenses (D'Alessandro and Turlings 2006) and deter feeding and oviposition by insect pests (War et al. 2011). By employing indirect-defense strategies, plants do not become fully resistant to herbivore damage but certainly reduce pest growth (Howe et al. 1996; Gatehouse 2002). To sum up, along with direct defenses, indirect defenses play an important role in HPR by providing phenotypic plasticity to the plants and enabling them to tolerate the stress (Agrawal 2010). Therefore, it is important for a breeder to understand the underlying resistance mechanism in plants while framing strategies to breed for resistance to insects.

3.4 R-Genes and Gene-for-Gene Hypothesis

The plant's innate immune response is highly polymorphic in its capacity to recognize and respond to biotrophs (Dangle and Jones 2001). There are two overlapping yet different forms of active plant defenses. One is basal plant defense, which restricts the invasion of virulent pathogen or insect, whereas the other recognizes the invading virulent pathogen or insect by employing plant's resistance (R) genes. The genetic basis of plant resistance was elucidated by H.H. Flor in the early 1940s (Flor 1942, 1956). Studying the flax rust pathogen, *Melampsora lini*, Flor demonstrated that plant-pathogen interactions were governed by specific interactions between pathogen *avr* (avirulence) gene locus and the alleles of the corresponding plant disease resistance (*R*) locus. When corresponding *R* and *avr* genes are present, respectively, in the host and the pathogen, disease resistance is expressed. If either is inactive or absent, disease results (Flor 1971). On varieties of flax (*Linum usitatissimum)* that have one gene for resistance to the avirulent parent race, F_2 cultures of the fungus segregate into monofactorial ratios. On varieties having 2, 3, or 4 genes

Table 3.1a Gene combinations and disease reaction

Virulence or avirulence genes in pathogen	R (resistance, dominant)	r (susceptible, recessive)
A dominant (Avirulence)	AR (−)[a]	Ar (+)[b]
a recessive (virulence)	aR (+)	ar (+)

[a](−) = resistant
[b](+) = susceptible

Table 3.1b Complementary interaction of two host genes for resistance (R1 and R2 loci) and the corresponding two pathogen genes (A1 and A2 loci) for virulence

Virulence (a) or avirulence (A) genes in the pathogen	Resistance (R) or susceptibility (r) genes in the plant			
	R1R2	R1r2	r1R2	r1r2
A1A2	–[a]	–	–	+
A1a2	–	–	+[b]	+
a1A2	–	+	–	+
a1a2	+	+	+	+

Source: Agrios (2006)
[a]– = Resistant
[b]+ = Susceptible

for resistance to the avirulent parent race, the F_2 cultures segregate into bi-, tri-, or tetrafactorial ratios (Flor 1971). These observations led to the theory of gene-for-gene complementarity between the host and the pathogen (Table 3.1a and 3.1b). Though the gene-for-gene hypothesis was postulated for disease resistance in plants, this concept has been applied with varying degree of proof to other host-pathogen (or host-pest) combinations, including viruses, bacteria, fungi, nematodes, and insects (Vander Plank 1978).

The mechanism of genetic vulnerability may be explained via the "gene-for-gene theory." Susceptible reaction occurs when the genes for resistance or susceptibility in the host match with corresponding virulence genes in the pathogen, also called matching interaction (Simmonds 1979). Basically, at the molecular level, it is the interaction between products of the genes controlling resistance in the host and pathogenicity in the pathogen (Higgins et al. 1998). Resistant reaction is the manifestation of interaction between products of alleles governing resistance in the host and those of avirulence in the pathogen (Staskawicz et al. 1995). Host plant expresses a susceptible reaction in the absence of genes for resistance in the host and the presence of corresponding genes for virulence in the pathogen or pest (Singh 2002). Though this is an oversimplification of the phenomenon, it laid the foundation for understanding the plant-pathogen interaction. The simplest model for this genetic interaction states that *R* products recognize *avr*-dependent signals and trigger signal-transduction events, which activate defense mechanisms and arrest pathogen growth. The plant's innate immunity response is highly polymorphic in its ability to recognize and to initiate plant-pathogen interaction to impart resistance. Specific *R*-mediated innate immunity is superimposed onto one or more basal defense pathways (Dangle and Jones 2001).

Martin et al. (1993) provided evidence of direct interaction of tomato *Pto* gene with *Pseudomonas syringae* effector *avr Pto* (from *Pseudomonas syringae* pv. tomato). Though *R*-gene-mediated resistance has not been established for tissue-chewing insects (i.e., Lepidoptera and Coleoptera), mapping of major *R*-genes in many important crops (Panda and Khush 1995) has proved that *R*-genes are an integral part of the active form of defense against piercing-sucking insect pests. Only a few of these dominant *R*-genes – which provide resistance against phloem feeders – have been cloned (e.g., *Mi-1.2*, *VAT*, and *BPH16*), and many more are extensively used in agricultural settings using marker-assisted breeding (Broekgaarden et al. 2011). A relatively small number of single dominant *R*-genes conferring resistance to phloem-feeding insects have been identified in different plant species (Table 3.2). In sorghum, accessions belonging to *Sorghum laxiflorum*, *S. australiense*, *S. brevocallosum*, *S. dimidiatum*, and *S. purpureosericeum* are highly resistant to sorghum shoot fly [*Atherigona soccata* (Rondani)] and spotted stem borer [*Chilo partellus* (Swin.)] (Venkateswaran 2003). *Sorghum angustum*, *S. amplum*, and *S. bulbosum* are resistant to sorghum midge, *Stenodiplosis sorghicola* (Coquillett) (Sharma and Franzmann 2001). The brown planthopper (BPH), *Nilaparvata lugens* Stål., is one of the most devastating rice pests that can be found

Table 3.2 Identified R-genes conferring resistance to insect pests

Crop	Gene(s)	Pest	References
Wheat (*Triticum aestivum*)	Several *H* genes	(*Mayetiola destructor)*	Wang et al. (2006) and Yu et al. (2009)
			McDonald et al. (2014)
	Several *Dn* genes	Russian wheat aphid (*Diuraphis noxia*)	Liu et al. (2005) and Peng et al. (2007)
Rice (*Oryza sativa*)	Several *Bph* genes	Brown planthopper (*Nilaparvata lugens*)	Du et al. (2009)
			Qiu et al. (2010)
			Tamura et al. (2014)
			Qiu et al. (2014)
			Myint et al. (2012)
			Wang et al. (2015)
	Several *Gm* genes	Gall midge (*Didymomyia tiliacea)*	Himabindu et al. (2010), Kumar et al. (2005)
Tomato (*Solanum lycopersicum*)	*Mi-1.2*	Potato aphid (*Macrosiphum euphorbiae*)	Rossi et al. (1998)
		Silverleaf whitefly (*Bemisia tabaci*)	Nombela et al. (2003)
Melon (*Cucumis melo*)	*Vat*	Cotton aphid (*Aphis gossypii*)	Klingler et al. (2001)
Medicago (*Medicago truncatula*)	*AIN*	Blue-green aphid (*Acyrthosiphon kondoi*)	Klingler et al. (2009)
Soybean (*Glycine max*)	Several *Rag* genes)	Soybean aphid (*Aphis glycines*)	Li et al. (2007), Zhang et al. (2009) and Zhang (2010)

Source: Updated and modified from Broekgaarden et al. (2011)

throughout the rice-growing areas in Asia. To date, 29 major BPH-resistance genes have been identified from cultivated *Oryza indica* as well as from wild species of rice and more than 10 genes have been fine-mapped to chromosome regions of less than 200 kb (Hu et al. 2016). Four BPH genes (*Bph14*, *Bph26*, *Bph17*, and *bph29*) have been cloned (Hu et al. 2016). The latest information on BPH-rice interaction has been provided by Jing et al. (2017). Jing et al. (2017) have focused on the genomics of BPH-rice interaction. They indicated that several BPH-resistance genes had been identified genetically and that 13 of these genes had been cloned, shedding light on the molecular basis of BPH-rice interaction. Their review indicates that resistance to BPH is mainly controlled by dominant genes and 31 BPH-resistance genes have been genetically identified.

Similarly, the green rice leafhopper (GRH), *Nephotettix cincticeps* Uhler, is a major leafhopper species that attacks cultivated rice and is found mostly in the temperate regions of East Asia. At least six GRH-resistance loci have been identified with the aid of DNA markers (Fujita et al. 2016). The Hessian fly [*Mayetiola destructor* (Say) (Diptera: Cecidomyiidae)] is one of the most destructive pests of wheat. Chen et al. (2004) characterized a gene coding for the secreted-salivary-gland-protein 11A1 (SSGP-11A1) from the Hessian fly, and later this group cloned and characterized three new genes coding for proteins designated as SSGP-11B1, SSGP-11C1, and SSGP-11C2. The functional relationship of these new genes with previously reported SSGP-11A1-encoding gene has indicated that this clustered superfamily might be important for Hessian fly virulence/avirulence (Chen et al. 2006). Tan et al. (2013) located two major QTL/genes encoding 12-oxo-phytodienoic acid reductase (OPR) and lipoxygenase (LOX) in bread wheat, which can be directly used in wheat breeding programs. Thirty-eight candidate single nucleotide polymorphisms (SNPs) for natural variation in defense against the cabbage whitefly were identified, and functional validation showed that four candidate genes affected whitefly performance (Broekgaarden et al. 2015).

The advent of molecular tools has provided major insights into structural features of *R*-genes and their role in conferring resistance (McDowell and Woffenden 2003). Although these genes confer resistance on a diverse group of organisms, such as viruses, bacteria, oomycetes, fungi, insects, and nematodes, there are prominent structural similarities in the gene products. These structural similarities were also observed among *R*-gene products from monocots and dicots, indicating that recognition and activation of plant-defense signal transduction have been maintained throughout the evolution. Like *R*-genes against pathogens, *R*-genes against insects are members of the nucleotide-binding site leucine-rich repeat (NBS-LRR) family of resistance genes (Kaloshian 2004). However, unlike plant-pathogen gene-for-gene interactions, only limited information is available on the *R*-genes involved in plant-insect interactions.

Cloning of *Mi* gene conferring resistance to the potato aphid led to the discovery that the gene for resistance to insects also contains the nucleotide-binding site leucine-rich repeat (NBS-LRR) motifs, as found in many resistance genes and was determined to be a member of the NBS-LRR family (Rossi et al. 1998). Pursuant to the genetic foundation laid by H.H. Flor's seminal studies on gene-for-gene model,

modes of receptor-effector recognition have been explored (Dodds and Rathjen 2010). Later, functional *R*-genes, identified and isolated from many crop species, have been found to encode resistance to bacteria, viruses, fungi, nematodes, and insects (Ellis et al. 2000). The largest class of *R*-genes encodes a nucleotide-binding site plus leucine-rich repeat (NBS-LRR) class of proteins. Their most striking feature is a variable number of carboxyl terminal LRRs. The LRR domains are found in diverse proteins and function as sites of protein-protein interaction, peptide-ligand binding, and protein-carbohydrate interaction (Jones and Jones 1997). Subsequently, Scheel (1998) hypothesized that many plant *R* proteins might be activated indirectly by pathogen-encoded effectors and not by direct recognition. The NBS-LRR activation in a network of cross talk between response pathways, *R* engagements in calcium influx, alkalinization of the extracellular space, protein kinase activation, production of reactive oxygen intermediates (ROIs), and transcriptional programming have been documented. Wurzinger et al. (2011) have discussed Ca^{2+}-dependent protein kinase (CDPK) and mitogen-activated protein kinase (MAPK) signaling with respect to potential cross talk and the subcellular localization of the involved components. Resistance-gene homologues in melon are linked to loci conferring disease and pest resistance (Brotman et al. 2002). Several NBS-LRR-related sequences were mapped to the vicinity of genetic loci that control resistance to papaya ringspot virus, *Fusarium oxysporum* race 1 and *F. oxysporum* race 2, and to the insect pest *Aphis gossypii*. *Bph14* gene conferring resistance to brown planthopper in rice encodes a coiled-coil, nucleotide-binding, and leucine-rich repeat (CC-NB-LRR) protein (Du et al. 2009).

It has been well established that, like plant-pathogen interaction, cloned genes for resistance to insects are family members of nucleotide-binding site, leucine-rich repeat (NBS-LRR). In analogy with pathogen recognition, recognition of insect herbivores by NBS-LRR protein is expected to take place through direct or indirect binding of insect effector molecules (Dodds and Rathjen 2010). Atamian et al. (2012) demonstrated that *Mi*-mediated response to aphids was clone specific and required common signaling components characterized for pathogen defenses in tomato.

R-genes conferring resistance to insects have been identified in several crops, for instance, in wheat for Hessian fly (Wang et al. 2006) and Russian wheat aphid (Peng et al. 2007), in rice for brown plant hopper (Qiu et al. 2010; Hu et al. 2016; Jing et al. 2017), and in melon for aphid (Klingler et al. 2001). Sharing structural similarity with *R*-genes against pathogens, the *R*-genes against insects have been demonstrated to be members of the nucleotide-binding site, leucine-rich repeat (NBS-LRR) family of resistance genes (Kaloshian 2004). A locus controlling resistance in barrel clover (*Medicago truncatula* Gaert.) to the blue alfalfa aphid (*Acyrthosiphon kondoi* Shinji) has been mapped to a chromosome region flanked by resistance-gene analogs predicted to encode the coiled-coil (CC)-NBS-LRR subfamily of resistance proteins (Klignler et al. 2005). The cloning and identification of aphid-resistance genes and resistance-gene candidates support the argument that aphid-plant interactions follow the gene-for-gene hypothesis. Several NBS-LRR sequences have also been cloned and mapped to the vicinity of genetic loci associated with resistance to

the cereal cyst nematode, *Heterodera avenae*, and the corn leaf aphid [*Rhopalosiphum maidis* (Fitch)] in barley (Ogbonnaya et al. 2001). Such information on the *R*-genes involved in plant-insect interactions should be useful for breeders in understanding and exploiting plant-pathogen gene-for-gene interaction in designing breeding strategies to develop insect-resistant crops (Broekgaarden et al. 2011).

Like plant-pathogen interactions, the interaction between wheat and medicago-blue-green aphids seems to involve a hypersensitive response, which is a form of programmed cell death (Grover 1995; Klingler et al. 2009). Hessian fly-resistant and Hessian fly-susceptible wheat lines were found to differ significantly for gene transcript abundance, cuticle permeability, and lipid composition (Kosma et al. 2010). On infestation, leaf-sheath epidermal permeability increased in susceptible wheat lines, whereas same was minimally affected in resistant lines, and changes in cuticle lipid profiling and transcript abundance were correlated (Kosma et al. 2010). In rice, mechanisms of resistance against the brown planthopper (BPH) seem to involve the deposition of callus in sieve elements of the phloem, which prevents the insect from sucking up phloem sap (Hao et al. 2008; Du et al. 2009).

Mi-1.2 gene, an *R*-gene, cloned from tomato, showed broad effectiveness toward several tomato phloem-feeding pests, viz., tomato potato aphid (Rossi et al. 1998), whitefly (Nombela et al. 2003), and potato psyllid (Casteel et al. 2006). *R*-gene-mediated resistance to insects has been found for phloem-feeding insects that require an intimate relationship with the host plant for successful colonization, whereas *R*-gene-mediated resistance has not been established for tissue-chewing insects (i.e., Lepidoptera and Coleoptera). Several examples of strong monogenic, natural resistance to phloem-feeding insects have indicated that in plants' innate immunity, individual cells have the capacity to perceive and respond to pathogen attack (Van Doorn and de Vos 2013).

Nearly all the cloned *R*-genes, expressing the dominant "gene-for-gene" mechanism, may be grouped into two major gene families, viz., the *Pto* receptor-kinase family that encodes intracellular serine threonine kinases, whereas the other family – the LRR (leucine-rich repeat) superfamily – encodes proteins with an LRR domain and exhibits hypervariability and confers recognition specificity (Brotman et al. 2002). Several studies have suggested that *R*-genes relative to resistance to insects belong to the supergroup of receptor-like kinases, possessing a nucleotide-binding site and leucine zip repeats. Relative to structural relationship of *R*-genes for resistance to insects with plant-resistance *R*-genes, TaXA21-A1, referred to as a wheat ortholog of OsXA21-like gene on chromosome 9 in rice, has not only explained the phenotypic variation in reaction to different stripe rust races but has also exhibited significant effects on resistance to powdery mildew and brown planthopper biotype BP (Liu et al. 2015).

In plants, many *R*-genes with diverse recognition specificities are available, which respond to a variety of microbial pathogens. Various genetic events, viz., gene duplication, divergence employing tandem or segmental duplication, recombination, unequal crossing over, transposable element activity, point mutation, and diversifying selection, have generated variations in *R*-genes (Qu et al. 2006;

Channamallikarjuna et al. 2010). Several *R*-genes exist in clusters of tandemly duplicated genes within the genome (Sharma et al. 2014).

Effector-triggered immunity (ETI) has been shown to display incredible robustness against pathogen attack and boost defense systems for rapid response (Cui et al. 2015). Each plant cell has the capacity to perceive and trigger response to the pathogen attack. The gene-for-gene model laid the foundation of receptor-effector recognition mechanism (Dodds and Rathjen 2010). Cui et al. (2015) proposed that, on the onset of host infection, different modes of interaction of NLR (nucleotide binding/leucine-rich repeat) with pathogen effectors occurred inside the cell. Specific NLR-effector recognition leads to ETI. The NLRs can recognize effectors directly in direct mode of NLR-effector recognition, whereas in indirect interaction, NLR binds to cofactor first, which is followed by a series of conformational modifications in effector molecules, thereby leading to initiation of ETI signaling (Cui et al. 2015). Earlier, "guard hypothesis" proposed by Vander and Jones (1998) postulated that R proteins recognized effectors indirectly. Effectors target host proteins other than R proteins and perturbation of those host targets then triggers the activation of R proteins.

Various families of transcription factors (TFs) are involved in regulation of immunity response by plants against any insect attacks and play an important role in the activation and fine tuning of plant's defense responses (Singh et al. 2002). Local and systemic changes in gene expression are mediated largely by transcription factors of the WRKY (a DNA-binding domain) and TGA families (Eulgem 2005). The WRKY domain is a 60-amino acid region that is defined by the conserved amino acid sequence WRKYGQK at its N-terminal end, together with a novel zinc-finger-like motif. The WRKY transcription factors participate in the control of defense-related genes either as positive or negative regulators and are essentially regulated at the transcriptional level (Ishihama and Yoshioka 2012). Transcriptionally suppressed *SlWRKY70*, a tomato ortholog of the *Arabidopsis thaliana WRKY70* gene, was needed for *Mi-1*-mediated resistance to aphids and nematodes in tomato (Atamian et al. 2012). In tobacco, the TGAs bind to the *as-1* element of the CaMV 35S promoter, a 20-bp element containing two TGACG boxes, and play a role in boosting transcription (Katagiri et al. 1989). The TGA family has been found to consist of ten members. TGA2 and TGA3 were found to bind to the pathogenesis-related (*PR-1*) promoter in the presence of salicylic acid (Johnson et al. 2003). A comprehensive genetic analysis revealed that plants appeared to deploy a broad spectrum of defense mechanisms, influencing multiple traits in response to combined stresses (Olivas et al. 2017). This recently available information on a wide range of plant responses, alteration of gene expression, and changes in cellular metabolism in response to broad defense activities has provided new insights into breeding strategies for resistance to insects.

3.5 Sources of Resistance

To breed for resistance to insects, it is important to identify sources of genes conferring resistance. As a source of variability, primary gene pool is the first choice of the breeder, as it could not only improve a crop agronomically but also confer resistance to insects. Harlan and de Wet (1971) considered primary and secondary gene pools to be the ones the breeder generally used, with tertiary gene pools defining the extreme outer limits of the potential gene pool of a crop. The transfer of resistance genes from secondary gene pool into a desired background is often a slow and tedious task. The tertiary gene pool consists of even more distantly related species or genera and pose difficulty in hybridizing cultivated species with wild relatives. It is well documented that wild species and/or non-domesticated crop relatives possess many valuable genes for resistance to insects (Clement and Quisenberry 1999). For example, wild species *Gossypium tomentosum*, *G. anomalum*, and *G. armourianum* are good sources of jassid resistance in cotton (Narayanan and Singh 1994). Resistance to brown planthopper and white-backed planthopper has been transferred from *Oryza officinalis* to cultivated rice (Jena and Khush 1990). Several introgression lines with genes from *O. officinalis*, *O. minuta*, *O. latifolia*, and *O. australiensis* have served as donors for resistance to brown planthopper (BPH) in rice (Jena and Kim 2010). Of the BPH-resistance genes identified in rice, 11 genes have been identified in wild rice, including *Bph11-Bph15* that came from *O. officinalis*; *Bph10* and *Bph18*that came from *O. australiensis*; *Bph20* and *Bph21* that came from *O. minuta*; and *Bph27* and *bph29* that came from *O. rufipogon* (Wang et al. 2015). For a more complete information on all the BPH-resistance genes, see Jing et al. (2017).

The resistance to large raspberry aphid (*Amphorophora agathonica* Hottes) in black raspberry (*Rubus occidentalis* L.) was first reported by Dossett and Finn (2010). Some accessions of *Lycopersicon pennellii*, a wild relative of tomato (*Lycopersicon esculentum*), are resistant to several important pests of cultivated tomato (Mutschler et al. 1996). Similarly, clones selected from the wild diploid species *Solanum berthaultii* have been shown to possess useful levels of resistance to the Colorado potato beetle (*Leptinotarsa decemlineata*), as well as to insects, such as aphids, flea beetles, leafhoppers, and potato tuber moth (Plaisted et al. 1992). While using wild species and/or non-domesticated crop relatives, even if fertile crosses can be made between the donor and recipient genotype, introgressing desirable genes for resistance to insects into cultivars is often a slow and cumbersome task (Plaisted et al. 1992). The backcross method of plant breeding is one of the ways in which the introduction of a specific gene from donor to recurrent parent is accomplished, but a major genetic drawback in conventional approaches is linkage drag. Linkage drag refers to the reduction in agronomic fitness of a cultivar because of the introduction of deleterious genes along with the beneficial gene(s). The linkage of undesirable alleles with the resistance quantitative trait loci (QTL) and hence co-introgression is a continuing problem (Boerma and Walker 2005). Three Japanese plant introductions, PIs 171451, 227687 and 229358, were identified as primary sources of genes for resistance to insects in soybean, but their linkage with poor

yield performance was a major obstacle in developing high-yielding insect-resistant soybean lines. However, now advances in molecular genetic technologies have facilitated the introgression of insect-resistance genes from conserved and unadapted germplasm into cultivated crops. With the help of molecular markers linked to traits of interest, indirect selection can be carried out to accelerate breeding progress (Balta et al. 2014); the development of resistant cultivars against different biotypes of brown planthopper (BPH) through marker-assisted selection (MAS) is a good example (Shabanimofrad et al. 2015). Breeding for resistance to insects in common bean by using a combination of phenotypic performance and QTL-based index has been shown to yield considerable progress (Tar'an et al. 2003). Advances in sequencing technology and functional genomics have facilitated cloning of genes for resistance to insects. *Bph14*, *Bph26*, *Bph17*, and *bph29* have been cloned via map-based cloning in rice, *Bph14* being the first cloned BPH-resistance gene originating from *O. officinalis* (Hu et al. 2016).

3.6 Mode of Inheritance of Resistance

The framework of breeding strategy to develop resistance to insects in crop plants depends upon the mode of inheritance of resistance. Plant resistance to insects is categorized as vertical and horizontal resistance. Vertical resistance is controlled by a single gene (monogenic) or a few genes (oligogenic), whereas horizontal resistance is controlled by many genes (polygenic), each producing a small effect (Marshall 1977; Simmonds 1979). Even though Van der Plank (1963, 1968) proposed these terms to describe only the plant-pathogen interactions, these are equally applicable to plant-insect interactions (Gallun and Khush 1980). Resistance under major genes refers to discontinuous variation, also called qualitative variation. With discontinuous variation, resistance in plants in a segregating population falls into distinct and separate phenotypic categories. The resistance controlled by polygenes exhibits continuous variation, called quantitative variation (horizontal resistance), where resistance does not fall into distinct resistant and susceptible phenotypic classes (Van der Plank 1968). At the genetic level, quantitative phenotypic variation can be explained by the combined action of many discrete genetic factors, each having a rather small effect on the overall phenotype, and environmental factors (Mather and Jinks 1971). Historically, many single genes have been incorporated to develop insect-resistant varieties. The resistance to BPH was found to be qualitative in nature and was reportedly controlled by a single gene (Athwal et al. 1971; Chen and Chang 1971). However, Jena and Kim (2010) have subsequently shown the involvement of two or more than two genes. Resistance to gall midge in rice and Hessian fly resistance in wheat and barley are other historical examples where monogenic nature of inheritance has been reported (Smith et al. 1994). Monogenic/oligogenic traits exhibit clear-cut susceptible or resistant classes in segregating populations. With a few exceptions, major genes have been identified in plants for resistance to only two groups of insects, the order Hemiptera and the dipteran family Cecidomyiidae. This contrasts with plant pathogens (viruses, bacteria, fungi, and

nematodes), where major genes for resistance to numerous species have been identified and used in plant breeding.

Horizontal resistance is often more durable than major-gene (vertical) resistance. Though major genes are relatively easy to identify in germplasm and to incorporate into commercial varieties or desired backgrounds, it is easier for a pathogen or an insect pest to overcome such resistance, as it is a matter of defeating a single gene or a few genes of the host through the counteractive generation of the corresponding virulent genes through mutation (Agrios 1978; Rubenstein et al. 2005). One strategy to delay the adaptation of pathogen is the pyramiding of several resistance genes, i.e., incorporating several resistance genes into a single cultivar (Brown 1995). So, in addition to application of durable-resistance genes, pyramiding multiple resistance genes is another efficient strategy to achieve durable resistance. In rice, marker-assisted pyramiding of two brown planthopper resistance genes, Bph3 and Bph27(t), not only significantly improved the BPH resistance but also reduced the yield loss caused by BPH (Liu et al. 2016).

Simulation models have predicted that if insect-adaptive alleles are recessive in nature and if strong nonallelic (epistatic) interaction exist in plant-resistance genes, the durability of pyramided genotypes/varieties would increase (Gould 1986). Horizontal resistance (HR), being polygenic and biotype non-specific, often exhibits a moderate level of resistance and, hence, does not exert intense selection pressure on insect population to evolve new biotypes. Therefore, polygenic resistance is often considered more durable than monogenic resistance as, among other reasons, adaptive alleles at multiple pest loci might be required to overcome multiple, unrelated plant-resistance factors (Yencho et al. 2000). For example, some resistance genes (*H* genes), which had been introgressed into wheat cultivars to control populations of Hessian fly, were defeated within 10 years after being first deployed (Cambron et al. 2010). Simmonds (1991) suggested that polygenically controlled horizontal resistance should be studied using biometric-genetic methods. Successful breeding programs aimed at developing durable horizontal resistance are environment-friendly and highly valuable for small farmers in the Third World, as such resistance minimizes the need for using chemical pesticides.

All the above factors make HR an ideal candidate for improving resistance to insects, but it is laborious to transfer horizontal resistance using conventional breeding methods. Moreover, strong environmental influences and dynamic nature of insects often complicate the identification, transfer, and selection of quantitative resistance and lead to inaccurate estimate of plant's true genetic potential. Statistical methods are available to study quantitative traits by developing appropriate experimental populations, but models used to study these traits are often complex and inadequate to precisely interpret the genetic effects of individual loci (Kang 1994; Young 1996). With the advent of molecular approaches, however, phenotypically neutral molecular markers can be used to dissect quantitative traits into discrete genetic loci, thereby allowing the study of effects of individual loci and increasing the selection efficiency by reducing environmental influence. Molecular-marker-assisted selection accelerates breeding progress (Tanksley et al. 1989) by not only helping track the introgressed gene(s) of interest but also by exercising

simultaneous selection against undesired genomic segments, thereby reducing the linkage drag. Deciphering of major gene interactions via molecular techniques not only hastens the breeding for resistance but also enhances understanding of virulence impacts on pathogen fitness (Mundt 2014).

3.7 Breeding Methods for Resistance to Insects

For various reasons, breeding for resistance to insects has not been as successful as breeding for disease resistance. One of the reasons is that efforts toward breeding for resistance to insects have not been as vigorous as toward resistance to diseases because, in most cases, it is relatively easy to control insect pests through insecticide use. Further, there are difficulties involved in ensuring adequate insect infestation for resistance screening, and transfer of traits related to resistance to insects is slow because of the complex and polygenic nature of their inheritance (Dhillion and Sharma 2012). Jenkins (1981) expressed that inheritance patterns for resistance to insects in plants were no different than those for other plant traits. Fundamentally, breeding methods for resistance to insects are the same as conventional breeding approaches for improving yield and quality (Kang et al. 2007). Jenkins (1981) emphasized, however, that several special aspects in a breeding program for resistance to insects must be considered, foremost among these being plant-insect interactions. There are some similarities, yet some marked differences exist between plant-insect interactions and plant-pathogen interactions. For example, insects can and do exercise choice. Their choices vary with the situation under which they are placed, such as monoculture versus a diversified crop culture. Detailed information about the interaction between the host and insect is required to empower both breeders and entomologists to enhance breeding efficiency. Breeders must take into consideration the life cycle of the insect, the infesting stage, and the relationship between the insect and the crop plant, together with the morphology, physiology, and genetic make-up of both the plant and the insect. It is worth emphasizing that resistance to a particular insect may not be permanent or/and may not affect other insects. In all breeding strategies, appropriate supplies of insects for artificial infestation and evaluation techniques for screening plant progenies must be ensured, as selection efficiency depends on the insect population, which, in turn, depends on various agroecological and environmental conditions. Steps must be taken to ensure that during selection, the most susceptible stage of plant coincides with optimum pest population. For example, to screen for resistance to gall midge in rice at Raipur, in the Indian state of Chhattisgarh (a hot spot for gall midge infestation), planting is generally delayed till July to synchronize maximum plant tillering with highest levels of pest population (Dhaliwal and Singh 2004). Progress in identifying and building levels of genetic resistance to insect pests depends on researcher's ability to distinguish, in each cycle of selection, the most resistant genotypes. Uniform infestation levels at appropriate stages of plant development are required for selecting resistant genotypes, reducing or eliminating "escapes," and for accumulating resistance genes (Maxwell and Jennings 1980). If efficient techniques for screening of

major insect pests are not available, breeders and entomologists rely on natural infestation. For many years, "hot spot" locations for the desired pest species were used for screening genotypes for resistance. However, studies have revealed reduced or no gains from screening based on natural infestation (Williams et al. 1978; Mihm 1985), as natural infestation is dependent on environmental conditions that are beyond researcher's control (Elias 1970). A good supply of eggs, larvae, or adult insects must be available for infesting plants in a breeding nursery. If the insects are reared in the laboratory, they must represent the wild population in vitality, biotype composition, and genetic structure, and they must be nourished so that their behavior and competitive ability are like those in the wild (Jenkins 1981). The screening and selection techniques must be simple and economical in utilization of limited resources, such as time and money (Kavitha and Reddy 2012). Generally, the scoring methods adopted to record insect damage are not quantified and not repeatable. Rigorous testing across many locations and years is required, as insects and pathogen species might widely differ from area to area (Hussain 2015).

Breeding is time-consuming and involves changing characteristics of a population across several generations by applying selection pressure on the population. The rate of achievement in a resistance breeding program depends on several factors (Agarwal and House 1982), some of which are listed below.

- Availability of stable donor lines possessing resistance to insects from diverse germplasm sources.
- Availability of adequate insect population and reliable, easy, and efficient techniques for screening for resistance to insects. The knowledge of the biology of the insect and the insect-plant and the insect-environment interactions is imperative to devise strategies to breed for resistance to insects. The information on hot spots for insect infestation is required, as during advanced breeding generations, screening of genotypes for resistance to insects in hot spots proves beneficial.
- Knowledge of the mechanism(s) of resistance to insects (tolerance, antixenosis, or antibiosis) is important.
- Knowledge of the mode of inheritance of resistance.
- Selection of correct breeding procedure.

There are several factors that affect pest/host-plant interactions, e.g., unintentional introduction of new pests and/or the emergence of new biotypes, the introduction of new cropping patterns, new agronomic practices, and the deployment of new varieties with hidden susceptibility to previously minor pests (Bosque-Perez and Buddenhagen 1992). Therefore, to devise pest-control strategies, it is essential to have dynamic breeding strategies to tackle active systems of pest/host-plant complexes (Bosque-Perez and Buddenhagen 1992). The interactions between plants and herbivores are exceedingly complex and multifaceted, even when they take place in simplified habitats that are characteristic of modern agriculture (Stout 2013).

The selection of plants resistant to insects first emerged as an art in the earliest times of agriculture. Even before the domestication of plants for agricultural purposes, the plants susceptible to arthropods would die before producing seeds. The

breeding strategy depends upon the breeding system of the crop (self-pollinated or cross-pollinated), means of reproduction (seed or asexual), and mode of inheritance (qualitative vs. quantitative). Crop breeding methodologies, both classic and modern, are explained by Kang et al. (2007). When breeding for resistance to insects, it is the responsibility of the development team to consider agronomic factors, including yielding ability, reproductive stability, uniformity of characters, tendency for weediness, potential vulnerability to attack by other pests, sensitivity to environmental stresses, and any undesirable characteristics of a new line (Kennedy and Barbour 1992). Generally, breeding programs are oriented toward higher productivity, and if a particular insect pest is of high economic importance, selection for resistance is coupled with high yield and quality. In the USA, the success attained in breeding for spotted alfalfa aphid was so spectacular that nearly all current alfalfa breeding programs include breeding for resistance to insects as a primary objective. However, sometimes, resistance to insects and productivity enhancement attributes are negatively related, e.g., for wheat stem sawfly, much of resistance in varieties is attributed to "solid-stem" character, but this trait is associated with low yield potential (wheat stem sawfly: Agrifacts.April2008. http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex3513/$file/622-26.pdf).

When genes for resistance are available in existing cultivars or germplasm collections, hybridization and selection can provide desired results by adopting pedigree, bulk, or backcross method of breeding. If the resistance source is only in wild relatives, then backcross is the appropriate procedure for transfer of desired level of resistance.

Often, the pedigree, mass-pedigree, and single-seed descent breeding methods suffice for transferring major resistance alleles and QTL from donors to elite breeding lines. Some form of backcrossing, such as recurrent backcrossing, inbred backcrossing, or congruity backcrossing (i.e., backcrossing alternately with either parent), becomes essential, as the genetic distance between the cultivar under improvement and the resistance-donor germplasm increases (Singh and Schwartz 2011). Hanson et al. (1972) described the development of alfalfa (*Medicago sativa* L.) populations having multiple resistance (resistant to four diseases and to two insect pests) through directed mass selection, also referred to as recurrent phenotypic selection. Along with multiple resistance, genetic potential for yield also increased during selection cycles. The coupling of mass selection with screening for resistance to insects can be done only if adequate natural pest population is available; otherwise artificial means of screening need to be adopted. Burton and Widstorm (2001) used mass selection in maize to improve agronomic performance and to maintain resistance to corn earworm and fall armyworm in exotic and southern US germplasm. Zuber et al. (1971) observed reduction of 208%in proportion of ears with earworm damage per generation after 10 cycles of mass selection in two maize populations.

Recurring cycles of the bulk-pedigree method of selection were used to develop significantly improved tolerance to leafhoppers in dry-bean breeding lines of different market classes of common bean (Kornegay and Cardona 1990). Singh and Schwartz (2011) reviewed breeding for resistance to insect pests and nematodes in

common bean and suggested that for a successful, broadly adapted commercial cultivar, resistance to multiple insect pests and nematodes and other biotic and abiotic stresses must be combined with stable high yield, seed quality, nutritional value, and desirable maturity and plant type. A few multiple-parent crosses with a considerably large number of F_1 seed (100) should be preferred over many single-crosses and backcrosses. This will, naturally, demand comparatively more time during hybridization to generate multiple-parent crosses, but this process should allow production of recombinants with resistance alleles/QTL for multiple pests in the shortest possible time. Finckh et al. (2000) emphasized the use of mixtures of varieties and species for functional diversity to reduce the risk of resistance breakdown by limiting pathogen and pest expansion. Mixtures are generally better buffered to tolerate yield losses caused by biotic and abiotic stresses. In composite populations, the frequency of resistance-conferring genes is increased and hence contributes to increased resistance.

The pedigree method of breeding is eminently suited to programs aimed at developing resistance to diseases and insects if resistance is governed by major genes, but it is not suitable for traits governed by minor genes. Various successful instances of the use of this breeding method for transfer of resistance to insects in rice are available (Khush 1980). Pedigree method involves hybridization between two selected parents, with at least one parent possessing strong resistance. After hybridization, selection begins in the F_2 generation. During F_3 to F_5 generations, superior plants from superior progenies rows are identified. Theoretically, about 92% homozygosity will be achieved by F_7 generation if a trait is governed by five genes. When targets for commercial breeding are also associated with resistance to insects, segregating lines must be exposed to proper insect pressure so that resistant segregants may be distinguished from susceptible ones. The breeder should expose the test lines to prevalent biotypes of insects for those areas for which they are being developed. The classical case of BPH susceptibility in rice in this regard further emphasizes proper selection of biotypes for screening. IR 26, a rice variety developed at the International Rice Research Institute (IRRI), Philippines, was found to be totally damaged by BPH in Kerala and at Hyderabad in 1975. Later, through the International Rice Testing Program (IRTP), it was confirmed that BPH biotype in South Asia was entirely different from the biotypes found in other rice-growing countries (Seshu and Kauffman 1980). To overcome the problem of variability within the insect population, an insect colony started from a single-pair mating of insects of known virulence is highly desirable. Insect damage is often related to the stage of growth and development of plant, and varieties under test should be uniform in maturity if inherent resistance is to be accurately measured.

Bulk method of breeding, proposed by Nilson Ehle in 1908, is a simple and most convenient method to attain inbreeding in the segregating generations after making an initial cross between desired parents. Since, in early generations, only natural selection operates, it is desirable to grow the generations in hot spots for insect pests for selection and perpetuation of only resistant plants. A natural insect population may be maintained in the field by using cultural practices that favor propagation of the insect species. In each generation, seed is bulked. Single-plant selection is

practiced from F_5/F_6 generation onward. This technique is used in the USA in breeding for resistance to Hessian fly, where wheat is planted, in the same area, year after year, during periods favorable for infestation. Artificially reared insect population may be transferred onto plants in the field or in the glasshouse. The resistance of new varieties/test genotypes is compared with that of resistant and susceptible check varieties. Deliberate selection may be practiced in the F_5 generation when a relatively high level of homozygosity has been achieved. When resistance to insects is polygenic in nature, selection for resistance in early generations is complicated because of the small magnitude of differences in resistance. Bulk method should not be a method of choice in this case, as it does not allow simultaneous screening for multiple pests (Khush 1977). Khush (1980) explored the possibility of using single-seed descent method in rice to improve traits governed by polygenes. Early generation population from multiple crosses involving three or four parents with minor resistance genes is proposed in bulk breeding. Artificial selection is not practiced till F_5 or F_6 generation. At the F_5 or F_6 stage, the bulk population is exposed to the targeted pest pressure, and plants with improved levels of resistance are identified and evaluated in progeny rows. Repeated bulk-pedigree cycles were followed to attain a high level of tolerance to leaf hoppers in dry-bean breeding lines of different market classes of common bean (Kornegay and Cardona 1990). Market classes for common bean refer to various categories of beans based on seed, size, and color.

Backcross breeding method is practiced to correct a defect in an otherwise productive cultivar/line (recurrent parent) by introducing a gene from another cultivar/line (nonrecurrent parent). The backcross method was proposed by Harlan and Pope in 1922 for cereal crops. Since 1922, backcrossing has become a widely used plant breeding approach in diverse crop species. To improve resistance to insects, an adapted but susceptible cultivar (recurrent parent) is crossed with a donor parent carrying resistance to insects. The initial hybridization is followed by backcrossing with recurrent parent. During this process, selection for resistance to insects is practiced regularly. Generally, it takes 4–6 backcrosses to sufficiently recover the genetic complement of the recurrent parent. The following formula may be used to theoretically estimate the recovery of the genetic complement of the recurrent parent during backcrossing:

$$\text{Recurrent parent (\%) genetic complement} = [1-(1/2)^{n+1}] \times 100,$$

where "n" is the number of backcrosses.

With each successive backcross, the progeny becomes more like the adapted variety (recurrent parent). If resistance is monogenic and dominant in nature, after four backcrosses, progeny will theoretically contain 96.875% genes from the recurrent parent (as per the above formula). The resistant plants will be heterozygous (*Rr*) for resistance and must be selfed for one generation to obtain true-breeding resistant plants (*RR*). If the genes for resistance being transferred to adapted variety are recessive, the progeny from each of the backcrosses will segregate into two genotypes (*RR* and *Rr*). As heterozygote (*Rr*) cannot be phenotypically separated

from the homozygote (*RR*) in this case, it would be necessary to self the progeny for one generation to find resistant (*rr*) plants before making the next backcross. Another possible procedure would be to backcross both the homozygous (*RR*) and heterozygous plants (*Rr*) to the recurrent parent and, at the same time, self each plant and test the selfed progenies for resistance. The backcross progeny from plants that prove to be heterozygous is then kept, and backcross progeny from homozygotes is discarded. This constitutes additional work for the breeder, but it saves one season.

While breeding for resistance to insects, reliable selection for resistance to insects (either by ensuring adequate natural pest population or use of artificial means) is essential in each generation. This process will make certain the transfer of genes for resistance to insects from the donor to the recurrent parent.

The backcross method has been used to transfer grassy stunt resistance from *Oryza nivara* to cultivated rice (Khush 1980). The inbred-backcross method was used to successfully introgress resistance to insects from *Lycopersicon esculentum* into cultivated tomato. Hartman and Clair (1998) discussed the effectiveness of the inbred-backcross method for introgressing genes for resistance to beet armyworm (*Spodoptera exigua* Hübner) in sugarbeet and to tomato fruitworm (*Helicoverpa zea* Boddie) in tomato.

Recurrent selection has been extensively used in many cross-fertilizing crops to improve economic traits. Primary objective of recurrent selection method is to gradually increase the frequency of favorable alleles and to maintain the genetic variability for further improvement (Hallauer and Darrah 1985). This method is basically used for improving traits that are inherited in a quantitative manner. Reciprocal recurrent selection simultaneously changes the gene frequencies in two populations so that overdominant, dominant, and partially dominant loci are all eventually utilized to maximize genetic advance (Comstock 1964). Only limited research efforts have been made on breeding for resistance to insects vis-à-vis productivity traits via recurrent selection. This may be attributed to the requirement of large-scale artificial insect rearing for infestation and post-infestation problems interfering with precise evaluation of genotypes for resistance to insects (Dhillon et al. 1993). Maize germplasm with superior resistance to *Chilo partellus* and *Busseola fusca* (Fuller) was developed through recurrent selection using a population developed from maize inbred lines exhibiting good general combining ability effects, which increased the frequency of favorable genes with additive effects. Although they did not use recurrent selection, Kang et al. (1995) reported that general combining ability (GCA) was more important than specific combining ability (SCA) for preference/non-preference of grain by maize weevils (*Sitophilus zeamais*) from analyses of two eight-parent diallels.

Recurrent selection method can be used for population improvement of both genetically narrow-based and broad-based populations. For a narrow-based population, about 1000 plants, and, for a broad-based population, about 3000–5000 plants may be sufficient to work with (Kang et al. 2007). The scheme for alternative recurrent selection (ARS) was proposed by Dhillon et al. (1993) to breed for resistance to maize borers [such as *Chilo partellus* (Swinhoe), *Sesamia inferens* (Walker)] in

maize. Recurrent selection based on S_1 families may be the best approach if there are no "escapes" during evaluation. The genetic gain per cycle of S_1 selection is generally expected to be higher than that from full-sib or half-sib selection (Dhillon and Khehra 1989). The S_1 selection involves the development of S_1 families in an off-season breeding nursery (season 1), evaluation of S_1 families (between and within-family selection), and recombination of the selected individuals during test season. This completes a cycle of S_1 selection in a year. Recurrent selection method to breed for fall armyworm resistance in maize was reported by Widstrom et al. (1992). They completed five cycles of selection and suggested that advanced cycles could serve as good sources of inbreds with intermediate to high levels of resistance to leaf feeding by larvae of the fall armyworm. Gillmore (1964) suggested that the reciprocal recurrent selection could be used to improve populations of some naturally self-pollinated crops in which plants with genetic male sterility would be freely wind-pollinated. Brim and Stuber (1973) used male-sterility-facilitated recurrent selection in rice for improving traits under polygenic control, such as partial resistance to blast.

The development of insect pest resistance in many important food crops has demonstrated the importance of breeding for this powerful trait by not only increasing the food productivity but also saving the environment from hazards of insecticides. Not only primary sources of resistance to insects have been used, but wild relatives have also been exploited to diversify the basis of and increase the levels of resistance to insect pests in different crops. With the advent of molecular tools, pyramiding of two or more genes for resistance to insects has been practiced for developing durable resistance. Identification and cloning of different genes for resistance to insects have expanded the tool kit of breeders. Closely linked molecular markers have facilitated the transfer of even quantitatively inherited resistance to insects. As per report from Emily Unglesbee, DTN staff reporter (February, 2017), Darwin's theory of evolution was on plain display this past year, as insects and weeds pushed many chemical and genetic crop protection tools to their breaking point, and insect resistance and weed resistance are likely to plague farmers in 2017. Because of the dynamic nature of pest/host-plant complexes and emergence of new pests resulting from climate change, cultivars with multiple resistance to insect pests will be in greater demand in the future for sustainable crop production worldwide. This requires consistent and concerted efforts of breeders, entomologists, and molecular biologists. For success in this arena, adequate funding and infrastructure must also be ensured.

Availability of information on plant-insect interactions has revealed that scientists need to investigate mutual plant responses to multiple stresses. *Arabidopsis thaliana* was subjected to a combination of stresses comprising attack by insect herbivores, *Pieris rapae* and *Plutella xylostella*, and infection by fungal pathogen *Botrytis cinerea* and drought stress. Genome-wide association analysis has led to the discovery of a limited overlap in the quantitative trait loci (QTL) underlying resistance to combined stresses (Davila et al. 2017). Several candidate genes involved in the biosynthesis of aliphatic glucosinolates and proteinase inhibitors involved in resistance to *Pieris rapae* and *P. xylostella*, respectively, were identified.

In nature, insect herbivory commonly occurs simultaneously or sequentially with other abiotic and biotic stresses (Stam et al. 2014). Such discoveries are intriguing for scientists and prompt them to explore communal plant responses and design improved strategies to control crop pests.

3.8 Conclusions

Biotic and abiotic stresses act as major constraints in increasing the productivity of crop plants. Breeding for resistance to insects has led to the development of hundreds of insect-resistant cultivars endowed with enhanced and stable yields and has emerged as an environmentally benign and economical method to minimize the damage by insect pests. A variety of structural and biochemical traits have been found associated with insect resistance in various crops; many of these traits have been successfully incorporated in commercial cultivars using conventional breeding approaches. The advent of molecular techniques has broadened the insect-resistant gene pool and enabled fast tracking their incorporation in elite germplasm. Many R-genes encoding for resistance to different groups of pests and pathogens have been identified and isolated from several crop species. Insect-resistance-conferring R-genes have been identified in wheat against Hessian fly and Russian wheat aphid, in rice against brown planthopper, and in melon against melon aphid. These R-genes share structural similarity with R-genes against pathogens. With the advent of molecular tools, pyramiding of two or more genes for resistance to insects has been practiced for developing durable resistance. Molecular approaches have, undoubtedly, facilitated the identification and transfer of resistance to insects across species, but the need for high-quality phenotypic analysis, coupled with reliable, affordable, and easy screening techniques, is of signal importance, for success. In future, there is a need to incorporate multiple resistance to important biotic and abiotic stresses in crop plants using a combination of conventional and molecular approaches. Further, the insect-resistant cultivars need to be highlighted as a tool in pest management so that farmers have the option of adopting such cultivars in areas where these pests pose a significant threat to their crops. Though the knowledge of science related to plant resistance to insects has increased many folds during the past decade, ever-increasing food demand and dynamic nature of plant-insect interactions will continue to pose a challenge for researchers.

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Advances in Breeding for Resistance to Hoppers in Rice

4

P.S. Sarao, Dharminder Bhatia, and D.S. Brar

Abstract

Rice productivity is hampered by a number of diseases and insects. Among the insects, hoppers including planthoppers and leafhoppers are typical phloem-sap feeders, which are very serious and damaging insect pests of rice in Asia. Many chemicals have been recommended for the control of planthoppers, but due to their feeding habit at the base of the plant, the farmers are unable to notice and effectively control these pests. Exploiting host plant resistance to hoppers and incorporating resistant genes in commercial cultivars are an alternative, economical and environment-friendly approach. To date, approximately 70 resistance genes against hoppers have been identified, and most of these genes have been tagged with molecular markers. Recently six genes for resistance to brown planthopper (BPH) in different lines have been cloned using map-based cloning. Based on molecular analysis of cloned genes, it appears that there is considerable similarity in the plant response to BPH infestation and fungal/bacterial pathogen attack. Marker-assisted selection (MAS) and pyramiding of genes for resistance to BPH and green rice leafhopper (GRH) have shown higher level and wide spectrum of resistance than their monogenic lines. In addition, transgenic approaches including RNAi have targeted various plant lectins and volatile compounds to generate resistance to hoppers. In context of changing climate, the major challenge for plant breeders is to breed varieties while taking care of changing populations of planthoppers and biotype development. Future research priorities

P.S. Sarao (✉) • D. Bhatia
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, India
e-mail: preetento@pau.edu; d.bhatia@pau.edu

D.S. Brar
School of Agricultural Biotechnology, Punjab Agricultural University, Ludhiana, India

Plant Breeding, Genetics, and Biotechnology Division, International Rice Research Institute, Los Baños, Philippines
e-mail: darshanbrar@pau.edu

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should concentrate on high-throughput screening of germplasm for field resistance to planthoppers, identifying and transferring new genes for resistance from different sources to broaden the gene pool of rice and identifying durable combination of genes for marker-assisted pyramiding.

Keywords
Hoppers • Rice • Germplasm screening • Genes/QTLs for resistance • MAS • Gene pyramiding • Molecular mechanism • RNAi

4.1 Introduction

Rice is the one of the most important cereals and is cultivated under highly diverse climatic and agroecological conditions. More than 90% of rice is produced and consumed in Asia. More than 3.5 billion people depend upon rice for more than 20% of their calories (Khush 2013). Sustained efforts are needed to increase the production and productivity of rice by 15–20% in the next 25 years to meet the demands of the ever-increasing population. A number of biotic (diseases, insect pests and weeds) and abiotic (drought, submergence, salinity, cold, etc.) stresses continue to reduce rice productivity. Hoppers, stem borer, leaf folder, Gundhi bug and gall midge are the important insect pests infesting rice. Among the hoppers, brown planthopper (BPH), *Nilaparvata lugens* (Stål); white-backed planthopper (WBPH), *Sogatella furcifera* (Horvath); green leafhopper (GLH), *Nephotettix* sp.; green rice leafhopper (GRH), *Nephotettix cincticeps* (Uhler); zigzag leafhopper (ZLH), *Recilia dorsalis* (Motschulsky); and small brown planthopper (SBPH), *Laodelphax striatellus* (Fallen) cause yield losses in rice to a variable extent and at various growth stages. These hoppers are also vectors of major viral diseases, such as grassy stunt, ragged stunt, rice stripe virus, black streak and tungro disease. Yield losses due to rice insect pests have been estimated at about 20–50% (Oerke et al. 1994; Prakash et al. 2007; Savary et al. 2012).

Planthoppers and leafhoppers are typical sap-sucking insect pests and cause serious damage to rice throughout Asia (Normile 2008; Heong and Hardy 2009). Hoppers cause significant yield losses leading to 'hopper burn'. Among the hoppers, BPH causes yield loss amounting to as high as 60% in India under epidemic conditions (Srivastava et al. 2009; Kumar et al. 2012). BPH has also been reported to cause damage in China, Korea, Japan and Vietnam. In 2005, there was loss of 2.7 m tons of rice due to direct damage by BPH, while this loss was 0.4 m tons in Vietnam due to two viruses, namely, grassy stunt and ragged stunt. WBPH has been reported to favour the hybrid rice crops in China and North Vietnam, whereas tungro disease epidemic by GLH was also reported from some areas (Heong and Hardy 2009). It is also difficult to notice these pests, and by the time plant damage becomes evident, significant loss in yield is inevitable. However the management of these

pests is possible with the regular monitoring of the crop (Sarao 2015), but it is very laborious and time-consuming. The two stages of hoppers, namely, nymphs and adults, suck sap from the leaf sheaths resulting in leaf yellowing, less tillering, reduction in plant height and more unfilled grains in panicles. In addition, there is reduction in chlorophyll, protein content of leaves and photosynthetic rate. Due to overfeeding by the hoppers, plants start wilting with first drying of outermost leaves followed by drying of the entire plant. At early stage, round yellowish patches appear which soon turn brownish due to drying up of the plants. These patches spread in concentric circles within the field, and this gives burnt appearance known as 'hopper burn' (Liu et al. 2008; Horgan 2009).

Many chemicals were recommended for the control of planthoppers (Sarao 2015), but due to their feeding habit at the base of the plant, the farmers are unable to notice and control these pests effectively. They perform a number of applications of insecticides under panic, which kills natural enemies and disrupts density-dependent control of the hoppers (Gorman et al. 2008). Extensive application of insecticides may affect behavioural, physiological and biochemical aspects of the insects leading to development of insecticide resistance in hoppers (Matsumura et al. 2009). Therefore the use of genetic resistance is the most effective measure for hopper management (Sarao et al. 2016). For sustainable hopper management, it is necessary to develop strategy involving proportionate balance between breeding for resistance and appropriate use of insecticides, so as to keep hopper population under economic threshold levels. However, cultivation of resistant varieties is an economical, efficient and environmentally sound strategy for hopper population management. These varieties provide pest control at essentially no cost to the farmers.

4.2 Screening for Resistance to Hoppers

Identification of genetic donors and different sources of resistance to hoppers is the primary need for breeding varieties. In addition, a large number of segregating plant materials also need to be screened. For the purpose, it is necessary to have reliable high-throughput screening techniques including availability of target insects of appropriate stages and good laboratory and screen house facilities. The germplasm can be screened rapidly by infesting plants at the seedling stage, during early mass-screening cycle in the glass house. This technique is economical in space, time and labour (Heinrichs et al. 1985). The selected resistant entries in the rapid screening method should be later screened under field conditions. In case of field screening, the location should be selected where high natural population of the pest is prevailing (hotspots).

Under greenhouse conditions, scoring of lines based on the degree of plant damage and number of insects used in infestation is very critical. Based on the initial scoring of the lines, majority of susceptible segregants/lines can be rejected, and the resistant ones can be further tested both in screen house and under field conditions.

4.2.1 Greenhouse Screening

The glass/greenhouse screening is the accelerated and effective method for assessing a large number of different germplasm lines (Myint et al. 2009; Li et al. 2010; Nanthakumar et al. 2012; Fujita et al. 2013; Sarao et al. 2016). Two methods used for screening are described as below:

4.2.1.1 Conventional Seedbox Screening

The conventional seedbox screening or standard seedbox screening test (SSST) is the most commonly used method for greenhouse screening. It is a rapid method for assessing large number of germplasm lines for planthopper resistance. The seeds of test material are sown in a single row of 3.5 cm apart in a seedbox of about 60 × 40 × 10 cm size. Suitable susceptible and resistant checks are sown in similar rows in the same box. Susceptible check (TN1) is sown as outer row which also acts as spreader row. In the centre of the box, half-susceptible and half-resistant material rows are sown. These boxes are placed in the water through galvanized iron trays containing water. Eight to twelve days after sowing, seedlings are thinned to about 20 plants per row. These seedlings are infested with about 8–10 (BPH and WBPH) and 3 (GLH) second to third instar nymphs per seedling. The insects are first cultured on TN1 plants in pots and then distributed uniformly on thinned seedlings by holding the base of the pot and lightly tapping and blowing these TN1 plants to dislodge the hopper nymphs on the seedlings.

For determining nonpreference parameter among lines, the settled planthoppers can be counted per germplasm line before grading for damage score in the tray. The grading of each entry in the seedbox is done when the susceptible check seedlings (TN1) in that box are about 90% dead. Scoring for each seedling in an entry is done using 0–9 scale as per standard evaluation system (SES) for rice. To compare entries a numerical rating system is used to score seedling damage: 0, no damage; 1, very slight damage; 3, first and second leaves of most plants are partially yellow; 5, pronounced yellowing and stunting or about half of the plants wilting or dead; 7, more than half of the plants wilting or dead; and 9, all plants dead (IRRI 2014). The average damage score of each germplasm line is designated as resistant (0–3.49), moderately resistant (3.50–5.49) and susceptible (5.50–9.00) following Heinrichs et al. (1985) and Sarao et al. (2016).

4.2.1.2 Modified Seedbox Screening Test (MSST)

This test was used to overcome some limitations of SSST and for better understanding of ‘field resistance’, that is, whether resistance is maintained or increases with plants age. The SSST is mostly qualitative, and entries with moderate levels of resistance because of tolerance or low levels of antibiosis or nonpreference usually are recorded as susceptible. Thus, the conventional test is modified to detect varieties with moderate levels of resistance. In this method, the plants are older at the time of infestation and fewer hoppers per seedling are placed. Plants are infested 20 days after sowing with 3 to 5, second to third instar nymphs per plant. In this test, the whole seedbox of infested seedlings in a screen cage (65 × 45 × 90 cm) is covered

to prevent the insects from escaping the tray. In this method mortality of the plants is caused by the progeny (F_1 population of planthoppers) rather than the initial source of infestation is the insects that cause the plant damage. The original nymphs mature and reproduce in the seedbox, and ultimately their offspring kill the plants (Velusamy et al. 1986).

These two methods have been extremely useful for inexpensive screening of the large volume of material required to find resistance genes/sources. Furthermore, they incorporate 'free choice', that is, the target insects can choose between the different varieties under test before initiating feeding (SSST and MSST) or oviposition (MSST) behaviour.

4.2.2 Field Screening

Field screening of germplasm is generally done in hotspots which include all life cycle aspects of the tested insect. For field screening, transplant two rows of a susceptible check such as TN1 on each side of test entry (Chelliah and Heinrichs 1980). To kill natural enemies, apply resurgence-inducing insecticide (spray of 0.002% deltamethrin or 0.02% methyl parathion) to the susceptible border rows starting at 20 days after transplanting (DAT). Next day after spray, observe the base of the plants so as to determine the population of spiders, mirid bugs and other predators. If they are still abundant, repeat the spray application the next day. Thereafter, repeat the sprays at 10-day interval up to 70 DAT, if necessary. After the first application of insecticides, the late instar nymphs at the rate of five insects/hill can be released to support the field population of BPH. Generally 25 BPH female adults/hill at maximum tillering and 100 BPH female adults/hill at flowering stage are required for valid test. When plants in the susceptible check start wilting, start grading all entries (Reissig et al. 1982; Heinrichs et al. 1985; Panda and Heinrichs 1983).

If by the resurgence technique cannot increase the population, then a polyethylene sheet can be placed around small field plots to prevent movement of BPH nymphs outside the plot and to prevent predators entering the test plot (Kalode et al. 1982).

4.3 Genetics of Resistance to Hoppers

Exploiting host plant resistance to hoppers and incorporating resistant genes in susceptible commercial cultivars are considered an economical and environmentally friendly approach. However, availability of good source(s) of resistance and identification of novel genes with linked markers are the utmost priority to achieve full potential of this approach. To locate the hopper resistance genes in germplasm lines, entomologists and breeders had worked tirelessly to study the inheritance of resistance to hoppers. Due to dedicated efforts of the scientists, a large number of donors for resistance to hoppers have been identified, and numerous varieties resistant to insects have been developed worldwide. Some of the key donors for

resistance include Mudgo, ASD7, Rathu Heenati, Ptb33 and wild species for BPH; Mudgo, Kasalath and Rathu Heenati for SBPH; N22, ADR52 and Guiyigu for WBPH; ASD7, DV85 and IR36 for GLH; and Rathu Heenati and Ptb33 for ZLH (see for more details in Brar et al. 2015). To date, more than 70 genes/QTLs for resistance to hoppers have been identified, and a significant number have been tagged with molecular markers (Fujita et al. 2013). A number of genes/QTLs for resistance to BPH (Table 4.1) and GLH have been reported, while limited information is available for other hoppers.

4.3.1 Genetics and Mapping of Resistance to BPH

Beginning with identification of sources of resistance to BPH in 1967 (Pathak et al. 1969), significant efforts have been done to search for host plant resistance to BPH. The earliest information on the genetics of BPH resistance was reported in 1970 (Athwal et al. 1971) with identification of *Bph1* and *bph2* as first two resistant genes. However development of DNA-based markers and QTL analysis in 1970–1980s helped to establish their linkage to specific region of rice genome. To date, 32 major genes designated from *Bph1* to *Bph32* for resistance to BPH have been identified from wild and cultivated rice germplasm. Of these, 25 have been mapped using restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD), simple sequence repeats (SSR), sequence tagged sites (STS) and insertions and deletions (InDel)-based markers (Table 4.1). These genes are located on seven (2, 3, 4, 6, 10, 11 and 12) of 12 rice chromosomes. The rice chromosome 12 contains eight genes including *Bph1*, *bph2*, *Bph7*, *Bph9*, *Bph10*, *Bph18*, *Bph21* and *Bph26* followed by six genes, *Bph3*, *bph4*, *Bph22*, *Bph25*, *Bph29* and *Bph32* on chromosome 6. Five genes, *Bph12*, *Bph15*, *Bph17*, *Bph20 and Bph27*, are located on chromosome 4. Four genes, *Bph11*, *Bph13*, *Bph14* and *Bph19*, are located on chromosome 3. One gene each, *Bph13*, *Bph30*, and *Bph28*, is located on chromosomes 2, 10 and 11, respectively (Table 4.1).

The *Bph1* (Hirabayashi and Ogawa 1995; Jeon et al. 1999; Sharma et al. 2002; Kim and Sohn 2005; Park et al. 2008; Cha et al, 2008) and *bph2* (Murata et al. 1998; Murai et al. 2001; Sharma et al. 2004; Sun et al. 2006), the first two resistant genes, were mapped on the rice chromosome 12. These two genes had shown resistance to BPH biotypes 1 and 2, prevalent at that time and soon deployed in rice mega varieties. In 1973, the first resistant rice cultivar, IR26, was released that contains *Bph1* (Khush 1971), followed by cultivars IR36, IR38 and IR42 with the *bph2* gene. However *Bph1* and *bph2* rapidly became obsolete in just 3–5 years because of the development of new BPH biotypes (Brar et al. 2015). This gave rise to the continuous efforts to identify and map novel sources of resistance to BPH to breed broad-spectrum and durable resistant varieties.

A broad-spectrum resistance gene, *Bph3*, was mapped against BPH biotype 2 in Rathu Heenati and Ptb33 using SSR markers. Two backcross populations were generated using both the donors for mapping *Bph3* locus. The BC_1F_2 was derived from cross of Ptb33/RD6, whereas BC_2F_2 was derived from cross between Rathu Heenati

Table 4.1 Some examples on genes for resistance to BPH in rice tagged with molecular markers

Gene	Chromosome[a]	Donor[b]	Marker	Marker type used	Population type	Reference(s)
Bph1	12L	IR28 (1)	XNpb248, XNpb336	RFLP	F_2/F_3	Hirabayashi and Ogawa (1995)
	12L	Gayabyeo (1)	RRD7, RG457, RG634	RAPD, RFLP, SSR	F_2/F_3	Jeon et al. (1999)
	12L	Mudgo (1)	em5814N, em2802N, R2708	AFLP, RFLP	F_2/F_3	Sharma et al. (2002)
	12L	Samgangbyeo (1)	BpE18-3	RAPD, STS	DH, F_2/F_3	Kim and Sohn (2005)
	12L	Samgangbyeo (1)	OsBphi 252	RDA clones, CAPS	NILs	Park et al. (2008)
	12L	Cheongcheongbyeo (1)	pBPH4, pBPH14	RAPD, SCAR, STS	RILs	Cha et al. (2008)
bph2	12L	NorinPL4	G2140	RFLP	F_2/F_3	Murata et al. (1998)
	12L	NorinPL4	KAM3, KAM4, KAM5	AFLP	F_4/F_5	Murai et al. (2001)
	12L	NorinPL4 (1)	KAM2, KAM3, KAM4	AFLP	F_5	Sharma et al. (2004)
	12L	ASD7 (1, 2)	RM463, RM7102	SSR	F_2/F_3	Sun et al. (2006)
Bph3	6S	Ptb33, Rathu Heenati, IR71033-121-15 (2)	RM589, RM588, RM586	SSR	BC_1F_2/BC_3F_2, F_2	Jairin et al. (2007a, b, c) and Liu et al. (2014)
bph4	6S	Babawee	RM217, C76A	SSR	F_2/F_3	Kawaguchi et al. (2001)
	6S	Babawee (4)	RM586-RM589	SSR	F_2/F_3	Jairin et al. (2010)
Bph6	4L	Swarnalata	RM6997-RM5742	SSR, STS	F_2/F_3, BC_2F_2	Qiu et al. (2010)

(continued)

Table 4.1 (continued)

Gene	Chromosome[a]	Donor[b]	Marker	Marker type used	Population type	Reference(s)
bph7	12L	T12	RM28295-RM313	SSR	F_2/F_3, BC_2F_1	Qiu et al. (2014)
Bph9	12L	Pokkali	OPR04,S2545	RAPD, RFLP	F_2, F_3/F_4	Murata et al. (2001)
	12L	Kaharamana (1)	RM463, RM5341	SSR	F_2/F_3	Su et al. (2006)
Bph10	12L	IR65482-4-136-2-2 (*O. australiensis IRGC100882*)	RG457	RFLP	F_2/F_3	Ishii et al. (1994)
	12L	IR54742 (*O. officinalis*) (1, 2, 3)	RG457L-B, RM260	STS, SSR	F_2/F_3	Lang and Bu (2003)
bph11	3L	IR54742-23-19-12-3-54 (*O. officinalis*) (1)	G1318	RFLP	F_2/F_3, RILs	Hirabayashi et al. (1998)
bph12	4S	GSK185-2 (*O. officinalis*)	G271, R93	RFLP	F_2/F_3	Hirabayashi et al. (1999)
Bph12	4S	B14 (*O. latifolia*) (1, 2)	RM261	SSR	F_2/F_3, RILs	Yang et al. (2002)
	4S	B14 (*O. latifolia*) (1, 2)	RM16459-RM1305	SSR	F_2/F_3, $BC_2F_{2:3}$	Qiu et al. (2012)
Bph13	2L	*960,044-112* (*O. eichingeri* acc. no. 105159)	RM250, RM240	SSR		Liu et al. (2001)
	3S	IR54745-2-21-12-17-6 (*O. officinalis*) (4)	AJ09b230, AJ09c	RAPD	RILs	Renganayaki et al. (2002)
Bph14	3L	B5 (*O. officinalis*)	SM1-G1318	SSR, STS	F_2, RILs	Du et al. (2009)
Bph15	4S	B5 (*O. officinalis*) (1, 2)	C820, S11182	RFLP, AFLP	F_2, F_5	Yang et al. (2004)
Bph17	4S	Rathu Heenati (1, 2)	RM8213-RM5953	SSR	F_2/F_3	Sun et al. (2005)
Bph18	12L	IR65482-7-216-1-2 (*O. australiensis*. acc. no. 100882) (Korean)	RM1022	SSR, STS	F_2/F_3	Jena et al. (2006) and Ji et al. (2016)
bph19	3S	AS20-1 (2)	RM6308-RM3134	SSR	F_2/F_3	Chen et al. (2006)

Bph20	4S	IR71033-121-15 (*O. minuta* acc. no 101141)/Korean Bio1	MS10-RM5953	SSR, STS	F_2/F_3	Rahman et al. (2009)
Bph21	12L	IR71033-121-15 (*O. minuta* acc. no. 101141)/(1, Korean)	RM3726-RM5479	SSR, STS	F_2/F_3	Rahman et al. (2009)
Bph22	6S	IR71033-62-24 (*O. minuta*)	RM19429, RM584, RM585	SSR	F_6	Harini et al. (2010)
Bph25	6S	ADR52/bio Chikugo-89	S00310	SSR	F_2, BC_3F_2	Myint et al. (2012)
Bph26	12L	ADR52/bio Chikugo-89	RM5479	SSR	F_2, BC_3F_2	Myint et al. (2012) and Tamura et al. (2014)
Bph27	4L	*O. rufipogon*, *acc. no. 2183* (2)	RM16853-RM16846	SSR	BC_1F_2	Huang et al. (2012)
	4L	Balamawee	Q5, Q20	SSR, InDels	F_2/F_3	He et al. (2013)
QBph11, *Bph28*	11L	DV85 (1, 2)	RM26656-RM26725	SSR, InDels	F_2/F_3	Su et al. (2005) and Wu et al. (2014)
bph20(t), *bph29*	6S	RBPH54 (*O. rufipogon)* (2)	RM435, RM540, BYL7, BYL8	SSR, STS, InDels	NILs	Yang et al. (2012) and Wang et al. (2015)
bph21(t), *bph30*	10S	RBPH54 (*O. rufipogon)* (2)	RM222, RM244	SSR, STS, InDels	NILs	Yang et al. (2012) and Wang et al. (2015)
Bph32	6S	Ptb33	RM19291, RM8072	SSR		Ren et al. (2016)

Modified from Fujita et al. (2013) and Brar et al. (2015)

[a]L, S = long and short arm of chromosome, respectively; [b]Biotypes used for screening for BPH resistance are given in parenthesis

and KDML105. The *Bph3* locus was mapped between two flanking SSR markers, RM589 and RM588, on chromosome 6S (Jairin et al. 2007a, b). The *Bph3* locus in Rathu Heenati was further physically mapped to 190-kb interval flanked by the markers RM19291 and RM8072 (Jairin et al. 2007c). *Bph3* has been widely used in marker-assisted selection (Jairin et al. 2009; Singh et al. 2011), revealing that the locus contains two valuable BPH resistance genes. Rice varieties deployed with *Bph3* more than 30 years ago still show resistance to BPH (Cruz et al. 2011). Both *Bph3* loci in Rathu Heenati and Ptb33 were later cloned and designated as *Bph3* gene and *Bph32* gene, respectively (Liu et al. 2014; Ren et al. 2016).

The recessive gene *bph4* was initially identified from *indica* rice, Babawee from Sri Lanka, and provides resistance against BPH biotypes 1–4 (Laxminarayana and Khush 1977). It was reported to have similar allele or closely linked to a dominant gene *Bph3* (Sidhu et al. 1979). Later based on trisomic analyses, *bph4* was assigned on rice chromosome 10 (Ikeda and Kaneda 1981). Kawaguchi et al. (2001) reported mapping of a recessive BPH gene *bph4* from Babawee on chromosome 6S using bulked segregant analysis with RFLP and SSR markers. However, *bph4* was again shown to be allelic to *Bph3* based on allelic tests with two different genetic backgrounds of rice (Jairin et al. 2010).

Kabir and Khush (1988) identified a resistance gene (designated as *Bph6*) against Bangladesh BPH population in a rice variety Swarnalata. The *Bph6* was later mapped using the F_2 and backcross populations and was located in the interval of SSR markers RM6997 and RM5742 on chromosome 4L. This gene was further delimited to a 25-kb region in the interval of STS markers Y19 and Y9 (Qiu et al. 2010). The recessive gene, *bph7*, was earlier identified in *indica* rice cultivar, T12, and found to be resistant to Bangladesh BPH population (mainly attributed to BPH biotype 4) (Kabir and Khush 1988). Qiu et al. (2014) reported fine mapping and assigning of *bph7* gene on rice chromosome 12 between SSR markers RM28295 and RM313 using F_2 and backcross populations. This was reported to explain 38.3% total phenotypic variation of resistance to BPH in the F_2 population.

Three BPH-resistant cultivars, Balamawee, Kaharamana and Pokkali, were reported to carry *Bph9* gene earlier. This gene was mapped on chromosome 12L in Pokkali (Murata et al. 2001) and Kaharamana (Sun et al. 2006). Later Balamawee was shown to be different from other two BPH-resistant cultivars based on various molecular-physiological characteristics of BPH such as settling behaviour including nymph preferences, nymph survival, honeydew and tolerance indices. The new gene was fine mapped in Balamawee and designated as *Bph27* (He et al. 2013). Gene *Bph10* introgressed from wild species is linked with RFLP clone RG457 on chromosome 12 (Ishii et al. 1994). In another study, STS markers were developed from RFLP clone RG457 and using the STS and SSR markers delimited the *Bph10* region between RG457L-B and RM260 on chromosome 12L (Lang and Bu 2003). Hirabayashi et al. (1998) identified *bph11* in *O. officinalis*-derived introgression line IR54742-23-19-12-3-54 on chromosome 3L with RFLP analysis of $F_{2:3}$ progenies and RILs.

A recessive gene designated as *bph12(t)* located on chromosome 4 using RFLP analysis of another *O. officinalis*-derived introgression line GSK185–2. The *Bph12*,

formerly designated as *Bph12(t)*, was earlier mapped to a 13.4-cM region on chromosome 4S using *O. latifolia*-derived introgression line 'B14' (Yang et al. 2002), which was further fine mapped to a 1.9-cM region using an F_2 and backcross population (Qiu et al. 2012). *Bph13* gene mapped on different location on chromosomes in two separate studies. Liu et al. (2001) reported identification and mapping of BPH resistance gene in *O. eichingeri* between two SSR markers, RM240 and RM250, respectively, on chromosome 2, whereas Renganayaki et al. (2002) mapped the *Bph13(t)* gene on chromosome 3 in *O. officinalis*-derived introgression line, IR54741-3-21-22 using a set of RAPD markers.

Huang et al. (2001) earlier identified and mapped *Bph14* and *Bph15* from an introgression line derived from *O. officinalis* 'B5' on chromosome 3L and on chromosome 4S, respectively. *Bph14* that showed stable resistance in different genetic backgrounds has been cloned using map-based cloning (Du et al. 2009). Yang et al. (2004) fine mapped *Bph15* locus using large population of 9472 F_2 individuals derived from a cross between a selected RIL of 'B5'-carrying *Bph15* and a susceptible cultivar, TN1. *Bph17* was identified and mapped from Rathu Heenati on chromosome 4S (Sun et al. 2005); however major BPH-resistant gene *Bph3* has been cloned from Rathu Heenati (Liu et al. 2014). Jena et al. (2006) identified *Bph18* in an introgression line, IR65482-7-216-1-2 derived from *O. australiensis*. The *Bph18* was identified as non-allelic to *Bph10* and mapped on the long arm of chromosome 12 flanked by the SSR marker RM463 and the STS marker S15552. The gene was utilized to develop durable broad-spectrum resistant varieties in Korea and provided resistance at both seedling and adult plant stages. Map-based cloning approach has been used to clone *Bph18* gene (Ji et al. 2016).

Rahman et al. (2009) identified and mapped two BPH resistance genes in *O. minuta* acc. IRGC101141 using F_2 population derived from a cross between resistant introgression line, 'IR71033-121-15', and a susceptible Korean japonica cultivar, 'Junambyeo'. The two genes were linked to molecular markers and designated as *Bph20(t)* on chromosome 4 and *Bph21(t)* on chromosome 12.

Myint et al. (2012) identified two BPH resistance genes, *Bph25* on chromosome 6S and *Bph26* on the chromosome 12 L in the *indica* cultivar ADR52. *Bph26* has been cloned using NILs in the background of Taichung 65 and found to be allelic to *bph2* present in cultivar ASD7 based on sequence analysis and feeding ability of BPH virulent biotype (Tamura et al. 2014). In a previous study, a recessive BPH resistance gene *bph18*(t) was identified from a wild rice accession (*O. rufipogon* accession GX2183), which shows a broad-spectrum resistance to BPH biotypes, including biotypes 1 and 2, Bangladesh, Cuu Long (Vietnam) and Pantnagar (India) (Li et al. 2006). However, Jena et al. (2006) reported same gene nomenclature in a different donor IR65482-7-216-1-2, derived from *O. australiensis*. Huang et al. (2012) further fine mapped *bph18*(t) using backcross population and renamed it to *Bph27*. In another study *Bph27* was mapped from Balamawee on chromosome 4L, though both the genes seem to be allelic in nature based on their position on the chromosome. Su et al. (2005) identified a major effect QTL in *indica* rice cultivar 'DV85' on chromosome 11 and designated as *Qbph11*. Later, *Qbph11* was fine mapped and designated as *Bph28* (Wu et al. 2014).

Yang et al. (2012) identified and mapped two recessive genes in *O. rufipogon*-derived introgression line, RBPH54 using BC_2F_2, which were tentatively named as *bph20(t)* and *bph21(t)*. Later, Wang et al. (2015) renamed *bph20(t)* and *bph21(t)* as *bph29* and *bph30* ,respectively, *and* cloned *bph29* using map-based cloning approach. Jairin et al. (2007a) mapped the *Bph3* locus on chromosome 6S using two backcross populations derived from Rathu Heenati and Ptb33. The BPH resistance locus seems to be two different valuable BPH resistance genes seeing the durability of resistance based on various MAS studies for deployment of this locus. Later, a dominant gene, *Bph32*, was cloned from the rice variety Ptb33 on chromosome 6S using bioinformatics analysis and a transgenic approach (Ren et al. 2016).

4.3.2 Small Brown Planthopper (SBPH)

Genes/QTLs for resistance to SBPH have been identified only recently. More than 30 QTLs for SBPH (Duan et al. 2007a, b, 2008, 2009, 2010; Tuyen et al. 2012; Zhang et al. 2014) have been identified from cultivated and wild species using SSST, MSST, antixenosis and antibiosis tests. The rice lines Mudgo, DV85, Kasalath, Rathu Heenati and wild rice *O. officinalis* have been used as resistance donors for identification of these QTLs.

4.4 Genomics of BPH-Resistant Genes: Cloning and Molecular Mechanism

Recently, six genes *Bph3*, *Bph14*, *Bph18*, *Bph26*, *bph29* and *Bph32* have been cloned using map-based cloning strategy (Table 4.2). The cloning of these genes has provided valuable information on the molecular basis of resistance. Of the six genes, three genes; *Bph14*, *Bph18* and *Bph26*, encode for coiled coil, nucleotide binding and leucine-rich repeat (CC-NBS-LRR) protein of NB-LRR family (Du et al. 2009; Ji et al. 2016; Tamura et al. 2014). NBS-LRR class of genes plays a vital role in resistance to plant diseases. During disease infection, these genes recognize the effectors delivered by pathogens and induce the downstream disease resistance reactions (Yue et al. 2012). Based on variability in the N-terminal region, plant NBS-LRR genes can be divided into several types. In rice, most

Table 4.2 Cloned BPH resistance genes in rice

Gene	Encoded protein	Plant defence response	Reference
Bph3	Lectin receptor kinases	Antibiosis	Liu et al. (2014)
Bph14	CC-NBS-LRR	Antibiosis	Du et al. (2009)
Bph18	CC-NBS-LRR	Antibiosis and antixenosis	Ji et al. (2016)
Bph26	CC-NBS-LRR	Antibiosis	Tamura et al. (2014)
bph29	B3 DNA-binding domain	Antibiosis	Wang et al. (2015)
Bph32	SCR domain	Antibiosis	Ren et al. (2016)

NBS-LRR-type genes are CC-NBS-LRR (CNL) with a coiled-coil domain at the N-terminus end (Monosi et al. 2004; McHale et al. 2006). *Bph18* and *Bph26* comprise of CC-NBS-NBS-LRR with two NBS domains, which is basically similar to CC-NBS-LRR. More than 400 NBS-LRR genes have been identified in the rice (*O. sativa* cv. Nipponbare) genome (Monosi et al. 2004), and only four genes encode for proteins where NBS domain is partially duplicated similar to *Bph18* and *Bph26* (Ji et al. 2016).

Bph3 is a cluster of three genes encoding lectin receptor kinases localized in plasma membrane belonging to G-type LecRK family. This family consists of an extracellular bulb-type lectin domain, a plant PAN-/APPLE-like domain, a transmembrane domain and an intracellular serine/threonine kinase domain. Lectin receptor kinases are large family of proteins present in plants and play a very important role in plant innate immunity against pests and diseases (Singh et al. 2013). A G-type lectin receptor kinase encoding gene *Pi-d2* from rice provides resistance against the rice blast caused by a fungal pathogen *Magnaporthe grisea* (Chen et al. 2006). *Bph29* has been a single-copy gene that encodes for B3 DNA-binding domain, a highly conserved domain found exclusively in transcription factors that interact with the major groove of DNA (Wang et al. 2015). Five classes of B3 domain-containing genes have been identified, and *Bph29* has the most similarity to RAV (related to ABI3/VP1, *Abscisic acid insensitive3*/*Viviparous1*) family. The *RAV1* gene of this family has been shown to play an important role in bacterial disease resistance in an earlier study (Sohn et al. 2006). However the role of B3 domain in insect resistance still needs to be elucidated. *Bph32* gene encodes for unknown protein containing a signal peptide and a SCOP d1gkna2 domain belonging to SCR (short consensus repeats) domain family of proteins. This family of proteins is considered to be a type of lectin or cell adhesion protein. The role of plant lectins has been identified to function as defence-related proteins that can act on insect glycoproteins or tissues to inhibit insect feeding (Ren et al. 2016).

BPH is a phloem-feeding insect that uses saliva sheath to establish the connection in the phloem tissue and suck sap with its stylet (Sogawa 1982). This action causes least physical injury to the host plant, thereby establishing prolonged and intimate interaction between insect stylets and plant cells (Du et al. 2009). In addition, BPH also acts as vector for the rice ragged stunt virus and rice grassy stunt virus transmitted by insect feeding to the phloem. As a consequence, the resistance factors are thought to be present within the phloem (Walling and Thompson 2012), and responses of the host plant to BPH probably have similarity with fungal or bacterial pathogens (Walling 2000, 2008). Site of expression of all the cloned resistance genes has been identified in the vascular bundles (phloem) of leaf sheath, the place of BPH attack on plants. In general, plants may respond to insect attack mainly by two defence mechanisms: antixenosis, which disturbs insect settling, colonization or oviposition, and antibiosis, which affects insect feeding, growth rate or survival. All the cloned BPH resistance genes employ antibiosis as a resistance mechanism, whereas *Bph18* is considered to employ both antixenosis and antibiosis (Ji et al. 2016). Further, callose deposition on phloem sieve plates and the cell walls of vascular tissue found to be important defence mechanism in plants responsible for

reduced insect feeding. Callose is produced enzymatically by the action of callose synthases in the presence of Ca^{2+}. It is located in the plasma membrane and deposited extracellularly around sieve plates (Will et al. 2013). BPH infestation caused upregulation of three callose synthase-encoding genes (*GSL1*, *GSL5* and *GSL10*) in both the wild-type and transgenic rice plants, whereas two genes responsible for decomposing the callose and occlusion of sieve tubes were slightly downregulated (Du et al. 2009). The upregulation of callose synthase genes responsible for producing callose and downregulation of callose decomposing genes reveal the importance of callose as a plant defence mechanism. Hao et al. (2008) also reported that activation of β-1,3-glucanase genes can open up sieve tube occlusions during BPH infestation in rice plants.

Two-branched innate immunity system (pattern-triggered immunity (PTI) and effector-triggered immunity (ETI)) has been recognized in plants in response to attack of diverse pathogens and insects (Jones and Dangl 2006). The cell surface-localized, pattern recognition receptors and cytoplasmic R proteins (mostly NB-LRR) are considered to build a two-tiered plant immune system. It has been considered that *R*-gene-mediated resistance can be easily overcome by pathogens that mutate and produce new effectors to counteract ETI (Jones and Dangl 2006), whereas PTI in general is supposed to confer broad-spectrum and durable resistance due to the conserved nature of pathogen-associated molecular patterns (Lacombe et al. 2010). Three BPH resistance genes (*Bph14*, *Bph18* and *Bph26*) that encode for cytoplasmic R proteins (CC-NBS-LRR) are supposed to induce ETI by recognizing the effectors resulting from insect feeding. These evidences provide interesting similarities between BPH and plant pathogens. It also suggests that rice *R* proteins may interact with BPH effectors in a gene-for-gene manner, and there are BPH *avr* (avirulence) genes for each BPH *R* gene in rice. On the other hand, lectin receptor kinase protein encoded in *Bph3*-mediated resistance has been suggested to function as extracellular ATP receptor or potential cell surface receptors for BPH-derived elicitors and can initiate PTI response (Liu et al. 2014).

In addition, plant defence responses to phloem-feeding insects that produce little injury to plants and perceived as pathogens involve the activation of salicylic acid (SA)-dependent and jasmonic acid (JA)-/ethylene-dependent signalling pathway (Walling et al. 2000). In *Bph14*-mediated insect resistance, genes involved in the SA synthesis pathway were found to be highly activated, whereas no difference was observed in the expression level of JA synthesis-related genes (Du et al. 2009). In case of *bph29*, upregulation *of* SA synthesis-related genes and downregulation of JA-dependent genes were observed by BPH infestation (Wang et al. 2015). In *Bph26*-mediated resistance, strong induction of both SA and JA synthesis-related genes with BPH infestation suggest that *BPH26* may activate JA- and SA-dependent resistance pathway. In *BPH18*, no significant difference was observed in the expression level of both the pathway-related genes (Ji et al. 2016). Based on molecular analysis of cloned genes, it appears that there is considerable similarity in the plant response to BPH infestation and pathogen attack. Further studies are needed on the frontiers of genomics research to understand molecular interaction between the host and pests and develop insect-resistant varieties.

4.5 Biochemical Mechanism of Resistance

The raised levels of biochemicals, phenolic acids and enzymes after planthopper infestation may play a prominent role in plant defence against planthoppers. Planthoppers first examine the plant surface for receiving chemical cues so as to find plants suitable for egg laying, settling or feeding (Woodhead and Chapman 1986). Female adults of BPH choose to sit on the plants treated with jasmonic acid (JA). The parasitism by parasitoid *Anagrus nilaparvatae* Pang et Wang was enhanced twice on JA-treated plants than on untreated control plants. JA application elevated the release of volatiles, namely, aldehydes, alcohols, monoterpenes, sesquiterpenes, methyl salicylate and n-heptadecane on treated plants. This shows that *A. nilaparvatae* utilized the plant-induced cues to locate BPH after JA treatment (Lou et al. 2005). In planthoppers, yeast-like endosymbionts (YLS) live intracellularly in the fat body cells (Chen et al. 2011). The presence of YLS in planthoppers helps them to use scarce nutrients so that they can affix the unfair composition of amino acids in plant phloem sap. The absence of YLS in planthoppers caused lower total protein concentrations, higher levels of nonlimiting free amino acids such as glutamine and aspartate and lower levels of leucine, an essential amino acid (Wilkinson and Ishikawa 2001). Many genes for BPH resistance are reported, but it is unknown that how these different genes are linked to biochemical products or pathways. This can also provide the way by which BPH adapt to resistant lines. If this information is made available, then scientist can select reliable plants based on phloem chemistry rather than assessing nymphal feeding and other tests.

The secondary and related compounds in rice plants played an important role in the defence against planthopper attack. The elevated ratio of longer to shorter carbon-chain substances and presence of shorter chain hydrocarbons on the rice surface served as barriers (Woodhead and Chapman 1986; Woodhead and Padgham 1988). Woodhead and Padgham (1988) distilled epicuticular waxes from IR22, IR46 and IR62 and observed feeding of planthoppers by managing plants by changing exogenous wax applications on different varieties. They observed an elevated ratio of longer to shorter carbon-chain compounds in IR46 and the presence of shorter chain hydrocarbons in IR22 which decided the planthopper feeding responses. Recently, Zhang et al. (2015) reported comparative transcriptional profiling from resistant and susceptible rice plants during early infestation by SBPH. They reported that with level of resistance in SBPH-resistant rice plants, genes involved in the very long-chain fatty acid biosynthesis were upregulated. These fatty acids are of 20 to 36 carbons and are required by plants for plant cuticle biosynthesis (Samuels et al. 2008; Shepherd and Wynne 2006). These very long-chain fatty acid production pathways have been united with plant defence against hoppers (Raffaele et al. 2009). These plant volatiles may be useful in studying the insect community make-up. Volatile organic compounds are released when insect attacks a plant, and these plays a major role in tritrophic interaction between plant, herbivore and parasitoids (Allmann and Baldwin 2010). The amount of biochemicals after insect infestation such as proteins, phenols and carbohydrates has been elevated with the enzyme activities of peroxidase, catalase and chitinase, whereas after hopper

infestation a reduced activity of superoxide dismutase, phenylalanine ammonia lyase and β-1,3-glucanase was observed. The phenolic acids, namely, vanillic acid, syringic acid, cinnamic acid and p-coumaric acids, were recorded in the plants after BPH infestation (Rani and Jyothsna 2010).

Against planthoppers, ovicidal resistance in japonica cultivars is a natural defence mechanism (Suzuki et al. 1996; Yamasaki et al. 1999; Yamasaki et al. 2000). It is highest at the maximum tillering stage. After oviposition by WBPH, there is formation of a watery lesion of benzyl benzoate around eggs at concentrations above 6.4 ppm at 25 °C. This concentration of benzyl benzoate causes up to 80% egg mortality, while non-watery lesions cause only 12% mortality (Suzuki et al. 1996). This solution of benzyl benzoate was present in the watery lesions of some japonica rice varieties and not in the intact rice plant tissues or in non-watery oviposition sites (Seino et al. 1996). The biosynthesis pathway of benzyl benzoate is upregulated due to WBPH oviposition. The solution may cause direct egg mortality or may affect WBPH symbionts; without symbionts eggs can't complete embryonic development (Seino et al. 1996). However, in case of BPH eggs, the ovicidal response was low, and the ranking of watery lesion can be associated with BPH egg mortality (Kiyonaga et al. 1997; Yamasaki et al. 2000). The chitin synthase (CHS) is required for chitin formation in insect cuticles and other tissues. These genes from BPH and SBPH were cloned, and reports say that BPH lacks *CHS2* and *CHS1* gene which can be efficient target genes for RNAi-based BPH control strategy (Wang et al. 2012).

4.6 Resistance to White-Backed Planthopper (WBPH)

Based on classical genetic analysis and mapping studies, 18 genes (*Wbphl*, *Wbph2*, *Wbph3*, *wbph4*, *Wbph5*, *wbph6 Wbph7(t)*, *Wbph8(t)*, *wbph9(t)*, *wbph10(t)*, *wbph11(t)*, *Wbph12(t)*, *WbphM1*, *WbphM2*, *wbphAR*, *WbphN*, *WbphO*, *Ovc)* have been identified for WBPH resistance (Fuzita et al. 2013; Ramesh et al. 2014). Classical genetic analysis has revealed several genes: *Wbph1* in Nagina 22, *Wbph2* in ARC 10239, *Wbph3* in ADR 52, *wbph4* in Podiwi-A8, *Wbph5* in N'diang Marie, *Wbph6* in Guiyigu and *Wbph7(t)* and *Wbph8(t)* in B5; an introgressed line from *O. officinalis* has been identified and designated. Sidhu et al. (2005) studied the inheritance of resistance in five cultivars. The resistance in Mudgo was governed by two independently inherited dominant genes and tentatively designated as *WbphM1 and WbphM2* from Mudgo. A recessive gene, *wbphAR*, conferred resistance in ARC11367, whereas resistance in NCS2041 and MO1 was conditioned by a dominant gene tentatively designated as *WbphN and WbphO*, respectively. Padmarathi et al. (2007) reported that recessive gene in ARC5984 and ARC6650 has similar allele to Podiwi (*wbph4*). He (2007) mapped *Wbph(t)* and *Wbph8(t)* on chromosome 4. Yamasaki et al. (2003) identified one major gene, *ovc*, and four QTLs for ovicidal response (formation of watery lesions and production of ovicidal substance,

benzyl benzoate) to WBPH in 'Asominori'. Recently, four major effect QTLs designated as *wbph9(t)*, *wbph10(t)*, *wbph11(t) and Wbph12(t)* have been mapped in Sinna Sivappu, a Sri Lankan landrace that showed resistance to both BPH and WBPH (Ramesh et al. 2014). The inheritance pattern in 255 $F_{2:3}$ families suggested single recessive gene of seedling damage score, two complementary recessive genes for antixenosis and single dominant gene for days to wilt. In addition to major WBPH-resistant genes, more than 70 QTLs associated with different components of WBPH resistance have been identified (Fujita et al. 2013) by analysing various rice experimental populations, including recombinant inbred line (RIL) populations (Yamasaki et al. 1999, 2003), doubled haploid (DH) populations (Geethanjali et al. 2009; Sogawa et al. 2009), introgression lines derived from wild rice species as the resistance donors (Tan et al. 2004) and backcross inbred lines (BILs) derived from interspecific crosses with wild rice species (Chen et al. 2010). WBPH and BPH often occur at the same time, though in varying proportions across time and space. It is thus imperative that breeding for resistance should target both hoppers (Bentur and Viraktamath 2008).

4.7 Resistance to Green Rice Leafhopper (GRH)

Green rice leafhopper (GRH) is predominant in the temperate regions of East Asia. At least six genes for resistance to GRH have been identified and mapped on chromosomes 3, 4, 5, 6, 8 and 11, respectively (Yasui et al. 2007). Tamura et al. (1999, 2004) identified two genes for resistance to GRH: *Grh1* on chromosome 5 in cultivar 'Pe-bi-hun' and *Grh6* on chromosome 4 in the Surinam cultivar SML17. Likewise, two genes, *Grh2* on chromosome 11 and *Grh4* on chromosome 3, were mapped in cultivars 'Lepe dumai' and 'DV85' in independent studies (Fukuta et al.1998; Yazawa et al. 1998; Kadowaki et al. 2003). The *Grh3* was located on chromosome 6 by Saka et al. (2006) in cultivar 'Rantaj emas 2' to a 4.6-Mb interval between markers C288B and C133A. This locus has been fine mapped further to 435-kb region between SSR markers RM20142 and RM20145 (Hur et al. 2015). Hirae et al. (2007) reported that both the cultivars 'Kanto-PL6' and 'Aichi80' carry *Grh3* based on virulent biotypes of GRH. The *Grh5* was identified from *Oryza rufipogon* acc. W1962 and mapped on chromosome 8 L using tightly linked simple sequence repeat (SSR) markers (Fujita et al. 2006). MAS has been used to develop near-isogenic lines (NILs) carrying *Grhl*, *Grh2*, *Grh4*, *Grh5* and *Grh6* in the background of japonica cultivar Taichung 65. Further pyramided lines carrying GRH resistance genes (*Grh2* and *Grh6*, *Grh4* and *Grh6*) developed in the background of Taichung 65 using NILs indicated significantly increased level of resistance to GRH (Fujita et al. 2010). Pyramided lines with different gene combinations (*Grh2* + *Grh4*), (*Grh2* + *Grh6*) and (*Grh4* + *Grh6*) showed higher nymph mortality than that of the NILs (Yasui et al. 2007).

4.8 Resistance to Zigzag Leafhopper (ZLH)

The zigzag leafhopper (ZLH) is prevalent in the tropical and subtropical regions of Asia. Heinrichs et al. (1985) reported donors (Rathu Heenati, Ptb21, Ptb33) for resistance to ZLH. Angeles et al. (1986) studied the resistance in cultivars Rathu Heenati, Ptb21 and Ptb33 to ZLH, WBHP, BPH and GLH. Based on resistance studies, single dominant gene in each donor was found to provide resistance to ZLH. These were designated as *Zlh1* in Rathu Heenati, *Zlh2* in Ptb21 and *Zlh3* in Ptb33.

4.9 Marker-Assisted Selection and Pyramiding of Genes/QTLs for Resistance to Hoppers

The field of durable resistance was once dominated by discussions on horizontal versus vertical resistance, however broadened substantially with understanding of various host pathogen studies. With the identification of number of genes/QTLs, MAS and gene pyramiding have emerged as an important approach for attaining the durable resistance. In a detailed study to examine the utility of resistant varieties and their associated resistant genes to BPH, Horgan et al. (2015) reported that only a few of the currently available BPH resistance genes showed durable resistance in monogenic rice lines carrying single resistant gene, whereas the traditional varieties known to carry two or more genes showed higher level of resistance indicating that pyramiding of two or more genes with strong to weak resistance could enhance the level of resistance. Classical breeding has successfully supported the development of a number of improved BPH-resistant genotypes. To further improve resistance of rice varieties, it could be emphasized the importance of combining all favourable and complementary physiological traits in a variety, rather than considering BPH resistance as a single trait. Pyramiding of different genes for resistance to bacterial blight (BB) is the model example on enhancing the level and spectrum of resistance to various pathotypes (Huang et al. 1997; Sanchez et al. 2000; Singh et al. 2001). As many as five genes for resistance to BB have been pyramided and combined, and a number of BB resistant varieties have been released in rice-growing countries including India, China, the Philippines, Thailand and Indonesia.

Identification of a tightly linked DNA marker is a prerequisite for marker-assisted selection and pyramiding of two or more genes in a single cultivar. The various institutes are directed towards marker-assisted backcrossing to introgress the favourable alleles for BPH resistance into elite rice lines, and to date many resistant genes have been tested for their linkage with markers (Sun et al. 2005; Jena et al. 2006; Fuzita et al. 2013; Brar et al. 2015). With the advances in molecular markers, a number of the BPH genes (*Bph1*, *bph2*, *Bph6*, *Bph7*, *Bph13*, *Bph15*, *Bph19*, *Bph20*, *Bph21*, *Bph25*, *Bph27* and *Bph28*) have been fine mapped (Table 4.1), and few genes (Table 4.2) have been cloned, which are suitable for marker-assisted selection for BPH resistance, albeit with varying levels of BPH virulence in different parts of Asia. Of the various resistant sources identified, the varieties Rathu Heenati, Ptb33,

MO1, IR71033-121-15, Balamawee and ADR52 in South Asia and Swarnalata in South East Asia have been indicated as potential donors for MAS, since these contain multiple genes for hoppers and most of them have been cloned and tagged with tightly linked molecular markers (Horgan et al. 2015). In an early effort to pyramid two BPH-resistant genes, *Bph1* and *Bph2* in background of a japonica line indicated that resistance level of the pyramided line was equivalent to that of the line carrying *Bph1* alone, but showed a higher level of resistance than the line carrying *Bph2* (Sharma et al. 2004). Later, a number of parental lines used in hybrid rice breeding in China that are pyramided with *Bph14* and *Bph15* through MAS showed higher level of BPH resistance than the lines carrying single gene (Li et al. 2006). Fujita et al. (2009) have evaluated the resistance of NILs (near-isogenic lines) and PYLs (pyramided lines) with *Bph25* and *Bph26* against BPH strains from East Asia. Their results indicated that a PYL containing both genes is resistance against several East Asian BPH strains. Furthermore, Myint et al. (2012) demonstrated that a PYL containing both genes could be effective despite the apparent low effectiveness of each gene alone in *Bph25* and *Bph26* monogenic NILs. Hu et al. (2012) evaluated a pyramided line carrying two resistance genes, *Bph14* and *Bph15*, for seedling damage, antixenosis and honeydew production and found to be more resistant than either the *Bph14*-NIL or the *Bph15*-NIL. Likewise pyramided line for *Bph12* and *Bph6* gene had lower nymph settling and survival and slower population growth and caused less damage compared to the monogenic lines (Qiu et al. 2012). Furthermore, MAS was used to pyramid three BPH resistance genes, *Bph14*, *Bph15* and *Bph18* in the background of elite restorer line, 9311 and its hybrids. The results showed that the *Bph15* have higher level of resistance than *Bph14* and *Bph18*, whereas *Bph14* was found slightly higher or similar as *Bph18* in resistance response against BPH (Hu et al. 2012). Recently, Liu et al. (2016) pyramided two dominant genes, *Bph3* and *Bph27*, using marker-assisted backcross programme, and the pyramided lines showed enhanced level of resistance than single gene.

The development of resistance for all other planthopper and leafhopper species using molecular breeding approaches is still severely limited by a scarcity of genetic information and availability of suitable markers. Six genes seem to be appropriate for MAS for resistance to GRH. Fujita et al. (2006) demonstrated that the pyramided line of *Grh2* and *Grh4* showed higher level of antibiosis than the lines carrying single resistance gene. However, three pyramided lines carrying different combinations of GRH resistance genes (*Grh2* and *Grh6*, *Grh4* and *Grh6* and *Grh5* and *qGRH4*) showed epistasis (Fujita et al. 2010).

For getting broad-spectrum and durable resistance, choice of gene combination for pyramiding is also very important. Genes in combination will be more durable, if these differ with respect to their molecular mechanism responsible for resistance to pathogen or insects. For example, a combination of *xa5* + *xa13* + *Xa21* is more successful and durable, because all the three genes provide resistance to bacterial blight with different molecular mechanism. Although pyramided lines can enhance resistance to hoppers, care should be taken in case of pyramided lines, as it is still unknown whether pyramided lines could lead to a more rapid adaptation of hoppers if the genes were sequentially deployed in a similar background variety. Tests of the

comparative durability of pyramided hopper-resistant rice lines in a similar genetic background have not been conducted, and there are many cases of naturally pyramided rice varieties against which wild hopper populations have already adapted.

4.10 Transgenic Approaches for Resistance to Hoppers

Transgenic rice was produced as early as 1988, since then a battery of genes have been introduced for various agronomic traits. Transgenic technology is now well established, and several varieties have been released for commercial cultivation. Transgenic crops occupy more than 180 million hectares globally (James 2015). In rice, *Bt* genes have been transferred into several genotypes which have shown resistance to stem borers; however, so far no commercial release has been made. Only a limited information is available on transgenic rice resistant to hoppers. Transgenic technology can be used as an approach for deployment of exotic resistance genes into the leading rice cultivars. These exotic resistance genes are shown to produce entomo-toxic effect in plants that affect the insect survival. A number of candidate genes to control hopper populations in rice have been reported. Of these mannose-binding protein encoding genes, 'snowdrop lectin' (*Galanthus nivalis* agglutinin, GNA) and 'garlic leaf lectin' (*Allium sativum* agglutinin from leaf, ASAL) have been demonstrated to control hoppers in rice in various studies (Powell et al. 1995; Majumder et al. 2004). Plant lectins have been reported to show severe effects on fecundity, growth and development of insects. The lectins produced by plants belonging to the family Amaryllidaceae show low or no toxicity towards higher animals, but are toxic to insects. Among the Amaryllidaceae lectins, the lectin from snowdrop, *Galanthus nivalis* L. agglutinin (GNA), is proved to be non-toxic to mammals and toxic to insects. The lectins are probably involved in the binding to receptors present on the midgut epithelial cells, thereby causing the insecticidal effect (Powell et al. 1998). The bound lectins inhibit absorption of nutrients or disrupt endocytosis of midgut cell lectins and other toxic metabolites (Eisemann et al. 1994). Expression of *GNA* or *ASAL* in rice plants has been shown to confer substantial resistance to BPH, WBPH and GRH in terms of increased insect mortality, retarded development and decreased fecundity (Rao et al. 1998; Sudhakar et al. 1998; Foissac et al. 2000; Tang et al. 2001; Sun et al. 2002; Nagadhara et al. 2003, 2004; Saha et al. 2006; Yarashi et al. 2008). Similarly, transgenic plants generated by introduction of *Dioscorea batatas* tuber lectin1 gene under the control of phloem-specific promoter of rice sucrose synthase-1 gene showed up to 30% reduced survival rate of BPH as compared to wild type (Yoshimura et al. 2012). Bala et al. (2013) reported that interaction of ASAL with NADH-quinone oxidoreductase (NQO), a key player in electron transport chain, may result in toxicity and loss of fecundity during BPH feeding on transgenic rice plants expressing ASAL. These studies indicate 'ASAL' as a prominent candidate gene against BPH attack.

RNAi (RNA interference) is an important approach for meeting the challenges imposed by crop insects with careful secretion of key enzymes/proteins (Gordon and Waterhouse 2007; Price and Gatehouse 2008; Rao Kola et al. 2015). Recently,

the method has shown another way to generate resistance against various insects in a number of studies (Aggarwal et al. 2012). The majority of studies on RNAi for insect control have targeted enzymes/proteins of the insect midgut as it is considered as the most effective target for the gene silencing. When three dsRNA targeting different sites within a gene encoding vascular ATP synthase subunit E (*V-ATPase-E*) were orally delivered into BPH insect, it resulted in decreased expression of the target gene (Li et al. 2011). Likewise, transgenic plants were generated using three genes, the hexose transporter gene *NlHT1*, the carboxypeptidase gene *Nlcar* and the trypsin-like serine protease gene *Nltry* by introducing dsRNA that expressed in the midgut of the BPH (Zha et al. 2011). When BPH feeds on transgenic plants, the expression of BPH genes were reduced by 40–70% in the third instar nymphs by day 4; however, no lethal phenotypic effect was observed.

Plants interact with different insects by releasing complex blend of volatile compounds. Rice plant induces the production of one of the most abundant volatile compound 'S-linalool' by feeding of BPH, whereas another constitutive produced volatile compound in rice, (E)-beta-caryophyllenes, is induced by feeding of chewing herbivores, but not by sucking pests like BPH. Both S-linalool and (E)-beta-caryophyllene have been reported to attract BPH parasitoid, *Anagrus nilaparvatae*, in the laboratory (Cheng et al. 2007). By silencing the two genes responsible for production of these volatile compounds, it was observed that inducible S-linalool attracted parasitoid and chewing herbivores but repel BPH. However, the constitutively produced (E)-beta-caryophyllene attracts both parasitoid and BPH resulting in an increased herbivore load. Therefore, silencing either signal (compound) resulted in the assemblage of specific insect community (Xiao et al. 2012).

The identification of suitable candidate genes to be used as targets is the primary requirement to use this technology. On the other hand, RNAi pathway in insects is yet not clear as compared to *Drosophila* (Burand and Hunter 2013). Therefore, RNAi pathway in the planthopper needs to be elucidated in order to efficiently use this technology to generate resistance against hoppers.

4.11 Future Priorities

Planthoppers pose a major challenge to rice production and sustainability particularly in the context of global climatic changes. However, advances in molecular marker technology and cutting-edge science of genomics offer new opportunities to meet the challenges of developing pest-resistant varieties. Some of the priorities to breed varieties resistant to hoppers are given below:

- Identification of resistant sources/donors involving diverse germplasm-primitive cultivars, landraces, traditional varieties and wild species of *Oryza*.
- Widening gene pool of rice through transfer of such genes governing resistance.
- Identify novel genes/QTLs governing resistance to hoppers preferably with different modes of resistance.

- Accelerate breeding and develop varieties with enhanced and wide spectrum of resistance, priority should be given on MAS and pyramiding of genes/QTL to different biotypes/insect populations, and combine multiple resistance to BPH, GLH and WBPH. Use gene-based MAS wherever possible.
- Develop high-throughput genotyping using new sequencing and molecular marker approaches and phenomics/phenotyping protocols to accelerate breeding efforts.
- Allele mining is emphasized to identify and incorporate desirable alleles for resistance.
- Develop isogenic lines for resistance to BPH, WBPH and GLH, and test such lines in different areas, regions and countries to deploy target genes for resistance in respective areas of rice cultivation.
- Explore transgenic technology including RNAi and gene editing as a long-term approach in developing germplasm resistant to hoppers.

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Distinguishing Proof and Utilization of Resistance of Insect Pests in Grain Legumes: Progress and Limitations

5

H.C. Sharma, Jagdish Jaba, and Sumit Vashisth

Abstract

Major food legumes including chickpea, pigeon pea, cowpea, field pea, lentil, faba bean, black gram, green gram, and *Phaseolus* beans play a vital role in food, nutritional security, and sustainable crop production. Several insect pests damage grain legumes, of which *Helicoverpa armigera*; *Maruca vitrata*; *Etiella zinckenella*; *Spodoptera litura* and *S. exigua; Melanagromyza obtusa*; *Ophiomyia phaseoli*; *Aphis craccivora* and *Bemisia tabaci*; *Empoasca* spp., *Megalurothrips dorsalis*, and *Caliothrips indicus*; *Mylabris* spp.; and *Callosobruchus chinensis* crusade extensive losses. Appreciable progress has been made in formulating techniques to evaluate germplasm, mapping populations, and genetically modified crops for resistance to insect pests under field and greenhouse conditions. No-choice and dual-choice cage screening techniques, detached leaf assay, and diet incorporation assays have been standardized to screen for resistance to major insect pests in grain legumes. However, some of these techniques cannot be used to screen against stem flies, pod fly, leafhoppers, thrips, and aphids. There is a need to develop methods for mass multiplication of aforesaid insects to undertake precise phenotyping for resistance to these insects. There is a necessity to identify lines with different resistance mechanisms/components of resistance for gene pyramiding to explicate cultivars with the stable source of resistance to insect pests. Prominent levels of resistance to the pod borers have been found in the wild accessions of chickpea,

H.C. Sharma (✉)
Dr. Y. S. Parmar University of Horticulture and Forestry, Nauni 173230, India

International Crops Research Institute for Semi-Arid Tropics (ICRISAT), Patancheru 502324, India
e-mail: hcsharma@ypsuniversity.ac.in

J. Jaba • S. Vashisth
International Crops Research Institute for Semi-Arid Tropics (ICRISAT), Patancheru 502324, India
e-mail: jaba.jagdish@gmail.com; sumitvashisth_hpau@yahoo.co.in

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pigeon pea, and cowpea, which can be exploited to introgress genes to heighten the levels and diversify the basis of resistance to insect pests to build host plant resistance a viable component of pest management in grain legumes for sustainable crop production.

Keywords
Grain legumes • Host plant resistance • Pod borers • Wide hybridization • Pest management • Wild relatives

5.1 Introduction

India is the highest producer and consumer of pulses in the world. Chickpea or Bengal gram (*Cicer arietinum*), pigeon pea or red gram or tur dal (*Cajanus cajan*), lentil (*Lens culinaris*), urdbean or black gram (*Vigna mungo*), mung bean or green gram (*Vigna radiata*), lablab bean (*Lablab purpureus*), moth bean (*Vigna aconitifolia*), horse gram (*Dolichos uniflorus*), pea (*Pisum sativum*), grass pea or khesari (*Lathyrus sativus*), cowpea (*Vigna unguiculata*), and broad bean or faba bean (*Vicia faba*) are some of the most important pulses used as food worldwide. Of these, chickpea, pigeon pea, mung bean, urdbean, and lentil are the major pulses grown in India. Food legumes are cultivated globally on an area of 70 million hectares with a production which is over 78 million tons and an average productivity of 846 kg ha-[1] (FAO 2012). In India, the overall pulse production for the year 2015–2016 was 17.33mt on an area of 24.89 million ha, with an average productivity of 758 kg ha^{-1}(Anonymous 2016). Chickpea is the most predominant pulse crop in India, accounting for 40% contribution of the total pulse production, followed by pigeon pea (18–20%), mung bean (11%), urdbean (10–12%), lentil (8–9%), and other legumes (20%) (Anonymous 2011). Madhya Pradesh (20.3%), Maharashtra (13.8%), Rajasthan (16.4), Uttar Pradesh (9.5%), Karnataka (9.3%), Andhra Pradesh (7.9%), Chhattisgarh (3.8%), Bihar (2.6%), and Tamil Nadu (2.9%) are the major pulse-producing states in India (Anonymous 2009). Food/grain legumes are the primary source of dietary protein and are an integral part of daily diet in several forms worldwide. Pulses supply significant nutritional and health benefits and are known to reduce several noncommunicable diseases such as colon cancer and cardiovascular diseases (Jukanti et al. 2012).

Several biotic and abiotic factors dissemble the production and productivity of grain legumes worldwide, of which insect pests are the predominant. Over the past five decades, significant progress has been made in developing improved cultivars and crop management practices, but there has been little increase in productivity. Grains are damaged by more than 150 species of insect pests, under unprotected conditions and in storage (Clement et al. 2000, Sharma and Upadhyaya 2016). Amid the many insect pests damaging food/grain legumes, the pod borers, *Helicoverpa armigera* (Hubner) is the most economically important pest of grain legumes in Asia, Africa, and Australia (Sharma 2001). The spotted pod borer,

Maruca vitrata (Geyer), is another major pest of cowpea and pigeon pea (Jackai and Adalla 1997; Sharma 1998), but it also damages other food/grain legumes, except chickpea and lentil (Sharma et al. 1999). The pod fly, *Melanagromyza obtusa* Malloch, and pod wasp, *Tanaostigmodes cajaninae* La Salle, both cause an extensive damage to pigeon pea in India. The leaf miner, *Liriomyza cicerina* (Rondani), is a significant pest of chickpea in West Asia and North Africa (Weigand et al. 1994). Pea pod borer, *Etiella zinckenella* Triet, is an important pest of pigeon pea, field pea, and lentil, while the aphid, *Aphis craccivora* Koch, infests all the food legumes, but it is a major pest of cowpea, field pea, faba bean, and *Phaseolus* beans. *Aphis fabae* (Scop.) is a major pest of faba bean and *Phaseolus* beans, and *Acyrthosiphon pisum* Harris is an important pest of field pea worldwide.

The whitefly, *Bemisia tabaci* Genn, infests all the crops, except chickpea crop, but is an important pest of *Phaseolus* spp. like black gram, and green gram and the defoliators, *Spodoptera litura* (Fab.) in Asia and *S. exigua* Hubner in Asia and North America, are occasional pests. Bihar hairy caterpillar, *Spilosoma obliqua* Walker, is a pest of green gram and black gram in North India, while the red hairy caterpillars, *Amsacta* spp., damage the rainy season pulses in south central India. Among sap-sucking pests, leafhoppers, *Empoasca* spp., infest most of the food/grain legumes but cause the most economic damage in black gram, green gram, and *Phaseolus* beans, and in the case of pod-sucking bugs, *Clavigralla tomentosicollis* Stal., *C. gibbosa* Spin., *Nezara viridula* L., and *Bagrada hilaris* Burm. are occasional pests, but extensive damage has been recorded in cowpea in Africa caused by *C. tomentosicollis* and in pigeon pea in India caused by *C. gibbosa.* Under storage conditions, bruchids, *Callosobruchus chinensis* L. and *C. maculatus* Fab, crusade extensive losses in storage in all the food legumes worldwide, and stink bugs (*Nezara viridula* (L.)) are the major damaging pest in soybean in Brazil (Borges et al. 2011). The pea weevil, *Bruchus pisorum* L., is an important pest of field pea and most vulnerable to attack major production areas (Clement and Quisenberry 1999; Mendesil et al. 2016).

5.2 Extent of Losses Due to Insect Pests in Grain Legumes

In India, insect pests lead to an approximate economic loss in yield of 15.00% of worth $2285.29 million (Dhaliwal et al. 2015). Pod borer, *H. armigera* – the single largest yield shrinking factor in food legumes – causes an estimated loss of US$ 317 million in pigeon pea and $328 million in chickpea (ICRISAT 1992). Worldwide, it causes an estimated loss of over $2 billion annually, despite over $1 billion value of insecticides used to control *H.armigera* (Sharma 2005). In general, the estimates of yield losses vary from 50 to 100% in the tropics and 5–10% in the temperate regions (van Emden et al. 1988). Another pod borer, *M. vitrata*, causes loss to be US$ 30 million annually (Saxena et al. 2002). In pigeon pea, yield losses due to pod borer 25–70%, pod fly 10–50%, *Maruca* 5–25%, and pod bug 10–30% have been reported (Sharma et al. 2010). Soybean aphid (*A. glycines*) can induce up to 58% yield losses in soybean crop (Wang et al. 1994) and annually $2.4 billion estimated

losses in yield (Song et al. 2006; Tilmon et al. 2011). Legume flower thrips (LFT), *M. sjostedti* Trybom, and cowpea *V. unguiculata* in tropical Africa cause yield losses ranging from 20% to 100% (Karungi et al. 2000). The avoidable losses in grain/food legumes at current production levels of 60.45 million tonnes would be nearly 18.14 million tonnes (at an average loss of 30%), worth at nearly US$ 10 billion (Sharma et al. 2008).

5.3 Resistance Screening Techniques

There are difficulties in screening and choosing for resistance to some important key pests, because of the lack of uniform insect infestations across locations and seasons, and it's also difficult to rear and multiply some of the insect species on artificial diets for artificial infestation. In pigeon pea and chickpea, the screening done by infesting crop plants with ten first-instar larvae and covering with a cloth bag placed all around a wire-framed cage (40 cm in diameter, 45 cm long) can be used to screen for resistance to the pod borer (Sharma 1998), using no-choice, dual-choice, or multi-choice assays, and plants may be evaluated for insect damage after 15 days of infestation, and this technique used to confirm the resistance under field conditions and find out resistance levels in various cultivars. Most of legume crops under laboratory condition may be screened by using detached leaf bioassay techniques (Sharma et al. 2001b, Sharma 2016) and by adjusting planting date, augmenting insect populations under field conditions, caging the crop plants with insects in the field, grouping of test material according to maturity and height, and tagging the inflorescences at flowering stage (Sharma et al. 2005a). In cowpea manifestation of tolerance to *Maruca* is affected by different phenology stages of crop (Dabrowski et al. 1983). Plants with five to seven shoots are most desirable to screening for resistance prior to flowering. Taking five eggs per plant, it was easy to differentiate among the resistant and susceptible lines and can be used as selection criteria (Jackai 1982, Oghiakhe et al. 1992a, b). For free and no-choice techniques need to be affirmed under field conditions for screening against major insect pest of legume crops (Echendu and Akingbohungbe 1989). The screening technique for whitefly, *B. tabaci*, in black gram genotypes may be based on whitefly resistance index (WRI) scores, symptoms, kind, and intensity of leaf injury categorized grades (I–V) for developing tolerant cultivars (Taggar et al. 2012).

5.4 Identification and Utilization of Resistance to Insects Pests

Significant effort has been made in recognition of sources of resistance to insect pests, but the orgins of resistance have not been utilized extensively in the crop breeding programs (Clement et al. 1994; Sharma and Ortiz 2002). Varieties with having improved yield factor are more prone to be susceptible to insect pests than the landraces (Lale and Kolo 1998). Lack of strategies for positive selection for

resistance to insect pests may result in more susceptibility in elite cultivars as compared to the landraces (Shaheen et al. 2006). Some of legume cultivars with resistance/tolerance to insect pests have been identified in pigeon pea, chickpea, cowpea, black gram, green gram, and field pea (Table 5.1). However, the levels of resistance/tolerance to pod borers are low to moderate but are quite more effective when deployed in combination with newer synthetic insecticides or natural plant products like neem seed kernel extract (NSKE) (Sharma and Pampapathy 2004). Cultivars with multiple resistance to insect pests and diseases will be in greater call for in future because of the needy concerns assorted with chemical control and environmental pollution and the changes in relative importance and severity of damage due to climate change. There is require to break the linkage amid insect pest resistance and susceptibility to diseases; e.g., in case of chickpea and pigeon pea, *H. armigera*-resistant cultivars are susceptible to wilt diseases (Sharma et al. 2005a).

Screening of various germplasms of chickpea and pigeon pea at ICRISAT (over 15,000 accessions for each crop) has led for identification of a few accessions which shows moderate levels of resistance to *H. armigera* (Lateef 1985; Lateef and Pimbert 1990). Based on wide testing of pigeon pea lines, such as PPE 45-2, BDN 2, ICPL 4, Bori, and T 21, ICPL 269 and ICPL 88039, early maturity; ICPL 332, ICPL 84060, LRG 41, and ICPL 187-1, medium maturity; and ICP 7035, medium-long maturity and vegetable type were ascertained to be resistant/tolerant to *H. armigera* (Sharma 2009; Srivastava and Joshi 2011). Of these, ICPL 88039 has been widely tested in the Indo-Gangetic Plains in North India, and it found to be suited for rice-wheat cropping system. ICPL 332WR was found to be promising in Andhra Pradesh, while ICP 7035 is opted by the farmers as a vegetable type. The cultivars GP 75, GP 118, GP 233, and GP 253 were confounded to be resistant to *M. obtusa*, evoking that resistance/tolerance to pod fly is not linked to maturity period and growth type of the genotype/cultivar (Moudgal et al. 2008). The cultivar ICPL 88034 and MPG 679 were showing low *Maruca* damage (10–25%) (Saxena et al. 1996).

The breeding efforts in chickpea have developed many *Helicoverpa*-resistant varieties such as C 235, Anupam, Pant G 114, ICCV 10, JG 74, Dulia, Pusa 261, Vijay, Vishal, ICCV 7, ICCV 10, and ICCL 86103 and were released for cultivation in India (Sharma et al. 2005b). The accessions (ICC 506 EB, ICC 10619, ICC 10667, ICC 4935, ICC 10243, ICCV 95992, and ICC 10817) have been confounded for resistance to *H. armigera*. The cultivar ICC 12475 chickpea showed resistance to *S. exigua* (Shankar et al. 2012). However, progenies of interspecific cultivated chickpea and a wild relative (*C. reticulatum*) showed high levels of resistance to *S. exigua*. Two accessions of *C. cuneatum* (ILWC 40 and ILWC 187) and 10 accessions of *C. judaicum* with high grades of resistance while 18 lines of *C. judaicum* and 4 lines of *C. reticulatum* and *C. pinnatifidum* have been identified with resistance to leaf miner in chickpea (Singh and Weigand 1994) and germplasm lines, viz., ILC 3800, ILC 5901, and ILC 7738, were identified and registered as sources of resistance to *Liriomyza cicerina*. Accessions DCP 923, JG 315, BG 1003, and BG 372 showed promise against bruchids, and genotypes GL 88341, BG 360, and RSG 524 were identified as resistant sources against root-knot nematodes (*Meloidogyne incognita* and *M. javanica*) (Indian Institute of Pulses Research 2015).

Table 5.1 Identification and utilization of host plant resistance to insect pests in grain legumes in India

Crop	Genotypes	References
Pigeon pea	Pod borer, *Helicoverpa armigera* ICPL 332[a], PPE 45-2, ICPL 84060, BDN 2, ICPL 4, Bori, T 21, ICP 7035, and ICPL 88039, ICC 12475, ICC 12477, ICCL 87317, ICCV 95992, ICPL 98003, ICPL 187-1, LRG 41ICPL 269, ICP 7203-1, ICPL 84060, ICPL 87119, ICPL 332	Lateef and Pimbert (1990), Kalariya et al. (1998), Parsai (1996, 2005), Sunitha et al. (2008a, b), Sharma (2009), Srivastava and Joshi (2011), Kumari et al. (2010a)
	Legume pod borer, *Maruca vitrata*	Saxena et al. (1996)
	ICPL 88034 and MPG 679	
	Pod fly *Melanagromyza obtusa*	Lateef and Pimbert (1990) Moudgal et al. (2008)
	ICP 10531-E1, ICP 7941E1, ICP 7946-E1, and ICP 7176-5. GP 75, GP 118, GP 233, and GP 253	
Chickpea	**Pod borer, *Helicoverpa armigera***	Dixit (2015), Lateef and Sachan (1990), Bhagwat et al. (1995), Das and Kataria (1999), Deshmukh and Patil (1995), Shankar et al. (2012)
	ICC 506, ICC 09314, ICC 738008, ICC 09104, 09116, ICCL 86105, ICC 14364, ICCV 7[a], ICCV 10[a], Dulia[a], C 235[a], JG 79[a], BJ 256[a], JG11, ICCL86111, Vijay, and Vishal. ICC 10667, ICC 10619, ICC 4935, ICC 10243, ICCV 95992, and ICC 10817	
	Leaf miner, *Liriomyza cicerina*	Singh and Weigand (1994), Girija et al. (2008)
	ILC 380, ILC 5901, and ILC 7738	Shankar et al. (2012)
	Beet armyworm *Spodoptera exigua*	Indian Institute of Pulses Research (2015)
	ICC 12475	
	Bruchid	
	DCP 923, JG 315, BG 1003, BG 372	
	Root-knot nematode	Indian Institute of Pulses Research (2015)
	Meloidogyne incognita and *M. javanica*	
Black gram	**Pod borer, *Helicoverpa armigera***	Lal (1987)
	Kalai[a], 338-3, Krishna[a], and Co 3[a], 4[a], and 5[a]	Soundararajan et al. (2010), Ponnusamy et al. (2014)
	CBG 08-011 and PLU 54; UH 82-5, IC 8219 and SPS 143	
	Jassid, *Empoasca kerri*	
	Sinkheda 1[a], Krishna[a], H 70-3, and UPB 1[a]	Dawoodi et al. (2010)
	Stem fly, *Ophiomyia phaseoli*	
	Killikullam[a], 338/3, P 58, Co 4[a], and Co 5[a]	
	Pink Pod borer *Cydia ptychora*	
	SKNU-03-03	

(continued)

Table 5.1 (continued)

Crop	Genotypes	References
Green gram	**Pod borer, *Maruca testulalis***	Lakshminarayan et al. (2008)
	J1, LM 11, P 526, and P 336	
	ML 337, ML 5, MH 85-61, and ML 325	Soundararajan et al. (2010)
	CGG 08-007 and CGG 08-028	
	Stem fly, *Ophiomyia centrosematis* Co 3	Devasthali and Joshi (1994)
	TAM-20, PDM-84-143 and Pusa-105 against *A. craccivora*, *A. kerri* (*Empoasca kerri*) and *M. undecimpustulatus*	
	Bruchids	Somta et al. (2008)
	V1128, V2817	
Field pea	**Pod borer, *Etiella zinkenella***	Lal (1987)
	EC 33860, Bonville[a], T 6113[a], PS 410, 2S 21, and 172 M.	Teshome et al. (2015)
	32,454, 235,002	
	Leaf miner, *Chromatomyia horticola*	
	P 402, PS 41-6, T 6113, PS 40, KMPR 9, P 402, and P 200	
Cowpea	**Pod borer, *Maruca vitrata***	Singh (1978), Lal (1987)
	TVu 946, VITA 4, VITA 5, Ife Brown, and Banswara[a]	Chanchal and Singh (2014)
	EC 394828, ET 116932, TVNu 946, Kashi Shyamal, Arka Suman, and Arka	Jackai (1981)
	Sumurudhi	
	Jassid, *Empoasca kerri*	
	TVu 123, TVu 662, JG 10-72, C 152, and 3-779 (1159)	
	Aphid, *Aphis craccivora*	
	P 1473, P 1476, IT82E-16, and MS 9369	Benchasri et al. (2007)
	Bruchids *Callosobruchus maculatus*	
	IT89KD- 288, IT99K-429-2 and IT97K-356-1	Obadofin (2014)

[a]Released for cultivation in India

Limited work has been done on insect resistance in lentil crop. Chhabra (1981) reported seven lines showed resistance to pea pod borer *E. zinkenella*. Chopra and Rajni (1987) ascertained resistance of bruchids, while Sharma and Yadav (1993) accounted resistance to aphid *A. craccivora* in some of the lentil accessions. Genotypic differences for susceptibility to aphid (*A. craccivora*), pod borer (*E. zinkenella*), and seed weevil have been noticed, but no efforts have been made to breed for resistance to these insect pests (Erskine et al. 1994).

The TVNu 946 cultivar showed high levels of resistance to *Maruca* across seasons and locations (Jackai 1981), and Oghiakh and Odulaja (1993) used the principal component analysis to study the variation patterns in 18 cultivars, 7 developmental

parameters of the pest on floral buds, flower, and sliced pods against *Maruca* in cowpea crop. Singh et al. (1996) accounted several improved cowpea varieties with combination of the resistance to aphid, thrips, and bruchid, and Nkansah and Hodgson (1995) confirmed resistance of TVu 801 and TVu 3000 to the Nigerian aphid strain but found that the two lines were susceptible to aphids from the Philippines. IT82E-16 displayed a high level of resistance to cowpea aphid *A. craccivora* (Benchasri et al. 2007), and the genotypes IT89KD-288 (V4) and IT89KD-391 (V2) had the outstanding performance against major insect pests of cowpea in southeastern agroecology of Nigeria (Onyishi et al. 2013). IT89KD- 288, IT99K-429-2, and IT97K-356-1 were resistant to *C. maculatus* (Obadofin 2014).

In case of green gram (*V. radiata*) cultivars PDM-84-139 and ML-382 were assuring against *Caliothrips indicus*, BM-112 for *Raphidopalpa* sp. (*Aulacophora* sp.) and PDM-84-143, TAM-20 and Pusa-105 against *A. craccivora*, *A. kerri* (*Empoasca kerri*) and *M. undecimpustulatus* (Devasthali and Joshi 1994) and MV 1–6 for grasshopper and cotton gray weevil. The cultivar MI-67-9 was resistant against bean aphid but was more susceptible to blue beetle. The sap-sucking jassid infestation was comparatively less in varieties MI-67-3 and MI-29-22 (Devesthali and Saran 1998). Talekar and Lin (1992) ascertained accessions V2709 and V2802 were highly resistant to both *C. chinensis* and *C. maculatus*, while the cultivated accessions V1128 and V2817 were also resistant (Somta et al. 2008) and moderately resistant in PLM 156 and V 1123 for both bruchid species (Dixit 2015). Lower pod borer complex damage was observed in CGG 08-007 and CGG 08-028 (Soundararajan et al. 2010), and resistance in TC1966, V2709, V2802, V1128, and V2817 was attributed due to presence of the biochemical compounds in the seeds (Talekar and Lin 1992; Somta et al. 2008).

The soybean cultivar IAC-100 with having PI 229358 and PI 274454 in its genealogy was formally released in Brazil, and it acquits resistance to stink bug complex (Rosseto 1989). Recently, the pink pod borer, *Cydia ptychora* (Meyrick), on urdbean/black gram was noticed in some of the regions in Gujarat (Dawoodi et al. 2009), and the variety SKNU-03-03 was showed least susceptible to pink pod borer (Dawoodi et al. 2010). Genotype PLU 648 was found resistant to *M. javanica*. Low pod borer complex damage was observed in CBG 08-011 and PLU 54 (Soundararajan et al. 2010). In field pea (*P. sativum*), accessions 32,454 (17%) and 235,002 (33%) had consistently low percent seed damage; incorporation of such promising accessions into pea breeding programs may lead to the exploitation of varieties with enhanced resistance against pea weevil, *B. pisorum* L., in Ethiopia (Teshome et al. 2015). However, lack of precision strategies in evaluating thousands of accessions for resistance to the target insect pests probably resulted in missing many potentially good sources of resistance. Therefore, high-throughput phenotyping has been used in recent times for large-scale evaluation of germplasm or breeding lines for resistance to sap-sucking insects.

5.5 Wild Relatives as Sources of Resistance to Insect Pests

The genes responsible for resistance to insect pests are quite rare in nature for the cultivated species, but they are quite frequent in the wild accessions of many crops. In few cases high levels of resistance in the cultivated germplasm of haricot bean, field pea (Clement et al. 2002), cowpea (Redden et al. 1983), and black gram (Dongre et al. 1996) have been reported. The wild relatives/accessions of pigeon pea and chickpea are authoritative sources of genes for resistance to insect pests. Over the past two decades, the authors ascertained a paradigm shift in identification and deployment of wild species of pigeon pea (Dhillon and Sharma 2012). In case of pigeon pea accessions ICPW 214 (*C. bracteata*), ICPW 141, ICPW 278, and ICPW 280 (*C. scarabaeoides*), ICPW 14 and ICPW 202 (*F. stricta*) have been reported to have resistance to pod fly *M. obtusa* and *T. cajaninae* (Sharma et al. 2003a). In case of *C. scarabaeoides* (L.) Thouars, *C. sericeus* (Benth. ex Baker) Maesen and *C. acutifolius* (F. Muell.) Maesen are highly resistant to *H. armigera* (Green et al. 2006), ICPW 1 (*Cajanus acutifolius*), ICPW 68 (*C. platycarpus*), ICPW 13 and 14 (*C. albicans*), ICPW 159 and 160 (*C. sericeus*), ICPW 83, 90, 94, 125, 137, 141 and 280 (*C. scarabaeoides*), ICPW 207 (*Paracalyx scariosa*) and ICPW 210 (*Rhynchosia aurea*) showed higher levels of antixenosis/non-preference for oviposition under no-choice, dual-choice and multi-choice conditions against pod borer, *H. armigera* (Sujana et al. 2008). High levels of antibiosis were found, when the *H. armigera* larvae reared on leaves and/or pods of *C. acutifolius* (ICPW 1), *C. sericeus* (ICPW 160), *P. scariosa* (ICPW 207), *C. cajanifolius* (ICPW 29), *C. scarabaeoides*, and *C. albicans*. The lyophilized leaf or pod powder was incorporated into the artificial diet, which can be used to assess antibiosis to *H. armigera*, and high levels of antibiosis were observed in diets having leaf and/or pod powder of some of the accessions of *C. acutifolius*, *C. lineatus*, *C. scarabaeoides*, *C. sericeus*, *C. platycarpus*, *P. scariosa*, and *R. aurea*. The postembryonic development period was prolonged, when insects reared on leaves and pods of wild relatives of pigeon pea. Wild relatives expressing high levels of antixenosis/non-preference and antibiosis can be used to increase the levels and diversify the bases of resistance to *H. armigera* in pigeon pea (Sujana et al. 2008). Efforts have also been made for transfering pod borer resistance from the wild relatives to the cultigens (Jadhav et al. 2012a; Mallikarjuna et al. 2011b). Accessions MA7, TT10, and H845 and accessions of wild relatives ICWP 016 (*Cajanus albicans*), ICWP 062 (*C. platycarpus*), ICWP 086, and ICWP 097 (*C. scarabaeoides*) were identified as resistant to *Meloidogyne javanica* (Dixit 2015).

Wild relatives/accessions of chickpea species, such as *Cicer bijugum C. reticulatumtum*., showed high levels of resistance to *H. armigera* (Sharma et al. 2005c, d), and accessions *C. pinnatifidum*, *C. bijugum*, and *C. echinosper* white mum (Davis) showed resistance to bruchid, *C. chinensis* L. (Singh and Ocampo 1998). Chickpea lines received from *C. reticulatum* and *C. echinospermum* were developed and showed for resistance to root lesion nematodes and *Phytophthora* root rot disease, but these lines are still undergoing backcrossing programs to retrieve the domesticated phenotype lines (T. Knights, personal communication). The recent studies

(Sandhu et al. 2005; Kaur et al. 2013) showed that *C. pinnatifi dum*, a valuable source for major biotic and abiotic stresses, can be crossed successfully with cultivated chickpea for the deployment of high level of resistance sources to *Botrytis* gray mold and *Ascochyta* blight (Kaur et al. 2013).

In lentil, for the first time sources of resistance to *Sitona* weevil (*Sitona crinitus* Herbst) obtained from its wild accessions of *Lens* species, accession ILWL 245 belongs to the species *L. culinaris* Medikus subsp. *orientalis* (Boiss.), and a total of 32 accessions including cultivated landraces, *L. c.* sp. *orientalis*, *L. nigricans*, and *L. lamottei* showed lower infestation rates than the susceptible check and were selected as potential sources of resistance to seed weevil (*Bruchus* spp.) (Bouhssini et al. 2008). However, the exploration of 571 accessions from 27 countries including wild species was screened for susceptibility to seed bruchids under unprotected conditions in Central Spain, and the wild species were *L. culinaris* Medikus subsp. culinaris, *L. nigricans* (M. Bieb.) Godr., *L. culinaris* Medikus subsp. orientalis (Boiss.) Ponert, and *L. lamottei* Cezfr., which showed lower infestation rates of seed bruchids (*Bruchus* spp.) than the local check "Lyda"(Ruiz et al. 2012). In India, an extensive research on bruchid species infesting lentil was carried out over the past 10 years at National Bureau of Plant Genetic Resources, New Delhi (Bhalla et al. 2004).

In soybean, wild relative PI 171444 (MG VI) was found to be the majorly resistant and exhibited antixenosis, antibiosis, and temporal separation (Kester et al. 1984), and the lines PI 229358, PI 227687, and PI 274454 expressed antixenosis-type resistance against *Anticarsia gemmatalis* (Hubner) (Lepidoptera: Noctuidae) (Hoffmann-Campo et al. 2006; Ortega et al. 2016) PI 227687 also provoked repellency to *Trichoplusia ni* caterpillars and adults of *Epilachna varivestis*, verified for the presence of volatile derivatives of their leaves (Liu et al. 1989). PI 567336A and PI 567598B were confirmed as the most resistant wild relatives and were characterized as having antibiosis resistance to kudzu bug (KZB), *Megacopta punctatissima* Montandon (Bray et al. 2016). For soybean cyst nematode, resistance source has been effectively exchanged from its wild-lasting soybean, *Glycine tomentella* Hayata (Riggs et al. 1998); however, its cultivars are still in an exploratory stage.

Recently, a draft genome sequence of mung bean was described (Kang et al. 2014), and sequence is useful for gene identification and development of DNA markers for specific trait(s) of interest in breeding program. Till date, various sources of resistance against bruchids have been identified in mung bean crop. Fujii and Miyazaki (1987) depicted first report on wild relatives of mung bean (*V. radiata* var. *sublobata*) and the accession TC1966 and ACC23 and ACC41 (Lambrides and Imrie 2000) and recently identified accession Sub2 in *Vigna radiata* var. *sublobata* for resistance to both bruchid species (Sarkar and Bhattacharyya 2015). The *Phaseolus* wild relatives are as of now by and by being screened for resistances to bruchids and other seed storage insect pests (Singh 2001, J. Beaver, individual correspondence, S. Beebe, individual correspondence, D. Debouck, individual correspondence). In case of wild relative of pea, *Pisum fulvum* (Sibth. & Sm.) is resistant to the bruchid, *Brichus pisorum* L. (Clement et al. 2002), while the wild relative of cowpea, *Vigna*

vexillata (L.) Benth, is resistant to pod-sucking bug, *Clavigralla tomentosicollis* Stal, and spotted pod borer, *M. vitrata* (Jackai and Oghiakhe 1989).

5.6 Mechanisms of Resistance to Insect Pests

Maxwell and Jennings (1980) defined insect resistance as "those heritable characteristics obsessed by the plant which regulate the ultimate degree of damage done by insects". Crop plants have developed various mechanisms of resistance, which have been classified as non-preference or antixenosis for oviposition and feeding; antibiosis showed in terms of reduced survival, prolonged development, and reduced fecundity; and recovery or tolerance to insect damage in terms of ability to withstand insect damage or production of additional branches, tillers of another flush of flowering, and fruiting bodies. All these mechanisms of resistance have been observed against different insects in various legume crops (Schoonhoven et al. 2005; Sharma et al. 2011).

5.6.1 Oviposition Non-preference or Antixenosis

Cowgill and Lateef (1996) and Sison et al. (1996) commemorated fewer eggs on the resistant/tolerant genotype ICC 506 EB than on ICC 4918 and ICCC 37. Comparatively lower egg laying was also recorded in hybrids based on ICC 12477, ICC 12478, ICC 12479, and ICC 506 EB as compared to the hybrids based on the susceptible check, ICCC 37, indicating that egg laying on F_1 hybrids is influenced by the parents and is inherited in the progeny (Narayanamma et al. 2007), and there is a positive correlation among numbers of eggs laid under laboratory and field conditions (Srivastava and Srivastava 1989). Antixenosis and antibiosis types of resistance have been ascertained against *C. chinensis* L. in chickpea and faba bean (Clement et al. 1994).

In case of pigeon pea, oviposition for non-preference was shown in ICPL 187-1, ICP 7203-1, ICPL 84060, ICPL 88039, T 21, and ICPL 332 under no-choice, dual-choice, and multi-choice conditions (Kumari et al. 2006). Wild *Cajanus* accessions (*C. acutifolius* and *C. sericeus*) were having extravagantly levels of antixenosis for oviposition of *H. armigera* (Sharma et al. 2009). Bean cultivars IAC-Harmonia, IAPAR-81, IPR-Eldorado, and IPR-Siriri were the less preferred for oviposition; and the IAC-Harmonia stretched the whitefly *B. tabaci* life cycle, expressing non-preference for feeding and/or antibiosis-type resistance (Silva et al. 2014). Cowpea variety TVNu 946 exhibits non-preference to *M. testulalis* for oviposition/egg laying when compared to Ife Brown and VITA 1 cultivars (Macfoy et al. 1983); there is no ovipositional antixenosis in some of cowpea cultivars to the pod borer by Valdez (1989). Trichomes on the pods of *V. vaxillata*, a wild relative of cowpea, are partially responsible for resistance to *C. tomentosicollis* Stal. (Chiang and Singh 1988). Singh (2002a, b) suggested that varieties with pigmented calyx, petioles, pods, and pod tips suffered least damage from legume spotted pod borer *M. vitrata*.

Durairaj et al. (2009) ascertained most of the wild relatives were found susceptible to aphids and other sucking insect pests, and both antixenosis and antibiotic type of resistance have been observed against *E. fabae*, *E. varivestis*, and *B. pisorum* L. (Clement et al. 1994). The pea varieties having yellow-green color are less preferred to the pea aphids than the blue-green ones (Painter 1951), and varieties deficient in certain amino acids are also shown to be resistant to the pea aphid *A. pisum* (Harris). In soybean varieties without pubescence were extensively damaged by the potato hopper, while those with pubescence seemed to be unaffected (Fehr 1987), and non-preference for oviposition is one of the major components in *H. zea* resistance in PI 2227687 soybean (Horber 1978).

5.6.2 Antibiosis

This mechanism of resistance is typically associated with plant biochemical parameters, like the presence of free amino acids, fatty acids, and fibers in the leaflets, which may have adverse effects on an insect that attempts to colonize it, affecting the biological performance of the insect (Panda and Khush 1995; Smith 2005). Antibiosis is a component of resistance to *H. armigera* in pigeon pea and chickpea, which is showed in terms of reduced larval survival, fecundity, and weight gain and prolonged larval development (Kumari et al. 2010b). Reduced larval and pupal weights and prolonged larval and pupal developmental periods were observed in insects reared on entire leaves or pods of ICPL 332, ICPL 84060, ICPL 88039, ICP 7035, and T 21. Similar effects were observed when larvae reared on artificial diet impregnated with lyophilized leaves or pods of aforesaid cultivars (Kumari et al. 2010a). Wild *Cajanus* accessions have high manifestations of antibiosis (*C. acutifolius* (Benth. ex Baker) Maesen) against pod borer (Sharma et al. 2009).

Antibiosis showed in terms of decreased larval, larval mortality, and pupal weights, extended larval and pupal periods, failure to pupate, and reduced fecundity, and egg viability contributed to antibiosis of resistance to *H. armigera* in chickpea (Srivastava and Srivastava 1989; Yoshida et al. 1995; Cowgill and Lateef 1996; Narayanamma et al. 2007). Larval survival and larval weight were lower on ICC 506 EB, ICC 12476, ICC 12477, and ICC 12478 when contrasted with that on ICCC 37. In addition, the isoflavonoids can interfere negatively with insect feeding, oviposition, and development (Harborne and Williams 2000; Simmonds 2003). The bean genotype IAC Una and Raz 49 were classified as highly susceptible and highly resistant, respectively, by Costa et al. (2013).

The cowpea cultivar MNC 99-541 F21 showed antibiosis against the whitefly *B. tabaci* biotype B, extending the life cycle of the insect, and genotypes Canapu, BRS-Urubuquara, and TE97-304 G-4 also showed antibiosis, causing high nymphal mortality (Cruz et al. 2014); Koona et al. (2002) accounted that TVnu 151 exhibited antibiosis for *C.tomentosicollis*, causing high nymphal mortality, and the larval survival of *M. vitrata* was low on cowpea variety TVNu 946, and it was due to the antibiotic and nutritional factors (Macfoy et al. 1983; Saxena 1989). Valdez (1989) observed only a slight effect of the host on larval survival, and Okech and Saxena

(1990) indicated that stem and pods act as antibiosis component of resistance in TVNu 946 and VITA 5. In general, antibiosis consequences are expressed in terms of weight and size of insects, sex ratio, and proportion of insects entering diapause (Basandrai et al. 2011). Four green gram accessions LM 131, V 1123, LM 371, and STY 2633 and three black gram accessions UH 82-5, IC 8219, and SPS 143 were found to be moderately resistant to bruchid *C. chinensis* having less percentage survival and prolonged developmental period as compared to susceptible check (Ponnusamy et al. 2014).

5.6.3 Tolerance

Ability to withstand insect damage that results in lower loss of grain yield indicates the ability of different genotypes to recover from insect damage. However, tolerance is more subject to variation because of environmental conditions than non-preference and antibiosis. The age or size and general vigor of the plant and size of the insect-resistant population also strongly influence the degree of tolerance.

Reduction in grain yield also renders a good measure of agronomic performance and the genotypic ability to withstand *H. armigera* damage. If there should arise an occurrence of chickpea, plant recuperation from harm recuperation by *H. armigera* was better if there should be an occurrence of ICC 506 EB, ICC 12476, and ICC 12479 when contrasted with the vulnerable check, ICCC 37 (Narayanamma et al. 2007). The misfortune in grain yield was lesser in the event of ICCV 2, ICC 12478, ICC 12479, and ICC 506 EB crosswise over crop phenology stages and pervasion technique conventions when contrasted with that on the vulnerable check, ICCC 37. Pigeon pea ICPL 187-1, ICPL 98008, ICP 7203-1, T 21, ICP 7035, and ICPL 332 showed moderate levels of resistance to *H. armigera* across planting dates. ICPL 187-1, ICPL 84060, ICP 7203-1, ICPL 87119, and ICPL 332 suffered lower loss in grain yield than the susceptible checks, ICPL 87 and ICPL 87091, under unprotected conditions (Kumari et al. 2010b).

5.7 Morphological and Biochemical Traits Associated with Insect Resistance

5.7.1 Phenological Traits

Pigeon pea genotypes having determinate growth habit, clustered pods, and dense plant canopy are more prone to be susceptible to pod borers, *H. armigera* and *M. vitrata*, than genotypes with non-clustered pods (Sharma et al. 1997), while the genotypes with smaller pods, pod wall thick and tightly fitting to the seeds, and a deep constriction between the seeds are less susceptible to *H. armigera* (Nanda et al. 1996). The varied plant growth types and maturity also influence genotypic susceptibility to pod fly, *M. obtusa*, but podwall thickness, trichome density, and amount crude fiber content are associated with resistance to *H.armigera* in pigeon

pea (Moudgal et al. 2008). Sharma et al. (2009) observed higher density of type "C" and "D" trichomes present in wild relatives of *C. scarabaeoides* and *C. sericeus*, and there are 5–6 traits that distinguish *C. cajanifolius* from pigeon pea such as flower morphology, pod color, morphology, pod constriction, seed color, and 100 seed weight (Mallikarjuna et al. 2012).

Pod wall thickness, plant growth habit, and crop duration influence pod borer *H. armigera* damage in chickpea (Ujagir and Khare 1988). Pubescence on the leaf tip is linked with reduced defoliation by *H. zea* (Boddie), *S. exigua* (Hubner), and *Pseudoplusia includens* (Walker) in soybean (Hulburt et al. 2004). The length of the peduncle and angle of pods influence expression of resistance to *M. vitrata* in cowpea (Soundararajan et al. 2013). Oghiakhe et al. (1991) reported that defoliated cultivars suffered lower damage than the undefoliated ones, and the cultivars TVu 946 and TVu 4557 having attributes of high length of the peduncle and angle of pods (Singh 1978) erect and profuse flowering in TVu 946 (Oghiakhe et al. 1992a, b) for resistance *M. vitrata* in cowpea. The bunched pods suffered greater damage by legume pod borer (Usua and Singh 1979). Pubescence in wild and cultivated cowpea *V. vexillata* and *V. unguiculata* badly affected oviposition, mobility, and food consumption by the legume pod borer in tests conducted with TVNu 729 (wild, highly resistant and highly pubescent), TVNu 946 (semi wild, moderately), and IT 82D-716 (cultivated, highly susceptible, and pubescent) (Oghiakhe 1995).

In green gram, fewer number of bruchid eggs were recorded on small and shiny seeds as compared to large and dull seeds, and in black gram, small and black seeds recorded lesser number of eggs as compared to large and green seeds (Ponnusamy et al. 2014); and the neoplasm formation, thicknesses of podwall, and micromorphological traits attributed for a reduced oviposition rate of female pea weevil on genotype 235,899-1 (Mendesil et al. 2016). In *Dolichus* bean, the foliage color, days to 50% flowering, flower color, pod color, pod texture, and fragrance influenced genotypic susceptibility to *M. vitrata* (Mallikarjuna et al. 2009).

5.7.2 Leaf Hairs and Trichomes

Leaf hairs (that do not produce glandular secretions) play a pivotal role in host plant resistance to insects. Wild relatives of pigeon pea such as *Cajanus scarabaeoides* and *C. acutifolius* with nonglandular trichomes are not preferred by *H. armigera* females for egg laying (Sharma et al. 2001a; Sujana et al. 2012). Trichomes (hair-like outgrowths on the epidermis of plants that produce glandular secretions) also play an important role in host plant resistance to insects. Hooked trichomes in bean vitiate the movement of the aphid, *A. craccivora* (Johnson 1953), and potato leafhopper, *E. fabae* (Pillemer and Tingey 1978). Glandular trichomes in pigeon pea are linked to *H. armigera* susceptibility (Peter et al. 1995; Sharma et al. 2001a; Green et al. 2003; Sujana et al. 2012).

Trichomes and their organic exudates in chickpea also influence the movement and feeding behavior of neonate larvae of *H. armigera* (Stevenson et al. 2005) and influence the feeding of spotted pod borer larvae, *M. vitrata*, in cowpea (Jackai and

Oghiakhe 1989) and cabbage looper, *Trichoplusia ni* (Hubner), in soybean (Khan et al. 1986). Trichomes on a wild relative of cowpea (*Vigna vexillata)* pods are partly responsible for resistance to the pod-sucking bug, *Clavigralla tomentosicollis* Stal. (Chiang and Singh 1988). The density and length of trichomes are linked with resistance to pod borers in short-duration pigeon pea, while trichome density on upper and lower surface parts of the leaf (390 and 452/9 mm^2), trichome length (3.5 mm), and trichome density (442.9 mm^2) and length (5.9 mm) on pods are positively correlated with the resistance to pod borer, *H. armigera* (Sunitha et al. 2008a).

Potential effects of trichomes on whiteflies may vary depending on trichome angle to the leaf surface, length and type, all factors potentially affecting adult oviposition, and immature attachment and feeding in black gram (Channarayappa et al. 1992), and the genotypes having shorter trichomes are inclined to resistance against *B. tabaci*. Another fact revealed that the black gram genotypes possessing erect trichomes were resistant to *B. tabaci*, and thus greater erectness of foliar trichomes seemed to disturb and retard the settling and probing (for oviposition and feeding) behavior of the whitefly in resistant genotypes of black gram (Lakshminarayan et al. 2008; Taggar and Gill 2012).

5.8 Biochemical Mechanisms of Resistance

5.8.1 Nutritional Factors

Nutritional parameters, viz., sugars, phenols, proteins, fats, sterols, and essential amino acids and vitamins, also influence on host plant suitability to insect pests. Total soluble sugars present in pigeon pea pod wall, which influence the pod damage by *H. armigera*. Apart from sugars, the protein content of the pod wall is also associated with susceptibility, while total sugars are associated with resistance to *M. obtusa* in pigeon pea (Moudgal et al. 2008). Higher sugar content present in flower (22%) and pods (10.6%) was responsible for the susceptibility of ICPL 88034, while higher phenol concentration in flowers (6.5%) and pods (9.3%) in ICPL 98003 was responsible for resistance. Protein percent in pods was significantly higher (25.5%) in susceptible ICPL 88034 when compared with resistant ICPL 98003 (16.5%) (Sunitha et al. 2008b).

Pea varieties deficient in certain amino acids, which influence for resistant to the pea aphid, *A. pisum* (Auclair 1963). Higher amounts of nonreducing sugars and lower amounts of starch in chickpea variety GL 645 attribute for its low susceptibility to *H. armigera* (Chhabra et al. 1990). Mung bean varieties with high sugar and amino acid content in leaves are resistant to whitefly, *B. tabaci*, and the jassid, *Empoasca kerri* (Ruth) (Chhabra et al. 1988). Soybean-resistant genotypes possessed high amount of fats, protein, and anti-nutritional factor (phenol and four to five times more trypisn inhibitors) than cowpea and chickpea (kabuli> desi) genotypes which contain high amount of carbohydrates and low amount of anti-nutrional factors and were susceptible toward *Callosobruchus* species (Sharma and Thakur 2014).

Nonprotein or unusual amino acids afford protection against herbivores in several plant species. The protective effect is elicited via their structural analogy to the most commonly occurring essential amino acids. Among these, L-canavanine, 2, 4-diamino butyric acid, azetidine-2-carboxylic acid, minosine, and 3-hydoxyproline have substantial growth inhibition effects on insects (Parmar and Walia 2001). L-canavanine is a structural homologue of L-arginine and takes place in over 1500 leguminous plant species. Some of the nonprotein amino acids also act as enzyme inhibitors; canaline – a hydrolytic product of canavanine – inhibits pyridoxal phosphate-dependent enzymes by forming a covalent bond (Ishaaya et al. 1991). Black gram cultivars NDU 5-7 and KU 99-20 registered higher peroxidase and catalase activities at 30 and 50 DAS under whitefly-stress conditions as compared with non-stressed plants (Taggar et al. 2012).

5.8.2 Secondary Metabolites

Plants also produce various defensive secondary metabolites in reaction to biotic and abiotic stresses. The secondary metabolites do not involve in the normal growth and development of plant but reduce its palatability of the plant tissues to the herbivores (Boerjan et al. 2003). Some of the secondary metabolites also influence in host finding, oviposition, feeding, and survival and growth and development of insects and play a major role in host plant resistance to insects in grain legumes. Among the secondary metabolites, plant phenols constitute one of the most common and widespread groups of defensive compounds, which play a pivotal role in host plant resistance against herbivores, including insects (Sharma et al. 2009; Usha Rani and Jyothsna 2010; Ballhorn et al. 2011). Qualitative and quantitative alterations in secondary metabolites and increase in activities of oxidative enzymes in plants in response to herbivore attack are a common mechanism of resistance to insects (War et al. 2013). Quercetin, quercitrin, and quercetin-3-methyl ether in the pod surface exudates of pigeon pea play a major role in host plant selection by *H. armigera* larvae in pigeon pea (Green et al. 2002, 2003). Stilbene, a phytoalexin, occurs at high concentrations in pigeon pea cultivars with resistance to *H. armigera* (Green et al. 2003). Total phenols and tannins present in the pod wall of pigeon pea are negatively associated with pod fly damage (Moudgal et al. 2008).

Protease inhibitors are another major class of anti-nutrional factors in chickpea and pigenopea, which have shown *H. armigera* microbial gut protease inhibitory activity in developing seeds of wild and cultivated chickpea (Parade et al. 2012). Amylase and protease inhibitors in pigeon pea showed to have an adverse effect on growth and development of *H. armigera* (Giri and Kachole 1998). There is appreciable variation in *H. armigera* gut protease inhibitory activity in developing seeds of chickpea (Patankar et al. 1999), and proteinase inhibitors from the nonhost plants (groundnut, winged bean, and potato) are more efficient in inhibiting the gut proteinases of *H. armigera* larvae than those from its favored host plants such as chickpea, pigeon pea, and cotton (Harsulkar et al. 1999). Amounts of trypsin inhibitor (TI) in desi chickpea cultivars ranged between 17 and 31 mg/g of sample. The TI

activity was greater in P-256 (39.47± 1.91 TUI/mg) than in Pusa Pragati (6.19 ± 0.56 TUI/mg) (Kansal et al. 2008). The wild relatives of pigeon pea belonging to *C. albicans*, *C. cajanifolius*, *C. sericeus*, *Flemingia bracteata*, and *Rhynchosia bracteata* showed high levels of resistance to *H. armigera* and exhibit high levels of protease inhibitors (*PIs*) activity under in vivo and in vitro against *H. armigera* gut proteinases (HaGPs) (Parade et al. 2012). Sterols and soybean leaf extract in combination with sucrose act as phagostimulant to the larvae of the cabbage looper, *Trichoplusia ni* (Hub.) (Sharma and Norris 1994a). Higher acidity in the leaf exudates of chickpea is linked with resistance to *H. armigera* (Srivastava and Srivastava 1989). The polar solvent extractable of the soybean genotype PI 227687 resistant to the cabbage looper, *T. ni*, contains daidzein, coumestrol, sojagol, and glyceollins. These compounds reduce feeding, survival, and growth and development of the cabbage looper, *T. ni* (Sharma and Norris 1991, 1994b). In soybean, pinitol confers resistance to *H. zea* (Boddie) (Dougherty 1976).

Malic acid in chickpea leaf organic acid exudates acts as an antifeedant and less palatable to the *H. armigera* larvae (Bhagwat et al. 1995). Oxalic acid exudates inhibit the growth and development of *H. armigera* larvae when incorporated into synthetic diet, while malic acid shows no growth inhibition on *H. armigera* (Yoshida et al. 1995, 1997). The chickpea having flavonoids judaicin 7-O-glucoside, 2-methoxy-judaicin, judaicin, and maakiain present in wild relatives of chickpea (*Cicer bijugum* and *C. judaicum*) have shown an antifeedant activity for the larvae of *H. armigera* (Simmonds and Stevenson 2001). In common bean genotypes, arcelin protein and trypsin inhibitors are the major secondary metabolites for resistance to bean weevil *Zabrotes subfasciatus* (Blair et al. 2010).

5.9 Inheritance of Resistance to Insects in Grain Legumes

Greater magnitude of σ^2 A (17.39) than σ^2 D (3.93) clearly showed preponderance of σ^2A in the inheritance of legume pod borer, *H. armigera* resistance (Narayanamma et al. 2013a). Gowda et al. (2005) ascertained that additive and dominance genetic variances were majorly predominant in early and medium maturity diallel trials, respectively. Additive as well as dominance components of genetic variances were equally important in the inheritance of legume pod borer *H. armigera* resistance in late maturity group. Such derivative nature of gene action controlling pod borer resistance in varied maturity groups has earlier been reported by Gowda et al. (1983) and Singh et al. (1991). Salimath et al. (2003) accounted in the involvement for both additive and nonadditive gene action in the inheritance of pod borer resistance, although their results were maturity non-specific. Cotter and Edwards (2006) reported that heritability of larval execution was maximum for neonates than for third-instar larvae in noctuid moth, *H. armigera*, on a resistant and a susceptible variety of the chickpea, *C. arietinum*. There was absence of genetic correlation between larval performance and oviposition preference, showing that female moths do not select the most suitable plant for their offspring.

Combining ability studies showed the preponderance of nonadditive type of gene action for resistance to *H. armigera* and *M. vitrata* in pigeon pea (Lal 1987). Verulkar et al. (1997) suggested the involvement of a single dominant gene in antixenosis mechanism of resistance in *C. scarabaeoides* to *H. armigera* and *M. obtusa*. Nonglandular trichomes, which are linked with resistance to *H. armigera* in *C. scarabaeoides*, are inherited as a predominant trait (Rupakala et al. 2005). The *H. armigera*-resistant parents, viz., ICC 506 EB, ICC 12478, ICC 12477, ICC 12479, and ICCV 2, proved to be the best general combiners for pod borer resistance with significantly negative gca effects and low pod borer damage (Narayanamma Lakshmi 2005; Sreelatha et al. 2008; Narayanamma et al. 2013b).The hybrids ICC 506 × ICC 3137, ICC 12477 × ICC 4918, ICC 12476 × ICC 3137, ICC 12479 × ICC 3137, and ICC 3137 × ICCV 2 showing significant and negative *sca* effects were having good specific combiners for resistance to pod borer damage done by *H. armigera*. Although there is a good balance between pod borer damage of crosses and their *sca* effects, the crosses (involving parents with contrasting gca effects) with significant *sca* effects need to be overworked for developing varieties on pod borer resistance and high grain yield parameters. Singh et al. (1997) could create pod borer-resistant chickpea line, ICCV 7, utilizing pedigree selection of the lines gotten from a combination of H 208 and BEG 482. Further, that the loci of pod borer resistant are different in different resistant sources (Dua et al. 2005), pyramiding of genes from different resistant sources will be effective in increasing the levels of pod borer resistance in chickpea. The identification and evaluation of breeding lines which have dual resistance to pod borer and *Fusarium* wilt, which help in IPM program (Singh et al. 1990; Lateef 1990; Lateef and Sachan 1990; Van Rheenen 1992; Chaturvedi et al. 1998; Sharma et al. 2003b), are important for increasing productivity of chickpea. Recently identified germplasm line (IPC 96-3 and FG 1235) having dual resistance to pod borer and *Fusarium* wilt (Harminder et al. 2005) could be used as potential donor source to develop chickpea varieties for sustainable crop production.

On the basis of specific combining ability estimates, the cross JAKI-9218×AKG-10-1 was found to be the best specific combination for seed yield, larval count, malic acid content, and percent of pod borer damage when compared to cross ICCV-2×Chandrapur Chanoli and JAKI-9218×Bushy Mutant (Jadhav and Vijaykumar 2015).The ratio of sca/gca was greater than one for seed yield per plant, larval count at vegetative and pod formation stages, and percentage of pod damage, thereby signifying the preponderance of nonadditive variance in the expression of these characters, whereas additive variance was found to be predominant in the expression of larval count at flowering stage and in malic acid content (Jadhav and Vijaykumar 2015). The identification of various breeding lines, viz., ICCL 87317, ICCL 87316, and ICCV 95992 having stable resistance to *H. armigera* and high grain yield potential, and germplasm lines, viz., ICC 12478, ICC 14876, and ICC 12479 having stable resistance to pod borer *H. armigera* and moderate yield potential (Sreelatha et al. 2003), could be used in heighten for pod borer resistance in elite agronomic traits. Similar results were reported by Singh and Singh (1990) in pigeon pea for pod fly resistance.

Since gca effects are the demonstration of additive properties of genes, parents selected based on gca effects will be useful for arising breeding lines with higher grain yield (Narayanamma et al. 2013b) and desirable levels of the trait of interest. Based on gca effects, the genotypes ICC-506 and ICCV-2 have good genetic potential for their utilization in further breeding programs for genetic improvement of pod borer *H.armigera* resistance in chickpea by using them as one of the parents in hybridization and isolating desirable segregants for resistance to pod borer. Most promisingly, the parent ICC-506 can be extensively used in the hybridization program to accelerate the pace of genetic improvement for pod borer resistance in chickpea. In lentil, ILWL 245 line is being used to transfer introgress resistance genes to cultivated and study the inheritance of *Sitona* weevil resistance in lentil (Bouhssini et al. 2008). Pathak (1988) studied the genetic resistance of cowpea aphid and reported a single dominant gene, designated as *Rac1* and *Rac2*. Ombakho et al. (1987) also studied in F1 and F2 generation of cowpea (TVU 310, ICV10, and ICV 11) and reported that resistant gene in TVU 310 and ICV 10 was designated by *Ac1*, while resistant gene in ICV11 was *Ac2*.

5.10 Wide Hybridization

Transferring gene from wild relative species to the cultivated species to confer an adaptive resistance to *H. armigera* is one of the potential options for crop improvement. Wild *Cajanus* species are the reservoir of many important trait-specific genes and can be utilized to improve the crop cultivars, enrich variability and diversity, and broaden the genetic base and the pre-breeding populations involving wild *Cajanus* species from its secondary gene pools (*C. cajanifolius* (ICPW 29), *C. scarabaeoides* (ICPW 281), *C. sericeus* (ICPW 159 and 160), *C. reticulatus*, *C. acutifolius* (ICPW12 and ICPW 004), *C. albicans* (ICPW 14)) and tertiary gene pools (*C. platycarpus* (ICPW 68), *Rhynchosia aurea*, *and R. bracteata*)) as donors for trait-specific genes and pigeon pea cultivars as recipients, while these crosses are being further advanced to develop introgression lines (ILs) with high levels of resistance to pod borer (Sharma and Upadhyaya 2016). The wild *Cicer* species such as *C. reticulatum*, *C. pinnatifidium*, and *C. echinospermum* showing high levels of resistance to *H. armigera* can be used in wide hybridization in crop improvement program (Sharma et al. 2005a, 2006). The cross-incompatibility among cultivated chickpea and its tertiary gene pool are post-zygotic (Mallikarjuna 2001; Babb and Muehlbauer 2005), and hence, there is a need to formulate bridge cross between tertiary and secondary gene pool and then use the progeny in further crosses with the cultigen. Recently introgression studies have been done on pod borer (*H. armigera*), pod fly, bruchid resistance, and other agronomic traits in pigeon pea for opting improved cultivar for sustainable crop production (Mallikarjuna et al. 2011a), and also advanced generation population from the cross-utilizing *C. acutifolius* as the pollen parent has shown resistance for pod borer damage (Mallikarjuna et al. 2007; Jadhav et al. 2012a), for opting variation for seed color and high seed weight. Some of the lines showed high level of resistance to pod borers and pod fly under

natural field conditions and for bruchid resistance studies for cultivated pigeon pea under storage conditions (Jadhav et al. 2012b).

There is lack of an authentic information of resistance to pea weevil in cultivated *P. sativum* accessions led to the geographical expedition and identification of resistant sources from its secondary gene pool of *Pisum*, which ensured in the breakthrough of pod and seed resistance in *P. fulvum* accessions (Clement et al. 2002). The *P. fulvum* accession ATC113 (PI 595933) was successfully crossed with *P. sativum* accession Pennant, and it produced interspecific progenies with having resistant traits in lines (Byrne et al. 2008), and the development of introgression line for pea weevil resistance into cultivated field pea was further confirmed by using advanced backcross lines of the original population (Aryamanesh et al. 2012). Development of first QTL markers is developed by interspecific hybridization among cultivated field pea and *P. fulvum* (resistance source) against pea weevil and identified three QTL regions associated resistance in cotyledon (linkage groups LG2, LG4, and LG5), pod wall/seed coat (linkage groups LG2 and LG5), and pod wall (on LG7) (Aryamanesh et al. 2014). Recently, Pandiyan et al. (2010) described a number of cross-sectional and cross- subgenus hybrids; amid these hybrids, the cross between *V. radiata* and *V. umbellata* is especially shown significant as *V. umbellata* possesses with a high level of resistance to bruchid beetles, one of the most serious and concern pests of *Vigna.*

5.11 Marker-Assisted Selection

As we know, pod borer (*H. armigera*) is perhaps the major threat to chickpea and pigeon pea in terms of production and productivity. Screening has been done over 5000 germplasm accessions divulged that still there is no resistant strain or source against this insect pest (Kumar et al. 2004). While few resistance sources were identified in the past in cultivated gene pool, they showed either inconsistency or low levels of resistance lending to their little development in breeding programs (Lateef 1990). Therefore, there is urgency to identify stable sources of genetic resistance in the crossable gene pool for pod borers to facilitate conventional genetic crop improvement programs. The use of undiscovered genes in existing gene pools and the utilization of wild relatives as a rich reservoir of resistance genes against both abiotic and biotic stresses should be given special attention to broaden the genetic base of breeding pool (Clement et al. 2009). In recent days, the development of newer molecular markers and other genomic sources has been quickened in major chickpea, pigeon pea, and some other pulse crops, and marker-assisted trait associations have been established for a number of important agronomic traits (Kumar et al. 2011). The wide pertinency of marker-assisted selection (MAS) has already been demonstrated in cowpea and pea crop, while in the case of lentil and faba bean, it is in infancy stage. The recent approach for the development resistance trait for major legume crops by deploying genomics-assisted breeding (GAB) holds promise in enhancing the genetic gains and discovery of genome-wide genetic markers, high-throughput genotyping/high-throughput phenotyping and sequencing platforms,

and high-density genetic linkage/QTL maps, and, more importantly, the availability of whole-genome sequence helps in speeding up the progress of genetic improvement of major pulses, which lead to rapid development of cultivars with higher yield, enhanced stress tolerance, and wider adaptability (Bhora et al. 2014).

Progress in marker-aided selection for development of resistance to insect pests in grain legumes though limited extent has been discussed by Sharma et al. (2008). Mapping the complex traits like resistance to pod borer, *H. armigera*, in chickpea is the only that just started (Lawlor et al. 1998). A cross between a wilt-resistant kabuli variety (ICCV 2) and a wilt-susceptible desi variety (JG 62) has been used to develop the first intraspecific genetic linkage map of chickpea using mapping population (Cho et al. 2002). This population has been further evaluated for resistance to pod borer *H. armigera*, and the data analysis is under progress. An interspecific population derived from ICC 4958 (*C. arietinum*) x PI 489777 (*C. reticulatum*) has been evaluated for opting resistance to beet armyworm, *S. exigua* (Hub.) (Clements et al. 2008), and pod borer, *H. armigera* (Sharma, H.C., Unpublished), and this population is being genotyped for identification of markers for resistance to these insects. Similarly another mapping population between Vijay and ICC 506EB has also been developed and evaluated for *H. armigera*, and in pigeon pea, also a mapping population between *C. cajan* and *C. scarabaeoides* is under development at ICRISAT (Upadhyaya HD, personal communication).

However, genetic improvement program has always been impeded with limited genetic variability under primary gene pool of pigeon pea, and its wild species present in the secondary and tertiary gene pools have been reported to carry forward resistance against major insect pests. However, till date deployment of resistance genes through conventional backcrossing has not been much successful. So now it especially calls for development of gene introgression through marker-assisted backcrossing (MABC) or advanced backcross breeding (AB breeding) for the development of improved insect pest-resistant cultivars (Choudhary et al. 2013). A cross among an aphid (*A. craccivora*)-resistant cultivated cowpea (IT 84S-2246-4) and susceptible wild cowpea (NI 963) has also been evaluated for aphid screening resistance and RFLP (restricted fragment length polymorphism) marker segregation (Myers et al. 1996). The RFLP marker bg4D9b was connected to the aphid resistance gene (Rac1), and furthermore, a few flanking markers in a similar linkage gathering (linkage bunch 1) have additionally been identified and described. Taran et al. (2002) identified the genetic linkage map of common bean. The genetic loci for resistance to potato leafhopper, *Empoasca fabae* (Harris), were detected by Murray et al. (2004). In green gram, TC1966 bruchid resistance gene has been mapped by adopting RFLP markers (Young et al. 1992). Resistance was mapped to a single locus on linkage group VIII (approximately 3.6 cM from the nearest RFLP marker), and based on RFLP analysis, a progeny was also identified in the F_2 population that maintained the bruchid resistance gene among a tightly linked double crossover. This progeny would be useful for developing bruchid-resistant mung bean lines and free of linkage drag. For introgression of the bruchid resistance gene in green gram, Yang et al. (1998) used RFLP marker-assisted selection in backcross breeding, while Kaga and Ishimoto (1998) studied genetic determination of a

bruchid resistance gene and its relationship to insecticidal cyclopeptide alkaloids, the vignatic acids in green gram. Villareal et al. (1998) reported random amplified polymorphic DNA (RAPD) markers have also been used to identify markers linked to the bruchid resistance in mung bean. The *Br* locus confirms a bruchid resistance in mung bean, *VrPGIP2* (encoding a polygalacturonase inhibitor) is a strong candidate gene for resistance, and *VrPGIP2* sequence genes were varied between resistant and susceptible lines (Chotechung et al. 2016). The gene was 25 cM from *pM151a*. Whenever pM151a and pM151b were conceived considered as alleles of a similar locus, the bruchid resistance genes were found 11.9 cM from its closest RAPD marker Q04 sub 900 and 5.6 cM from pM151. The progress has been made for the crosses between field pea (*P. sativum*) and the wild species *(P. fulvum*) to locate molecular marker resistance gene to pea weevil in (Byrne et al. 2002). There have been no definitive efforts that has been made to identify QTLs associated with insect resistance in pigeon pea (Sharma 2009), but mapping population based on *C. cajan* x *C. scarabaeoides* has been developed and is under evaluation stage for resistance to *H. armigera* to identify QTLs linked for resistance to pod borer in pigeon pea.

To date, the sources of cowpea aphid (CPA) resistance and major quantitative trait loci (QTL) reported only for peanut crop (Herselman et al. 2004) and *M. truncatula* (Kamphuis et al. 2012). Genetic mapping for CPA resistance in cowpea would facilitate for identifying syntenic areas in other legumes, as they may confabulate similar physiological responses against CPA infestation (Kamphuis et al. 2013). Development of African cowpea introgresses resistance allele genes from IT97K-556-6 into susceptible local blackeye varieties (CB27) by backcrossing with the help of recombinant inbred line (RIL) for aphid resistance (Huynh et al. 2015). Genome solution for a major QTL associated with the *Rk* locus in cowpea for resistance to root-knot nematodes *Meloidogyne* spp. has significance for plant breeding programs and characterization R gene by Huynh et al. (2016). Muchero et al. (2010), working on the cross from the foliar thrips susceptible IT93K503-1 and the resistant black-eyed cowpea cultivar "California Blackeye No. 46" (CB46), identified three QTLs on the linkage groups 5 and 7. These QTLs' (*Thr- 1*, *Thr-2*, and *Thr-3*) peaks were collocated with the AFLP markers ACCCAT7, ACG-CTC5, and AGG-CAT1 and were linked with foliar damage caused by *T. tabaci* and *F. schultzei*. These urging researches paved the way forward for genetic characterization of major insect pest resistance in cowpea and disease causes > 15% yield loss in West Africa and impacts production in Asia and South America negatively. In addition, other putative candidate marker-assisted selection (MAS) for insect or disease resistance in cowpea was reported (Timko and Singh 2008).

Resistance to bruchid has been reported in few mung bean cultivars (Somta et al. 2006; Somta et al. 2008); however, some of mung bean breeders have keen interest in identifying new sources of resistance to this important pest from other Asian *Vigna* species such as *V. umbellata* and *V. nepalensis* (Pandiyan et al. 2010; Somta et al. 2008). It is reported that the bruchid and mung bean bug were controlled by a single dominant gene in the F1 and F2 seeds of mung bean and two QTLs were identified for bruchid resistance, and a QTL for bean bug resistance was detected.

These new markers will be further used for cloning of the resistance genes to bruchid and bean bug in the future (Hong et al. 2015). There are several reports analyzing resistance to mung bean yellow mosaic virus (MYMV) in different germplasms, and both recessive and dominant genes have been implicated. The resistant variety SML-668 has two recessive genes for resistance. Sudha et al. (2013) reported that the resistance of mung bean variety "KMG189" is controlled by a single recessive gene. Development of mung bean yellow mosaic Indian virus (MYMIV) resistance, either using the wild mung bean accessions (*V. radiata* var. *sublobata*) or some of the breeding line from Pakistan, has found a common major resistance QTL (variously named MYMIV'9_25, qMYMIV1, qMYMIV4) (Chen et al. 2013; Kitsanachandee et al. 2013). This locus was detected in different locations/regions, years, sources of resistance, and scoring systems. The locus was having specific markers; therefore, these could be used in marker-assisted selection for resistance breeding program.

The mung bean yellow mosaic virus resistance (MYMIV) has been found in some accession of black gram, and this resistance gene has been further mapped using SSR markers (Gupta et al. 2013). An SSR marker nearly linked to the resistant locus was found that could be used for marker-assisted selection. Kushida et al. (Kushida et al. 2013) recently studied some accessions of *V. minima*, and *V. nakashimae* showed a high level of resistance to all races of soybean cyst nematodes in Japan, and these resistant sources are being used in azuki breeding, since the soybean cyst nematode is an increasingly problematic pest on legumes in Hokkaido, Japan. *V. nakashimae* has been used to develop an interspecific linkage map with *V. umbellata* (Somta et al. 2006). QTL-M and QTL-E enhance soybean resistance to major insects; pyramiding these QTLs with cry1Ac increases protection against Bt-tolerant pests, presenting an opportunity to effectively deploy Bt with host plant resistance genes (Ortega et al. 2016).

5.12 Transgenic Resistance to Insects

The first successful genetic transformation of chickpea with *cry1Ac* gene, which inhibit the growth and development of *H. armigera*, was reported by Kar et al. (1997). Genetic transformation of chickpea using *Cry1Ac* gene has been reported by many workers subsequently (Indurker et al. 2007; Mehrotra et al. 2011). A second gene, *Cry2Aa*, was also incorporated for pyramiding with existing *Cry1Ac* in chickpea lines (Acharjee et al. 2010). Mehrotra et al. (2011) generated pyramided genes *Cry1Ac* and *Cry1Ab* chickpea; however, pyramiding of two or more combination of genes with different modes of action is preferred for effective management of the insect pest. Ganguly et al. 2014 reported chickpea expressing fused *cry1Ab/Ac* constitutively for resistance to *H. armigera* using pod-specific *msg* promoter from soybean to different transgenic lines has also been reported. Homologous ubiquitin and RuBisCO small subunit (rbcS) promoters used to transcribe *cry1Ac* in transgenic chickpea both constitutively and in a tissue-specific manner through *Agrobacterium*-mediated transformation of chickpea var. ICCV89314 (Chakraborty et al. 2016).

The toxicity of commercial Bt formulation and Cry1Ab and Cry1Ac to *H. armigera* larvae was reduced significantly when the *H. armigera* larvae were fed on diets amended with antibiotics, suggesting that gut microbes may be one of the factors conferring resistance/susceptibility to insects in *Bt* transgenic crops (Paramasiva et al. 2014).

In recent days, Cowpea aphid, *A. cracciovra*, also causes significant yield losses in chickpea, an important pulse crop in the Indian subcontinent, where transgenic chickpeas expressing the *Allium sativum* leaf agglutinin (ASAL) gene resulted in a significant reduction in survival and fecundity of cowpea aphid (Chakraborti et al. 2009). A new management strategy such as upregulating secondary metabolites, which are toxic to insect pests (Gatehouse 2002), or introducing RNAi technology for insect control by silencing endogenous genes of insects could be new strategy to develop genetically modified chickpea (Gordon and Waterhouse 2007).

Transgenic pigeon pea plants with *cry1Ab* and soybean trypsin inhibitor (*SBTI*) genes have been reported (Sharma et al. 2006) but have not been found to be effective for controlling *H. armigera* (Gopalaswamy et al. 2008). Developed transgenic chickpea expressing cowpea trypsin inhibitor (Thu et al. 2003) and α-amylase inhibitor (Shade et al. 1994; Schroeder et al. 1995; Sarmah et al. 2004) showed resistance to bruchid species. Transgenic pea with expression of α-amylase inhibitor has also been developed for resistance to pea weevil (Morton et al. 2000).

Ikea et al. (2003) detailed the fruitful hereditary change of cowpea utilizing the molecule particle gun bombardment of shoot meristem system. A productive and stable cowpea change/recovery framework has been created as of late (Popelka et al. 2006), so that transgenic cowpea is currently a reality. By and by, there is no distinguished cowpea assortment indicating solid imperviousness to bruchids. Interestingly, high resistance was depicted in the wild relative *Vigna vexillata*; however, nonviable seeds coming about because of their cross make this approach improper to exchange these qualities to the developed species (Fatokun 2002). Be that as it may, fake eating regimen bioassay performed on cowpea weevils recommended that α-amylase inhibitor 1 (αAI-1) confined from regular bean (*Phaseolus vulgaris*) would be utilized against these vermin assaults (Ishimoto et al. 1999).

Right now, huge advance has been made on cowpea hereditary change which may turn out to be without further ado accessible for the African ranchers. The qualities utilized are the Cry1Ab communicating the delta endotoxin of *Bacillus thuringiensis* (Bt) ssp. kurstaki and the α-amylase inhibitor 1 (αAI-1) to target, individually, the unit borer (M. vitrata) and *C. maculatus* and *C. chinensis* (Abrol 1999; Popelka et al. 2006; Tarver et al. 2007; Adesoye et al. 2008; Huesing et al. 2011). Every one of these reviews permitted Solleti et al. (2008) to present the αAI-1 quality under bean phytohemagglutinin promoter, in "Pusa Komal," a financially imperative Indian cultivar, and to create fruitful transgenic plants which unequivocally restrained the improvement of *C. maculatus* and *C. chinensis* in insect bioassay. Due to the outcrossing observed among crops and crop to wild, the introduction of transgenic cowpea harboring insect-resistant gene in African agriculture would be a threat for the non-GM crop and their wild relatives (Williams and Chambliss 1980; Asiwe 2009). Lüthia et al. (2013) who preceded *αAI-1* gene is a cotyledon-specific promoter into the breeding line IT86D-1010 and the Japanese cultivar "Sasaque"

that both showed 100% larval (*C. chinensis* and *C. maculatus*) mortality in the seeds of transgenic lines. Currently, several genes of interest such as herbicide imazapyr, α-amylase inhibitor 1 (against bruchids), Cry1Ab, and Cry1Ac (against *Maruca*) have been brought in successfully into commercially important cultivars of cowpea, and the genes are transmitted in Mendelian fashion (Abaye et al. 2014). Investigations executed by Jackai et al. (1997) showed that the insect pests of cowpea controlled by several other different forms of Bt crystal toxins and this basic information was further used by Adesoye et al. (2008) and Bakshi et al. (2011) to introduce *Cry1Ab* in cultivars (TVu 201, Ife Brown, IT90K-277-2, IT90K-288, and IT90K- 391) and *Cry1Ac* genes in cultivar (Pusa Komal) in various cowpea genotypes, and their experiment results showed that the transgenes were carried in Mendelian fashion to the progenies which showed significant reduction of larvae survival and weight. These findings were confirmed by several other authors as the introduction of this gene in pea (Shade et al. 1994; Schroeder et al. 1995; Morton et al. 2000; Sousamajer et al. 2007), adzuki bean (Ishimoto et al. 1996), and chickpea (Sarmah et al. 2004; Ignacimuthu and Prakash 2006) conferred resistance against bruchid beetles.

5.13 Potential and Limitations of HPR to Insects in Grain Legumes

Crop protection includes application of synthetic pesticides, weedicides, etc. for protecting crops against pests and diseases and has largely been helpful in curbing the losses; however, their haphazard application leads to an adverse effect on environment and health hazards in human beings. The crop improvement efforts have been underway over a long period to develop varieties/cultivars with resistance to insect pests in grain legumes (Sharma 2005, 2016). Nevertheless, host plant resistance can be used as a primary constituent of pest control, as along with cultural, biological, and chemical control and as a check against the released susceptible cultivars, apart from the use of molecular approaches for the development of insect pests resistant cultivars of legumes. Adaptation of genetic alternatives, such as introgression/pyramiding of genes/quantitative trait loci associated, wide hybridization, and marker-assisted selections for development of insect pest-resistant cultivars, on the other hand, is much an ecological and eco-friendly approach (Khera et al. 2013). Special importance has been given on the current status and prospects of deploying newer molecular host plant resistance techniques and breeding approaches for developing improved cultivars with high resilience to major insect pests stress to achieve maximum genetic yield potential in all the legume crops. As we know, plant resistance to insects is the key factor of any pest management system because:

- It is specific to target insects or group of pests and generally has no adverse effects on the nontarget organisms in the ecosystem.
- Plant resistance effects on insect pest population are cumulative over sequential generations for particular pest because of bringdown survival, delayed development, and lower fecundity.

- The most of insect-resistant crop cultivars carry moderate to high level of resistance across cropping season. In contrast, the insecticides must be applied frequently in order achieve satisfactory control of pest populations.
- HPR is easy to be compatible with other strategies of pest control, and it also improves the efficiency of other methods of pest management.

However, host plant resistance is not the only nostrum for solution for all the insect pest problems in agroecosystem. It needs a long time for the exploitation of plant genotypes/cultivars with resistance to insect pests. Some mechanisms of plant resistance may involve the diversion of plant morphological traits or biochemical traits for the production of defense chemicals and other physiological processes that helps in obtaining yield (Mooney et al. 1983). Although concentration of natural defense chemicals responsible for resistance is low in plant tissues, the total amount per hectare may be high (Mitra and Bhatia 1982). Some plant defense chemicals also affect the food nutrition quality. Most of genotypes with resistance to *H. armigera* are susceptible to *Fusarium* wilt in both pigeon pea and chickpea (Sharma 2005). There is a need to generate baseline information on the inheritance of resistance to insect pests in grain legumes 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 basis of resistance for sustainable production of grain legumes. 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 do not have a negative effect on the quality of the product.

5.14 Conclusions

Conventional methods of protecting the legume crops from insect pests are inadequate to meet the growing demand for pulses in future. Accuracy and preciseness of phenotyping for resistance to insect pests remain a major critical limitation. Improved higher-version phenotyping systems will have a substantial impact on both MAS and conventional breeding in order to develop cultivars resistant to insect pests, in addition to there is a need of more strategic research that feeds into these endeavors. There are very limited reports concerning about the role of application of MAS for developing resistant cultivars in grain legumes. Be that as it may, those accessible neglects to exhibit an expansion in proficiency of MAS over conventional breeding methodologies. A combination of morphological, biochemical, and molecular markers is needed to introgress insect resistance genes from both cultigens germplasm and wild relatives of grain legumes to accelerate the process of developing cultigens with resistance to enhance the crop productivity and improve the livelihoods of the farming community.

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Breeding for Aphid Resistance in Rapeseed Mustard

6

Sarwan Kumar and S.S. Banga

Abstract

The productivity of oilseed brassicas is severely affected by aphid pests. Among the different aphid species, turnip/mustard aphid, *Lipaphis erysimi* (Kaltenbach), is the key pest of oilseed brassicas in Indian subcontinent inflicting 35.4–91.3% losses under different agroclimatic conditions. The development of an aphid-resistant cultivar offers an effective, economic and eco-friendly method of its management which requires the availability of a crossable source of resistance. Brassica plants employ a plethora of biophysical and biochemical defence mechanisms against insects, which range from surface waxes and trichomes to production of toxic biochemicals such as glucosinolates, isothiocyanates, lectins, volatiles, alkaloids, etc. Such resistant plants can be identified by an effective screening protocol, and the gene(s) of interest can be transferred to the desirable agronomic background by conventional breeding or marker-assisted selection. Not much progress has been made in breeding for resistance in brassicas against aphids primarily due to non-availability of resistant source within the crossable germplasm as well as lack of knowledge on its trait genetics. Though some success has been achieved to introgress the gene of interest to a desirable agronomic background, it has complex and elaborate breeding requirements. An alternate strategy to conventional breeding is the use of insect-resistant transgenes through genetic engineering, but this strategy has its own associated issues. Thus, the

S. Kumar • S.S. Banga (✉)
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana 141004, India
e-mail: sarwanent@pau.edu; nppbg@pau.edu

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development of aphid-resistant cultivars requires more research on aphid-plant interactions to identify either an effective aphid resistance gene or a phenomenon that can lead to a new mechanism of resistance.

Keywords
Brassica • Defence • Host plant resistance • *Lipaphis erysimi* • Screening techniques

6.1 Introduction

Crop brassicas belong to the family Brassicaceae. It is a major angiosperm family that includes nearly 375 genera and 3200 species (LeCoz and Ducombs 2006). Members of this family provide major sources of oilseeds, vegetables and condiments. Canola (*Brassica napus*); Indian mustard (*B. juncea*); *B. rapa* ssp. *oleifera*, viz., *toria* and brown *sarson*; and Abyssinian mustard (*B. carinata*) account for almost 13% of the vegetable oil supplies of the world. Besides its economic importance, Brassicaceae are of special significance in the study of insect-plant interactions as all members produce glucosinolates, which have a great influence on such relationships. Further, the genome of the closely related *Arabidopsis thaliana* has been sequenced, which can provide ready access to genetic and genomic resources (Hegedus and Erlandson 2012). *A. thaliana* is ideal as a model system for the study of insect-plant interactions at genetic and molecular level (Mitchell-Olds 2001). This chapter focuses on various aspects of breeding for resistance to mustard aphid in rapeseed-mustard. We also discuss various aspects of aphid biology, host-pest interactions and factors associated with resistance responses of the host.

6.2 The Aphid Complex of Brassicas

Aphids are global pests. Despite forming a small insect group, they inflict serious damage to agricultural crops (Remaudière and Remaudière 1997; Dedryver et al. 2010). They belong to family Aphididae and comprise approximately 5000 species (Smith and Chuang 2014), of which nearly 100 are very damaging for crop plants (Blackman and Eastop 2000, 2007). The main aphids infesting brassica crops are cabbage aphid [*Brevicoryne brassicae* (L.)], turnip/mustard aphid [*Lipaphis erysimi* (Kaltenbach)*/Lipaphis pseudobrassicae* (Davis)], shallot aphid [*Myzus ascalonicus* Doncaster], peach-potato aphid [*Myzus persicae* (Sulzer)], potato aphid [*Macrosiphum euphorbiae* (Thomas)], corn root aphid [*Aphis maidiradicis* Forbes] and root-feeding aphid species, namely, cabbage root aphid/poplar petiole gall aphid [*Pemphigus populitransversus* Riley] and bean root aphid [*Smynthurodes betae* Westwood] (Blackman and Eastop 2000). *B. brassicae*, a native to Europe and worldwide in distribution, is a major pest on vegetable brassicas in most European countries with strong yield reducing impacts. It is a brassica specialist insect that

feeds on phloem sap of its host plants (Cole 1997). Though a primary pest of vegetable brassicas, it also infests other species in genus *Brassica* (Cole 1994a, b, 1997; Kift et al. 2000). *L. erysimi* is a native to eastern Asia (Blackman and Eastop 2000). It is the most serious pest of oilseed brassica, especially in India and other subtropical regions of the world. It may cause 10–90% productivity losses, depending upon the agroclimatic conditions, intensity of population development and crop growth stage (Singh and Sachan 1994; Ahuja et al. 2009). *L. erysimi* is also a vector of ten non-persistent plant viruses like cabbage black ring spot and mosaic diseases of cauliflower, radish and turnip (Blackman and Eastop 1984; Rana 2005). It is a brassica specialist and can develop only on brassicaceous plants. Generally, *B. rapa* and *B. juncea* are better hosts than other *Brassica* species (Rana 2005).

Peach-potato aphid, *Myzus persicae*, is a generalist pest with a host range of more than 400 plant species (Quaglia et al. 1993). It is a major vector of more than 100 plant viruses including potato virus Y and potato leaf roll virus and various mosaic viruses, including western yellows (Ponsen 1972; Eskanderi et al. 1979; Bwye et al. 1997). It is cosmopolitan, polyphagous and an efficient vector of plant viruses. It possesses wide genetic variation for colour, life cycle, host plant relationships and mechanisms of insecticide resistance. Although many consider it to have originated from China, the native place of its primary host *Prunus persica*, others believe it to be a native of Europe (Blackman and Eastop 2007).

6.3 Aphid Biology

Aphids are the specialized phloem sap feeders. Their ability to rapidly exploit the ephemeral habitats makes them serious pests. High reproductive potential and dispersal capacities add to their wide adaptability (Dedryver et al. 2010). Aphids exhibit parthenogenetic viviparity – a process that limits the need for males to fertilize females and obviate egg stage from the life cycle. Thus, aphids reproduce clonally and give birth to young ones. Embryonic development of an aphid begins before its mother's birth leading to telescoping of generations. These attributes permit aphids to efficiently exploit the periods of rapid plant growth, conserve energy and allow rapid generation turnover. Nymphs of certain aphid species can reach maturity in as little as 5 days (Goggin 2007). Parthenogenesis sets them apart from other Hemiptera and has a great influence on their biology. Many species of aphids also exhibit alternation of generations. Evolution of alternating hermaphrodite generations with a series of parthenogenetic, all-female generations dates back to Triassic period (Blackman and Eastop 2007). Coupled with viviparity, this reduces the development period and permits rapid multiplication of aphids. Further, to conserve energy for maximizing their reproduction and survival, aphid colonies exhibit wing dimorphism to produce highly fecund wingless (*apterae*) morphs or less prolific winged (alate) progeny that can disperse to new host plants depending on the resource availability. All these strategies contribute to aphids' success and their abundance in temperate zones. An enormous propagation rate precipitates abnormally high population under favourable conditions (Goggin 2007).

6.3.1 Aphid Life Cycles

Most of the aphid species display relatively complicated life cycles, and each of these life cycles has morphs which specialize in reproduction, dispersal and survival under adverse conditions. Based on how aphids utilize their host plants, life cycle can be of two types: heteroecious or host alternating and monoecious/autoecious or non-host alternating. Heteroecious aphids live on one plant species (primary host) in winter and migrate to another taxonomically unrelated plant species (secondary host) in summer and again migrate to primary host in autumn. On the primary host plant, eggs are laid by females after mating with males. However, on the secondary host plant, they reproduce parthenogenetically. Aphids that interrupt parthenogenetic reproduction with sexual reproduction are termed as holocyclic. In contrast to host-alternating aphids, non-host-alternating aphids remain either on the same or closely related host species throughout the year. They complete both sexual and parthenogenetic life cycle on the same host species. There are also species which do not produce eggs and are known as anholocyclic. Some species can live both holocyclic and anholocyclic lives, simultaneously across wide geographies (Bhatia et al. 2011). However, monoecy and heteroecy can coexist rarely (Williams and Dixon 2007). The presence of both sexual and asexual life cycle ensures that aphids take advantage of both parthenogenesis and genetic recombination that help them to evolve.

Lipaphis erysimi is a holocyclic species with a chromosome number of 2n = 10 (Blackman and Eastop 2000). Although it produces parthenogenetically in warmer climates, a holocyclic reproduction has been reported in western Honshu, Japan, on cruciferous crops (*B. rapa*, *Raphanus sativus*) (Kawada and Murai 1979). A chromosome number of 2n = 8 and differing in karyotype from holocyclic populations have been reported from Northern Europe. Most anholocyclic parthenogenetic populations have 2n = 9, probably derived from eight chromosomes through dissociation of one autosome to produce a small, unpaired element. Though sexual morphs have been reported from North India, populations were mostly anholocyclic (Blackman and Eastop 2007).

Brevicoryne brassicae is a monoecious species that exhibits holocyclic life cycle with parthenogenetic reproduction in warmer climates as well as during warmer periods of temperate climates. However, with the fall in temperature during autumn, males are also produced (Blackman and Eastop 1984), which mate with the females to produce eggs for overwintering. As per Hines and Hutchison (2013), about 15 overlapping generations are passed in a crop season in the United States.

Myzus persicae exhibits holocyclic life cycle, and it overwinters as egg stage on its primary host (peach and related trees). In the subsequent spring or summer season, fundatrix/fundress (the winged stem mother) returns as alate emigrants to secondary host plants and multiplies to apterous and alate viviparae (Moran 1992; Bhatia et al. 2011). The wingless female then gives birth to young ones by parthenogenesis and multiplies at a very fast rate. This results in large aphid populations on different crop plants. When the temperature starts falling late in the season, some of the apterous viviparae turn into apterous oviparae and alate viviparae into alate

males. These males and females start sexual reproduction and lay eggs on the primary host plant (Stern 1995). At the end of winters, females (stem mothers) hatch from the eggs the next spring season and start reproducing parthenogenetically (Bhatia et al. 2011).

6.3.2 Aphid-Host Plant Interactions

Aphids are specialized phloem sap feeders which insert their needle-like stylets in the plant tissue avoiding/counteracting the different plant defences. They withdraw large quantities of phloem sap while keeping the phloem cells alive. In contrast to the insects with biting and chewing mouthparts which tear the host tissues, aphids penetrate their stylets between epidermal and parenchymal cells to finally reach sieve tubes with slight physical damage to the plants, which is hardly perceived by the host plant (Bhatia et al. 2011). The long and flexible stylets move through intercellular spaces in the apoplasm of the cell wall (Giordanengo et al. 2010), although stylets also make intracellular punctures to probe the internal chemistry of a cell (Zust and Agrawal 2016). The high pressure within sieve tubes helps in passive feeding (Bhatia et al. 2011). During the stylet penetration and feeding, aphids produce two types of saliva. The first type is dense and proteinaceous (including phenoloxidases, peroxidases, pectinases, β-glucosidases) that forms an intercellular tunnelled path around the stylet in the form of sheath (Felton and Eichenseer 1999; Zust and Agrawal 2016). In addition to proteins, this gelling saliva also contains phospholipids and conjugated carbohydrates (Urbanska et al. 1998; Miles 1999; Cherqui and Tjallingii 2000; Sharma et al. 2014). This stylet sheath forms a physical barrier and protects the feeding site from plant's immune response (Will et al. 2012, 2013). When the stylets encounter active flow of phloem sap, the feeding aphid releases digestive enzymes in the vascular tissue in the form of second type of 'watery' saliva. The injection of watery saliva (E1) prevents the coagulation of proteins in plant sieve tubes, and during feeding the watery (E2) saliva gets mixed with the ingested sap which prevents clogging of proteins inside the capillary food canal in the insect stylets (Bhatia et al. 2011; Sharma et al. 2014; Zust and Agrawal 2016). Though the actual biochemical mode of action that inhibits protein coagulation is unknown, the calcium-binding proteins of aphid saliva are reported to interact with the calcium of plant tissues. This results in suppression of calcium-dependent occlusion of sieve tubes and subsequent delayed plant response (Will et al. 2007, 2009, 2013). This mechanism of feeding is more specialized and precise, which helps the aphid to avoid different allelochemicals and indigestible compounds found in other plant tissues (Schoonhoven et al. 2007). In addition to this, aphid saliva also contains non-enzymatic reducing compounds, which in the presence of oxidizing enzymes inactivate different defence-related compounds produced by plants in response to the insect attack (Miles 1999).

There are commonalities of events during initial plant reaction to insect feeding or pathogen infection. These include protein phosphorylation, calcium influx, membrane depolarization and release of reactive oxygen species (ROS), such as

hydrogen peroxide (Garcia-Brugger et al. 2006). These lead to activation of phytohormone-dependent pathways. In response to infestation/infection, different phytohormone-dependent pathways are activated. Ethylene (ET) and jasmonate (JA) pathways are activated by different necrotrophic pathogens (Thomma et al. 2001) and grazing insects (Maffei et al. 2007), while salicylate (SA)-dependent responses are induced by biotrophic pathogens (Thomma et al. 2001). These responses lead to the production of various defence-related proteins and secondary metabolites with antixenotic or antibiotic properties. In the event of infestation by aphids, a SA-dependent response was seemingly activated. In contrast, JA-dependent genes were repressed (Zhu-Salzman et al. 2004; Thompson and Goggin 2006; Gao et al. 2007; Walling 2008). All these responses lead to the manipulation of the plant metabolism to ensure compatible aphid-plant interactions.

6.3.3 Aphid Endosymbionts

The phloem sap is a highly unbalanced diet composed principally of sugars and amino acids with high C:N content. The most of the amino acids are present at very low concentrations. Despite their nutritionally poor diet, aphids exhibit high growth and reproduction rates. Since aphids directly feed on the sugars and amino acids, their assimilation efficiency is very high. In addition, essential amino acids required by their growth and development are synthesized by symbiotic bacteria present in their body. These include primary (obligate) symbionts and secondary (facultative) symbionts. *Buchnera aphidicola* (gamma-3 proteobacteria, *Escherichia coli*, is also a member of this group) is the most common vertically transmitted primary symbiont present in most aphid species (Munson et al. 1991; Oliver et al. 2010). Some species of aphids also bear other bacteria, i.e. 'secondary symbionts'. These include several species of gamma-proteobacteria such as *Serratia symbiotica*, *Regiella insecticola* and *Hamiltonella defensa* (Chen et al. 1996; Chen and Purcell 1997; Fukatsu et al. 2000, 2001; Darby et al. 2001; Sandstrom et al. 2001; Haynes et al. 2003; Russell et al. 2003; Moran et al. 2005; Oliver et al. 2010). *B. aphidicola* is a coccoid hosted in the cytoplasm of specialized cells called mycetocytes/bacteriocytes in the haemocoel of insect. These endosymbionts upgrade the aphid diet by converting non-essential amino acids to essential amino acids. The evolution of symbiotic relationship with endosymbionts has enabled aphids to exploit new ecological niches, i.e. to feed on the plant phloem sap which is otherwise the nutritionally poor diet.

6.4 Plant Defence Responses Against Insects

Brassicas possess an array of defence mechanisms against different biotic stressors including insect herbivores. These include surface waxes, trichomes, plant secondary metabolites and different volatiles, which provide varying degree of protection against insects feeding on them. Such defence mechanisms can be constitutive or

inducible and direct or indirect defences. The constitutive defences comprise physical and chemical barriers that exist before insect attack (preformed/innate defences). These may be the ancient defences involving different plant receptors that recognize microbial cell surface molecules, signal transduction pathways that induce transcription of defence-associated genes and antimicrobial effectors, cationic peptides and proteins (Boman 1995; Borregaard et al. 2000; Thomma et al. 2002 as cited from Ahuja et al. 2009). In contrast, inducible defences are induced following invasion of an insect herbivore. This kind of defence is particularly important when the defence is bioenergetically expensive and insect attack is frequent and unpredictable (Haukioja 1999). The defences that show their effect on the herbivore through synthesis of toxins are called direct defences, while the defences that affect herbivores through the attraction of natural enemies of insects are called indirect defences (Dicke 1999). Brassica plants release different volatile compounds to attract natural enemies of insects that feed on them. This release of volatile organic compounds is construed as a 'cry or call' for help by the plant from herbivore predators. The different defence components of brassica plants are discussed in the following subsections.

6.4.1 Biophysical Defences

Many morphological and anatomical characters may influence the suitability of a plant as host to the insect (Southwood 1986). These characters may include epicuticular wax, trichomes, depth of vascular bundles, etc. The epicuticular wax is the first site of interaction between insect and its host plant, and hence, its chemical composition is critical for an insect to feed, probe or oviposit on a plant. The waxes are complex mixtures of very-long-chain lipids substituted with primary alcohols, aldehydes, fatty acids and alkyl esters, all of which primarily occur with even-numbered chain lengths and hydrocarbons, secondary alcohols and ketones with predominance of odd chain lengths (Walton 1990). Waxiness has been found to hinder *L. erysimi* from reaching the undersurface of leaves, where it normally feeds during the vegetative plant stage (Åhman 1990). However, Lamb et al. (1993) reported that elevation of leaf wax did not improve the resistance of *B. napus* or *B. oleracea* (kale and collard) to *L. erysimi*. The neonate larvae of diamondback moth, *Plutella xylostella* L., have been shown to spend more time walking at a faster pace on waxy line of cabbage compared to that on non-waxy one (Eigenbrode et al. 1991). The young larvae of mustard beetle, *Phaedon cochleariae* (Fab.), find it difficult to climb the heavily waxed culm of cabbage on waxy cultivars and failed to reach their feeding site, while they easily walked on the non-waxy cultivars (Stork 1980). Although waxy trait is responsible for resistance to insect pests, glossiness is not a preferred trait in vegetables. Increased resistance to *P. xylostella* was observed in *B. oleracea* and *B. rapa* genotypes having glossy leaves (Ulmer et al. 2002). A significant increase in the feeding by flea beetle, *Phyllotreta cruciferae* (Goeze), was observed after removal of epicuticular wax from leaves of *B. napus* and *B. oleracea* particularly from the area where wax was removed (Bodnaryk 1992) and

most difference in feeding preference was explained by the presence of leaf wax. Reifenrath et al. (2005) observed an increase in *P. cochleariae* activity after removal of leaf wax, suggesting that wax occludes stimulatory signals such as glucosinolates, and they suggested that the resistance was primarily antixenosis. The importance of waxes on leaf surface has received increased attention in the recent years due to their association with polar compounds like glucosinolates, the key host recognition signals for specialist insects (Badenes-Pérez et al. 2010; Städler and Reifenrath 2009). Badenes-Pérez et al. (2010) reported the presence of glucosinolates on leaf surface of three *Barbarea* species but not on the surface of test *B. napus* genotype. The leaf surface wax has been reported to affect even the third trophic level. The aphids' parasitoid host recognition behaviour is influenced by aphid cuticular waxes which in turn are related to the plant surface waxes (Muratori et al. 2006).

Trichomes may also influence leaf herbivory by insects. The trichomes are small, sometimes branched, hair-like structures that are produced from cells of aerial epidermis, produced by most plant species (Werker 2000). Glandular trichomes produce secondary metabolites (e.g. flavonoids, alkaloids, terpenoids) which can either repel or trap insects or can be poisonous (Duffey 1986). The trichome producing morphotype of *Arabidopsis lyrata* was reported to be less damaged by insect herbivores than the glabrous form (Loe et al. 2007). The non-glandular trichomes, unlike glandular trichomes, do not produce secondary metabolites but mainly function as structural defence against small herbivores by interfering with insect movement on the plant surface (Southwood 1986). The insects feeding on trichome-bearing plants show poor weight gain due to poor nutritive value of cellulose-rich trichomes resulting in increased mortality. *B. nigra* lines having high number of trichomes supported less growth of *Pieris rapae* (L.) and increased mortality of *P. cruciferae* (Traw and Dawson 2002). Agrawal (1999) reported an increase in trichome density after insect damage in *Raphanus raphanistrum.* Similarly, Traw (2002) reported an increase in the trichome density as well as glucosinolate level after feeding by *P. rapae* in black mustard. Trichome-bearing pods of *Sinapis alba* were reported to be resistant to flea beetle, while glabrous pods of cultivated *Brassica* species are readily attacked (Lamb 1980).

Expression of *A. thaliana* myb-like transcriptor factor, GLABRA3 (GL3) in *B. napus*, resulted in the production of a dense coat of trichomes on the adaxial leaf surface (Gruber et al. 2006), and *P. xylostella* larvae had difficulty in feeding on these lines and grew slower (Adamson et al. 2008). Despite their negative effects on herbivore insects, trichomes may have their effect at the third trophic level. For example, trichomes on the leaves of trichome-bearing line of *Arabidopsis thaliana* affected the movement of aphid predator, *Episyrphus balteatus* (De Geer), and resulted in reduced performance (Wietsma 2010). Further, trichomes play an important role in the acceptance of host plants for oviposition (Sadeghi 2002), and there was comparatively less oviposition on *A. thaliana* line having higher trichome density (Wietsma 2010).

Before reaching the sieve tubes for feeding, aphid stylets had to pass through different cell layers such as the epidermis, endodermis, cortex and pericycle. The

plants with densely packed cell layers may pose hindrance to the stylets and, hence, may be less preferred (Henning 1966). Moderate resistance to aphids in *B. carinata*, *B. alba* and *Eruca sativa* has been attributed to this factor (Malik 1981). The depth of sieve tubes is an important factor in resistance of a plant to aphids. Aphids must have long stylets to feed on plant tissues with deeply localized vascular bundles (Gibson 1972). Further, such aphids will require more energy to probe deep into the plant tissue, while aphids with short stylets will starve and die (Berlinski 1965).

6.4.2 Biochemical Defences

6.4.2.1 Glucosinolates and Myrosinase-Glucosinolate System

Glucosinolates (GSLs) of brassica plants are a class of secondary metabolites. These amino acid-derived, secondary plant products containing β-D-thioglucose and sulphonated oxime moieties are found almost exclusively in the order Capparales (Halkier and Gershenzon 2006). They are a large group of naturally occurring, non-volatile, sulphur-containing, organic anionic compounds and are reported to be present in 16 plant families (Fahey et al. 2001). GSLs include approximately 140 naturally occurring thioglucosides that mainly differ in their R-group substitutes (Fenwick et al. 1983), and 30 of these are present in *Brassica* species (Bellostas et al. 2007). Although the glucosinolates may confer resistance to insects which feed on them, their breakdown products released after myrosinase hydrolysis can be more toxic. Myrosinase (thioglucoside glucohydrolase, EC 3.2.3.1) catalyses the cleavage of glucosinolates to produce an aglycone moiety (thiohydroxamate-*O*-sulfonate), glucose and sulphate. The aglycone moiety, being unstable, rearranges to form isothiocyanates (ITCs), thiocyanates, nitriles, amines, oxazolidine-thiones and epithionitriles depending upon the glucosinolate being hydrolysed and the reaction conditions (Rask et al. 2000; Sadasivam and Thayumanavan 2003). The concentration of glucosinolates varies widely depending upon different species, plant parts and agronomic and climatic conditions (Font et al. 2005; Tripathi and Mishra 2007). A drastic decline in the concentration of glucosinolates (mainly aliphatic ones) occurs in *B. napus* seeds during the first 7 days of imbibition, while *de novo* synthesis of indolyl glucosinolates and an aromatic glucosinolate (gluconasturtin) takes place concomitantly. Gluconasturtin is not initially present in the seed. During the subsequent growth period, some more glucosinolates also accumulate (Clossais-Besnard and Larher 1991). On the other hand, glucosinolates occur in low concentrations in the fully expanded leaves (Porter et al. 1991). With the start of the reproductive phase of plant, i.e. during flowering, there is a reduction in the concentration of glucosinolates in vegetative plant parts as well as in inflorescence, which otherwise has relatively large amounts of glucosinolates. In contrast to this, during maturation of seeds, glucosinolate synthesis occurs in siliques which are then transported to the seeds through pod shells (Rask et al. 2000). The levels of glucosinolates can also be influenced by environmental conditions. An increase in the concentration of glucosinolates occurs in brassica plants under drought conditions (Bouchereau et al. 1996; Jensen et al. 1996). However, there is no consistent

relationship between glucosinolate concentration and water stress since increased levels of glucosinolates are also observed in plants grown under moist conditions compared to those grown in dry soil (Louda and Mole 1991). In intact plant tissues, glucosinolates and myrosinase are housed separately and individually where these are inactive thus preventing self-toxicity (Jones and Vogt 2001). This intracellular localization of myrosinase has been widely investigated. Lüthy and Matile (1984) propounded 'the mustard oil bomb hypothesis' for this organization. As per this hypothesis, glucosinolates are present in the myrosin grains (vacuoles) of myrosin cells, while the myrosinase is associated with the membranes in the cytoplasm. However, later studies proved that glucosinolates (Kelly et al. 1998) are present in vacuoles of different types of cells, while myrosinases are localized in the myrosin cells (Thangstad et al. 1991; Höglund et al. 1992; Kissen et al. 2009) scattered across the plant tissues. Myrosin cells carry myrosin grains (Bones et al. 1991; Kissen et al. 2009), forming a continuous reticular system or myrosin body (Andreasson et al. 2001; Ahuja et al. 2009). Tissue damage caused by insect feeding brings glucosinolates and myrosinase together, precipitating immediate release of glucosinolate-breakdown products (Bones and Rossiter 2006). Such defensive responses (or 'mustard oil bomb') play multiple roles in plant-insect interactions (Rask et al. 2000; Kissen et al. 2009). These defend the plants against the attacks by generalist feeders (Rask et al. 2000) but at the same time expose them to attack by specialist feeders (Renwick 2002; Bjorkman et al. 2011). Glucosinolates are feeding and oviposition stimulants for more than 25 insect species of the orders Coleoptera, Lepidoptera and Diptera (Hopkins et al. 2009). As a consequence of coevolution, insects like *B. brassicae* and *L. erysimi* (both crucifer specialists) can sequester glucosinolates from host plant to protect themselves from predators. These insects can synthesize their own thioglucosidase endogenously, which is spatially separated in the insect body from sequestered glucosinolates in their non-flight muscles. When an insect is crushed or fed upon by a predator, thioglucosidase hydrolyses the sequestered glucosinolates (glucosinolate concentration in haemolymph is normally 15–20 times more than those in the leaf tissue) to produce toxic products (Bridges et al. 2002; Rossiter et al. 2003). These products taste badly and also release volatiles to alarm other insects in the colony. In comparison, the generalist aphid, *M. persicae*, excretes glucosinolates in its honeydew (Hopkins et al. 2009). Another example of coevolution is the production of a glucosinolate sulfatase enzyme (GSS) by the diamondback moth, *P. xylostella* (specialist) (Ratzka et al. 2002), and desert locust, *Schistocerca gregaria* (Forskål) (generalist) (Falk and Gershenson 2007). GSS desulphonates glucosinolates to produce desulphoglucosinolates which are not amenable to hydrolysis by myrosinase. Thus, the production of toxic isothiocyanates is prevented. This enables the insects to feed on glucosinolate-rich plants (Ratzka et al. 2002; Falk and Gershenson 2007). In contrast, *P. rapae* is able to manipulate glucosinolate hydrolysis reaction in such a way that instead of toxic isothiocyanates, less toxic nitriles are formed (Wittstock et al. 2004). Glucosinolates are also known to stimulate larval feeding and oviposition by adults of the large white butterfly, *Pieris brassicae* (L.), and small white butterfly, *P. rapae* (Renwick et al. 1992; Smallegange et al. 2007). These also stimulate

oviposition by *P. xylostella* (Renwick et al. 2006). Many insects such as *B. brassicae* (Nottingham et al. 1991) and *P. xylostella* (Renwick et al. 2006) carry receptor neurons that can detect isothiocyanates to find host location.

Buxdorf et al. (2013) experimented with *Arabidopsis thaliana* mutants having varying levels of glucosinolates and glucosinolate-breakdown products to study the effects of these phytochemicals on phytopathogenic fungi. It was observed that *Alternaria brassicicola* was more strongly affected by aliphatic glucosinolates and isothiocyanates as decomposition products. *B. cinerea* also induced glucosinolate accumulation at a level higher than that by *A. brassicicola*. For *A. brassicicola*, the type of glucosinolate-breakdown product was more important than the type of glucosinolate from which that product was derived. For example, the sensitivity of the *Ler* background and the sensitivity gained in Col-0 plants expressing epithiospecifier protein depended upon the type of breakdown products, both of which accumulate simple nitrile and epithionitriles, but not isothiocyanates. Correlations between identical compounds in different plant tissues permit (co-)regulation of their biosynthesis or emission. The glucosinolate content seemed positively correlated in leaves and other tissues indicating independent regulation of emission (Sotelo et al. 2014; Gupta et al. 2015). However, none of the leaf or flower volatiles was positively associated with gluconapin, glucobrassicanapin or the sum of all glucosinolates in either leaves or flowers. The lack of consistent positive correlations between VOCs and major defence compounds may indicate that plants avoid eavesdropping by specialist herbivores to locate their host plants. Negative correlations may indicate chemical trade-offs for synthesis of the secondary metabolites.

Although glucosinolates play a defensive role in plants against herbivorous insects, there have been concerns regarding increased insect susceptibility of canola cultivars with exceptionally low level of these compounds. Such concerns may be far-fetched since low glucosinolate levels in such cultivars are confined mainly to the seeds (Milford et al. 1989). Also, high and low glucosinolate cultivars did not differ in their susceptibility to pod midge (*Dasineura brassicae*) (Åhman 1982). Extensive studies in India with both *B. napus* and *B. juncea* canola have shown no reasons to believe that canola quality cultivars were more susceptible than their non-canola counterparts. In fact, the inheritance mechanism of glucosinolates in *B. juncea* seemed to be different in leaves and seeds. Major QTLs accounting for a large variation in seeds or leaves were not co-localized (Gupta et al. 2015). Though there are no supporting references, low glucosinolate plants may be less attractive to specialist insects for which these compounds serve as attractants and feeding stimuli (Gabrys and Tjallingii 2002; Mewis et al. 2002). This is supported by the work of Giamoustaris and Mithen (1995) who reported that increase in the content of glucosinolates in *B. napus* resulted in increased feeding damage by the specialist insects, flea beetles [*Psylliodes chrysocephala* (L.)] and greater incidence of small white butterfly (*P. rapae*), while the damage by generalist pests, i.e. pigeons and slugs, was reduced. Further, glucosinolate-rich flower tissues are preferred more by *P. brassicae* and sustain higher growth compared to leaf tissues (Smallegange et al. 2007) indicating the selective role of glucosinolates to elicit feeding in this specialist insect and the adaptation of the insect to use these compounds to its advantage.

6.4.2.2 Phytoalexins and Phytoanticipins

Phytoalexins are antimicrobial secondary metabolites produced *de novo* by plants in response to biotic or abiotic stresses (Bailey and Mansfield 1982; Pedras and Yaya 2010), while phytoanticipins are constitutive defences already present in the plant irrespective of the stress. Plant secondary metabolites can be phytoalexins in one plant species and phytoanticipins in the other.

Polyphenolics – phenolic acids, flavonoids and lignans, terpenoids, phytosterols and alkaloids – have been associated with plant defences. Phenolics, especially the condensed tannins, are feeding deterrents to several pests on *B. napus* (Meisner and Mitchell 1984; Muir et al. 1999). These act by inactivating digestive enzymes (Nguz et al. 1998) or through antibiotic effects (Duffey and Stout 1996). A sinapic acid – precursor of sinapine – has been found to deter the oviposition by *Delia radicum* (L.) on cauliflower plants (Jones et al. 1988). Flavonoids show both stimulatory and deterrent effects on insects feeding on brassica plants. Quercetin and kaempferol from *Armoracia rusticana* stimulated feeding by *Phyllotreta armoraciae* (Koch) (Nielsen et al. 1979) and *P. xylostella* (van Loon et al. 2002). In contrast, isorhamnetin-3-sophoroside-7-glucoside and kaempferol 3,7-diglucoside found in *B. napus* were deterrent to *Mamestra configurata* (Walker), at levels higher than those found in vegetative tissues (Onyilagha et al. 2004). The phytosterols, strophanthidin and strophantidol, found in *Cheiranthus* and *Erysimum* species, exhibited feeding deterrent action against flea beetle species, *Phyllotreta undulata* (Kutschera), *Phyllotreta tetrastigma* (Comolli) and *P. cochleariae* (Nielsen 1978). Camalexin-deficient *A. thaliana* mutants showed greater susceptibility to the cabbage aphid, *B. brassicae* (Kusnierczyk et al. 2008), suggesting the role of camalexin in insect resistance.

6.4.2.3 Volatile Compounds

Volatile compounds are associated with plant-insect communication, plant-pathogen communication and plant-plant communication (Baldwin et al. 2002). These volatiles can be monoterpenes, sesquiterpenes, indole or 'green leafy volatiles' (Tumlinson et al. 1999). The hydrolysis of glucosinolates leads to the production of volatile thiocyanates, isothiocyanates and nitriles. Cabbage seed weevils, *Ceutorhynchus assimilis* (Paykull), are attracted to 3-butenyl and 4-pentenyl isothiocyanate in *B. napus*, but not to 2-phenylethyl isothiocyanate (Bartlet et al. 1993). Similarly, cabbage root fly, *Delia brassicae* L., was attracted to 4-methylthio-3-butenyl isothiocyanate and 1-cyano-4-methylthio-3-butene produced after glucosinolate hydrolysis in *Raphanus sativus* (Ellis et al. 1980). Though different herbivore insects use these volatile compounds as cues to locate their hosts, these also serve as a means of indirect defence against the herbivores. Plants release volatiles following insect attack to attract natural enemies that keep a check on the herbivore insect population. Volatile z-jasmone not only repels *L. erysimi* but also attracts its parasitoids on brassica plants (Birkett et al. 2000). Blande et al. (2007) have reported the attraction of the aphid parasitoid, *Diaeretiella rapae* (M'Intosh) towards semiochemicals produced by turnip plants after feeding by *L. erysimi* (specialist) and *M. persicae* (generalist). Pope et al. (2008) studied the orientation

response of cabbage aphid, *B. brassicae*, and its parasitioid, *D. rapae*, to alkenyl glucosinolate hydrolysis products. The electroantennogram responses indicated peripheral odour perception in *D. rapae* females to all the 3-butenylglucosinolate hydrolysis products.

6.4.2.4 Lectins

Lectins are found across a range of plant, microbial and animal tissues (Nachbar and Oppenheim 1980; Komath et al. 2006; Michiels et al. 2010; Vandenborre et al. 2011). These are the proteins which selectively bind with carbohydrate moieties of glycoproteins that are located on animal cell surface. Lectins incorporated in artificial diets have been shown to reduce performance of several insect pests (Murdock et al. 1990; Powell et al. 1993; Sauvion et al. 2004a; Vandenborre et al. 2011). Although the actual mechanism of insecticidal action is not clearly known, these are not adequately metabolized by digestive enzymes. These can be lethal due to their affinity to epithelial cells in the insect gut (Vasconcelos and Oliveira 2004). They can bind with gut proteins (e.g. glycosylated proteins) with high affinity (Macedo et al. 2004; Sauvion et al. 2004b). Since, lectins interact with mono- and oligosaccharides, the insecticidal activity may involve a specific carbohydrate-lectin interaction with glycoconjugates on the surface of digestive tract epithelial cells (Macedo et al. 2004), precipitating nausea, vomiting and diarrhoea. They may also cause membrane disruption of epithelial cell microvilli of insects fed upon diet containing lectins (Hart et al. 1988). Lectins show biological activity against a range of sap-sucking insects (Foissac et al. 2000; Powell 2001). *Brassica fruticulosa* – a wild relative of cultivated brassicas – appeared to possess resistance against the cabbage aphid, *B. brassicae* (Cole 1994a, b; Ellis and Farrell 1995; Ellis et al. 2000) as well as to *L. erysimi* (Kumar et al. 2011). A high concentration of lectins appeared responsible for the resistance. Feeding preference/choice tests have shown that *L. erysimi* had maximum feeding preference for *B. rapa* ssp. brown *sarson* cv. BSH 1. Least preference was reported for *B. fruticulosa*. The antixenosis to feeding in *B. fruticulosa* has been reported earlier for cabbage aphid, *B. brassicae*. Monitoring of feeding behaviour of this species by electrical penetration graph (EPG) revealed a significant reduction in the duration of passive phloem uptake on *B. fruticulosa* compared to the susceptible *B. oleracea* var. capitata cv. 'Offenham Compacta'. There was either quick withdrawal of stylets from sieve elements or disrupted phloem uptake (Cole 1994a).

6.5 Host Resistance Against Aphids

Brassica plants are among the oldest cultivated plants known to humans with documented records dating back to ca. 1500 BC (Raymer 2002). The domestication of brassica plants resulted in the narrowing of their genetic base. The breeding efforts in brassica plants were largely focused on high yield and desirable quality traits such as low glucosinolates and erucic acid content, and little attention was paid by plant breeders to maintain adequate level of insect and/or disease resistance. All this

led to loss of genes employed by their ancestors to ward off insect herbivores. It may be possible to remobilize lost defensive genes which requires the screening of a large brassica germplasm for resistance against insects which further requires a quick and efficient screening methodology.

6.5.1 Screening Methodology

Many attempts have been made to identify sources of resistance in primary gene pool of crop *Brassica* species (Brar and Sandhu 1978; Amjad and Peters 1992; Sekhon and Åhman 1992; Bhadoria et al. 1995; Saxena et al. 1995). The literature on the screening techniques for aphid resistance has been reviewed extensively by Bakhetia and Bindra (1977). Available screening techniques are summarized in this section.

6.5.1.1 Screening at Seedling Stage

Screening at seedling stage is always desirable since screening at adult plant stage is often laborious and time consuming. However, no serious attempt has been made to correlate seedling stage resistance with the adult plant resistance. Bakhetia and Bindra (1977) have tried to develop seedling screening methodology which is compatible with adult plant evaluation which is based on the seedling mortality at a defined aphid population level. Population levels of 11, 20, 20 and 30 wingless aphids and 1 ml and 3 ml aphids (1 ml = about 600 nymphs + wingless adults) per plant appeared optimal for resistance screening at cotyledonary, 2-leaf, 4-leaf, 6-leaf, flower bud initiation and flowering stages, respectively (Sekhon and Åhman 1992). The results obtained at all the test stages were comparable when screening was conducted under optimum level of aphid population per plant. The effect on the survival and fecundity was also similar at all the stages studied. Despite its advantages, this screening technique is not widely used for brassica germplasm screening against aphids.

6.5.1.2 Screening at Adult Plant Stage

Adult plant screening is the most widely used method for screening against aphids. Though it is laborious and time consuming, it reflects the resistance shown by plants under actual field conditions. It is based on the different injury symptoms manifested upon aphid feeding such as yellowing, curling, crinkling of leaves, drying of flower buds and flowers and shrivelling of developing pods. Different workers have adopted different grading systems, but the one published by Bakhetia and Sandhu (1973) is generally adopted for screening at adult plant stage. A major limitation of this method is the failure to account for different phenologies of the test genotypes. Late flowering genotypes are sometimes misclassified as resistant as flowering initiations in late genotypes may coincide with season end high temperatures, which are invariably less than congenial for aphid infestation.

Different injury grades are given to the test entries on the basis of degree of insect damage.

Aphid infestation index (AII)	Description
0	Free from aphid infestation. Even if a single wingless aphid is present, the plant is considered infested. Plants showing excellent growth
1	Normal growth, no curling or yellowing of the leaves, except only a few aphids along with little or no symptoms of injury. Good flowering or pod setting on almost all the branches
2	Average growth, curling and yellowing of a few leaves. Average flowering and pod setting on all the branches
3	Growth below average, curling and yellowing of the leaves on some branches. Plants showing some stunting, poor flowering and little pod setting
4	Very poor growth, heavy curling and the yellowing of leaves, stunting of plants, little or no flowering and only a few pods forming. Heavy aphid colonies on plants
5	Heavy stunting of plants, curling, crinkling and yellowing of almost all the leaves. No flowering and pod formation. Plants full of aphids

A specific injury grade is given to every observed plant, and the aphid infestation index (AII) is worked out by multiplying the number of plants falling under each grade with the respective grade number. The AII is calculated at pre-flowering, flowering and pod formation stages as

$$\text{Aphid Infestation Index} = \frac{(0\times a)\pm(1\times b)\pm(2\times c)\pm(3\times d)\pm(4\times e)\pm(5\times f)}{a+b+c+d+e+f}$$

where a, b, c, d, e and f are the number of plants falling under each injury grade.

The different test entries are classified into different resistance categories based on the AII as

Aphid infestation index (AII)	Reaction
0.00–1.50	Resistant
1.51–2.50	Moderately resistant
2.51–3.50	Susceptible
> 3.50	Highly susceptible

The higher the AII, the lower the level of resistance in an entry

6.5.1.3 Other Screening Methods

Only limited attempts have been made to develop a screening technique based on the biology of mustard aphid, despite its significance in identifying sources of resistance. According to Bakhetia and Bindra (1977), it is possible to develop such a criterion for screening since nymphal survival, fecundity, longevity and reproduction are similar at all the plant growth stages. Singh et al. (1965) and Malik (1981) have also reported fecundity to be inversely related to resistance. Aphid population at a particular stage and an increase in the population during a given time interval can also be used in germplasm screening (Bakhetia and Sekhon 1989). More recently, Kloth et al. (2015) have demonstrated the use of automated video tracking for phenotyping of plants for resistance to aphids. Though this method can be used

to screen a large number of accessions at a time, it has the limitation that it uses the leaf discs instead of intact plants and, hence, does not reflect the actual resistance exhibited by plants. The resistance effect was partially lost in the leaf discs. However, this limitation can be overcome by the use of electrical penetration graphs (EPG) (Tjallingii 1988; Trebicki et al. 2012) which uses the intact leaf instead of leaf disc, but this technique has its own high equipment cost limitation.

6.5.2 Breeding for Aphid Resistance

Three different mechanisms are responsible for imparting insect resistance to plants: antixenosis, antibiosis and tolerance. Antixenosis is rarely effective under no-choice conditions since insects can learn to feed on the less preferred plant. In contrast, antibiosis puts a selection pressure on the insects, and there is always a risk of development of insect biotypes, a danger not applicable to tolerance. Tolerance imparts least pressure on the insect to adapt. A sustainable resistance results from amalgamation of all three mechanisms (Smith 1989).

Different breeding methods have been used to develop resistant cultivars. These include intervarietal hybridization, induced mutagenesis or autotetraploidy. *B. napus* strains and colchicine-induced tetraploid *toria* (*B. rapa*) appeared more resistant to mustard aphid in contrast to diploids (Rajan 1961; Singh et al. 1965; Jarvis 1970; Gill and Bakhetia 1985; Kalra et al. 1987), and the resistance was attributed to be due to antibiosis; however, these were cytogenetically unstable. Many workers have also attempted to artificially synthesize alloploids of *B. napus* (Prakash and Raut 1983) and *B. rapa* x *Eruca sativa* (Agnihotri et al. 1990 as cited from Sekhon and Åhman 1992), but these were not resistant to the aphids.

In the past, Lammerink (1968) attempted to develop cabbage aphid-resistant variety of rape after selection in the F_3 generation of the cross (Broad Leaf Essex rape x Colder Swede) x giant rape. He also attempted recurrent selection in the crosses involving purple top white Globe and Sjodin turnip for breeding mustard aphid-resistant variety. Recently Kumar et al. (2011) reported wild *B. fruticulosa* (Plate 6.1) to be resistant to mustard aphid and described attempts at the introgression of resistance gene(s) from *B. fruticulosa* to *B. juncea*. *B. fruticulosa* have been previously reported to possess resistance against the cabbage aphid, *B. brassicae* (Cole 1994a, b, Ellis and Farrel 1995, Ellis et al. 2000). Study of feeding behaviour of *B. brassicae* electronically by electrical penetration graph (EPG) showed a large reduction in the duration of passive phloem uptake from *B. fruticulosa* compared to *B. oleracea* var. capitata cv. 'Offenham Compacta'. There was either quick withdrawal of stylets from sieve elements or disrupted phloem uptake (Cole 1994a). Ellis and Farrel (1995) concluded that resistance of *B. fruticulosa* was due to high levels of both antixenosis and antibiosis. The resistance in *B. fruticulosa* due to antibiosis against *D. radicum* has also been reported by Jenson et al. (2002). *Rorippa indica* is another wild crucifer which is resistant to mustard aphid, and the genes conferring resistance have been recently identified by Bandopadhyay et al. (2013). Sarkar et al. (2016) have cloned, purified and characterized a novel *R. indica*

Plate 6.1 (**a**) *Brassica fruticulosa* – a wild crucifer resistant to mustard aphid (**b**) Susceptible introgression line (**c**) One of the resistant introgression lines

defensin (RiD) which is toxic to *L. erysimi*. This aphid resistance trait can also be successfully introgressed to the cultivated backgrounds as demonstrated by somatic hybrids and their backcross progenies (Mandal 2003; Dutta 2007).

In addition to this, different workers have attempted to induce mutations in *B. juncea* for aphid resistance through chemical (Srinivasachar and Verma 1971) and physical mutagens (Srinivasachar and Malik 1972; Labana 1976), but all these efforts did not yield any result.

6.5.3 Genetic Engineering for Aphid Resistance

An alternative strategy to conventional breeding is the transgenic technology. For phloem-feeding insects, the different strategies can be employed such as expression of protease inhibitors, RNA interference (RNAi), antimicrobial peptides and repellents.

The *Cauliflower mosaic virus* (CaMV) 35S promoter is used to control transgene expression in many transgenic plants (Will and Vilcinskas 2013) which regulates the expression of a β-glucuronidase (GUS) reporter gene for the expression of dsRNA to protect the plants against the coleopterans (Baum et al. 2007) and aphids (Pitino et al. 2011).

The phloem-specific promoters can be used for phloem-specific expression of defence-related compounds against aphids. This would lead to more targeted expression of defence-related compounds with little/no exposure to the nontarget insects. This would also limit GM-associated bioenergetics investment of plant by avoiding the expression of defence-related compounds in plant tissues in the absence of pest attack. The *SUC2* promoter that regulates the *AtSUC2* sucrose-H^+ symporter gene is restricted to the plant phloem which produces aphid toxic proteins. This green florescent protein is transferred through the sieve elements where aphids actually feed (Imlau et al. 1999). Protease inhibitors (PIs) can also be used to confer resistance in plants against different insects including aphids by genetic engineering. These small peptides/proteins reduce or inhibit the activity of proteases required for digestion of proteins. They have been shown to be toxic to a number of pests belonging to order Lepidoptera, Coleoptera and Orthoptera (Boulter et al. 1989). Their potential as insecticidal proteins has also been explored in aphids. PIs ingested with phloem sap may disrupt the digestion of proteins in aphid gut and hence can interfere with normal amino acid assimilation leading to the reduction in growth and subsequent pest damage. The expression of trypsin inhibitors and other PI-like chymotrypsin inhibitors has already been achieved in the phloem of transgenic plants (Dannenhoffer et al. 2001; Kehr 2006). The cysteine protease inhibitor of barley, HvCPI-6, inhibited the performance of *M. persicae* and *Acyrthosiphon pisum* (Harris) in artificial diet (Carrillo et al. 2011). Similarly, cysteine protease inhibitors, oryzacystatin I (OC I), inhibited the growth of *M. persicae*, *A. gossypii* and *A. pisum* (Rahbé et al. 2003). A reduction in adult weight, fecundity and biomass of *M. persicae* fed on transgenic *B. napus* expressing (OC I) was observed in comparison with those fed on control plants. PIs were also shown to defend white cabbage

cultivars and *A. thaliana* against *B. brassicae* (Broekgaarden et al. 2008). PIs, thus, show detrimental effects against aphids, and their use in aphid management, therefore, appears to be an effective strategy for pest management.

Lectins are another class of proteins that have toxic effects on aphids and have the potential to be used for aphid control through genetic engineering. These are the proteins that selectively bind carbohydrates and the carbohydrate moieties of glycoproteins and can be poisonous. Lectins have been reported to show biological activity against a wide range of insects, especially the sap-sucking insects (Foissac et al. 2000; Powell 2001). Genes encoding wheat germ agglutinin from *Triticum* spp. (Kanrar et al. 2002), ACA from *Allium cepa* (Hossain et al. 2006), fusion ASAL from *A. sativum* and ACA from *A. cepa* (Hossain et al. 2006) have been introduced into Indian mustard, *B. juncea*, that provide protection against the mustard aphid, *L. erysimi.* These transgenic plants showed significant toxic effect against *L. erysimi* as evidenced by bioassays under controlled conditions.

Another method of aphid control through transgenic technology is the RNA interference (RNAi), which involves gene suppression at the level of RNA and involves post-translational RNA-mediated gene silencing. The transgenic plants that delivered dsRNA to aphids resulted in inhibition of Rack1 (located in the gut) and C002 (located in the salivary gland) proteins in peach-potato aphid, *M. persicae* (Pitino et al. 2011). The transformed plants of tobacco and *A. thaliana* resulted in reduction in fecundity of aphids with up to 60%t silencing in feeding aphids. Although salivary proteins (Mutti et al. 2006, 2008) and gut proteins (Shakesby et al. 2009) are the most promising RNAi targets for insects with piercing and sucking mouthparts such as aphids, the other targets may include transporters in the bacteriocyte plasma membrane required for nutrients' transport between aphids and their endosymbiont, *Buchnera aphidicola*.

6.6 The Way Forward

Plant resistance to aphids has great potential in managing populations of these important insect pests. Earlier efforts by plant breeders have focused on host plant resistance as a single component of pest management, and hence, greater emphasis was laid on screening for virtual immunity to aphids. Such extremely high level of resistance can result from very high level of toxic (to aphids) substance in the plant, which has many disadvantages such as continuous selection pressure on the insect population to develop resistant biotypes, possible side effects on natural enemies as well as yield drag. Thus, for sustainable pest management, partial resistance to insects has the potential for the future. Such partially resistant cultivars can be integrated with other methods of pest management, which is the main feature of IPM. The effective IPM strategy against aphids infesting rapeseed-mustard could not be developed due to a lack of resistant variety. This is primarily because of lack of in-depth knowledge about the mechanism of resistance. Though transgenics conferring resistance to aphids have been developed, their efficacy in reducing aphid

populations had been evaluated under controlled environments, and field testing of such transgenics is still awaited.

In addition to the inherently or transgenically expressed toxins in plants, other methods to reduce aphid populations on plants can also be developed. Since aphids utilize many secondary plant compounds especially volatiles in host plant recognition, plants can be genetically manipulated to alter their volatile profile, and limited success has been achieved under laboratory conditions (Beale et al. 2006; Schnee et al. 2006). It is a well-known fact that aphids reproduce at exceptionally high rate. A single mother aphid can produce 5.9 billion offspring in 6 weeks (Dixon 2005). Thus, disrupting the host recognition process of a mother aphid can significantly reduce the offspring population. However, this is a theoretical concept, and there is no report highlighting the validity of this strategy. Another potential area of research is the genetic manipulation of induced resistance in plants which is influenced by jasmonic acid (JA), salicylic acid (SA) and ethylene. The associated signalling pathways can be altered genetically to enhance the innate plant resistance level.

An effective and sustainable aphid management requires the adoption of integrated pest management (IPM) strategy. Since host plant resistance forms the core of any IPM programme, there is no effective IPM programme against aphids infesting brassica crops due to the lack of resistant crop cultivars. Rather than complete resistance to aphids, it is the partial resistance that has greater potential for the future, to maintain sustainability of pest management systems.

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Breeding for Resistance to Insect Pests in Maize

7

Chikkappa G. Karjagi, J.C. Sekhar, Soujanya P. Lakshmi, S.B. Suby, Jaswinder Kaur, M.G. Mallikarjuna, and Pradyumn Kumar

Abstract

The production of maize is constrained by various biotic stresses particularly insect pests. Infestation of insect pests on standing crop and stored grains not only reduces yield but also affects the quality of grains. The strategy for enhancing host plant resistance (HPR) is one of the cheapest, safe and sustainable methods for managing insect pests. Being a leading contributor to the world cereal basket, maize suffers from various insect pests. Maize has undergone various improvements through diverse breeding tools starting from selection to the present transgenic approaches to minimize the losses due to insect pests. This chapter provides an overview on major insect pests of maize, their distribution across the globe, methods of screening germplasm for resistance to insect pests, identification of sources of resistance, mechanisms of insect resistance, genetic nature of resistance and application of novel breeding methods for development of insect-resistant cultivars of maize.

Keywords

Maize • Insect pests • Stem borers • Insect resistance • Transgenic maize

C.G. Karjagi • J.C. Sekhar • S.P. Lakshmi • S.B. Suby • J. Kaur • P. Kumar (✉)
Indian Institute of Maize Research, Pusa Campus, New Delhi 110 012, India
e-mail: chikkappagk@gmail.com; jcswnc@rediffmail.com; soujanyak.scientist@gmail.com; subsb@gmail.com; jasspau@yahoo.com; pradyumn.kumar@gmail.com

M.G. Mallikarjuna
Indian Institute of Maize Research, Pusa Campus, New Delhi 110 012, India

Division of Genetics, Indian Agricultural Research Institute, New Delhi 110 012, India
e-mail: mgrpatil@iari.res.in

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7.1 Introduction

Maize (*Zea mays* L. ssp. *mays*) originated in central Mexico from its closest progenitor teosinte (*Zea mays* L. ssp. *parviglumis*). The domestication of maize started between 6000 and 10,000 years ago (Ortega et al. 1980). The spontaneous natural mutations, subsequent selection, fixation and improvement have resulted into tremendous genetic diversity in maize germplasm; this has led to differentiation of maize into different types, viz. sweet corn, popcorn, high-lysine maize, high-tryptophan maize, etc. Based on kernel colour, each type of maize can be further classified into yellow, white, blue, etc. The tremendous genetic diversity and plasticity have allowed it to grow in varied agroclimatic conditions. It is being grown in tropical, subtropical and temperate climate across the globe from equator to 45° N/S. In tropics, it can be grown in places as high as 3300 m above sea level (Ortega et al. 1980). It has the highest genetic yield potential among cereals and is considered the queen of cereals. Being a leading contributor towards the global cereal production, it is known for its multifaceted usages for feed, food, fuel and fibre (Yadav et al. 2015). Presently it is being cultivated on approximately 184 million hectares in more than 166 countries. The global area, production and productivity of maize are increasing continuously from the 1950s. Presently the global maize production is around 1021 million metric tonnes with an average productivity of ~ 5 t/ha (FAOSTAT 2014). The major reason of continuous increase in maize production is due to sustained efforts towards developing high-yielding cultivars. However, various biotic and abiotic constraints affect the global maize production. It was reported that 9% of the world maize crop is lost annually due to insect pests (James 2003). However, the losses due to different insect pests differ from region to region; for instance, *Chilo partellus* (Swinhoe) and *Sesamia inferens* (Walker) are the most destructive insect pests affecting productivity of maize in Asian countries (Siddiqui and Marwaha 1993) causing 25–40% yield losses depending on pest population density and phenological stage of the attacked crop (Khan et al. 1997). Numerous efforts made in breeding for insect-resistant cultivars have played a significant role in reducing the losses caused by insect pests. Among the insect pests attacking maize, stem borers play a major role in reducing maize yield through damaging the leaves, stems, ears and kernels. The major damage symptoms contributing to severe yield loss are dead hearts, foliar damage and stem tunnelling (Mathur and Rawat 1981) (Table 7.1).

The distribution and intensity of insect pests of maize vary spatially as well as temporally. The infestations on maize plant also differ from insect to insect as well as with stage of plant. In general, there is no crop stage of maize which is free from insect attack. In fact, storage insects lay their eggs on cobs/kernels in the field immediately after crop attains physiological maturity. Globally there are about two dozen major insect pests of maize, viz. European corn borer [*Ostrinia nubilalis* (Hübner)], Asian corn borer or Oriental corn borer [*Ostrinia furnacalis* (Guenee)], spotted stem borer [*Chilo partellus* (Swinhoe)], Mediterranean corn borer or pink stem borer [*Sesamia nonagrioides* (Lefebvre)] or pink borer [*Sesamia cretica* (Led)], African maize borer [*Sesamia calamistis* (Hmps)], pink stem borer [*Sesamia*

Table 7.1 Ingredients of artificial diets of *Chilo partellus* and *Sesamia inferens*

Chilo partellus (Siddiqui et al. (1977)		*Sesamia inferens* (Reddy et al. (2003)	
Ingredient	Quantity	Ingredient	Quantity
Green gram powder	75 g	Fraction A	–
Wheat powder	20 g	Green gram grain flour	75 g
Yeast powder	5. 0 g	Maize grain flour	20 g
Ascorbic acid	1. 7 g	Brewer's yeast	8 g
Methyl paraben	0. 8 g	Sorbic acid	1 g
Sorbic acid	0. 4 g	Vitamin E	0. 3 g
Multivitamin	1capsule	Methyl parahydroxybenzoate	2 g
Vitamin E	0. 4 g	Ascorbic acid	1. 7 g
Streptomycin sulphate	0. 5 g	Sugar	15 g
Agar-agar powder	6 g	Casein	5 g
Formaldehyde 40%	1 mL	Cholesterol	1 g
Distilled water	390 mL	Dried maize leaf and stem powder	15 g
		Common salt	0.3 g
		Distilled water	400 mL
		Fraction B	
		Agar-agar	12 g
		Distilled water	250 mL
		Formaldehyde 40%	1 mL

inferens (Walker)], African maize stalk borer [*Busseola fusca* (Fuller)], African sugarcane borer [*Eldana saccharina* (Walker)], Southwestern corn borer [*Diatraea grandiosella* (Dyar)], American sugarcane borer [*Diatraea saccharalis* (Fabricius)], neotropical corn borer [*Diatraea lineolata* (Walker)], corn earworm [*Helicoverpa zea* (Boddie)], corn rootworm complex [*Diabrotica* spp.], fall armyworm [*Spodoptera frugiperda* (J. E. Smith)], maize leafhopper [*Cicadulina mbila* (Naude)], corn leaf aphid [*Rhopalosiphum maidis* (Fitch)], greater rice weevil or maize weevil [*Sitophilus zeamais* (Motschulsky)] and angoumois grain moth [*Sitotroga cerealella* (Olivier)] which together account for substantial yield losses in different countries (Ortega and De Leon 1974; Guthrie 1989). In addition, there are several minor insect pests of maize in different parts of the globe which may also cause yield losses albeit to a lesser extent than the major pests.

Several strategies have been adopted to control the losses caused by these insect pests. Among various strategies, the use of chemical insecticides is the major one across the globe, but it results in ecological damage, environmental pollution, human health hazards and development of resistance in the insect pests. Therefore, host plant resistance (HPR) has emerged as the most effective alternative and economical approach to control insect pests. Studies of insect resistance in maize began in the early 1900s. In the USA, the efforts towards breeding insect-resistant maize cultivars started somewhere around the 1920s after the discovery of European corn borer in 1917 in the USA (Guthrie 1989). Breeding insect pest-resistant cultivars can not only effectively reduce the loss and improve maize yield but also improve

the quality by controlling fumonisin contamination (Santiago et al. 2013). The rate of success in breeding-resistant cultivars depends on availability of broad germplasm base, efficient reliable screening techniques, knowledge of resistance mechanism, mode of inheritance, selection of right breeding procedure, etc. Scores of comprehensive reviews have been published regarding sources of resistance, genetics of resistance and their use in development of insect-resistant maize cultivars against different insect pests by employing various breeding methods under insect resistance breeding programmes (Welcker et al. 1997; Guthrie 1989; CIMMYT 1989; Ortega et al. 1980). Further identification, development and utilization of sources of resistance against different insect pests of maize have been comprehensively covered by Mihm (1997), and the readers are advised to go through the above monograph for more detailed information. The present chapter briefly discusses the distribution of major insect pests of maize across the globe, screening techniques for identification of resistant germplasm, genetics of HPR and the use of novel breeding methods for development of insect-resistant cultivars of maize.

7.2 Distribution of Maize Insect-Pest Complex

The relative prevalence of most damaging insects of maize and their importance across different geographical regions of the world was covered extensively by Ortega et al. (1980). The situation is not much different even today. However, the brief accounts of a few major insects are given here.

O. nubilalis is a very serious pest of both sweet corn and grain corn. It was first observed in North America near Boston, Massachusetts, in 1917, but is now well distributed in the temperate region of the Northern Hemisphere comprising North America, Europe, the Middle East and North Africa. The number of generations varies from one to four per year; however, the major losses in maize are caused by two generations. It feeds on every part of the plant except the roots. *O. furnacalis* occurs in eastern region of Southeast Asia and the Philippines and attacks all parts of the maize plant. However, the yield losses are greatest when it infests during reproductive stage of the plant. The most common feeding site of late-/final-instar larvae is the stalk.

C. partellus (Swinhoe) occurs in West, South and Southeast Asia and Northeast and South Africa. It infests maize plants in all stages; however, the major loss is caused when it attacks maize plant in early whorl stage (four-leaf stage). The larvae immediately after hatching feed on leaves and later bore into stem to make a tunnel. It feeds mainly on soft tissues of leaf and then enters into stem through whorl where it cuts the growing point resulting in drying up of central shoot and formation of dead heart. It is active from March to October ('kharif' season) and has 6–7 overlapping generations. It undergoes hibernation in larval stage in the stubbles and stalks during winter season. It causes heavy damage to maize crop resulting from 24 to 80% yield losses in different agroclimatic regions (Panwar 2005; Panwar et al. 2001; Kumar and Mihm 1996).

S. inferens (Walker) causes severe losses in West, South and Southeast Asia. In India *S. inferens* is one of the principal insect pests of maize particularly during winter ('rabi') season. It attacks leaf, stem, silk, tassel and immature cobs; the larvae feed under leaf sheath and remain there during early stage of growth (4–8 leaf stage), later enter into central shoot and cause death of central leaf, the growing point, much the same way as *C. partellus* resulting in death of the plant. Severe infestation results in stunted plant growth and appearance of cob and tassel at one place. It has migrating tendency and may attack a number of plants. It has 4–5 generations a year. The losses due to *S. inferens* in winter range from 25.7 to 78.9% (Chatterjee et al. 1969). *S. nonagrioides* and *S. cretica* are found in Mediterranean basin, Middle East and some parts of northern Africa. *B. fusca* occurs throughout mainland sub-Saharan Africa. Initially it feeds on young terminal leaf whorls making small holes and 'windowpanes' (patches of transparent leaf epidermis). The first generation bore in the main stem, whereas the second-generation caterpillars bore in the cobs causing significant losses. *E. saccharina* is indigenous to Africa and is widely distributed in sub-Saharan Africa comprising Burundi, the Democratic Republic of Congo, Kenya, Rwanda, Tanzania and Uganda. The major symptoms of the insect damage are stem tunnelling and/or breakage including cob damage. *Diatraea saccharalis* is native to the Western hemisphere; it is a minor pest of sweet corn in Americas. Both *D. saccharalis* and *D. grandiosella*, however, cause serious damage in subtropical and tropical regions of Central and Latin America and the southern USA. *H. zea* is distributed across the Americas with the exception of Northern Canada and Alaska. It attacks maize plant mostly on tassel and silk. The grown-up larvae enter the cob from the top and feed on the apical grains first. Since it attacks in the later stages of the crop, the losses in yield are not high, but it reduces the market value of crop especially of sweet corn.

7.3 Conceptual Framework of Host Plant Resistance

Development of resistant cultivars is one of the most economical and ecologically sound methods of insect pest management (Jenkins 1981). Reginald Painter gave framework on host plant resistance in his book, *Insect Resistance in Crop Plants*, which guided the applied research towards development of insect-resistant cultivars. Painter defined resistance as 'the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect' (Painter 1951). He introduced three 'mechanisms' or 'bases', viz. 'non-preference', 'tolerance' and 'antibiosis' through which host plant resistance gets manifested. As per Painter (1951), 'antibiosis' includes all adverse effects of resistant plants on insect survival, physiology, growth and development, fecundity, etc. The term 'non-preference' is self-explanatory which describes avoidance of plant as host with respect to food, colonization through oviposition and shelter. The term 'tolerance' was defined as the ability of the plant to support insect populations that would severely damage as well as withstand insect injury yet does not have much loss in terms of economic yield and/or quality as compared to susceptible plants

under same level of infestation/damage. The concept of host plant resistance given by Painter was most widely accepted at global level and has been extensively used for managing pests and diseases in several crops including maize in the last over 60 years. The concept of host plant resistance has not changed much since Painter (1951) except the substitution of the term antixenosis for non-preference by Kogan and Ortman (1978). But the definition of resistance evolved over a period without changing the core meaning of the term; Smith (2005) defined resistance as the 'sum of the constitutive, genetically inherited qualities that result in one cultivar or species being less damaged than a susceptible plant lacking these qualities' by keeping the definitions of antibiosis, antixenosis and tolerance the same as that of Painter. However, recently Stout (2013) has discussed the weakness of framework given by Painter and proposed dichotomous framework with a major division between resistance (plant traits that limit injury to the plant) and tolerance (plant traits that reduce the amount of yield loss per unit injury). The proposal of dichotomous scheme was to align the basic and applied research on plant resistance. Nonetheless, the identification of sources of resistance is prerequisite for exploitation of host plant resistance. Several studies have been conducted to identify the sources of resistance against major insect pests of maize across the globe and to understand the underlying mechanisms of resistance.

7.4 Mechanisms of Resistance

The specific adaptation features at phenotypic levels play an important role in establishing the first line of defence against insect pest attack. A good understanding of the mechanism(s) and bases of resistance is needed for establishing differences among resistant genotypes. For example, a tight husk prevents the entry of cob earworm as well as fall armyworm, thus protecting the crop from damage (Guthrie 1989). In fact, specific chemical compounds, present in silk, like maysin, AM-maysin (apimaysin, methoxymaysin), flavones and chlorogenic acid (CGA), were supposed to provide resistance to corn earworm. The correlation study between silk maysin concentrations and 8-day old corn earworm larval weights has shown highly significant negative association ($r \approx -0.80$, $P < 0.0001$). It was also supposed that silk browning was also closely associated with silk maysin concentrations and antibiosis (Guo et al. 1999). Chlorogenic acid (CGA) in silks has also been associated for resistance to corn earworm and was supposed to act in similar fashion as that of maysin on *H. zea*. The genetic basis of chlorogenic acid (CGA) in silks has been attributed to two candidate QTLs located on *p1* and *qtl2* locus affecting the biosynthesis of CGA. It has been mapped by using three different F_2 populations derived from crosses A619 × Mp708, A619 × Mo6 and Mo6 × Mp708 (Bushman et al. 2002). The recent studies have shown that additional gene *a1* (tightly linked to SH2) also has significant effects on silk maysin, AM-maysin, and chlorogenic acid concentrations, the silk antibiotic chemicals, along with *p1* gene which was reported earlier. The successful selection for *p1* in sweet corn through backcross methods along with *a1* has increased the sweet corn resistance to corn earworm (Guo et al. 2004). Gundappa et al. (2013) found that phenolic acids (ferulic acid and *p*

coumeric acid) are negatively correlated with leaf injury and tunnel length caused by *C. partellus* at all plant stages. Bioassay of neonate larvae of *C. partellus* by diet incorporated with phenoic acids resulted in increased mortality and retarded the development and growth.

It was observed that resistance to shoot fly is primarily due to non-preference for oviposition under field conditions. Rao and Panwar (2001) observed that resistant varieties to shoot fly had low carotenoid, nitrogen and crude protein contents compared to susceptible ones.

Zakka et al. (2013) reported that physical factors alone are not responsible for grain resistance to *Sitophilus* sp. in maize. Nwosu et al. *(*2015) identified resistant maize genotypes 2000SYNEE-WSTR and TZBRELD3C5 and found antixenosis and antibiosis as mechanisms of resistance to *S. zeamais*. In the recent past, Garcia-Lara and Bergvinson (2014) reported that kernel hardness and pericarpin in the kernel are the major factors responsible for resistance to *S. zeamais*. It was reported that simple phenolic acids, diferulates, heteroxylans and extensins, are associated with resistance to *S. zeamais* (Ayala-Soto et al. 2014). Resistance to *S. oryzae* in maize is conferred by several biophysical, anatomical and biochemical traits (Soujanya et al. 2016). In the case of *S. nonagrioides*, the combination of antibiotic pith and stem resistance is responsible for conferring resistance (Ordás et al. 2002). Thus, it is evident that usually there is more than one factor responsible for resistance to insect pests.

7.5 Screening Techniques for Insect Resistance

The ability to develop resistant cultivars depends on the precision of resistance screening techniques. Comparisons of per cent yield loss due to pest damage provide a relative measure of their resistance. In India, the entomology programme under All India Coordinated Research Project (AICRP) on maize conducts experiments at different centres to measure the level of resistance against *C. partellus* and *S. inferens* based on leaf injury rating (LIR). The yield loss is directly proportional to LIR which is an estimation of antibiosis contribution to resistance. However, there is variation among genotypes in leaf-feeding resistance with respect to yield loss which reflects the tolerant component. The effective and reliable screening technique helps in determining the accurate level of insect resistance in a large number of genotypes. Hot spot locations for certain pests are usually considered for screening the material under natural pest infestation. In these locations, planting date of the crop should be adjusted in such a way that the susceptible stage of the crop synchronizes with the peak activity period of pest. This can be determined by conducting population dynamic studies either by using attractant traps or by monitoring pest infestation at regular intervals. Screening under natural infestation is not so reliable and takes a long time to identify lines with stable resistance; therefore, artificial infestation techniques have been standardized for evaluating maize germplasm against stem borers. Advances in insect rearing techniques and reliable, simple and robust scoring methods used to evaluate infestation and to identify resistant material have greatly facilitated the breeding programmes for insect resistance.

7.5.1 Spotted Stem Borer

The small piece of butter paper bearing 10–15 black-head stage eggs is pinned into the whorl of the plant on 10–12-day-old maize crop. These are sufficient to cause appreciable leaf feeding and dead heart formation. The second infestation is also required if rainfall occurs after the first release. Since a large number of larvae are required for artificial infestation, a widely accepted method has been developed for mass rearing of *C. partellus* on artificial diet (Siddiqui et al. 1977). Because, mass rearing of *C. partellus* on natural diet is cumbersome and requires excessive handling which predisposes the larvae to mechanical injury, artificial diet is therefore, preferred over natural food.

7.5.2 Pink Stem Borer

Maize plant is most receptive to *S. inferens* at 10–15 days after germination, thereby resulting in maximum dead-heart formation and grain yield reduction. The infestation at anthesis stage should not be done because the plants develop in-built tolerance with advancement in age of the crop. For infestation of plants by *S. inferens* larvae, poppy seeds are mixed with neonate larvae and 10–12 larvae are dispensed with Bazooka or plant inoculators. LIR scale for *S. inferens* developed by Reddy et al. (2003) has been adopted for evaluation. Screening under artificial infestation is required to confirm resistance observed in natural pest infestation conditions. Similar to spotted stem borer, mass rearing of pink stem borer on natural food is time consuming due to regular change of cut pieces of stem. Mass rearing on artificial diet (Reddy et al. 2003) is an important prerequisite for obtaining large number of larvae for artificial infestation, which provides the base for host plant resistance studies.

7.5.3 Shoot Fly

Screening of inbred lines against shoot fly, *Atherigona* spp., cannot be done under artificial conditions as it is very difficult to rear in the laboratory. In hot spot locations such as Delhi and Ludhiana, in India, it is being carried out under natural conditions by fish meal technique under AICRP on maize under entomology programme during the spring season (February–May). Based on per cent dead hearts, the genotypes of maize are classified. Recently, a susceptibility index to classify maize genotypes against shoot fly has been developed by Kumar et al. (2014).

Susceptibility Index = {(Percentage of plants oviposited/10) + (Number of eggs laid per plant * 10) + (Percentage of dead hearts/10)}/3

7.5.4 Storage Insect Pests

Post-harvest losses due to insect pests especially *S. oryzae* are the major constraint in grain storage. It can cause losses either directly by consumption of grains or indirectly by creating favourable environment for the establishment of other pests/fungi during storage (Tefera et al. 2010) and by reducing quality (Gethi 2002). It was reported that 80% losses occur for untreated maize grain stored in traditional structures depending on the period of storage (Boxall 2002). The incorporation of insect resistance trait in breeding programme for the reduction of post-harvest losses is an effective and eco-friendly management option (Somta et al. 2006). Mass rearing of *S. oryzae* is necessary to screen the germplasm to identify resistant sources, which are carried out effectively on conditioned maize kernels adjusted to moisture content of 12%. The procedure involves release of 200 adults of *S. oryzae* in a jar (1 litre capacity) containing 500 g maize grain. The adults oviposit for 7 days; after 7 days, all the adults are removed, and the grains are kept at 28 ± 1 °C and 70% RH for the development of their progenies. Adequate numbers of jars are prepared to meet the pest population requirement of genotypes to be screened.

In order to screen the germplasm for resistance against *S. cerealella*, 15 pairs of newly emerged adult moths are released per jar containing 100 kernels of maize germplasm. The jars are kept for 7 days for oviposition (Garcia-Lara et al. 2009). The jars of genotypes under testing were kept under controlled conditions at 27 ± 1 °C and 70% RH. The adults were observed for the mortality after a week. The F_1 progeny emergence from each jar is recorded for a period of 2 months from the day of release of adults. Classification of maize genotypes has been done by the method developed by Dobie (1977) under no-choice conditions. The susceptibility index, ranging from 0 to 11, was used to classify the maize genotypes: 0–3, least susceptible; 4–7, moderately susceptible; 8–10, susceptible; and ≥11, highly susceptible.

7.6 Sources of Resistance to Different Insect Pests

To develop insect-resistant genotypes, it is essential to identify, characterize and categorize effective sources of resistance. The probability of finding a source of resistance depends on the genetic diversity existing within their germplasm as well as the insect populations prevalent in a region. Screening of native as well as exotic germplasm is the routine procedure to identify resistant germplasm for different insect pests. The resistant sources for different insect pests have been identified across the globe by screening thousands of maize genotypes over a period under natural and/or artificial infestation condition. To identify the reliable sources of resistance, there is a need to evaluate the diverse sets of germplasm collected across different geographical regions for several years under artificial infestation (Xinzhi et al. 2012).

The extensive screening of many germplasm collections at different regions across the globe has been undertaken. Malvar et al. (2004) screened diverse

landrace collections against European corn borer (ECB) and pink stem borer (PSB) and identified resistant sources for stem and ear damage under various maturity groups like very early (PRT0010008, GRC0010085), early (PRT00100120, PRT00100186), midseason (GRC0010174) and late season (ESP0070441). Velasco et al. (1999) identified the following synthetic cultivars BSCB1(R)C11 of field corn and NE-HY-13A(S)C1, NE-HY-13B(S)C1 and AS11of sweet corn as sources of resistant to Mediterranean corn borer (MCB) and European corn borer (ECB) after screening under artificial infestation. He also observed that the resistant sources have one or the other field corns in their pedigree and hypothesized that field corns are relatively more resistant than sweet corn. Thus, the resistance source differs depending on the genetic background. The presence of high insect resistance in the above landraces may be due to high selection pressure or single origin. Further, several MCB-resistant genotypes of different maturity were also identified.

In India, several workers have screened different kinds of germplasm to identify the resistance sources against insect pests. Sekhon and Sajjan (1990) reported antibiosis in CM 500 to *C. partellus* which was evident only 20 days after germination. Likewise, Singh and Marwaha (1996) studied the growth and development of *C. partellus* and obtained minimum growth index (0.96) in Antigua Gr. 1. Panwar et al. (2000) evaluated 43 inbred lines against *C. partellus*, under artificial infestation during *kharif* (rainy) season and under heavy natural infestation against shoot fly species during spring season, and it was found that two inbreds, namely, IPA 34-10-13-3-1-1-#-2-1 and IPA 3-6-14-2-#-1, were moderately resistant to borers, *C. partellus* and *Atherigona* spp. These inbreds may be designated as multiple pest-resistant sources and should be used while developing varieties or single-/double-cross hybrids. Similarly, the maize lines, viz. MIRTC4Am F 36-8-2-2-8, MIRTC4Am F 1018-2-2-8, MIRTC4Am F 28-8-1-1-8 and MIRTC4Am F 110-8-1-1-8, were found tolerant to *C. partellus* (Panwar et al. 2001). Kumar et al. (2005) reported Antigua groups 1 and 2, CML-139 and CML-67, to be resistant against *C. partellus*. Sekhar et al. (2014) reported six genotypes, viz. PFSRS2, AEBYC534-1-1, P390AM/CMLC4F230-B-2, AEBCYC534-3-1, CML384X176F3-100-9 and P63C2-BBB-17B to be resistant to *C. partellus.* In the recent past, Rajasekhar and Srivastav (2013) screened maize genotypes against *C. partellus* and found no sign of dead hearts in HUZQPM 242, HUZQPM 246, QPM 193, CM 119, AH 411, HUM 152, NMH 9858, HUZM 185 and HUZM 217. An antibiosis mechanism has been noticed in VIM 325, VIM 308 and VIM 322 in terms of low larval survival, less larval and pupal periods and low growth index when screened against *C. partellus* in maize (Abdalla and RaguRaman 2014). Some maize genotypes showing antibiosis to *C. partellus* were also identified which include AES 805, Ill 1656, K41, NC 27, yellow no. 2, Ganga 101, Arbhavi Local, Jalandhar Local, Antigua Gr. 1, Vijay, J 12, Jawahar and Ganga 5.

Sekhar et al. (2004) screened 62 maize genotypes against *S. inferens* under artificial infestation, out of which eight lines, viz. P391C2 F 147-2-2-1-1-B-B-B-B-B, P391C2 BcF3-1-1-2-1-B-B, MIRT C4AmF86-B-3-1-B, MIRTCAmF86-B-3-1-B, MIRT C4AmF110-B-1-1-B, PT963112-B-B-B-B-B-B, MIRT C4AmF36-B-2-B

and PT963128-B-B-B-B-B-B, were found resistant. In other studies Reddy and Sekhar (2002) and Sekhar et al. (2014) reported several inbred lines, namely, WNZPBTL 9 (3.2), WNZPBTL 8 (3.5), CML 338 (3.6), WNZ EXOTIC POOL DC2 (3.1), CML 424 (3.2) and WNZPBTL 9-1 (3.4), which recorded LIR less than resistant check CM 500 (3.8) for *S. inferens* infestation. Sekhar et al. (2008) categorized CML421, CAO3141, CAO3120 and CAO0106 inbred lines and single crosses CML429 × CML474 and CML421 × CML470 as highly resistant and CML427 × Pop 147-F2-#-105-2-1-B-1-B*4 and CML426 × CML470 crosses as highly susceptible to *S. inferens* based on 1–9 scale of LIR. Khalifa et al. (2013) determined resistance to the pink stem borer, *S. cretica*, in 20 exotic maize populations with different genetic backgrounds and found that populations of Tamps. 23 and Antigua have relatively good level of resistance to infestation by the larvae.

Shahzad et al. (2006) screened ten maize cultivars, viz. EV-5098, Sahiwal-2002, Golden (full season yellow), EV-6098, EV-6089, Sadaf, Pak Afgoyee (full season white), EV-1098, Agaiti-2002 and Agaiti-85 (short season yellow), against shoot fly during spring season; among them EV-5098, EV-6098, Agaiti-2002 and EV-1098 were found to be resistant. Recently, 68 inbred lines were evaluated against shoot fly during spring 2015 at Delhi and Ludhiana under AICRP Maize Entomology programme. CML420 (8.3), ACC. 263, 214 (9.1), WINPOP 8 (9.1) AEB (Y) (10.0%) and CML49 (10.0) recorded less than 10.0% dead hearts (Annonymous 2016).

As adult weevils of *Sitophilus* feed, mate and oviposit inside the grains, resistance of maize grain is a trait connected to the whole caryopsis. Utilization of HPR to reduce storage losses has been underutilized in maize (Pingali and Pandey 2001). Several workers identified sources of resistance to *Sitophilus* species in maize. Soujanya et al. (2015) identified WNCDMR11R 0913, WNCSKNY 4854 (2) and WNCDMR19RYDWS 1518 as moderately resistant to *S. oryzae* based on Dobie's index (4–7).

Studying different damaging symptoms and their correlation among themselves helps in identification of critical damaging symptoms for indirect selection for resistance. Since insect pests cause damage in different parts of the plant and at different stages of the plant, it is not necessary that resistance in one stage or one part of the plant will show resistance at another stage or another part. However, depending on the material used in the study, a strong negative correlation between insect damage and yield was observed (Bohn et al. 1999; Cartea et al. 1999; Butron et al. 1999b, 2009, 2012). Similarly, Krakowsky et al. (2007) also observed negative genotypic correlations between ECB susceptibility and a subset of QTLs determining ADF (cellulose + lignin), which is one of the cell wall components. On the contrary, Butrón et al. (1999a) did not get any correlation between stem and ear damage resistance traits while evaluating germplasm against MCB damage. Thus, the results of the above-mentioned studies indicate the necessity of identification and selection of resistant materials separately for each plant part as well as crop stage.

7.7 Genetics of Resistance

The resistant sources are the basic materials for genetic studies. Several efforts have been made across the globe towards the genetic characterization of regional maize collections to identify native sources of resistance to damage caused by different insect pests of maize. Knowledge on genetics of resistance is useful in deciding breeding methodology and breeding strategies to be adopted. Breeding for stem borer resistance in maize is challenging because the trait is quantitative and involves polygenes with low heritability (Sharma et al. 2007). Several studies have been conducted on genetics of resistance to maize insect pests. The studies of genetics of resistant trait do not differ from the genetic studies of any plant trait for that matter but involve an additional component; the plant-insect interaction, a biological relationship. The lack of knowledge of genetics does not necessarily prevent establishment of insect resistance breeding programmes. In the past, insect-resistant genotypes were developed without the knowledge of either the mechanisms or the mode of inheritance. However, the detailed breeding plans cannot be formulated without the knowledge of genetics. The knowledge and understanding with respect to genetic basis of resistance would increase the efficiency of breeding insect-resistant genotypes. Development of appropriate genetic materials is the prerequisite for the genetic studies. Selection of highly contrasting and extreme phenotypes, viz. resistant and susceptible, and development of F_1 hybrids by making crosses between them is the first step towards development of different kinds of genetic material which aids in genetic studies. The most widely used genetic materials are F_2s, $F_{2:3}$s and BC_1F_1s with parent 1 and parent 2 to understand the genetics. The resistance trait must be studied and considered in relation to association with other characters. The ultimate objective of studying the genetics is to utilize resistant resources in breeding programme for development of cultivars which not only resist the damage caused by insect pests but also give higher yield. Studies on genetic basis for antibiosis, an important mechanism of resistance or tolerance, have shown that antibiosis is largely determined by additive effects especially stem antibiosis indicating underlying chemical basis for resistance.

7.7.1 European Corn Borer

Genetics of resistance to European corn borer (ECB) is one of the highly studied areas in maize across different genetic backgrounds in the world. The studies started as early as the 1920s when the pest was first observed in 1917 in Boston, Massachusetts. One of the pioneer studies by Penny and Dicke (1956) reported the existence of at least three gene pairs which are involved in leaf-feeding resistance. The study also indicated partial phenotypic dominance of susceptibility over resistance. Later studies indicated that resistance is largely governed by additive type of gene action. The resistance to early stage of development is based on production of specific chemicals like DIMBOA, whereas in later stage, it is the thickening of the cell wall and its composition (Butron et al. 2010; Ordas et al. 2010). It was found that the concentration of neutral detergent fibre (NDF), acid detergent fibre (ADF)

and lignin contributed towards increased resistance to second-generation ECB. This information was revealed while studying the relationship between plant composition and ECB resistance in the three maize populations, viz. BS9(CB), WFISILO and WFISIHI (Ostrander and Coors 1997).

7.7.2 Mediterranean Corn Borer

The studies on genetic effects have shown that stalk tunnelling resistance to *S. nonagrioides* is determined largely by additive genetic variance in majority of the studies across diverse set of germplasm as compared to dominance effects. Both additive and dominance gene effects equally play an important role in ear resistance to MCB (Cartea et al. 1999; Butron et al. 1999a, 2009; Velasco et al. 2004). The correlation studies have shown that general appearance of the ear is a good indicator of ear resistance to MCB. It was found that ear resistance was dominant over susceptibility (Cartea et al. 2001).

7.7.3 Spotted Stem Borer

Pathak and Othieno (1990) studied inheritance of resistance to *C. partellus* and reported both additive and nonadditive gene effects. The genetic analysis for resistance to the spotted stem borer in three maize crosses revealed highly significant additive gene effects for leaf feeding, dead hearts and stem tunnelling (Pathak 1991).

7.7.4 Pink Stem Borer

Sekhar et al. (2015) investigated the genetics of resistance to *S. inferens* and reported that additive × additive (I) followed by dominance (D) and additive (A) gene effects are responsible for resistance. In another study, Santosh et al. (2012) reported that negative additive and dominance effects and positive additive × dominance (j) and dominance × dominance (l) epistatic interaction govern the pink stem borer resistance in maize.

7.7.5 Shoot Fly

There are no studies on genetics of resistance against *Atherigona* spp. in maize. However, much research work has been done against shoot fly in sorghum, but the genetic gains were quite low. Mohammed et al. (2016) studied inheritance of resistance to sorghum shoot fly and found higher values of variance due to specific combining ability (σ^2s), dominance variance (σ^2d) and lower predictability ratios than the variance due to general combining ability (σ^2g) and additive variance (σ^2a) for shoot fly resistance traits.

7.7.6 Maize Weevil

Several researchers worked on genetic analysis of resistance in maize to *Sitophilus* spp. (Castro-Alvarez et al. 2015; Derera et al. 2014; Dari et al. 2010). Zunjare et al. (2015) studied the genetic analysis of resistance to *S. oryzae* and reported that additive and nonadditive gene actions were important for imparting resistance against *S. oryzae*. In majority of the promising crosses having desirable SCA effects, one of the parents had desirable GCA effects, which indicates the possibility for generation of resistant crosses and found narrow sense heritability for grain weight loss (29.41%) and number of insect progeny (32.55%) as moderate magnitude. However, it was reported that nonadditive gene action was more important than additive gene action for weevil progeny emergence (Dhliwayo et al. 2005). In another study, Kim and Kossou (2003) also reported that maize weevil resistance was controlled by additive and nonadditive gene actions and the inheritance was quantitative and polygenic. It is possible to develop promising inbred lines with higher degree of resistance through transgressive segregants generated from two diverse resistant inbreds (Castro-Alvarez et al. 2015).

7.8 Breeding for Insect-Resistant Cultivars

The information regarding the right kind of genetic material for developing insect-resistant cultivars is the first step in breeding for insect resistance. It should be approached with interdisciplinary teams. Since resistance is an outcome of the complex interaction between host plant and insects, screening under natural infestation is highly challenging to get the reliable data, because the mobile nature of insects can cause uneven distribution with respect to its number and stay time at the fixed site under natural infestation (Guthrie 1989). Thus, plant material should be infested uniformly under artificial condition to distinguish resistant *vis-a-vis* susceptible. The process of development of resistant cultivars to various insect pests starts with the use of resistant sources in breeding programme. Several breeding methods are available; a breeder has to choose the most appropriate method depending on the objective (Fig. 7.1). In fact, plant breeders have developed resistant sources without the knowledge of genetics of resistance. However, in most of the cases, the genetics of resistance and the objective of the breeder decide the type of breeding method to be followed. The information on the genetics of resistance greatly increases the breeding efficiency. Thus genetic information and breeding objectives determine the type of breeding method to be followed. However, the most important trait to be considered in breeding for insect resistance and evaluation of level of defence against is the relative higher yield level under infested conditions (Butron et al. 1999a).

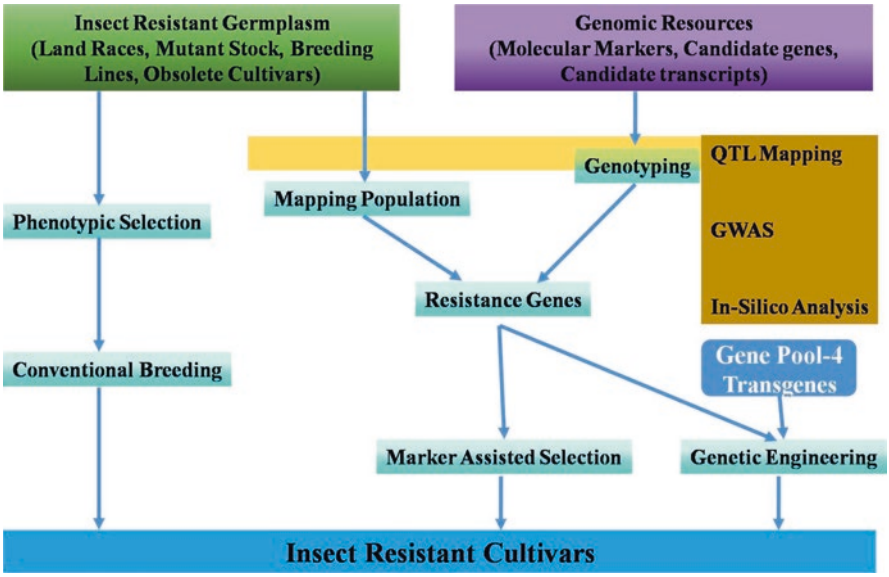

Fig. 7.1 The comprehensive approach for breeding insect-resistant maize by integrating conventional breeding and advanced techniques

7.8.1 Selection Criteria

The purpose of breeding for insect pest resistance is to reduce yield loss; therefore, selection for resistance should be based on the criterion of avoiding yield loss. However, selection for insect resistance cannot be on any single trait, and it differs from insect to insect. Since different parts of the plants get affected, the use of selection index, by considering several traits along with yield, would help in determining the resistance level against insect pest damage. Butron et al. (1998) computed an index to measure stem damage and ear damage by MCB. He used damage index under artificial infestation to evaluate antibiosis; the regressions of yield loss on the damage index were used to separate the genotypes into four groups to measure antibiosis and/or tolerance level.

7.8.2 Development of Synthetics and Composites Through Recurrent Selection

In any breeding programme, selection against insect pest attack under artificially infested condition should usually be more rewarding for development of insect-resistant genotypes. The measure of insect resistance is either in the form of reduced leaf defoliation or stem or stalk tunnel length but the symptoms of insect damage should be robust for the plant breeders to make the right decision in selection.

Historically, conventional breeding techniques have been adopted while breeding for insect resistance. Mihm (1985) documented comprehensively the efforts made by CIMMYT, Mexico while developing a subtropical source population with multiple borer resistance (MBR population). The methodology followed was recombination and recurrent selection under artificial infestation with Southwestern corn borer (SWCB), sugarcane borer (SCB), European corn borer (ECB) and fall armyworm (FAW). Diverse source populations obtained from different organizations were used for development of MBR population. The SWCB resistance sources were from Mississippi State University, CIMMYT population 47 and the Islands of Antigua, whereas the ECB-resistant sources were procured from Cornell University and the University of Missouri. Mugo et al. (2001) have reviewed the intricacies of breeding methods followed by CIMMYT for development of MBR population.

Klenke et al. (1986) developed a corn synthetic (BS9) specifically with resistance to ECB throughout the life of the plant by following recurrent selection from the base population BSSCO. Malvar et al. (2004) have proposed to develop broad-based MCB and ECB-resistant composites for short and long duration by utilizing landraces PRT0010008, FRA0410090, PRT00100186 and ESP0090214 and ESP0090033, PRT00100530, GRC0010174 and ITA0370005, respectively, through inter-mating. Sandoya et al. (2008) used maize synthetic EPS12 as base population to develop MCB- and ECB-resistant inbred lines by three cycles of recurrent selection. The selection has decreased the tunnel length at the rate of −1.80 cm per cycle. In general, breeding methods do differ across different types of insects; nevertheless improved resistance against one insect pest may increase the resistance to other pests as well due to clustering of genes determining resistance mechanisms (Groh et al. 1998; Cardinal et al. 2001; Jampatong et al. 2002; Ordas et al. 2009, 2010).

Recurrent selection can be employed to enhance the level of resistance in the population which can be used to derive inbred lines with higher degree of resistance to weevils. Garcia-Lara and Bergvinson (2014) observed 2–3-fold increase in the level of resistance against *S. zeamais* by three cycles of intra-population recurrent selection. Sekhar et al. (2010) observed significant response to cyclic improvement in resistance to *S. inferens* in eight maize genotypes.

7.8.3 Development of Hybrids and Their Evaluation Under Artificial Infestation Condition

Development of hybrids and their evaluation under artificial infestation condition is also being practised for development of resistant cultivars. Even efforts were made to identify and exploit the heterotic pattern by making flint × flint crosses for resistance to *S. nonagrioides*. Based on variety effects and cross performance, the heterotic pattern Basto/Enano levantixo (stem resistance) × Longfellow (positive variety effects for grain yield) has been recommended for obtaining high-yielding flint maize hybrids tolerant to *S. nonagrioides* infestation (Soengas et al. 2004).

7.8.4 QTL Mapping

Identification and location of genes conferring resistance will facilitate the understanding of genetic mechanism of resistance. Further, comparing genomic locations identified through different studies using different sources helps to combine the resistant genes from different germplasm sources to enhance the level of resistance. The different germplasm sources contribute different gene conferring resistance, which is evident in the study conducted by Krakowsky et al. (2002) where De811 and B52 do contain different genomic regions for resistance to ECB. It was discussed in the above sections that evaluation of maize germplasm under artificial infested conditions is most important for identification, selection and development of insect-resistant cultivars. The associated challenges are also numerous while evaluating the germplasm due to influence of growing conditions or environment on expression of resistant trait (Willmot et al. 2004; Sandoya et al. 2008; Mahmoud et al. 2016). Artificial infestation is time consuming and laborious and requires highly skilled manpower to achieve the desired results in the field. The advancement in molecular tools and techniques has led to identification of genomic regions responsible for resistant reaction through genomic mapping by using DNA-based molecular markers.

Maize is the first crop for which a complete molecular map was developed (Helentjaris et al. 1986). The knowledge with respect to number, genomic positions and genetic effects of quantitative trait loci (QTL) determining resistance to different insect pests would avoid the laborious phenotypic selection and also simplify selection process during breeding for insect resistance. QTL mapping is a powerful tool for efficient identification and characterization of novel insect-resistant genes. Development of powerful molecular genetic tools allows genome-wide association studies to dissect the molecular variation underlying variation in insect resistance (Madhusudhana, 2015; Chan et al. 2010; Kump et al. 2011). Several studies have been conducted on QTL mapping of resistance traits to different insect pests in maize depending on the importance of pest.

7.8.4.1 European Corn Borer

Several studies have been undertaken for mapping genomic regions conferring resistance to ECB in different mapping populations developed in diverse sets of germplasm. Bohn et al. (2000) mapped the QTLs for resistance against the ECB in F_3 families derived from a cross D06 (resistant) × D408 (susceptible), early maturing European dent germplasm. The study revealed six QTLs for tunnel length and five QTLs for stalk damage resistance, which together explained 50% of genotypic variance. Cardinal et al. (2001) mapped QTL determining resistance to stalk tunnelling by ECB in maize by using RILs derived from B73 × B52 cross. The study has detected nine QTLs for ECB tunnelling, which accounted for 59% of the genetic variation. Six of the nine QTLs were from resistant parent, B52, and were responsible for decreased tunnelling. One digenic interaction was also detected between QTLs for ECB tunnelling. Further, it was observed that most of the QTLs detected were located on the genomic regions determining one or more cell wall components

like neutral detergent fibre (NDF), acid detergent fibre (ADF) and acid detergent lignin (ADL) content (Cardinal and Lee 2005). Krakowsky et al. (2002) used F_3 populations for mapping QTLs conferring resistance to stalk tunnelling by ECB. The study identified seven QTLs distributed on chromosomes 1, 3, 4, 5 and 8, which explained 42% of the phenotypic variation. In another study, QTLs conferring resistance to leaf-feeding damage by first-generation ECB as well as stalk tunnelling by second-generation ECB have been mapped using $F_{2:3}$ mapping population derived from a cross B73Ht (susceptible) × Mo47 (resistant). The study led to the identification of nine QTLs on chromosomes 1, 2, 4, 5, 6 and 8 for leaf-feeding resistance by first-generation ECB along with seven QTLs for stalk tunnelling resistance by the second-generation ECB on chromosomes 2, 5, 6, 8 and 9 (Jampatong et al. 2002; Sharopova et al. 2001). It was observed in both studies that there was consensus with respect to co-localization of several QTLs identified for resistance to other stem borers of maize including resistance to stalk tunnelling in other maize populations. Krakowsky et al. (2004) reported ten QTLs conferring resistance to stalk tunnelling by the ECB using 191 RILs of maize population derived from B73 (susceptible) × De8 (resistant), which together explained 42% of the phenotypic variation. Papst et al. (2004) used test cross approach to evaluate the lines and map QTLs determining resistance to stalk tunnel length in the same population, D06 (resistant) × D408 (susceptible), which Bohn et al. (2000) had used. Orsini et al. (2012) reported two and one QTL for resistance to stalk breakage and leaf feeding by second- and first-generation ECB, respectively. The identified QTLs explained 36 and 25% of genotypic variance with moderate heritability of 0.69 and 0.43, respectively. The study used test cross progenies of DH lines derived from KW4773 (P_R) and WBB53(P_S) belonging to stiff-stalk synthetic. The QTLs identified were consistently located on the genomic regions around the previously reported genomic regions.

7.8.4.2 Mediterranean Corn Borer

In two separate experiments, QTLs determining resistance to MCB or PSB have been mapped, by using IBM population derived from a cross B73 × Mo17 (Ordas et al. 2009) and RIL population (Ordas et al. 2010). The numbers of QTLs identified in these experiments are two and three, respectively, on chromosomes 1, 9 and 1, 3 and 8, respectively, which explained 18 and 7.5% of the phenotypic variance. The studies concluded that the possibility of marker-assisted selection (MAS) for improving resistance to MCB is less due to low percentage of phenotypic variance. Another reason may be that the character is determined by a large number of QTLs each contributing a small proportion towards resistance reaction. The study detected the presence of pleiotropism or linkage between genes affecting resistance and agronomic traits. Samayoa et al. (2014, 2015) reported quantitative trait loci for yield performance under infestation with *S. nonagrioides* and located six QTLs for resistance traits.

7.8.4.3 Southwestern Corn Borer

Six QTLs explaining 53.3% of genotypic variance for resistance to the first generation of SWCB [leaf damage ratings (LDR)] have been identified in $F_{2:3}$ lines derived from a cross CML131 (susceptible) × CML67 (resistant). In another mapping population derived from Ki3 (susceptible) × CML139 (resistant), seven QTLs have been identified, of which three are common between both the mapping populations (Bohn et al. 1997). The extension of the same study led to identification of nine and five QTLs determining resistance to leaf-feeding damage (LFD) by the first generation of SWCB in two RIL mapping populations derived from cross CML131 (susceptible) × CML67 (resistant) and Ki3 (susceptible) × CML139 (resistant), respectively, with moderate level of heritability (0.50–0.75). The QTLs identified explained about 52% and 35.5% of the phenotypic variance, respectively. Further, it was also observed that many of the QTLs identified were located in genomic regions, where QTLs determining leaf protein concentration or leaf toughness are located. This further corroborates the chemical basis of resistance (Groh et al. 1998). In another study, Brooks and Barfoot (2015) also mapped eight QTLs conferring resistance to leaf feeding by SWCB using the F_2 population which explained 20% of the phenotypic variation; QTL identified on chromosomes 1, 5 and 9 correspond to previously identified regions by Groh et al. (1998).

7.8.4.4 Sugarcane Borer

Bohn et al. (1997) and Groh et al. (1998) identified ten and eight mostly identical QTLs, identified for the first generation of SWCB for SCB explaining 98.2 and 52% of the genotypic and phenotypic variation, respectively, in $F_{2:3}$ and RIL mapping population derived from CML131 (susceptible) × CML67 (resistant), respectively.

7.8.4.5 Fall Armyworm

Brooks and Barfoot (2015) identified seven QTLs in the same mapping population, which was used for QTL mapping for SWCB, and found that all the QTLs together explained 14% of the phenotypic variation. Similar to what was observed by Groh et al. (1998) for SWCB and SCB, three QTLs on chromosomes 6, 9 and 10 were conferring resistance to leaf-feeding damage by both SWCB and FAW. It was also interesting to note that the QTLs identified on chromosomes 6 and 9 corresponded to insect resistance genes, *mir* family and *glossy15*, respectively, confirming possibility of the common genomic regions determining resistance to different insect pests.

7.8.4.6 Maize Weevil

S. zeamais (Motsch.) occurs across the globe and causes severe loss in stored grain especially in tropical regions. García-Lara et al. (2009) analysed genomic regions responsible for resistance to stored grains by using $F_{2:3}$ populations derived from a cross CML290 (susceptible) × Muneng-8128 C0 HC1-18-2-1-1 (resistant). The most widely used component traits, viz. grain damage (GD), grain weight losses (GWL), MW susceptibility index (Dobie index, DI) and numbers of adult progeny (AP), were used along with putative components of resistance, viz. grain hardness

and pericarp/grain ratio to measure resistance to storage grain. The study has identified 21 QTLs ranging from 3 (AP) to 7 (DI) QTLs for different component traits which together explained 10 (AP) to 28 (GD) and 23 (AP) to 78 (DI) % phenotypic and genotypic variation, respectively, for different traits. The study also reported narrow sense heritability 48.0% and 45.0% for grain weight loss and number of insect progeny, respectively. The study was further extended to understand the underlying biochemical basis of resistance to stored grain resistance by identifying several QTLs for 11 traits, viz. p-coumaric acid (p-CA), cis- and trans-ferulic acid (FA), four isomers of diferulic acids (DiFA), phenolic acid amides (p-coumaroyl-feruloyl putrescine [CFP] and diferuloyl putrescine [DFP]), total DiFA and total phenol acids (PhA). The QTLs identified explained 25–47 and 50–98% phenotypic and genotypic variation, respectively, along with co-localization at QTLs identified for cell wall-bound compounds suggesting strong association for MW resistance (García-Lara et al. 2010).

7.8.5 Marker-Assisted Selection

The ultimate utility of identification of genomic regions conferring resistance to different insect pests in a breeding programme is to mobilize such specific QTLs into different genetic backgrounds via MAS to develop resistant cultivars. But inconsistency of QTLs detected across environments is a common characteristic, which complicates implementation of marker-assisted selection posing serious problem towards breeding for insect resistance (Groh et al. 1998). Several MAS strategies have been proposed, from simple backcross programmes to more complex population improvement strategies. Bohn et al. (2001) observed MAS using only molecular marker information is less efficient than conventional phenotypic selection (CPS). On the contrary, Willcox et al. (2002) integrated the QTL mapping for leaf-feeding resistance to first-generation Southwestern corn borer along with marker-assisted backcross breeding. Three putative QTLs linked to leaf-feeding resistance to first-generation SWCB were identified on chromosomes 7, 9 and 10, which together accounted 28% of the total phenotypic variation. The study evaluated BC_2F_3 lines, selected by two methods, viz. marker-assisted selection via QTL-linked markers and conventional selection under SWCB infestation. It was observed that both MAS and conventional selection produced comparable lines indicating that MAS is equally effective. The results are encouraging for undertaking large-scale MAS for development of insect-resistant cultivars by introgression of QTLs conferring resistance into otherwise well-adopted cultivars. Further, Flint-Garcia et al. (2003) and Samayoa et al. (2015) also concluded from their study that MAS is feasible for the introgression of resistance trait without any penalty on yield.

QTL mapping facilitates the development of molecular markers and enhances marker-assisted introgression of resistance traits into economically important cultivars of crops (Varshney et al. 2005; Bergelson and Roux 2010). The whole-genome-based selection is bringing lots of excitement towards increasing the efficiency of MAS by targeting all sets of genes (minor as well as major genes) determining

resistance, which looks promising towards developing resistance to various insect pests. Foiada et al. (2015) have already tried towards the same for ECB stalk damage and concluded that efficiency of MAS for ECB stalk damage resistance can be increased considerably when progressing from a QTL-based towards a genome-wide approach. The advances in molecular tools and techniques have brought significant improvement in the efficiency of breeding methods. In fact, they have accelerated the rate of development of new cultivars by reducing the breeding time.

7.8.6 Transgenic Approach for Development of Insect-Resistant Cultivars

Genetic engineering of crops for insect resistance aims at enhancing the resistance of plants towards insect pests through introduction and expression of specific DNA sequences in the crop plants. The introduced sequences code for the protein or over-expression of the native sequences to code for the metabolites which possess insecticidal activity or disturb the metabolism of insect severely. Within less than two decades from the first commercial release, insect-resistant transgenic crops have been widely accepted in the global agriculture due to significant socio-economic approach (Koziel et al. 1993). Several transgenic approaches are available to combat the insect pest damage in crop plants. The transgenics possess non-plant-based transgenes with plant-based transgenes and combinations of several transgenes.

7.8.6.1 Transgenics with Non-plant-Based Transgenes

Several non-plant-based genes have been transferred and expressed in plants through genetic engineering approach. Transgenics based on genes encoding cry proteins of *Bacillus thuringiensis* are widely adopted in the global agriculture, since the release of GM maize with Bt Cry proteins in 1996. Separate strains of Bt produce a variety of crystal toxins with distinct host range. At least ten genes encoding different Bt toxins have been engineered into plants (Schuler et al. 1998). Among these, Cry1Ab-based maize hybrids were widely adopted against European corn borer (Koziel et al. 1993) and Cry3Bb against the root cutworms. Besides these, several novel Bt insecticidal proteins have been isolated and the efficiency against various pests was demonstrated. Vip3, a single-chain vegetative insecticidal protein, and Cry34/Cry35 are known to be active against lepidopteran larvae and root worms (coleopteran), respectively, with a broader range of toxicity as compared to earlier Cry proteins (Moellenbeck et al. 2001; Fang et al. 2007). The insecticidal property of avian egg white protein avidin was successfully demonstrated. The insecticidal activity of avidin arises as a result of biotin sequestration (Morgan et al. 1993). The engineered maize plants for avidin resulted in more than 2.0% expression levels of avidin of total protein in seed and showed high resistance towards red flour beetle, *T. castaneum*, and other coleopteran pests (Kramer et al. 2000). In addition to these approaches, the production of dsRNA in plants to target the insect metabolism through RNAi is another well-established technology in insect molecular biology. In maize, transgenics producing dsRNA against V-type ATPase of corn rootworm

showed suppression of mRNA in the insect and reduction in damage as compared to controls (Baum et al. 2007).

7.8.6.2 Plant Defense Gene-Based Transgenics

A plant poses static (pre-synthesized insecticidal compounds) and active (production of insecticidal compounds in response to wounding and insect damage) defence mechanisms to defend against insect pests. Proteinase inhibitor (P_i) proteins are the small proteins of 4 to 25 kDa, which interfere with the digestive process of insects. The transformed plants with proteinase inhibitor showed resistance to *S. inferens* and *C. suppressalis* in rice (Xu et al. 1996), *S. cerealella* in wheat (Altpeter et al. 1999) and *S. litura* in tobacco (Yeh et al. 1997). Similarly, α-amylase inhibitors in plants showed high insecticidal activity through inhibition of starch digestion. The α-amylase inhibitor of the common bean (αAI-Pv) transformed pea, tobacco and adzuki bean showed resistance to lepidopteran and coleopteran group of insects (Altabella and Chrispeels 1990; Schroeder et al. 1995; Ishimoto et al. 1996). Lectins are carbohydrate-binding proteins, some of which are toxic to insects belonging to Homoptera, Coleoptera, Lepidoptera and Diptera. The most likely mechanism of entomotoxic activity of lectins involves interaction with different glycoproteins or glycan structures, which leads to interference with a number of physiological processes (Macedo et al. 2015). Transgenic maize events containing the gene-encoding snowdrop lectin (*Galanthus nivalis* L. *agglutinin*) with phloem-specific promoter showed enhanced resistance to aphids and Asian corn borer, *O. furnacalis* (Guenee) (Wang et al. 2005a, b).

7.8.6.3 Transgenics with Multiple Insecticidal Toxins

The single transgene specificity towards major target pests may result in transformation of secondary or minor pests into primary and severe pests. Therefore, stacking or pyramiding of multiple transgenes to ensure the durability of resistance or/and target the multiple insect pests, especially secondary pests, is warranted. The transgenic maize hybrid containing six insect resistance genes active against corn rootworm and lepidopteran pests (rootworm, *cry34Ab1* + *cry35Ab1*, modified *cry3Bb1*; lepidoptera, *cry1F,cry1A.105, cry2Ab2*) confers solution to both groups of pests with long-lasting durability (Gatehouse 2008). Additionally, the development of gene construct with single translation machinery but coding sequences of two or more insecticidal genes results in fusion proteins against multiple insect pests. Transgenic rice and maize plants engineered with coding sequences for δ-endotoxin Cry1Ac and the galactose-binding domain of the nontoxic ricin B chains showed resistance to larvae of stem borer (*C. suppressalis*) and leaf armyworm (*S. littoralis*) (Mehlo et al. 2005).

7.9 Conclusions

Maize has diverse usages, such as human food, animal feed and raw material for several maize-based industries. The efforts are therefore being made to meet the growing demand through continuous development of new cultivars with increasing level of resistance against insect pests and diseases and higher yield. In recent years, it has been considered as crop of industrial importance as 30% of US maize produced is being used for biofuel production. The demand for maize is increasing across the globe. However, the new challenges are emerging due to depleting natural resource base, increased cost of cultivation and changing scenario of biotic and abiotic stresses especially under climate change scenario. Breeding for insect pests' resistance in maize has been challenging because of the complexities in genetic control. The conscious effort towards breeding insect-resistant cultivars was missing in most of the developing countries. Further work is required to gain knowledge on gene action imparting resistance. Efforts have been made in employing molecular tools such as integration of MAS into the conventional breeding programmes for improved resistance.

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Breeding for Insect Resistance in Sorghum and Millets

8

P. Sanjana Reddy, Vitthal R. Bhagwat, G. Shyam Prasad, and Vilas A. Tonapi

Abstract

Sorghum and millets are crucial to food, fodder, and nutritional security in arid and semiarid tracts of the world. Sorghum is vulnerable to several insect pests. Among them, shoot fly, spotted stem borer, greenbug, midge, and head bugs are the most important worldwide. The pearl millet and small millets are relatively less subjected to pest attack and are more susceptible to diseases though sporadic instances of insect attack are reported. However, stem borers and grain midge are of regular occurrence in pearl millet. White grubs in India and spike worms in West Africa are assuming importance. The chapter covers the resistance sources, resistance mechanisms, resistant traits, gene action governing the major traits, and biotechnological advances for the economically important pests in sorghum and millets. Several genotypes resistant to shoot fly and to a lesser extent to stem borer, midge, aphids, and shoot bug have been identified. Development of multiple pest- and disease-resistant cultivars is emphasized.

Keywords

Sorghum • Pearl millet • Small millets • Resistance mechanism • Shoot fly • Biotechnology

8.1 Introduction

Sorghum and millets are crucial to the food and fodder security in the arid and semi-arid parts of the world. These crops are cultivated in harsh environments where it is difficult to grow other crops. Millets are small-grained grasses mostly grown in

P. Sanjana Reddy (✉) • V.R. Bhagwat • G.S. Prasad • V.A. Tonapi
ICAR-Indian Institute of Millets Research, Rajendranagar, Hyderabad 500030, India
e-mail: sanjana@millets.res.in; Bhagwat@millets.res.in; shyam@millets.res.in

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developing countries. Globally sorghum is grown on 41 million hectares producing 64.2 million tons of grain (Rao et al. 2015). In India, which has 16% of the world sorghum area, sorghum is grown in both rainy (*kharif*) and post-rainy (*rabi*) seasons (Tonapi et al. 2011). The millets are grown in harshest regions of Sahel in Africa and in South Asia's semiarid zone. They include foxtail millet, finger millet, proso millet, kodo millet, barnyard millet, little millet, teff, and fonio. The most important countries growing pearl millet are India, Nigeria, Chad, Niger, Mali, Tanzania, China, and former USSR. Finger millet is adapted to both tropical and temperate climates. It is consumed as a staple food in Eastern Africa and Asia. Foxtail millet is prominently cultivated in Europe, China, India, Indonesia, the Korean peninsula, and the former USSR. Proso millet is mostly suited to temperate climates. It is widely cultivated in the Russian Federation, Ukraine, Kazakhstan, Australia, Argentina, and the USA (Irén Léder 2004). Among the millets, four crops are prominently cultivated in Africa: pearl millet (the most widely grown with 76% area), finger millet (19%), teff (9%), and fonio (4%) (Obilana 2003). In the Asian continent, India and China are the two important and highly populated countries, where millets are exclusively grown, although semiarid regions of Nepal, Myanmar, and Pakistan produce millets in small quantities. The world statistics refer to pearl millet as millet though finger millet and foxtail millet are added in a few countries. Pearl millet is the most widely grown of all millets, and it has the highest yield potential of all millets under drought and heat stress. Based on the world statistics, India has the largest acreage under pearl millet contributing to nearly 40% of the world's output producing about 11 million tons of grain per year. Pearl millet is grown in about 30 million hectares worldwide, largely in Africa (18 million hectares) and Asia (10 million hectares). In the USA, about 607,000 hectares of pearl millet are cultivated annually mostly in North Dakota, Nebraska, South Dakota, and some southeastern states including Georgia and Florida where it is used as hay and a summer grazing crop (Dewey et al. 2009). Millets are important for food, nutrition, and fodder security in these regions. Among all these crops, sorghum has the largest acreage worldwide and is grown for diverse uses for food, fiber, forage, ethanol, and sugar production (Liu et al. 2009). Pearl millet is the next important millet crop cultivated across the globe. The other species of millets have regional preferences and confined to smaller regions in individual countries. The fonio is an indigenous West African crop comprising of two species, *Digitaria exilis and Digitaria iburua*. It is grown on small farms in Africa and is world's fastest maturing cereal. Small quantities of white fonio are grown in sub-Sahelian Western Africa with Mali having the highest acreage under it. Black fonio is grown sporadically in Togo, Nigeria, and Benin. In Latin America, millets are grown to a limited extent in Argentina. Proso millet cultivation is concentrated in the Russian Federation, Kazakhstan, and Ukraine. Production of millets in North America, Australia, and Europe is extremely limited (ICRISAT and FAO 1996)

Though the millets are widely cultivated and got adapted in many parts of the world, several studies suggest that most of them originated in tropical West Africa, as the greatest number of both wild and cultivated forms exists in Africa. They have migrated and adapted in different countries. Unlike in developed countries, where

millets are utilized as feed, they have been important food staples particularly in Asia and Africa. In East Asia, millets have been in cultivation since the past 10,000 years (Manju and Khurana 2014). Of the total global output estimated 28 million tons, developing countries, mainly in Asia and Africa, account for 94% of production. Of this, pearl millet accounts for about 15 million tons, foxtail millet for 5 million tons, proso millet for 4 million tons, and finger millet for over 3 million tons. In developing countries, millets are grown under marginal conditions with limited application of improved technologies except in some areas where commercialized farming utilizing hybrids is taken up. These crops are usually grown on light, well-drained soils that are poor in organic matter content, without irrigation or chemical fertilizer, although exceptions occur. Sorghum is more susceptible to insect pests, while reports on economic losses due to insect pests in other millets are limited (ICRISAT and FAO 1996).

The distribution of sorghum insect pests is well studied by Guo et al. (2011). Among the 150 insect species, more than 100 of them are found in Africa (Kruger et al. 2008). The greenbug, sorghum midge, fall armyworm, and corn borers are the major pests in North America (Munson et al. 1993; Wu and Huang 2008; Damte et al. 2009). Grasshoppers cause more damage in South America. Sorghum shoot fly, corn rootworm, and corn borers are important pests in Asia, Europe, and Africa. Sorghum aphid and sorghum midge cause severe damage in Australia (Guo et al. 2011). Resistance of plants to insects enables a plant to avoid or inhibit host selection, inhibit oviposition and feeding, and reduce insect survival and development, tolerate, or recover from injury from insect populations that would cause greater damage to other plants of the same species under similar environmental conditions (Smith 1989). Resistance of plants to insect damage is determined by combination of heritable morphological and/or biochemical characters of the plants that also determines the relative degree of damage caused by the insects. The inability of a plant to serve as host to an insect is termed as antixenosis. Thereby, the insect changes its host plant for feeding and oviposition for its survival (Sharma 1997). Originally the term non-preference was proposed to describe such behavior by Painter (1951). The term "antixenosis" was proposed by Kogan and Ortman (1978) to replace the term proposed earlier. The adverse effects of the physicochemical characteristics of the host plants on the biology of an insect feeding on it are termed as "antibiosis." The young larvae and eggs are affected, and in chronic cases, it leads to mortality of older larvae, pupae, and adults. The surviving individuals may have reduced body size and weight, prolonged period of development, and reduced fecundity. The allelochemicals, growth inhibitors, and morphological barriers in the plant lead to antibiosis mechanism of resistance (Sharma 1997). The tolerance mechanism of resistance is defined as the ability of plants to withstand or recover from damage caused due to insects as compared with damage on a susceptible cultivar. After the insect infestation, the tolerant plant recover and depict new growth or outgrow an insect infestation due to their inherent genetic capability From an agronomic perspective, the tolerant cultivars produce a greater yield than plants of a susceptible cultivar. The tolerance mechanism often occurs in combination with antixenosis and antibiosis mechanisms (Sharma 1997).

8.2 Sorghum

Insect pests are one of the major detrimental factors for grain and fodder sorghum production in farmer's fields. Sorghum is mostly grown under rainfed subsistence farming system and is vulnerable to pest attack at all stages of its growth. Use of excessive insecticides has caused damage to the environment apart from the development of new biotypes in insects. Breeding for crop varieties with resistance to harmful insects has been observed as the best way to tackle the pests, especially in areas where farmers are poor in resources. Therefore, host plant resistance is an important component of integrated pest management system. Extensive work on breeding for insect resistance has been done in sorghum, while very few reports are available on other millets.

Sorghum is attacked by several species of insect pests from sowing to harvest. Nearly 150 species are recorded as pests of sorghum. Among them, shoot fly, spotted stem borer, greenbug, sorghum midge, and head bugs are the most important worldwide (Sharma 1993). Earlier studies have estimated the losses due to insect pests to be around 32% in India (Borad and Mittal 1983), 9% in the USA, and 20% in Africa.

Only a few of the insect pests are economically important such as shoot fly, stem borer, midge, mite, earhead bugs, and aphids. These pests are discussed in detail in this chapter to illustrate concepts of breeding for resistance to these pests. The success of any resistance breeding program depends on the availability of diverse genetic resources from which resistant sources can be selected, standardization of screening techniques, knowledge of resistance mechanism, mode of inheritance, and selection of suitable breeding procedures. Pedigree breeding methods are used to attain short-term gains and in breeding for resistance to a single pest. However random-mating populations can serve as a long-term approach for developing lines with resistance to several major insects. As insect pests cause damage at two stages – shoot and earhead – two pest-resistant populations using ms_3 and ms_7 genetic male sterility genes can be developed.

8.2.1 Shoot Fly, *Atherigona soccata* (Rondani) (Muscidae: Diptera)

Shoot fly is a major biotic constraint to sorghum production causing considerable losses in both the rainy and post-rainy seasons. It attacks sorghum at the seedling stage. The sorghum plants below 30-days in age are damaged by larvae feeding on growing point. Thus, the central leaf dries up, resulting in typical deadheart symptoms. The late-sown rainy season and early-sown post-rainy season sorghum crops are more vulnerable to shoot fly infestation. Due to damage to the main plant, the losses are heavy due to decrease in grain and fodder yields. Plant resistance to shoot fly appears to be a complex controlled by a number of componential characters, which finally sum up in the expression of resistance to shoot fly (Dhillon 2004). Several resistant sources have been identified by earlier workers (Tables 8.1 and 8.2).

Table 8.1 Resistant and/or less susceptible genotypes of sorghum reported against major insect pests

Crop/pest	Resistant/promising genotypes	References
Shoot fly	IS Nos 844, 923, 1034, 1057, 1061, 1071, 1082, 1096, 1104, 1199, 1456, 2122, 2162, 2195, 2269, 2291, 2309, 2312, 2394, 2705, 3962, 4224, 4522, 4646, 4660, 4661, 4663, 4666, 4712, 4776, 5072, 5092, 5210, 5214, 5285, 5333, 5469, 5470, 5480, 5484, 5490, 5511, 5538, 5566, 5469, 5490, 5613, 5619, 5622, 5623, 5633, 5636, 5642, 5648, 7094, 8315, 8320, 12611, 18368, 18369, 18471, 18577, 18584	Krishnananda et al. (1970), Jotwani and Srivastava (1970), Rao et al. (1972), Soto (1974), Singh et al. (1978), Sharma et al. (1977), Singh and Jotwani (1980b), Borikar et al. (1982), Khurana and Verma (1985), Taneja and Leuschner (1985), Sharma and Rana (1985), Raina et al. (1984), Unnithan and Reddy (1985), Mote et al. (1986), Nimbalkar and Bapat (1987), Jadhav et al. (1988), Omori et al. (1988), Singh and Verma (1988) and Patel et al. (1989)
Stem borers	IS Nos 1044, 1082, 1119, 2122, 2123, 2146, 2168, 2169, 2291, 2309, 2312, 2375, 2376, 4273, 4546, 4637, 4576, 4757, 4776, 4881, 4981, 5075, 5253, 5429, 5469, 5470, 5480, 5538, 5566, 5571, 5585, 5604, 5619, 5622, 7223, 8811, 9608, 10711, 12308, 13100, 13674, 17742, 17745, 17747, 17750, 17948, 17966, 18333, 18366, 18551, 18573, 18577, 18578, 18579, 18580, 18548, 18585, 18662, 18667, 20643, 21969, 22039, 22091, 22145, 22507, 23411, 23962, 24027, 2162, 2263, 18328, 18349, 10370, 10364, 178, 3962, 4213, 12497, 18479, 18323, 18326, 18427, 4405, 18584, 18676, 5613, 18517, 5629, 2205, 2235, 1054	Taneja and Leuschner (1985), Reddy (1985), Jotwani et al. (1978) and Patel and Sukhani (1989)
Midge	DJ 6514, ICSV 745, QL 39, PM 15936-2, ICSV 197, IS Nos 957C, 1257C, 1832C, 2144C, 2508C, 2549C, 2579C, 2660, 2663, 2685C, 2740C, 2816C, 3017C, 3390C, 3472, 3574C, 4411, 4870, 5977, 6170, 7005, 7132C, 7193C, 8100C, 8112C, 8232C, 8237C, 8887, 10712, 12572C, 12608C, 12612C, 12664C, 12666C, 18563, 21873, 21881	Johnson et al. (1973), Gowda and Thontadaraya (1976), Kulkarni et al. (Kulkarni et al. 1978, Page Page 1979) and Sharma et al. 2002
Aphid	TAM 428, IS 1144C, IS 1366C, IS 1598C, IS 6416C, IS 6426C, IS 12661C, and IS 12664C, SLB 80, ICSV 93046, SLR 31	Teetes et al. (1995) and Bhagwat et al. (2014)
Shoot bug	Genotypes of Kafir Suma and Dwarf Hegari, I 753, H 109, GIB, 3677B, and BP 53 (IS 1055), MSH65, SPH 1388, SPV nos 475, 678, 736, 741, 756, 775, 819, 858, CSV 10, IS 19349	Khan and Rao (1956), Agarwal et al. (Agarwal et al. 1978) and Rajasekhar (1989), Chandra Shekar (1991) and Chandra Shekar et al. (Chandra Shekar et al. 1993a, b)
Head bug	IS 18657, IS 18677, PJ 8K(R), IS 17610, IS 17645, IS 21443 and IS 17618	Singh and Rana (1992), Chandra Shekar (1991), Chandra Shekar et al. (Chandra Shekar et al. 1992, Chandra Shekar et al. 1993a, b) and Sharma and Lopez (1992)

Table 8.2 Resistant or less susceptible genotypes of pearl millet reported against various insect pests

Crop/pest	Resistant/promising genotypes	References
Shoot fly	IP 241, PT 1939, MS 6317, PT 1522, PT 1930, IP 863, PT 1836, MS 6112	Appadurai et al. (1981)
	JFB 801, JFB 812	Pandey et al. (1985)
	MP 16, MP 19, MP 31, MP 53, MP 67	Kishore (1996a)
	Pusa 23	Kishore (2000)
Spotted stem borer	A 10, A 21P1, A 63, A 66, A 163, A 280, A 281	Sandu et al. (Sandhu et al. 1976)
	MP 19, MP 2I, MP 31, MP 39, MP 47, MP 53, MP 56, MP 60, MP 63, ICMS 7703, ICMS 7704, WCC 75, IVPS 77	Kishore (1996a)
	PUSA 23, PUSA 383, MP 489	AICPMIP (2010)
	MP 508	AICPMIP (2011)
	RAJ 171	AICPMIP (2012)
Millet stem borer	CIVT, Sadore local	ICRISAT (1983)
	Zongo	Gahukar (Gahukar 1984)
	INMB 106, INMB 218, INMB 155	Ndoye et al. (1986)
Oriental armyworm	Souga Local 4, 700112, PIB 228, and D 1051	Sharma and Davies (Sharma and Davies 1982)
	IP 6577, PIB 228, IP 6069, IP 6251, and IP 5836	Sharma and Sullivan (2000)
Spike worm	Ex-Bornu and Souna, HKP, Zongo 3, Nieluve, Bou	Vercambre (1976, 1978)
	Souna, 314 HK 78, ICMS 7819, ICMS 7838, IBV 8001, M 24–38, Nigerian composite, HKB Tif, CIVT, HKP, Zongo, Nieluva, Boudouma, IBMV 8392, INMG 52, INMV 5001, SRM-Dori, P3 Kolo, ITV 8001, Kassblaqa, Yolusee-Nial, Tara Yombo	Ndoye et al. (1986)
	Souna, KH-78, IBV 8001, ICMS 7819	Ndoye and Gahukar (1987)
Spike worm	IBMV 8302, INMG-1, INMG-52, ITMV 8001	ICRISAT (1984)
Earhead caterpillars *Eublemma silicula*	29 MD, 146, RSK, 268, Pusa 605, MLBH 104	Kishore (1996a, 1996b)
Earhead caterpillar, *Helicoverpa armigera*	MH 1910, MH 1984, MP 533, HHB 67 Imp, Nandi 61, 86M64	AICPMIP (2014)
Shoot bug	26J, 78J, 98, 103, 107TD, RSJ, RSK, 13073, 6D, 29MD, 146	Kishore (1996a)

(continued)

Table 8.2 (continued)

Crop/pest	Resistant/promising genotypes	References
Pyrilla	IP Nos. 22B, 36D, 44, 79, 214, 263, 1266, 1301, 1345, 1395, 1402	Pradhan (1971)
	79, 1395, 263, 1307, j-98, 1301, 1402, 44265, 23B, 1362	Jotwani (1978)
	36 D, IP Nos. 44, 79, 214, 263, 1266,1301,1307, 1345, 1395, 1402, 1708	Kishore (1996a)
White grubs	RSK Nos.1086, 213, 315,1826, 833	Kishore (1996a)
Gray weevil	NHB 5	Singh and Singh (1977)
	MP 17, MP 3I, MP 38	Kishore (1996a)
Leaf roller	36 D, 29 MD, 146, MP 31	Kishore (1996a)
Greenbug	GAHI 1	Stegmeier and Harvey (Stegmeier and Harvey 1976)
	C-591, Pak-75211, Pak-75212, Pak-75219, Pak-75194, Pak-75227, Pak-75238 Pak-75272, Pak- 75276, WCA-78, C-47, Pak-75322, Pak-75323, Pak-75329, Pak-75331, Pak-75334, Pak-75337, Pak-75338, Pak- 75339, Pak-75353, Pak-75359	Akhtar et al. (2012)
Chinch bug	TifGrain 102	Ni et al. (2007)
	04-7049, 05-5212a, 05-5206a, 04-7041, 02-7978, 02- 7747, 04-7040	Maas and Ni (2009)
	07F-1226, 07F-1229, 07F-1231, 07F-1235, 07F-1238, 07F-1239, 07F-1240	Xinzhi et al. (2009)
	59464B and 59668M-1	Rajewski et al. (Rajewski et al. 2009)

Starks' interlards and fish meal technique have been proven to be effective in creating uniform and desired levels of shoot fly infestation (Soto 1974; Sharma et al. 1992). Antixenosis is the primary resistance mechanism to shoot fly (Soto 1974; Singh and Jotwani 1980b; Raina et al. 1984; Taneja and Leuschner 1985). The germplasm lines IS 1034, IS 2146, IS 2265, IS 2309, IS 3962, IS 4664, IS 5566, IS 5604, IS 18369, and IS 18551 (<40% plants with eggs) show antixenosis for shoot fly. The shoot fly resistance levels in the identified germplasm sources vary with density of insect population and are influenced by the environment (Sharma and Nwanze 1997; Dhillon et al. 2005). Looking into the complexity of resistance

mechanism and its interaction with the environment, it is crucial to identify the genotypes with different resistance mechanisms to diversify the basis of resistance and pool the genes contributing the resistance toward this insect (Riyazaddin et al. 2015). Importance of trichomes on the undersurface of the leaves in governing tolerance to shoot fly has been reported by several workers (Maiti et al. 1980; Taneja and Leuschner 1985). The resistant lines also exhibit glossy leaves during seedling stage. This may be possibly due to reflection of light from the leaves and chemicals present in the surface waxes. The first instar larva is inhibited from reaching the shoot tip by rapid growth of the seedlings (Taneja and Leuschner 1985; Omori et al. 1988). Other traits such as percentage of nitrogen, total sugars, reducing sugars, moisture, and leaf chlorophyll content are higher in susceptible cultivars, while silica bodies, amino acids, phosphorus, and total phenols were higher in resistant cultivars (Singh and Jotwani 1980a; Mate et al. 1988; Patel and Sukhani 1990; Khurana and Verma 1983).

Shoot fly resistance is quantitatively inherited and controlled by additive gene action as has been reported by majority of workers (Nimbalkar and Bapat 1987; Singh and Verma 1988). However, the genetics of resistance parameters is controlled by shoot fly pressure. The midparental heterosis was realized only under low shoot fly infestation, while no heterosis was observed under high shoot fly pressure (Rana et al. 1981; Dhillon et al. 2006). The additive × additive interaction among the nonallelic interactions was found to be important for most of the resistance contributing traits. The additive component increases with heavy infestation, but dominance component remains intact (Borikar and Chopde 1980). The predominance of additive and additive × additive gene effects suggests that among the breeding methods, progeny selection would be more effective for improving the shoot fly resistance while selecting for other desirable attributes simultaneously (Patil et al. 2005). Four traits, trichome density, glossy intensity, eggs per plant, and percent deadhearts, were significantly correlated among themselves. Using a population of 210 RILs made between the shoot fly-susceptible parent, 27B, and shoot fly-resistant parent IS2122, Aruna et al. (2011) identified QTL for shoot fly resistance and the associated traits.

8.2.2 Stem Borer, *Chilo partellus* (Swinhoe) (Crambidae: Lepidoptera)

Several species of stem borers attack sorghum in different regions (Nwanze 1997). Among them, the spotted stem borer, *Chilo partellus,* is predominant in Asia and eastern and southern Africa (Kumar et al. 2006). Starting from 1 month after germination, stem borer attacks all stages of the crop. Except the plant roots, all parts of the plant are vulnerable to the attack. In the initial crop growth stage, the larvae feed on the leaves in the whorl of the plant causing deadhearts. In the later stages of crop

growth, they feed on the stem causing stem tunneling and feed on the panicle by boring finally resulting into chaffy heads. The world germplasm collections (30,000 germplasm accessions) were screened for spotted stem borer by Indian national sorghum improvement program and ICRISAT (Kumar et al. 2006). Several resistance sources were identified (Table 8.1). Among the resistant sources, ovipositional non-preference, reduction in the feeding of first instars on young leaves, less number of deadheart formation, decrease in stem tunneling, and lower signs of leaf damage were identified as resistance mechanisms (Chapman et al. 1983; Dabrowski and Kidiavai 1983; Woodhead and Taneja 1987; Sharma and Nwanze 1997; Kumar et al. 2006). Natural screening can be done at identified hotspot locations. The late-sown rainy season crop (first and third week of July) is more prone to stem borer damage in India. Artificial infestation can be done by releasing first instar larvae in the plant whorls using Bazooka applicator. The traits such as epicuticular wax and ligular hairs play a significant role by obstructing larval migration (Bernays et al. 1983). Genotypes with rapid elongation of internodes and early panicle initiation showed less damage due to stem borer at early vegetative and flowering stages, thereby showing less damage to growing point (Taneja and Woodhead 1989). Also, resistant genotypes were shown to depict a narrow angle between the leaf and stem (Woodhead and Taneja 1987). Genotypic differences for larval establishment have been reported (Singh and Rana 1989; Berg van den and Westhuizen van der 1997). The pest has a prolonged life cycle (larval, pupal, and the total development period) on the resistant genotypes (Singh and Rana 1984, 1989; Saxena 1990, 1992; Verma et al. 1992) resulting in reduction of number of generations in a season/year. Antibiosis mechanism of resistance is also expressed in terms of reduced pupal weight (Singh and Verma 1988; Verma et al. 1992) and low pupation and adult emergence (Singh and Verma 1988). The development of *C. partellus* is affected when it feeds on few resistant genotypes due to secondary plant substances in the leaves and/or less nutrients in the diet. These include low sugar content (Swarup and Chaugale 1962); greater amounts of amino acids, tannins, total phenols, neutral detergent fiber (NDF), acid detergent fiber (ADF), and lignins (Khurana and Verma 1982, 1983); and silica content (Narwal 1973) in sorghum genotypes having adverse effects on insect survival and development and thereby associated with resistance to *C. partellus* in sorghum. However under unfavorable growth conditions, genotypic resistance is poorly expressed. The inheritance of resistance to stem borer is quantitative in nature and with low heritability (Singh et al. 1980). The resistance to stem borer attack at different growth stages of the plant, such as leaf feeding, stem tunneling, and deadheart formation, is inherited differently (Pathak 1985). The additive and additive × additive type of gene action governs leaf feeding, while the stem tunneling is under the control of dominant genes. Hence, repeated screening of breeding material for several generations is recommended to improve selection for resistance to stem borer (Kishore et al. 1984).

8.2.3 Midge, *Stenodiplosis sorghicola* (Coquillett) (Cecidomyiidae: Diptera)

Midge is a small fly with orange-red color. It lays eggs inside the florets during flowering. The maggots feed on developing seeds resulting in poor grain yield. The damaged panicles are empty. The individual spikelets that are damaged by midge have pupal case attached to it or have a small exit hole on the upper glume. The life cycle of the midge is shorter in summer than in winter. The Johnson grass, *Sorghum halepense*, and pearl millet, *Pennisetum americanum*, serve as alternate hosts for the sorghum midge. The peak periods of infestation in South India usually occur in the crops sown April, June, August, and October. However, the developmental stages were active throughout the year, and the pest shows no diapause (Natarajan and Chellaiah 1985). The resistant sources for midge are given in Table 8.1. Breeding for midge resistance is an important component of sorghum improvement programs in Asia, Africa, Australia, and the Americas (Henzell et al. 1997) as host plant resistance is an effective means of keeping midge populations below economic threshold levels (Sharma 1993). Screening for sorghum midge resistance in hotspot locations is an effective means for testing resistance. The hotspots are Bhavanisagar, Dharwad, and Pantnagar in India, Farakoba in Burkina Faso, Sotuba in Mali, Alupe in Kenya, and Kano in Nigeria. For initial testing of large populations, early planting of susceptible sorghums with a range of days to flowering is suggested. The peak midge density occurs during October. The resistance in the promising lines is confirmed by using a no-choice head cage technique.

Oviposition non-preference is the most important mechanism of resistance to sorghum midge (Sharma 1985; Franzmann 1993; Rossetto et al. 1984; Sharma et al. 1990; Waquil et al. 1986a). Antixenosis to visiting adults is also observed in some sorghum genotypes (Sharma and Vidyasagar 1994; Waquil et al. 1986b). The survival and development of midge larvae is adversely affected on some midge-resistant genotypes (Sharma et al. 1993b; Waquil et al. 1986b). Short, tight, and hard glumes, faster grain development between the third and seventh day after anthesis, closed spikelets and panicle compactness, and tannin content of the grain are associated with resistance to sorghum midge (Murty and Subramaniam 1978; Rossetto et al. 1984; Sharma et al. 1990). Diarisso et al. (1998) suggested that in the resistant sorghum genotypes, the spikelets remained open for a short time thus evading the midge damage. Resistance to sorghum midge is also influenced by the chemical constituent of the grain that caused differential expression of resistance among the sorghum genotypes (Sharma et al. 1993b).

Based on testing in several environments (seasons and locations), the germplasm lines IS 3461, IS 8884, IS 8887, IS 8891, IS 19476, IS 22806, and AF 28 showed moderate to high levels of resistance to midge (Sharma et al. 1999). The inheritance to sorghum midge resistance is mainly governed by additive type of gene action, while cytoplasmic effects are also reported (Widstorm et al. 1984; Agrawal et al. 1988). In a few parents, dominance in gene action is also seen. The genotypes DJ 6514 and TAM 2566 have good general combining ability for midge resistance and widely used (Patil and Thombre 1985). Based on testing in India and Africa, it is

reported that both the parents need to have resistance to midge to produce midge-resistant hybrids and resistance is specific to the region of evaluation (Sharma et al. 2004b). In Australia, single source of midge resistance has been incorporated in sorghum hybrids that are being widely grown by the farmers (Henzell et al. 1997; Franzmann 1996; Jordan et al. 1996). Hence, there is a chance of breakdown of resistance as when a cultivar is planted continuously over large areas for several consecutive seasons, it results in evolution of new biotypes. Hence, diverse sources of resistance and diverse cultivars need to be grown to avoid severity of insect attack.

8.2.4 Aphid, *Melanaphis sacchari* (Zehntner) (Aphididae: Hemiptera)

The sugarcane aphid is an important pest in Asia, Africa, Australia, and the USA (Sharma and Nwanze 1997). In many sugarcane-growing countries, it acts as a vector for sugarcane yellow leaf virus (Smith et al. 2000). The abaxial surface of older sorghum leaves are attacked by the nymphs and adults of *M. sacchari*. They secrete a sugary solution/honeydew which fall on the lower leaves and ground below on which sooty molds giving a black appearance (Narayana 1975). In India, the pest is majorly reported on post-rainy season crop. The peak attack is observed in January when the post-rainy sorghum crop was between flowering and milk stage and declined thereafter till maturity (Waghmare et al. 1995). The crop is usually prone to terminal drought stress that intensifies the damage due to the sugarcane aphid (Raetano and Nakano 1994). The resistant sources for aphids are given in Table 8.1. For screening under natural conditions, the material should be sown during late rainy season in July and early post-rainy season in October. Under greenhouse conditions, leaf cage technique can be used to study aphid multiplication and growth rates by confining aphid females with the leaves and counting the number of aphids produced in 15 days. The aphid infestation is recorded on a 1–9 scale. The loss in grain yield in the infested plots is compared with that of non-infested plots (Sharma et al. 1991).

Tolerance to aphid is associated with small and narrow leaves; less number of leaves and low drooping of leaves at seedling stage (Mote and Kadam 1984); greater plant height; greater internode length, thereby maintaining greater distance between two leaves; waxy leaf surface (Mote and Shahane 1994); and epicuticular wax on the ventral surface of the leaves. Faster multiplication has been observed on genotypes with higher concentration of nitrogen, sugar, free amino acids and total chlorophyll (Mote and Shahane 1994; Tsumuki et al. 1995). The genotypes with high contents of potassium, phosphorus, and polyphenols (Mote and Shahane 1994), Aconitic acid (Rustamani et al. 1992) are less preferred by the aphids. Due to infestation, the total phenol content reduced by 18.5 to 55.8% over the healthy leaves, while War et al. (2012) suggested an increase in the phenol content. The phenol content of the aphid-infested leaves is not related to the tannin content of grains (Sharma and Dhillon 2005).

Resistance is controlled by dominant gene action and single dominant gene controlling resistance to aphids was reported by Chang (1981). However, other reports indicated the significant dominant and additive variances and complementary interaction (Hsieh and Pi 1988). In the cross M35-1 (susceptible) × R354 (resistant), observations on aphid population at various time intervals (51, 58, 65, 72, 86, 93 DAE and at maturity) showed that the inheritance of aphid resistance was governed by two dominant genes with duplicate effects (Deshpande et al. 2011). Cytoplasmic male sterility system also contributed toward aphid resistance (Dhillon et al. 2006). The restorer lines have a dominant effect on the inheritance of aphid resistance in hybrids (Sharma et al. 2004a, 2006).

8.2.5 Greenbug, *Schizaphis graminum* (Rondani) (Aphididae: Hemiptera)

Greenbug is one of several aphids that infest cereal grains (Teetes and Pendleton 2000; Royer 2007). Apart from sorghum, it is an important insect pest of winter wheat (*Triticum aestivum* L.). It is distributed widely across the globe and found throughout the Middle East, southern Europe, Africa, central western and central Asia, and North and South America (Blackman and Eastop 2000). More than 70 grasses and cereals were found to serve as hosts for greenbug. Greenbug is also a vector of the viruses and was shown to predispose sorghum to charcoal rot (Teetes et al. 1973). It is an economically important pest especially in temperate parts of the world affecting sorghum productivity (Teetes 1980). With a loss estimated at $274 million annually (Eddleman et al. 1999). The common symptoms in the plants include chlorosis and red necrotic spots (van Emden and Harrington 2007). Among the different biotypes of greenbug discovered on sorghum, biotype I is of economic importance (Harvey et al. 1991; Kofoid et al. 1991; Teetes and Pendleton 2000). Among the many control measures, host plant resistance is found to be important in the control of greenbug.

A large collection of about 40,000 sorghum germplasm accessions were evaluated for greenbug resistance, which resulted in identification of 21 resistant sources. Among these 21 lines, PI 607900 outperformed other lines with a damage rating of 1.1 (Huang 2011). This sorghum line PI 607900 (KS 97) was identified as an important source of resistance to biotype I, an important biotype of greenbug. This genotype was genetically distinct from other known resistant sources (Tuinstra et al. 2001; Wu et al. 2006) and had good general combining ability toward greenbug biotype I resistance (Tuinstra et al. 2001; Wu and Huang 2008). Resistance to greenbug biotype I was governed by a complimentary gene action between two major dominant genes (Tuinstra et al. 2001). According to Painter (1951), resistance to any insect pest can be classified under three categories: antibiosis, antixenosis, and tolerance. The resistance to greenbug can be classified under antibiosis and tolerance (Wilde and Tuinstra 2000). The inheritance of resistance to greenbug biotype I is under the control of polygenes (Agrama et al. 2002; Katsar et al. 2002; Nagaraj et al. 2005; Wu and Huang 2008). The genes for resistance to different greenbug

biotypes were mapped on sorghum chromosome SBI09 (Agrama et al. 2002; Katsar et al. 2002; Wu et al. 2007). Aphid-resistant plants are characterized with specific responses involving a gene-for-gene interaction, and resistance in such a case involves loci containing nucleotide-binding site-leucine-rich repeat (NBS-LRR) sequences (Dogimont et al. 2010).

8.2.6 Shoot Bug, *Peregrinus maidis* (Ashmead) (Delphacidae: Hemiptera)

The shoot bug/corn planthopper damages the host plant by piercing the vascular tissues and sucking sap from the leaves, leaf sheaths, and stem. The adults and nymphs are found inside the leaf whorl and on the inner side of the leaf sheath, causing reduced plant vigor, stunting, and yellowing of leaves and predisposing the plant to moisture stress. The corn planthopper is a pest of corn in many tropical and subtropical corn-growing regions throughout the world, including Hawaii (Singh and Rana 1992). In India, shoot bug causes up to 41% yield losses (Hosmani and Chittapur 1997). Resistance sources have been reported in sorghum (Table 8.1), and few of these are linked to virus diseases transmitted by *P. maidis* (Table 8.1). Natural screening can be done at hotspot locations with selection of suitable sowing date. For artificial screening under field conditions, mass rearing of the insect should be done on susceptible cultivar CSH 1, interlards should be planted first with CSH 1, and infestation carried out in test entries and drought conditions are simulated. The brachypterous and macropterous adults, total eggs, and nymphal population per plant are counted, and plant damage is calculated as the percentage of damaged plants to the total plants at 45, 60, and 70 days after emergence. The resistant plants showed tan plant pigment and tightly wrapped leaves around the stem (Agarwal et al. 1978). Antixenosis for oviposition is found to be the primary mechanism of resistance as depicted by significantly low rate of oviposition on resistant as compared to susceptible genotypes and positive and significant correlation between oviposition and plant damage (Singh and Rana 1992). The genotypes IS 18676, IS 19349, and IS 18677 were identified to host fewer nymphs and adults consistently at 30, 45, and 60 days after germination and hence showed a high degree of antixenosis (Shekar et al. 1993).

8.2.7 Head Bug, *Calocoris angustatus* (Lethiery) (Miridae: Hemiptera)

Sorghum head bugs (C. *angustatus*) in India and *Eurystylus oldi* Poppius in West Africa cause immense losses to sorghum yields (Sharma 1993). With the introduction of early-flowering, high-yielding cultivars with compact panicles in West Africa, head bugs have increased in recent years, and they predispose the panicles to grain mold thus increasing the losses. Hence, the screening for head bugs and grain molds are combined. In such a regional sorghum head bug and grain mold

resistance trial conducted at 15 and 13 research stations located in 10 West and Central African countries, respectively, two cultivars, namely, IS 14384 and CGM 39/17-2-2, exhibiting consistently high levels of resistance to both head bug and grain mold over years and localities were obtained. At all localities except in Benin, Chad, and Guinea, the *E. oldi* was the dominant head bug species (Ratnadass et al. 2003).

The nymphs and adults of head bug suck the sap from the developing grains resulting in both qualitative and quantitative losses. The infestations are high during August–September in the rainy season crop. The germplasm accessions and improved lines with resistance to head bug are given in Table 8.1. Natural screening can be carried out in hotspot locations that include Hyderabad, Bhavanisagar, Kovilpatti, Coimbatore, Palem, and Dharwad in India. For artificial screening, infester row technique is followed. Four rows of mixed maturity cultivars or early-flowering sorghums (40 to 45 days) are sown 20 days earlier for every 16 rows of test material. Test material must be sown in two dates to prevent escape in the early- and late-flowering lines. To avoid the problem of variation in flowering, no-choice head cage technique is followed. Observations should be taken on head bug counts, grain damage rating, grain yield, grain weight and floaters, and germination percentage.

The traits that are less preferred by head bugs include colored grain with high tannin content; long, hard, and less hairy glumes; compact panicles; >50% grain covered with glumes; and hard corneous grain (Sharma et al. 1993a, b, c). To increase the resistance levels as well as to diversify the resistance base, sorghum genotypes that are showing non-preference to adults, harboring low rates of population (antibiosis), and showing tolerance to head bug feeding can be used in a breeding program (Kumari et al. 2000). The inheritance of resistance is due to partially dominance with the genes having both additive and nonadditive gene action (Sharma et al. 2000). Other studies have shown that the resistance is controlled by recessive genes and it does not have without maternal influence. The gene action is predominantly nonadditive, while additive gene action is also found in some cases (Showemimo et al. 2006). However, cytoplasmic nuclear male sterility influences the resistance in hybrids, and both the parents need to be resistant to head bugs (Dhillon et al. 2006). It has been found that response to selection in early generation using pedigree selection method can be realized for achieving resistance to sorghum head bug and this method is reliable considering the time and resources (Showemimo et al. 2006).

8.2.8 Multiple Pest Resistance in Sorghum

The sorghum crop experiences severe damage by two or more insect pests as well as one or more pathogens during the crop-growing season. Hence, it is desirable to breed for multiple disease resistance. There are several studies showing multiple resistances to sorghum insects. The germplasm lines IS 18551, IS 2195, PS 28060-3 (Nwanze et al. 1991), IS 2205 (Patel et al. 1989), ICSV 705, IS 4881, and IS 13 674

(Jalaluddin et al. 1995) and hybrids HC 171 (Singh and Lodhi 1995) and HH 1 (Verma and Singh 2000) are found to be resistant to sorghum shoot fly and spotted stem borer and IS 22 464 with resistance to spotted stem borer and midge (Nwanze et al. 1991). However, resistance to some of the pests has not been successfully combined. Genotypes resistant to shoot fly and stem borer are susceptible to midge and vice versa (Sharma 1993). Since the resistance to sorghum insect pests is largely governed by additive gene action, resistance is needed in both parents to produce insect-resistant hybrids, and resistant parents can be bred through selection method of breeding (Sharma et al. 1996).

8.2.9 Employing Biotechnological Tools for Pest Resistance in Sorghum

Several quantitative trait loci (QTLs) have been identified in insect resistance breeding programs and summarized by Subudhi et al. (2002) and Sharma et al. (2005). By multiple QTL mapping, Satish et al. (2009) discovered 29 QTLs for shoot fly resistance. Most of these were found in syntenic maize genomic regions. This indicates that the resistant genes are in maize and sorghum (Guo et al. 2011). For greenbug resistance, three QTLs were found to be governing resistance against greenbug biotype I, and five QTLs were found to be associated with biotype K accounting for 9–19.6% of phenotypic variation (Nagaraj et al. 2005), and Wu and Huang (2008) identified two QTLs on chromosome 9 (accounting 6–80% variation). Chang et al. (2006) reported a single dominant gene controlling aphid resistance and mapped an SSR marker linked with this gene on linkage group 9. For head bug resistance, three significant and seven putative QTLs were identified by Deu et al. (2005) from a cross between head bug-resistant sorghum cultivar Malisor 84-7 and head bug-susceptible cultivar S 34. For midge resistance, two linkage groups were associated with antixenosis, and these two genetic regions explained 12 to 15% of the phenotypic variation, i.e., for egg number/spikelet under no-choice cage conditions. About 34.5% of the phenotypic variation for the difference in egg and pupal counts (antibiosis) was explained by one genetic region (Tao et al. 2003).

Much progress has been made in the past decade in the identification of molecular markers for various biotypes of greenbug. The molecular markers were utilized to identify greenbug-resistant sorghum genotypes as well as their utilization in marker-assisted breeding programs for developing greenbug-resistant sorghum cultivars. The molecular markers have also helped in dissecting the genes for greenbug resistance and in better understanding the genetic basis and mechanism of resistance (Yencho et al. 2000). Thus, they were extensively utilized in diverse studies. Across the world, five independent QTL mapping experiments were taken up in sorghum to identify genes contributing towards resistance to four different greenbug biotypes (Agrama et al. 2002; Katsar et al. 2002; Nagaraj et al. 2005; Wu et al. 2007; Wu and Huang 2008). These studies involved seven distinct sources of resistance and resulted in identification of multiple genomic regions responsible for resistance toward greenbug biotypes C, E, I, and K. For the economically important

greenbug biotype I, Katsar et al. (2002) identified three loci located on chromosomes SBI05, SBI06, and SBI07 conferring resistance to it. The chlorophyll loss due to greenbug injury was estimated, and nine genomic regions were identified that showed both biotype-specific and biotype-nonspecific resistance and tolerance to biotypes I and K (Agrama et al. 2002). Of these seven QTLs that were responsible biotype-specific resistance and tolerance to greenbug damage, three markers present on chromosomes SBI02, SBI05, and SBI09 were linked with biotype I-specific resistance and tolerance. Similarly, Nagaraj et al. (2005) quantified the chlorophyll loss as an indicator to greenbug damage. They identified three QTLs present on the sorghum chromosome SBI01 and SBI04 for biotype I resistance and tolerance. Recently, Wu and Huang (2008) have shown a major QTL located on sorghum chromosome SBI09 responsible for resistance to greenbug biotype I. Based on these studies and from the resistant sources used, it can be seen that multiple regions of the genome are responsible for resistance against greenbug. Some of the alleles in these genomic regions were specific to the biotype and some nonspecific or contributed toward general resistance. Though extensive studies were made in the direction of developing resistant cultivars against greenbug, progress toward developing cultivars with economically important greenbug biotype I resistance has been slow. The identification of new sources needs to be taken up on a massive scale. Considering the meager sources of resistance, the resistance to aphid attack is thought to be governed by very few resistance loci and alleles (Dogimont et al. 2010).

Different transcriptomic studies have emphasized the role of signaling compounds and defense-activated genes (Huang 2007). The cysteine proteinase inhibitors were downregulated, and genes such as Xa1, antimicrobial proteins, and other signaling compounds were upregulated in response to greenbug damage in sorghum as detected by suppression subtractive hybridization (Park et al. 2006). The differential expression of 82 greenbug-responsive genes was identified in plants infested with greenbug in another transcriptomic study. This included a LRR-containing glycoprotein sequence and other defense-related proteins (Zhu-Salzman et al. 2004). All these studies have indicated the significant role of plant R genes through signal transduction pathway in defense against greenbug attack.

The Bt crops have gained popularity in corn, cotton, and soybean for insect pest management and are commercially viable covering large areas under cultivation (James 2009). However, the Bt genes currently used are efficient against Lepidopteran pests. The sucking pests, such as aphids, are not sensitive to normal Bt proteins (Guo et al. 2011). Some progress has been made in developing stem borer-resistant sorghums through transgenic approach. Girijashankar et al. (2005) developed transgenic sorghum plants expressing a synthetic cry1Ac gene under a wound-inducible promoter mpiC1. The Bt-transgenic sorghum plants showed partial tolerance against first instars of the spotted stem borer. There have been limitations in the utilization of Bt crops. There is every chance that the targeted insect pests can develop resistance to the Bt crops (Tabashnik et al. 2009) and resurgence of nontarget pests is not ruled out due to change in pest ecology (Lu et al. 2010). Hence, stacking multiple Bt genes for insect resistance management can be one of the options for controlling an array of pests (Bates et al. 2005; Lu et al. 2010).

8.3 Pearl Millet

Nearly 500 species of insects have been reported on pearl millet worldwide (Sharma and Davies 1988). Among these, stem borer and grain midge are frequently seen. White grubs are prominent in India, while spikeworms assume importance in the sub-Sahelian zone of West Africa. However, grain yields are only moderately reduced due to pest damage in pearl millet in India. Insect damage in pearl millet can occur on foliage, flowers, as well as seeds and has been recorded across all plant growth stages, i.e., third-leaf stage, fifth-leaf stage, head initiation, flag leaf stage, boot stage, 50% stigma emergence, milk stage, and dough stage (Maiti and Bidinger 1981). The possibilities of controlling insect pests by breeding cultivars with durable resistance need to be explored. In future breeding for insect pest resistance research in this crop, the areas that need to be given due emphasis are the survey of the endemic areas, the development and use of effective screening techniques for insect pests, identification of resistant sources, and developing cultivars resistant to major pests (Williams and Andrews 1983).

8.3.1 White Grubs, *Holotrichia consanguinea* (Blanch) (Melolonthidae: Coleoptera)

White grubs are a serious problem in pearl millet-growing areas of Rajasthan. The grubs feed on the roots and live inside the soil at depths of 2–25 cm. Seedlings die and mature plants remain stunted in growth due to the attack of white grubs. The germplasm lines IP numbers 205, 213, 225, 252, 256, 314, 315, 323, 375, 427, 432, 467, 476, 478, 501, 513, and 514 (Pradhan 1971) and IP numbers 432, 835, 1158, 1365, 1411, 1450, 1538, 1546, and 1550 have been reported to be resistant/less susceptible to white grubs (Kishore 1991a).

8.3.2 Shoot Fly, *Atherigona approximata* (Malloch) (Muscidae: Diptera)

The shoot fly is a common pest of pearl millet in Gujarat and Tamil Nadu states of India. The damage is caused by the larvae feeding on the growing point causing "deadheart" during the seedling stage, whereas in advance stages, they feed on earheads and cut down panicles. The late-sown crop suffers higher damage. The cultivars derived from Togo germplasm are susceptible to shoot fly. The lines IP 241, IP 863, PT 1522, PT 1930, PT 1939, M86317, MS6112 (Singh and Marwaha 1996), P 280, P 354, P 566, P 2714, P 2776, P 2917, PS 730 (Appadurai et al. 1981), CO 7, MH 365, MH 475 and MH 491 are resistant to shoot fly. Under artificial field conditions, shoot fly populations can be monitored through fish meal traps (Taneja and Leuschner 1985). For germplasm evaluation, susceptible cultivar was planted in 4 rows (as infester rows) 20 days earlier than the test material planted in 20 rows in between infester rows. Fish meal was spread in the infester rows 1 week after

seedling emergence. Plants with deadhearts, number of eggs per plant, leaf feeding, and panicle damage were measured.

8.3.3 Stem Borer, *Chilo partellus* (Swinhoe) (Crambidae: Lepidoptera)

Larval feeding leads to leaf scars and deadhearts. Larvae tunnel inside the stem leading to chaffy panicles. The lines P1, A 10, A 21, A 63, A 66, A 163, A 280, and A 281 (Sandhu et al. 1976), Pusa 23 and Pusa 841 × 303 (Singh and Marwaha 1996), and INMB 106, INMB 218, and INMB 155 (Ndoye et al. 1986) were less susceptible to stem borer. Crop residue from the previous season may be spread in the field for artificial screening. Number of exit holes can be used for evaluation of resistance. Stem borer can also be reared on artificial diets and distributed in leaf whorls by Bazooka applicator. Infested plants rated physically on 1–9 scale for the leaf area consumed, plants with deadhearts, stem tunneling, and chaffy panicles can be used to evaluate resistance. Hairiness of leaves and leaf sheath partly explains the resistance to borer (Ajayi 1985).

8.3.4 Genetics of Resistance

The studies on genetics of insect resistance in millets are scanty. Pearl millet inbreds and hybrids were evaluated for resistance to chinch bug at Lincoln, NE, and Tifton, GA, USA. The inbreds 59464B and 59668M-1 were the most frequently identified resistant lines. Inbred Tift 99B was susceptible. When insect damage among hybrids made with Tift 454 was evaluated, resistance tended to be dominant or overdominant in expression. Inbred lines 03GH707 and Tift 454, developed at Tifton, were resistant only in some assessments at Tifton, but not at Lincoln. Location-specific resistance influenced by environmental conditions or genetic differences in the insect populations between the two locations was observed. The line 16RmR1, developed at Lincoln, was susceptible in both the Lincoln experiments, but not at Tifton. The line 03GH706, on the other hand, was susceptible in some Tifton assessments, but was not among the most susceptible inbreds in the Lincoln experiments. Data suggested multilocation evaluations to effectively identify resistance to chinch bug feeding in pearl millet (Rajewski et al. 2009). Wilson et al. (2000) suggested that expression of resistance is a quantitative trait and can vary across locations and seasons. Resistance is not always fully dominant; both positive and negative general combining ability for plant damage were observed in diallel crosses of pearl millets from Africa. Generally, hybrids were found to be more resistant than the parental inbreds. The resistance sources for chinch bug among the elite US grain pearl millet lines and their high heritability for resistance make it amenable for incorporation of the trait through selection in the pearl millet breeding program (Maas and Ni 2009).

8.3.5 Resistant Sources

The identification of sources of resistance to major pests of pearl millets is of utmost importance, which will provide material for breeders for the development of resistant varieties and hybrids (Kishore 1996a, b; Kishore 1995). The pearl millet germplasm, varieties, and hybrids found resistant or promising against various pests under different experiments, trials, and nurseries worldwide are compiled (Table 8.2).

8.3.6 Mechanisms of Resistance

In general host plant resistance to insects is based on direct or indirect defense mechanisms, which are inherently present or induced upon herbivore attack (Schoonhoven et al. 2005). Direct defense mechanism involves physical or chemical plant traits that by themselves interfere with the physiology or behavior of the herbivore and are the main determinant of plant resistance. Morphological characteristics are known to contribute to plant resistance to insect pest (Norris and Kogan 1980). Studies on the mechanisms of resistance in millets against insect have been scanty. Most of the statements made are based on the field observations recorded in routine screenings with meager data to support the statements.

8.3.6.1 Antibiosis

In stem borers, differences exist in the initial levels of infestation between genotypes and infestation shifted with crop age and phenology. Such changes were due to differences in the biophysical and chemical constituents among varieties at various physiological growth stages, which play a role in affecting pest populations. It was suggested that traits like size, thickness, and hardness of stem may affect progeny development in stem feeders. Ndoye (1977) also suggested that in local pearl millet cultivar Zongo, a secretion in the galleries where the larvae are lodged may serve as a resistance mechanism. Some pearl millets were found associated with *Heliocheilus albipunctella* attack. Low level of damage on long and compact panicles was observed and was not affected by the number and length of floral peduncles (Vercambre 1978). Gahukar (1984) investigated the relationship between *H. albipunctella* damage and bristle length, position, panicle length, compactness, and diameter and found that a relationship existed between compactness and damage. Resistance was expressed by a slower rate of plant damage by chinch bugs to resistant pearl millet genotypes as compared to the susceptible ones (Rajewski et al. 2009). The chinch bug-infested plants had lower photosynthetic rate than the non-infested control plants.

8.3.6.2 Antixenosis

In pearl millet, though *Heliocheilus* emergence coincided with panicle exertion, it showed low panicle damage (ICRISAT 1983, 1984) which was attributed to ovipositional non-preference or antibiosis against larval feeding. Non-preference for

oviposition may be due to the presence of involucral bristles, their density, length, and orientation. Bristle length was one of the few characters found associated with *Heliocheilus* infestation. Bristles on panicles of pearl millet also contributed to reduced damage caused by blister beetle, *Psalydolytta fusca* Olivier (Gahukar 1988, 1991). Long-duration cultivars (Sanio, NKK, Sadore, Torini, and Haini-Kiei) escaped pest attack. Compact spikes were less preferred for oviposition. Incorporation of these characters in high-yielding cultivars was suggested (Gahukar 1987). Long awns on the spike of pearl millet and lack of covering by the flag leaf were found to be associated with resistance to *Anatrachyntis simplex* Walsingham (Sandhu et al. 1977).

In finger millet, several lepidopterous larvae infest the earheads at the maturity. The total damage varies and depends upon the variety and the season indicating variation existing among the varieties and their interaction with environment for resistance. The more compact or tightfisted the panicles, the more is the susceptibility to attack as such panicles provide a congenial microclimate for the larvae to hide within the closed head (Murthi and Harinarayana 1989; Sharma et al. 1998). The presence of high number of vascular bundles was linked to susceptibility to pink borer (Prem Kishore and Jotwani 1980).

8.3.6.3 Tillering Capacity

It is an adaptive form of tolerance of the native grasses to stem injury and may result in an overall increase in head production and yield (Nwanze 1985). Local genotypes of pearl millet are reported to produce tillers profusely under moderate to low attack by borers and still produce reasonable yields. Harris (1962) and Nwanze (1989) indicated higher yields of millets under low borer infestation due to profuse tillering.

8.3.6.4 Pseudo-resistance

Infestation of *Heliocheilus* results in severe damage to panicle and yield loss when the peak of moth emergence period coincides with the panicle exertion. Hence, the early as well as the late varieties of pearl millet evaded the pest infestation. It was shown that extent of crop damage was directly related to the period of crop maturity and head exertion (ICRISAT 1984). The short-cycle pearl millet cultivar, "Souna millet," was reported to have escape mechanism from blister beetle damage (Gahukar 1991). Coop et al. (1993) reported that millet grains compensate for meloid damage through enlargement of grains in neighboring undamaged glumes. Typically, hybrid pearl millet plants grow so vigorously that severe damage by chinch bugs and yield loss are not observed (Maas and Ni 2009). Jotwani (1978) opined that early-maturing lines of finger millet were less susceptible to earhead caterpillars. Late-sown millets generally evade attack by white grubs, but crops may be infested severely later in the season (Singh et al. 2004).

8.4 Small Millets

The small millets in India include six cereal crops such as finger millet (*Eleusine coracana*), foxtail millet (*Setaria italica*), kodo millet (*Paspalum scrobiculatum*), proso millet (*Panicum miliaceum*), barnyard millet, and little millet. Compared to other coarse grain crops, pests are not of economic importance in small millets though shoot fly is an emerging pest in little millet, proso millet, and foxtail millet. Other pests that are reported include stem borer, grasshoppers, gray weevil, earhead caterpillars, root and shoot aphids, and *Helicoverpa* in finger millet. The varietal trials are routinely screened for multipest resistance especially stem borer in finger millet, and shoot fly in kodo millet, little millet, proso millet, foxtail millet, and barnyard millet (AICSMIP 2015). The identification of sources of resistance to major pests of millets is of utmost importance, which may provide material for breeders for the development of resistant varieties and hybrids (Kishore 1995, 1996a, b). The millet germplasm, varieties, and hybrids found resistant or promising against various pests under different experiments, trials, and nurseries worldwide are compiled and presented in Table 8.3.

8.4.1 Resistant Traits

In finger millet, several lepidopterous larvae infest the earheads at the maturity. Total damage varies considerably with the variety, the season, and other factors. The more compact or tightfisted the panicles, the more is the susceptibility to attack as such panicles provide a congenial microclimate for the worms to multiply or to hide within the closed head (Murthi and Harinarayana 1989, Sharma et al. 1998). The presence of high number of vascular bundles was linked to susceptibility to pink borer (Prem Kishore and Jotwani 1980). High trichome length and density in little millet (*Panicum miliaceum* L.) induced non-preference for oviposition by shoot fly. The susceptible genotypes were vigorous in growth (higher plumule, coleoptile, and radical length) than the resistant genotypes (Gowda et al. 1996). Jotwani (1978) opined that early-maturing lines of finger millet were less susceptible to earhead caterpillars. Late-sown millets generally evade attack by white grubs, but crops may be infested severely later in the season (Singh et al. 2004). Late-maturing finger millet varieties had severe incidence of pink borer and grey weevils than the early and mid-late varieties (Lingappa 1979). The rusty plum aphid (*Hysteroneura setariae*) is often found infesting the leaves, stem, and shoots of finger millet in large numbers. Aphids were found in higher frequency on mid-late than early and late varieties (Nageshchandra 1981).

Table 8.3 Resistant or less susceptible genotypes of small millets reported against various insect pests

Crop/pest	Resistant/promising genotypes	References
Finger millet		
Pink borer	VR 94, C 180, PR 722, S 81-10	Jotwani (1978)
	IE 932, IE 982 and IE 1037	Lingappa (1979)
Gray weevil	PES 9, 144, 224, KM 1, 14, HR 228, JNR 1008, T36-B	Kishore and Jotwani (1980)
	KM 1, RAU 1, RAU 3, INNDAF 7, INDAF 8, HR 374, HR 1523, HR 154, PES 110, PES 400, WR 9, VL 110	Murthi and Harinarayana (1989)
	HR-154, PES-176, JNR-852	Kishore (1991b)
	IGRFM 08-4, VL 352, GPU 88, TNEC 1234, KMR 344, DHFM V 10- 2-1, GK 1, VL 376, GPU 89, PPR 1040, GK 2	Sasmal (2015)
Chilo partellus	PES 172, KM 1, PR 202, LES 224, IE 169	Kundu et al. (1980)
Earhead worms	Indaf 7, Indaf 8, PR 202, PR 202, PR 177, HR 374, HR 1523, PES 110, PES 1877, TNAU 1877, TNAU 294, VL 110	Murthi and Harinarayana (1989)
	HR 174, JAN 852, B7-43, PR 1044, PES 8, PES 176, INDAF 5, T 20-1, PES 144, CO-10, KM 14	Prem Kishore and Jotwani (1980)
Aphid	PES 176, RAU 1, HR 374	Murthi and Harinarayana (1989)
Kodo millet		
Shoot fly	Accession nos. 6, 10, 12, 21p, 22, 44, 48, 221, 227, 232, 278, Bulk, 291, 296	Sandhu et al. (1977)
	Germplasm: 6, 11, 20, 21, 29, 32, 39, 42, 45, 50, 60,106, 110, 113, 117, 119, 120, 121, 131, 142, 155, 158, 160, 170, 172, 173, 178, 180, 185	Murthi and Harinarayana, (Murthi and Harinarayana 1989)
	Varieties: RPS 40-1, RPS 40-2. RPS 62-3, RPS 61-1, RPS 69-2, RPS 72-2, RPS 75-1, RPS102-2, RPS 107-1, RPS 114-1, RPS 120-1, IQS 147-1, CO 2, Keharpur	
	RPS 811, 902, 904, 905, 929, 941, 946, 967, 968	Jain et al. (2014)
Foxtail millet		
Shoot fly	GS No. 101, 107, 110, 112, 119, 124, 128, 129, 132, 142, 150, 151, 155, 156, 157, 160, 167, 170, 172, 174, 175.	Murthi and Harinarayana (1989)
	Varieties: RAU 1, 2, 6 ISe 119, 185, 358, 700, 700, 702, 703, SIA 5, 36, 67, 242, 326, 395, SE 21-1, SIC 1, 2 CO 3.	
Flea beetles	Germplasm: 2, 12, 33, 47, 62, 64, 73, 89, 101, 111, 116, 117, 118, 123, 125, 129, 157, 167, 168, 170, 179, 182, 201, 213, 219	Murthi and Harinarayana (1989)
	Varieties: SIA 1432, 1557, 1583, 1720, 2423, 2424, 2425, SE 21.1, TNAU 18, TNAU 82, Chitra	

(continued)

Table 8.3 (continued)

Crop/pest	Resistant/promising genotypes	References
Armyworms	Germplasm: 12, 29, 39, 102, 103, 104, 116, 117, 123, 125, 138, 157, 167, 168, 169, 198, 201, 219	Murthi and Harinarayana (1989)
	Varieties: SIA 1557, 1583, 1720, 2423, 2424, 2425, 2425, SS 21-1, ITS 69, SIC 31	
Leaf rollers	Germplasm: 26, 39, 73, 101, 121, 123, 126, 128, 137, 144, 170	Murthi and Harinarayana (1989)
	Varieties: SIA 1432, 2423, 2424, 2425, SE 21-1, SIC 28	
Little millet		
Shoot fly	GPMR No. 7, 17, 18, 20, 22, 26, 46, 53, 78, 84, 92, 98, 101, 104, 106, 107, 112, 114, 115, 116, 117, 124, 132, 134, 136, 141, 148, 149, 163, 169, 170, 171, 172, 175	Murthi and Harinarayana (1989)
	Varieties: PRC 2, 3, 7, 8, 9, 10, 11, 12 RPM 1-1, 8-1, 12-1, 41-1, RAU 1, 2, K 1, CO 2, Dindori 2-1	
Proso millet		
Shoot fly	GPMS No.101, 102, 105, 108, 112, 114, 115, 117, 122, 123, 124, 125, 126, 135, 136, 138, 148, 152, 153, 155, 156, 157, 159, 164	Murthi and Harinarayana (1989)
	Variety: RAUm1, 2, 3, MS 1307, 1316, 1437, 1595, 4872, PM 29-1, BR 6, CO 1	
Barnyard millet		
Shoot fly	GECH No. Variety 102, 106, 108, 111, 120, 123, 127, 142, 149, 151, 157, 180, 205, 210, 218, 224, 226, 227, 230, 235, 236, 240, 241, 246, 247, 248, 250, 260, 276, 288, Bhageshwar Local-2	Murthi and Harinarayana (1989)
	Variety: VL 8, 13, 21, 24, 30, 31, 32, ECC 19, 18, 20, 21, RAU 7, KE 16, K 1, PUNE 2386	

8.5 Conclusions

Of late, there is an increasing focus on the utilization of millets as to attain the food, nutritional, and fodder security especially in the arid and semiarid tracts. Sorghum and millets grow rapidly, tolerate abiotic stresses and can thrive and yield relatively well under marginal farming conditions in a short time period. Sorghum is gaining importance as a bioenergy crop worldwide to produce "next generation" fuels. Insect pests are becoming a major problem in sorghum production and to a limited extent in other millets. Among them, shoot fly, stem borer, greenbug, head bugs, and sorghum midge are the most important worldwide in sorghum-growing areas. Identifying new sources of resistance for the major pests of sorghum, surveying for pests in millets, and building host plant resistance are the research objectives in almost all crop improvement programs across the world.

Antixenosis is the primary mechanism of resistance to shoot fly. Shoot fly resistance is quantitatively inherited and controlled by additive gene action. The genotypes identified with shoot fly resistance can be effectively utilized in breeding programs, and genetic gains can be realized through selection. For stem borer resistance, genotypic resistance is poorly expressed in unfavorable growth conditions with inheritance being quantitative in nature with low heritability. Hence, screening the progenies repeatedly is suggested. Oviposition non-preference is an important resistance mechanism for controlling sorghum midge. Additive type of gene action controls the inheritance of resistance to sorghum midge, while cytoplasmic effects are also reported. Resistance to sugarcane aphid is controlled by dominant gene action involving one to two dominant genes. The aphid resistance is influenced by the type of cytoplasmic male sterility in the female lines, while the restorer lines have a dominant effect on the expression of resistance to aphids in hybrids. Greenbug biotype I is an economically important biotype. Two major dominant genes with complimentary gene action controlled its inheritance. Antixenosis for oviposition can be exploited for bringing in resistance for shoot bug, and resistant sources have been identified. For head bug, the resistance is inherited as a partially dominant trait controlled by both additive and nonadditive gene action. Cytoplasmic nuclear male sterility influences the resistance in hybrids, and both the parents need to be resistant to head bugs. Several germplasm lines with multiple resistance have been identified and can be deployed to tackle multiple pests at a time. QTLs have been identified for resistance to shoot fly, greenbug, midge, and aphid in sorghum. The QTLs identified provide the basis for marker-assisted selection. Compared to other coarse grain crops, pests are not of economic importance in small millets though shoot fly is an emerging pest in little millet, proso millet, and foxtail millet. Information on the key pests of pearl millet and small millets with respect to data on economic injury levels, yield loss, effectiveness of natural enemies are less. The resistant sources and traits were identified for few pests in small millets.

Identification of new sources of resistance is the need of the hour. In germplasm evaluation for pest resistance, there is a need for improving the screening techniques for increasing the precision of screening and revisit the selection criteria for resistance to insect pests. Integrated pest management systems should be emphasized, and genetic resistance should be combined with other desirable plant characters and resistant traits. Once the genes are identified, gene pyramiding for incorporating multiple resistance to insect pests and diseases in high-yielding cultivars should be taken up. In sorghum and pearl millet, where CMS system is in place, the insect resistance genes should be incorporated into hybrid parental lines so as to be able to develop hybrids with increased resistance levels. For improving transformation efficiency, protocols need to be standardized and simplified. The genomic tools and molecular markers should be extensively utilized in marker-assisted breeding and gene editing in future sorghum breeding programs. For achieving these targets, a collaborative program involving research institutions, industry, and international organizations is required rather than working in isolation.

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Breeding for Insect Resistance in Cotton: Advances and Future Perspectives

9

Ramesh Arora, Sanjeev Kumar Kataria, and Paramjit Singh

Abstract

Cotton crop was domesticated independently in separate parts of the world and comprises of at least four cultivated species and several geographical races. The crop is attacked by a wide variety of insect pests, which cause enormous losses in yield and lower the quality of fibre. Major efforts have been directed towards development of cultivars resistant to sucking pests (especially jassid and whitefly) and bollworms and budworms. Selection of hairy jassid resistant/tolerant genotypes in Africa and India are among the earliest examples of exploitation of host plant resistance in minimizing crop losses due to insect pests. While this trait helped in successfully managing the jassid problem, it led to increased susceptibility to whitefly and some bollworm species. Although several morphological and biochemical traits were found associated with resistance to one or more pests, the same traits resulted in increased susceptibility to other pests. A spectacular success in the development of bollworm- and budworm-resistant cotton was achieved with the development of Bt-transgenic cotton incorporating a gene encoding for delta-endotoxin from the soil-inhabiting bacterium, *B. thuringiensis*. A stacking of two or more resistance genes has helped to improve

R. Arora
Department of Entomology & Zoology, Eternal University, Baru Sahib, Himachal Pradesh 173101, India
e-mail: arorarame@gmail.com

S.K. Kataria (✉) • P. Singh
Punjab Agricultural University, Regional Station, Bathinda 151 001, India
e-mail: k.sanjeev@pau.edu; paramjit.2006@pau.edu

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the activity spectrum of Bt cotton against several lepidopteran pests. Issues concerning biosafety of Bt cotton and management of resistance to Cry toxins in target pests are also discussed.

Keywords
Upland cotton • Genetic diversity • Insect resistance • Sucking insects • Bollworms and budworms • Transgenic cotton

9.1 Introduction

The cotton genus, *Gossypium*, contains around 50 species, grown for the fibre (cotton lint) obtained from the long seed hairs as well as for the oil obtained from the seeds. Cotton fibre has exercised a profound influence on humans from times immemorial. With a history going back to antiquity, the fibre has maintained its pristine purity and importance to this day. Currently, cultivated cotton is the single most important natural fibre crop in the world. Cotton fibre from *Gossypium* species has been a fibre component of textiles and other manufactured items for more than 5000 years in the New World (Damp and Pearsall 1994). Cotton cultivation in the Old World began from India, where it was grown for more than 6000 years since the pre-Harappan period. Indians used cotton for clothing, towels and sheets and sold these items as luxuries to the Chinese and Parthians (Dineen 1988). It even finds mention in the Rigveda, the oldest scripture of the Hindus in India (Sethi et al. 1960).

Gossypium includes species that originated in both the Old World and New World tropical and warm-temperature regions. It was domesticated independently in separate parts of the world. The four most widely cultivated species today are *G. arboreum* (tree cotton), *G. herbaceum* (Levant cotton) from the Old World, *G. barbadense* (Sea Island cotton or Pima cotton) and *G. hirsutum* (upland cotton, which accounts for the largest share of world production) from the New World (Wendel et al. 2009).

The world commercial production of cotton in 2016–2017 was 105.3 million bales from an area of 29.46 million hectares and a productivity of 756 kg/ha (National Cotton Council of America 2017). More than 100 countries are involved in the production of cotton and other related activities with China, India, USA, Pakistan, Uzbekistan and Brazil as the leading producers. The estimates of the United States Department of Agriculture for 2015–16 and 2016–17 indicate that India has displaced China to become the largest producer of cotton, while still maintaining the largest area under cotton. India has also sustained its position as the second largest consumer of cotton after China, as well as the second largest exporter of cotton next to the USA. However, the productivity of seed cotton in India (496 kg/ha) was still way below Australia (2038 kg/ha), China (1484 kg/ha), Brazil (1524 kg/ha), USA (870 kg/ha) and even Pakistan (552 kg/ha) during 2015 (National Cotton

Council of America 2016). Several biotic (insect pests, diseases, weeds) and abiotic (salinity, reduced moisture) stresses act as major constraints in attaining high productivity of cotton.

9.2 Insect Pests Damaging Cotton

Cotton ecosystems throughout the world harbour a wide variety of insects including pests, non-pest herbivores, natural enemies, pollinators and casual visitors. The number of insect species found in the crop may range from a few hundreds to more than a thousand. However, the number of pest-insect species ranges from around 20 to 60 with 5–10 key pests in most production systems (Luttrell et al. 1994). The important insect pests may be categorized into four groups: sucking pests (jassid, whiteflies, aphids, thrips, mirid bugs, stink bugs, mites); bollworms (pink, spotted, spiny and New World and Old World bollworms), budworms and boll weevil; defoliators (leaf rollers, leafworms, tobacco caterpillar, leaf perforator, cabbage looper, armyworms, cotton looper) and stem borers; and lint stainers (red cotton bug, dusky cotton bug) (Arora et al. 2006). Some of these pests like the heliothines, jassids, aphids, whiteflies and mites are polyphagous, and one or more species are recorded in each cotton-growing zone. Others, like the boll weevil and pink bollworm are specialized cotton feeders with a limited geographical distribution (Matthews 1999). For details on the distribution, nature of damage, life history and methods of control of all the important arthropod pests of cotton, the reader is referred to the excellent treatises on cotton pests edited by Matthews and Tunstall (1994) and King et al. (1996). The cotton plant, through its capacity for continued flower bud production and vegetative growth, can compensate for quite considerable damage, especially in varieties of an indeterminate growth habit, and so the damaging effect of an insect depends on the stage at which infestation occurs and other factors, such as availability of moisture, nutrients and temperature (Matthews 1999).

9.3 Genetic Diversity in Cotton

The genetic resources of cotton are extensively dispersed globally across five continents and consist of approximately 45 diploids (A–G and K genomes, $2n = 2 \times = 26$) and 5 tetraploid species (AD genomes, $2n = 4 \times = 52$) that belong to genus *Gossypium* in family Malvaceae (Lubbers and Chee 2009). To a large extent, the differences in cotton genomes are the result of geographical isolation: the 'C' genome is confined to Australia (10 species) and 'D' genome to America (12 species), while genomes 'A', 'B' and 'E' are found in Africa and Asia. Genomes 'F' and 'G' comprise one species each, which do not fit into the original five groups (Munro 1994). 'A' genome is the only one which produces cotton lint. It is found in the wild species *G. herbaceum* var. *africanum* in Southern Africa, which seems to be the nearest existing species to the wild ancestors of the cultivated cottons (Fryxell 1979).

9.3.1 Geographical Spread and Cotton Races

The cotton-growing areas of the world lie between 42°N and 33°S; outside these limits the summers are either not long enough or not hot enough for the cotton plant to complete its growth cycle (Munro 1994). Cotton is known to defy well-established Vavilovian principles as it acquired novel genetic variation during the course of its spread to new areas, which unlike other crops is much more than the variation found in their respective centre of origin (Gumber et al. 2014).

More than 90% of the world's cotton is supplied by modern cultivars of *G. hirsutum,* while *G. barbadense* provides long, strong and fine fibres and is cultivated in some areas of Central Asia, Egypt, Sudan, India, the USA and China. *G. arboreum* is a significant crop in India and Pakistan, while *G. herbaceum* is cultivated in some region of Africa and Asia (Wendel et al. 2009). The centre of origin of *G. hirsutum* is considered to be in Mexico, but diverse forms are spread throughout Central America and the Caribbean (Campbell et al. 2010).

Hutchinson et al. (1947) classified the diverse morphological forms of *G. hirsutum* into seven geographical races, viz. 'yucatanense', 'punctatum', 'palmeri', 'latifolium', 'marie-galante', 'morrilli' and 'richmondi'. Of these seven, punctatum, latifolium and marie-galante have dispersed the farthest with latifolium being considered the race from which modern cultivated 'upland' cotton was derived. During the botanical collection surveys, all races other than 'yucatanense' were strongly associated with humans and their activities (Lubbers and Chee 2009). The history of domestication of cotton and its impact on phenotypic and genetic traits has been discussed by Lubbers and Chee (2009).

The diversity of *G. hirsutum* germplasm base is currently narrow. However, there are many sources of diversity available from the primary, secondary and tertiary gene pools (Stewart 1995). The primary gene pool comprises all of five tetraploid AD species, viz. *G. hirsutum* L., *G. barbadense* L., *G. tomentosum* Nuttall ex Seemann, *G. mustelinum* Miers ex Watt and *G. darwinii* Watt. These species share the same genome chromosome constituency and can form fertile hybrids with cotton. The secondary gene pool includes A, B, D and F genome diploid cotton (20) species, which are relatives of the ancestral parents that gave rise to AD genome. The tertiary gene pool includes C, E, G and K genome diploid (25) species. The chromosomes of these species are quite divergent from the A to D genomes, and utilizing them for transferring tetraploids requires more extreme methods such as chromosome doubling and the use of bridge species (Stewart et al. 2010; Lubbers and Chee 2009).

9.3.2 Germplasm Collections

The exploitation of wide genetic diversity in *Gossypium* spp. necessitates establishment of germplasm collections for their utilization in crop improvement. Several cotton germplasm banks exist in the world, but the availability of the accessions are generally quite limited. To protect the worldwide economic value of cotton and

cotton by-products, coordinated efforts to collect and maintain cotton genetic resources have been going on for more than 200 years. Campbell et al. (2010) presented an overview of the origin and expansion of cotton collections around the world. Currently, there are eight major dedicated cotton germplasm collections present in Australia, Brazil, China, France, India, Russia, the USA and Uzbekistan. The International Plant Genetic Resources Institute (IPGRI) has designated the *Gossypium* collections in the USA and India as the world cotton germplasm collections. In addition, some other international or national institutes also have limited germplasm collections as listed below. The following is a summary of these collections as described by Campbell et al. (2010).

9.3.2.1 USA

The US-sponsored cotton germplasm explorations date back to the early 1900s. Since 1960, these collections have been maintained by the National Centre for Genetic Resources Preservation (NCGRP). Currently, nearly 10,000 accessions covering 45 *Gossypium* species are maintained in the collection. The collection is subdivided into seven different parts: (i) variety collection, (ii) primitive landrace collection, (iii) *G. barbadense* collection, (iv) Asiatic (A genome species) collection, (v) wild species collection, (vi) genetic marker collection and (vii) a base collection (i.e. NCGRP) of all materials in Parts 1–6 and new plant introductions (Percival et al. 1999). Parts 1–5 constitute the working collection, which is routinely seed propagated and distributed by the USDA-ARS at College Station, Texas.

9.3.2.2 India

The Indian cotton germplasm collection is maintained as a working collection by the Central Institute of Cotton Research (CICR) at Nagpur and Coimbatore and as a permanent storage collection at the National Bureau of Plant Genetic Resources (NBPGR) in New Delhi. The collection consists of 10,227 accessions that represent almost entirely cultivated accessions of *G. hirsutum, G. barbadense*, *G. arboreum* and *G. herbaceum*. It also includes race stock accessions of each cultivated species, 26 wild species and 32 synthetic introgressed derivatives.

9.3.2.3 China

The Chinese cotton germplasm collection is housed by the Chinese Academy of Agricultural Sciences in Beijing, Anyang and Hainan Island. A working collection is housed at Anyang, a long-term collection at Beijing and an in vivo collection of wild species at Hainan Island. The total collection consists of 8868 accessions of all the 4 cultivated species and 41 wild species.

9.3.2.4 France

The French cotton germplasm collection is housed by the French Centre de Coopération Internationale en Recherche Agronomique pour le Développement (CIRAD) in Montpellier, France. The collection contains 3070 accessions representing 5 tetraploid species and 27 diploid species.

9.3.2.5 Brazil

The Brazilian collection is maintained by the Brazilian Agricultural Research Corporation (Embrapa) at the National Centre for Genetic Resources and Biotechnology. There are about 4361 accessions representing mainly *G. hirsutum* and *G. barbadense* along with 26 diploid species and the other 3 tetraploid species.

9.3.2.6 Australia

Cotton collections in Australia reside in two places: the Commonwealth Scientific and Industrial Research Organization (CSIRO Plant Industry), Narrabri, NSW, and the Australian Tropical Grains Germplasm Centre (ATGGC), Biloela, QLD. The CSIRO collection consists of 542 *G. hirsutum* accessions, 63 *G. barbadense* accessions and 30 races and wild diploid species. The ATGGC collection consists of 1080 accessions mainly of *G. hirsutum* and a small number of accessions of 27 other *Gossypium* species.

9.3.2.7 Russia

The current Russian cotton germplasm collection better known as the VIR collection is housed at Vavilov Institute of Plant Industry (VIR) in St. Petersburg. It consists of 6322 accessions comprised of 24 diploid species, 3 tetraploid species and several diploid and tetraploid hybrids. Seventy percent of the VIR collection is represented by *G. hirsutum* cultivars, landraces and germplasm lines.

9.3.2.8 Uzbekistan

Cotton germplasm collections in Uzbekistan reside in three locations: the Cotton Breeding Institute of Agriculture Ministry, the Institute of Genetics and Plant Experimental Biology at the Academy of Sciences of Uzbekistan and the National University of Uzbekistan at Tashkent. In total, there are >20,000 accessions including isogenic, inbred lines, recombinant inbred lines and elite AD allotetraploid lines, along with wild primitive and extant representatives of the A to G and K genome species.

In spite of these extensive collections, there are species which are not conserved or are under-represented in these collections. Species that are not conserved include the E genome species *G. benadirense* Mattei, *G. bricchettii* (Ulbrich) Vollesen and *G. vollesenii* Fryxell and the K genome species *G. anapoides* Stewart, Wendel and Craven. Most of the K genome species are under-represented in the collections. Habitat loss and potential species loss are lending an urgency to collecting efforts that has not previously existed (Campbell et al. 2010).

9.4 Breeding for Resistance to Insect Pests

In the absence of protection provided by pesticides, the mean losses inflicted by insect pests in cotton were predicted to be a whopping 84% (O'erke et al. 1994). In India, actual mean yield losses of 50–60% were attributed to insect pests even with

the adoption of crop protection measures before the advent of Bt cotton (Arora and Dhaliwal 1996). Due to the enormous losses caused by a multitude of insect pests in cotton, major efforts have been directed at developing insect-resistant cultivars with emphasis on leafhoppers, whitefly, thrips and bollworms and budworms.

9.4.1 Leafhoppers

Several species of leafhoppers or jassids are serious pests of cotton crop around the world. The important ones are *Amrasca biguttula* (Ishida) in India, *Jacobiella facialis* (Jacobi) and *J. lybica* (Bergevin and Zanon) in Africa, *Amrasca terraereginae* (Paoli) in Australia, *Empoasca decipiens* Paoli in Egypt, *Empoasca distinguenda* Paoli in Zaire and South Africa and *Empoasca dolichi* Paoli in Somalia (Matthews 1999).

The Indian cotton jassid, *A. biguttula*, is widely distributed in India, and in addition to cotton, it also feeds on okra, potato, brinjal and some wild plants. Adults are about 3 mm long and greenish yellow during the summer, acquiring a reddish tinge in the winter. Injury to plants is caused both by the adults and nymphs which suck sap from the foliage and due to the injection of toxins into the plant tissues. The attacked leaves turn pale and then rust red. With change in appearance, the leaves also turn downwards, dry up and fall to the ground. Owing to the loss of plant vitality, the cotton bolls may also drop off resulting in loss of yield (Atwal 1986).

Some of the earliest work on host plant resistance was done for the selection of jassid (*J. facialis*)-resistant/jassid (*J. facialis*)-tolerant genotypes in Africa (Painter 1951). Hairiness was found to be associated with resistance to jassid. An extensive screening of cotton germplasm revealed that without exception, the resistant types were hairier than the susceptible ones. Zululand hybrid was the most resistant, although all hairy plants were not necessarily resistant (Parnell 1925). The selection 44 from a variety 'Uganda' had considerable tolerance as well as generally lower populations of leafhoppers. Later, strain A 2106 was found highly resistant to leafhoppers (Parnall et al. 1949).

In India also, hairy genotypes were found tolerant to *A. biguttula*. The selected genotypes included 4F, LSS and 289F/43 (Afzal and Abbas 1944). But U4 from Africa was susceptible to jassid in India. Likewise, in Australia, hairy variety Miller 41J was found to be resistant to *A. terraereginae* as were crosses of Miller x U4 (Marriott 1943).

Although pubescence has been widely exploited as a resistance characteristic against jassid, it imparts susceptibility to several other major pests especially whitefly and some bollworm species. There is thus a need to look for other traits imparting jassid resistance. Sikka et al. (1966) observed that hair density on the midrib was not important, but the density and hair length on the leaf lamina were involved in jassid resistance. Batra and Gupta (1970) indicated that in addition to the hair length and density of hairs on midrib or leaf lamina, the thickness of palisade tissues was also important in imparting resistance to cotton cultivars against jassid. Khan and Agarwal (1984) observed that varieties of cotton with hair length on the midveins of

the ventral surface of leaves longer than the ovipositor of females were not preferred for egg laying. Murugesan and Kavitha (2010) conducted a detailed analysis of physico-chemical characteristics associated with jassid resistance in cotton and observed that plant height, internodal length, trichome density on the ventral surface of the leaves, hair length and hair density on midrib had negative association with leafhopper damage as well as oviposition. Among the biochemicals, free gossypol in cotton leaves has been reported to be negatively correlated with number of eggs of cotton jassid (Singh and Agarwal 1988), while protein content had no significant effect (Murugesan and Kavitha 2010).

9.4.2 Whitefly

Several whitefly species infest cotton, the most important of which is the sweet potato whitefly *Bemisia tabaci* (Gennadius), which is nearly cosmopolitan in distribution. The banded-wing whitefly, *Trialeurodes abutilonea* (Haldeman), has been recorded in the USA, Mexico and the West Indies. The greenhouse whitefly, *Trialeurodes vaporariorum* Westwood, is also a secondary pest of cotton in California (Leigh et al. 1996). The silverleaf whitefly *B. argentifolii* Perring and Bellows is considered biotype B of *B. tabaci* by many (Commonwealth Agricultural Bureaux International 2017a).

The sweet potato whitefly is a cosmopolitan phloem-feeding insect that lives on a diverse range of herbaceous host plants, numbering over 900. *B. tabaci* possibly originated in India and spread to different parts of the world through transport of infested plant products (Global Invasive Species Database 2015). Besides cotton, *B. tabaci* is a major pest of ornamentals, vegetables and grain legumes, causing damage directly through feeding on phloem and deposition of honeydew on leaves or indirectly through the transmission of plant pathogenic viruses in the genera *Begomovirus* (*Geminiviridae*), *Crinivirus* (*Closteroviridae*) and *Carlavirus* or *Ipomovirus* (*Potyviridae*) (Jones 2003).

It has been observed since the 1950s that morphologically indistinguishable populations of *B. tabaci* differ with respect to host range, host plant adaptability and plant virus transmission capabilities (Brown et al. 1995). Recent molecular and phylogenetic studies have revealed that *B. tabaci* is a complex of 11 well-defined genetic groups containing at least 34 morphologically indistinguishable species, which are merely separated by a minimum of 3.5% mtCOI nucleotide divergence (Dinsdale et al. 2010; De Barro et al. 2011; Commonwealth Agricultural Bureaux International 2017a).

In contrast to leafhoppers, several studies have demonstrated that smooth-leaf trait conferred lowered whitefly susceptibility (Pollard and Saunders 1956; Mound 1965; Bindra 1985; Venugopal Rao et al. 1990; Chu et al. 1998; Walker and Natwick 2006). Another plant morphological trait contributing to lowered whitefly susceptibility was okra-leaf trait (Jones et al. 1974; Chu et al. 1999; Walker and Natwick 2006). Among the wild cottons, *G. thurberi* was found to possess high level of resistance to whitefly by Walker and Natwick (2006). Based on their studies, these

authors concluded that the high level of resistance in *G. thurberi* seemed to be due to unknown factors above and beyond smooth- and okra-leaf traits. Khalil et al. (2015) studied the impact of leaf hairiness and other physicomorphic plant characters on whitefly susceptibility and reported that whitefly population correlated positively with hair density on leaf lamina and vein and length of hairs on leaf midrib, but it correlated positively with hairy density on midrib and veins as well as length of hairs on leaf midrib. Among the other factors, whitefly population exhibited negative response with gossypol glands on leaf lamina, midrib and veins and with plant height. Jindal (2004) reported that cotton genotypes 'Supriya' and 'NHH 44' were resistant to whitefly. Trichome length and distance from lower leaf surface to nearest vascular bundles were negatively correlated, while compactness of vascular bundles and leaf lamina thickness were positively correlated with development duration of whitefly. Egg laying by the pest was negatively correlated with compactness of vascular bundles but positively correlated with leaf lamina thickness. Epicuticular waxes were positively correlated with number of eggs laid. However, none of these characteristics has been found to impart sufficient level of resistance to whitefly in commercial American cotton cultivars.

Since the development of bollworm-resistant Bt-transgenic cotton, efforts have been made to incorporate resistance to whitefly and other sucking pests in transgenic cotton. Recently, Shukla et al. (2016) reported identification of a protein (Tma 12) from an edible fern, *Tectaria macrodonta* (Fee), that is insecticidal to whitefly. Transgenic cotton lines expressing Tma 12 at about 0.01% of total soluble protein were resistant to whitefly infestation in contained field trials. In view of its proven safety, Tma 12 is a promising candidate gene that could be pyramided with Bt toxin genes to develop transgenic cotton resistant to bollworms as well as whitefly.

9.4.3 Thrips

The thrips are among the important insect pests damaging young cotton plants. Several researchers have observed decreases in yield from thrips or increases in yield when seedling thrips were controlled (Cook et al. 2011). Among these, the onion thrips, *Thrips tabaci* (Lindeman), western flower thrips, *Frankliniella occidentalis* (Pergande), and flower thrips, *F. tritici* (Fitch), are the most important. Both adults and larvae of thrips feed on the contents of plant epidermal cells. Damaged areas of leaves do not develop in a normal manner causing leaves to twist. Distortion, malformation and tearing of leaves occur at the site of injury as leaf size increases. Seedling damage by thrips may result in reduction in plant height and leaf area and may even delay crop maturity due to its impact on growth parameters (Cook et al. 2011).

Genetic variation in thrips resistance exists among cotton species and genotypes within cultivated species (Ballard 1951; Hawkins et al. 1966; Zhang et al. 2014). Many lines in *G. barbadense* and *G. arboreum* are more resistant than *G. hirsutum* genotypes (Stanton et al. 1992; Zhang et al. 2013). The plant characteristics contributing to thrips resistance included pilosity (Quisenberry and Rummel 1979) and

being glandless (Zhang et al. 2014), while okra-leaf shape was more susceptible than normal-leaf cotton (Syed et al. 1996; Chen et al. 2006). Based on extensive evaluation, Zhang et al. (2011, 2013, 2014) observed Acala 1517-08, Acala 1517-99 and Pima as more resistant to thrips than other commercial cultivars. The glandless cotton may, however, not impart resistance to all thrips species as the same has been reported to be more susceptible to onion thrips *T. tabaci* in China (Fang et al. 1995), India (Bhatnagar and Sharma 1991) and Pakistan (Arif et al. 2004). As per Arif et al. (2004), hair density on midrib had a positive correlation, while length of hairs on veins and gossypol glands on veins and midrib showed a negative correlation with *T. tabaci* population.

9.4.4 Bollworms and Budworms

Several species of bollworms and budworms attack the fruiting bodies of the cotton plants, the most important being the heliothines, pink bollworm and spotted and spiny bollworms. In India Kranthi and Russel (2009) reported that for nearly 2 decades before the advent of bollworm-resistant transgenic cotton, these pests caused yield losses to the extent of 70–80% even after the adoption of plant protection measures. Among these, *Helicoverpa/Heliothis* species are the major pests. These four major species are found on a wide range of wild and cultivated host plants, with the later larval instars preferentially feeding upon the fruiting bodies.

Helicoverpa armigera Hubner popularly known as the Old World bollworm or African cotton bollworm is a cosmopolitan, polyphagous pest of cotton, which also attacks a wide range of legumes, vegetables, cereals, oilseeds and ornamentals. The larvae bore into the flower buds; the attacked buds show bracteoles spread out and curled downwards. Larger larvae bore into maturing green bolls, and young bolls fall after larval damage. Leaves and shoots may also be attacked, especially at high pest population densities (Commonwealth Agricultural Bureau International 2017b).

Helicoverpa punctigera (Wallengren) known as the Australian bollworm and endemic to Australia shares the damage with the more notorious species, *H. armigera*. The two species combined represent the most significant agricultural insect pests in Australia (Matthews 1999).

The tobacco budworm, *Heliothis virescens* (Fabricius), is a native of North America found throughout the eastern and southwestern USA. It disperses northward annually and can be found in New England, New York and southern Canada during late summer. It also occurs widely in the Caribbean and sporadically in Central and South America. Tobacco budworm attacks several field crops including tobacco, cotton, alfalfa, clover, flax and soybean and is sometimes also recorded feeding on vegetable and ornamental plants (University of Florida Entomology & Nematology 2017). Budworm larvae damage bolls and squares by chewing holes into the base of bolls.

American cotton bollworm, *Helicoverpa zea* (Boddie), commonly known as cotton bollworm, corn earworm and tomato fruitworm, is confined to the New World

and occurs throughout the Americas from Canada to Argentina. It is a polyphagous pest damaging a wide range of crops including cotton, corn, sorghum, tomato, legumes and vegetable crops. In cotton, squares, flowers and young bolls are attacked. Young shoots and leaves can also be damaged, especially in the absence of fruiting structures (Commonwealth Agricultural Bureau International 2017c).

The pink bollworm *Pectinophora gossypiella* Saunders is a worldwide pest of cotton and is the key cotton pest in North and South America and Asia (O'erke et al. 1994). The pink bollworm larvae enter the cotton buds, flowers and bolls shortly after emergence from eggs and feed internally on the fruiting bodies. The pink bollworm causes failure of buds to open properly, fruit shedding, lint damage and seed loss (Commonwealth Agricultural Bureau International 2017a).

The *Earias* species attacking cotton include the spotted bollworm, *Earias vittella* (Fabricius), and spiny bollworm, *E. insulana* (Boisduval), in India, *E. biplaga* Walker in Africa, *E. huegeliana* Gaede in Australia and *E. cupreoviridis* Walker in China (Pearson and Maxwell-Darling 1958). The larvae of both *E. insulana* and *E. vittella* cause damage by boring into growing shoots, buds, flowers and bolls. As soon as the terminal shoot of young cotton is bored, the growing tip loses its turgidity and droops. The larvae can cause excessive shedding of fruiting bodies, and the circular holes produced by larvae in the fruiting bodies remain filled with excreta.

Before the advent of DDT and other synthetic organic insecticides in 1940s, several varietal traits especially earliness and short duration were incorporated into commercial cotton cultivars to minimize damage by late season boll weevils, bollworms and other pests (Bottrell and Adkisson 1977). When organic insecticides became available, breeders began to develop longer duration cultivars which produced more lint and were more profitable than the short-season cultivars (Adkisson et al. 1982). Several morphological and biochemical traits were found associated with lower bollworm damage and incorporated into commercial cultivars for lowering bollworm damage (Smith 1992; Jenkins and Wilson 1996).

Among the morphological traits conferring resistance, nectariless improved resistance to *H. zea* and *H. virescens*. Glabrous or smooth-leaf lacking pubescence reduced oviposition by the pests (Lukefahr et al. 1971; Robinson et al. 1980). Pubescence also adversely affected the mobility and survival of young *H. virescens* larvae (Ramalho et al. 1984). The characteristics imparting resistance to pink bollworm include nectariless, okra leaf, super-okra leaf and earliness (Ingram 1994). Stiffness of shoot tips contributed to resistance against spotted bollworm (Singh 1989).

An important biochemical conferring resistance to bollworms and tobacco budworms is gossypol, which adversely affects development of lepidopteran larvae (Jones et al. 1988). Several studies have demonstrated the effectiveness of gossypol and other allelochemicals like catchin, quercitin and condensed tannins in retarding growth of bollworm and tobacco budworm (Bell and Stipanovic 1977; Chan et al. 1978; Waiss et al. 1981; Jenkins et al. 1983; Narayanan et al. 1990; Taneja et al. 1994). Stipanovic et al. (1988) reported that hemigossypolone and the heliocides H_1, H_2, H_3 and H_4 were also associated with resistance to *Heliothis*/*Helicoverpa* spp.

However, none of these characteristics provided stable and high level of resistance for incorporation in commercial cultivars. Moreover, the requirements for resistance to one or a group of pests often resulted in increased susceptibility to some other pests. A spectacular success in the development of bollworm (Lepidoptera)-resistant cotton has been achieved with genetically engineered transgenic cotton developed during the 1990s (Peferoen 1997; Helider and Boulter 1999). Genetic engineering of crops enables introduction of one or more useful genes from microorganisms or plants into commercial cultivars and reduces the time needed to introgress introduced character into an elite genetic background (Helider and Boulter 1999). The insect-resistant transgenic cotton, also known as Bt cotton, incorporates a gene from the soil-inhabiting entomopathogenic bacterium *Bacillus thuringiensis* Berliner in the cotton plant (Peferoen 1997). In addition to endospores, *B. thuringiensis* produces a parasporal crystal in the sporangium at the time of sporulation. The insecticidal toxicity of *B. thuringiensis* in susceptible insects is largely due to the crystal protein (abbreviated as Cry protein), and different Bt strains produce one or more distinct Cry proteins. Numerous Bt Cry toxins have been isolated and characterized (Hofte and Whiteley 1989; Crickmore et al. 1998). The updated Bt toxin lists, their dendrograms and further details are available at the Bt toxin nomenclature website (Crickmore et al. 2016).

The Cry protein is produced in the form of a protoxin, which is degraded by proteolytic enzymes in the alkaline midgut of the susceptible insects into an activated toxin which then attaches with the specific receptor on the brush border of midgut epithelial cells to cause pathological effects ultimately leading to insect mortality (Sanahuja et al. 2011). Each Cry protein has a specific and rather narrow spectrum of activity against some insect species (Jurat-Fuentes and Jackson 2012), while being safe to all other organisms (Siegel 2001; Naranjo et al. 2008).

The natural enemies including parasitoids and predators are not adversely affected by the Cry toxin (Romeis et al. 2006; Naranjo 2011). Rather, recent studies have indicated strengthening of biological control in transgenic cotton due to reduced usage of insecticides (Lu et al. 2012). The only major problem encountered in large-scale adoption of foliar *B. thuringiensis* applications was its rapid degradation on the plant surface (Arora 2015). Therefore, successful efforts were made to clone Cry protein genes and incorporate these in crop plants (Nester et al. 2002; Sanahuja et al. 2011). Initially, the expression levels of Cry proteins in experimental plants were not sufficient for insecticidal activity (Peferoen 1997). Substantial increases in expression levels have since been achieved using strong promoters and enhancers and by engineering the codon usage to bring it more in line with the plant-preferred codon usage (Helider and Boulter 1999). Consequently, the expression levels of Cry proteins in transgenic plants have increased to over 100 times those obtained using native Bt genes (Wong et al. 1992). More than 20 Bt genes have so far been incorporated into cotton, corn, soybean and other important crops for lepidopteran and/or coleopteran activity (Shera and Arora 2015).

The genetically engineered cotton called Bollgard incorporates a *cry1Ac* gene from *B. thuringiensis*. The technology developed by Monsanto was used to transfer the Bt gene into the Delta and Pine Land varieties (Coker type) using DP5415 and

DP5690 as recurrent parents. The D&PL brand Bt varieties were designated as NuCOTN 33^{B} and NuCOTN35^{B}, respectively, and were the first Bt cotton varieties released for commercial cultivation in the USA in 1996 (International Cotton Advisory Committee 1995, 1997). It was released as 'Ingard' in Australia by Deltapine and Cotton Seed Distributors, both subsidiaries of Monsanto (Fitt 2003). In China, the Chinese Academy of Agricultural Sciences developed Bt cotton by using modified Bt fusion gene (*cry1ab*, *cry1Ac*) inserted in local varieties, which was commercially released in 1997 (Pray et al. 2001). The primary target pests successfully managed by these varieties included various species of bollworms and budworms including *Helicoverpa* spp., *Heliothis* spp., *P. gossypiella* and *Earias* spp. (Naranjo 2011). Bt cotton also reduced survival of other lepidopteran such as armyworms, cabbage loopers, leaf perforators and soybean loopers (Hardee et al. 2001). The adoption of Bt cotton in USA, Australia, China, India and other countries resulted in a sharp decline in insecticide application to cotton crop, increased the yield of seed cotton and benefited cotton growers through improved income (International Cotton Advisory Committee 2001a; Brookes and Barfoot 2015). The reduced insecticide usage also helped to increase the abundance of natural enemies in Bt cotton fields (Lu et al. 2012).

In spite of its widespread adoption, the control of some of the bollworm and defoliator pests of cotton with the *cry1Ac* Bt cotton was not achieved up to the desired level (Fitt et al. 1988; Forrester et al. 1998; Hardee et al. 2001). Therefore, stacked Bt cotton (Bollgard II or BG II) with two cry genes (*cry1Ac*, *cry2Ab*) was developed (International Cotton Advisory Committee 2001a, b). This two-toxin cotton was first planted in 2003 in the USA and in 2006 in India (International Cotton Advisory Committee 2003a; Fabrick et al. 2015). The BG II cotton genotypes provided for a broader spectrum of activity against the lepidopteran pests (International Cotton Advisory Committee 2003a; Naranjo 2011). The *cry2Ab* gene in Bollgard II ensured good control of the fall armyworm *Spodoptera frugiperda*, beet armyworm *S. exigua*, cabbage looper *Trichoplusia ni* and soybean looper *Pseudoplusia includens*, in addition to bollworms and budworms already controlled by Bollgard (International Cotton Advisory Committee 2003a). It has also been observed to provide better protection from the tobacco caterpillar *Spodoptera litura*, a sporadic pest of cotton in India (Mann et al. 2010), and red bollworm, *Diparopsis watersi*, in Burkina Faso in Africa (International Cotton Advisory Committee 2004b). Bollgard II also produces the β-D-glucoronidase (GUS) marker protein to facilitate detection of plants capable of producing *cry2Ab* (International Cotton Advisory Committee 2008). Further, in view of large-scale adoption of Bt cotton, reports of field-evolved resistance to *cry1Ac* containing Bollgard cotton by the pink bollworm from Gujarat, India, were received by 2008 (Dhurua and Gujar 2011). Double-stacked cotton is believed to help in managing resistance to Cry toxins (Ferre et al. 2008; Tabashnik et al. 2009).

In addition to endotoxins (Cry toxins), some strains of *B. thuringiensis* also produce exotoxins during the vegetative phase. These toxins are known as vegetative insecticidal proteins (VIPs) and a large number of such proteins have been isolated from different *B. thuringiensis* strains (Crickmore et al. 2016). While Monsanto

produced Bollgard and Bollgard II cottons, Syngenta came up with transgenic cotton containing VIP 3A, which was selectively toxic to a number of lepidopteran insects (Mascarnhas et al. 2003; International Cotton Advisory Committee 2003b). Similarly Dow Agrosciences came up with its own version of Bt cotton called 'Widestrike' containing *cry1Ac* and *cry1F* genes from *B. thuringiensis*. It provided season-long protection from a broad spectrum of lepidopteran pests (International Cotton Advisory Committee 2004a) and was released for commercial cultivation during 2005 in USA. Investigations into the comparative efficacy of Bollgard II and Widestrike cottons against different lepidopteran pests by a number of researchers revealed that both the stacked genotypes were effective against all the important lepidopteran pests. However, the Widestrike cotton with Cry1Ac and Cry1F was highly effective and provided better control of *S. frugiperda* as compared to Bollgard II cotton with Cry1Ac and Cry2Ab toxins (International Cotton Advisory Committee 2008). The Widestrike 2 cotton was released for commercial cultivation in Australia, Brazil, Costa Rica and Mexico besides the United States. In addition to these countries, the Bollgard II was adopted in Columbia, India and South Africa (International Cotton Advisory Committee 2014).

Recently Bollgard III and Widestrike 3, with three-stacked insect resistance genes have been developed. Both Bollgard III and Widestrike 3 contain *vip 3A* in addition to *cry 1Ac* plus *cry 2Ab* genes in the former and *cry 1Ac* plus *cry 1F* genes in the latter genotype (International Cotton Advisory Committee 2014; Whitehouse et al. 2014). Bollgard III was granted regulatory approval for commercial cultivation in Australia in 2014 and Brazil in 2016 with the hope that the additional toxin (VIP 3A) will reduce the selection pressure for resistance to Bt toxins and extend the life-span of Bt cotton.

9.5 Concerns About Bt Cotton

Any new technology comes with its own set of advantages and limitations, and transgenics are no exception. The major areas of concern in case of Bt cotton include impact on non-target organisms, development of resistance to Bt toxins and broader socio-economic impacts on the adopting farmers (Naranjo et al. 2008).

9.5.1 Toxicity to Non-Target Organisms

The season-long expression of Bt toxins in cotton plants has aroused concerns about their safety to nontarget organisms, especially the natural enemies encountered in the cotton ecosystem. Several studies have revealed that there are no meaningful impacts of Bt cotton on predator populations (Naranjo et al. 2005; Romeis et al. 2006; Gatehouse et al. 2011).

Lu et al. (2012) carried out an extensive analysis of predator populations in Bt cotton at 36 locations across China over a 20-year period (1990–2010). The authors reported a marked increase in abundance of three types of generalist arthropod

predators (ladybirds, lacewings, spiders). These predators helped to provide natural control of the aphid pests reducing the need for pesticide sprays. The biocontrol services by the conserved predators even extended to the neighbouring crops of maize, peanut and soybean.

In contrast, specialist parasitoid population was adversely affected by reduced host abundance and/or reducing individual fitness through indirect host-mediated effects within Bt-susceptible hosts (Romeis et al. 2006). However, a meta-analysis of several of these studies revealed the overall impacts on arthropod communities were significantly less than those encountered in pesticide-treated conventional cotton (Marvier et al. 2007; Gatehouse et al. 2011). Based on analysis of 360 published studies and scores of meta-analyses on the subject, Naranjo (2011) concluded that unlike conventional bred insect-resistant plants that may sometimes be detrimental to natural enemies, Bt crops have been documented to be essentially benign to a wide range of nontarget invertebrates.

9.5.2 Pest Resistance to Bt Toxins

The selection pressure exerted by the application of highly toxic insecticides to manage nefarious pests has resulted in the development of insecticide resistance in hundreds of species of insect pests. In case of transgenic crops including Bt cotton, the insect pests are continuously exposed to minute amounts of Cry toxins throughout their lifespan. Therefore, probability of development of resistance to these toxins is quite high (Kaur and Arora 2015). Such resistance has been termed as field-evolved resistance and defined as a genetically based decrease in susceptibility of a population to a toxin caused by exposure of the population to the toxin in the field (Tabashnik et al. 2014).

The Bt cotton was first released in 1996, and within a couple of years, Gould (1998) expressed fears about the long-term sustainability of Bt crops due to the ability of insect pests to adapt to these toxins. However, the first report of increasing tolerance of cotton bollworm, *H. armigera* to Cry1Ac cotton in China appeared a decade later (Li et al. 2007). Since then, another two cotton pests, pink bollworm for India (Dhurua and Gujar 2011) and *H. zea* from the USA (Tabashnik et al. 2013), have been suspected to have developed resistance to Bt cotton containing Cry1Ac toxin. In addition, Downes et al. (2010) have reported incipient resistance to cry2Ab (Bollgard II) toxin in *H. punctigera* from Australia.

The refuge (non-Bt cotton or other hosts) coupled with high dose has been the major strategy for delaying pest resistance to Bt crops including cotton (Tabashnik et al. 2008; Tabashnik et al. 2013). The strategy has worked well to the extent that no major cotton crop failures due to pest outbreaks on Bt cotton have been reported from anywhere in spite of some reports of development of pest resistance to one or more Bt toxins (Kaur and Arora 2015). The high-dose refuge strategy works by diluting the frequency of resistant allele and delaying the production of a resistant pest population (Gould 1998; Ives et al. 2011). Non-Bt cotton plants have been used as refugia in the USA, Australia, India and elsewhere, while China has relied on

natural refugia of non-Bt alternate host plants of *H. armigera*, the primary target of Bt cotton in China (Wan et al. 2012; Lu et al. 2013). The natural refugia of alternate non-Bt host plants have also worked to an extent in Australia (Sequeira and Playfield 2001) and India (Ravi et al. 2005). But the alternate host strategy cannot be applied for pink bollworm, which is a rather specific pest of cotton.

The second major strategy for delaying development of resistance has been the pyramiding of Bt genes in cotton (Naranjo 2011). The *cry1Ac* gene (Bollgard) was pyramided with *cry2Ab* (Bollgard II) or *cry1F* (WideStrike) to produce double-stacked insect-resistant Bt cotton (International Cotton Advisory Committee 2008). With the advent of these genotypes, the refuge requirements have also generally become less stringent (US Environmental Protection Agency 2007; Carriere et al. 2015).

Carriere et al. (2015) conducted a meta-analysis of 38 studies that reported the effects of 10 Bt toxins used in transgenic corn and cotton against 15 species of insect pests. Surprisingly, they found that compared with optimal low level of insect survival, survival on currently used pyramids was often higher for both susceptible insects and insects resistant to one of the toxins in the pyramid. The researchers concluded that cross-resistance and antagonism between toxins used in pyramid was common. Further, the authors suggested directed pyramid design based on their own and similar studies in future.

Several alternate strategies including the use of seed mixtures, mosaics and tissue-specific and stage-specific toxin expression, combining Bt toxins with biological control and deploying additional microbial or plant genes along with Bt genes have been proposed and tried on a limited scale (Gould 1998; Tabashnik et al. 2013; Kaur and Arora 2015; Carriere et al. 2016).

9.5.3 Socio-economic Impact

Transgenic cotton is now grown in 22 countries and the European union, spanning six continents: Africa (Burkina Faso, South Africa, Sudan), Asia (China, India, Japan, Myanmar, Philippines, Pakistan, Singapore, South Korea, Taiwan), Europe (European union), Oceania (Australia, New Zealand), South America (Argentina, Brazil, Colombia, Paraguay) and North America (Canada, Costa Rica, Mexico, USA) (International Service for the Acquisition of Agri-biotech Applications 2017). Numerous studies conducted across major cotton-growing countries during the last three decades have revealed substantial economic, environmental and social benefits from the cultivation of Bt cotton (International Cotton Advisory Committee, 2000; Shelton et al. 2002; Smale et al. 2006; Mayee and Choudhary 2013; Brookes and Barfoot 2015; Choudhary and Gaur 2015).

Beginning with an area of 0.8 million hectares in the USA, Mexico and Australia, transgenic cotton (insect resistant plus herbicide tolerant) was grown over 75% of the more than 31 million hectares in 2016–2017 (James 2015). With an adoption rate of more than 95%, India has emerged as the largest producer of cotton in the world. In the 13-year period, 2002–2014, India tripled its cotton production from

13 million bales to 39 million bales. The increase in Bt cotton hectares from 50,000 in 2002 to 11.6 million in 2014 represents an unprecedented 230-fold increase during the same period. India more than doubled its share of global cotton production from 12% in 2002 to 25% in 2014. The yield of seed cotton increased from 308 kg/ha in 2001–2002 to 570 kg/ha in 2013–2014. This achievement was combined with a sharp decline in insecticide use on cotton from 46% of total insecticide use in agriculture in 2001 to 20% in 2011. Additionally, cotton seed oil production rose from 0.46 million tonnes in 2002–2003 to 1.5 million tonnes in 2013–2014 (Choudhary and Gaur 2015). In spite of such spectacular performance, increase in suicide rate of cotton farmers since the 1990s has been cited as evidence for failure of Bt cotton in India. One of the environmentalists even called it genocide. Suicides are a complex issue dependant on many factors. A recent analysis of factors contributing to farmer's suicide concluded that implicating Bt cotton in such cases was not based on facts and there has been no increase in farmer's suicide rate since the introduction of Bt cotton (Gilbert 2013). The near total adoption of Bt cotton by more than 7 million predominantly small and marginal cotton growers is itself biggest proof of the profitability and utility of transgenic technology for the farmers.

9.6 Outlook

Transgenic insect-resistant cotton has helped to minimize losses caused by bollworms/budworms and other lepidopteran pests. But whitefly and other sucking pests continue to cause serious damage to cotton crop. In addition, there are reports of bollworms becoming resistant to *cry1Ac* and *cry2Ab* genes. Therefore, there is a need to locate new resistance genes, which can be incorporated into commercial cotton cultivars. Induced defences (Zarate et al. 2007) and RNAi-based gene silencing (Chen et al. 2015) appear promising for developing future insect-resistant cultivars. The recent characterization of Tma 12 protein from a fern is another promising step towards developing whitefly-resistant cultivars (Shukla et al. 2016). In addition, application of *Isaria fumosorosea* (a fungal pathogen of whitefly) expressing dsRNA of whitefly immunity-related gene may aid in developing RNAi technology for whitefly management (Chen et al. 2015). The efforts of the Institute of Cotton Research (ICR) of the Chinese Academy of Agricultural Sciences (CAAS) have resulted in the sequencing and assembling of the genome of *G. arboreum* (Li et al. 2015). This may lead to identification of insect resistance genes in the crop and ultimately lead to development of specifically targeted insect-resistant cultivars. There is an urgency to integrate transgenic insecticidal cultivars with other components of pest management to minimize pest damage as well as to extend the useful life of insecticidal proteins (Naranjo 2011). The combined efforts of agronomists, breeders, biotechnologists and crop protection scientists may lead towards a sustainable cotton production and protection system in future.

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Breeding Avenues in Fruit Crops for Imparting Resistance Against Insect Pests

10

Krishan Kumar, P.K. Arora, and M.I.S. Gill

Abstract

Insect pests cause huge losses to crops directly or indirectly, and fruit crops are not an exception to this statement. The application of insecticides for minimizing qualitative and quantitative losses in fruit crops is not only hazardous to consumers but also results in undesirable environmental and ecological consequences. The development of insect-resistant fruit varieties is an ecofriendly alternative to chemical control and is a durable solution to the menace of insect pests. The host plant resistance against insect pests is based on certain structural and biochemical features of the plants. The transfer of traits to the elite germplasm through conventional breeding is often limited by the long pre-bearing juvenile phase of the fruit crops. The genomics-assisted breeding, which is the integration of genomic tools with conventional breeding, can prove helpful in overcoming these shortcomings. Among the genomics approaches, biparental mapping, association mapping and genomic selection have direct relevance in genetic improvement of fruit crops. The biparental mapping helps in locating the gene/QTLs for insect pest resistance. Through this approach, the host plant resistance against leaf miner in citrus, woolly apple aphid and rust mite in apple, gall mite in black currant and aphid in raspberry has been mapped. Similarly, the use of genetic

K. Kumar • P.K. Arora (✉)
Regional Research Station, Punjab Agricultural University, Abohar 152116, India
e-mail: kkshorti@pau.edu; parshotamarora@pau.edu

M.I.S. Gill
Department of Fruit Science, Punjab Agricultural University, Ludhiana 141004, India
e-mail: hodhort@pau.edu

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engineering-based approaches like transgenesis, cisgenesis, RNAi and other potential techniques, which could enhance the fruit crop resistance against insect pests, has been discussed in this chapter.

Keywords
Fruit breeding • Insect pests • Host resistance • Genomics • Genetic engineering

10.1 Introduction

The food and nutritional security is among the basic human needs and plays a pivotal role in global human development. The adequacy of fruits along with cereals, vegetables and pulses is a must to achieve nutritional security. The fruits being rich in vitamins, minerals and antioxidants are an indispensable component of nutritional security. The daily intake of fruits has been known to reduce the risk of various kinds of diseases such as coronary heart diseases, stroke, cancer, diabetes and cataract (Van Duyn and Pivonka 2000). The fruits are a rich source of vitamins like vitamin A, vitamin C and vitamin B. The vitamins (vitamins A and C) along with polyphenols like anthocyanin present in deep-coloured fruits like strawberry, coloured grapes, pomegranate, etc. and flavonoids like naringin in grapefruit serve as the antioxidants. The antioxidants act as scavengers of free radicals that are produced during various metabolic reactions in the body (Zhang et al. 2015). The antioxidants by virtue of capturing the free radicals prevent oxidative damage to the tissues and thereby protect mankind from different diseases. The minerals like potassium in banana, plum and apricot prevent the chances of hypertension and subsequently prevent stroke and heart diseases, while folic acid present in citrus fruits can prevent direct damage to DNA (Van Duyn and Pivonka 2000).

The adequate availability of the fruits must be ensured for achieving nutritional security. At global level, the current fruit production is 676.67 million tonnes from an area of 59.62 million ha. China, India and Brazil are the three leading fruit-growing countries in terms of area and production (Anonymous 2016). The global population is projected to rise to at least 9.0 billion by 2050, and a matching increase in the global fruit production will also be required to feed this population. As per FAO report, to meet the fruit demand of world population in 2050, the fruit production must be increased by 33% from the production level of 2005–2007 (Linehan et al. 2012). This can be achieved by increasing the productivity of fruit crops, which is greatly affected by various biotic and abiotic stresses. In the category of biotic stresses, apart from diseases, insect pests cause heavy yield losses. As per 1996 estimates, insects cause 6% fruit crop losses despite the use of insecticides, and in the absence of insecticide protection, these losses reach up to 23% (Krattiger 1997). Breeding insect pest-resistant fruit varieties is the only environment-friendly and permanent solution to overcome the losses caused by insect pests.

10.2 Host Plant Resistance

The plants exhibit resistance to the insect herbivores through either of the three mechanisms, viz. *antixenosis* (acting as deterrent for oviposition or serving as antifeedant), *antibiosis* (negatively affecting the growth and development of the insect) and *tolerance* (able to induce growth and comparable yield even in the presence of insect attack). At a time, either one or combination of these mechanisms might operate in host plants constitutively or transiently. However, a resistance formed by the combination of all the three mechanisms is most effective and durable (Ahman 2009).

The *antixenosis* is to ward off the insect at its first line of attack. It is facilitated by plant's structural features alone or in combination with the biochemical attributes. In *antibiosis*, the insect appears on the plant but its growth and development is slowed down by virtue of inherent plant metabolites mainly secondary metabolites. The structural and biochemical features which generally make up the plant defence system are briefly discussed hereunder.

10.2.1 Structural Features

In this category, there are certain morphological traits, which make the host plant less preferred by the insects. These morphological traits form the first line of defence against the insect herbivores (War et al. 2012). These morphological variations confer a fitness advantage to the resistant individual compared to the susceptible ones. The structural features such as the presence of spines, thorns or thin layer of hairs (trichomes) on the leaves, toughened or hardened leaves (Hanley et al. 2007; War et al. 2012) and epicuticular wax (Khederi et al. 2014) have been reported in plant defence against insects. These features make the host plants less preferred for either oviposition or feeding (War et al. 2012).

Of the above features, trichomes not only affect the ovipositional behaviour, feeding and larval nutrition of insect pests (Handley et al. 2005) but also sometimes secrete secondary metabolites such as flavonoids, alkaloids and terpenoids that make the plant poisonous and repellent or help in trapping the herbivores, thus forming a structural and chemical defence (Hanley et al. 2007; Sharma et al. 2009).

10.2.2 Biochemical Features

Plants during the metabolism produce certain secondary metabolites, which are not directly useful for plant growth, but their presence in plants makes the tissue unpalatable to insects (Howe and Jander 2008). The secondary metabolites are encompassed by phenolics and its derivatives and defensive proteins including enzymes.

The phenolics are one of the most common and widespread group of compounds, which play a major role in crop defence against insect pests (Usha Rani and Jyothsna 2010; War et al. 2011; Sharma et al. 2009). Of the various phenolic compounds,

lignin, quinines, tannins and flavonoids have been reported to be involved in defence against insect herbivores (War et al. 2012). Lignin, a phenolic heteropolymer, defends the plants by increasing the roughness of the leaves that ultimately hampers the movement of herbivores during feeding and also reduces the nutritional content of leaves (Mellway et al. 2009). Quinines on the other hand are produced as a result of oxidation of phenols. They affect insect pests either due to direct toxicity or by virtue of covalent binding to the leaf proteins. The quinine-bound proteins are rendered indigestible to the insects (Duffey and Stout 1996; Bhonwong et al. 2009). Similar to the quinines, tannins also reduce nutrient absorption efficiency in the insect pests. Tannins are bitter polyphenols and due to astringent nature act as feeding deterrents (War et al. 2012). They also precipitate the proteins nonspecifically, thereby decreasing the nutritive value of consumed food.

There is wide spectrum of plant defence proteins that are involved in plant defence against insect herbivores. The plant defence proteins include mainly the lectins, proteinase inhibitors and oxidative enzymes.

Lectins are the carbohydrate-binding proteins and are stable in the insect midgut. These upon ingestion by the insect bind to the glycosyl group of epithelial membrane of the digestive tract and cause damage to the epithelial membrane and interfere with the nutrient digestion and absorption. Due to their stability over a range of pH, they serve as the potential insecticides. In this category, *Galanthus nivalis* L. agglutinin (GNA), *Phaseolus* haemagglutinin (PHA) and wheat germ agglutinin (WGA) have been studied against many insect pests (Vandenborre et al. 2011).

Proteinase inhibitors (PIs) are a class of defensive proteins, which bind to the digestive enzymes in the insect gut and inhibit their activity, thereby reducing protein digestion resulting in the shortage of amino acids that leads to slow development or starvation of amino acids (Azzouz et al. 2005).

The oxidative enzymes, namely, peroxidases, polyphenol oxidases and lipoxygenases, are usually upregulated in plant system upon herbivore attack (War et al. 2012). These enzymes are usually produced by the plant under oxidative stress to scavenge the reactive free radicals, but in the process, they also form certain compounds which are toxic to the insects. *Peroxidases* improve plant defence by involvement in the processes like lignification, suberization, auxin metabolism and wound healing (He et al. 2011; Heng-Moss et al. 2004; Sethi et al. 2009). These also produce phenoxy and other oxidative radicals by reacting with the phenols, which are toxic upon ingestion by the insects (Chen et al. 2005; Zhang et al. 2008). *Polyphenol oxidases* form o-quinones, which are highly reactive intermediate compounds that readily polymerize. Under alkaline conditions, these alkylate the essential amino acids and reduce the nutritional quality of food (Bhonwong et al. 2009; Zhang et al. 2008), while under acidic conditions, quinone is converted into semiquinones that give rise to reactive oxygen species, which are toxic to the insects (Bhonwong et al. 2009; Zhang et al. 2008). *Lipoxygenases* catalyse hydroperoxidation of polyunsaturated fatty acids, resulting in the formation of fatty acid hydroperoxides. The hydroperoxides are enzymatically or chemically degraded to unstable and highly reactive aldehydes, ketones, epoxides and reactive oxygen species such as hydroxyl radicals,

singlet oxygen, superoxide ion and peroxyl, acyl and carbon-centred radicals (Maffei et al. 2007; Bruinsma et al. 2009).

The sources of resistance to various insect pests in fruit crops and the type of resistance are enumerated in Table 10.1. In apple, the infestation of apple codling moth (*Cydia pomonella*) and green apple aphid (*Aphis pomi*) was positively correlated with fruit quality and high yield in 'Fiesta' × 'Discovery' population (Stoeckli et al. 2009). The infestation of codling moth was more in ripe fruits, while the attack of green apple aphid was more on vigorous trees producing more number of fruits. The infestation behaviour of these two insects indicates to the role of primary and secondary metabolites in plant defence (Stoeckli et al. 2011). At immature firm stage, most of the energy is directed towards production of secondary metabolites, which ensures the minimum herbivore attack, while at ripe stage, these secondary metabolites are mostly converted into edible carbohydrates.

In banana, the resistance against weevil is due to the hardness of the corm (Arinaitwe et al. 2016). In citrus, the donors for resistance against various insect pests are available in the germplasm (Table 10.1). The Asian citrus psyllid (*Diaphorina citri*) is the key pest of citrus around the world (Westbrook et al. 2011). The nymphs of the insect feed exclusively on the young elongating flush and retard the leaf and shoot development (Michaud 2004). In addition, the nymphs while feeding also excrete honeydew, which invites sooty mould (Arora et al. 2005). However, the devastating economic damage of this insect comes from its ability to carry the phloem-limited gram-negative bacteria, *Candidatus Liberibacter* spp., which causes citrus greening disease or huanglongbing (HLB) (Bove 2006). The survey of the citrus and related germplasm revealed that *Casimiroa edulis* and *Zanthoxylum ailanthoides*, the members of subfamily *Toddalioideae* and family *Rutaceae*, exhibited high resistance against psyllid. The psyllid neither used *Casimiroa edulis* for oviposition nor was it used for feeding by the nymphs and adults, while the *Zanthoxylum ailanthoides* was used only for resting purpose by the adults. Besides the above two sources, the other germplasm, which showed resistance to all the three stages of insect, included *Poncirus trifoliata* (CRC 4007), *Poncirus trifoliata* (CRC 3549), *Glycosmis pentaphylla* and *Clausena harmandiana* (Westbrook et al. 2011). Out of the different sources cited above, *Poncirus trifoliata* is cross compatible with the species in genus *Citrus* and therefore can be used for imparting resistance to this important pest through conventional and molecular breeding. The other sources, *C. edulis*, *Z. ailanthoides*, *G. pentaphylla* and *C. harmandiana*, are the distant relatives of genus *Citrus*, and their resistance can be used via cisgenesis or intragenesis (Rommens et al. 2007).

Citrus leaf miner (*Phyllocnistis citrella* Stainton) is a serious pest of nursery and grown-up citrus trees. The adult oviposits on the young elongating leaves, while the larva emerging from these eggs feeds on epidermal cell layers of developing leaves by making serpentine mines (Belasque et al. 2005). The affected leaves become curled and twisted and the heavy infestation also stunts the plant growth. Besides this, the wounds caused to the leaves also serve as an entry point for the bacterium, *Xanthomonas citri* subsp. *citri*, a causal agent of Asiatic citrus canker. Host sources harbouring resistance to this insect pest include *Casimiroa edulis* and *Zanthoxylum*

Table 10.1 Source and basis of resistance to insect pests of economic importance in different fruit crops

Fruit crop	Insect pest	Source of resistance	Basis of resistance	References
Banana	Banana weevil (*Cosmopolites sordidus*)	*M. acuminata* subsp. *microcarpa* acc. Borneo	–	Arinaitwe et al. (2016)
Citrus	Asian citrus psyllid (*Diphorina citri*)	Sexually compatible to genus *Citrus*: *Poncirus trifoliata*	Antixenosis and antibiosis	Westbrook et al. (2011)
		Sexually incompatible distant relatives: *Casimiroa edulis*, *Zanthoxylum ailanthoides*, *Glycosmis pentaphylla*		
	Citrus leaf miner (*Phyllocnistis citrella*)	Sexually crossable donors with genus *Citrus: Microcitrus* hybrid (CRC 1485), *Poncirus trifoliata* 'Simmons trifoliate' (CRC 3549), *xMicrocitronella* sp. (CRC 1466), *Microcitrus australis* (3673), *M. australasica* (CRC 1484), *Eremocitrus glauca* (CRC 4105)	–	Richardson et al. (2011)
		Sexually incompatible distant relatives: *Glycosmis pentaphylla*, *Bergera koenigii*, *Casimiroa edulis*, *Zanthoxylum ailanthoides*		
		Poncirus trifoliata	–	Bernet et al. (2005)
	Citrus root weevil (*Diaprepes abbreviatus* L.)	*Glycosmis pentaphylla*	Antibiosis (Dehydrothalebanin)	Shapiro et al. (1997) and Shapiro et al. (2000)
		Glycosmis pentaphylla, *Microcitrus australis*, *Eremocitrus glauca*, *Severinia buxifolia*, *Triphasia trifolia*, *Citrus hystrix* and *Balsamocitrus dawei*	Antixenosis and antibiosis	Bowman et al. (2001)
Mango	Fruit fly (*Bactrocera dorsalis*)	Langra and EC-95862 (*Mangifera indica*)	Antibiosis	Verghese et al. (2012)

ailanthoides L. from the subfamily *Toddalioideae*, and *Glycosmis pentaphylla* and *Bergera koenigii* from *Aurantioideae* had zero or very low abundance of leaf miner larvae (Richardson et al. 2011). The resistance from the above described sources cannot be incorporated into the elite scion/rootstock genotypes through hybridization-based crop improvement methods due to their sexual incompatibility with cultivated species of *Citrus*. However, *Poncirus trifoliata* 'Simons trifoliate' is cross compatible with *Citrus* and can be used in crop improvement through classical breeding (Richardson et al. 2011).

Citrus root weevil (*Diaprepes abbreviatus*) is a devastating insect pest of citrus and damages the cultivated trees by larval feeding on roots. The *Balsamocitrus dawei*, a member of family *Rutaceae*, showed high level of host resistance by exhibiting minimum root damage and inhibiting the larval growth of the weevil. Apart from this genus, *Glycosmis pentaphylla*, *Eremocitrus glauca*, *Microcitrus australis*, *Severinia buxifolia*, *Triphasia trifolia* and *Citrus hystrix* also suppressed the larval growth of the weevil (Bowman et al. 2001). The resistance sources showed antibiosis kind of resistance to the insect, and HPLC analysis of the extracts in *Glycosmis pentaphylla* revealed that *dehydrothalebanin*, a metabolic byproduct of phenyl alanine, was the main biochemical responsible for it (Shapiro et al. 2000; Shapiro et al. 1997).

Fruit fly in mango is a quarantine pest. The fruits infested with fruit fly do not get the suitable market due to the fear of its introduction and spread into non-host countries. The varieties Langra and EC-95862 are resistant to fruit fly, while the varieties like Alphonso, Benganpalli and Totapuri are susceptible to the fruit fly infestation (Verghese et al. 2012). The differential resistance of the varieties underlies in the concentration of the phenolics in the peel and pulp. The peel phenolics concentration in resistant varieties was in the range of 42.37–53.12 mg/g in peel and 2.33–2.36 mg/g in pulp. The corresponding phenol values for the susceptible varieties were 6.06–13.56 mg/g in peel and <0.60 mg/g in pulp. In no-choice tests, it was found that fruit fly also oviposits in Langra and EC-95862, but due to higher phenolics in the peel and pulp of these varieties, the maggots fail to pupate. The resistance in these mango varieties is therefore of antibiosis type (Verghese et al. 2012).

10.3 Techniques to Improve Fruit Crops Against Insect Pests

The techniques to introduce resistance against insect pest in fruit crops include conventional breeding techniques, genomics-based breeding techniques and genetic engineering-based techniques. The first two techniques use the sexually compatible resistant germplasm for cross-breeding with cultivated varieties/rootstocks. During crossing, besides the target gene, other genes are also brought in from the donor genotype. The last technique relies on changing the expression of single-target trait by modifying the expression of responsible gene (genetic editing) or addition of a new resistance gene from plants, animals or other kingdoms (trans-/cis-genesis).

10.3.1 Conventional Breeding Techniques

Most of the present-day fruit cultivars are the result of the chance seedling selection by the growers. However, among the classical breeding techniques, which have regularly been used in systematic breeding, are controlled hybridization and induced mutagenesis, and these are also useful in the context of improvement of fruit crops against insects.

10.3.1.1 Hybridization

It is the controlled cross-pollination of a selected maternal genotype with pollen of the desired male parent. Among fruit crops, the modern domesticated strawberry and pear are the product of natural hybridizations. The first systematic breeding in fruit crops was initiated by Thomas Andrew Knight, who improved several fruit crops like apple, pear, peach, cherry, strawberry, nectarine, etc. through hybridization followed by selection (Janick 2012). In apple, 'Fuji' apple, a release of Japanese breeding programme ('Ralls Janet' × 'Delicious'), is now the leading world cultivar. The 'Del Monte Gold' a hybrid variety of pineapple from Hawaii is superior to 'Smooth Cayenne' (a spineless sport of 'Cayenne'). However, there is no information on the improved insect pest-resistant fruit varieties through hybridization-based approach.

The improvement against various biotic and abiotic stresses through hybridization can be achieved in the cases, where the gene of interest is present in related cultivars/species and the crop/variety is sexually crossable. However, long juvenile phase, pre- and postpollination barriers and polyembryony are some of the hurdles that limit the success of conventional breeding in developing insect pest-resistant genotypes in fruit crops. The situation becomes even more complicated for the fruit breeders, when the genes for conferring resistance to insect pests are not available in the primary gene pool, and from the secondary gene pool, these are difficult to transfer alone without the supplementation of other undesirable traits.

10.3.1.2 Mutation Breeding

This is another classical technique, which could be useful in bringing the change in host genes responsible for resistance against insects. These changes can be introduced with the use of mutagens. The mutagens have been used in two ways in fruit crops: in vivo mutation breeding and in vitro mutation breeding. Under in vivo mutation breeding, the seed or budwood is treated with LD_{50} dose of the mutagen (dose at which 50% of the treated material respond compared to untreated), and the surviving plant material is subsequently evaluated phenotypically in the field. The use of in vivo mutation breeding has assisted in the production of as many as 50 cultivars in fruit crops, and some notable examples include pear cv. Gold Nijisseiki with resistance to black spot disease (Yoshioka et al. 1999), Pusa Nanha papaya with dwarf growth habit (Ram 1981) and seedless cultivars in citrus fruits (Hearn 1986; Gulsen et al. 2007; Roose and Williams 2007; Vardi et al. 2008). The in vitro mutation breeding combines the use of mutagens with tissue culture cycle. Under in vitro mutation breeding, any plant part which can regenerate into complete

plantlet is used as explants. The in vitro mode of mutation breeding can prove even more advantageous in fruit crop improvement, as it allows rapid regeneration of explants pre- and post-mutagen treatment and is also useful in screening of the final regenerated plantlets in quick time. Under in vitro mutation breeding, the explants like shoot tips, nodal segments, leaves, callus, etc. have been used for mutation induction followed by screening the mutated cells/tissues for tolerance against filtrates of various disease-causing pathogen (Bhagwat and Duncan 1998; Masuda and Yoshioka 1997) and abiotic stresses like salt (Kumar et al. 2010). Both physical (gamma rays, X-rays, UV rays, thermal neutrons and heavy ion beam) and chemical (EMS, MMS, MNH, etc.) mutagens have been used for mutation induction (Jain 2005). The technique largely has enabled the production of varieties with improved fruit traits or enhanced disease resistance in fruit crops. There is limited information on the application of technique for the development of insect pest-resistant fruit varieties.

10.3.2 Genomics-Based Breeding Techniques

It involves the use of genomic tools (molecular markers) for the improvement of fruit crops. The direct techniques which constitute a part of the genetic improvement are biparental mapping, association and genomic selection. The use of genomics can expedite the varietal development in fruit crops.

10.3.2.1 Biparental Mapping

This technique is useful where the resistance is controlled by the major gene. The controlled crosses are performed between the two contrasting parents such as pest resistant and susceptible, to develop a linkage map. The linkage map is developed on the principle of recombination during meiosis. In biparental mapping approach, there are four steps:

(a) Development of mapping population
(b) Identification of polymorphic markers between the parents and genotyping of the population with polymorphic markers
(c) Linkage analysis and map construction
(d) Fine mapping or high-resolution mapping

10.3.2.1.1 Development of Mapping Population

The fruit crops are highly heterozygous in nature and have long juvenile phase. Thus, it is very difficult to develop ideal mapping population, viz. recombinant inbred lines (RILs), doubled haploids (DH) and near-isogenic lines (NILs) in fruit crops. In these crops, F_1 population, where marker data can be analysed in two-way pseudo-testcross manner (de la Rosa et al. 2003; Mehlenbacher et al. 2006; Gisbert et al. 2009; Gulsen et al. 2010), half- or full-sib-derived populations (Brennan et al. 2008) and in some cases F_2 (Dillon et al. 2006; Sargent et al. 2006; Blas et al. 2009) populations have been used for mapping purpose (Table 10.3). The size of the

population may vary from 50 to 250 for initial map development, but for high-resolution mapping, larger-sized populations are required.

10.3.2.1.2 Identification of Polymorphic Markers Between the Parents and Genotyping of the Population with Polymorphic Markers

Available DNA markers are screened against the genomes of the parents to find out the polymorphic ones (that can differentiate the two parents). Earlier, the mapping began with the marker systems, viz. RFLP, RAPD and AFLP, and gradually has been taken over by SSRs and SNPs. The polymorphic markers are screened against the individuals of the population, and data is recorded as per its similarity with the banding pattern of the parents.

10.3.2.1.3 Linkage Analysis and Map Construction

Linkage analysis between the markers is generally calculated by computer programs such as MAPMAKER (Lander et al. 1987), JoinMap (Stam 1993) and GMENDEL (Echt et al. 1992). The genetic distance between them is calculated based on mapping functions such as Haldane and Kosambi. The linkage maps based on molecular markers are available in most of the fruit crops, and highly saturated maps are also available in fruit crops such as apple, grapes, *Citrus* and *Prunus* (Table 10.2).

10.3.2.1.4 Gene/QTL Mapping

After the development of linkage map, the next step is to locate the gene/quantitative trait loci (QTLs) controlling traits of importance on the either linkage group(s) of the map. For this, the correlation between the genotypic (marker data) and phenotypic data is established using software packages like Map Manager QTX [for single marker analysis (Manly et al. 2001)], Map Maker/QTL [for simple interval mapping (SIM) (Lincoln et al. 1993)] or QTL Cartographer [for composite interval mapping (CIM) (Basten et al. 2002)]. Mapping gives information regarding the position of the gene controlling resistance to particular insect pest/disease or other trait. Genes/QTLs conferring resistance to certain insect pests have been mapped on the linkage map of few fruit crops (Table 10.3). Among these, the genes for aphid and rust mite resistance in apple and gall mite resistance in black currant are the major genes, while the resistance for leaf miner in citrus is under the control of polygenes.

10.3.2.1.5 High-Resolution Mapping

Once the linkage between a gene/QTL with the marker is established, the next step is to fine map the gene-containing region with additional markers as the genetic distance (cM) on the linkage map does not reflect the true physical distance in the genome. But, it is quite difficult to delimit the gene-containing region with the small population size.

To obtain the new linked markers within the previously mapped region, the size of the population is either increased or other additional progenies sharing the same resistant parent in their pedigree are screened to find out any possible recombinant

Table 10.2 Fruit crops with available molecular maps

Fruit crop	Parents/populations used	Marker type and number	Total map length (cM) and linkage groups (LG)	References
Apple	'Fiesta' × 'Discovery' progeny	475 AFLPs, 235 RAPDs, 129 SSRs and 1 SCAR	1371 cM, 17 LG	Liebhard et al. (2003)
Apricot	81 F_1 individuals of cross 'Goldrich' × 'Valenciano'	AFLP, RAPD, RFLP and SSR markers	Goldrich, 511 cM Valenciano, 467.2 cM	Hurtado et al. (2002)
	F_1 progeny of 'Stark Early Orange' × 'Tyrinthos'	180 AFLPs, 29 SSRs	602 cM	Vilanova et al. (2003)
Banana	180 F_1 individuals of cross 'Borneo' × 'Pisang Lilin' (*Musa acuminata*)	167 SSR and 322 DArT markers	1197 cM, 11 LG	Hippolyte et al. (2010)
Ber	F_1 seedlings of cross *Ziziphus jujuba* cv. 'JMS2' × *Z. acidojujuba* 'Xing 16'	2748 restriction site-associated DNA markers	913.87 cM, 12 LG	Zhao et al. (2014)
Citrus	F_1 progeny of 'Clementine mandarin' × 'Orlando tangelo'	609 [385 SRAP, 97 RAPD, 95 SSR, 18 ISSR, peroxidase gene polymorphism (POGP) and 2 resistance gene analog (RGA)] markers	Clementine, 760 cM, 9 LG; Orlando tangelo, 740 cM, 9 LG	Gulsen et al. (2010)
Cranberry	362 individuals from the cross of two cranberry selections	4648 SNPs and 201 SSRs	1112 cM, 12LG	Covarrubias-Pazaran et al. (2016)
Black currant	Full sibling progeny between lines (SCRIS36/1/100) × (EMRS B1834)	AFLP, SSR (both genomic and EST based) and SNP markers	–	Brennan et al. (2008)
Grapes	'Syrah' × 'Pinot Noir', 'Syrah' × 'Grenache', 'Cabernet Sauvignon' × 'Riesling'	1134 markers (350 AFLPs, 501 SNPs, 283 SSRs)	1443 cM, 19 LG	Vezzulli et al. (2008)
Guava	Three mapping populations	AFLPs and SSRs	1379 cM, 11 LG	Rodriguez et al. (2007)

(continued)

Table 10.2 (continued)

Fruit crop	Parents/populations used	Marker type and number	Total map length (cM) and linkage groups (LG)	References
European Hazelnut	'OSU252.146' × 'OSU 414.062' F_1 progeny	249 RAPDs and 20 SSRs	OSU252.146, 661 cM OSU 414.062, 812 cM and 11 LG	Mehlenbacher et al. (2006)
Litchi	'Maguili' × 'Jiaohesanyuehong' F_1 population	312 (169 AFLPs and 143 RAPDs) markers	1040.43 cM, 16 LG	Liu et al. (2010)
Loquat	'Algerie' × 'Zaozhong 6' Progeny	SSRs and AFLPs	Algerie, 900cM; Zaozhong 6, 870cM, 17 LG	Gisbert et al. (2009)
Mango	'Jin-wang' × 'Irwin'	6594 specific-locus amplified fragment (SLAF) markers	3148.28 cM, 20 LG	Luo et al. (2016)
Olive	F_1 progeny of 'Leccino' × 'Dolce Agogia'	61 RAPDs, 21 AFLPs, 8SSRs & 4 RFLPs	Leccino, 2765 cM (22 major and 17 minor LG); Dolce Agogia, 2445 cM (27 major and 3 minor LG)	de la Rosa et al. (2003)
Papaya	F_2 progeny of interspecific cross 'AU9' × 'Sun Up'	712 SSRs, 21 AFLP and 1 morphological marker	Major LG -9; minor LG -5	Blas et al. (2009)
Pear	102 F_1 individuals of cross 'Bayuehong' × 'Dangshansuli	3143 SNP markers and 98 SSRs	2243.4 cM, 17 LG	Wu et al. (2014b)
Prunus	Almond cv. 'Texas' × Peach cv. 'Earlygold'	235 RFLPs, 11 isozymes and 96 SSRs	522 cM, 8 LG	Joobeur et al. (1998) and Aranzana et al. (2003)
	BC_1 progeny of (*Prunus persica* × *P. ferganensis*) × *P. persica*	78 RFLPs, 63 AFLPs, 57 SSRs, 16 RAPDs and two morphological markers	665 cM,8 LG	Verde et al. (2005)

Fruit crop	Parents/populations used	Marker type and number	Total map length (cM) and linkage groups (LG)	References
Black raspberry	115 F_1 seedlings of ORUS 3021-2 × ORUS 4153-1 (♂)	399 SNP, 70 SSRs and 12 high-resolution melting (HRM) markers	ORUS 3021-2, 779.4 cM, 7 LG	Bushakra et al. (2015)
			ORUS 4153-1, 892.1 CM, 7 LG	
Red raspberry	F_1 progeny of 'Heritage' × 'Tulameen'	SNPs and SSRs	Heritage, 462.7 cM, 7 LG	Ward et al. (2013)
			Tulameen, 376.6 cM, 7 LG	
Strawberry	*Fragaria vesca* × *F. nubicola* derived F_2 population	175 SSRs, 6 gene specific and 1 SCAR marker	424.3cM, 7 LG	Sargent et al. (2006)
Sweet cherry	166 siblings of 'Rainier' × 'Rivedel' cross	3830 SNPs, 34 SSR markers	Rainier, 549.5 cM	Guajardo et al. (2015)
			Rivedel, 582.6 cM	
	100 individuals of 'Wanhongzhu' and 'Lapins' cross	SNP, SSR and self-incompatibility S-locus	849.0 cM	Wang et al. (2015)

Table 10.3 Insect pest-resistant genes/QTLs mapped with molecular markers in fruit crops

Fruit crop	Pest	Population used	Mapped with or between markers on linkage group	References
Apple	Aphid (*Dysaphis devecta*)	'Prima' (aphid susceptible) × 'Fiesta' (aphid resistant) F_1 progeny	*Sd1* gene between a SCAR marker 2B12a (0.4 cM) and SSR marker SdSSRa (0.9 cM) on LG7	Cevik and King (2002)
	Rust mite (*Aculus schlechtendali*)	'Fiesta' × 'Discovery' F_1 progeny	The AFLP marker E35M42-0146 (20.2 cM) and the RAPD marker AE10-400 (45.8 cM) on LG7 of 'Fiesta'	Stoeckli et al. (2009)
Citrus	Leaf miner (*Phyllocnistis citrella*)	Maps: *Poncirus trifoliata* (Pa) based on 63 markers, *Citrus aurantium* based on 157 markers	One antibiosis QTL with marker CR7 on LG 7 of Pa map	Bernet et al. (2005)
			Another antibiosis QTL with marker S2-AS4.800 on sour orange linkage map	
			Six antixenosis QTLs also mapped	
Black currant	Gall mite (*Cecidophyopsis ribis*)	Full sibling progeny between gall mite-susceptible (SCRIS36/1/100) × gall mite-resistant (EMRS B1834) lines	*gmr* gene at 4.0 cM from AFLP marker E41M88-280	Brennan et al. (2009)
Black raspberry	Aphid (*Amphorophora agathonica*)	115 F_1 seedlings of aphid susceptible, ORUS 3021-2 (♀) and aphid resistant, ORUS 4153-1 (♂)	Ag4 mapped with SNP marker S99_32802	Bushakra et al. (2015)

between the gene and previously linked markers. This strategy has been followed for fine mapping the Sd1 gene conferring resistance to biotype 1 and 2 of aphid in apple (Cevik and King 2002). For increasing the density of the markers in the vicinity of the gene-containing region, most of the researchers have used AFLP markers, as these are easy to construct and no prior sequence information is required for their development. Once the tightly linked AFLPs are found, they are converted into PCR amenable SCAR (sequence-characterized amplified region) markers (Brennan et al. 2009). The step of high-resolution mapping is useful for marker-assisted breeding and for cloning of the genes, which can be used for incorporation through genetic engineering.

The markers showing linkage with the gene of trait are suitable for marker-assisted selection, if they either co-segregate or show close linkage (at less than 1 cM ideally) with it. The markers can be used in selection of the genotypes resistant to insect pests efficiently (Brennan et al. 2008); nonetheless, so far, it has not substituted the phenotype-based screening in fruit crops.

10.3.2.2 Population Mapping/Association Mapping

In biparental mapping population, the marker trait association or linkage is established based on the recombination that has occurred during the genesis of mapping population (Khan and Korban 2012). Further, to use the identified QTL in marker-aided breeding, the QTL is fine mapped by creating the additional number of crosses. As different QTLs segregate in different mapping populations, the QTLs identified and mapped through single or few mapping populations are often useful only in a single or a few genetic backgrounds and are of no utility in a wide range of genetic backgrounds (Sorkheh et al. 2008; Kenis et al. 2008). Fruit crops are characterized by long juvenile phase, due to which, the generation and maintenance of segregating populations is difficult in these crops (Khan and Korban 2012; Rikkerink et al. 2007). Many traits are governed by more than one gene in these crops (Iwata et al. 2016). For such complex traits, there are many alleles which determine the total phenotype. The biparental mapping approach considers only the alleles present in the outbred parents, and therefore, a maximum of four alleles would segregate for a trait in this approach (Khan and Korban 2012). To take an account of the total phenotype, the information about all the possible alleles contributing towards the phenotype is necessary. The correlation establishment of genotype with phenotype in domesticated and natural population can provide this information, and the process of estimating this association is called *association mapping*. This mapping approach identifies QTL based on the historic recombination in a panel of diverse germplasm via the presence of linkage disequilibrium (LD) between markers (usually SNPs) and QTL, i.e. the nonrandom association of alleles (Zhu et al. 2008). The principle of this approach is that LD tends to be maintained between loci over many generations. High LD is expected between loci in tight linkage, while recombination should have eliminated LD between unlinked loci (Breseghello and Sorrells 2006).

Since the association mapping considers all possible recombination events that have occurred in the population from the origin of marker trait associations (Myles et al. 2009), the resolution with which a QTL marker association is established is high. The approach involves identification of the trait of interest and establishment of diverse panel, high-throughput genotyping of the panel, phenotyping of the panel for the trait of interest and establishment of association of the phenotypic trait with the genotypic markers by studying the population structure, linkage disequilibrium and LD decay. In the first step, a set of diverse individuals, which usually represent the whole population for the trait of interest, is to be identified. In fruit crops, the researchers have used either the diverse panel, for instance, in banana (Sardos et al. 2016) and grapes (Nicolas et al. 2016), or segregating population derived from the

progenitor wild germplasm, which represent the whole domestication of the crops, for instance, in strawberry (Hancock et al. (2016).

The next steps in the process are to genotype and phenotype the panel. The genotyping initially has been performed with the already available markers like simple sequence repeat (SSR) markers in peach (Cao et al. 2012), SSR, randomly amplified polymorphic DNA (RAPD), sequence-tagged sites (STS) and candidate gene markers in pear (Iwata et al. 2013). With the availability of whole genome sequence in large number of fruit crops and emergence of cost-effective next-generation sequencing technology, the association mapping is being adopted with the whole genome, and the strategy is termed as genome-wide association studies (GWAS) (Myles et al. 2009). For the whole genome genotyping, the SNP-based genotypic arrays and the techniques like genotype by sequencing (GBS), which simultaneously detects the SNPs, are being used. During the association mapping, since the whole genome information is made available, along with the SNP-based polymorphism, copy number variation is also explored as sometimes the functional phenotypic variation may also occur due to structural change in the chromosomes (Khan and Korban 2012).

The attractive feature of genome-wide association studies at this step is that in few cases, the researchers have provided public access to the genotypic and phenotypic information of the studied populations. Such information can surely reduce the cost associated with the genomics of other researchers working on the same aspect. In this connection, the genotypic information on segregating population of strawberry (Hancock et al. 2016) and on diverse panel of banana (Sardos et al. 2016) can be assessed on request by the institutions globally.

The final step to establish association between the genotype and phenotype is accomplished through LD mapping. The open-source software like TASSEL (Bradbury et al. 2007) and STRUCTURE (Pritchard et al. 2000) are used for this purpose. The examples of genome-wide association studies in fruit crops are described in Table 10.4.

However, in the above tabulated studies, there is no report for associating genes/QTLs for insect pest resistance. The approach, however, can prove immensely useful in identifying QTLs with a high resolution for insect pests like citrus leaf miner and other such pests, where resistance is under the control of more than one gene.

10.3.2.3 Genomic Selection

Genomic selection (GS) is a useful technique in selection of the favourable individuals based solely on the predictive value of genetic markers (Meuwissen et al. 2001). It involves two main stages: in the first stage, a training population (TP) is phenotyped and genotyped in the similar manner as explained under GWAS. The information here is used to develop a model of breeding value. Second, a separate breeding population (BP) is genotyped, and the model derived from stage 1 is applied to estimate each individual's genomic estimated breeding value (GEBV), which is used for selection.

Table 10.4 Association mapping in fruit crops for different traits

Fruit crop	Population size	Markers and their number	Traits associated	References
Apple	1200 seedlings	2500 SNPs	6 traits (weighted cortical intensity, fruit firmness, acidity, fruit splitting, internal browning and bitter pit)	Kumar et al. (2013)
Banana	104 genotypes	5544 SNP markers	Seedlessness	Sardos et al. (2016)
Grapes	279 cultivars	501 SNPs and 20 SSRs	–	Nicolas et al. (2016)
Peach	104 landraces	53 SSR markers	10 traits (chilling requirement, flowering time, ripening time, fruit development period, fruit weight, flesh texture, flesh firmness, flesh adhesion, red pigment in the flesh and flesh colour around the stone)	Cao et al. (2012)
Pear	76 cultivars	162 markers (155 SSRs, 4 RAPD-STS, 2 ACC synthase genes, 1 S-RNase gene)	9 traits (number of spurs, vigour of tree, harvest time, fruit size, fruit shape, fruit firmness, acidity, total soluble solids and resistance to black spot)	Iwata et al. (2013)
Strawberry	106 individuals of '*Fragaria virginiana*' × '*F. chiloensis*' cross	2474 SNP markers	4 traits (plant vigour, daughters per mother, fruit weight and yield)	Hancock et al. (2016)

The GS differs from association mapping in term of computation analysis (Begum et al. 2015). The software package GS3 (Muranty et al. 2015) has been used for estimation of GEBV in genomic selection studies.

In fruit crops, the genomic selection is useful in the selection of individuals for choosing the parents for crossing and early evaluation of bred material. The approach has been used in apple, pear and grapevine. In apple, it has been used for fruit quality traits (Kumar et al. 2013; Muranty et al. 2015); in pear, it has been used for vegetative and productive quality traits (Iwata et al. 2013).

10.3.3 Genetic Engineering-Based Techniques

It is a set of technologies that are used to change the genetic makeup of cells, including the transfer of genes from within and across species boundaries. It includes the approaches like transgenics, RNAi and genetic editing tools like SSNs.

10.3.3.1 Transgenics

The technology of introduction of gene(s) in the host genome is called genetic transformation. The process of introduction, integration and expression of trans (foreign) gene(s) in the host is called transgenesis, and so raised fruit crops are called transgenics. The first transgenic was produced in tobacco (1982), closely followed by a fruit crop (papaya), which was later commercialized in 1998. The genetic transformation requires gene construct, a method of gene introduction and selection and regeneration, and testing of transgenic plants.

10.3.3.1.1 Gene Construct

Gene construct is made up of gene of interest (transgene) and the selectable marker gene. Both the two mentioned genes have their own promoters, coding regions and terminator sequences as in normal genes.

10.3.3.1.2 Gene of Interest

The fruit crops have been transformed with genes of diverse origins like encoding insecticidal proteins of bacterium (McGranahan et al. 1988; Dandekar et al. 1993; Dandekar et al. 1994; James et al. 1993), plant origin (Graham et al. 1997; Yang et al. 2000) and synthetic reconstructs (Tao et al. 1997) to effectively control the target insect.

The genes of the bacterium *Bacillus thuringiensis* have commonly been employed for generation of insect pest-resistant transgenic fruit crops (Table 10.5). The insecticidal property of bacterium *Bacillus thuringiensis* lies in its Cry and Cyt series of toxins. These two types of toxic proteins have selective preference for insects of different orders. Cry proteins are effective against the insects of orders Lepidoptera, Coleoptera, Hymentoptera and Diptera, while Cyt toxins are useful only against dipteran insects. Both these series of toxins are pore-forming proteins, and their primary action is to lyse midgut epithelial cells by inserting into the target membranes (Aronson and Shai 2001; de Maagd et al. 2001; Bravo et al. 2007).

Among the genes of plant origin, *GNA* (*Galanthus nivalis agglutinin*) gene from snowdrop lectin (*Galanthus nivalis*) and *CpTi* (cowpea trypsin inhibitor protein) from cowpea have been used in fruit crops. The *GNA* gene is effective against the homopteran insects like aphids for which *cry* genes are not useful. The *GNA* gene controls aphids by producing *lectin* protein, which in turn binds in the gut and causes surface lesions (Eisemann et al. 1994) and, by this, induces mortality in the aphids. On the other hand, the gene CpTi inhibits the function of enzyme trypsin (a protease) in the insects, which is required for food digestion in the insects. Consequently, due to breakage in the supply of essential amino acids, insect death occurs (Ismail et al. 2010).

Table 10.5 Fruit crops transformed with insect pest-resistant genes

Fruit crop	Insect pest	Transgene	Expression of the transgene	References
Apple	Coddling moth (*Cydia pomonella*)	Cry1Ac and ICP	Low-level expression of the target gene	Dandekar et al. (1993) and James et al. (1993)
Cranberry	Black-headed fireworm (*Rhopobota naevana*)	*Btk-ICP* from *B. thuringiensis* var. kurstaki	No effective control during bioassays	Serres et al. (1992)
Grapefruit	Aphid	GNA	–	Yang et al. (2000)
Juneberry	–	*Bacillus thuringiensis* var. kurstaki gene encoding for toxin I-ID73	–	Hajela et al. (1993)
Persimmon	Oriental moth (*Monema flavescens*)	Synthetic *cry1Ac*	Significant insect mortality in the bioassays	Tao et al. (1997)
Strawberry	Vine weevil (*Otiorhynchus sulcatus*)	CpTi	–	Graham et al. (1997)
Walnut	Coddling moth (*Laspeyresia pomonella*)	Cry1Ac	Increased level of larval mortality	McGranahan et al. (1988) and Dandekar et al. (1994)

10.3.3.1.3 Selectable Marker Genes

The selectable marker genes provide a competitive advantage to the transformed cells and selectively promote their growth over the non-transformed cells in the regeneration medium containing the selective agent. Some commonly used selectable agents for genetic transformation are mentioned in Table 10.6.

Of the different selectable marker genes, *nptII* gene coding for resistance to antibiotic kanamycin has been used mostly for the initial selection of the putative transgenics. But, the long presence of the antibiotic genes in the transgenics has raised concerns in the commercialization of these crops due to the potential risks associated with the transfer of these genes to environment or medically related bacteria or from transgenic plant product as food to intestinal micro-organisms (Darbani et al. 2007). Due to these speculated risks with the antibiotic resistance genes, the use of alternative selectable markers or marker-free transgenics programme has been initiated by the researchers (Upadhyaya et al. 2010).

The alternative marker genes, which do not have toxic effects on the environment and human health like *manA* gene from *E. coli* and *daoI* (D-amino acid oxidase) gene from yeast *Rhodotorula gracilis*, have been utilized in fruit crops. The *manA* as a selectable marker gene has been used in papaya (Zhu et al. 2005), apple (Degenhardt et al. 2006) and citrus (Ballester et al. 2008) with good transformation

Table 10.6 Commonly used selectable marker genes along with their selective agent (Scutt et al. 2002)

Selectable marker gene	Substrate used for selection
Neomycin phosphotransferase (*nptII*)	Kanamycin, neomycin
Hygromycin phosphotransferase (*hptII*)	Hygromycin B
Gentamycin acetyl transferase (accC3/accC4)	Gentamycin
Streptomycin phosphotransferase (SPT)	Streptomycin
Phosphinothricin acetyl transferase (*bar*)	L-phosphinothricin (PPT)
Phosphomannose isomerase (*manA*)	Mannose

efficiency. The gene *dao1* encodes the enzyme D-amino acid oxidase which catalyses the oxidative deamination of toxic D-amino acids and has been utilized as the selectable marker gene in apple cultivars (Hattasch et al. 2009). Another category is visual markers like *gfp* (from jellyfish), which gives green colour on expression and as such does not need any substrate for its expression. With the availability of *egfp* (mutant *gfp* with enhanced expression), it has been used as visual marker in several fruit crops, e.g. citrus, papaya, apple, etc.

After differentiating the transformed cells from the non-transformed one, the selectable marker is of no further use to the plant cell; instead it is a potential risk. Therefore, stress is laid on the production of marker-free transgenics, which involves selection of the putative transformants with the help of selectable markers initially followed by their removal from the plant system. Marker-free transgenics have been obtained in both highly efficient, e.g. strawberry, and relatively recalcitrant system, e.g. apple (Schaart et al. 2004).

10.3.3.1.4 Methods of Gene Introduction

Out of the various methods, *Agrobacterium* (vector mediated) and particle bombardment (vectorless) are the methods of choice for the gene introduction or transfer. *Agrobacterium* can stably transfer the genes in single copy in the euchromatin region while particle bombardment has the advantage of transferring more than one gene at a single time. Although the commercialized transgenic fruit tree (papaya) was produced with the aid of particle bombardment, most of the researchers have relied upon *Agrobacterium* for gene transfer in fruit crops. In citrus, supplementation of the existing *Agrobacterium*-mediated method with sonication and vacuum infiltration has increased the transformation efficiency (De Oliveira et al. 2009).

10.3.3.1.5 Selection, Regeneration and Testing of Transgenics

The pre-requisite for the transformation of fruit crops is the reliable tissue culture regeneration protocol. The plants regenerated in medium containing marker genes are further verified for their transgenic status by PCR and western blotting techniques. Once the transgene has been confirmed in the plants, these have to pass through glasshouse screening, confined and open-field trials with the permission from the regulating agency of the particular country before getting the commercial status.

Among fruit crops, papaya varieties, namely, 'Rainbow' and 'Sun Up' resistant to papaya ring spot virus, have only been commercialized so far. Another transgenic 'Honey Sweet' plum, showing resistance to plum pox virus, has been cleared for cultivation in the USA (Scorza et al. 2013). Any of the transgenic fruit variety showing resistance to insect pests has not been commercialized till date. To make use of the technology, transgenic trap crop strategy is also suggested (Dandekar et al. 2002). In this strategy, insect pest-resistant transgenic plants of variety or crop are grown together with commercial variety of the same or different crop. The insect pest after feeding on the transgenic plants of trap variety/crop gets killed, and the main crop survived from the insect attack. Here, the trap crop is primarily meant for protection of crop (variety) of interest from insect pest and not for the commercial income, and thereby, it addresses the concerns of the consumers as well. This strategy has been followed for walnut, where menace of codling moth is controlled by using transgenic plants of apple as the trap crop (Dandekar et al. 2002).

10.3.3.2 RNA Interference

It is a homology-dependent gene silencing process, where the short dsRNA such as small interfering RNA (siRNA) or microRNA (miRNA) mediates in the reduction or complete suppression of the target gene expression. The phenomenon was first observed by Napoli et al. (1990) in their genetic transformation experiments of petunia, an annual flowering herb. However, the molecular basis of this mechanism was revealed 8 years later by Fire et al. (1998) in the nematode *Caenorhabditis elegans*, and the phenomenon was termed as RNA interference (RNAi).

10.3.3.2.1 Mechanism of RNAi

The mechanism of RNAi has been studied extensively in the context of siRNA and miRNA. To initiate the process of RNAi in the host cells, the precursor molecule is dsRNA or primary miRNA transcript (pri-miRNA). The dsRNA can be introduced either externally and could also be produced endogenously by the host cell itself or through virus infection. The pri-miRNA on the other hand is the transcriptional outcome of endogenous miRNA genes by RNA polymerase II in the nucleus. The transcribed product or externally introduced miRNA transcript is 5′ capped and 3′ adenylated dsRNA with a stem loop. The pri-miRNA is cleaved by a microprocessor complex (comprising Drosha and microprocessor complex subunit DCGR8) to form precursor miRNA (pre-miRNA), a duplex that contains 70–100 nucleotides. The pre-miRNA from nucleus is transported to the cytoplasm by exportin 5 protein (Lam et al. 2015).

The dsRNA molecule is recognized by a dsRNA binding protein RDE 4 (Grishok et al. 2000) and subsequently cleaved by processor enzyme called Dicer (Ribonuclease type III enzyme) into small RNA molecules of 21–25 long nucleotide fragments with 2 base pair hangs at 3′ end (Zamore et al. 2000). Similarly, the pre-miRNA is cleaved by Dicer into 18–25 nucleotides in the cytoplasm.

After genesis of the small RNA molecules (siRNAs/miRNAs), the process of RNAi is carried forward by the RNA-induced silencing complex (RISC), which is a complex ribonucleoprotein. It has different subunits of which helicase (Stevenson

2004), Argonaute, a multidomain protein having RNAase H-like activity (Elbashir et al. 2001), has so far been studied. The helicase subunit induces unwinding of the siRNA duplex, and subsequently, the antisense strand is kept as guide while the sense or passenger strand is cleaved. The miRNA process differs at this step slightly as after unwounding of the miRNA duplex, the passenger strand is released and not cleaved. The synthetic duplex siRNAs, if introduced externally, skip the dicer step in the host cell and are directly loaded in the RISC complex and follow the rest of the steps in a similar manner (Grishok et al. 2001).

Now depending upon the small RNA molecule (siRNA/miRNA-RISC complex), the gene silencing could occur in different ways. The siRNA cause silencing of the target gene by either degrading the mRNA transcript (Molesini et al. 2012) or inhibiting the transcription through methylation of the promoter region of the gene. The miRNA, on the other hand, induces gene silencing by blocking translation (Lam et al. 2015).

10.3.3.2.2 Status and Factors Affecting the Success of RNAi in Insect Pests of Fruit Crops

The RNAi in context with the insect pests of fruit crop is in experimental phase, the examples of which are listed in Table 10.7. The technique has been tested for a range of genes by employing different inducer molecules (dsRNA/siRNA) with different modes of introduction against insect pests of fruit crops.

10.3.3.2.3 Target Gene

To effectively use RNAi in insect pest management, the first step is to identify the gene crucial for the insect pest metabolism. Initially, the researchers observed RNAi effects in insect pests by targeting single gene (Turner et al. 2006; Chen et al. 2008) and later for more than one gene (Borgio 2010; Rosa et al. 2010; Li et al. 2011) (Table 10.7).

The findings of Borgio (2010); Rosa et al. (2010) and Li et al. (2011) suggest that for observing best RNAi response, the target insect should initially be tested against different genes. This could help in finding out the key gene of insect metabolism and silencing or downregulation of which could cause mortality in the insect.

10.3.3.2.4 Type of Inducer RNA Molecules

Of the four different inducer molecules, viz. dsRNA, siRNA, miRNA and tasiRNA, only dsRNA and siRNA have been applied against the insect pests of fruit crops (Table 10.1). There is a report of Upadhyay et al. (2011) against whitefly (*Bemisia tabaci*), where efficiency of the two inducer molecules siRNA and dsRNA has been compared. Both the molecules were equally effective in downregulating the studied genes.

10.3.3.2.5 Method of Introduction into the Host Cell

To evaluate the potential of RNAi against insect pests in fruit crops, the microinjection, artificial diet and genetic engineering have been evaluated.

Table 10.7 Examples of RNAi used against insect pests of fruit crops

Insect pests	Host fruit crop	Type of inducer molecule	Target gene (s)	Method of dsRNA introduction	RNAi response	References
Light brown apple moth (*Epiphyas postvittana*)	Apple	dsRNA	Carboxylesterase	Larval feeding	Effect persistent up to adult stage	Turner et al. (2006)
Oriental fruit fly (*Bactrocera dorsalis*)	Guava, mango, ber, citrus	dsRNA	Female-specific double-sex (*Bddsx*) gene	Abdominal microinjection	Reduced expression of *Bddsx* and Bdyp1genes	Chen et al. (2008)
					Delayed ovary development and reduced number of mature eggs	
					27% of female progeny had deformed ovipositor	
			Genes encoding ribosomal protein Rpl19, V type ATPase D subunit, the fatty acid elongase Noa and a small GTPase Rab11	Direct feeding and by feeding bacteria expressing these genes	Direct feeding was more responsive than that of bacterial feeding for RNAi	Li et al. (2011)
					Silencing of rab11 killed 20% of adult flies. Egg production was affected by dsRNA of *noa* and *rab11* genes	
Glassy-winged sharpshooter (*Homalodisca vitripennis*)	Grapes, almond and citrus	dsRNA	Actin	Transfection	Tenfold decrease in the mRNA of actin genes and altered phenotypes	Rosa et al. (2010)

In microinjection, the inducer molecules are injected in the body cavity for facilitation of its circulation in the haemolymph, which allows its quick effects to be observed in most of the receiving cells (Price and Gatehouse 2008). The microinjection is a very cumbersome technique and is not feasible for the insects of very small size such as whitefly (Upadhyay et al. 2011). Moreover, the injection caused injury cannot be differentiated from the RNAi effects.

In the method of artificial diet, the insects are fed with the artificial diet containing inducer molecules (dsRNA/siRNA) for their key genes to induce the RNAi response (Turner et al. 2006; Li et al. 2011). The diet-based assay has an added advantage, as once RNAi for a particular gene is found effective, the inducer molecule could be made available as insecticide/pesticide formulation.

The introduction of dsRNA of genes crucial for insect metabolism into plants is another method for observing RNAi. Due to constitutive expression of dsRNA, the insect pests could be controlled effectively in this method. However, there is no such example of this approach in fruit affecting insect pests.

10.3.3.2.6 Cell Autonomous Versus Systematic RNAi

The RNAi in the literature has been classified broadly as: *cell autonomous* RNAi and *systemic* RNAi. In the *cell autonomous* RNAi, the silencing effect of the gene is limited to the cell receiving the dsRNA molecule, whereas in *systemic* RNAi, the expression of the target gene is not only knocked out in the recipient cell, but it is also spread systemically to the neighbouring cells and therefore affects the whole insect. For the control of insect pests through RNAi, systemic spread of knockdown effect of the target gene in the system of the insect is essential. The initial RNAi studies on *Drosophila melanogaster* suggested the absence of systemic RNAi in insects. This was probably due to the lack of gene RdRP (coding for enzyme RNA-dependent RNA polymerase) in insects, which was responsible for spreading the siRNA signal in the model organism *C. elegans*. It indicated that the RNAi could be useful for functional genomics studies in insects but would have limited role in their management. This was the belief until the two independent studies (Tomoyasu and Denell 2004; Bucher et al. 2002) on coleopteran insect *Tribolium castaneum* gave proof of systemic RNAi in insects. However, a recent genome comparison of *C. elegans* and *Tribolium* has revealed that *Tribolium* lacks *C. elegans* like RdRP gene. Therefore, systemic RNAi in *Tribolium* could be due to either the other gene having RdRP-like activity or altogether a different mechanism (Tomoyasu et al. 2008). Studies of Turner et al. (2006) on light brown apple moth and Li et al. (2011) on fruit flies have given evidences for long-term effects of RNAi in insects. The effects vary from reduced expression of the target gene to decreased egg-laying potential of the insect, deformed ovipositor, etc. Moreover, the effects are not only limited to the midgut region but are also expressed in other parts of the body. These results indicate that in insects the RNAi is not limited to a particular cell. Now, it is the question whether the RNAi is systemic in all the insects or it is limited to few insects. If it is systemic in all the insects which could be revealed by future investigations, it will be the effective tool in the management of insect pests, and if the systemic RNAi is

limited to only few insects, its use in the integrated insect pest management could be limited only for those insects.

10.3.3.3 Genome Engineering/Genetic Editing

It is a recently evolved technique which aims at the improvement of target trait either through site-specific mutation induction or through replacement of the target gene sequences with the desired DNA sequence. The mutation mode of the technique has largely been exploited for trait improvement (Voytas and Gao 2014). This mode of the technique differs from the conventional technique of induced mutagenesis in terms of specificity. In conventional mutagenesis, mutations are random, and to identify the desirable phenotype, many samples are to be screened. In this technique, the change is brought only in the target gene while maintaining the integrity of the rest of the genome. Though RNAi also offers to deactivate the expression of a single gene, sometimes the control is not complete.

The process of genetic editing is based on the operational harmony of the engineered endonucleases and cell DNA repair mechanism (Voytas and Gao 2014). The engineered endonucleases induce double-stranded breaks at the desired site in the genome, which activate the cellular DNA repair mechanisms. The cells repair the damage to dsDNA through two different mechanisms: non-homologous end joining (NHEJ) or homologous recombination (HR). It is the mode of DNA repair mechanism, which determines the final change at the target site. The NHEJ-mediated repair mechanism induces mutational (insertion/deletion/translocation) changes, while the HR-mediated repair mechanism replaces the endogenous gene with the introduced DNA template (Osakabe and Osakabe 2014).

The prerequisite for the targeted mutations is the prior sequence information of the target gene, sequence-specific nucleases (SSNs) and their cellular introduction and an efficient regeneration system to ultimately produce the altered plantlets.

There are currently four major classes of SSNs: engineered homing endonucleases or meganucleases, zinc finger nucleases (ZFNs), transcription activator-like effector nucleases (TALENs) and clustered regularly interspaced short palindromic repeats (CRISPR)/Cas9 reagents (Voytas and Gao 2014). Of these, CRIPSR/Cas9, due to being simple, inexpensive, easy to design and efficient (Kanchiswamy et al. 2015b), are the preferred choice for genetic editing.

The step of introduction of sequence-specific nucleases is the most critical, which could determine final fate of the technique. The nucleases have been delivered into the cell as DNA, mRNA or protein. Of these three ways, the SSNs introduced as proteins display high efficiency as the proteins immediately upon introduction become functional. The off-target effects are also reduced as the proteins are also rapidly degraded (Kanchiswamy et al. 2015a). The regenerated plants from such genetically edited plant cells are likely to bypass the GMO legislations as there is no trace of foreign DNA in the altered plants.

In context of the chapter, there is no example on the use of SSNs for the improvement of fruit crops. However, with the availability of whole genome sequence information in fruit crops like apple (Velasco et al. 2010), Japanese apricot (Zhang et al. 2012), wild and cultivated strawberry (Shulaev et al. 2011; Hirakawa et al. 2014),

Chinese and European pears (Wu et al. 2013; Chagné et al. 2014), peach (Verde et al. 2013) and few of the tropical and subtropical fruit crops like sweet orange (Wu et al. 2014a), grapes (Jaillon et al. 2007) and papaya (Ming et al. 2008), the technique is likely to make an impact in the field of targeted trait improvement in fruit crops. The essential pre-requisite is to identify the target gene and its function, where the change is required. In relation to the use of the technique for inhibiting the pests of fruit crops, it is essential to identify the genes, whose expression the pest tailors to suit to its needs.

10.4 Conclusions

Insect pests are one of the productivity as well as quality-limiting factors in fruit crops. The host plants exhibit resistance against insect pests by certain structural and biochemical features. The long juvenile phase and sometimes complex inheritance of the traits makes their direct transfer difficult through conventional breeding techniques. Genomics-based techniques can expedite the pace of variety development. Out of the different genomics approaches, biparental mapping has so far been utilized to impart resistance against insect pests in fruit crops. The loci conferring resistance to aphid and rust mite in apple, gall mite in black currant, aphid in raspberry and leaf miner in citrus have been mapped. The transgenic technology can prove vital for improvement in a single trait of an otherwise elite variety. The transgenic papayas (Rainbow and Sun Up) with resistance to ring spot virus, being cultivated commercially in Hawaii, are the direct evidence for the success of this technology in fruit crops. However, none of the insect-resistant fruit crops has come up commercially. The experimentation on approaches like marker-free transgenics and the use of genes of plant origin or from the cross-compatible species in fruit crops is also going on. The growing of transgenics as trap crops as demonstrated in walnut for codling moth also looks an attractive strategy for control of insect pests. The RNA interference is being carried out by targeting various key genes in insects. So far, it has been tested for insects, namely, fruit fly, light brown apple moth and glassy-winged sharpshooter. The significant lab outcome of RNAi can be commercialized in the form of sprayable technology.

10.5 Future Thrusts

The introduction of resistance in elite fruit cultivars against insect pests is an eco-friendly option to manage the losses associated with them. To achieve this, the classical breeding techniques need to be complemented with modern innovative biotechnological approaches. The genomics-based techniques like association mapping and genomic selection can prove very useful in this regard. Both these approaches use diverse set of genotypes for the trait of interest. The advantage of these techniques is that there is no direct need of generating segregating population and the generated information can also prove useful to the other breeders in their

native crop improvement programmes. The pre-requisite is to generate first line of information on these techniques in the context of insect pests of fruit crops.

The genetic engineering-based approaches hold promise in adding or altering a single trait without bothering for linkage drags often associated with crossbreeding. Few transgenic fruit varieties have been released for commercial cultivation in fruit crops, but the acceptance of products of the technology in general faces public opposition. However, the use of genes of plant origin and introduction of marker-free technology may prove a silver lining in the adoption of this technology and in turn reaping the desired targeted benefits. There is a need to stress upon cloning the resistance genes from the native germplasm through map-based gene cloning (by using biparental mapping) and to utilize them through *cisgenesis* or *intragenesis* (manipulating the expression of the host genes by alteration in promoters or other elements). The genetic editing, one of the recently evolved genetic engineering-based approaches, holds promise in modifying the expression or replacing a single gene. The research should be oriented on host-insect pest interaction to identify the plant genes, which the insect pest tailors to suit its needs. Later, the modification or replacing such genes can help in developing insect pest-resistant fruit crop varieties. Thus, there are immense biotechnological-based breeding avenues for genetic improvement of fruit crops against insect pests.

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Breeding for Stem Borer and Gall Midge Resistance in Rice

11

Gurpreet Singh Makkar and J.S. Bentur

Abstract

Breeding for insect-resistant varieties has been central to the integrated pest management as it offers a viable and ecologically acceptable approach. Status of progress made in breeding and adoption of resistant varieties against stem borers versus gall midge presents two contrasting scenarios. The conventional resistance breeding for yellow stem borer has not gained much impetus due to the lack of resistance sources in cultivated rice (*Oryza sativa* and *O. glaberrima*) gene pool, want of efficient insect rearing and varietal screening protocols, and inherently complex genetics of resistance. Hence, alternative approaches like wide hybridization to introgress resistance from other species of *Oryza*, transgenic approach to deploy *Bt cry* and other insecticidal genes and RNAi approach are being actively pursued. In contrast, high level of gall midge resistance is available in the crossable gene pool, insect rearing and greenhouse screening methods are well developed, genetics of resistance are well studied, molecular markers linked to R genes are developed, and many resistant rice varieties have been released for commercial cultivation and well adopted by farmers. To date 7 gall midge biotypes and 11 plant resistance genes have been reported. Nonetheless, the diversity in insect pest populations and continuous selection of virulent biotypes necessitate supplementation of conventional breeding techniques with molecular and transgenic approaches. Recent advances in the molecular breeding techniques and transgenic rice biotechnology present a great scope

G.S. Makkar (✉)
Department of Plant Breeding & Genetics, Punjab Agricultural University, Ludhiana 141 004, Punjab, India
e-mail: gsmakkar@pau.edu

J.S. Bentur
Directorate of Rice Research, Rajendranagar, Hyderabad 500 030, India
e-mail: jbentur@yahoo.com

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for enhanced varietal tolerance to biotic stresses. Status and prospects in this field are presented in this chapter.

Keywords
Breeding • Gall midge • Insect resistance • Molecular approaches • Rice • Stem borer

11.1 Rice Stem Borer and Yield Losses

Among the biotic stresses, insect pests continue to be a major limitation in realizing the potential yield of rice. Among various insect pests ravaging the rice fields, stem borers (SBs) are the most important ones (Bandong and Litsinger 2005). Stem borers are ubiquitous pests in all rice ecosystems with 50 known species representing three families, Pyralidae, Noctuidae (Lepidoptera), and Diopsidae (Diptera). However, yellow stem borer (YSB) *Scirpophaga incertulas* (Walker) and white stem borer (WSB) *S. innotata* (Walker) (Lepidoptera: Pyralidae) are the most important with *S. incertulas* comprising more than 90% of the borer population in rice in India. 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 earhead 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). Further, in irrigated ecosystem, 1% dead heart resulted in 0.3% or 12 kg/ha loss whereas 1% white earhead caused 4.2% or 183 kg/ha loss in grain yields; the loss due to 1% infestation in both phases of damage was 4.6% or 201 kg/ha. White earhead damage had a much greater impact on rice yield in the irrigated ecosystem than due to dead heart, as the latter occurs later in the season 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. 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). In India, the yield losses due to yellow stem borer (YSB) infestation ranged from 3 to 95% (Senapati and Panda 1999), and this pest accounts for 50% of all insecticides used in rice field (Huesing and English 2004). Recovery or prevention of 5% of the losses due to stem borers could feed approximately 140 million people for 1 year (Datta 2000).

11.1.1 Yellow Stem Borer (YSB; *Scirpophaga incertulas*): Distribution, Biology, and Damage Potential

Of the reported stem borer species, yellow stem borer (YSB), *Scirpophaga incertulas* (Walker) (Lepidoptera: Pyralidae), assumes utmost significance (Shu et al. 2000;

Sarwar 2012) and is prevalent in all rice-producing areas of Asia (Cohen et al. 2000), Southeast Asia (Bandong and Litsinger 2005; Pathak 1968), and India in particular (Catling et al. 1987; Chelliah et al. 1989; Satpathi et al. 2012). It is commonly found in Afghanistan, Bangladesh, Burma, India, Nepal, Philippines, Taiwan, China, Japan, Sri Lanka, Vietnam, Thailand, Malaysia, Singapore, Sumatra, Java, Borneo, Sumba, and Sulawesi. The incidence of this monophagous pest may spread throughout the growing season (Shepard et al. 1995). It prefers aquatic environments where there is continuous flooding ranging from tropical lowland rice to highly preferred deepwater rice. It inflicts serious damage at all stages of the crop; larval damage to tillers during the vegetative stage results in "dead heart" symptoms (drying up of central shoot), and damage during reproductive stage results in "white ears/white heads/white earheads" (panicles with chaffy, unfilled grains). Second larval instar attaches to the tiller and bores into the stem. The egg mass of YSB is covered with brownish hairs from the anal tufts of the female. Individual eggs are white, oval, and flattened. A full-grown larva has brown head and prothoracic shield and measures about 20 mm. The pupa is pale green and enclosed in a white silk cocoon. Fresh cocoon is pale brown and turns dark brown with time. The female moth has a pair of black spots at the middle of each whitish, light brown to yellowish forewing. The male is smaller and has two rows of black spots at the tip of the forewings. Both sexes of adults are strongly attracted to light sources near rice fields during the season and signal the initiation of a fresh brood. Rainfall and relative humidity are the major determinants strongly influencing the relative abundance of stem borer populations. However, development of stem borer life stages is strongly driven by temperature. Cooler temperature coupled with changes in day length may induce diapause or temporary arrest in development of mature larvae. Pervasive distribution and chronic pattern of its infestation often result in recurrent yield loss. The YSB larvae cause serious damage to rice tillers at vegetative stage (Salim and Masih 1987) and at panicle emergence stage (Taylor 1996; IRRI 2000), although the damage to tillers at vegetative stage is largely compensated. The lowest yields often result from white earhead damage when infestation occurs at or just after the prebooting stage (Bandong and Litsinger 2005).

11.2 Strategies Toward Insect Resistance Breeding with Special Reference to Yellow Stem Borer

Insecticides are commonly preferred at the farmer level for stem borer management, though often insecticidal applications fail to deliver desired results (Sarwar et al. 2005), because the insect larvae feed inside the stem pith and remain out of the reach of many insecticides. The application of pesticides may also pose various threats including environmental contamination, evolution of resistant biotypes, and poisoning of aquatic fauna. Therefore, the foremost challenge is to strengthen integrated pest management (IPM) programs through incorporation of host plant resistance (HPR) as its integral component for improved productivity and sustainability. Rice breeding programs are often emphasized on insect-resistant rice varieties as

they have a better ability to withstand the insect damage attained by means of genetic manipulation (Sarwar et al. 2010). Among the two potential sources for enhancing host plant resistance against insect pests, the first comprised of the natural resistance systems primarily existing in rice germplasm and their wild relatives, while the second one comprised of potentially exploitable heterologous resistance systems which are often found in organisms like bacteria (Sharma et al. 2003). Conventionally, host plant resistance to insects involves quantitative traits at several loci. Several programs of resistance breeding are still based on visual and phenotypic selection, and majority of these have focused on vertical resistance involving a single major gene. The conventional resistance breeding for YSB has not gained much impetus due to the lack of resistance sources in cultivated rice (*O. sativa* and *O. glaberrima*) gene pool (Bhattacharya et al. 2006), want of efficient insect rearing and varietal screening protocols, and inherently complex genetics of resistance. The lack of a high level of resistance against the yellow stem borer had virtually stalled development of resistant varieties in the past (Bentur 2006). Hence, alternative approaches like wide hybridization to introgress resistance from other species of *Oryza*, transgenic approach to deploy Cry proteins from *Bt*, and other insecticidal genes are actively pursued. Advances in biotechnology have provided several novel means for breeding of horizontal resistance and sustainable pest resistance with fusion genes (Wan 2006). However, for thorough understanding of resistance mechanism at the molecular level, the resistance genes must be cloned, and their structure and functions must be interpreted (Deka and Barthakur 2010).

Rice is rich in germplasm resources: cultivated and wild, the cultivated rice consisting of two species, *Oryza sativa* L., referred to as Asian cultivated rice, and *Oryza glaberrima* Steud., referred to as African cultivated rice. In addition, there are 22 wild species in the genus *Oryza*. The International Rice Genebank maintains more than 1,05,000 types of Asian and African cultivated rice and 5000 ecotypes of wild relatives. Likewise, many major rice-producing countries have established national germplasm banks. Together, these germplasm collections contain genes that can be used to meet a broad range of research objectives (Zhang 2007).

Relatively small genome size (~ 430 Mb), availability of a dense physical map and molecular markers (Chen et al. 2002; Wu et al. 2002), availability of high-density genetic maps, whole-genome microarrays (for profiling expression of all of the genes in the entire life cycle of rice growth and development), availability of ~ 40,000 full-length cDNA clones (Kikuchi et al. 2003; Liu et al. 2007), a large number of expressed sequence tags (ESTs), rich forward and reverse genetics resources (Hirochika et al. 2004), and complete genome sequence (Sasaki et al. 2002) have opened up a wide spectrum of opportunities for enhancement of biotic stress tolerance in rice. Rice has nearly 55,986 genes, of which nearly 600 genes have been identified in rice which affect the biotic and abiotic stresses, coloration of plant parts, and morphological, physiological, and biochemical traits, including more than 30 genes conferring resistance to various insect pests. Such germplasm and genomic resources have provided an unprecedented opportunity for development of enhanced varietal tolerance to biotic stresses through new molecular improvisations for resistance breeding.

11.2.1 Stem Borer Resistance Through Conventional Breeding and Molecular Markers

Even though no high level of resistance against YSB was reported in the primary gene pool of rice, conventional breeding has led to development of rice varieties like Ratna, Sasyasree, and Vikas which derive moderate level of resistance from the donor source TKM6. Efforts were made to develop markers associated with YSB resistance using W1263 as the donor parent. More recently attempts are being made to introgress YSB resistance from wild species like *O. longistaminata*. However, no product has so far been released for cultivation.

11.2.2 Stem Borer Resistance Through Transgenics

To date, it has not been possible to find endogenous genes imparting desired levels of insect resistance (Schuler et al. 1998), and thus transgenic rice biotechnology offers a potent, cost-effective, and environment-friendly option. In this pursuit, genetic transformation techniques based on recombinant DNA technology have shown high success for incorporation of resistance conferring genes from unrelated sources into commercially important crop plants (Bennett 1994; Dhaliwal et al. 1998).

For the development of insect-resistant transgenics, several plant-incorporated protectants (PIPs) hold potential. The term PIP was designated by the EPA to describe the substances that are incorporated in plants to protect them from damage caused by insect pests and diseases. A PIP is defined as the pesticidal substance that is produced in a plant and the genetic material necessary to produce that substance. *Bt* or *cry* genes derived from the soil bacterium, *Bacillus thuringiensis*, have been the most successful group of related genes used commercially for genetic transformation of crop plants. *Bt* genes encode for insecticidal proteins which are filled in crystalline inclusion bodies produced by the bacterium on sporulation (Cry protein, Cyt protein) or expressed during bacterial growth (Vip protein). In addition, possibilities need to be explored to combine non-*Bt* insecticidal genes (like lectins, proteinase inhibitors, or ribosome-inactivating proteins), secondary plant metabolites, small RNA viruses, and vegetative insecticidal proteins (Vips) from *Bt* and related species with most widely exploited *Bt* genes for providing durable resistance. Efforts made so far are summarized in Table 11.1.

11.2.3 Stem Borer Resistance with *Bt* Genes

The crystal insecticidal proteins (Cry toxins or delta-endotoxins) encoded by *Bacillus thuringiensis* (*Bt*) genes show high toxicity to Lepidopterans (Whiteley and Schnepf 1986; Cohen et al. 2000), Dipterans (Andrews et al. 1987), and Coleopterans (Krieg et al. 1983; Herrnstadt et al. 1986). *Bt* Cry proteins are toxic to insects (BANR 2000) and nontoxic to humans and other animals. The first *Bt* toxin

Table 11.1 Transgenic rice genotypes developed/evaluated for resistance against stem borers and other lepidopteran pests

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
1.	Xiushui 134	*cry1Ac,cry1Ig,G10* (EPSPS gene)	*Agrobacterium*	Maize ubiquitin promoter (pUBi)/modified cauliflower 35S promoter	SSB, LF and glyphosate	Field trial	Zhao (2015)
2.	Tobacco plant	Deletion mutant (Ndv200) *BtVip3BR* gene	*Agrobacterium*	2X35S CaMV	YSB, cotton BW (*Helicoverpa armigera*), black cut worm (*Agrotis ipsilon*), cotton leaf worm (*Spodoptera littoralis*)	Lab studies	Gayen et al. (2015)
3.	Rice	dsRNA	–	–	Plant hoppers and stem borer	–	Li et al. (2015)
4.	Zhejing-22, Kongyu- 131	*Ds-Bt*	*Agrobacterium*	–	SSB	Field trial	Gao et al. (2014)
5.	Ariete	*mpi-pci* fusion gene	*Agrobacterium*	mpi promoter	SSB	Lab studies	Quilis et al. (2014)
6.	mfb-MH86	*cry1Ab* gene	–	Ubiquitin promoter	SSB and other lepidopteran pests	Pilot testing stage	Wang et al. (2014)

7.	Rice	*cry1Ac,cry1I*-like gene	*Agrobacterium*	pGreen	LF, SSB	Field trial	Yang et al. (2014)
8.	Minghui 63 (Elite Indica restorer line)	*cry1Ab*, *cry1Ac*, *cry1C,cry2A*	*Agrobacterium*	Maize ubiquitin promoter	YSB, SSB, LF	Field trial	Yang et al. (2011)
9.	Bt-DL	*cry1Ab*	–	–	SSB	Field trial	Zhang et al. (2011)
	Bt-KF6	*cry1Ac*, *CpTI* genes	–	–	SSB	Field trial	
	Bt-SY63	*cry1Ab* and *cry1Ac* fusion gene	–	–	SSB	Field trial	
10.	G6H1, G6H2, G6H3, G6H4, G6H5, and G6H6	*cry1Ab* and *Vip3H* fusion gene	–	–	SSB, PSB	Lab cum Field trial	Chen et al. (2010)
11.	Under development	*cry1Aa*, *cry1Ab*, *cry1Ac*, *cry1Ba,cry1Ca*	–	–	PSB, SSB	Lab studies	Gao et al. (2010)
12.	*Oryza sativa*	*cry1B* and *cry1Aa* fusion gene	Biolistic transformation	Phosphoenolpyruvate carboxylase (PEPC) promoter	YSB	Lab studies	Kumar et al. (2010)
13.	*Oryza sativa*	*cry1Ia5*	–	–	Stem borer, *Chilo agamemnon*	Lab studies	Moghaieb (2010)
14.	Zhonghua 11 (*Oryza sativa* L. ssp. japonica)/RJ5 line	*cry1C*	*Agrobacterium*	rbcS promoter	YSB, SSB, LF	Field trials	Ye et al. (2009)

(continued)

Table 11.1 (continued)

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
15.	Minghui 63 (Elite Indica restorer line)	Ten transgenic lines (two *cry1Ac* lines, three *cry2A* lines, five *cry9C* lines)	–	–	YSB, SSB	Field trial	Chen et al. (2008)
16.	Khazar, Neda and Nemat	*cry1Ab* gene	–	–	SSB	Field trial	Kiani et al. (2008)
17.	Korean varieties, P-I, P-II, P-III	*cry1Ab*	*Agrobacterium*	Maize ubiquitin promoter	YSB	Field trial	Kim et al. (2008)
18.	Minghui 63 (Indica restorer line)/ T(1Ab)-10	*cry1Ab* gene	*Agrobacterium*	–	YSB, LF	Field trial	Tang and Lin (2007)
19.	Pusa Basmati 1 and Taraori Basmati (Indica rice) and TNG 67 (Japonica rice)	*PINII* (potato proteinase inhibitor)	*Agrobacterium*	Pin2 wound inducible promoter	YSB	Lab and greenhouse studies	Bhutani et al. (2006)
20.	Elite Vietnamese	*cry1Ab-1B* (translationally fused gene) and *cry1A/cry1Ac* (hybrid Bt gene)	–	Maize ubiquitin promoter and rice actin-1 promoter	YSB	Lab studies	Ho et al. (2006)

21.	Basmati 370 (Indica rice)	*cry1Ac*, *cry2A*	Biolistic	Ubiquitin promoter and CaMV35S promoter	YSB	Lab studies	Riaz et al. (2006)
22.	Basmati line B-370 (Indica rice)	*cry1Ac*, *cry2A*	–	–	YSB, LF	Field trial	Bashir et al. (2005)
23.	Minghui 63 (Indica restorer line)	*cry2A*	*Agrobacterium*	Maize ubiquitin promoter	YSB	Field trial	Chen et al. (2005)
24.	Senia and Ariete	*mpi* gene (maize proteinase inhibitor)	Particle-bombarded and *Agrobacterium*	Maize ubiquitin 1 promoter	SSB	Lab studies	Vila et al. (2005)
25.	Indica rice	*cry1Ab*, *cry1Accry1C*, *cry2A*, *cry9C*	–	–	YSB, SSB	Lab studies	Alcantara et al. (2004)
26.	Ariete and Senia	*cry1B* or *cry1Aa*	–	ubi1 promoter or mpi promoter	SSB	Field trial	Breitler et al. (2004)
27.	IR58025A, IR58025B and Vajram (Indica rice)	CRY1AB,CRY1AC genes; *bar* gene for herbicide resistance	*Agrobacterium*	Maize ubiquitin promoter; CaMV 35S promoter (for BAR gene)	YSB	Lab studies	Ramesh et al. (2004b)
28.	Pusa basmati 1 (Indica rice)	*cry1Ac, Xa21*	Biolistic	–	YSB, BLB	Lab studies	Gosal et al. (2003)
29.	Basmati (Indica rice)	*cry1Ac*, *cry2A*	Biolistic	PEPC promoter and PB10 (pollen-specific) promoter	YSB	Small-scale field trial	Husnain et al. (2003)

(continued)

Table 11.1 (continued)

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
30.	IR-64, Pusa Basmati-1 and Karnal Local (Indica rice)	*cry1Ac*	*Agrobacterium* and biolistic	Maize ubiquitin promoter	YSB	–	Raina et al. (2003)
31.	Rajalele (Javanica progenies)	*cry1Ab*, snowdrop lectin *gna*	–	–	YSB, plant hopper	–	Slamet et al. (2003)
32.	IR 68899B and IR68897B (maintainer lines) MH63 and BR827-35R (restorer lines)	*chimeric Bt gene*, *cry1Ab*; *cry1Ab*/*cry1Ac* fusion gene	–	35S and PEPC promoters; actin I promoter	YSB, LF	Field trials	Balachandran et al. (2002)
33.	IR 72 (Indica rice)	*Bt* fusion gene (for insect resistance), *Xa21* gene (for BLB), chitinase gene (for sheath blight)	Reciprocal crossing of two transgenic homozygous IR72 lines parental lines transformed independently	–	Insect resistance, BLB of rice, Sheath blight	Lab studies	Datta et al. (2002)
34.	Pusa Basmati-1, IR-64 and Karnal Local (Indica rice)	*cry1Ac* gene	Biolistic/*Agrobacterium*	Maize ubiquitin-1 promoter	YSB	Lab studies	Khanna and Raina (2002)
35.	Minghui 81	*cry1Ac* gene	Particle bombardment	Maize ubiquitin- 1 promoter	SSB	Field trial	Zeng et al. (2002)

36.	"Xiushuill" and "Chunjiang 11"	spider insecticidal gene	*Agrobacterium*	–	LF, SSB	Lab studies	Huang et al. (2001)
37.	IR64 (Indica rice)	*cry1Ab*	–	–	YSB	–	Maiti et al. (2001)
38.	M7 and Basmati 370 (Indica rice varieties)	*cry1Ac*, *cry2A*, snowdrop lectin *gna*	Particle bombardment	Maize ubiquitin-1 promoter, CaMv 35S promoter	YSB, LF, BPH	–	Maqbool et al. (2001)
39.	KMD1 and KMD2	CRY1AB gene	–	–	SSB, YSB	Field trial	Ye et al. (2001)
40.	Pusa Basmati 1 (Indica rice)	*cry1Ab*, *Xa21*	Biolistic	–	YSB and BLB of rice	–	Gosal et al. (2000)
41.	Indica rice	*cry1A, cry1Ab, cry1Ac, cry1C* and *cry2A*	–	–	YSB	–	Intikhab et al. (2000)
42.	KMD1 (Japonica elite line)	*cry1Ab*	–	–	YSB	–	Shu et al. (2000)
43.	Minghui 63 (Indica CMS restorer line) and its derived hybrid rice Shanyou 63	*cry1Ab* and *cry1Ac*	Biolistic	Rice actin- 1 promoter	LF, YSB	Field trials	Tu et al. (2000)

(continued)

Table 11.1 (continued)

Sl. no.	Recipient genotype/rice subspecies	Trans gene(s)	Method of transformation	Promoter used	Reported resistance against	Stage of study	Reference (s)
44.	PR16 and PR18	*cry1Ab*	–	Maize ubiquitin promoter	YSB	Lab studies	Ye et al. (2000)
45.	Vaidehi (Indica rice)	*cry1Ab*	–	–	YSB	–	Alam et al. (1998)
46.	Maintainer line IR68899B	*cry1Ab*	Biolistic	35S constitutive promoter	YSB	Lab studies	Alam et al. (1999)
47.	Japonica rice	*cryIAb*, *cryIAc*, *hph* and *gus* genes	*Agrobacterium*	Maize ubiquitin promoter, the CaMV35S promoter, and the *Brassica* Bp10 gene promoter	YSB, SSB	Lab studies	Cheng et al. (1998)
48.	Indica and Japonica rice	*cry1Ab*	–	–	YSB	–	Datta et al. (1998)
49.	Basmati 370 and M7 (Indica rice)	*cry2A*	Particle bombardment	CaMV35S promoter	YSB and LF	Lab studies	Maqbool et al. (1998)
50.	Aromatic rice, Tarom molaii	*cry1Ab*	–	–	YSB		Ghareyazie et al. (1997)
51.	Indica, Japonica	*cry1Aa, cry1Ac, cry2A, cry1C*	–	–	YSB		Lee et al. (1997)

52.	IR64 (Indica rice)	CRY1AC	Particle bombardment	Maize ubiquitin 1 promoter	YSB	Lab studies	Nayak et al. (1997)
53.	Japonica, Taipei 309 and Taipei 85–93. Indica, Minghui 63 and Qingliu Rai	*cry1A*, *cowpea proteinase inhibitor* gene	–	–	YSB	–	Wu et al. (1997a)
54.	Japonica, Taipei 309	*cry1Ab*	Particle bombardment	Rice actin-1 promoter	YSB	Lab studies	Wu et al. (1997b)
55.	Japonica rice	*PINII* (potato proteinase inhibitor)	–	–	PSB	Lab studies	Duan et al. (1996)
56.	IR58 (Indica rice)	*cry1Ab*	Particle bombardment	CaMV35S	Mortality of YSB+SSB and feeding inhibition of LF and another leaf folder, *Marasmia patnalis*	Lab studies	Wunn et al. (1996)

SSB striped stem borer/Asiatic rice borer (*Chilo suppressalis*), *LF* leaf folder (*Cnaphalocrocis medinalis)*, *YSB* yellow stem borer (*Scirpophaga incertulas*), *PSB* pink stem borer (*Sesamia inferens*), *BPH* brown plant hopper (*Nilaparvata lugens*)

gene was discovered in 1901 by Ishiwaki in diseased silkworms, cloned in 1981, and genetically engineered into japonica and indica rice plants in 1988 and 1990, respectively. Field evaluations of *Bt* rice have been reported since 2000, and these studies primarily focus on *cry1A* genes (Shu et al. 2000; Tu et al. 2000). Shu et al. (2002) reported a line KMD1 transformed with a synthetic *cry1Ab* gene, conferring resistance to eight lepidopteran pest species, including YSB under laboratory as well as under natural infestation. Since then several rice lines expressing insecticidal genes with lepidopteran activity [*cry1Aa, cry1Ab, cry1Ac, cry1Ab/Ac, cry1C,* cry2A, *CpTI* (cowpea trypsin inhibitor), etc.] and hemipteran activity [snowdrop lectin (*Galanthus nivalis* agglutinin) *gna* gene and *Pinellia ternata* agglutinin – *pta*] have been developed and tested. Iran was the first country to release *Bt* rice for commercial cultivation in 2004. Likewise, China permitted the commercial production of *Bt* rice lines Huahui No. 1 (CMS restorer line) and *Bt* Shanyou 63 (a hybrid of Huahui No.1 and Zhenshan 97A, a CMS line), both lines expressing *cry1Ab/Ac* fusion gene, which contains a copy of the synthetic DNA sequence with two genes: the CRY1AB and the CRY1AC (Chen et al. 2011). These genes encode the respective *Bt* toxins, lethal to Lepidoptera, whereas *Bt* Shanyou 63 provides resistance to rice stem borer and leaf folder (Tu et al. 2000). In India, IR62 was the first transgenic rice-expressing *Bt* gene (Nayak et al. 1997). Subsequently, various transgenic *Bt* (Cry1Ab, Cry1Ac) rice varieties (IR64, Karnal Local, etc.) resistant to YSB have been produced (Khanna and Raina 2002; Ramesh et al. 2004a, b); however, Cry proteins are ineffective against sap feeders. But currently, no GM rice variety has been commercially released in India.

11.2.4 Strategies for Successful Deployment of *Bt* Genes

Early breakdown of the resistance is a major limitation which itself poses the challenge of maintaining the durability of the resistance. Development of durable resistance strategies may involve gene pyramiding or gene stacking as one of its potential components. The use of multiple genes with different mode of action against the same pest or a range of pests delays the development of resistance. Gene pyramiding of *cry1Ac*, *cry2A*, and snowdrop lectin gene, *gna*, in transgenic rice was more effective against a variety of insects than any single gene (Maqbool et al. 2001; Loc et al. 2002). Further, stacking of *Bt* genes with *gna* gene imparted relatively higher and broader resistance to lepidopterans and in addition to hemipterans, which are otherwise not controlled by *Bt* alone (Maqbool et al. 2001; Ramesh et al. 2004a). Preliminary field testing of transgenic rice lines carrying c*ry1Ab*, *Xa21*, and *gna* genes has also been conducted in India (Bentur 2006). Recent investigation suggested that Cry1Ab or Cry1Ac could be combined with Cry1C, Cry2A, or Cry9C for durable resistance in transgenic rice as Cry1Ab and Cry1Ac compete for the same binding site in YSB (Alcantara et al. 2004).

11.2.5 Stem Borer Resistance with Genes and Proteins Other than *Bt*

Discovery of a number of insecticidal proteins like protease inhibitors, ribosome-inactivating proteins, lectins, antibodies, and insect peptide hormones provides several novel options for deriving resistance from sources other than *Bt* solely or in combination with *Bt.* Plants themselves may be the source of these non-*Bt* genes with insecticidal activity (Sharma et al. 2004). Protease inhibitors are antimetabolites acting against a wide range of insect pests, and the genes encoding for these are a component of plant's natural defense system against insect damage. Several transgenic rice plants expressing protease inhibitors have been field tested including those with synthetic gene coding for winged bean trypsin inhibitors WTI-1B (Mochizuki et al. 1999), oryzacystatin, cowpea trypsin inhibitors, potato proteinase inhibitors II, and soybean Kunitz trypsin inhibitors (Tyagi and Mohanty 2000; Sharma et al. 2004). In addition, transgenic rice plants with barley trypsin inhibitor BTI-CMe have been tested for resistance against rice weevil *Sitophilus oryzae* (Alfonso-Rubi et al. 2003). Cowpea trypsin inhibitor (*CpTi*) transgene has also been used for deriving resistance to stem borer (Brar and Khush 2007). Likewise, plant lectin (heterogeneous group of sugar-binding proteins) genes have shown protection in particular to homopterans (sap-sucking insects: BPH, WBPH, GLH), apart from lepidopterans and coleopterans. However, snowdrop lectin (*Galanthus nivalis* agglutinin) gene, *gna*, stacked with *Bt* genes imparted relatively higher and broader resistance to lepidopterans and homopterans than *Bt* alone (Maqbool et al. 2001; Ramesh et al. 2004a). Further, extensive research is needed on cloning of insecticidal protein coding genes specifically for the stem borers.

11.2.6 RNA-Mediated Crop Protection Against Rice Yellow Stem Borer

RNA interference (RNAi) or RNA silencing has emerged a promising research tool for silencing, downregulating, or controlling the expression of the key insect genes especially where the resistance sources are rare in the primary gene pool of the host plant. As we understand that double-stranded RNA (dsRNA) is an important regulator of gene expression in many eukaryotes (Meister and Tuschl 2004), a sequence-specific suppression of target insect gene is achieved through exogenous application and endogenous expression of dsRNAs, which degrades the target complementary endogenous messenger RNA (mRNA) transcripts within the cell. It works through 21–24 nucleotide small RNAs which are processed through a set of core enzymatic machinery involving Dicer and Argonaute proteins (Mohanpuria et al. 2015). RNAi-mediated silencing of target insect gene may lead to growth inhibition, developmental aberrations, reduced fecundity, and mortality (Baum and Roberts 2014). Kola et al. (2015) discussed the role of various potential insect genes encoding key enzymes/proteins for developing an effective insect control by RNAi approach including acetylcholinesterase, cytochrome P450 enzymes, amino peptidase N,

allatostatin, allatotropin, tryptophan oxygenase, arginine kinase, vacuolar ATPase, chitin synthase, glutathione-S-transferase, catalase, trehalose phosphate synthase, vitellogenin, hydroxy-3-methylglutaryl coenzyme A reductase, and hormone receptor genes. Kola et al. (2016) reported that YSB larvae fed on dsRNA designed from two genes of rice yellow stem borer (YSB), cytochrome P450 derivative (CYP6), and Aminopeptidase N (APN) have detrimental effect on larval growth and development of the insect. Cytochrome P450 monooxygenases (cytochrome P450s) are found in virtually all living organisms (Kola et al. 2015) and perform an important role in the metabolism of xenobiotics such as drugs, pesticides, and plant toxins (Scott 2008). In insects, cytochrome P450s play a predominant role in the metabolism of insecticides, which often results in the development of insecticide resistance in insect populations (Zhou et al. 2010). On the other hand, the aminopeptidase N (APN) group of exopeptidases are abundant proteins on the midgut brush border of insect larva (Adang 2013). APNs in lepidopterans received initial attention because they function as receptors for *Bt* Cry1 insecticidal toxins. It plays an important physiological role in dietary protein digestion (Marchler-Bauer et al. 2015). Inhibition of its activity in the midgut can result in detrimental effect on larval growth and development and lead to larval mortality (Reed et al. 1999). Expression of APNs was found in midgut and malpighian tubules (Wang et al. 2005). These genes can be deployed to develop YSB resistance in rice using RNAi approach. However, to achieve an effective RNAi response for YSB control in rice, careful identification of specific target insect enzymes and proteins, efficient delivery methods of introducing dsRNA into insect cells/bodies, and stabilization of dsRNAs during and after delivery are certain key issues which need immediate concern.

11.3 Gall Midge – An Overview

The Asian rice gall midge (ARGM) *Orseolia oryzae* (Wood-Mason) (Diptera: Cecidomyiidae) was first reported as an unidentified pest of rice in Bihar, India, by Riley (1881). Though first identified as *Cecidomyia oryzae* Wood-Mason (Cotes 1889), the pest was later renamed as *Pachydiplosis oryzae* (Felt 1921), and subsequently as *Orseolia oryzae* (Gagné 1973). A related species in western Africa was named as African gall midge, *O. oryzivora* (Harris and Gagne 1982). The introduction and widespread cultivation of dwarf and high-yielding rice cultivars resulted in extensive gall midge problem. A significant portion of rice yield is lost to ARGM damage in several rice-growing countries including India, China, Thailand, Sri Lanka, Myanmar, Indonesia, Bangladesh, and Vietnam (Bentur 2015). The conservative economic estimate of yield losses from gall midge is about US$ 500 million in Asia and US$ 80 million in India alone. In India, it is rated as third most important pest of rice in terms of spread and severity of damage and yield loss (Bentur 2015), next to stem borers and plant hoppers. ARGM occurs in most states in India except north-western states like Punjab and Haryana. It is essentially a monsoon pest and prefers high humidity and moderate temperature with peak activity extending between last week of August and first week of October (Rajamani et al. 1979).

The pest has a short life cycle (19–23 days) under normal temperatures (22–28 °C) and constant humidity (~85% RH), with sex ratio (male to female) of 1:3 usually. Adult fly is pink in color and looks like a mosquito. Mating occurs during dawn or dusk (crepuscular), and a single female lays an average of 125–150 eggs which usually hatch on the fourth day. Feeding and salivary secretion of maggots turn the growing shoot meristem into a gall chamber, which after elongation develops into a tubular gall commonly known as silver shoot or onion leaf. The affected tillers bear no panicle or grains resulting in significant economic loss. An economic estimate of annual yield loss from gall midge is pegged at Rs. 3300 million (Bentur et al. 2003) in southern India alone. In contrast, the maggots fail to induce gall formation on the resistant varieties, and perish in 2–4 days after hatching. Several promising sources of resistance were identified in greenhouse screening and field evaluation of rice germplasm. This made the host plant resistance as the most viable option for successful management of the gall midge for the last several decades.

11.3.1 Rice-Gall Midge Interactions

Classical approaches in rice breeding for gall midge resistance were pursued during the late 1950s which later led to successful release of the first gall midge (GM)-resistant variety "Kakatiya" in 1975. Since then, more than 100 rice varieties resistant to gall midge have been released for cultivation, and in this the availability of greenhouse rearing and screening protocols played a significant role. Systematic evaluation of over 25,000 accessions of rice germplasm has led to identification of more than 500 sources of resistance to gall midge (Bentur et al. 2011; Bentur 2015), and majority of these are landraces from northeastern states of India. Differential reaction of same genotype against gall midge populations at different rice-growing areas reflected intraspecific variations and helped in the detection of its geographically distinct populations (biotypes). Biotypes, in general, refer to the intraspecific category of insect populations with similar genotypes for biological attributes. They represent evolutionary transients in the process of speciation and develop through natural selection acting upon genetic variations within the pest populations. Roy et al. (1969) first suspected the occurrence of gall midge biotypes (GMB). Kalode and Bentur (1989) characterized three distinct biotypes of gall midge, based on 13 years of data on field evaluation of differentials in the country. Subsequently, reports on the emergence of new virulent biotypes appeared. Recently, a seventh biotype, GMB4M, was reported (Vijayalakshmi et al. 2006). Several reports (Bentur et al. 1987; Srinivas et al. 1994; Nair and Devi 1994) associated the selection of virulent biotypes to extensive cultivation of resistant varieties of rice. With the detection of gall midge biotypes, screening of resistant germplasm accessions against the characterized biotypes was undertaken aggressively to understand the range of resistance (Kalode and Bentur 1988; Bentur et al. 1994). Investigations on genetics of rice gall midge resistance at Indira Gandhi Agricultural University (IGAU), Raipur, further led to characterization of ten gall midge resistance (R) genes designated as *Gm1* through *Gm10*. Identification of *Gm11* gene from

breeding line CR57-MR1523 (Himabindu et al. 2010) finally raised the number of characterized gall midge-resistant genes to 11. Nair et al. (2011) reported gene-for-gene relation between R genes in rice and gall midge biotypes. Each of the biotypes showed a specific range of virulence against R genes, and likewise each R gene conferred resistance to specific biotypes, which implies that none of the R genes conferred resistance to all biotypes and none of the biotypes showed virulence against all the R genes. The range and pattern of resistance displayed by rice gene differential varieties against the seven known biotypes are presented in Table 11.2. Based on the similarity in range of resistance, R genes were categorized into four groups. Rice plant and gall midge have been known to exhibit compatible or incompatible interaction. In the first case, virulent insect successfully establishes on a susceptible rice plant leading to gall formation and completion of insect life cycle. However, in incompatible interaction, the host rice plant is resistant, and the insect fails to establish and is killed within 24–48 h of feeding. The major component of varietal resistance against rice gall midge is antibiosis (Modder and Alagoda 1972; Hidaka 1974; Kalode 1980), and the defensive role of phenols against gall midge in resistant varieties is also reported (Amudhan et al. 1999). However, no antixenosis mechanism is involved. The maggots feeding on resistant varieties are either killed on feeding or unable to molt to second instar. So far, tolerance as a mechanism of resistance against gall midge is only reported in rice cultivar CR1014 (Prakasa Rao 1989).

Bentur and Kalode (1996) reported two types of resistance reactions exhibited by resistant rice plants in response to gall midge feeding; HR^+ type is characterized by symptoms of tissue necrosis at the site of maggot feeding and HR- type in which no tissue necrosis occurs, but the insect mortality is observed. Addition of this information in the Table 11.2 further suggested diversity in R genes in terms of spectrum of resistance and type of resistance. Of the 11 known R genes, only *Gm1* and *Gm8* confer HR- type resistance, while the other 9 genes provide HR+ type resistance.

11.3.2 Tagging, Mapping, and Cloning Gall Midge Resistance Genes in Rice

The use of marker-assisted selection (MAS) with PCR (polymerase chain reaction)-based molecular markers for gene pyramiding has met with encouraging results. To date PCR-based linked molecular markers have been developed for 8 of the 11 resistance genes (Yasala et al. 2012). While four of the genes, viz., *Gm2*, *gm3*, *Gm6*, *Gm7*, have been noted as a cluster on chromosome 4, two genes *Gm4* and *Gm8* are located on chromosome 8. For most of these genes, flanking markers are available, which can be used to effectively transfer them. Three of the genes, viz., *gm3*, *Gm4*, and *Gm8*, have been cloned through map-based approach, and candidate genes for these have been identified as NB-ARC (LOC_Os04g52970.1) (Sama et al. 2014), NBS-LRR (LOC_Os08g09670.1) (Divya et al. 2015), and proline rice protein (Dutta et al. 2014), respectively. Based on the gene sequence information, functional markers have been developed for these three genes (Dutta et al. 2014).

Table 11.2 Nature and effectiveness of gall midge resistance genes in rice against different biotypes

Group	Source	Gene	Chr. no.	HR type	Reaction to gall midge biotype							References
					GMB1	GMB2	GMB3	GMB4	GMB5	GMB6	GMB4M	
I	W1263	*Gm1*	9	−HR	R	S	R	S	R	R	S	Reddy et al. (1997)
II	Phalguna	*Gm2*	4	+HR	R	R	S	S	R	S	S	Mohan et al. (1994)
II	ARC5984	*Gm5*	?	+HR	R	R	R	S	R	S	S	Kumar et al. (1998b)
II	Dukong 1	*Gm6*	4	+HR	R	R	R	S	R	S	S	Tan et al. (1993)
II	RP2333-156-8	*Gm7*	4	+HR	R	R	R	S	R	S	S	Kumar et al. (1999)
II	Madhuri -L9	*Gm9*	7	+HR	R	R	R	S	R	S	S	Shrivastava et al. (2003)
II	BG308	*Gm10*	?	+HR	R	R	R	S	R	S	S	Kumar et al. (2005)
III	CR57-MR1523	*Gm11*	12	+HR	R	R	R	R	S	S	S	Himabindu et al. (2010)
IV	RP2068	*gm3*	4	+HR	R	R	R	R	S	S	R	Kumar et al. (1998a)
IV	Abhaya	*Gm4*	8	+HR	R	R	R	R	S	S	R	Srivastava et al. (1993)
IV	Jhitpiti/Aganni	*Gm8*	8	−HR	R	R	R	R	S	S	R	Kumar et al. (2000)
V	TN1	None	–	–	S	S	S	S	S	S	S	–

After Bentur et al. (2011)

HR hypersensitive reaction, *GMB* gall midge biotype, *R* resistant, *S* susceptible, *Chr* rice chromosome number, ? not determined

[a]Groups are based on the spectrum of resistance conferred by the gene across gall midge biotype

11.3.3 Pyramiding of Gall Midge-Resistant Genes in Rice

Gene pyramiding offers an excellent approach to incorporate wide range and durable resistance against gall midge in rice. Better insights into the genetics of resistance, R (resistant) gene mapping, allelic relationships, and linkage are necessary for pyramiding of resistant genes. Resistance against gall midge is conferred by a single gene (monogenic) which facilitates pyramiding. However, one of the major problems that has impeded the long-term success of gall midge-resistant varieties released so far is the continuous evolution of new virulent biotypes against the deployed resistant genes. Distinct major genes for gall midge resistance are effective against different biotypes, and this differential reaction offers a promising tool for pyramiding resistant genes. Combining resistant genes in a variety is surely a gateway to an effective and durable resistance; however, which gene combinations will provide desired durability needs investigation. The suggested approach is to combine the genes with different mechanism of resistance in good agronomic background. To date, most of the gall midge-resistant varieties developed so far derive their resistance mainly from *Gm1*, *Gm2*, *Gm4*, and *Gm11* genes, and thus these are less likely candidates for pyramiding. The virulence against *Gm2* and *Gm11* genes has already been reported at several locations across India. However, *Gm1* gene exhibited continued durability for more than 30 years of its deployment, and resistant variety "Abhaya" carrying *Gm4* gene has not been cultivated widely. Based on the available information on resistance nature, frequency of alleles conferring virulence against R genes (Bentur et al. 2008), genetics of virulence, and fitness cost associated with virulence, the best combination of genes suggested is *Gm4+Gm8* or *gm3+Gm8* (Bentur 2015).

11.3.4 Virulence Monitoring in Gall Midge Populations

Widespread cultivation of gall midge-resistant varieties often resulted in evolution of new virulent biotypes which caused resistance breakdown in single-gene-resistant varieties. As a curative measure, developing varieties with durable resistance through gene pyramiding is a viable option. The use of marker-assisted selection (MAS) with PCR (polymerase chain reaction)-based molecular markers for gene pyramiding has yielded encouraging results. To date PCR-based molecular markers have been developed for 8 of the 11 resistance genes. However, the selection of candidate genes for pyramiding needs thorough understanding of the virulence composition of the pest populations in the target area, the genetics of plant resistance, and insect virulence, as the rice-gall midge interaction is a gene-for-gene one. A modified F_2 screen method has been developed for monitoring virulence in gall midge populations (Bentur et al. 2008; Andow and Bentur 2010). Tests based on this method across the country revealed high level of virulence against resistance-conferring *Gm2* plant gene. Further, studies at Warangal revealed a slower rate of virulence development against *Gm1*, while a rapid increase in frequency of virulence allele in gall midge conferring adaptation to *Gm2*, the plant resistance gene,

was observed. As the single recessive gene, *$_v$Gm2*, conferring virulence against *Gm2* (Bentur et al. 1992) follows sex-linked inheritance, it results in less durability of resistant gene (*Gm2*) in host plant since such virulence gets fixed in population faster than the autosomal inherited virulence gene. Similar studies also established low levels of virulence against *Gm8* and high levels against *Gm11*.

11.3.5 Durable Deployment of Gall Midge-Resistant Varieties

The deployment of gall midge-resistant varieties of rice often led to the emergence of resistance-breaking biotypes that suppress the yield benefit provided by the resistance. Cohen et al. (2004) suggested that besides the genetic makeup of the varieties under cultivation, the frequency of alleles for adaptation to host, genetics of virulence, and fitness cost associated with virulence as the decisive factors in shaping evolution rate of new biotypes. They further compared various deployment strategies for gall midge-resistant rice varieties including sequential release of varieties containing single-resistant gene, release of variety with two resistant genes pyramided and seed mixtures of gall midge susceptible variety, and release of single R gene or pyramided variety through the use of various simulation models. The results of these simulation studies revealed that (1) the release of a single variety with two pyramided resistant genes provides longer duration of resistance than the combined term of resistance of two single-gene varieties released sequentially and (2) the incorporation of a susceptible variety into the seed mixture usually prolongs the durability of resistant varieties. However, deliberate efforts are needed to investigate how farmers' main leverages (choice of resistant variety, resistance deployment strategy, and cultural practices) can be best combined to achieve resistance durability while minimizing yield losses.

11.3.6 Insect Virulence Genes *vis-à-vis* Biotype Evolution

Gall midge biotypes have been encountered in association with cultivation of resistant crop cultivars, and in this case, a gene-for-gene relationship between pest virulence and host plant resistance has been discussed earlier. Knowledge of occurrence of gall midge biotypes is a prerequisite to design crop improvement programs for incorporating pest resistance. To slow down the process of biotype selection, crop cultivars with broad genetic bases are needed. On the other hand, knowledge of genes and pathways involved in insect virulence and evolution of biotypes is strongly needed. Sinha et al. (2012a) identified more than 80,000 ESTs each from gall midge feeding on resistant as well as susceptible host. Comparative transcriptome analysis of these two sets of ESTs led to identification of several virulence and avirulence genes of gall midge besides development of 2303 EST-based and 2756 SNPs markers. Sinha et al. (2012a) successfully cloned two genes *Ooprot1* and *OoprotII*. RT-PCR analysis established that both these genes were upregulated in gall midge larvae feeding on resistant host than in larvae feeding on susceptible host

suggesting their role in detoxification of plant resistance factors. Likewise, a secretory salivary protein coding gene, oligosaccaharyl transferase (*OoOST*), has been cloned and characterized (Sinha et al. 2012b), and its expression was found to be seven times higher in salivary glands of larvae feeding on susceptible host than in those feeding on resistant ones, indicating their role in insect virulence. They further found another overexpressed gene, *OoNDPK*, coding for nucleoside diphosphate kinase in gall midge maggots feeding on susceptible plants. Better understanding of insect virulence genes, pathways involved in insect virulence, and interaction of virulence genes with host genotypes may be helpful in delaying the evolution of resistance-breaking evolutionary transients in target insect population.

11.4 Conclusions and Prospects

Forgoing account of our understanding insect-plant interactions and efforts to develop resistant rice cultivars against stem borers and gall midge bring home the following conclusions. The rice stem borer, mainly YSB, association has come to an evolutionary equilibrium with YSB attaining monophagous status and adopting k strategy of population structure. In other words, rice offers no threat to the insect, and insect in turn does not challenge the plant's survival. It is "live and let others live" equilibrium. Superimposed on this state is the mankind's demand for food which does not compromise on even a marginal yield loss due to the stem borers. While classical breeding approach did not provide high level of host plant resistance, mainly due to the evolutionary equilibrium, novel biotechnological approaches outlined in the text above are more likely to bring "success." This would mean an unprecedented selection pressure on the insect. It would certainly be naive to undermine the insect's genetic plasticity to respond to this pressure. Studies have clearly shown high frequency of alleles conferring resistance against Cry toxins in populations of YSB in the Philippines (Bentur et al. 2000) and SSB populations in China even without deployment of *Bt* rice. It is thus imperative also to invest on development of effective deployment strategies along with focus on transgenic and other approaches for stem borer resistance.

In contrast, rice-gall midge interactions may be in a state of evolutionary flux. This is reflected in the diversity in defense pathways that have coevolved in the plants, simultaneously and independently across rice-growing regions of the world. The Thailand land race "Siam 29" has distinct resistance mechanism (conferred by *Gm2* with HR+ type) in comparison with Indian land race "Eswarakora" (with *Gm1* and HR- type). Evolutionary biologists propose formation of gall to restrict and captivate the invading insect itself as the plant defense. Ingenious adaptation of the insect against this first line of defense has rendered the plant more prone and secure host for the gall former. This parallel evolution is the battle for survival (Bentur et al. 2016) which may be further considered in association with r/k strategy of the pest population dynamics which display typical "buck and boost" cycles. The take-home message is likely that no single approach would provide lasting resistance to the gall midge. Hence novel approaches need to be continuously explored to stay one step ahead of this evolutionary miracle pest.

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Breeding for Insect Resistance in Mung Bean and Urd Bean

12

Harpreet Kaur Cheema, Aditya Pratap, and G.K. Sujayanand

Abstract

Mung bean and urd bean are important warm season food legumes grown in tropical and subtropical regions of the world and contribute significantly to the nutritional security of vegetarian people. However, high incidence of insect pests in these crops is a major constraint in achieving their potential productivity and resulting in yield instability over the years. Their chemical control is costly and inconsistent and has detrimental environmental effects. Host plant resistance is an economical, durable, environmentally safe and ecologically acceptable means of managing these pests. This chapter outlines the sources of resistance available for major insect pests of mung bean and urd bean, mechanisms of resistance, breeding methods for evaluation of genetic resources, alien gene introgression, genetic transformation and prospects in breeding for insect resistance in mung bean and urd bean.

Keywords

Breeding strategies • Insect resistance • Food legumes • Mung bean • Urd bean

H.K. Cheema (✉)
Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana 141004, India
e-mail: hkcheema@pau.edu

A. Pratap • G.K. Sujayanand
ICAR-Indian Institute of Pulses Research, Kanpur 208024, India
e-mail: adityapratapgarg@gmail.com; sujay2020@gmail.com

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12.1 Introduction

Mung bean (*Vigna radiata* (L.) R. Wilczek) and urd bean (*Vigna mungo* (L.) Hepper) are important warm season grain legumes serving as important sources of human food and are in great demand, especially by vegetarian people. On global level, specific data for mung bean and urd bean are not available; however, among pulses, the data for dry beans (including *Phaseolus* spp. and *Vigna* spp.), which account for one of the largest groups, is available (FAOSTAT 2015), wherein India, Myanmar and Brazil are the major producers. Mung bean is an ancient and economically one of the most important Vigna crop in Asia, particularly in the Indian sub-continent, and is becoming popular in other continents as well. The world production area of mung bean is about 5.5 million ha (Weinberger 2003) with an estimated global production of 2.5–3 mt (Tomooka et al. 2005). India is the primary mung bean producer, contributing 65% of the world production, but most of the produce is consumed locally (Vijayalakshmi et al. 2003). China, Myanmar, Vietnam and Thailand are the major exporters of mung bean grain and products (Srinives et al. 2007). Black gram is grown largely in South and Southeast Asia but to a lesser extent, compared to mung bean. India, Burma and Thailand are the major producers. Together, mung bean and urd bean occupied an area of 6.26 million ha with a production of 3.46 million tonnes in India (Department of Agriculture and Cooperation 2016). These crops are cultivated over a wide range of agroclimatic zones in India. There has been a phenomenal increase in area, production and productivity of these crops during the past 40 years, especially in spring/summer season, primarily due to the development of short duration, disease-resistant and high-yielding varieties along with plant protection and production technologies (Kooner et al. 2006). However, the occurrence of high incidence of insect pests is a major constraint in achieving high crop productivity and is responsible for yield instability over the years. About 115 and 198 insect species are reported to feed on these crops in India and the world, respectively (Kooner et al. 2006; Chhabra and Kooner 1998). Among these, 17 insect pests have been identified as key pests under Indian conditions which exact a heavy toll on yield (Kooner et al. 2006). These include *Ophiomyia phaseoli* (Tryon), *Bemisia tabaci* (Gennadius), *Empoasca* spp., *Polyphagotarsonemus latus* (Banks), *Aphis craccivora* Koch, *Spodoptera litura* (Fabricius), *Maruca* spp., *Helicoverpa armigera* (Hubner), *Lampides boeticus* Linnaeus, *Megalurothrips distalis* (Karny) and *Callosobruchus* spp. The strategies for managing these insect pests include integration of agronomic and cultural management, host plant resistance (HPR), biological control, natural pesticides and judicious use of chemical pesticides. Efforts should be made for maximizing host plant resistance as it has proven to be an effective, economical, durable, environmentally safe and acceptable means of managing biotic stresses. HPR is a sustainable approach and is also compatible with other components of integrated pest management (IPM).

12.2 Sources of Resistance

The major sources of genetic variation for improving resistance against insect pests include germplasm collections from local sources, introduction and acquisition of germplasm from exotic sources, wild accessions and recombinants resulting from crossings of selected parents of all sources (Keneni et al. 2011).

The Vigna species, in general, show a wide distribution in the tropics and subtropics (Anishetty and Moss 1988). Both mung bean *V. radiata* and urd bean *V. mungo* originated in the Indian sub-continent (Condolle 1883; Zukovskij 1962). The primary centre of diversity for mung bean has been suggested to be the central Asian region (Vavilov 1926), and India is the likely centre of domestication where it was domesticated as early as 1500 BC (Smartt 1985). Therefore, large numbers of wild relatives are available in India. The progenitors of mung bean (*V. radiata* var. *sublobata*) and urd bean (*V. mungo* var. *silvestris*) are found as weeds in cultivated and wasteland areas of India (Singh et al. 1974; Chandel et al. 1984) and in wetlands in subtropical regions of northern and eastern Australia (Lawn and Cottell 1988).

12.2.1 Cultivated/Primary Gene Pool

Several workers in the past have reported resistance in mung bean and urd bean germplasm against various insect pests; most have reported lack of complete and/or stable resistance and use terms such as moderate resistance, tolerance or least susceptible in comparison/relative to other entries screened in the collection (Chhabra et al. 1988; Sahoo and Hota 1991; Fargali et al. 1996; Naqvi et al. 1995; Khattak et al. 2004).

12.2.1.1 Agromyzid Flies, *Ophiomyia* spp. and *Melanagromyza* spp.

The main agromyzid flies infesting beans are legume seedling fly, *Ophiomyia phaseoli* (Tryon)/*O. centrosematis* (de Meijere), *Melanagromyza obtusa* (Malloch) and *M. sojae* (Zehntner). These flies can cause up to 90% infestation in mung bean (Sehgal and Ujagir 1985). The insect inserts eggs on the underside of young leaves. Maggots mine into the leaves and petioles and also bore into the stem resulting in withering, drooping and death of the plant. Stem infestation leads to a distinct zigzag tunnelling and reddening (sometimes pale) may be observed with maggots or pupae inside. Apart from the exit holes, the plants initially appear healthy on the outside. The pest has been reported to cause 5–20% and 3–62% damage on an average in mung bean and urd bean, respectively (Sharma et al. 2011).

Abate (1990) found that CIAT accession nos. G05253, G05773, G02005 and G02472 out of more than 1500 bean germplasm lines tested were highly resistant to bean fly and were recommended for the use in breeding programmes; the mechanism of resistance was found to be tolerance. Talekar (1990) screened mung bean cultivars against stem borer, *Ophiomyia* spp., and reported three resistant cultivars, viz., V 2396, V 3495 and V 4281. In urd bean, highly resistant lines such as UG 218, PDU 1, PDU 5, AKU 7, CO 305, UP 95-1 and LBG 707 have been identified against

stem flies (Gupta and Kumar 2006). Lal (1987) reported mung bean cultivar Co 3 and urd bean cultivars Karaikal, Killikum, 338/3 and P58 as less susceptible to stem fly.

12.2.1.2 Sweetpotato Whitefly (*Bemisia tabaci* (Gennadius))

The sweetpotato whitefly, *Bemisia tabaci* (Gennadius), is a cosmopolitan insect pest of many agriculturally important crops in the world. It is a major threat to successful cultivation of urd bean and mung bean. The nymphs and adults suck sap from leaves lowering the vitality of plants and secrete honey dew on which sooty mould grows resulting in blackening and drying of leaves leading to total failure of the crop (Chhabra and Kooner 1980a). Moreover, it is a vector of mung bean yellow mosaic virus (MYMV). Workers have reported 17–71% avoidable losses due to whitefly in these crops (Saxena 1983; Chhabra 1992; Mansoor-Ul-Hassan et al. 1998). Chemical control is the most common means of managing whitefly; however, it often fails to provide adequate control thereby necessitating alternate management strategies. Host plant resistance offers a low-cost, practical, long-term solution for maintaining lower whitefly populations and reducing crop losses (Bellotti and Arias 2001).

Screening of germplasm against whitefly and jassid is being carried out using various screening techniques; the most common include population counts per leaf (Khattak et al. 2004; Singh et al. 2008; Nadeem et al. 2014) and number of adults per split cage (Kooner and Cheema 2007a) under natural conditions in hot spots and the newly devised screening method of whitefly resistance index (WRI; based on leaf injury grade) under screen house conditions (Taggar et al. 2013). Screening of more than 2000 genotypes of rainy season mung bean against whitefly over a period of about 25 years at Punjab Agricultural University (PAU), Ludhiana, India, resulted in identification of 43 accessions as resistant (Chhabra and Kooner 1980b, 1981–93, 1992a, b, 1993, 1994, 1998; Chhabra et al. 1980, 1981b-93, 1988; Kooner 1998; Kooner and Cheema 2007a; Kooner et al. 1977, 1979, 2005). Kooner et al. (1997) screened 504 germplasm lines of mung bean and found that ML 1, ML 6, ML 7, P 290, P 292, P 131, P 293, P 325, P 364 and 11,148 were least susceptible to *B. tabaci* and MYMV. Yadava and Dahiya (2000) reported ML 803, ML 839, PDM 91-249 and PBM 5 as good source of resistance against whitefly. NM-92 has been reported as resistant to whiteflies (Khattak et al. 2004). Similarly, Bhatnagar and Dahiya (2005) found that MH 96-1 harboured lower whitefly population. Kooner and Cheema (2007a) identified genotypes ML 1265 and ML 1229 as resistant donors for whitefly. Both the genotypes have been used by the breeders in the crossing programme of rainy season mung bean, and ML 1265 was subsequently released in the Punjab state as a high-yielding variety tolerant to whitefly. Singh and Singh (2014) found mung bean genotypes TMB 36 and RMG 1004 out of 30 genotypes screened against whitefly as resistant/tolerant at Varanasi, India. Mung bean genotypes MH 3153 (Nadeem et al. 2014) and ML 1774 and ML 1779 (Cheema et al. 2015) were observed to be least affected by whitefly incidence. Out of ten mung bean varieties, Pant U 30 was found tolerant to whitefly (Sahoo and Hota 1991).

About 1400 urd bean genotypes have been screened in about 15 years against whitefly, jassid and MYMV, and 28 were identified as resistant against whitefly at PAU, Ludhiana (Chhabra and Kooner 1981a, 1981b–93, 1995a, b, 1998; Chhabra et al. 1984, 1993; Kooner et al. 1994). Varieties LBG 17, SEL 37, Pant U 30 and Sarla were found most promising against whitefly (Sahoo and Sahu 1991). Lowest incidence of whitefly was recorded on urd bean cultivar Pant U 19 by Prasad et al. (2005) at Ranchi, India. Kumar et al. (2004) reported RB-4, RB-32 and PDU-3 as superior to standard check T-9. Entry IPU-95-13 was identified as tolerant to whitefly (Sharma et al. 2004), while genotype KU 99-4 was found promising against whitefly (Bhatnagar and Dahiya 2005; Kooner and Cheema 2007b). Out of 22 germplasm lines tested at Jammu, India, Singh et al. (2008) reported that KARS 114 had least susceptibility to whitefly attack and was high yielding and suggested its utilization in imparting resistance for further conventional/mutation breeding programmes for urd bean improvement. Among 44 urd bean genotypes screened against whitefly, the lowest incidence was observed on genotypes ACM05-007 and TPU-4 (Kumar and Singh 2014). Taggar et al. (2013) categorized urd bean genotypes KU 99-20 and NDU 5-7 as moderately resistant to whitefly on the basis of whitefly resistance index (WRI; based on leaf injury grade) as they recorded WRI of 1.50, while the susceptible genotypes had WRI ranging from 2.59 to 3.05. The authors also suggested that optimum period for differentiation of susceptible and resistant urd bean genotypes could be taken between fifth and sixth week after release of whiteflies in multiple choice test under screen house conditions. Moreover, whitefly population could be counted from any of the canopies (upper/middle/lower) for screening urd bean genotypes.

12.2.1.3 Green Jassid (*Empoasca* spp.)

Green jassids, also known as green leafhoppers, *Empoasca kerri* Singh-Pruthi, *E. motti* Singh-Pruthi and *E. terminalis* Distant, are sucking insect pests common during vegetative stage of plant growth (Chaudhary et al. 1980; Chhabra et al. 1981a, b; Litsinger et al. 1988). The adults and nymphs suck cell sap from underside of the leaves and reduce the vitality of the plants.

Chhabra et al. (1988) screened 29 cultivars of mung bean and identified three cultivars, viz., ML 337, ML 423 and ML 428, to be least susceptible to the jassid. Kooner (1998) screened 48 genotypes of mung bean and reported ML 508 and ML 537 possessing resistance against *Empoasca* spp. Many mung bean and urd bean genotypes mentioned for whitefly resistance have been reported to be resistant/tolerant to jassids by different workers (Chhabra and Kooner 1980a, 1981a, b, 1993, 1994, 1995a; Chhabra et al. 1981b, 1993). At Varanasi, Pandey and Misra (1992) identified five crosses of F_2 and F_3 generations of mung bean, viz., ML 5 x PIMS 1, PIMS 1 x P 226, ML 5 x P 226, T 44 x UPM 79-3-4 and ML 80 x UPM 79-3-4, as least susceptible to jassid and pod borers. Entries TAM-20, PDM-84-143, Pusa-105, MI-67-3 and MI-29-22 were reported as promising against *E. kerri* (Devesthali and Joshi 1994; Devesthali and Saran 1998). Lal (1987) reported urd bean cultivars from Badnapur (Krishna, H 70-3, No. 55 and UPB 1) as less susceptible to jassid. Sahasrabudhhe and Patil (2000) screened some cultivars of urd bean and identified

Sindkheda 1-1 as promising against *E. kerri*. Ujagir and Sehgal 1997 reported Pant U 19 with lowest incidence of jassid. Singh and Singh (2014) reported genotypes TMB 36 and Pusa 1271 as resistant/tolerant with minimum population of jassid as compared to 28 other mung bean genotypes. Genotype MH 3153 was observed to be resistant to jassid (Nadeem et al. 2014). Out of five mung bean genotypes screened, NM-92 was resistant against jassids in Pakistan (Khattak et al. 2004). Among the ten urd bean genotypes, KBG 06016 recorded minimum leafhoppers which was on par with the standard checks VBN 5 and VBN 4 (Justin et al. 2015). Kumar and Singh (2014) screened 25 different genotypes, and TU-631 had minimum number of leafhoppers.

12.2.1.4 Cowpea Aphid (*Aphis craccivora* Koch)

The nymphs and adults of cowpea aphid or black aphid, *Aphis craccivora* Koch, suck the plant sap from young plants especially on leaflets, stems and pods. Young leaves become twisted on continuous feeding. Aphids excrete honeydew which results in growth of sooty mould (Sharma et al. 2011).

Sahoo and Hota (1991) screened mung bean genotypes against *A. craccivora* and found that 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 were resistant. Chhabra et al. (1986) tested 30 urd bean genotypes and identified LU 335, LU 274, LU 332 and LU 470 as moderately resistant to *A. craccivora* and M 1-1 as highly resistant. Entries LU 15, LU 178, LU 190 and LU 194 were also reported to possess resistance (Chhabra et al. 1981-93). Of 20 cultivars screened for resistance to *A. craccivora* in Madhya Pradesh, TAM-20, PDM-84-143 and Pusa-105 were found promising (Devesthali and Joshi 1994). Sahasrabudhhe and Patil (2000) reported that urd bean cultivar Sindkheda 1-1 was quite promising against *A. craccivora*. More recently, among ten urd bean genotypes, the minimum aphid population was recorded in KBG 05007, and it was on par with standard check, VBN 4 (Justin et al. 2015).

12.2.1.5 Bean Blossom Thrips (*Megalurothrips distalis* (Karny))

Nymphs and adults of bean blossom thrips or flower thrips *Megalurothrips distalis* (Karny) feed on the pedicles and stigma of flowers, causing flower shedding and deformity of inflorescence and ultimately high-yield reduction of the crop which in some cases reach 100% (Kooner et al. 1983; Chhabra and Kooner 1985a, b).

Malik (1990) observed that summer mung bean genotypes SML 77, UPM 82-4 and Pusa 107 were resistant to *M. distalis* under natural as well as screen house conditions. Screening germplasm of summer mung bean against bean thrips at PAU, Ludhiana, resulted in identification of about 30 least infested lines (Chhabra and Kooner 1985b, 1988, 1992c; Chhabra and Malik 1992; Cheema et al. 2007). Mung bean cultivars Co 3, Co 4 and Co 5 from Coimbatore have been reported to be less susceptible to thrips (Lal 1987). Chhabra (2001) reported that mung bean genotypes PIMS 2 and PIMS 3 at Badnapur, CO 3 at Coimbatore and ML 5 and ML 337 at Durgapura were resistant to thrips. NM-92 has also been reported to be resistant to thrips in Punjab, India, and Pakistan (Khattak et al. 2004; Kooner et al. 2005). Singh and Singh (2014) recorded minimum thrips infestation in ML 1628, Pusa 1171 and

ML 1464 and reported these as resistant/tolerant. MH 3153 recorded lowest number of thrips per leaf among eight advanced mung bean genotypes/cultivars in Pakistan (Nadeem et al. 2014). In urd bean, highly resistant lines such as PDU 5, KB 63, UG 567 and UH 804 have been identified against thrips (Gupta and Kumar 2006). Of 25 urd bean genotypes, ACM05-007 was found least infested with thrips followed by AKU 10-1 (Kumar and Singh 2014). Pant U 19 was found to be least susceptible to thrips (Ujagir and Sehgal 1997; Katare et al. 1998; Prasad et al. 2005) at Pantnagar and Ranchi.

12.2.1.6 Cotton Bollworm (*Helicoverpa armigera* (Hübner))

Cotton bollworm, better known as gram pod borer, *Helicoverpa armigera* (Hübner), is a polyphagous insect pest infesting mung bean at all stages of development. The larvae feed on the foliage when young and on the seed in the pods in later stages. The grown-up larvae feed voraciously on the leaves, buds, flowers and pods and may result in heavy losses in yield.

Sources of heritable resistance to pod borers in mung bean and urd bean are scanty, and screening for resistance is difficult due to variable insect population pressures across seasons and locations. Mung bean cultivars J1, LM 11, P526 and P336 from Durgapura, Rajasthan, and Co3 from Coimbatore, Tamil Nadu, and urd bean cultivars Kalai and 338-3 from Badnapur, Maharashtra, have been found to be less susceptible to pod borer (Lal 1987). Chhabra et al. (1988) screened rainy season mung bean and reported that genotypes ML 337, ML 423 and ML 428 were resistant to the pest. Sahoo and Hota (1991) screened some mung bean entries and identified JRUM 1, JRUM 11, JRUM 33, DPI 703, LAM 14-2, UPM 83-6, UPM 83-10, Pusa 115, PDM 116 and ML 353 as least susceptible to the pest. Among the ten genotypes/cultivars screened, GM-2K-5, GM-9926 and GM-2K-3 were found to resistant to *H. armigera* (Umbarkar et al. 2011). Jayasekera and Ariyaratne (1988) reported some mung bean lines at Maha Illuppallama Research Station, Sri Lanka, having moderate tolerance to damage by pod borers. These lines were 76-187 x MI-5-28, Type 51 (CES-55 x MI-3-133F)- 2F and Type 51 x 76-187-4F. Likewise, in urd bean, highly resistant lines such as UG 737, PLU 557 and TAU 1 have been identified against pod borers (Gupta and Kumar 2006). Genotypes KUG 503 and UH 08-5 have been reported with minimum pod damage (Kumar and Singh 2014).

12.2.1.7 Legume Pod Borer (*Maruca vitrata* (Fabricius))

Legume pod borer or spotted caterpillar, *Maruca vitrata* (Fabricius), earlier known as *Maruca testulalis* (Zhang) is a cosmopolitan pest that occurs in tropical and subtropical regions worldwide. It is absent from North Africa and the temperate regions of Europe and North America (Taylor 1978). The adult lays the eggs on the abaxial surface of leaf, the petals of flowers and on the flower buds. The larva webs the leaves, flowers and pods together and feeds from inside. A larva may consume 4–6 flowers before pupation. Third instar larva bores into pods and damages the developing grains (Sharma et al. 2011). Pod damage may be as high as 50% (Choragudi et al. 2015).

Mung bean accessions V 2109, V 4270, V 2106 and V 2135 were identified as source of resistance to pod borer, *M. testulalis* (AVRDC 1981). Screening of mung bean germplasm against this insect resulted in identification of JRUM 1, JRUM 11, JRUM 33, DPI 703, LAN 14-2, UPM 83-6, Pusa 116 and ML 353 as tolerant (Sahoo and Hota 1991). Chhabra et al. (1988) reported mung bean cultivars, viz., LU-3, LU-15, LU-33, LU-173, LU-190, LU-196, LU-397, LU-426 and LU-434, as resistant to pod borers such as *Lampides boeticus* Linnaeus, *M. vitrata* and *H. armigera*. Sahoo et al. (1989) studied the varietal susceptibility of mung bean and reported that PDM-54-146, ML 131 and ML 372 genotypes recorded consistently lower pod and grain damage (0–5%) by *M. testulalis*, *Catochrysops cnejus* Fabricius and *L. boeticus*. Pant U 19 had lowest pod damage caused by *C. cnejus*, *L. boeticus* and *H. armigera* at Ranchi, India (Prasad et al. 2005). Likewise, genotypes ML 65, B-101 and B-103 were found to be resistant against *Maruca* in mung bean at Port Blair, Andaman, India (Gangwar and Ahmed 1991). Swarnalatha (2007) reported that LGG 505, ML 267, LGG 502, LGG 407, LGG 460 and LGG 485 were resistant to *M. testulalis* as compared to other genotypes. Entries MGG 364, MGG 365 and MGG 363 were found tolerant with *Maruca* pod borer damage of 11.6–14.6% (Choragudi et al. 2012). Later, Choragudi et al. (2014) recorded 5 of 110 genotypes tested, viz., KM-9-128 (3.5%), KM-9-136 (5.8%), RMG-492 (8.34%), LGG-527 (9.5%) and LGG-538 (10.0%), as tolerant to *M. vitrata*, while none was found resistant. Entries MGG 358, MGG 359, MGG 360, MGG 364, MGG 366 and MGG 367 were found to be moderately susceptible, which in an earlier study by Choragudi et al. (2008) gave tolerant reaction. This emphasizes the need for multi-season and multilocation screening as spatial and temporal variation seems to play a role in response of various genotypes against the pest. In black gram, nine entries, viz., CBG 08-009, CBG 08-014, CBG 08-045, CBG 08-057, PLU 102, 5-16-7, PLS 364/42, KU 301 and CBG 08-040, were found to be moderately resistant to pod borers, viz., *M. vitrata*, *H. armigera*, *L. boeticus* and *Riptortus linearis* (Fabricius), in both rainy and winter seasons (Soundararajan and Chitra 2014). Among 25 different genotypes of urd bean, KUG-503 recorded the minimum pod borer damage (Justin et al. 2015).

12.2.1.8 Bean Butterfly (*Lampides boeticus* (Linnaeus))

Bean butterfly or pea blue butterfly, *Lampides boeticus* (Linnaeus), lays bluish green, sculptured eggs on young buds. Larvae are green, oval and flat in shape, and they feed on leaves, buds, flowers and bore into the pods.They pupate in soil or plant debris (Sharma et al. 2011).

Chhabra and Kooner (1980a) screened mung bean material against pea blue butterfly and identified genotypes ML 1, ML 3, ML 5 and ML 170 as resistant. Upadhyay et al. (1998) screened urd bean material and identified DU 4, T9, CO 5, KBG 512, AC 220, KB 63, P 58, 7282-1, AC 229, PLU 572, 338/3, Karaillal, Killilkum and Judadir as resistant to the butterfly. Likewise, Sahoo and Hota (1991) screened some genotypes and found JRUM 1, JRUM 11, JRUM 33, DPI 703, LAM 14-2, UPM 83-10, Pusa 115, PDM 116 and ML 353 as least susceptible to the pest.

12.2.1.9 Bruchids, *Callosobruchus* spp.

Bruchids are the most devastating and widespread insect pests of stored pulses that can infest the seeds in the field as well. The bruchids infesting mung bean and other *Vigna* species are oriental cowpea bruchid, *Callosobruchus chinensis* (Linnaeus); four-spotted bean weevil, *Callosobruchus maculatus* (Fabricius); pulse weevil, *Callosobruchus analis* (Fabricius); lentil bruchid, *Callosobruchus phaseoli* (Gyllenhal); and Mexican bean weevil, *Zabrotes subfasciatus* (Boheman). In case of severe infestation, there is a heavy loss of germination (47.53–79.60%) and altered flavour and nutritive value of grains that reduces the marketability and acceptability of pulses (Singh and Sharma 1982; Divya et al. 2013). Breeding resistance to bruchids in mung bean and urd bean is valuable for providing a sustainable method to minimize storage losses. Earlier, no mung bean accessions were found to be resistant to this pest at Asian Vegetable Research and Development Centre (AVRDC) (Talekar and Lin 1981), but later screening of around 500 accessions provided accessions, V1128, V2709, V2802, VM 2011 and VM 2164, with moderate to high level of *C. chinensis* resistance (AVRDC 1990; Talekar 1988; Talekar and Lin 1992). Later, two of these accessions (V 2802, V 2709) were confirmed to possess complete resistance to *C. chinensis* and *C. maculatus* (Somta et al. 2007).

Urd bean is known to be immune to *C. chinensis*, but it is susceptible to *C. maculatus* though it prolongs the latter insect's developmental period (Srinives et al. 2007). Rasul et al. (1989) reported that Mash 59 and Mung 6601 were less damaged by *C. analis* than other varieties. Four mung bean accessions (LM 131, V 1123, LM 371 and STY 2633) and three urd bean accessions (UH 82-5, IC 8219 and SPS 143) were found moderately resistant to *C. chinensis* with less percentage survival and prolonged developmental period (30.5–31.5 days) as compared to susceptible check (Duraimurugan et al. 2014). Similarly, accessions KM-12-5 and P-S-16 were found relatively resistant against *C. analis* (Soumia et al. 2015).

12.2.1.10 Other Minor Insect Pests

Galerucid beetle, *Madurasia obscurella* Jacoby, is a foliage and root feeder of mung bean (Menon and Saxena 1970; Gupta and Singh 1984) and urd bean (Dhuri and Singh 1983). Its larvae damage 25% and 60% of the root nodules of mung bean and urd bean, respectively (Srivastava and Singh 1976). Lal (1987) reported several mung bean and urd bean cultivars from Badnapur, Maharashtra, and Kanpur, Uttar Pradesh, as less susceptible to galerucid beetle.

Pink pod borer, *Cydia ptychora* (Meyrick), is a defoliator and pod and seed feeder of mung bean in India (Lal et al. 1980; Sepswasdi et al. 1990). Among the ten urd bean varieties screened, Dawoodi et al. (2010) found SKNU-03-03 as least susceptible to *C. ptychora* with minimum larval population and lowest damage to pods and grains.

Table 12.1 Potential sources of insect resistance in *Vigna* species

Character	Species	References
Resistance to bruchids	*V. riukiuensis*	Tomooka et al. (1992)
	V. reflexo-pilosa	Tomooka et al. (1992)
	V. radiata var. *sublobata*	Fujii and Miyazaki (1987)
		Kaga and Ishimoto (1998)
		Miyagi et al. (2004)
	V. umbellata	Tomooka et al. (2000)
		Kashiwaba et al. (2003)
		Somta et al. (2006)
	V. tenuicaulis	Tomooka et al. (2000)
	V. nepalensis	Somta et al. (2008)
Resistance to cowpea storage weevil	*V. vexillata*	Ng (1990) and Birch (1986)
	V. reticulata	Ng (1990)
	V. oblongifolia	Ng (1990)
	V. luteola	Ng (1990)
Insect resistance in the form of pubescens	*V. unguiculata* ssp. *dekindtiana* var. *pubescens*	Ehlers and Hall (1997)
Pronounced antibiosis to cowpea moth *Cydia ptychora*	*V. unguiculata* ssp. *mensensis*	Ezueh (1981)
Bean fly (*O. phaseoli*, *O. centrosematis, M. sojae*) resistance	*V. reflexo-pilosa*	Egawa et al. (1996)
Resistance to pod bug	*V. unguiculata* ssp. *dekindtiana* TVNu 151	Koona et al. (2002)

12.2.2 Wild Species as Source of Resistance

Wild relatives of *Vigna* can offer sources for imparting resistance to several biotic and abiotic stresses (Table 12.1) besides improving yield and quality traits (Pratap et al. 2012).

Resistance to bean flies (*Ophiomyia phaseoli*, *O. centrosematis* and *M. sojae*) (Ng 1990), pod-sucking bug *Clavigralla tomentosicollis* Stal and pod borer *M. vitrata* (IITA 1988) has been found in *V. vexillata*. High levels of resistance to *O. phaseoli* and two other agromyzids, *O. centrosematis* and *Melanagromyza sojae*, was found in *V. glabrescens* Maréchal et al. accession V 1160 (Talekar and Hu 1993). Likewise, Egawa et al. (1996) have reported bean fly resistance in *V. reflexo-pilosa* Hayata.

TC 1966, an accession of wild relative of mung bean, *V. radiata* var. *sublobata* (Roxburgh) Verdcourt, is well known to possess complete resistance to five species of bruchids, *C. analis*, *C. chinensis*, *C. maculatus*, *C. phaseoli* and *Z. subfasciatus* (Fujii and Miyazaki 1987; Fujii et al. 1989; Kaga and Ishimoto 1998; Lambrides and Imries 2000; Miyagi et al. 2004). However, the resistance to bruchids is linked with undesirable seed properties (Fernandez and Talekar 1990; Mei et al. 2009) and is in the repulsion phase with resistance gene for mung bean yellow mosaic virus derived from NM 92 (Chen et al. 2013). Lambrides and Godwin (2007) reported TC 1966 as susceptible to Australian strains of *C. maculatus*. Tomooka et al. (2000) reported that cultivated ricebean *Vigna umbellata* (Thun.) Ohwi and Ohashi accession was found to be more useful as bruchid resistance source than *V. radiata* var. *sublobata* (Tomooka et al. 1992) as indicated by chemicals in ricebean cotyledons. Gill (2013) reported ricebean genotype LRB 535 having minimum *C. maculatus* adult emergence and growth index (2.22% and 0.07, respectively) as compared to recommended mung bean variety PAU 911 (ML 1265) of Punjab, India, where it was maximum (94.44% and 4.28, respectively). Wild urd bean, *Vigna mungo* var. *silvestris* Lukoki et al., has also been reported to have widespread resistance to bruchids (Fernandez and Shanmugasundaram 1988; Kasiwaba et al. 2003). Fujii et al. (1989) identified accessions PLU 416 and TC 1966 of *Vigna mungo* var. *silvestris* and *V. radiata* var. *sublobata*, respectively, as bruchid resistant. Other potential sources of resistance to bruchids include *V. glabrescens* (Fernandez and Shanmugasundaram 1988; Talekar 1988), *V. riukiuensis* (Ohwi) Ohwi & H. Ohashi and *V. reflexo-pilosa* (Tomooka et al. 1992), *V. tenuicaulis* N. Tomooka & Maxted (Tomooka et al. 2000), *V. vexillata* (L.) A. Rich (Birch et al. 1986) and *V. nepalensis* Tateishi & Maxted (Somta et al. 2008).

12.3 Mechanisms of Resistance

12.3.1 Agromyzid Flies

The agromyzid fly or bean fly resistance mechanism was investigated in mung bean accession V 4281, and it appeared to be antibiosis (Talekar 1987). Lin and Rose (1976) screened 3000 mung bean accessions in China and studied the mechanism of resistance and found a positive correlation between the thickness of mung bean leaf and bean fly infestation rate. This implied that bean flies preferred to feed or lay eggs in thick-leaved varieties. Accession V 1160 had significantly smaller and less pubescent first trifoliate leaves, significantly smaller and thinner petioles and glabrous stems with shorter and thinner internodes. It exhibited antixenosis as bean fly adults made lesser feeding/oviposition punctures in leaves of this resistant line as compared to the susceptible mung bean breeding line, VC 1973A (Talekar and Hu 1993). Thus, both antixenosis and antibiosis were involved in imparting resistance against bean fly.

12.3.2 Sweetpotato Whitefly and Green Jassid

Several biophysical and biochemical parameters responsible for resistance against sucking pests, mainly whitefly and jassid, have been suggested by various workers. Plant morphology especially leaf surface characteristics can influence feeding, oviposition and shelter behaviour of whitefly. Taggar and Gill (2012) reported that resistant urd bean genotypes had narrow, thin and highly pubescent leaves having short but erect trichomes, while the longer trichomes in susceptible genotypes lay flat posing little hinderance to oviposition and feeding. Lakshminarayan et al. (2008) also reported that whitefly-resistant genotypes of mung bean possessed thinner leaf lamina and shorter trichomes on the lower surface of the leaf. Chand and Varma (1980) reported more leaf hairs per cm^2 in whitefly-resistant varieties of mung bean and urd bean than the susceptible ones. The resistant varieties had single, hooked, 3–4 septate leaf hairs, while susceptible ones had single, straight, non-septate leaf hairs.

Several biochemical components influence the response of a genotype towards insect attack. Chhabra et al. (1981b) while studying the mechanism of resistance in mung bean against whitefly reported that biochemicals like phenols, amino acids and non-reducing sugars were responsible for imparting resistance to the insect. High contents of total phenols, free amino acids and low content of non-reducing sugars at vegetative stage imparted resistance to *B. tabaci* in urd bean and mung bean (Chhabra et al. 1984, 1993; Kooner et al. 1994; Patel and Srivastava 1990). Enhanced activities of the enzyme peroxidase and catalase in resistant urd bean genotypes NDU 5-7 and KU 99-20 suggested bioprotection of plants against *B. tabaci* infestation (Taggar et al. 2012). Moreover, higher levels of o-dihydroxy phenols and total phenols were continuously produced and maintained in resistant genotypes (NDU 5-7, KU 99-20) to provide protection from invading whiteflies. The tannin and flavonol contents increased to 11.1 and 7.1%, respectively, in resistant plants after whitefly infestation (Taggar et al. 2014). Thus, genotypes possessing higher total phenols may be selected for the use in whitefly resistance breeding programmes.

12.3.3 Cowpea Aphid

Raju and Panda (1983) reported that the adult aphid larviposited more on the susceptible mung bean variety ‘Shining’ and least on the tolerant varieties ‘Kopergaon’ and ‘Green 4’. The adult aphid attained significantly higher fecundity, higher body weight, short nymphal period and longer duration on the susceptible variety.

12.3.4 Bean Thrips

Low content of free amino acids, total phenols, total minerals, total sugars, non-reducing sugars, calcium and potassium and high content of total carbohydrates

were thought to be responsible for the resistance in mung bean lines SML 99 and SML 100 (Chhabra et al. 1994).

12.3.5 Legume Pod Borer

Jayadeep and Srinivasan (2007) observed a significant and positive correlation between total sugar, reducing sugar, non-reducing sugar, amino acids and proteins with pod damage, whereas negative correlation prevailed between phenolic content in pods with pod damage in urd bean by legume pod borer *M. vitrata*.

12.3.6 Bruchids

Bruchid resistance in mung bean could be a result of antibiotic factors and hairy pods (Talekar 1996). In case of urd bean, delayed development period and low adult emergence were attributed to seed weight, seed coat width and phenol content in the seeds (Patel et al. 2003). Duraimurugan et al. (2014) observed that in mung bean, lesser number of eggs were recorded from small and shiny seeds as compared to large and dull seeds, while in urd bean, small and black seeds recorded lower number of eggs as compared to large and green seeds. Resistance in *Vigna mungo* var. *silvestris* against bruchids is reported to be of antibiosis nature as supported by observations on reduced survival, smaller-sized adults and longer developmental period (Dongre et al. 1996; Souframanien and Gopalakrishna 2007). Soundararajan et al. (2013) observed that resistance in this *Vigna* species had possible components of both antixenosis and antibiosis recorded in terms of less oviposition by *C. maculatus* on accessions VBN-VS 6, 7, 9, 18, 21 and 24 and reduced seed damage, prolonged development and low adult emergence on accessions VBN-VS 9, VBN-VS 21 and VBNVS 24.

Multiple seed factors are responsible for resistance against bruchids, i.e., the presence of α-amylase inhibitors, trypsin inhibitors and polyphenol and tannin content (Ishimoto and Kitamura 1989). The resistant genotype VM 2164 had significantly higher trypsin inhibitor activities than susceptible genotypes. The globulin of VM 2164 adversely affected the bruchid egg deposition (Landerito et al. 1993). The two chemical factors, vignatic acid (Sugawara et al. 1996; Kaga and Ishimoto 1998) and VrCRP (cysteine-rich protein of the plant defensin family) (Chen et al. 2002), were also isolated from *V. sublobata* accession TC 1966 and its progenies. However, one individual identified in the BC_2F_2 population retained vignatic acids despite its bruchid susceptibility (Kaga and Ishimoto 1998). Thus, vignatic acids were not confirmed as the principal antibiotic factors directly responsible for bruchid resistance in mung bean crossed with TC 1966, but these could possibly facilitate the use of map-based cloning strategies to isolate the Br gene. A peptide compound 'GIF-5' toxic to the bruchids was also identified from a similar material that was used for isolating vignatic acids (Kaga et al. 2000).

12.4 Genetics of Resistance

Genetics of resistance need to be studied in order to formulate detailed breeding plans to increase efficiency of developing insect resistant genotypes that are also high yielding. Distabanjong and Srinives (1985) reported that the resistance to bean fly *O. phaseoli* in mung bean was due to additive gene.

The bruchid resistance was found to be controlled by a single gene as reported by several workers (Kitamura et al. 1988; Tomooka et al. 1992; Young et al. 1992; Cheng et al. 1996; Srinives 1996; Miyagi et al. 2004; Lawn and Rebetzke 2006). Sun et al. (2008) crossed a resistant variety from India, V 2709, with a susceptible variety, Zhonglü 1, from the World Vegetable Centre, AVRDC. Segregation of the F_2, BC_1F_1 and F_3 populations showed that bruchid resistance of V 2709 was controlled by a single dominant locus named *Br2*. Recently, the inheritance of seed resistance to two insects, *C. chinensis* and bean bug *Riptortus clavatus* Thunberg, was examined in a mung bean cultivar, Jangan mung bean, developed by backcrossing with the resistant donor V 2709 (Hong et al. 2015). The resistance to bruchid and bean bug was found to be controlled by a single dominant gene in the F_1 and F_2 seeds, and the resistances were either different or closely linked with each other. Sarkar et al. (2011) reported that bruchid resistance in Indian sublobata is controlled by a major dominant gene but might have varying degrees of expressivity. Somta et al. (2007) also suggested modifying genes contributed to the resistance of V 2709 to bruchid. Such modifiers were also reported to be involved in bruchid resistance in wild mung bean by Kitamura et al. (1988). Liu et al. (2016) reported intrinsic differences caused by differentially expressed genes (DEGs) and sequence-changed-protein genes (SCPs) of mung bean and transposable elements (TEs) as the likely modifier factors determining bruchid resistance. Recently, Chotechung et al. (2016) indicated that gene encoding a polygalacturonase inhibitor (polygalacturonase-inhibiting protein PGIP) designated as *VrPGIP2* is very likely the gene at the *Br* locus responsible for bruchid resistance in mung bean.

In case of urd bean, the resistance to *C. chinensis* infestation appeared to be conditioned by a homozygous recessive gene (Fernandez and Talekar 1990), whereas the resistance to *C. maculatus* was indicated to be controlled by two dominant duplicate genes *Cmr1* and *Cmr2* (Dongre et al. 1996). Similarly, inheritance of bruchids was studied in F_2 generation, and the results confirmed in the F_3 generation of a TU 94-2 x *V. mungo* var. *silvestris* cross (Souframanien and Gopalakrishna 2007). The segregation showed a good fit to a 15:1 ratio ($p = 0.466$) indicating the presence of two dominant duplicate genes for resistance to *C. maculatus*.

12.5 Breeding Strategies

12.5.1 Conventional Breeding Methods

Various methods of breeding including mass and bulk selection, pedigree method and backcross method or their modifications may be applied for developing

insect-resistant cultivars depending on the mode of inheritance and the number of genes controlling resistance under given conditions (Keneni et al. 2011). Introduction, pure line selection, recombination breeding/hybridization and mutation breeding have been successfully employed to develop new varieties of mung bean and urd bean for various traits (Fernandez and Shanmugasundaram 1988; Tickoo et al. 2006; Singh et al. 2011).

Although bruchid resistance gene in TC 1966 was used to develop mung bean-resistant lines (Tomooka et al. 1992; Watanasit and Pichitporn 1996), no commercial-resistant variety was released to farmers mainly due to uncertainty on safety of the resistant seeds for human consumption (Srinives et al. 2007). There was only one bruchid-resistant mung bean variety 'Jangan Nokdu' officially released to farmers in Korea, which was developed by employing V 2709 as the resistant donor (Lee et al. 2000). However, a single-resistant cultivar based on a single resistance gene is considered less durable, as the insects co-evolve with the host plants and can usually overcome the resistance sooner or later (Srinives et al. 2007). Such a study was conducted by Lin et al. (2005) who showed that seeds of VC 6089A (a mung bean, *Vigna radiata*, bred by using a wild Vigna species, *V. sublobata* (accession no. TC 1966)) had high level of resistance with more than 96% of the bruchid eggs failing to develop into adults. Mortality of surviving bruchids raised for five generations on VC 6089A also remained higher than 96%; however, female adults maintained high fecundity. Thus, the possibility of beetles developing resistance to the resistant mung bean VC 6089A could not be excluded. Hence, development of multiple-resistant cultivars is an effective way to slow down the evolution of resistance.

12.5.2 Molecular Approaches

Biotechnological approaches, such as marker-assisted breeding, tissue culture, in vitro mutagenesis and genetic engineering, can contribute to speeding up of classical breeding in overcoming major problems, such as lack of natural sources of genetic resistance to biotic and abiotic stresses and sexual incompatibility (Cook and Varshney 2010).

12.5.2.1 Target-Oriented Experimental Populations

Recombinant inbred line (RIL) populations are preferred for mapping of traits of interest owing to their genetically stable nature (Chen et al. 2007). In mung bean, interspecific/intersubspecific and intraspecific mapping populations were developed to genetically analyze beneficial traits such as resistance to bruchid (Young et al. 1992; del Rosario et al. 1997; Kaga and Ishimoto 1998; Somta et al. 2007; Sarkar et al. 2011; Isemura et al. 2012; Schafleitner et al. 2016).

12.5.2.2 Molecular Markers and Linkage Maps

In the past, there have been several efforts to develop molecular markers and linkage maps associated with agronomic traits for the genetic improvement and, ultimately,

Table 12.2 Examples of QTL mapping in mung bean and urdbean and *Vigna*-interspecific crosses for insect resistance

Crop	Population	Number of markers	Remarks	References
Mung bean	F_2 (VC 3890 x *V. radiata* var. *sublobata* TC 1966)	153 RFLP	Bruchid resistance	Young et al. (1992)
	V. radiata var. *sublobata* x mung bean	RFLP	Bruchid resistance	Reeves (1993)
	BC_2F_2 (Isogenic lines) TC 1966 x cultivated mung bean or BC_2F_2 (NM 92 x TC 1966) x TC 1966	8 RAPD	Bruchid resistance	Kaga and Ishimoto (1998)
	F_{12} RIL (*V. radiata* NM 92 x TC 1966)	10 RAPDs, 7 CAPs and 6 AFLPs	1 QTL for bruchid resistance	Chen et al. (2007)
	RIL (NM 92 x TC 1966)		1 QTL for bruchid resistance	Chen et al. (2013)
	F_2 (460 individuals) *V. radiata* x TC 1966	4 CAPs, 1 SSR, 1 STS	2 QTLs for bruchid resistance, one QTL for bean bug resistance	Hong et al. (2015)
	F_{12} RIL (TC 1966 x NM92)	6000 SNPs	1 QTL for bruchid resistance	Schafleitner et al. (2016)
	F_7 RIL (*V. radiata* V 2802 x NM 94)		1 QTL for bruchid resistance	Schafleitner et al. (2016)
Urd bean	F_8 RIL (*V. mungo* var. *mungo* (cv. TU 94–2, bruchid susceptible) x *V. mungo* var. *silvestris* (bruchid resistant)	86 RAPD, 47 SSR, 41 ISSR, 254 AFLP	8 QTLs for bruchid resistance	Souframanien et al. (2010)
Vigna-interspecific	F_2 (74 individuals) *V. umbellata* x *V. nakashimae*	175 markers (74 RFLP, 101 SSR)	5 QTLs for bruchid resistance	Somta et al. (2006)

breeding for cultivar development to increase the average yields of mung bean (Kim et al. 2015). However, only a few examples of such approaches in mung bean and urd bean for insect resistance are available (Table 12.2). In legume species, linkage mapping-based approaches have been successfully employed for mapping genes/QTL for resistance to biotic stresses, tolerance to abiotic stresses and several agronomic traits (Chamarthi et al. 2011). Transfer of insect resistance such as that for

bruchids from resistant *Vigna* genotypes into popular mung bean and urd bean lines can be accomplished efficiently through interspecific or intraspecific crosses aided by the use of molecular markers linked to bruchid resistance genes (Nair et al. 2013). Linkage maps based on restriction fragment length polymorphism (RFLP), random amplified polymorphic DNA (RAPD) and simple sequence repeat (SSR) markers are available for interspecific crosses of mung bean and resolve 11 linkage groups (Humphry et al. 2002; Zhao et al. 2010). Single nucleotide polymorphism (SNP) markers are highly abundant in the genome and may provide an appropriate marker resource for molecular breeding. The small genome size of mung bean (515 Mb/1C) makes this species highly accessible either for full genome sequencing or a reduced representation library sequencing effort, paving the path to generate many SNP markers (Moe et al. 2011).

QTL mapping in common bean is available for leaf hopper *Empoasca* spp. (Murray et al. 2004), thrips *Thrips palmi* Karny (Frei et al. 2005), bean-pod weevil *Apion godmani* Wagner (Blair et al. 2006) and bruchids (Blair et al. 2010a, b) and for resistance to onion thrips, *Thrips tabaci* (Linderman), common blossom thrips *Frankliniella schultzei* (Trybon) (Muchero et al. 2010), bean flower thrips *Megalurothrips sjostedti* (Trybon) (Omo-Ikerodah et al. 2008) and *Aphis craccivora* (Huyn et al. 2015) in cowpea. This encourages us to undertake such work in mung bean and urd bean as well which can lead to identification of QTL imparting major portion of resistance for quantitatively governed traits.

Out of the 63 RAPD markers and 113 sets of SSR/STS primers used in bulked segregant analysis, two markers, OPC-06 and STSbr2, were found to be linked with the bruchid resistant locus *Br2* (Sun et al. 2008). Further analysis suggested that the genetic distances between these two markers and *Br2* locus were 11.0 and 5.8 cM, respectively. In urd bean, Souframanien (2005) was successful in identifying PCR-based markers (Genbank Accessions DQ 094299 and DQ 094300) linked with bruchid resistance using F_8 RIL population of the cross *Vigna mungo* (cv. TU 94-2) with *V. mungo* var. *silvestris*. Souframanien et al. (2010) identified two QTLs, Cmrae1.1 and Cmrae1.2, for percentage *C. maculatus* adult emergence in urd bean, on linkage group (LG) 3 and 4, respectively, and six QTLs for developmental period, (two QTLs Cmrdp1.1 and Cmrdp1.2 on LG 1; three QTLs Cmrdp1.3, Cmrdp1.4 and Cmrdp1.5 on LG 2; and one QTL Cmrdp1.6 on LG 10). It has also been reported that the azuki bean SSR markers can be widely used for Asian *Vigna* species (Chaitieng et al. 2006; Datta and Souframanien 2006; Gupta et al. 2013).

Reports indicate involvement of a single dominant gene '*Br*' for imparting resistance against bruchids in accession TC 1966 of wild mung bean *Vigna radiata* var. *sublobata* (Kitamura et al. 1988; Fujii et al. 1989; Young et al. 1992). Furthermore, this gene has been mapped on linkage group VIII (LG8), nearly 3.6 cm away from RFLP marker pR 26 (Young et al. 1992). Kaga and Ishimoto (1998) showed that resistance-imparting gene (vignatic acid gene), '*Va*' co-segregated with bruchid resistance and mapped to a single locus at the same position as the cluster of markers, thereby suggesting a single dominant gene or a cluster of genes controlling the production of vignatic acid analogs. Menancio-Hautea et al. (1993) constructed a linkage map where bruchid resistance gene was located to a 13 cm interval flanked

by RFLP markers. Kaga and Ishimoto (1998) reported three RAPD markers, viz., BEXA08, BEXA99 and BEXC49 tightly linked to the resistance gene. They converted the RAPD markers to RFLP probes. The RFLP markers located on either side of '*Br*' gene were found to be tightly linked at 0.7 cM. The mapping data in linkage map constructed by Isemura et al. (2012) showed that the gene-encoding resistance protein VrD1 differed from the bruchid resistance gene *Br1* reported by Kitamura et al. (1998). The SSR marker designed from the bruchid resistance gene *Vigna radiata* defensin 1 (VrD1) (Chen et al. 2002) was mapped to the upper region of LG1. On the other hand, Young et al. (1992) and Kaga and Ishimoto (1998) mapped bruchid resistance gene *Br1* to LG8 of the map by Menancio-Hautea et al. (1993), which corresponds to LG2 of this mung bean map. Miyagi et al. (2004) developed two PCR-based markers sequence tagged site (STS br1 and STS br2) closely linked with a major locus conditioning bruchid, *C. chinensis* resistance. STSbr 1 generated a codominant marker, while STSbr 2 generated a dominant marker. Cheng et al. (2005) identified two codominant PCR markers closely linked with bruchid resistance alleles.

To facilitate transfer of bruchid resistance, a genetic linkage map was constructed based on an interspecific F_2 mapping population between *V. umbellata* and *V. nakashimae* (Ohwi) Ohwi & H. Ohashi consisting of 74 plants (Somta et al. 2006). A total of 175 DNA markers (74 RFLPs and 101 SSRs) were mapped on 11 linkage groups spanning a total length of 652 cM. Comparison of the genome map of azuki bean and this interspecific genome map showed that 114 (94.2%) markers were located on the same linkage groups in both maps. The marker order was also highly conserved between the two maps.

Recently, Hong et al. (2015) constructed a genetic linkage map 13.7 cm in length with six markers. Here, two QTLs were identified for bruchid resistance, and one QTL for bean bug resistance was detected. One of the QTLs for resistance to bruchid was shared with the QTL for bean bug resistance. Schafleitner et al. (2016) developed and validated SNP markers tightly linked to bruchid resistance loci of two different resistance sources. One higly significant QTL associated with bruchid resistance was mapped to chromosome 5 on genetic maps of two RIL populations (Table 12.2). Liu et al. (2016) provided whole-genome scaffold sequences for a bruchid-resistant mung bean line and obtained a list of putative *Br* genes on chromosome 5 and candidates of molecular markers for selecting resistant lines to help develop bruchid-resistant mung bean varieties.

The practical application of marker-assisted selection (MAS) in legumes for the genetic improvement of resistance or tolerance to stress has generally remained limited, being mainly hampered by lack of investment and the genetic complexity of most stress-related traits (Dita et al. 2006). Sarkar et al. (2011) validated the tightly linked marker STSbr, and Chen et al. (2013) identified QTL for bruchid resistance that may serve in generating superior genotypes with durable bruchid resistance by MAS for quick and accurate screening of germplasm in the future. More efficient regeneration protocols recently established for many legumes should encourage legume researchers resume to the use of techniques such as double haploidy (DH) breeding, wide hybridization and mutagenesis in breeding programmes.

On the other hand, crops without appropriate regeneration protocols may also be improved by mutagenesis through TILLING (Dita et al. 2006). Distant hybridization breeding can further be accelerated using molecular marker-assisted breeding procedures (Kumar et al. 2011a).

12.5.2.3 Omics Research

Recently, there has been an increasing interest in the genetic and genomic analysis of mung bean. The recent release of a reference genome of the cultivated mung bean (*V. radiata* var. *radiata* VC 1973A) and an additional de novo sequencing of a wild relative (*V. radiata* var. *sublobata*) has provided a framework for mung bean genetic and genome research, which can further be used for genome-wide association and functional studies to identify genes related to specific agronomic traits (Kim et al. 2015). Van et al. (2013) obtained a total of 305,504 SNPs in mung bean by exploiting the sequence information of two mung bean genotypes, viz., Sunhwanokdu and Gyeonggijaerae 5. The validated genome-wide SNP markers could enrich the current molecular resources and might be of value for the construction of a mung bean genetic map and the investigation of genetic diversity in mung bean. Kim et al. (2014) provided the whole-genome sequence of a bruchid susceptible mung bean (*V. radiata* var. *radiata* VC 1973A). Recently, Liu et al. (2016) have reported the whole-genome sequence of a bruchid-resistant RIL and an increased number of available gene annotations for mung bean, by 14,500 genes.

Lin et al. (2016) used omics-related technologies to study the mechanisms of bruchid resistance in seeds of the nearly isogenic lines (NILs) VC 1973A (bruchid susceptible) and VC 6089A (bruchid resistant). A total of 399 differentially expressed genes (DEGs) were identified between the two lines by transcriptome sequencing. According to transcriptome and proteome data, only three DEGs/DPs, including resistant-specific protein (*g39185*), gag/pol polyprotein (*g34458*) and aspartic proteinase (*g5551*), were identified and located on chromosomes 5, 1 and 7, respectively. Both *g39185* and *g34458* genes encoded a protein containing a BURP domain.

12.5.2.4 Alien Gene Introgression Through Distant Hybridization

For crop improvement, genes imparting resistance to various biotic stresses are not always available within the cultivated species. Sometimes they may be found among the wild relatives but are not easily introgressed. Continuous vigorous efforts are needed to evaluate the wild gene pool under field and controlled conditions since some of the wild species can prove to be important reservoir of useful genes. Introgression of alien genes from wild species can not only diversify and broaden the genetic base of cultivated material but also provide genes for biotic stress resistance. Gene transfer from wild gene pool is highly tedious due to factors like lack of homology between chromosomes of participating species in the cross, pre- and post-fertilization barriers between wild and cultivated species, etc. Sometimes, wild gene introgression is also associated with linkage drag (Pratap et al. 2014; Kumar et al. 2011b). Kumar et al. (2007) reported cross incompatibility, embryo abortion at early growth stage and inviability or sterility of F_1 hybrids/subsequent progenies

as the major pre-fertilization barriers in *V. radiata* x *V. umbellata*. Singh (1990) and Pratap et al. (2014) reviewed a wide spectrum of hybridization work in the genus *Vigna*. Although successful transfer of many desirable traits has been successfully accomplished in *Vigna* species from wild genetic resources, the actual release of new cultivars from distant crosses is scanty. In India, only three mung bean cultivars, viz., HUM 1, Pant Moong 4 and IPM 99-125 and one urd bean cultivar, Mash 1008, have been developed from mung bean × urd bean crosses (Pratap et al. 2014). There are only a few successful examples of gene introgression from wild genetic resources in *Vigna* against insect pests, and release of such a cultivar still remains unachieved. Transfer of bruchid resistance from wild *Vigna* species is difficult due to cross incompatibility. Various strategies have been devised to overcome crossability barriers in order to access wild gene pools. Successful hybridization between *V. radiata* and *V. glabrescens* resulted in four pure lines carrying moderate resistance to thrips (AVRDC 1990).

To achieve successful gene transfer from the wild relatives to cultivated *Vigna*, several supportive techniques are there which have been employed with variable success.

Embryo Rescue Techniques Hybrid plants could be obtained successfully through embryo rescue technique in the reciprocal cross *V. mungo* x *V. radiata* (Gosal and Bajaj 1983a, b; Verma and Singh 1986), *V. mungo* x *V. umbellata* (Biswas and Dana 1975; Chen et al. 1983) and *V. radiata* x *V. radiata* var. *sublobata* (Sharma and Satija 1996). Interspecific hybrids between *V. radiata* (cv. Kamphaeng Saen 2) and *V. umbellata* (cv. Miyazaki) were successfully obtained by rescuing the 12-day-old embryos on MS medium supplemented with 1 mg/L IAA, 0.2 mg/L kinetin and 500 mg/L casein hydrolysate (Chaisan et al. 2013).

Bridge Species The useful genes available in the secondary and tertiary gene pools can be introgressed into the cultivated species by involving a third species called bridge species. This is done when direct hybridization between cultivated and wild species does not result in fertile hybrids. Bruchid resistance in ricebean was successfully transferred to azuki bean by using bridge species *V. nakashimae* (Tomooka et al. 2000, 2003).

Irradiation Techniques Irradiation has been used to recover fertile plants in F_1 and subsequent generations in interspecific crosses in *Vigna*. Pandiyan et al. (2008) reported increased pod set in interspecific *V. radiata* x *V. umbellata* crosses developed from gamma ray-irradiated parental lines.

Growth Hormones The process of introgression of desirable traits from related species to cultivated ones needs increased employment of in vitro culture techniques. Gupta et al. (2002) successfully regenerated plant hybrids using in vitro culture of immature embryos using growth regulators to overcome crossability barriers in *V. radiata* x *V. umbellata*. A true-breeding *V. mungo* × *V. radiata* derivative was

reciprocally crossed with *V. angularis*, and the pollinated pistils were treated with GA3 after 24 and 78 h of pollination (Kumar et al. 2011b).

Polyploidization Ploidy level induction of plant cells by colchicine treatment is a useful technique in plant breeding helping in resolving interspecific hybrid sterility problems (Miyashita et al. 2009). Using this technique, successful crosses have been attempted between *V. radiata* × *V. mungo* (Pande et al. 1990). The hybrid sterility problem between the interspecific hybrids obtained from the cross *V. radiata* (cv. "Kamphaeng Saen 2) × *V. umbellata* (cv. Miyazaki) was resolved by colchicine treatment applied at 2 g/L (Chaisan et al. 2013). Three out of twenty hybrid seedlings were successfully induced from diploid to tetraploid which were subsequently able to produce flowers and set pods normally.

Genetic Transformation In the last three decades, significant progress has been made towards development of reproducible protocols for generation of transgenic vignas that permit the expression of alien genes in cultivated background (Pratap et al. 2014). Sonia et al. (2007) successfully generated morphologically normal and fertile transgenic plants of mung bean with two transgenes, *bar* and α-amylase inhibitor *αAI*. Cotyledonary node explants were transformed by co-cultivation with *Agrobacterium tumefaciens* strain EHA105 harbouring a binary vector pKSB that carried bialaphos resistance (*bar*) gene and *Phaseolus vulgaris* α-amylase inhibitor-1 (*αAI-1*) gene. Green transformed shoots were regenerated and rooted on medium containing phosphinothricin (PPT). Overall transformation frequency was 1.51%.

12.6 Conclusions

Productivity of food legumes is affected by number of biotic stresses, and, therefore, there is a need to lay more emphasis within breeding programmes on identification and incorporation of insect pest resistance genes in addition to improving yield and quality of these crops. Host plant resistance is compatible with other methods of insect pest management and has no adverse effect on the environment. Major thrust needs to be given to host plant resistance studies on important insect pests such as stem fly, thrips, whitefly, jassids, borers and bruchids in the integrated pest management programmes for mung bean and urd bean. Insect-resistant cultivars are usually safer for human consumption as well as beneficial to the farmers. Improved natural and artificial screening of germplasm against insect pests on a multilocation plane can provide stable-resistant donors for the use in crop improvement programmes. The mechanisms involved in and the inheritance of resistance should be known for formulating effective breeding plans to develop insect-resistant, high-yielding cultivars. Thus, insect resistance should also be given emphasis while identifying new varieties for farmers. Although several reported resistant donors have been used in crossing programme by the breeders, the levels of resistance to many insects are not high in cultivated germplasm. Since strong resistance is not much available, an option could be explored wherein moderately resistant or

tolerant or relatively less susceptible material having very strong agronomic traits and high-yielding components is released as a variety to manage insect pests with moderate chemical interventions as a means of IPM. Thus, the primary aim of breeding for insect resistance should be to achieve a satisfactory level of sustainable resistance attuned with yield and quality, thereby reducing the insecticide load.

Concerted efforts are needed to screen diverse germplasm sources for identification of desirable traits followed by the use of appropriate breeding and molecular methods and techniques for transferring those traits in mung bean and urd bean cultivars. Although successful transfer of various desirable traits has been successfully accomplished in *Vigna* species from wild genetic resources, the actual release of new cultivars from distant crosses is scanty. There are only a few successful examples of gene introgression from wild genetic resources in *Vigna* against insect pests, and release of such a cultivar remains unachieved. Identification of high crossability genes in *Vigna* can bring non-crossable species within the ambit of alien gene transfer technology. Advances in wide crossing techniques such as embryo culture and development of novel crossing strategies such as the use of mentor pollen technique and the use of growth hormones will further make wild gene pools of many crops even more accessible. At the same time, efforts are needed towards establishment of universal genetic transformation protocols and in vitro regeneration techniques.

The continuing advances in structural genomics and genetic engineering will result in new strategies for alien gene introgression. Recently, Sakai et al. (2015) presented a genome database of the genus *Vigna*, Vigna Genome Server ('VigGS', http://viggs.dna.affrc.go.jp), based on the recently sequenced azuki bean genome. VigGS will contribute to genomic research into plant biotic and abiotic stresses and to the future development of new stress tolerant Vigna crops. Finally, integrated breeding using conventional and genomic tools and alien gene detection through molecular and cytogenetic approaches will help in successfully employing the alien gene transfer technologies for the genetic amelioration of various *Vigna* species for insect resistance and other useful traits.

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Insect Biotypes and Host Plant Resistance

13

Gaurav K. Taggar and Ramesh Arora

Abstract

The green plants and herbivorous insects are engaged in a constant struggle for dominance. Humans usually intervene in this struggle by developing pest-resistant genotypes and other pest management tactics. Upon failure of a previously successful tactic to which the insect population has apparently adapted, the latter is often considered to be a novel or distinct entity and termed as a "biotype." The success of host plant resistance (HPR) strategy is constantly challenged by the occurrence of resistance-breaking insect biotypes. In general, the term "biotype" usually designates an intraspecific group of organisms that are not morphologically distinguishable, but differ by a biological function. Variation among individuals within populations has always been the focus of population genetics. However, the term "biotype" includes the entities that are not consistent either within or between biotypes, and their underlying genetic composition and origins, while generally unknown, are likely heterogeneous within and variable between biotypes. Biotypes may differ in some biological parameters, including detoxification pathways, reproductive rate, dispersal, virus vectoriality, and capacity to damage plants, and are well defined by microsatellite polymerase chain reaction (PCR)-based DNA markers. Insect biotypes feeding on different species of host plants are particularly well documented. To slow down the process of biotype selection, crop cultivars with broad genetic bases are needed.

G.K. Taggar (✉)
Department of Plant Breeding & Genetics, Punjab Agricultural University, Ludhiana 141 004, India
e-mail: gauravtaggar@pau.edu

R. Arora
Department of Entomology & Zoology, Eternal University, Baru Sahib, Himachal Pradesh 173101, India
e-mail: arorarame@gmail.com

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The durability of host plant resistance can be enhanced by identifying a wide array of potential insect-resistant genes and ensuring their incorporation in commercially important cultivars.

Keywords
Insect biotype • Coevolution • Host plant resistance • Plant defenses • Biotype management

Plants defend themselves from herbivore damage through a plethora of structural and chemical defenses. These defenses may have exerted enormous selection pressure on the insects resulting in the evolution of counter-defenses (adaptations) in herbivorous insects. The process of plant defense and insect counter-defense is fast tracked in the agroecosystem where humans purposely select insect-resistant plants for cultivation. In this process, the eighteenth and early nineteenth centuries saw the development and cultivation of several insect-tolerant cultivars. However, with the discovery of Gregor Mendel's basic tenets of heredity and plant hybridization in the late nineteenth century, this approach of breeding of insect-resistant plants received scientific impetus. Host plant resistance (HPR) has become an important component of integrated pest management (IPM), and several scientists have tried to define it in their own words. Painter (1951) defined it as "the relative amount of heritable qualities possessed by the plant which influence the ultimate degree of damage done by the insect in the field." In practical agriculture, resistance represents the ability of a certain variety to produce a larger crop of good quality than do ordinary varieties at the same level of insect population. Panda and Khush (1995) further extended it as "any degree of host reaction less than full immunity." The breeding of resistant cultivars is a continuous process as genes for insect resistance in the cultivars may gradually be overwhelmed by the development of insect biotypes possessing essential genetic attributes of overcoming the corresponding properties of insect-resistance genes in plants.

13.1 Biotype Concept

Herbivorous insects are commonly known to escape the tactics deployed for their management. As per Downie (2010), when a previously known successful weapon for pest management fails, the insect population has apparently revamped itself to it and is often considered to be a new or distinct entity, given the nonformal category "biotype." It is a fact that the phenotypic variation is omnipresent in natural populations and interpretation of the nature of phenotypic distinctness requires an elucidation of the genetic and environmental variation that causes it, which requires a thorough understanding of the hierarchic structure of alleles within loci, genes within individuals, individuals within populations, and populations within species (Downie 2010).

The biotype concept has been reviewed by several authors over the years (Thorpe 1930; Smith 1941; Eastop 1973; Claridge and den Hollander 1983;

Diehl and Bush 1984; Saxena and Barrion 1987; Downie 2010). Printz (1937) and Painter (1941) applied the term "biotype" to situations where the insect response was indifferent to crop plants developed for their resistance to insect feeding.

Biotypes have been defined as populations within an arthropod species that show variations in their ability to effectively use a trait deployed by a plant cultivar (Gallun and Khush 1980; Wilhoit 1992; Pedigo 1999). A routine method of identifying biotypes is by exposing a set of plant cultivars, each possessing a different insect-resistant gene(s) that reacts differentially to a given insect biotype (Starks and Burton 1972; Saxena and Barrion 1983; Tomar and Prasad 1992; Ratcliffe and Hatchett 1997). Nielson et al. (1970) defined biotype as the populations that can reproduce and survive on cultivars developed for resistance to a particular insect or can resist insecticides. As per Gallun (1978), a biotype is an individual or a population whose phenotype is determined by the interaction between plants having different genes for resistance and the larvae's ability or inability to survive on and stunt the plant. However, Saxena and Barrion (1987) opined that the term biotype is an intraspecific category referring to insect populations of similar genetic composition for a biological attribute. The biotype populations may be partially and temporarily sympatric, allopatric, or parapatric with other compatible populations but differ in one or more biological attributes. Granett et al. (2001) have tried to clarify the concept of biotypes, strain, and host race: "strain designates a population arising from a single collection or clonal individual; biotype is a category designating shared phenotypic traits; host race is a biotype that is better adapted to a specific host than are other biotypes."

The gene-for-gene relationship between insect virulence genes and the genes for plant resistance is very much alike to that explained by Flor (1971) for the genes contributing pathogen resistance in plants and the corresponding genes for virulence in the pathogens. The virulence or avirulence of an insect biotype to a gene contributing to plant resistance depends on the extent of interaction between the resistance genes in the host plant and virulence genes in the insect. Upon recognition of the gene products of the avirulent insect by the defense system of the resistant plant, the insect finds it difficult to infest a resistant plant. On the other hand, when a resistant plant is unable to distinguish insect gene products, the virulent insect biotype overcomes the plant resistance gene(s). Puterka and Burton (1990) suggested that insect biotypes originate from a pre-existing variability for virulence or mutations resulting from sexual recombination or from the exposure to plant resistance gene selection pressure resulting in a variation in the insect virulence gene frequency. The level of resistance exerted by the plant resistance gene, the initial virulence gene frequency, and the extent of interaction between the genotype, the insect, and the environment decide the intensity and duration of virulence gene expression.

However, Claridge and Den Hollander (1983) opined that insects capable of reproducing parthenogenetically are different in kind to those reproducing bisexually. Many insects reproducing by means of parthenogenesis fall outside the scope of the biological species concept, because such organisms multiply without any exchange of genetic material with other organisms. With the passage of time, new

mutants may evolve, resulting in new forms which may differ in some important traits, such as host or other habitat requirements. In pea aphid, *Acyrthosiphon pisum* (Harris), with the adaptation of parthenogenetic clones to different species of host plants, the new biotypes arise annually (Frazer 1972). According to Claridge and Den Hollander (1983), there is a little evidence to suggest that gene-for-gene relationship is usual or indeed common for insect-plant feeding relationships. The existence of a gene-for-gene relationship has been clearly established in case of Hessian fly, the only biparental species of insect.

Claridge and Den Hollander (1983) further argued to dispense away with the term "biotype" due to the confusion of two distinct schools of thought. The first concept applies both to individuals and to populations of a species which share certain biological characteristics, usually concerning virulence on different host varieties (synonymous with host race), with little or no knowledge of their genetic bases. The second is a very specific concept concerning the gene-for-gene relationship, in which a gene for virulence in a pest is known to correspond with a specific gene for resistance in the host plant. While considering the two schools of thoughts, the first one appears to be of little importance and may be potentially misleading as in case of the rice brown planthopper. However, the specific concept holds limited applicability since it is dependent upon the detailed genetic analyses which are available in very few cases.

Downie (2010) echoed the call given by Claridge and Den Hollander (1983) to dispense with the term and extended that the segregation of alleles and dynamics of gene frequencies (genotypic variation) should be the criteria for understanding the differences in virulence to host plant resistance and resistance should be deployed against genetically distinct populations not imagined homogenous "biotypes." The entities falling under the umbrella term "biotype" are not consistent either within or between biotypes, and their underlying genetic composition and origins, while generally unknown, are likely heterogeneous within and variable between biotypes.

The use of the term biotype suffers from some problems due to limited knowledge about the genetic makeup of different insect biotypes (Smith 2005). A major tenant of Flor's (1971) concept assumes that there exist single-gene relationships between the host plant and the pest. However, as per Wilhoit (1992), the insect biotypes may refer to populations expressing a particular set of virulence genes or to those insect populations reacting in the same fashion to a set of plant differentials with more than one gene. Mitchell-Olds and Bergelson (2000) suggested that the use of a gene-for-gene concept may be oversimplified due to the recent innovations in the field of plant genomics and that a "gene-for-genome" concept will allow simultaneous evaluation of several resistance genes involved in potentially overcoming a pest virulence gene. A thorough understanding of the genome-wide changes in the reaction of several plant resistance genes to an insect pest is required. For this to happen, the researchers must rely on existing gene models and a working definition of biotypes that include both individuals and populations that exhibit virulence to different genes in insect-resistant plant genotypes (Smith 2005).

13.2 Insect Biotypes in Important Crop Pests

The development of insect biotypes limits the prediction of their available host range, thus complicating the management strategies in different commercial crops. The biotypes may render the previously known resistant crop cultivars to succumb to insect injury, leading to economic losses. Continuous development of arthropod pest biotypes poses a continuous threat to the stability of resistant crop varieties as well as to the sustainability of the breeding programs focused on insect resistance. The development of abundant biotypes of rice insect pests hampered the progress of the breeding programs in several rice-growing countries in Asia (Saxena and Rueda 1982; Saxena and Barrion 1985).

Insect biotype development has been documented in several orders of insects (Thorpe 1930, 1940; Smith 1941). Classical cases of biotype development like in case of grape phylloxera, European corn borer, Hessian fly, corn leaf aphid, greenbug, and pea aphid (Painter 1951) laid the foundation for reorienting the breeding strategies in major crops. According to Pathak (1970), insect biotypes have been known to be developed in at least eight species of insect pests affecting agricultural crops. Saxena and Barrion (1987) documented biotypes to occur in 36 arthropod species belonging to 17 families from six orders. Aphids contribute almost half of these pest species with known biotypes.

Later, van der Arend (2003) listed biotype developments in several insect pests, majority of which overlapped with those documented by Saxena and Barrion (1987). It was Smith (2005), who updated this list of arthropod biotypes associated with plant resistance genes and gave a comprehensive overview of the existing biotypic diversity among arthropod pests in major crops like fruits, legumes, cereals (maize, rice, wheat), and several vegetables. Almost 18 different arthropod species belonging to orders Homoptera, Diptera, Acari, and one species of Coleoptera have been documented to develop virulent biotypes to plant resistance genes (Smith 2005). Parthenogenetic reproduction plays an immense role in contributing greatly toward the successful development of resistance-breaking biotypes in 10 of the 18 aphid species. Since aphids outnumber the entire documented cases of arthropod biotypes, the review by Smith and Chuang (2014) dealt in detail about the physiological, behavioral, genetic, and molecular cues regulating aphid host selection and the genetics and genomics of developed and deployed aphid-resistant cultivars. In their work, these authors documented 17 aphid species comprising more than 50% of all arthropod biotypes to demonstrate virulence. In some of these cases, the selection pressure exerted by the monogenic-based antibiosis resistance leads to the development of virulence in the aphid.

Many cases of emergence of several new resistance-breaking biotypes have been documented in several crop cultivars. Table 13.1 lists the documented cases of arthropod biotype development, till date, in various crop plants. About 50 arthropod species belonging to 20 families from seven orders have been so far documented to exist as biotypes in various agricultural crops across the globe. Majority of the arthropod biotypes have been documented to exist in the order Hemiptera (33) followed by Diptera (6), Coleoptera (4), Lepidoptera (3), Thysanoptera (2),

Table 13.1 Resistance-breaking arthropod biotypes documented in various agricultural crops

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
1	*Acyrthosiphon kondoi* Shinji	Blue alfalfa aphid	Hemiptera	Aphididae	Lucerne (*Medicago sativa*)	2	Frazer (1972) and Auclair (1978), Nielson and Lehman (1980) and Zarrabi et al. (1995)
2	*Acyrthosiphon pisum* (Harris)	Pea aphid	Hemiptera	Aphididae	Lucerne (*Medicago sativa*), dyer's whin (*Genista tinctoria*), winged broom (*G. sagittalis*), common sainfoin (*Onobrychis viciifolia*), and horseshoe vetch (*Hippocrepis comosa*)	15	Harrington (1943), Cartier et al. (1965), Auclair (1978), Frazer (1972) and Peccoud et al. (2015)
3	*Agromyza oryzae* (Munakata)	Rice leaf miner	Diptera	Agromyzidae	Rice (*Oryza sativa*)	2	Saxena and Barrion (1987)
4	*Amphorophora agathonica* Hottes	Large raspberry Aphid	Hemiptera	Aphididae	Red raspberry (*Rubus idaeus*)	6	Converse et al. (1971) and Dossett and Kempler (2012)

5	*Amphorophora idaei* (Born)	Large raspberry aphid	Hemiptera	Aphididae	Red raspberry (*Rubus idaeus*)	5	Panda and Khush (1995), Birch et al. (1996, 2002), Gordon et al. (1999), Jones et al. (2000), Jennings (1988) and Dossett and Kempler (2012)
6	*Amphorophora rubi* (Kaltenbach)	Raspberry aphid	Hemiptera	Aphididae	Red raspberry (*Rubus idaeus*)	4	Briggs (1959, 1965), Knight et al. (1960), Keep and Knight (1967), Keep et al. (1970) and Saxena and Barrion (1987)
7	*Aphis craccivora* Koch	Cowpea aphid	Hemiptera	Aphididae	Cowpea (*Vigna unguiculata*)	2	Ansari (1984), Kusi et al. (2010), Aliyu and Ishiyaku (2013), Jones (1967), Watson and Okusanya (1967), Jones (1967) and Saxena and Barrion (1987)
					Groundnut (*Arachis hypogaea*)	2	
					Bush sitao (*Vigna unguiculata sesquipedalis*)	5	
8	*Aphis fabae* Scopoli	Bean aphid	Hemiptera	Aphididae	Broad bean (*Vicia faba*)	2	Pathak (1970)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
9	*Aphis glycines* Matsumura	Soybean aphid	Hemiptera	Aphididae	Soybean (*Glycine max*)	3	Kim et al. (2008), Hill et al. (2010) and Michel et al. (2011)
10	*Aphis gossypii* Glover	Cotton or melon aphid	Hemiptera	Aphididae	Cotton (*Gossypium* spp.) and melon (*Cucumis melo*)	2	Wang et al. (2016), Vanlerberghe-Masutti and Chavigny (1998), Najar-Rodriguez et al. (2008), Xu et al. (2014) and Wang et al. (2004b)
11	*Aphis nasturtii* (Kaltenbach)	Buckthorn aphid	Hemiptera	Aphididae	Potato (*Solanum tuberosum*)	2	Saxena and Barrion (1987)
12	*Aulacorthum solani* (Kaltenbach)	Foxglove aphid	Hemiptera	Aphididae	Potato (*Solanum tuberosum*)	1	Saxena and Barrion (1987) and Miller et al. (2009)

13	*Bemisia tabaci* (Gennadius)	Sweet potato whitefly	Hemiptera	Aleyrodidae	Cotton (*Gossypium* spp.), okra (*Abelmoschus esculentus*), cassava (*Manihot esculenta*), squash (*Cucurbita maxima*), potato (*Solanum tuberosum*), sweet potato (*Ipomoea batatas*), tomato (*Solanum lycopersicum*)	34 cryptic species	Brown et al. (1995), Cervera et al. (2000), Nombela et al. (2003), Moya et al. (2001), De Barro et al. (2005), Dinsdale et al. (2010), De Barro et al. (2011) and Boykin and De Barro (2014)
14	*Brevicoryne brassicae* (Linnaeus)	Cabbage aphid	Hemiptera	Aphididae	Vegetables	2–4	Lammerink (1968) and Dunn and Kempton (1972)
15	*Callosobruchus maculatus* (Fabricius)	Cowpea weevil	Coleoptera	Chrysomelidae	Cowpea (*Vigna unguiculata*)	1	Shade et al. (1996)
16	*Chaetosiphon fragaefolii* (Cockerell)	Strawberry aphid	Hemiptera	Aphididae	Strawberry (*Fragaria ananassa*)	2	Saxena and Barrion (1987)
17	*Chlorops oryzae* Matsumura	Rice stem maggot	Diptera	Chloropidae	Rice (*Oryza sativa*)	2	Saxena and Barrion (1987)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
18	*Cydia* (*Laspeyresia*) *pomonella* (Linnaeus)	Coddling moth	Lepidoptera	Tortricidae	Apple (*Malus* spp.), plum (*Prunus domestica*), walnut (*Juglans regia*)	3	Phillips and Barnes (1975) and Saxena and Barrion (1987)
19	*Daktulosphaira vitifoliae* (Fitch)	Grape phylloxera	Hemiptera	Phylloxeridae	Grapes (*Vitus* spp.)	2	Granett et al. (1985), Williams and Shambaugh (1988), Song and Granett (1990), Omer et al. (1999) and Martinez-Peniche (1999)
20	*Dasineura* (*tetentsi*) *oxycoccana* (Johnson)	Blueberry gall midge	Diptera	Cecidomyiidae	Blackcurrant (*Ribes nigrum*)	2	Hellqvist (2001)
21	*Diuraphis noxia* (Kurdjumov)	Russian wheat aphid	Hemiptera	Aphididae	Wheat (*Triticum* spp.)	11	Kiriac et al. (1990), Shufran et al. (1997), Zsuzsa et al. (2001), Basky (2003), Haley et al. (2004), Smith et al. (2004), Merrill et al. (2014), Tolmay et al. (2007) and Jankielsohn (2011)

22	*Dysaphis plantaginea* (Passerini)	Rosy apple aphid	Hemiptera	Aphididae	Apple (*Malus* spp.)	3	Alston and Briggs (1977) and Rat-Morris et al. (1999)
23	*Eriosoma lanigerum* (Hausmann)	Wooly apple aphid	Hemiptera	Aphididae	Apple (*Malus* spp.)	3	Sen Gupta (1969), Gupta and Miles (1975) and Young et al. (1982)
24	*Frankliniella occidentalis* (Pergande)	Western flower thrips	Thysanoptera	Thripidae	Cucumber (*Cucumis sativus*)	2	De Kogel et al. (1997)
25	*Lepidosaphes ulmi* (Linnaeus)	Oystershell scale	Hemiptera	Diaspididae	Apple (*Malus* spp.)	2	Gharib (1978) and Saxena and Barrion (1987)
26	*Macrosiphum euphorbiae* (Thomas)	Potato aphid	Hemiptera	Aphididae	Tomato (*Solanum lycopersicum*)	2	Goggin et al. (2001) and Srinivasan and Alvarez (2011)
27	*Mayetiola destructor* (Say)	Hessian fly	Diptera	Cecidomyiidae	Wheat (*Triticum* spp.)	16	Gallun and Reitz (1971), Ratcliffe et al. (1994), Naber et al. (2000) and El Bouhssini et al. (2001)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
28	*Muellerianella fairmaire* (Perris)	Leafhopper	Hemiptera	Delphacidae	Common velvet grass (*Holcus lanatus*)	1	Drosopoulos (1976, 1977)
29	*Myzus persicae* (Sulzer)	Green peach aphid	Hemiptera	Aphididae	Tobacco (*Nicotiana tabacum*), cabbage (*Brassica oleracea* var. *capitata*), peach (*Prunus persica*)	3	van Emden et al. (1969) and Saxena and Barrion (1987)
30	*Nasonovia ribisnigri* (Mosley)	Currant-lettuce aphid	Hemiptera	Aphididae	Lettuce (*Lactuca sativa*)	2	van der Arend et al. (1999)
31	*Nephotettix cincticeps* (Uhler)	Green rice leafhopper	Hemiptera	Cicadellidae	Rice (*Oryza sativa*)	2	Sato and Sogawa (1981)
32	*Nephotettix virescens* (Distant)	Green leafhopper	Hemiptera	Cicadellidae	Rice (*Oryza sativa*)	3	Heinrichs and Rapusas (1985), Takita and Hashim (1985) and Panda and Khush (1995)
33	*Nilaparvata lugens* (Stal)	Brown planthopper	Hemiptera	Delphacidae	Rice (*Oryza sativa*)	4	Verma et al. (1979), Heinrichs (2001), Huang et al. (2001), Jena and Kim (2010) and Bhogadhi et al. (2015)

34	*Orseolia oryzae* (Wood-Mason)	Asian rice gall midge	Diptera	Cecidomyiidae	Rice (*Oryza sativa*)	11 (Indian-7, Chinese-4)	Heinrichs and Pathak (1981), Takita and Hashim (1985), Mohan et al. (1994), Rajyashri et al. (1998), Katiyar et al. (2000) and Vijaya Lakshmi et al. (2006)
35	*Ostrinia nubilalis* (Hubner)	European corn borer	Lepidoptera	Crambidae	Corn (*Zea mays*)	4	Kim et al. (1967), Chiang et al. (1968) and Saxena and Barrion (1987)
36	*Phaedonia inclusa* Stal	Soybean leaf beetle	Coleoptera	Chrysomelidae	Soybean (*Glycine max*)	1	Saxena and Barrion (1987)
37	*Rhagoletis cerasi* (Linnaeus)	European cherry fruit fly	Diptera	Tephritidae	Sweet cherry (*Prunus avium*), apple (*Malus* spp.)	2	Boller and Bush (1974), Prokopy et al. (1988) and Bush (1993)
38	*Rhopalosiphum maidis* (Fitch)	Corn leaf aphid	Hemiptera	Aphididae	Barley (*Hordeum vulgare*), corn (*Zea mays*), sorghum (*Sorghum bicolor*)	5	Cartier and Painter (1956), Painter and Pathak (1962), Singh and Painter (1964) and Wilde and Feese (1973)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
39	*Saissetia oleae* (Olivier)	Black scale	Hemiptera	Coccidae	Citron melon (*Citrullus lanatus* var. *citroides*)	1	Saxena and Barrion (1987)
40	*Schizaphis graminum* (Rondani)	Greenbug	Hemiptera	Aphididae	Barley (*Hordeum vulgare*), wheat (*Triticum* spp.), oats (*Avena sativa*), sorghum (*Sorghum bicolor*)	11	Curvetto and Webster (1998), Kindler and Hays (1999), Kindler et al. (2001), Porter et al. (2000), Harvey and Hackerott (1969), Kindler and Spomer (1986), Porter et al. (1982), Puterka et al. (1988), Teetes et al. (1975) and Wood (1961)
41	*Sitobion* (*Macrosiphum*) *avenae* (Fabricius)	English grain aphid	Hemiptera	Aphididae	Wheat (*Triticum* spp.)	3	Lowe (1981)
42	*Sitophilus oryzae* (Linnaeus)	Rice weevil	Coleoptera	Curculionidae	Split peas (*Pisum sativum*), adzuki bean (*Vigna angularis*)	2	Holloway (1984, 1985) and Holloway and Smith 1985

43	*Therioaphis maculata* (Buckton)	Spotted alfalfa aphid	Hemiptera	Aphididae	Lucerne (*Medicago sativa*)	6	Nielson et al. (1970), Nielson and Lehman (1980) and Panda and Khush (1995)
44	*Therioaphis trifolii forma maculata* (Buckton)	Spotted alfalfa aphid	Hemiptera	Aphididae	Alfalfa (*Medicago sativa*), clover (*Trifolium* spp.)	2	Nielson et al. (1970), Sunnucks et al. (1997b), Milne (1998a, b) and Saxena and Barrion (1987)
45	*Thrips tabaci* Lindeman	Onion thrips	Thysanoptera	Thripidae	Tobacco (*Nicotiana tabacum*), dead nettle (*Lamium purpureum*), onion (*Allium cepa*)	2	Zawirska (1976), Brunner et al. (2004), Toda and Murai (2007), Diehl and Bush (1984), Fekrat et al. (2014), Nault et al. (2006), Kobayashi and Hasegawa (2012), Jacobson et al. (2013), Westmore et al. (2013) and Saxena and Barrion (1987)

(continued)

Table 13.1 (continued)

No.	Arthropod species	Common name	Order	Family	Crop	Number of biotypes documented	Reference(s)
46	*Trialeurodes vaporariorum* (Westwood)	Greenhouse whitefly	Hemiptera	Aleyrodidae	Vegetables	2	Lei et al. (1998)
47	*Tribolium castaneum* (Herbst)	Red flour beetle	Coleoptera	Tenebrionidae	Sorghum grain (*Sorghum bicolor*)	2	Coulibaly (1993)
48	*Yponomeuta padella* (Linnaeus)	Small ermine moth	Lepidoptera	Yponomeutidae	Hawthorn (*Crataegus monogyna*)	1	Raijmann (1992) and Saxena and Barrion (1987)
49	*Aceria tosichella* Keifer	Wheat curl mite	Acari: Prostigmata	Prostigmata	Goat grass (*Aegilops tauschii*)	6	Malik et al. (2003) and Harvey et al. (1995, 1997, 1999, 2001)
50	*Tetranychus urticae* Koch	Red spider mite	Acari: Trombidiformes	Tetranychidae	Tomato (*Solanum lycopersicum*)	1	Foster and Barker (1978)

Trombidiformes (1), and Prostigmata (1). Aphids continue to outnumber all other arthropod species as far as biotype development is concerned with as many as 24 species recorded on different host plants. Due to the enormous variations in aphid host plant specificity and reproductive biology, the avoidance of aphid virulence throws challenges to crop protection (Smith and Chuang 2014). However, enough evidence exists whereby the development of insect biotypes can be delayed or avoided through combined plant breeding and pest management efforts.

13.3 Factors Responsible for Biotype Evolution

The possible causes for biotype evolution have been reviewed by several workers (Ruggle and Gutierrez 1995; Porter et al. 1997; Birkle and Douglas 1999; Smith 2005; Michel et al. 2011). As per Xiang Dong et al. (2004), the insect biotypes have their genetic bases, including the mutation or change in the sequence of enzymes and chromosomes, assortive mating and genetic differentiation of population, and, of course, sexual reproduction. Puterka and Burton (1990) suggested several factors such as selection pressure exerted by the resistance genes, mutations, or preexisting differences in virulence; sexual recombinations may lead to the development of insect biotypes. However, the initial virulence gene frequency, the category of resistance exhibited by the plant resistance gene, and the interaction between the genotype, the pest, and the environment ultimately decide the intensity and duration of virulence gene expression.

There exists a direct correlation between the use of insect-resistant cultivars and the subsequent evolution of new insect biotypes. Biotype development in several insects is related to variations in the composition of the resistance genes in the deployed resistant cultivars. The question of how greenbug, *Schizaphis graminum* (Rondani), biotypes develop has been answered at the population, organism, and gene levels (Smith 2005). However, as per Porter et al. (1997), there exists no correlation between the occurrences of new greenbug biotypes with the deployment of greenbug-resistant wheat cultivars. Since the resistance in *Gb3*, *Gb4*, *Gb5*, and *Gb6* has never existed in a wheat cultivar in the field, therefore, the gene-for-gene relationship had no effect on the development of biotypes of *S. graminum*. In case of sorghum, the relationship between the use of resistant hybrids and the evolution of new biotypes has been established in only three of the 11 biotypes of greenbug. However, no clear relationship evidence has been established even within these three biotypes (Sharma 2009).

Biotype selection is also dependent upon the geographic extent to which resistant cultivars are planted throughout the insects' host range (Smith 2005). Besides, the selection of insect biotypes on previously resistant cultivars may also be attributed to improper insecticide application, lack of crop rotation, or improper management practices such as elimination of alternate (weed) hosts. Large-scale monoculture of same rice cultivars in several countries, as well as indiscriminate applications of insecticides for hopper control, leads to the evolution of hopper biotypes in Southeast Asia (Smith 2005). Planting of early *Mayetiola destructor* (Say)-resistant wheat

cultivars over a wide geographical range may also contribute to the evolution of virulence (Smith 2005). Several non-crop cultivar factors have also been documented to play a likely role in the development of biotypes (Porter et al. 1997). Examples include non-crop host adaptation by *S. graminum* (Powers et al. 1989), large variations in *S. graminum* clonal diversity (Shufran et al. 1992; Shufran and Wilde 1994), and autumn sexual reproduction of the greenbug on cool season grasses, especially blue grass (Puterka et al. 1992). The greenbug summer populations on wheat die before sexual forms are produced, thereby eliminating the chances that individuals produced on summer crop plants result in biotypes (Smith 2005). This idea is well supported by the identification of a biotype on Western wheat grass (Anstead et al. 2003) with a unique virulence profile, thereby establishing the fact that noncultivated grasses are closely involved in the development of what have become recognized as *S. graminum* biotypes.

Michel et al. (2011) presented a comprehensive overview of the genetic basis for biotype development in homopterans, particularly aphids. In ecological levels, the natural enemies, the symbionts, the selection capacity to the host plants, and the resistance to insecticides are the possible reasons for the evolution of aphid host biotypes. Biotypes have been known to be intrinsically associated with host plant resistance, particularly many species within the family Aphididae (Smith 2005). Relationships between symbiotic bacteria and insects are well documented. Such intricate relationships are known to have a considerable effect on the host biology, can be obligatory or facultative for the host, and are known to be involved in host plant utilization, reproductive manipulation, nutrition, and ability to withstand environmental variations (Bourtzis and Miller 2006).

Many bacterial endosymbionts such as *Buchnera*, *Hamiltonella*, *Rickettsia*, *Arsenophonus*, *Regiella*, *Serratia*, etc. act as a source of essential amino acids to their carriers, the aphids, and may, therefore, be involved in aphid defense as well as biotype development (Ruggle and Gutierrez 1995; Birkle and Douglas 1999; Moran and Wernegreen 2000; Wille and Hartman 2009; Oliver et al. 2010). These endosymbionts have been documented to be involved with different insect biotypes, presumably because of the diversity in the nutrients and amino acids afforded by different host plants (Simon et al. 2003a; Chiel et al. 2007). For instance, it has been indicated that virulence to lucerne (alfalfa) varieties is symbiont based (Ruggle and Gutierrez 1995). There are several cases depicting the close associations between insects and their endosymbionts. These symbionts have been found to play a very crucial role in development, reproduction nutrition, speciation, and defense against natural enemies of their host insects (Baumann 2005; Douglas 1998; Gregory et al. 2000; Oliver et al. 2003; Stouthamer et al. 1999). There exists a large diversity of the bacterial microbes harbored by the brown planthopper, and the results of Tang et al. (2010) provide enough evidence of symbiotic relationships between specific bacterial microbes and biotypes of *N. lugens*. There are also evidences that some biotypes of *N. lugens* differ in DNA polymorphisms, isozymes, and small morphological features (Claridge et al. 1984; Latif et al. 2009; Shufran and Whalon 1995). However, the exact mechanism of conferring virulence in *N. lugens* biotypes is still not clear.

Studies conducted by Chiel et al. (2007) have revealed an interesting fact related to *Bemisia tabaci* B biotype and the bacteria it carries in Israel: all B biotype *B. tabaci* hosts *Hamiltonella*, but they have not been found to carry either *Wolbachia* or *Arsenophonus*. On the contrary, *Arsenophonus* and *Wolbachia* have frequent association with the Q biotype, with the latter having no association with *Hamiltonella* in Israel. Interestingly, *B. tabaci* Q biotype populations from other regions of the world showed infection with *Hamiltonella* and *Cardinium*, while only the A biotype showed infection with *Fritschea* in the United States (Baumann 2005). *Rickettsia* is the only symbiont that is commonly detected in both biotypes of *B. tabaci* and is also the only bacterium found in very high concentration throughout the insect body (Gottlieb et al. 2006, 2008), and being intracellular, this bacterium affects some biological aspects of the insect. Correlations between the symbiont profiles and biotypes of Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) and *S. graminum*, have recently been revealed (Pinheiro et al. 2014; Anathakrishnan et al. 2014), but their genetic underpinnings have not yet been explored.

Secondly, since most of the sap sucking insects feed exclusively on plant phloem, there is an induction of consistent responses within plants through interactions with aphid saliva (Mutti et al. 2008). Such responses highlight the role of the salivary glands in insect biotype adaptation (Michel et al. 2011). Specific factors found in aphid saliva play an immensely important role in biotype adaptation as has been implicated in earlier research. For instance, resistance breakdown in sorghum is a result of higher activity of pectin methylase in saliva of *S. graminum* biotypes (Dreyer and Campbell 1984). Furthermore, certain saliva-related proteins may be involved in *D. noxia* biotype adaptation against wheat (Lapitan et al. 2007).

Thirdly, the complex life cycle is the biggest factor which aids the aphids to develop into new biotypes (Michel et al. 2011). Most species are holocyclic (alternating between primary and secondary hosts) and heteroecious (undergoing sexual and asexual reproduction), although variations and phenotypic plasticity are common (Moran 1992; Blackman and Eastop 2000, 2007). Since the generation time is very short in aphids, any modification or adaptation that evolves during the asexual stage can quickly become common. However, very little information is available about the genetic mechanisms of biotype evolution in aphids, despite the frequency at which biotypes evolve. Only in a few studies (Dreyer and Campbell 1984; Lapitan et al. 2007) have mechanisms been explained, but the gene(s) involved remain elusive.

Based on analysis of these specific insect-plant interactions, future plant resistance programs should concentrate on the use of the most effective resistance genes irrespective of what effect these genes may have on insect population genetics. The evolution of insect biotypes with a high reproductive potential should be anticipated when developing plant resistance to insect pests. The high reproductive potential of aphids coupled with parthenogenetic mode of reproduction and clonal diversity suggests that new biotypes will continue to evolve in the future (Smith 2005). In a few cases, the development of insect virulence has also been promoted by the higher expression of genes controlling antibiosis.

13.4 Biotechnological Tools for Biotype Identification/ Analysis

Morphology has been used historically to separate species when identifying and describing insect taxa. Among the many groups of insects, however, morphological characters can vary with respect to environmental factors within a single species or be as convergent and cryptic among closely related species as to be of limited usefulness (Calvert et al. 2005). The term "biotype" usually designates an intra-specific group of organisms that are not morphologically distinguishable but differ by a biological function (Eastop 1973). Although host plant response remains the main criterion for identification of insect biotypes, but it is often laborious and time-consuming. Therefore, other methods based on morphological characters (Starks and Burton 1977), isozymes (Abid et al. 1989), and mitochondrial DNA (Shufran et al. 2000) have been utilized to assess genetic relationships among biotypes or to develop alternative identification procedures. In such cases, studies of their biology and molecular profiles become essential to defining species and characterizing populations (Calvert et al. 2005). At the molecular level, protein and DNA polymorphisms can be combined with studies of biological characteristics by using experimental or technological approaches: electrophoresis of allozymes, analysis of randomly amplified polymorphic DNAs (RAPDs), and nucleic acid sequence comparisons of nuclear or mitochondrial DNA markers (Calvert et al. 2005). However, it has not been possible to fully distinguish all insect biotypes using these methods.

For solving routine taxonomic and ecological problems regarding biotype or cryptic status of insect, various molecular tools have been utilized. Various allozymes, RFLP, RAPD, microsatellite, and mtDNA-based markers have been used for differentiating biotypes and sympatric species (Laroche et al. 1996; Hoy et al. 2000; Hufbauer et al. 2004). For exploring the genetic differences between insect biotypes, DNA-based techniques are increasingly being applied (Birkle and Douglas 1999) and are particularly valuable for the study of aphids (Hales et al. 1997). For instance, consistent differences between greenbug, *S. graminum*, biotypes that use different sorghum cultivars have been revealed using restriction analyses of mitochondrial DNA (mtDNA) (Powers et al. 1989) and between alfalfa aphid, *Therioaphis trifolii* (Buckton), biotypes using different legume crops (Sunnucks et al. 1997b). Consistent differences in microsatellite profiles have also been unraveled in the English grain aphid, *Sitobion avenae* (Fabricius), collected from wheat and cocksfoot (De Barro et al. 1995; Sunnucks et al. 1997a). Furthermore, significant variations in ribosomal spacers have been detected for the large raspberry aphid, *Amphorophora idaei* (Born), infesting various raspberry cultivars (Birch et al. 1994).

Random amplified polymorphic DNA-polymerase chain reaction (RAPD-PCR) has been successfully applied to reveal distinctive patterns among some greenbug biotypes (Black et al. 1992; Aikhionbare et al. 1998; Lopes-da-Silva et al. 2004). Using several types of midge DNA analyses, biotypes of the Asian rice gall midge, *Orseolia oryzae* (Wood-Mason), have been identified. Based on DNA

polymorphisms related to amplification by RAPD primers, Behura et al. (1999) developed a PCR-based assay to differentiate between the Indian *Orseolia* biotypes. The SCAR (sequence-characterized amplified region) primers could differentially amplify the DNA of the six Indian biotypes, as well as that of the African gall midge, *O. oryzivora* (Harris and Gagne). The AFLP (amplified fragment length polymorphism) cluster analyses have been utilized to closely evaluate the composition of the Chinese and Indian *O. oryzae* groups (Katiyar et al. 2000).

Molecular techniques and DNA-based markers have led to tagging of several plant resistance genes and mapping of virulence genes and their subsequent cloning for insect biotypes. The SCAR method has been utilized for the identification of the biotype of *O. oryzae* (Behura et al. 1999) and *Anopheles quadriannulatus* (Fettene and Temu 2003). It has been observed that the insecticide applications affect the balance of both B and Q biotypes of *B. tabaci* that have different inherent levels of resistance to insecticides (Horowitz et al. 2005). Therefore, to select a suitable strategy to manage different biotypes of *B. tabaci*, SCARs can play an integral role in the rapid identification of biotypes. So far, *B. tabaci* cryptic species have been distinguished using a variety of genetic markers (Gawel and Bartlett 1993; Wool et al. 1993; Cervera et al. 2000; De Barro 2005) with the recent focus shifting toward sequencing a portion of the mitochondrial cytochrome oxidase I (mt-COI) gene (Boykin et al. 2007; Dinsdale et al. 2010; De Barro et al. 2011). However, for species identification, the conventional molecular-based methods, such as polymerase chain reaction, require expertise in laboratory techniques and access to expensive laboratory equipment (e.g., thermocyclers), besides being time-consuming as well.

Among the molecular markers, RAPD-PCR is most commonly used to discriminate the *B. tabaci* biotypes. For successfully distinguishing *B. tabaci* B biotype and non-B biotypes, De Barro and Driver (1997) screened four random primers. For differentiating the B, Q, and newly found T biotypes distributed in Italy, Simon et al. (2003a) used methods such as RAPD-PCR, esterase electrophoresis spectra, and silverleaf symptom. The sequence analysis of DNA fragments in specific regions such as the mitochondrial cytochrome oxidase I (COI) and ribosome internal transcribed spacer 1 (ITS1) can also be used to distinguish *B. tabaci* biotypes (Frohlich et al. 1999; De Barro et al. 2000). For identifying insect species and biotypes, several studies on specific primer set applications are gradually becoming common (Behura et al. 1999; Kethidi et al. 2003; Wang et al. 2004a). Wang et al. (2004a) developed the specific primer set, Baf/Bar, for *B. tabaci* biotype B, through which it was indicated that *B. tabaci* biotype B existed in Taiwan. However, upon mitochondrial COI sequence analysis, it was revealed that in Taiwan, *B. tabaci* also included the An and Nauru biotypes, besides the biotype B (Hsieh et al. 2006). In order to rapidly amplify a target DNA sequence using four to six specially designed primers, Notomi et al. (2000) and Nagamine et al. (2002) used the loop-mediated isothermal amplification of DNA (LAMP) as one of the methods. Recently, LAMP assays have been used successfully to distinguish between Middle East-Asia Minor 1 (MEAM1) and Mediterranean (MED) regions' cryptic species of *B. tabaci* by two research groups (Adachi et al. 2010; Hsieh et al. 2012).

13.5 Management of Insect Biotypes

Host plant resistance is a cost-effective and sustainable approach to reduce insect damage and increase yield potential of plant varieties. Evolution of biotypes among insect populations is a potential threat to the durability of host plant resistance. Biotypes have long-lasting implications for pest management as the failure to identify distinct populations can have serious consequences (Bush and Hoy 1983). Large-scale cultivation of resistant cultivars exerts a constant selection pressure on insect populations, paving the way for the evolution of new biotypes (Kindler and Hays 1999; Naber et al. 2000). The successful utilization of certain insect-resistant varieties may be seriously constrained in time and space by the occurrence of new biotypes of the target pest. Hence, continuous and systematic evaluation of new germplasm must be explored to identify new genes for resistance (Sharma 2009). For conferring resistance to new insect biotypes, some of the known resistance genes could be pyramided and tested for efficacy. The pyramided major genes or quantitative trait loci (QTLs) may provide stable resistance and improve yield potential of cultivars. In such situations, one has to adopt the strategy of breeding crop cultivars for polygenic resistance or constantly search for new resistance genes followed by their introgression into high-yielding cultivars (Jena and Kim 2010). To delay or overcome the evolution of insect biotypes, cultivars with diverse mechanisms of resistance having stable expression against the prevalent insect biotypes should be utilized in a breeding program (Sharma 2009).

Still, much research is needed to determine the influence of emerging insect biotypes on resistant crop cultivars and to determine the relative frequencies and distributions of biotypes. Several methods have been suggested to maximize the use of host plant resistance to brown planthopper (and in general homopteran pests) in pest management. Sequential release of varieties with diverse resistance traits, the use of multilines with vertical resistance, and polygenic resistance with moderate resistance (horizontal resistance) received wide acceptability (Khush 1979;Panda and Khush 1995). However, these methods failed in practical applications, mainly due to the difficulties in developing a spectrum of activities that could satisfy the above criteria. In order to prevent the evolution of new biotypes in the field, gene pyramiding of known resistance genes in commercial rice varieties seemed to be insufficient unless the resistance-breaking mechanism of BPH to each resistance gene was considered (Horgan 2009; Chen 2009). Many doubts have arisen about the possibilities of developing high-yielding crop cultivars with the higher level of resistance to insect pests. This assumption is based on the fact that the energy and other resources that the plants divert for resistance would not be available for the growth and reproduction of the plant. For instance, van Emden (1991) concluded that partial host plant resistance was more important than the high level of resistance to insects.

Michel et al. (2011) suggested that the durability of host plant resistance can be preserved along with the management of evolution of insect virulence by introducing diverse soybean aphid-resistant genes and varieties. In addition, the possibility of gene pyramiding and geographically varying *Rag* (resistant to *Aphis glycines*

Matsumura) gene deployment may extend the life of host plant resistance (Porter et al. 2000; Smith 2005). The integration of all the tactics will be necessary to extend the durability of host plant resistance in soybean and slow the evolution of soybean aphid biotypes.

For biotype management, a thorough knowledge of the insect systematics and biology is a prerequisite. Such kind of information is absolutely required for both the establishment of management measures in the most severely affected areas and the prediction of risks associated with the insect pests. In order to characterize biotypes to map their occurrence, a comprehensive approach utilizing molecular tools and detailed morphological studies is absolutely necessary (Navia et al. 2013). This can be possible through the concerted efforts of researchers across regions, countries, and continents. A prior knowledge of the identity of the biotype in each geographical region would be very useful in integrated pest management practices. The use of biotype-specific SCAR primers in a single PCR with an unknown genomic DNA sample of a given biotype would enable entomologists and plant breeders to identify the biotype prevalent in that region in the shortest possible time and to avoid deploying any crop variety known to be susceptible to that biotype (Behura et al. 1999). Area-wide rigorous monitoring and surveillance programs should be initiated to detect and map the occurrence of insect biotypes. Improving pest prediction capabilities, cataloging the range of important host plant species, and establishing varietal impact under insect pressure are of utmost importance. In the newly affected areas, continuous screening of resistance of a commercial crop cultivar to this biotype should be taken on a priority basis.

Keeping into consideration the risks of biotype evolution, a single strategy of deployment of insect-resistant genotypes alone may be a risky proposition. For broadening the genetic base of resistance and enhancing its durability against different insect biotypes, the traditional breeding efforts need to be blended with alternative breeding strategies. For successful gene pyramiding, there is a need to explore new sources of resistance constantly, which can further be characterized and mapped using genetic markers (Dossett and Kempler 2012). Durable resistance will only come from combining multiple resistance sources, until strong sources of horizontal resistance are identified. For new sources to be efficiently combined to maintain their durability and prevent future breakdown of resistance, mapping studies will be necessary to identify markers and linkages for insect-resistant genes (Dossett and Kempler 2012). A comprehensive knowledge about the biology of resistance mechanisms will be imperative for judging how durable novel sources of resistance may be and how effective they will be at the objective of delaying the evolution of new insect biotypes. The risk of emergence of new biotypes could be reduced to a much greater extent by adopting well-planned monitoring strategy coupled with integrated biotype management practices that provide multiple selective pressures (Raffa 1989).

To avoid the selection of arthropod biotypes, an amalgamation of plant breeding and pest management practices is vital (Smith 2005). It has been observed that cultivars possessing tolerance mechanism against insects exert minimum selection pressure on pest populations to evolve virulence (Heinrichs 1986). On the contrary,

those cultivars exhibiting antibiosis, where high levels of chemical and physical factors have resulted in selection for virulent individuals, are comparatively unstable than tolerant cultivars. Therefore, the utilization of a cultivar possessing moderate levels of antibiosis or with a blend of antibiosis, antixenosis, and tolerance could serve as an effective management practice (Smith 2005). This is further supported by the results of Basky (2003) which provide evidence that virulent *D. noxia* populations are unable to overcome tolerance but possibly overcome the antibiosis component of several different wheat resistance genes.

Development and adoption of improved arthropod pest management techniques can result in enhanced arthropod natural enemy fauna and delay the biotype development as has happened in the case of *N. lugens* (Smith 2005). To monitor the onset of new biotypes, surveillance and sampling programs should be initiated in different geographical locations and from diverse host plants. The method of differentiation of arthropod biotypes (host differentials or PCR-based assays) should be accurate and should give the most efficient differentiation of biotypes in an insect population. As per Smith (2005), a sound pest management approach aiming at slowing down the development of insect biotypes should focus on planting different genotypes with resistance genes to specific biotypes in different geographical areas. Smith (2005) and van Emden (2007) opined that the use of insect-resistant crop plants with horizontal resistance and moderate levels of resistance that blend well with other management strategies should be the key for all breeding programs focused on delaying the onset of insect biotypes. There is a dire need to identify new and diverse insect-resistant genes that express tolerance resistance or more moderate levels of antibiosis resistance in pest management.

13.6 Conclusions

Host plant resistance is an integral component of integrated pest management as well as varietal improvement programs. Continuous planting of crop cultivars with single major genes (R) may predispose them to certain virulent insect biotypes, thus limiting their sustainability and performance. Therefore, efforts should be oriented toward broadening the genetic base of resistance, both monogenic and polygenic. As biotype shifts may occur, rendering previously efficient genes, susceptible to the new biotypes, agricultural entomologists should undertake regular and systematic arthropod biotype surveillance programs that can help the plant breeders in evolving insect-resistant cultivars. Inability to recognize their existence in nature can have serious consequences in pest management programs (Diehl and Bush 1984). There are hundreds of insect-resistant genes deployed in improved cultivars globally, but the continual evolution of virulent biotypes dictates the need for the identification of new sources of resistance and for MAS systems to identify and track these genes. The refinement and increased use of MAS techniques and MAS centers should be encouraged to accelerate the rate and accuracy of breeding crop plants for insect resistance. From this increased understanding, there should emerge strategies to better manage these economically damaging pests in a sustainable manner.

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