Host Plant Resistance to Insect Pests in Wheat

5

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

Abstract

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

Keywords

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

---

A. Sharma (✉)
Center for Biological Control, College of Agriculture and Food Sciences, Florida A&M University, Tallahassee, FL, USA
e-mail: anamika.sharma@famu.edu

V. Mendu
Department of Plant Sciences and Plant Pathology, Montana State University, Bozeman, MT, USA

G. V. P. Reddy
USDA-ARS Southern Insect Management Research Unit, Stoneville, MS, USA

S. Kumar, M. Furlong (eds.), *Plant Resistance to Insects in Major Field Crops*,
https://doi.org/10.1007/978-981-99-7520-4_5

5.1 Introduction

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

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

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

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

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

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

5.2.1 Sources of Resistance

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

5.2.2 Screening Germplasm Collections and Identification of Resistant Varieties

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

5.2.3 Crossbreeding with Related Species and Genetic Mapping

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

5.3 Factors Influencing the Expression of Resistance in Wheat to Arthropods

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

5.3.1 Genetic Factors

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

5.3.2 Environmental Factors

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

5.3.3 Physiological Factors

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

5.3.4 Arthropod Factors

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

5.4 Techniques Used to Measure Pest Resistance

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

5.5 Inheritance of Arthropod Resistance in Wheat

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

5.6 Constitutive Versus Induced Host Resistance

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

5.7 Transgenic Approach for Arthropod Resistance

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

5.8 Arthropod Biotypes and Development of Resistant Varieties

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

5.9 Historical Review of Plant Resistance to Wheat Pests

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

5.10 Major Arthropod Pests of Wheat

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

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

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

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

5.10.2 Aphids

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

5.11 Incorporation of Resistant Wheat Varieties into IPM Programs

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

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

5.12 Conclusion

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

References

Abbas MST (2018) Genetically engineered (modified) crops (*Bacillus thuringiensis* crops) and the world controversy on their safety. Egypt J Biol Pest Control 28:52. https://doi.org/10.1186/s41938-018-0051-2

Achhami BB, Reddy GVP, Sherman JD, Peterson RKD, Weaver DK (2020) Antixenosis, antibiosis, and potential yield compensatory response in barley cultivars exposed to wheat stem sawfly (Hymenoptera: Cephidae) under field conditions. J Insect Sci 20:9. https://doi.org/10.1093/jisesa/ieaa091

Aljbory Z, Aikins MJ, Park Y, Reeck GR, Chen M (2020) Differential localization of Hessian fly candidate effectors in resistant and susceptible wheat plants. Plant Direct 4:e00246. https://doi.org/10.1002/pld3.246

Altpeter F, Diaz I, McAuslane H, Gaddour K, Carbonero P, Vasil IK (1999) Increased insect resistance in transgenic wheat stably expressing trypsin inhibitor CMe. Mol Breeding 5:53–63

Archer TL, Peairs FB, Pike KS, Johnson GD, Kroening M (1998) Economic injury levels for the Russian wheat aphid (Homoptera: Aphididae) on winter wheat in several climate zones. J Econ Entomol 91:741–747

Arif MA, Waheed MQ, Lohwasser U, Shokat S, Alqudah AM, Volmar C, Borner A (2022) Genetic insight into the insect resistance in bread wheat exploiting the untapped natural diversity. Front Genet 13. https://doi.org/10.3389/fgene.2022.828905

Armstrong JS, McNew RW (1976) Resistance in wheat to the greenbug, *Schizaphis graminum* (Rondani) (Homoptera: Aphididae): mechanism and inheritance. Crop Sci 16:828–830

Berzonsky WA, Ding H, Haley SD, Harris MO, Lamb RJ et al (2003) Breeding wheat for resistance to insects. Plant Breeding Rev 22:221–296. https://doi.org/10.1002/9780470650202.ch5

Bockus WW, Bowden RL, Hunger RM, Morrill WL, Murray TD, Smiley RW (2010) Compendium of wheat diseases and pests, 3rd edn. The American Phytopathological Society, Minnesota

Buntin GD, Flanders KL, Slaughterand RW, Delamar ZD (2004) Damage loss assessment and control of the cereal leaf beetle (Coleoptera: Chrysomelidae) in winter wheat. J Econ Entomol 97:374–382

Cai QN, Ma XM, Zhao X, Cao YZ, Yang XQ (2009) Effects of host plant resistance on insect pests and its parasitoid: a case study of wheat-aphid–parasitoid system. Biol Control 49:134–138

Cao HH, Pan MZ, Liu HR, Wang SH, Liu TX (2015) Antibiosis and tolerance but not antixenosis to the grain aphid, *Sitobion avenae* (Hemiptera: Aphididae), are essential mechanisms of resistance in a wheat cultivar. Bull Entomol Res 105:448–455

Crespo-Herrera L, Singh RP, Reynolds M, Huerta-Espino J (2019a) Genetics of greenbug resistance in synthetic hexaploid wheat derived germplasm. Front Plant Sci 10:782. https://doi.org/10.3389/fpls.2019.00782

Crespo-Herrera LA, Singh RP, Sabraoui A, El-Bouhssini M (2019b) Resistance to insect pests in wheat—rye and *Aegilops speltoides* Tausch translocation and substitution lines. Euphytica 215: 123

Dhaliwal GS, Jindal V, Dhawan AK (2010) Insect pest problems and crop losses: changing trends. Indian J Ecol 37:1–7

Domingo JL (2016) Safety assessment of GM plants: an updated review of the scientific literature. Food Chem Toxicol 95:12–18

Duan X, Hou Q, Liu G, Pang X, Niu Z, Wang X, Zhang Y, Li B, Liang R (2018) Expression of Pinellia pedatisecta lectin gene in transgenic wheat enhances resistance to wheat aphids. Molecules 23:748

El-Bouhssini M, Ogbonnaya FC, Chen M, Lhaloui S, Rihawi F, Dabbous A (2013) Sources of resistance in primary synthetic hexaploid wheat (*Triticum aestivum* L.) to insect pests: Hessian fly, Russian wheat aphid and Sunn pest in the Fertile Crescent. Genet Resour Crop Evol 60:621–627

El-Bouhssini M, Amri A, Lhaloui S (2021) Plant resistance to cereal and food legume insect pests in North Africa, West and Central Asia: challenges and achievements. Curr Opin Insect Sci 45:35–41

Elek H, Werner P, Smart L, Gordon-Weeks R, Nádasy M, Pickett J (2009) Aphid resistance in wheat varieties. Commun Agric Appl Biol Sci 74:233–241

El-Wakeil NE, Volkmar C, Sallam AA (2010) Jasmonic acid induces resistance to economically important insect pests in winter wheat. Pest Manag Sci 66:549–554

FAO (2014) Food and agricultural organization of United Nations, Food and Agriculture Organization, Statistics Division (FAOSTAT). FAOSTAT

FAO (2022) Food and agricultural organization of United Nations FAO's Statistical Yearbook for 2022. https://www.fao.org/newsroom/detail/fao-s-statistical-yearbook-for-2022-goeslive/en#:~:text=Sugarcane%20is%20the%20world's%20largest,factor%20of%203.7%20since%202000. Accessed Mar 2023

Fedak G, Armstrong KC (1980) Production of trigeneric (barley × wheat) × rye hybrids. Theor Appl Genet 56:221–224

Garcia M, Martinez M, Isabel D, Santamaria ME (2021) The price of the induced defense against pests: a meta-analysis. Front Plant Sci 11. https://doi.org/10.3389/fpls.2020.615122

Gebretsadik KG, Zhang Y, Chen J (2022) Screening and evaluation for antixenosis resistance in wheat accessions and varieties to grain aphid, *Sitobion miscanthi* (Takahashi) (Hemiptera: Aphididae). Plants 11:1094. https://doi.org/10.3390/plants11081094

Herbert DA, Van Duyn JW Jr, Bryan MD, Karren JB (2007) Cereal leaf beetle. In: Buntin GD, Pike KS, Weiss MJ, Webster JA (eds) Handbook of small grain insects. Entomological Society of America, Lanham, MD, p 120

Kamran A, Asif M, Hussain SB, Ahmad M, Hirani A (2013) Major insects of wheat: biology and mitigation strategies. Crop Prod. Accessed on 17 Feb 2023. https://doi.org/10.5772/55799

Kassa MT, Haas S, Schliephake E, Lewis C, You FM, Pozniak CJ, Krämer I et al (2016) A saturated SNP linkage map for the orange wheat blossom midge resistance gene Sm1. Theor Appl Genet 129:1507–1517

Kher SV, Dosdall LM, Cárcamo HA (2011) The cereal leaf beetle: biology, distribution and prospects for control. Prairie Soils Crop 4:32–41

Kisten L, Tolmay VL, Mathew I, Sydenham SL, Venter E (2020) Genome-wide association analysis of Russian wheat aphid (*Diuraphis noxia*) resistance in Dn4 derived wheat lines evaluated in South Africa. PLoS One 28(15):e0244455

Koch A, Wassenegger M (2021) Host-induced gene silencing—mechanisms and applications. New Phytol 231:54–59

Li C, Chen M, Chao S, Yu J, Bai G (2013) Identification of a novel gene, *H34*, in wheat using recombinant inbred lines and single nucleotide polymorphism markers. Theor Appl Genet 126: 2065–2071

Luo K, He D, Guo J, Li G, Li B, Chen X (2023) Molecular advances in breeding for durable resistance against pests and diseases in wheat: opportunities and challenges. Agronomy 13:628. https://doi.org/10.3390/agronomy13030628

McCauley D (2020) A Pith(y) solution to a growing problem. CSA News 65:6–11

Mondal S, Rutkoski JE, Velu G, Singh PK, Guzmán C, Bhavani S, Lan C, He X, Singh RP (2016) Harnessing diversity in wheat to enhance grain yield, climate resilience, disease and insect pest resistance and nutrition through conventional and modern breeding approaches. Front Plant Sci 7. https://doi.org/10.3389/fpls.2016.00991

Morrill W, Weiss M (2007) Wheat stem sawfly. In: Buntin G, Pike K, Weiss M, Webster J (eds) Handbook of small grain insects. Entomological Society of America, p 120

Moudrý J, Konvalina P, Stehno Z, Capouchová I, Moudrý J Jr (2011) Ancient wheat species can extend biodiversity of cultivated crops. Sci Res Essays 6:4273–4280

Nasrollahi S, Badakhshan H, Sadeghi A (2019) Analyzing Sunn pest resistance in bread wheat genotypes using phenotypic characteristics and molecular markers. Physiol Mol Biol Plants 25: 765–778

Nilsen KT, N'Diaye A, MacLachlan PR, Clarke JM, Ruan Y, Cuthbert RD, Knox RE, Wiebe K, Cory AT, Walkowiak S et al (2017) High density mapping and haplotype analysis of the major stem-solidness locus SSt1 in durum and common wheat. PLoS One 12:e0175285

Onstad DW, Knolhoff L (2014) Arthropod resistance to crops. In: Onstad DW (ed) Insect resistance management. Academic Press, Oxford, pp 293–326

Peirce ES, Cockrell DM, Mason E, Haley S, Peairs F, Nachappa P (2022) Solid stems and beyond: challenges and future directions of resistance to wheat stem sawfly (Hymenoptera: Cephidae). J Integr Pest Manag 13:29. https://doi.org/10.1093/jipm/pmac023

Porter DR, Webster JA (1976) Resistance in wheat to the Hessian fly. Crop Sci 16:227–230

Porter DR, Webster JA (1982) Mechanisms of Hessian fly resistance in wheat. Entomol Exp Appl 31:335–343

Porter DR, Webster JA (2000) Russian wheat aphid-induced protein alterations in spring wheat. Euphytica 111:199–203

Qi T, Guo J, Peng H, Liu P, Kang Z, Guo J (2019) Host-induced gene silencing: a powerful strategy to control diseases of wheat and barley. Int J Mol Sci 20:1

Royer TA, Pendleton BB, Elliott NC, Giles KL (2015) Greenbug (Hemiptera: Aphididae) biology, ecology, and management in wheat and sorghum. J Integr Pest Manag 6:19. https://doi.org/10.1093/jipm/pmv018

Sardesai N, Nemacheck JA, Subramanyan S, Williams CE (2005) Identification and mapping of *H32*, a new wheat gene conferring resistance to Hessian fly. Theor Appl Genet 111:1167–1173

Sarthi G, Singh AK, Sharma V (2022) Genetic basis of arthropod resistance in cereals. In: Plant defense against insect pests. Springer, Cham, pp 173–207

Shanower TG, Hoelmer KA (2004) Biological control of wheat stem sawflies: past and future. J Agric Urban Entomol 21:197–221

Shelton AM, Zhao JZ, Roush RT (2002) Economic, ecological, food safety, and social consequences of the deployment of *Bt* transgenic plants. Annu Rev Entomol 47:845–881

Shiferaw B, Smale M, Braun HJ, Duveiller E, Reynolds M, Muricho G (2013) Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. Food Security 5:291–317

Smith CM (2005) Plant resistance to arthropods-molecular and conventional approaches. Springer, Dordrecht, p 423

Smith CM, Clement SL (2012) Molecular bases of plant resistance to arthropods. Annu Rev Entomol 57:309–328

Smith CM, Harris MK (1989) Registration of KSU29, KSU30, and KSU31 wheat germplasms resistant to greenbug and Russian wheat aphid. Crop Sci 29:248–248

Subramanyam S, Sardesai N, Puthoff DP, Meyer JM, Nemacheck JA, Gonzalo M, Williams CE (2006) Expression of two wheat defense-response genes, Hfr-1 and Wci-1, under biotic and abiotic stresses. Plant Sci 170:90–103

Tadesse W, Sanchez-Garcia M, Tawkaz S, El-Hanafi S, Skaf P, El-Baouchi A, Eddakir K, El-Shamaa K, Thabet S, Gizaw AS, Baum M (2019) Wheat breeding handbook at ICARDA. https://hdl.handle.net/20.500.11766/10723

Tadesse W, Harris M, Crespo-Herrera LA, Mori BA, Kehel Z, El-Bouhssini M (2022a) Insect resistance. In: Reynolds MP, Braun H (eds) Wheat improvement-food security in a changing climate-CIMMYT. Springer, pp 361–378

Tadesse W, El-Fakhouri K, Imseg I, Rachdad FE, El-Gataa Z, El-Bouhssini M (2022b) Wheat breeding for hessian fly resistance at ICARDA. Crop J 10:1528–1535

Tan CT, Yu H, Yang Y, Xu X, Chen M, Rudd JC, Xue Q, Ibrahim AMH, Garza L, Wang S, Sorrells ME, Liu S (2017) Development and validation of KASP markers for the greenbug resistance gene Gb7 and the Hessian fly resistance gene H32 in wheat. Theor Appl Genet 130:1867–1884

Tan MK, El-Bouhssini M, Wildman O, Tadesse W, Chambers G, Luo S, Emebiri L (2018) Development of SNP assays for hessian fly response genes, Hfr-1 and Hfr-2, for marker-assisted selection in wheat breeding. BMC Genet 19:50

Tang G, Liu X, Chen GH, Witworth RJ, Chen MS (2018) Increasing temperature reduces wheat resistance mediated by major resistance genes to *Mayetiola destructor* (Diptera: Cecidomyiidae). J Econ Entomol 111:1433–1438

Van Emden HF (2017) Host-plant resistance. In: van Emden HF, Harrington R (eds) Aphids as crop pests, 2nd edn. CABI, Boston, MA, pp 515–532

Wu H, Sparks C, Amoah B, Jones HD (2003) Factors influencing successful Agrobacterium-mediated genetic transformation of wheat. Plant Cell Rep 21:659–668

Würschum T, Leiser WL, Langer SM, Tucker MR, Miedaner T (2020) Genetic architecture of cereal leaf beetle resistance in wheat. Plants 9:1117. https://doi.org/10.3390/plants9091117

Xu X, Li G, Carver BF, Puterka G (2020) Identification of wheat germplasm resistant to major Russian wheat aphid biotypes in the United States. Crop Sci 60:1428–1435. https://doi.org/10.1002/csc2.20041

Zanganeh L, Madadi H, Allahyari H (2015) Demographic parameters of *Diuraphis noxia* (Hemiptera: Aphididae) and *Hippodamia variegata* (Coleoptera: Coccinellidae) recorded in the context of *D. noxia* infesting resistant and susceptible cultivars of wheat. Eur J Entomol 112: 453–459

Zhang M, Wang H, Yi Y, Ding J, Zhu M, Li C, Guo W, Feng C, Zhu X (2017) Effect of nitrogen levels and nitrogen ratios on lodging resistance and yield potential of winter wheat (*Triticum aestivum* L.). PLoS One 12(11):e0187543

Zhang J, Li H, Zhong X, Tian J, Segers A, Xia L, Francis F (2022) Silencing an aphid-specific gene SmDSR33 for aphid control through plant-mediated RNAi in wheat. Front Plant Sci 13: 1100394

Zhao C, Escalante LN, Chen H, Benatti TR, Qu J, Chellapilla S (2015) A massive expansion of effector genes underlies gall-formation in the wheat pest *Mayetiola destructor*. Curr Biol 25: 613–620

Zhu Y, Qian W, Hua J (2010) Temperature modulates plant defense responses through NB-LRR proteins. PLoS Pathog 6:e1000844

Zukoff A, McCornack BP, Whitworth RJ (2023) Wheat insect pest management 2023. Kansas State University