

Multiple Aphid Resistance from Alien Sources and its Chromosomal Location in Bread Wheat

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Alnarp

Doctoral Thesis
Swedish University of Agricultural Sciences
Alnarp 2014

Acta Universitatis Agriculturae Sueciae
2014:62

Cover: Three aphid species that attack wheat. *Rhopalosiphum padi* (left),
Sitobion avenae (top-right) and *Schizaphis graminum* (bottom-right)
(photo: Leonardo A. Crespo Herrera)

ISSN 1652-6880
ISBN (print version) **978-91-576-8072-3**
ISBN (electronic version) **978-91-576-8073-0**
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Print: SLU Service/Repro, Alnarp 2014

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Abstract

Wheat (*Triticum aestivum*) is a very important cereal crop and is cultivated worldwide on more than 200 million hectares annually, with an average grain yield of about 3 t/ha. A number of diseases and pests are known to affect wheat production, with aphids being important insect pests. The aphid species that commonly attack wheat are *Schizaphis graminum*, *Rhopalosiphum padi*, *Sitobion avenae*, *Diuraphis noxia* and *Metopolophium dirhodum*. These aphids can reduce wheat yields by up to 40% solely due to feeding and by over 60% when their feeding transmits viral diseases. One way to reduce aphid damage is through plant breeding and growing resistant varieties. The aims of this thesis were to: 1) identify novel sources of resistance to multiple aphid species in a wheat-alien genetic stock; 2) determine the utility of those resistance sources in the field; 3) review the utility of rye as a source of resistance to biotic stresses in wheat; and 4) locate genomic regions associated with aphid resistance in a synthetic hexaploid wheat (SHW). Under laboratory conditions, certain wheat genotypes carrying the 1R chromosome from rye reduced both *R. padi* and *S. avenae* growth, the most resistant ones by 24 and 34% relative to the control, respectively. Certain *Aegilops speltoides*-derived wheat lines displayed hardly any chlorosis due to *S. graminum* and reduced aphid colony weight by up to 68% compared with the control. The results of laboratory and field evaluations were in good agreement. The most resistant wheat-rye genotype reduced *R. padi* field population development by 33% relative to the control, while the *A. speltoides*-derived line reduced *S. graminum* field population development by up to 75%. Certain rye-derived genotypes carrying resistance to one or two aphid species also showed resistance to fungal diseases such as powdery mildew and *Septoria tritici* blotch. Five quantitative trait loci (QTL) associated with aphid resistance were found in the SHW mapping population. One QTL for *R. padi* antibiosis is located on chromosome arm 4BL, two QTL for *R. padi* tolerance on 5AL and 5BL, and two QTL for *S. graminum* resistance on 2DL and 7DL. An epistatic interaction that enhanced *R. padi* tolerance was also detected. The sources of resistance identified here have potential applications in wheat breeding programmes aiming to incorporate aphid resistance.

Keywords: Wheat breeding, rye, *Aegilops*, synthetic hexaploid wheat, quantitative trait loci, antibiosis, antixenosis, tolerance, greenbug, bird cherry-oat aphid, English grain aphid.

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Dedication

To *Sybil* and my little *Leo*
who have been “*strong as a lion*”

A name is just an approximation to the nature of things
Carlos Fuentes

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List of Publications

This thesis is based on the work contained in the following papers, which are referred to by their Roman numerals in the text:

- I Crespo-Herrera, L.A., Smith, C.M., Singh, R.P. & Åhman, I. (2013). Resistance to multiple cereal aphids in wheat–alien substitution and translocation lines. *Arthropod-Plant Interactions* 7(5), 535-545.
- II Crespo-Herrera, L.A., Singh, R.P. & Åhman, I. Field population development of bird cherry-oat aphid and greenbug (Hemiptera: Aphididae) on wheat-alien substitution and translocation lines. (Submitted).
- III Crespo-Herrera L.A., Garkava-Gustavsson L. & Åhman I. Rye revisited as a source of resistance to diseases and pests in wheat – exemplified by lines with rye chromatin in the same wheat background. (Manuscript).
- IV Crespo-Herrera L.A., Akhunov E., Garkava-Gustavsson L., Jordan K.W., Smith C.M., Singh R.P. & Åhman I. (2014). Mapping resistance to the bird cherry-oat aphid and the greenbug in wheat using sequence-based genotyping. *Theoretical and Applied Genetics*. (In press).

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The contribution of Leonardo A. Crespo Herrera to the papers included in this thesis was as follows:

- I Planned and conducted the experiments, analysed the data and wrote the main part of the manuscript.
- II Planned and conducted the experiments, analysed the data and wrote the main part of the manuscript.
- III Planned the experiment together with co-authors, analysed the data and wrote the main part of the manuscript.
- IV Planned and conducted the experiments together with co-authors, analysed the data and wrote the main part of the manuscript.

Abbreviations

AUCPD	Area under the curve of population development
Bgt	<i>Blumeria graminis</i> f. sp. <i>tritici</i> ; powdery mildew
BYDV	Barley yellow dwarf virus
CIMMYT	International Maize and Wheat Improvement Center
FHB	Fusarium head blight
GBS	Genotyping-by-sequencing
Hx	Hydroxamic acids
MAS	Marker-assisted selection
MRGR	Mean relative growth rate
QTL	Quantitative trait loci
RILs	Recombinant inbred lines
<i>rm</i>	Intrinsic rate of increase
SBS	Selected-bulk selection
SHW	Synthetic hexaploid wheat
SNP	Single nucleotide polymorphism
STB	<i>Septoria tritici</i> blotch
UPOV	International Union for the Protection of New Varieties of Plants

1 Introduction

Wheat (*Triticum aestivum* L.) is one of the most commonly grown plant species in the world. According to the Food and Agriculture Organization of the United Nations¹, 216 million hectares of wheat were harvested in 2012. This area represents 15.5% of the world's arable land. In 2012, global wheat production was about 675 million tonnes, of which 47% was produced in Asia, 29% in Europe and 16% in the Americas, and global average wheat yield was 3.1 t/ha. Global average consumption was 66 kg/capita in 2009, but there are geographical regions where consumption is much higher, such as in Central Asia (166 kg/capita), Western Asia (153 kg/capita), North Africa (141 kg/capita) and southern Europe (117 kg/capita).

The world's population is continuously increasing and is projected to be more than 9 billion by 2050. This population growth is co-occurring with other factors such as a dietary shift in developing countries, climate change, which is compromising wheat yields due to abiotic factors, and the constant pressures of biotic stresses (Hawkesford *et al.*, 2013). Consequently, there is a great need to produce wheat in a more sustainable manner and increase its supply by 2-3% annually to meet the increasing demand. However, wheat yields at present are increasing at less than half the required rate. According to Hawkesford *et al.* (2013), from the production perspective there are three key challenges to be overcome in achieving a sufficient wheat supply: 1) to increase yield potential; 2) to protect yield potential; and 3) to increase resource use efficiency. In order to tackle these challenges, it is critical to adopt a multidisciplinary approach that can identify and improve the contribution of relevant traits in wheat production.

Among the biotic factors that limit wheat production, aphids are considered a major threat by significantly reducing grain yields if not controlled. These insects cause two major types of damage: 1) they deplete plant resources by

¹. FAOSTAT: <http://faostat3.fao.org/faostat-gateway/go/to/home/E> accessed in February 2014.

feeding and 2) they transmit viral diseases. Feeding damage can reduce wheat yields by up to 40% (Voss *et al.*, 1997; Kieckhefer & Gellner, 1992). When feeding is combined with transmission of barley yellow dwarf virus (BYDV), the yield reductions can be by over 60% (Riedell *et al.*, 2003).

Chemical control is currently the most widely used method to reduce aphid damage in agriculture. Commercial farms rarely apply insecticides based on aphid samplings. Chemical control is instead frequently driven by other factors, such as the value of the planted crop, 'good' or 'bad' growing seasons and the economic benefit of applying more than one chemical product in one spraying (Nansen & Ridsdill-Smith, 2013). Although chemical control can be justified when aphid outbreaks occur, in the absence of alternative control methods, the indiscriminate use of insecticides has a negative impact on the environment and human health, and also carries the risk of the pests developing resistance to the products used.

The most viable alternative to control aphids is by means of genetic resistance in cultivars. This method is environmentally friendly, economically sound and easy for farmers to use. By incorporating resistance to aphids into wheat cultivars, farmers are given access to a cheap control method present in the seed that they obtain for planting.

The incorporation of resistance into wheat is facilitated by detailed characterisation and understanding of the genetic basis of such resistance. Therefore, the work presented in this thesis aimed to characterise and contribute information on new resistance sources to multiple aphid species that are pests of wheat.

2 Background

2.1 Plant resistance to insects

Plant resistance to insects can be defined as the plant characteristics that are genetically ruled and result in the insect pest inflicting less damage on a plant compared with another plant of the same species lacking such genetic characteristics (Smith, 2005).

The first classification of plant resistance, based on the response of plant genotypes across several disease races, is attributed to Van der Plank (1966; 1963), who separated resistance into vertical and horizontal types (Figure 1). Later, Flor (1971) developed the gene-for-gene concept to describe the co-evolution of plant-parasite systems in the vertical type of resistance. Even though the conceptual frameworks developed by Van der Plank and Flor were first applied to phytopathology, they can also be applied to plant resistance to insects.

According to the mode of inheritance, plant resistance can be classified into qualitative (vertical) and quantitative (horizontal). The term qualitative is used to describe a type of resistance that is controlled by single genes, usually with large phenotypic effects, so-called major genes. In most cases they are dominant, and thus display resistance source phenotypes when offspring genotypes are heterozygous at the locus of interest. Qualitative resistance is typically race-specific and when deployed at large scale it has low durability due to strong selection pressure put on the pests (McDonald & Linde, 2002).

Quantitative resistance is governed by so-called minor genes, usually with small phenotypic effects that act in an additive manner. In heterozygous offspring genotypes, minor genes tend to display intermediate phenotypic values compared with those of the parental genotypes. Quantitative resistance is commonly considered non-race specific and durable, since it does not pose

strong selection pressure on the pests and the boom-bust cycles are absent (McDonald & Linde, 2002).

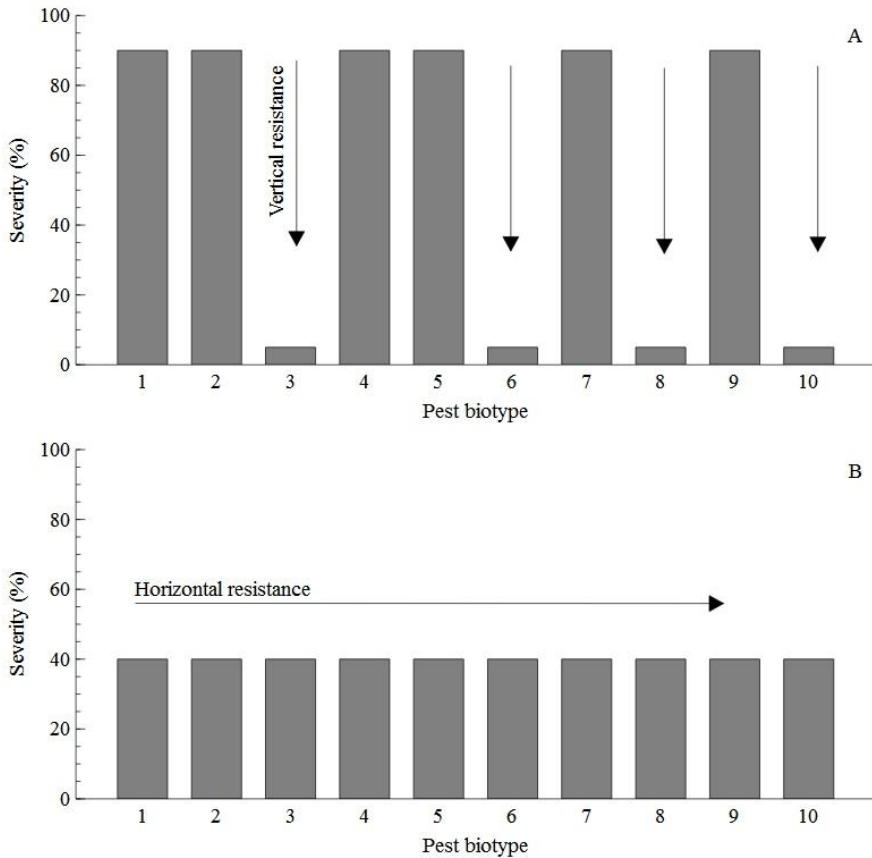


Figure 1. Visual representation of the Van der Plank concepts of (A) vertical (qualitative) resistance and (B) horizontal (quantitative) resistance.

Depending on the effect that plant resistance has on insect performance, insect behaviour and plant performance, Painter (1941) classified resistance as antibiosis, non-preference and tolerance, respectively. The non-preference category was renamed “antixenosis” by Kogan and Ortman (1978) to describe a plant characteristic rather than an insect behaviour. All three categories of resistance are frequently present in resistant plants. Although one category may dominate over the other two, it is often difficult to separate their individual effects.

2.1.1 Antibiosis

The term antibiosis has the Greek roots *anti* (= against, opposed to) and *bio* (= life). It is used to define the plant characteristics that negatively impact on insect physiology and consequently affect life history traits. For instance, antibiotic plants tend to cause longer developmental periods, higher mortality rates, reduced growth, lower fecundity, *etc.*

Antibiotic characteristics are mainly conferred by plant substances that are non-nutritional (allelochemicals). Allelochemicals are substances that can be induced upon insect damage or can be present constitutively in resistant plant genotypes. Examples of these compounds are the hydroxamic acids (Hx) such as DIMBOA and DIBOA. Concentrations of Hx have been shown to be negatively correlated with aphid performance (Ni & Quisenberry, 2000; Givovich & Niemeyer, 1996; Givovich *et al.*, 1994). The genes that are involved in the synthesis of DIMBOA and DIBOA are well characterised by Nomura *et al.* (2002) and Nomura *et al.* (2003) and are known to be present in the homologous chromosomes 4 and 5 of wheat. Wheat relatives with typically high Hx concentrations are the species carrying the B genome, such as *Aegilops speltoides* Tausch. and *Triticum dicoccum* L., whereas *Aegilops tauschii* Coss., the carrier of the D genome, has low concentrations of Hx (Niemeyer *et al.*, 1992).

While allelochemicals are commonly involved in conferring antibiosis, morphological structures of the plant can also result in insect mortality. Wheat trichomes, for instance, are reported to cause punctures on eggs of the cereal leaf beetle (*Oulema melanopus* [L.]). These punctures cause egg desiccation and may also cause the death of larvae due to damage in their alimentary canal at feeding (Papp & Mesterhazy, 1992; Wellso, 1979; Wellso, 1973). However, there is no strong evidence suggesting that trichomes cause antibiosis to aphids in wheat.

The measurement of antibiosis in plants requires the evaluation of life history traits. One of the most common methods is to build life tables that record different aspects of insect performance (longevity, mortality, number of offspring per female, *etc.*) from which the intrinsic rate of increase (*rm*) is calculated. The *rm* is widely used to describe the proportion by which a population increases from one time unit to the next (Krebs, 2009) and, particularly for aphids, it is expressed as (Wyatt & White, 1977):

$$rm = 0.74 * \ln(M) / d$$

where *M* = number of aphids produced until the first offspring starts to give birth to new aphids and *d* = pre-reproductive time.

Another method to measure antibiosis is by estimating the mean relative growth rate (MRGR). The MRGR is highly correlated to the *rm* parameter in aphids (Leather & Dixon, 1984; Dewar, 1977). The MRGR requires the quantification of initial and final aphid weight when exposed to the plants, and is calculated as (Blackman, 1919):

$$MRGR = \frac{\ln W_f - \ln W_i}{t}$$

where W_i = initial aphid weight, W_f = final aphid weight and t = duration of the experiment.

Alternatively, it is possible to quantify only the final aphid weight (Figure 2). This screening method has been shown to be effective in finding resistance sources in wheat and barley (Crespo-Herrera *et al.*, 2013; Cheung *et al.*, 2010).



Figure 2. Wheat seedling infested with *Rhopalosiphum padi* nymphs 4 days prior to weighing on a microbalance to calculate aphid growth relative to that on a control plant.

2.1.2 Antixenosis

The term antixenosis derives from the Greek roots *anti* (= against, opposed to) and *xenos* (= foreign). It is used to describe the plant characteristics that negatively affect the host finding and host acceptance processes of insects. Consequently, antixenotic plants have a reduced number of aphids per plant or plant structure (leaf, tiller, spike, *etc.*). Low feeding rate can be another form of antixenosis.

Insect vision, olfaction, gustation and thigmoreception are involved in the three phases of host finding: 1) searching (orientation); 2) recognition (landing and probing); and 3) acceptance (feeding and reproduction). Although vision provides information about the potential host's size, colour and shape, chemoreception (olfaction and gustation) is the most important aspect for host finding and acceptance (Gillot, 2005). For instance, high concentrations of constitutive compounds such as Hx derived from glucosides can deter aphids from settling on wheat plants (Elek *et al.*, 2014). There are also volatiles that are released upon insect damage (methyl salicylate and cis-jasmone) and when perceived by the olfactory system of aphids, they can have a repelling effect (Pickett & Glinwood, 2007; Bruce *et al.*, 2003; Birkett *et al.*, 2000; Pettersson *et al.*, 1994).

Powell *et al.* (2006) suggested that the most important factor for aphids accepting or rejecting a plant as a host is the information they receive in the stylet insertion and probing phases. When probing, aphids take small sap samples, which are transported to the pharyngeal taste organ. There are three phases involved in plant penetration: 1) pathway phase; 2) xylem phase; and 3) phloem phase. Acceptance or rejection of a plant as a host is mostly carried out at the phloem phase (Pettersson *et al.*, 2007). However, host acceptance also depends on the ability of the aphids to penetrate the plant tissue and reach the phloem, which can be limited by morphological or anatomical structures (Smith & Chuang, 2014)

Antixenosis is generally measured as the differential level of attractiveness of plant genotypes. Evaluations are usually performed in free-choice tests, where the plant genotypes to be tested are randomly planted and exposed to the insects in round or rectangular pots (Webster & Inayatullah, 1988). Antixenosis can also be measured in no-choice tests and recorded as the level of host acceptance after a certain period (Ninkovic & Åhman, 2009).

Despite the fact that antixenosis can affect the initial colonisation rates of aphids (Webster & Inayatullah, 1988), it can be an insufficient plant defence. Since monoculture dominates today's agricultural systems, insect feeding choices are limited and they may eventually infest antixenotic cultivars in the absence of susceptible ones. Furthermore, antixenosis may not contribute to reducing the spread of viral disease. On the contrary, virus spreading may increase as aphids may be constantly searching for acceptable hosts.

2.1.3 Tolerance

The ability of a plant to withstand and/or recover from insect damage without compromising insect physiology or behaviour is the definition of plant tolerance. This category of resistance is complex and involves several plant

physiological processes, such as those related to photosynthesis, nutrient uptake, allocation patterns, re-growth, *etc.* (Boyko *et al.*, 2006; Rosenthal & Kotanen, 1994).

Studies of gene expression in aphid-tolerant genotypes have shown the up-regulation of transcription sequences corresponding to compounds that regulate photosynthesis, photorespiration, protein synthesis, antioxidant production and detoxification (Boyko *et al.*, 2006). Other possible responses are the prevention of cell wall modification due to aphid feeding, and down-regulation of genes responsible for the synthesis of secondary metabolites related to basal plant defences (Reddy *et al.*, 2013). However, these plant responses may vary depending on the aphid species, since it is known that different aphid species can induce different physiological responses in plants (Franzen *et al.*, 2008; Ni *et al.*, 2002).

Despite its complexity, plant tolerance is an attractive trait to incorporate into cultivars, as it has the advantage of not putting any selection pressure on aphid populations which can eventually overcome the other two resistance categories. Therefore, tolerance is expected to be durable and stable across time. It may also facilitate combination with other control methods, as actions to control aphids are often taken too late. The combination of antibiosis and tolerance to aphids can reduce the spread of viruses in the field, and at the same time reduce aphid damage. Furthermore, it can provide a wider window for plant breeders to identify and develop new resistant cultivars if antibiosis is overcome.

The measurement of tolerance requires the assessment of aphid damage to the plants. Therefore, plant traits that are known to be affected by aphid feeding are good candidates for measurement. These traits are specific to certain aphid species. For those that cause clear plant symptoms, it is possible to measure tolerance by estimating chlorophyll losses with a portable device (SPAD meter) and/or by rating symptoms such as chlorosis and leaf roll (Sotelo *et al.*, 2009; Lage *et al.*, 2003). However, for those aphid species that do not cause such symptoms, other plant physiological parameters affected by aphid feeding may be used (Franzen *et al.*, 2008).

The assessment of plant growth reduction is a relevant parameter of tolerance (Dunn *et al.*, 2007). This is measured by exposing the plant genotypes to at least two treatments, of which one must be non-infested and the other aphid-infested at a certain density. The experimental settings for this type of evaluation need to be very stringent, since it requires plants with the same starting size among treatments. Another complication to identifying tolerance arises from the fact that all three categories of resistance are often expressed in single plant genotypes. This makes it difficult to separate tolerance from the

other categories, since less biomass reduction can also be caused by *e.g.* higher mortality rates of aphids or lower acceptance of resistant plant genotypes. To account for this confounding effect, it is crucial that the plants have approximately the same aphid density over time.

2.2 Wheat aphids and resistant germplasm

2.2.1 Aphids as pests of wheat

Aphids are a large group of small and soft-bodied insects that feed from plant phloem. They have varied and complex life cycles. In general, most of the species overwinter in the egg stage and hatch in the spring as females which reproduce parthenogenetically. Later, winged individuals migrate to a secondary host. Several generations are often born on the same plant, and when the population density becomes high or the nutritional quality of the host becomes low, winged individuals develop and migrate to infest another host plant (Triplehorn & Johnson, 2005). Later in the season, when the temperature decreases and nights become longer, holocyclic aphids enter into their sexual phase. This part of their life cycle takes place on their primary host, which is commonly unrelated to their secondary host (Triplehorn & Johnson, 2005; Hales *et al.*, 1997). Aphid populations that do not undergo sexual reproduction are called anholocyclic, as opposed to holocyclic.

The most important aphid species attacking wheat are: greenbug (*Schizaphis graminum* [Rondani]), bird cherry-oat aphid (*Rhopalosiphum padi* L.), English grain aphid (*Sitobion avenae* [Fabricius]), Russian wheat aphid (*Diuraphis noxia* [Mordvilko]), and rose grain aphid (*Metopolophium dirhodum* [Walker]). These species are globally distributed in the wheat producing regions, with certain geographical differentiation. For instance, *D. noxia* has not been reported in Australia and *S. graminum* is absent as a pest in northern Europe.

Greater attention has been given to *D. noxia* and *S. graminum* in studying wheat resistance mechanisms and developing resistant cultivars. In contrast, *R. padi*, *S. avenae* and *M. dirhodum* have not been studied extensively and resistance to these species has not been purposely incorporated into wheat cultivars. Possibly because *D. noxia* and *S. graminum* cause clear plant symptoms on the plants, it is more feasible to select resistant plants from breeding populations and thus obtain wheat cultivars carrying the desired resistance. The other three species do not cause clear plant symptoms, and therefore it is more difficult to select resistant progeny from segregating populations.

2.2.2 Sources of resistance to aphids in wheat

Hexaploid wheat arose 8,000 years ago in the Near East (Matsuoka, 2011) from spontaneous hybridisation between the tetraploid species *Triticum turgidum* L. and the diploid species *A. tauschii*. Therefore, hexaploid wheat is an allopolyploid species composed of three genomes (A, B and D) with seven pairs of chromosomes each (Faris *et al.*, 2002). Studies have established that the donor of the A and D genome is *Triticum urartu* Tum. ex Gan. and *A. tauschii*, respectively (Dvorak *et al.*, 1988; McFadden & Sears, 1946). The origin of the B genome is not completely clarified yet. However, there are indications that *A. speltoides* is the donor (Dvorak & Zhang, 1990).

Resistance to aphids is found in all three gene pools of wheat. According to chromosome homology, the species in the primary gene pool are hexaploid landraces, along with the donors of the A and D genomes. The species that have at least one homologous genome in common with wheat are placed in the secondary gene pool. These include the polyploid species of the *Triticum* and *Aegilops* genera, such as *Triticum timopheevii* Zhuk. and diploid species of the *Aegilops* section *Sitopsis* that carry the S genome, which is related to the B genome. (Feuillet *et al.*, 2008; Friebe *et al.*, 1996).

The tertiary gene pool contains the most distantly related species to wheat; for instance species of *Secale* and *Thinopyrum* belong to this group. The chromosome pairing patterns with wheat in this last group are ruled by the *Ph1* locus in chromosome 5B (Feuillet *et al.*, 2008; Friebe *et al.*, 1996). Transfer of desirable characteristics from species belonging to the primary and secondary gene pool is possible via homologous recombination, whereas the transfer of desirable loci from the tertiary gene pool requires chromosome engineering techniques, for instance by exploiting the centric breakage-fusion of univalents during meiosis, use of *ph1* mutants, radiation methods and tissue culture (Feuillet *et al.*, 2008; Friebe *et al.*, 1996).

Synthetic hexaploid wheats (SHW) have served as an important source of resistance to several biotic constraints of wheat production, since resistance can be incorporated from some of the wild relatives (Ogbonnaya *et al.*, 2013). Such resistance has been found particularly against *S. graminum*, but also against *R. padi* (Crespo-Herrera *et al.*, In press). SHW are produced by the interspecific cross of a tetraploid species carrying the A and B genomes with the diploid *A. tauschii*, followed by a chromosome doubling process (Figure 3).

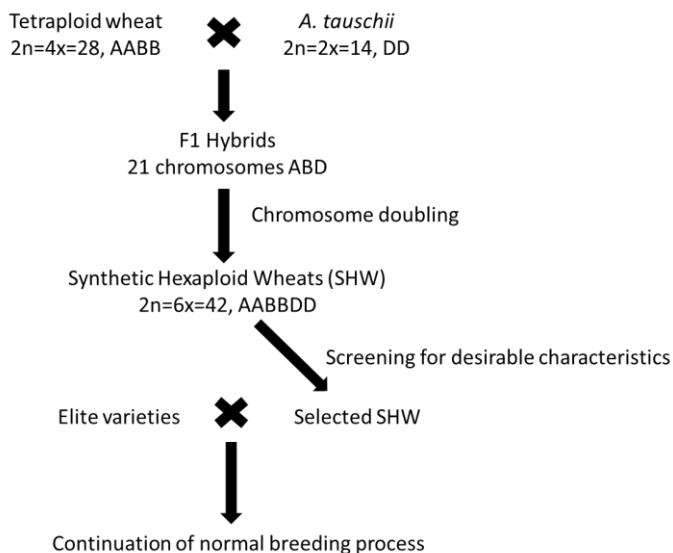


Figure 3. Development of synthetic hexaploid wheats (SHW). Modified from: Mujeeb-Kazi (1995).

Rye, *Secale cereale* L. ($2n=2x=14$), has also been extensively used to incorporate relevant agronomic characteristics into wheat (Rabinovich, 1998). Naranjo *et al.* (1987) reported homoeologous pairing patterns of wheat chromosome groups 1, 2, 3, 5 and 6 with chromosomes 1R, 2R, 3R, 5R and 6R of rye. This feature makes it possible to produce chromosome substitution and translocation lines by different methods, for instance by recovering spontaneous translocations (Jiang *et al.*, 1994; Lukaszewski & Gustafson, 1983; Sears, 1981), applying irradiation treatments (Jauhar & Chibbar, 1999; Sebesta & Wood, 1978), tissue culture of embryos (Friebe *et al.*, 1990; Lapitan *et al.*, 1984), use of *ph1* mutants (Lukaszewski, 1995) or applying okadaic acid treatments (Knight *et al.*, 2010). Four main rye sources have been used to incorporate rye chromatin into wheat, two from Germany, one from Japan and one from the USA (Rabinovich, 1998). However, that from Petkus rye has been mostly deployed, as (1B)1R substitution or 1BL.1RS translocations (Rabinovich, 1998).

The extent to which wheat-rye translocations have been used in the development of cultivars varies over time and among countries, and there are no recent surveys published. At the International Maize and Wheat Improvement Center (CIMMYT), 60% of the advanced wheat germplasm during the 1990s carried a 1BL.1RS translocation (Rabinovich, 1998). In China, nearly 42% of the wheat cultivars released between 1960 and 2000 were (1B)1R genotypes (Zhou *et al.*, 2007).

2.2.3 *Schizaphis graminum*

Schizaphis graminum, commonly known as greenbug, most probably originates from the Middle East. Its distribution in the wheat growing areas of the world encompasses Asia, Southern Europe, Africa and North and South America (Blackman & Eastop, 2007). Nymphs are characterised by a light green colour with a dark-green longitudinal dorsal strip and dark-tipped siphunculi (Stoetzel, 1987). *Schizaphis graminum* feeds on several genera of the Poaceae and it is a vector of the SGV strain of BYDV (Gray & Gildow, 2003).

Feeding by *S. graminum* causes chlorosis and necrotic spots at the feeding sites on susceptible plants (Figure 4). This feature allows the evaluation of relatively large germplasm sets to identify potential resistance sources.

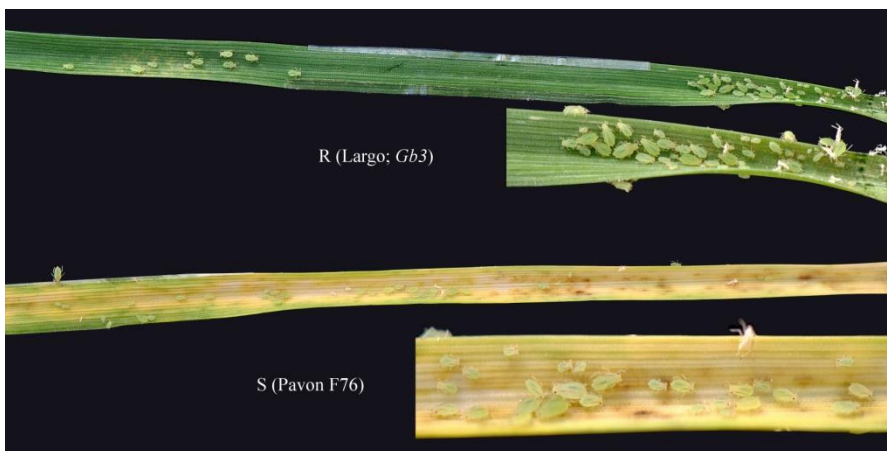


Figure 4. Plant damage caused by individuals of *Schizaphis graminum* biotype E after 15 days of feeding on the resistant (R) wheat cultivar Largo, carrying the *Gb3* resistance gene, and on the susceptible (S) wheat cultivar Pavon F76.

Efforts to transfer *S. graminum* resistance to wheat have been underway in the USA since the 1950s (Berzonsky *et al.*, 2003; Porter *et al.*, 1997). From these breeding and resistance characterisation efforts, several resistance genes have been found in wheat and/or wheat relatives (Porter *et al.*, 1997). Fourteen *S. graminum* resistance genes have been reported to date, of which one was found in durum wheat (*Triticum turgidum* L.), one in *A. speltoides*, one in bread wheat, two in *Secale cereale* L. and nine in *A. tauschii* (Table 1). Seven of the nine genes from *A. tauschii* are either allelic or tightly linked to the *Gb3* gene (Table 1). So far resistance loci to *S. graminum* have been found in chromosomes 7S, 7D, 1R, and also likely in 2D (Crespo-Herrera *et al.*, In press).

Table 1. *Schizaphis graminum* resistance genes, origin, chromosome location, linked markers and resistance to biotypes.

Gene	Germplasm	Species origin	Chromosome	Markers	Biotype resistance ¹⁴
<i>Gb1</i> ¹	DS 28A	<i>T. turgidum</i>	Not mapped		A, F, J
<i>Gb2</i> ^{2,3}	Amigo; TAM107 and TAM200	<i>S. cereale</i>	1AL.1RS	<i>XIA294</i>	B, C, J
<i>Gb3</i> ^{4,5}	Largo	<i>A. tauschii</i>	7DL	<i>Xgwm037</i> ; <i>Xwmc634</i>	C, E, H, I, J, K
<i>Gb4</i> ^{6,7}	CI 17959	<i>A. tauschii</i>	7DL [†]		C, E, I, J, K
<i>Gb5</i> ^{7,8}	CI 17882; CI 17884 and CI 17885	<i>A. speltooides</i>	7S(7A)		C, E, I, J, K
<i>Gb6</i> ^{3,9}	GRS1201	<i>S. cereale</i>	1AL.1RS	<i>XIA294</i>	B, C, E, G, I, J, K
<i>Gb7/Gbx2</i> ^{5,10}	W7984	<i>A. tauschii</i>	7DL	<i>Xwg420</i> ; <i>Xwmc671</i>	C,E, I, K
<i>Gba</i> ¹¹	CETA/ <i>A. tauschii</i> Wx1027	<i>A. tauschii</i>	7DL [†]	<i>Xwmc671</i> ; <i>Xbarc53</i>	I, E ^o
<i>Gbb</i> ¹¹	CROC 1/ <i>A. tauschii</i> Wx224	<i>A. tauschii</i>	7DL [†]	<i>Xwmc671</i> ; <i>Xbarc53</i>	I [†]
<i>Gbc</i> ¹¹	68111/Rugby//Ward// <i>A. tauschii</i> TA2477	<i>A. tauschii</i>	7DL [†]	<i>Xgwm671</i> ; <i>Xgdm150</i>	I [†]
<i>Gbd</i> ¹¹	Altar 84/ <i>A. tauschii</i> TA2841	<i>A. tauschii</i>	7DL [†]	<i>Xgwm671</i> ; <i>Xwmc157</i>	I [†]
<i>Gbx1</i> ¹¹	Wichita/TA1695//2*Wichita	<i>A. tauschii</i>	7DL [†]	<i>Xwmc157</i> ; <i>Xgdm150</i>	I [†]
<i>Gby</i> ¹²	Sando's 4040	<i>T. aestivum</i>	7A	<i>Xpsr119</i> ; <i>Xpr1B</i> ; <i>Xbcd98</i> are 99.77% correlated to Gby	I [†]
<i>Gbz</i> ¹³	KSU97-85-3	<i>A. tauschii</i>	7DL [†]	<i>Xwmc671</i> ; <i>Xbarc53</i> . <i>Xwmc157</i> is completely linked to Gbz	I [†]

Source: ¹ Curtis *et al.* (1960); ² Sebesta & Wood (1978); ³ Lu *et al.* (2010); ⁴ Joppa & Williams (1982); ⁵ Weng *et al.* (2005); ⁶ Martin *et al.* (1982); ⁷ McIntosh *et al.* (2012); ⁸ Tyler *et al.* (1985); ⁹ Porter *et al.* (1991); ¹⁰ Weng & Lazar (2002); ¹¹ Zhu *et al.* (2005); ¹² Boyko *et al.* (2004); ¹³ Zhu *et al.* (2004); ¹⁴ Burd & Porter (2006).
^o No data available on other GB biotypes. [†] Allelic or closely linked to *Gb3* gene. Table taken from: Crespo Herrera (2012).

There are *S. graminum* biotypes which are virulent to germplasm with certain resistance genes. Contrary to the common view that this aphid species defeated the resistance genes due to strong selection pressure, Porter *et al.* (1997) demonstrated that *S. graminum* populations with virulence to the known resistance genes were already present in nature before the deployment of resistant cultivars in agriculture. Later, Burd and Porter (2006) identified unique virulence patterns in various *S. graminum* populations, and also showed that biotypes E and I are the most commonly associated with wheat. In addition, Weng *et al.* (2010) demonstrated that the biotypic differentiation of *S. graminum* is strongly related to host species associations.

So far, most of the loci associated with *S. graminum* resistance act in a gene-by-gene fashion and, except for the gene *gb1*, which is recessive, all the genes listed in Table 1 are dominant major genes. Therefore, when resistance genes are pyramided in single plant genotypes, they do not provide higher resistance levels compared with plant genotypes carrying single resistance genes, even though the avirulence patterns can be expanded due to the combination of genes conferring resistance to different aphid biotypes (Porter *et al.*, 2000). The predominance of major genes for *S. graminum* resistance can possibly be explained by the fact that most previous studies have measured resistance traits in a qualitative rather than a quantitative manner.

However, if quantitatively inherited resistance traits were to be found, the accumulation of resistance loci might further enhance resistance levels due to additive effects and may increase the durability of resistance. The number of studies on quantitative inheritance of *S. graminum* resistance is limited. There are a few reported quantitative trait loci (QTL) that confer antixenosis (Castro *et al.*, 2004). However, these results still require validation steps.

2.2.4 *Rhopalosiphum padi*

Rhopalosiphum padi is commonly referred to as bird cherry-oat aphid. Apterous females have a pear-shaped body. The colour of this aphid varies from green-olive to light yellow-green, with a distinctive red-orange pigmentation at the distal section of the abdomen (Figure 5). The siphunculi are swollen and constricted near to the flange (Blackman & Eastop, 2007; Stoetzel, 1987). *Rhopalosiphum padi* is an efficient vector of BYDV, particularly the strain PAV, and strain RPV of cereal yellow dwarf virus (CYDV) (Gray & Gildow, 2003). Unlike *S. graminum* and *D. noxia*, *R. padi* does not cause visible feeding symptoms on the plants (Franzen *et al.*, 2008). However, gas-exchange, content of carotenoids and the efficiency of photosystem II are affected (Franzen *et al.*, 2008). The damage is evident as plant growth reduction. Yield can be reduced by 31% solely due to direct feeding (Voss *et al.*, 1997) and by up to 62% when damage is combined with BYDV infection (Riedell *et al.*, 2003).

The geographical origin of *R. padi* is uncertain, as it is a cosmopolitan species. Molecular techniques and population modelling have shown that there are two *R. padi* lineages that differ in their reproductive strategy (Macfadyen & Kriticos, 2012; Delmotte *et al.*, 2003; Simon *et al.*, 1996; Simon *et al.*, 1991): a holocyclic lineage with the sexual reproduction phase on the primary host (*e.g.* *Prunus padus* in Europe and *P. virginiana* in North America) and the parthenogenetic phase on Poaceae species during summer; and an anholocyclic

lineage that occurs on grasses all year around at latitudes where winters are mild.



Figure 5. *Rhopalosiphum padi* individuals feeding on a wheat seedling.

So far, wheat cultivars have not been deliberately bred for *R. padi* resistance and no differences in virulence patterns among aphid populations have been reported. The lack of clear plant symptoms and the polyphagy and wide adaptation of this species make it difficult to find sources of resistance with adequate protection levels that can be deployed in elite wheat germplasm.

Resistance to *R. padi* has been found in several wheat relatives, for instance *Agropyron elongatum* (Host.) Beauv., *Agropyron intermedium* (Host.) Beauv., *Agropyron repens* (L.) Beauv. and *Elymus angustus* Trin. (Tremblay *et al.*, 1989), and also in hexaploid wheat (Dunn *et al.*, 2011).

Other studies have shown that rye chromatin introgressed into wheat may confer *R. padi* resistance. However, it is important to consider the source and chromosome that is transferred into wheat (Crespo-Herrera *et al.*, 2013; Hesler *et al.*, 2007). In particular, the 1R chromosome from certain rye sources has shown seedling resistance under laboratory conditions and also reduced growth rate of aphid populations in the field.

No *R. padi* resistance genes have been reported to date. However, one study on QTL mapping of *R. padi* resistance in wheat showed that resistance-related traits, such as plant biomass reduction and reduced individual aphid growth, can be inherited in a quantitative manner (Crespo-Herrera *et al.*, In press). It has also been shown that a significant part of the phenotypic variation in tolerance can be explained by epistatic effects (Crespo-Herrera *et al.*, In press). There are currently no other genetic studies available on wheat, despite the fact that *R. padi* is a serious pest of this crop and an efficient vector of BYDV.

2.2.5 *Sitobion avenae*

Commonly known as English grain aphid, *Sitobion avenae* individuals are yellow-green or red-brown. They have a prominent pale cauda and black, cylindrical siphunculi that are less than twice as long as the cauda. The femora are typically black mainly towards the distal section (Blackman & Eastop, 2007; Stoetzel, 1987). This aphid species does not cause clear symptoms on the plants and it is a vector of the strains MAV and PAV of BYDV. Unlike the other aphid species attacking wheat, it performs better at early plant reproductive stages than at vegetative stages, particularly at flowering (Watt, 1979). Although the damage (up to 21% yield reduction) caused by *S. avenae* is significant, it is generally regarded as less deleterious than *R. padi*, *S. graminum* and *D. noxia* (Voss *et al.*, 1997; Kieckhefer & Kantack, 1980).

The origin of *S. avenae* is considered to be European, and it is currently distributed in all Europe, North and South Africa, east India, Nepal, China and North and South America (Blackman & Eastop, 2007). It overwinters on species of Poaceae. There are lineages that differ in their strategy of reproduction (Dedryver *et al.*, 1998; Newton & Dixon, 1988): 1) a lineage that exhibits only parthenogenesis, unable to produce sexual morphs; 2) a clone that only produces males and parthenogenetic females; 3) a cyclic parthenogenetic lineage capable of producing both sexes; and 4) a lineage derived from the last group and classified as an intermediate clone, which partly turns into sexual morphs after a certain period.

Resistance to *S. avenae* has been found in wheat relatives such as *Triticum monococcum* L., *Triticum boeoticum* Boiss., *Triticum araraticum* Jakubz., *Triticum dicoccoides* (Körn. ex Asch. & Graebner) Schweinf. and *T. urartu* (Migui & Lamb, 2004; Migui & Lamb, 2003; Di Pietro *et al.*, 1998). To date, only one gene has been mapped (*Ra-1*), on chromosome 6AL of the durum wheat line C273 (Liu *et al.*, 2011). Crespo-Herrera *et al.* (2013) also found resistance in seedlings of wheat lines carrying rye chromatin. Such resistance is conferred by chromosome 1R of certain rye origin.

2.2.6 *Diuraphis noxia*

Commonly known as Russian wheat aphid, apterae of *Diuraphis noxia* have a convex and elongated body shape, with a yellow-green or grey-green colour. Their siphunculi are pale, short and truncated, and almost as long as they are wide. *D. noxia* is also distinguished by the presence of a supra-caudal process at the eighth abdominal tergite (Stoetzel, 1987). This aphid species is regarded as an inefficient vector of BYDV (Damsteegt *et al.*, 1992). Feeding symptoms consists of characteristic leaf roll that is caused by toxin injection. Leaves can also present white, purple and yellow streaks, and ears become bent if infested (Blackman & Eastop, 2007; Berzonsky *et al.*, 2003). Yield reduction due to feeding damage is reported to be up to 40% in winter wheat (Kieckhefer & Gellner, 1992). The advantage in deploying *D. noxia*-resistant cultivars in the field was demonstrated by Randolph *et al.* (2003), who showed that resistant cultivars had only 1% yield reduction under aphid infestation compared with a non-infested treatment.

The origin of *D. noxia* is central Asia, between the Caucasus Mountains and the Tian Shan (Berzonsky *et al.*, 2003; Puterka *et al.*, 1993). Nowadays it is widely distributed in East Asia, South Africa, North and South America, south and central Europe, North Africa and the Middle East, but has not been reported in Australia so far. Recent studies claim that the most probable migration pattern of this species from its centre of origin to the Americas was through South Africa, Mexico and then USA-Chile-Argentina (Zhang *et al.*, 2014). However, Botha (2013) suggests that *D. noxia* migrated into the Americas directly from its centre of origin. This aphid species may occur as both holocyclic and anholocyclic forms and it only feeds on Poaceae species. These are mostly wheat and barley, but it can also feed on rice, rye and oats (Blackman & Eastop, 2007; Stoetzel, 1987).

Extensive research has been undertaken to understand and characterise the resistance to *D. noxia* in wheat (Smith *et al.*, 2010; Boyko *et al.*, 2006; Smith *et al.*, 1991). The first resistance sources were reported by Toit (1989) in common wheat accessions from Iran and Russia. To date, 11 resistance genes have been reported (Table 2), of which five are allelic or tightly linked (*Dn1*, *Dn2*, *Dn5*, *Dn6* and *Dnx*).

Eight biotypes have been reported in the USA since 1986, when *D. noxia* was first observed in North America. This biotype diversity is believed to have emerged due to the selection pressure caused by resistant cultivars. However, non-cultivated hosts may play a significant role in maintaining new biotypes (Weiland *et al.*, 2008). Halt wheat, released in 1994, was the first cultivar carrying resistance to *D. noxia* in the USA (Smith *et al.*, 2004; Quick *et al.*, 1996) and it was not until 2003 that a new biotype appeared, designated RWA-

2 or biotype 2 (Haley *et al.*, 2004). Later, in 2006, three new *D. noxia* biotypes were identified (RWA-3, RWA-4 and RWA-5), of which biotype 3 is virulent to all 11 genes reported so far (Burd *et al.*, 2006). In 2008, biotypes 6, 7 and 8 were reported (Weiland *et al.*, 2008). Virulence patterns in other countries have also been studied. Populations from Chile, Czech Republic and Ethiopia are reported to be virulent to the *Dn4* resistance gene, which is the most widely deployed gene in wheat cultivars. However *Dn6* has been reported to be effective against these populations (Smith *et al.*, 2004).

Table 2. *Diuraphis noxia* resistance genes, origin, chromosome location, linked markers and resistance to biotypes.

Gene	Germplasm	Species origin	Chromosome	Markers	Biotype resistance ^{8,9,10}
<i>Dn1</i> ¹	PI 137739	<i>T. aestivum</i>	7DS	<i>Xgwm111</i>	1
<i>Dn2</i> ^{1,5}	PI 262660	<i>T. aestivum</i>	7DS	<i>Xgwm111</i>	1
<i>Dn3</i> ²	SQ24	<i>A. tauschii</i>		<i>Not mapped</i>	1
<i>Dn4</i> ^{3,5}	PI 372129	<i>T. aestivum</i>	1DL	<i>Xgwm106; Xgwm337</i>	1, 4, 5 and 6
<i>Dn5</i> ¹	PI 294994	<i>T. aestivum</i>	7DS	<i>Xgwm111</i>	1, 5 and 8
<i>Dn6</i> ³	PI 243781	<i>T. aestivum</i>	7DS	<i>Xgwm111; Xgwm44</i>	1, 4, 5, 6, 7 and 8
<i>Dn7</i> ^{4,6}	Turkey 77	<i>S. cereale</i>	1RS	<i>XHor2; Xscb241</i>	1, 2, 5, 6, 7 and 8
<i>Dn8</i> ¹	PI 294994	<i>T. aestivum</i>	7DS	<i>Xgwm635</i>	1
<i>Dn9</i> ¹	PI 294994	<i>T. aestivum</i>	1DL	<i>Xgwm642</i>	1
<i>Dnx</i> ¹	PI 220127	<i>T. aestivum</i>	7DS	<i>Xgwm111</i>	1, 6, 7 and 8
<i>Dn1881</i> ⁷	1881	<i>T. turgidum</i>	7BS	<i>Xgwm46; Xgwm333</i>	1

Source: ¹ Liu *et al.* (2001); ² Nkongolo *et al.* (1991); ³ Liu *et al.* (2002); ⁴ Lapitan *et al.* (2007); ⁵ Ma *et al.* (1998); ⁶ Marais *et al.* (1994); ⁷ Navabi (2004); ⁸ Burd *et al.* (2006); ⁹ Haley *et al.* (2004); ¹⁰ Weiland *et al.* (2008). Table taken from: Crespo Herrera (2012).

The *D. noxia* resistance genes listed in Table 2 are major genes conferring a qualitative type of resistance. There are some QTL studies for *D. noxia* resistance reporting genomic regions associated with traits related to plant tolerance and antibiosis (Ricciardi *et al.*, 2010; Castro *et al.*, 2004), but no further characterisation of these has been made to date.

2.2.7 *Metopolophium dirhodum*

Commonly known as rose grain aphid, *M. dirhodum* apterae are yellow-green, with a greener stripe along the dorsum, similar to *S. graminum*. However unlike *S. graminum*, the siphunculi are often pale, not reticulated, and the body shape is elongated (Stoetzel, 1987). Another difference between *M. dirhodum* and *S. graminum* is that in alate individuals of the former the medial vein of the fore wing is forked twice, whereas in *S. graminum* it is forked once (Stoetzel, 1987).

Metopolophium dirhodum is a holocyclic species that overwinters in wild and cultivated plant species of *Rosa*. The secondary hosts are species of Poaceae, Cyperaceae and Juncaceae (Weber, 1985). This species is a vector of strains PAV and MAV of BYDV.

In terms of host resistance, *Metopolophium dirhodum* is one of the least studied of all aphid species that attack wheat. Despite being considered a minor pest, it can reduce grain yield by up to 15% in winter wheat when plants are infested at booting stage (Watt & Wratten, 1984).

3 Objectives

There were four main objectives of the work presented in this thesis. These were:

I. To identify novel sources of resistance to multiple aphid species in a wheat-alien genetic stock (Paper I).

II. To determine under field conditions the resistance level of sources identified as resistant in laboratory screenings (Paper II).

III. To screen for disease resistance in the wheat-alien genetic stock previously screened for resistance to aphids (Paper III).

IV. To study the genetic basis of *Rhopalosiphum padi* and *Schizaphis graminum* resistance in a mapping population derived from a cross between a spring bread wheat and a synthetic hexaploid wheat (Paper IV).

4 New sources of resistance to aphids in wheat

4.1 Wheat-alien substitution and translocation lines (Papers I and II)

A genetic stock of 64 wheat-alien substitution and translocation lines, all in the background of the spring wheat cultivar Pavon F76, was evaluated for resistance to three aphid species that may attack wheat in major cultivated regions globally. This stock has different rye and *A. speltoides* origins and was developed by Lukaszewski (2008; 2006; 2000; 1997; 1995; 1993), Brunell *et al.* (1999), Kim *et al.* (2004) and Lukaszewski *et al.* (2004). The evaluations consisted of two major studies: 1) screening of all entries in the stock under controlled conditions for resistance to *R. padi*, *S. avenae* and *S. graminum* (Paper I); and 2) testing a subset of genotypes from the laboratory study under field conditions to assess their aphid resistance (Paper II).

A set of rye cultivars was also evaluated for *R. padi* resistance in laboratory screenings, since most of the lines constituting the stock carry rye as an alien source. These screenings showed that resistance to *R. padi* can be found in rye at levels similar to a highly resistant control (Figure 6), an accession of *Hordeum vulgare* L. ssp. *spontaneum* (C. Koch) Thell. (Cheung *et al.*, 2010). From these results, it was concluded that rye can be a valuable source of *R. padi* resistance for wheat.

The evaluation of the Pavon F76 genetic stock (Paper I) with *R. padi* and *S. avenae* indicated that seedling resistance (presumably antibiosis) to both of these aphid species can be found in single lines carrying chromosome 1R, particularly (1A)1R_e, (1B)1R_e, 1AL.1RS_e, 1BL_v.1RS_e (1D)1R_{pr} and (1D)1R_{pr}.1D₅₊₁₀₋₂. These genotypes showed reduced *R. padi* growth of between 75.8 and 85.3% of that in the control Pavon F76. These same plant genotypes had *S. avenae* growth of between 65.7 and 75.5% relative to the control. In

addition, the genotypes (1D)1R_e, 1AL.1RS_{am}, (1A)1R_{inv}, 1AL.1RS_{rh} and 1BL.1RS_e were found to be resistant only to *S. avenae*.

Adult plant evaluations were conducted in a subset of genotypes (Paper I), since *S. avenae* populations normally peak at early reproductive stages. Interestingly, only the 1AL.1RS_{am} genotype showed resistance at the adult plant stage. These results are in agreement with previous resistance patterns found by Migui & Lamb (2004). The mechanisms behind this phenomenon have not been identified as yet, but one possible explanation is differences in secondary metabolites produced at seedling and adult plant stages.

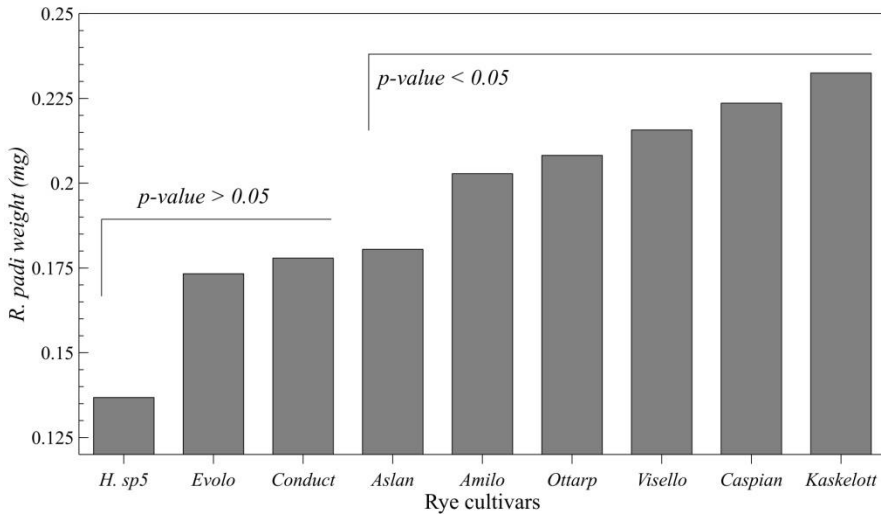


Figure 6. Mean weight (mg) of *Rhopalosiphum padi* nymphs in eight commercial varieties of rye after 4 days of exposure to test plants. *H. sp5* = *Hordeum vulgare* ssp. *spontaneum* #5 (resistant control). The *p*-values correspond to significance levels compared with the resistant control in *t*-tests.

Resistance to *S. graminum* has previously been found in wheat carrying rye and *A. speltoides* chromatin (Table 1). In Paper I, resistance was only found in *A. speltoides*-derived genotypes 7A.7S-L7, 7A.7S-L5 and 7A.7S-Gb5, the latter carrying the gene *Gb5*. The results indicated that both tolerance, in the form of less chlorosis, and antibiosis can be components of the resistance in these genotypes. However, tolerance seems to be the major component in 7A.7S-L7 *S. graminum* resistance. Further evaluations are required to characterise the mechanisms underlying the resistance.

Attempts were made in Paper II to evaluate the yield protection conferred by the genotypes (1B)1R_e, 1AL.1RS_{am}, (1D)1R_{pr}, 1AL.1RS_e and 7A.7S-L5 grown in the field under aphid pressure. These genotypes were planted in

north-west Mexico in a split-plot experimental design with two treatments (aphid-infested and non-infested) and three sowing dates during the 2012-2013 growing season. The aphid populations in the field were not sufficiently large to inflict significant differences in yield and yield components. Nonetheless, significant differences in aphid population densities were found among genotypes identified as resistant and susceptible under controlled conditions (Figure 7). Heritability estimates across sowings were 0.79 and 0.56 for *R. padi* and *S. graminum*, respectively, which indicates that most of the phenotypic variation observed was due to the plant genotypes rather than the environment. However, a significant interaction between genotype and sowing date was found, so the results shown in the lower graph in Figure 7 must be interpreted with caution. Genotypes 1AL.1RS_e and (1D)1R_{pr} reduced *R. padi* field populations across all sowing dates, by 32.8% and 24.1%, respectively. Genotype 7A.7S-L5 reduced the *S. graminum* field population by 74.8, 74.1 and 48.5% in the three sowings compared with the control (Paper II). These results were well in line with previous findings in the laboratory experiments (Paper I).

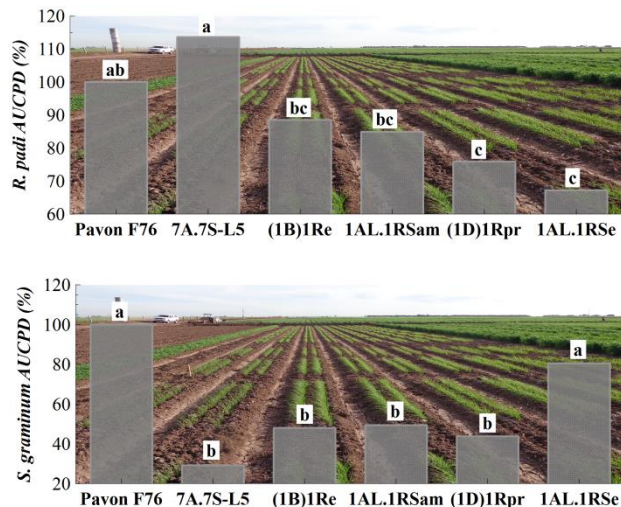


Figure 7. Area under the curve of aphid population development (AUCPD) relative to the susceptible control Pavon F76 in genotypes evaluated in the field across three sowing dates. Genotypes with different letters are significantly different at $p < 0.05$ in Fisher's LSD test.

4.2 Disease resistance of wheat-alien lines with known responses to wheat aphids (Paper III)

Rye was reviewed as a source of resistance to different biotic constraints of wheat, with the genetic stock in the background of the cultivar Pavon F76 being taken as an example. It can be advantageous for breeding purposes if resistance to both pests and diseases is found in single translocations. Since there is no recombination between homoeologous chromosomes of wheat and rye in the presence of the *Ph1* locus or the absence of chemical treatments, the rye segment is inherited as a block when crossed with wheat lacking the same homoeologous rye chromosome. However, a disadvantage of this feature is that the alien chromatin may also confer undesirable characteristics, and thus further efforts are required to reduce the amount of the alien source in the wheat genome.

Rye has been widely studied as an important source of desirable agronomic characteristics in wheat. Resistance to leaf rust (*Puccinia triticina* Erikss.), yellow rust (*P. striiformis* var. *striiformis* Westend), stem rust (*P. graminis* Pers. f. *sp. tritici* Erikss. and E. Henn.) and powdery mildew (*Blumeria graminis* [DC.] f. *sp. tritici* Em. Marchal) has been identified in different rye sources. Chromosome 1R from Petkus rye has been the most frequently deployed source since the 1960s. It carries *Lr26*, *Yr9*, *Sr31* and *Pm8* resistance genes for leaf rust, yellow rust, stem rust and powdery mildew, respectively. Other favourable characteristics associated with this translocation are yield improvement and wide adaptation (Villareal *et al.*, 1998; Villareal *et al.*, 1996; Villareal *et al.*, 1994; Villareal *et al.*, 1991). However, there are many other rye resistance sources apart from Petkus rye (An *et al.*, 2013; Zhuang *et al.*, 2011; Lu *et al.*, 2010; Ren *et al.*, 2009; Luo *et al.*, 2008; Tang *et al.*, 2008; Hysing *et al.*, 2007; Malik *et al.*, 2003; Dundas *et al.*, 2001; Marais *et al.*, 1994; Friebe *et al.*, 1990; Heun & Friebe, 1990).

In Paper III, a list of 2470 lines and varieties carrying alien introgressions (Schlegel, 2014) was matched with the varieties released by countries affiliated to the International Union for the Protection of New Varieties of Plants (UPOV). The data indicated that in Chile, 34% of the commercial varieties released between 2000 and 2013 carry rye introgressions, whereas in Russia and Australia this proportion is 1-2%. Schlegel's compilation matched 15% of commercial varieties registered in the database of the Journal of Plant Registrations of the USA².

². <http://www.ars-grin.gov/cgi-bin/npgs/html/csrlist.pl?> Accessed on February 2014

The Pavon F76 stock was screened for resistance against powdery mildew (Bgt), Fusarium head blight (FHB; *Fusarium* spp.) and *Septoria tritici* blotch (STB; *Mycosphaerella graminicola* [Fückl]) in disease nurseries managed by Lantmännen Lantbruk during summer 2013. The stock was planted at three locations; one in Sweden and two in Germany. Resistance against Bgt was also evaluated in a greenhouse assay with a Swedish isolate from the wheat cultivar Revelj. Moreover, attempts were made to evaluate BYDV damage in a greenhouse experiment but, possibly due to growing conditions, the evaluation was unsuccessful. In addition, a review was made of previous studies that had evaluated the agronomic performance of the stock.

Several genotypes carrying 1R chromatin had low scores for one or more diseases, and four of these had previously been found to be resistant to *R. padi* and *S. avenae*. Many of the genotypes carrying 2R, 3R, 4R, 5R and 6R also had low scores for one or more diseases.

The Kendall's Tau correlation coefficient showed no correlation ($Tau=0.036$, $P=0.71$) between scores of STB in Sweden and Germany. This may indicate that STB strains in those locations are different from each other, and also that the resistance observed in the stock may be race-specific.

4.3 Wheat genomic regions associated with *R. padi* and *S. graminum* resistance (Paper IV)

With the objective of identifying the genetic basis of resistance to *R. padi* and *S. graminum* in the SHW CWI76364, in Paper IV an F6 mapping population was studied, consisting of 140 recombinant inbred lines (RILs) derived from the cross of this SHW and the spring wheat cultivar Seri M82 (aphid susceptible). The population was phenotyped for resistance to these two aphid species. The presence/absence of pubescence in RILs was also scored. Aphid growth and plant biomass reduction due to *R. padi* feeding were measured under controlled conditions. Symptoms due to *S. graminum* feeding were scored in a greenhouse assay and population density of *S. graminum* was estimated in a field trial. A genotyping-by-sequencing (GBS) approach was used to identify genomic regions associated with resistance traits.

A genomic region on chromosome 4BL was found to be associated with *R. padi* growth and was designated *QRp.slu-4BL*. This region is located 14.6 cM from the pubescence locus in the same chromosome arm. However, no association between these two traits or any other resistance measurement was found. *QRp.slu-4BL* is located in the same chromosome arm in which genes responsible for the synthesis of Hx have previously been mapped (Nomura *et*

al., 2002). It would be of great interest to determine whether there is an association between Hx concentrations in the mapping population and *QRp.slu-4BL*.

Two genomic regions associated with tolerance (plant biomass reduction) to *R. padi* were found on chromosome 5AL and 5BL and designated *QRp.slu-5AL* and *QRp.slu-5BL*, respectively. These two QTL appeared to act in an additive fashion (Figure 8). An epistatic interaction was detected between *QRp.slu-5AL* and a locus in chromosome 3AL, which was designated *EnQRp.slu-5AL*. This epistatic interaction significantly explained about 5% of the total phenotypic variation and appeared to enhance tolerance to *R. padi* (Figure 9).

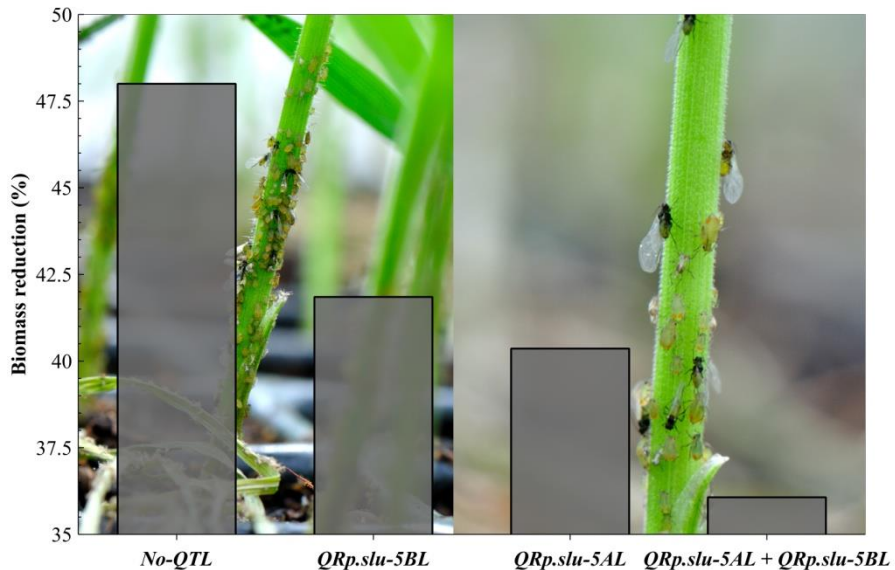


Figure 8. Individual and combined effects of the *QRp.slu-5AL* and *QRp.slu-5BL* genomic regions on plant biomass reduction due to *R. padi* feeding in 140 recombinant inbred lines (RILs). Labels on the x-axis refer to RILs without and with one or both QTL markers.

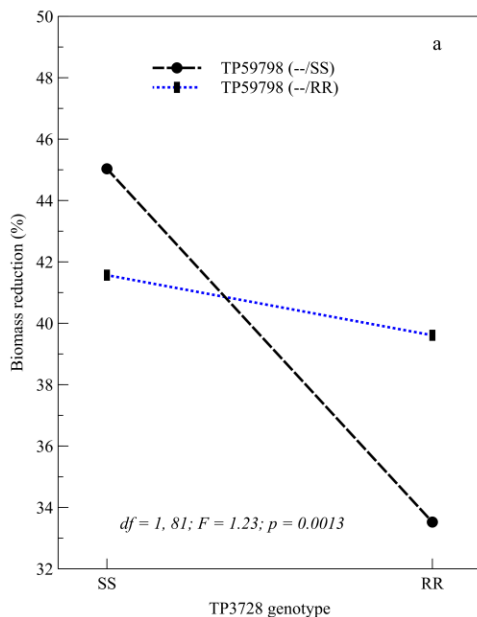


Figure 9. Interaction plot of the GBS markers linked to *QRp.slu-5AL* (TP3728) and *EnQRp.slu-5AL* (TP59798). The labels SS and RR indicate whether alleles originate from the resistant (RR) or susceptible (SS) parent. Degrees of freedom (*df*), *F*-value (*F*) and *p*-value (*p*) from the analysis of variance are indicated.

Evaluation of *S. graminum* resistance in the greenhouse assay resulted in the identification of a genomic region associated with plant symptoms to aphid infestation in chromosome 7DL. This is putatively the gene *Gba*, previously mapped in the SHW CETA/A. *tauschii* Wx1027 (Zhu *et al.*, 2005), which carries the same *A. tauschii* source as CWI76364. This was the only region found to be associated with plant symptoms. The locus was also associated with the number of *S. graminum* per tiller in the field together with a new QTL on chromosome 2DL, designated *QGb.slu-2DL*. These two regions (*Gba* and *QGb.slu-2DL*) appeared to act in an additive fashion (Figure 10).

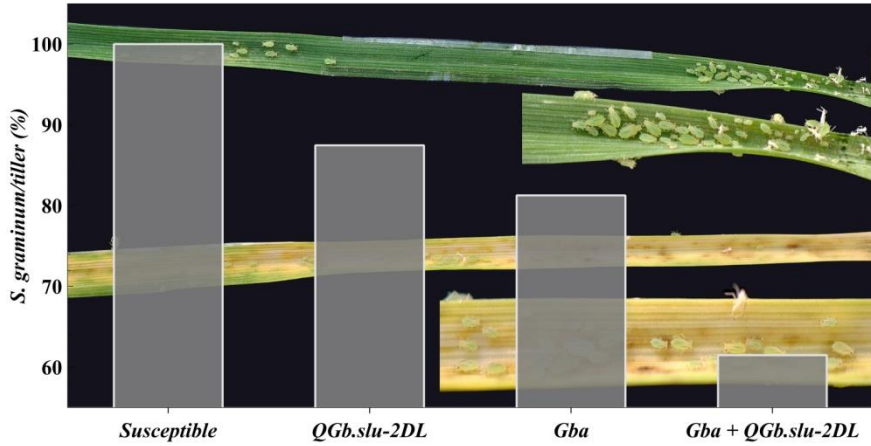


Figure 10. Individual and combined effects of the putative gene *Gba* and the *QGb.slu-2DL* genomic region on the relative number of *S. graminum*/tiller in the field. Labels on the x-axis refer to the susceptible parent (Seri M82) and RILs carrying one or both QTL markers.

5 Wheat breeding for aphid resistance

Unlike many other breeding components that are well incorporated into current wheat breeding pipelines, aphid resistance demands considerable logistic efforts. It is difficult to incorporate aphid resistance without sacrificing other breeding components and benefits of breeding strategies. Wheat improvement simultaneously requires the selection of high yielding lines, well adapted to the growing conditions, with tolerance to abiotic factors as well as resistance to diseases and sometimes pests other than aphids.

Complications arise because conventional breeding programmes often require large population sizes of segregating generations, where the best individuals are selected in the field. At the same time, it is critical to have high and homogeneous aphid populations across time and space in order to accurately select aphid-resistant plants based on their phenotypic response. Furthermore, when the targeted aphid species does not cause symptoms on the plants, it is very difficult to carry out phenotypic selection and the identification of resistant progeny is only possible by phenotyping for the category of resistance to be transferred. It is also important to evaluate whether aphid resistance is associated with undesirable agronomic traits. Thus pre-breeding plays an important role in transferring aphid resistance.

Nowadays, molecular markers can substitute for phenotypic evaluations. Therefore, accurate identification and characterisation of resistance sources, along with gene mapping, are crucial for the efficient incorporation of aphid resistance into wheat. The next generation sequencing technologies allow efficient identification of single nucleotide polymorphisms (SNP) associated with aphid resistance in large populations. This information can be used in marker-assisted selection (MAS), which reduces phenotyping in breeding material and makes it possible to select individuals carrying a desired resistance gene(s). Aphid resistance breeding would greatly benefit from MAS, as phenotyping would be reduced. Besides, studies have shown that it is necessary to pyramid aphid resistance genes to have resistance to multiple

aphid species and their biotypes. Thus gene mapping and/or gene discovery are crucial steps to incorporate aphid resistance in wheat by means of MAS.

Based on the work presented in Papers I-IV, a plant breeding strategy to incorporate aphid resistance was devised (Figure 11). The strategy is intended to be applied in a conventional wheat breeding approach based on limited back-crossing and a selected-bulk selection (SBS) method.

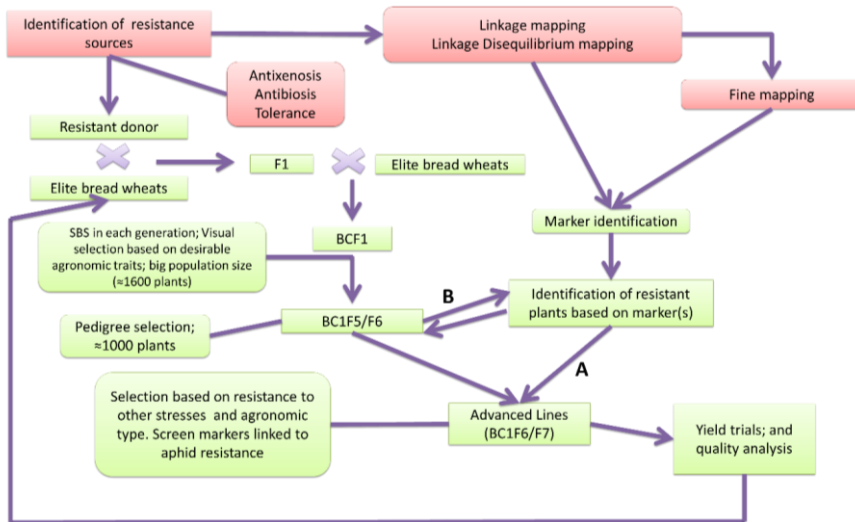


Figure 11. Wheat breeding strategy for the incorporation of aphid resistance under a limited backcrossing and selected-bulk selection (SBS) approach with the aid of molecular markers. A) Marker screening at late generations during pedigree selection; B) marker analysis of the advanced lines at the end of the selection process. The strategy requires the identification and genetic understanding of aphid resistance sources to efficiently incorporate genes of interest. Taken from: Crespo Herrera (2012).

6 Conclusions and future prospects

The studies conducted within the framework of this thesis allowed new resistance sources to aphids to be found in a genetic stock where rye- and *A. speltoides*-derived lines had resistance to one or two aphid species (Papers I-III). The results of the field studies agreed well with those of evaluations made under controlled conditions. The lines that appeared to be resistant in seedling assays also reduced the aphid population size in the field. These results indicate that rye and *A. speltoides* are valuable sources of resistance to aphids and to other biotic stresses for wheat, as shown in the disease resistance evaluations.

Genomic regions associated with aphid resistance traits were successfully mapped in a SHW. Paper IV is the first publication in wheat to map resistance to *R. padi* and a genomic region for *S. graminum* resistance not reported previously. These results require further investigation in order to fine-map the genomic regions. However, all sources identified throughout Papers I-IV already have potential applications in wheat breeding programmes aiming to incorporate aphid resistance in their elite material.

From the work in Papers I-IV, a number of prospects emerged on how to carry on the study of wheat resistance to aphids in the plant materials used. These are:

- To evaluate the plant materials for resistance against *D. noxia*.
- To study the inheritance of resistance to *R. padi* and *S. avenae* in the wheat-rye translocation lines identified.
- To study the mechanisms behind the seedling and adult plant resistance to *S. avenae*.
- To study the resistance patterns to *S. graminum* in the *A. speltoides*-derived lines and determine whether such differences are due to different loci present in the *A. speltoides* chromatin.
- To determine the levels of yield losses due to aphid feeding in the resistant germplasm identified.

- To determine whether there is a correlation between Hx concentrations and *R. padi* resistance in the mapping population derived from the SHW CWI76364.
- To study the molecular mechanisms behind the epistasis interaction detected in the expression of *R. padi* tolerance.
- To conduct validation steps of the QTL found for resistance to *R. padi* and *S. graminum* with other aphid populations and other environments.
- To conduct genetic studies to study the inheritance of each QTL found in the mapping population.
- To fine-map the new QTL for resistance to *R. padi* and *S. graminum*.
- To use the sequence information of the SNPs associated with the resistance QTL to produce easy-to-use markers such as STS or KASP.
- To transfer the resistance identified here into elite wheat germplasm.
- To explore the suitability of new breeding tools such as genomic selection to incorporate and combine different categories of resistance to multiple wheat aphids.

The knowledge that has been accumulated throughout the history of aphid resistance research in wheat is highly valuable and provides great opportunities to successfully deploy resistance in elite germplasm. However, further efforts are required to characterise and incorporate resistance into commercial varieties.

Farmers would benefit greatly if aphid-resistant varieties could be grown, since insecticide treatments would be reduced and thus wheat could be grown in a more sustainable manner, with less damaging effects on the environment. Furthermore, for farmers without the possibility to apply chemical control, aphid resistance in cultivars would alleviate their yield losses and improve their income.

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Acknowledgements

As the last four years went by, several people contributed in different ways to the completion of my studies. I am thankful to all the persons I met in Sweden, as in different moments and for different reasons, they were all present in my everyday life while I was away from Mexico. I am also thankful to all my friends and family back in my homeland, from whom in the distance and in Mexico itself I received a lot of support.

Several people have contributed to the completion of this PhD project, and I want to start thanking my three supervisors, as their guidance and support was a major component of my PhD: *Inger Åhman*, who was willing to take the chance in accepting me as her student and since then on, was always a source of knowledge, encouragement and positive inputs; under her supervision I had enough freedom to try and explore different things for my studies, which was a fundamental part of my PhD education. *Larisa Gustavsson*, who also accepted to co-supervise my studies and always contributed with the best of her to my PhD project; she always gave encouragement and held interesting discussions with me. *Ravi P. Singh*, who first introduced me to the world of wheat breeding and gave me the opportunity to work for the wheat program at CIMMYT where the subject of this PhD project arose; ever since, he always shared his knowledge and vision, and had always time to answer all my questions.

I am also very thankful for the kind support I received from: *Michael Smith*, who allowed me to conduct part of my work in his lab at KSU; he provided valuable inputs and feedback to my work and undoubtedly played an important role in the completion of my studies. *Eduard Akhunov* and *Katherine Jordan*, who kindly had me in their lab at KSU to conduct part of my work; as they shared their knowledge and experience with me, they also had important contributions to the completion of my studies.

I want to acknowledge the financial support provided by the Monsanto's Beachell-Borlaug International Scholars Program, and all members of the Panel of Judges that considered this PhD project to be funded.

At SLU I want to thank *Vehbo Hot*, who shared his practical experience and was a great support during my studies. Thanks to *Jan-Eric Englund* and *Estelle Proux-Wéra* who provided support in different stages of my studies. Thanks to *Ida Lager*, *Dharani Burra*, *Rui Ruan*, and *Johannes Albertsson* as they shared their views in various subjects and provided help whenever I needed it. To *Mary McAfee* for her help in language editing. Thanks to the staff in Alnarp Repro Unit for their professional service in printing.

Thanks to the Lantmännen Lantbruk team, as they provided support in disease evaluations.

At CIMMYT, I want to thank *Pawan Singh* for his trust and support since we met. Thanks to *Julio Huerta* for sharing his knowledge and always holding nice informative conversations. To *Jose Crossa*, who provided valuable advice on data handling. Also to *Jorge Montoya*, *Ramon Delgado*, *Chito*, *Lalo*, *Vicente Morales* and *Juan Ramirez*, for their help in conducting field trials and germplasm management. Thanks to the staff at CIMMYT's germplasm bank for providing plant materials.

To *Eric Lopez* and *Fredrik Reslow* for their friendship.

I am thankful to my parents, *Leonardo Crespo* and *Luminosa Herrera*, my brother *Tedy Crespo*, and sisters *Isamar Crespo* and *Divina Crespo*. Together they are a continuous source of unconditional support.

I am also thankful to my closest family, *Sybil* who has been very supportive and understandable throughout this period and also to my little *Leo* who has been as supportive and understandable as a beautiful baby can be.