HOST RELATIONSHIPS OF THREE APHID SPECIES ON WHEAT IN THE GENUS *Triticum*: POTENTIAL FOR CROP RESISTANCE IN SPRING WHEAT

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Dedicated to my Wife

Monicah Muthoni

and our children,

Mishek, Mary and Grace

and my mother

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ABSTRACT

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Aphids are the most cosmopolitan insect pests of common wheat, *Triticum aestivum* L. and durum wheat, *Triticum durum* Desf. and occasionally cause serious yield losses. Host plant resistance is a desirable aphid management strategy in regions such as North America, where the crop has a narrow profit margin.

Genetically diverse cultivated and wild wheats were used as tools for investigating the potential of crop resistance in the management of cereal aphids: *Rhopalosiphum padi* L., *Sitobion avenae* (Fabricius) and *Schizaphis graminum* (Rondani) which are pests of adult plants of spring wheat. Because relatively little information is available on resistance to aphids in adult wheat plants, the first step was to determine methods that might be used to investigate this resistance, and then to characterize the level of resistance. The second step was to assess whether the low level of resistance generally observed in modern cultivated wheats can be attributed to domestication. The third step was to focus the search for resistance to *S. avenae* in adult plants on *Triticum monococcum* L., because it's genome is one of the smallest in the genus, it is the

progenitor of domesticated wheats, and it is suspected of being more resistant to aphids than modern wheats.

Biomass relationships between the aphids and the wheats were quantified to estimate resistance. Degrees of resistance were quantified by plant biomass loss during infestation. The antibiosis component of resistance was measured by comparing aphid biomass gain on susceptible check and test lines. The tolerance component of resistance was estimated as plant biomass loss per unit biomass gained by aphids. Cultivated Canadian Spring wheats (Canadian Western Red Spring, Canadian Prairie Spring and Canadian Western Amber Durum) exhibited low levels of resistance to aphids, although Canadian Western Red Spring was more resistant than the highly susceptible Canadian Prairie Spring wheat. There was no correlation between seedling resistance and adult plant resistance among wheats tested at the two growth stages. Resistance shown by seedling plants was largely antibiosis, and resistance shown by adult plants was largely tolerance. The level of resistance was associated with the degree of domestication, with the frequency of resistant accessions being high in the least domesticated diploid wheats and low in the most domesticated hexaploid wheats. However resistant wheats were identified at all ploidy levels. Resistance in wheats is not general to all the aphid species, but species-specific in different wheats. Several accessions of the diploid *T. monococcum* have high levels of resistance to *S. avenae*. Overall, spike biomass more effectively estimated resistance than did foliage biomass. Seedling resistance to aphids cannot be used to predict adult plant resistance. The potential use of wild wheats in screening and plant breeding programs for resistance to aphids is discussed.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

FOREWORD

This thesis is written in manuscript style according to the format of the Bulletin of Entomological Research. Chapter 1 is a general introduction and outlines the problem being investigated. Chapter 2 contains a literature review of host relationships of cereal aphids and wheats in the genus *Triticum*. Chapters 3, 4 and 5 are manuscripts each of which represents a separate research topic; these combined form the body of the thesis. Chapter 3 reports on levels of resistance of spring wheats to three aphid species and the methods used to investigate this resistance. Chapter 4 reports on assessment of whether the low levels of resistance observed in modern cultivated wheats can be attributed to domestication. Chapter 5 contains a research report on screening *Triticum monococcum* L. for resistance to one aphid species, *Sitobion avenae* (Fabricius). Chapter 6 is a general discussion which relates the information contained in the manuscripts and previous research reported in Chapter 2, and describes broader implications of the findings. Chapter 7 consists of a summary of the significant findings, conclusions and suggested future studies. Literature cited contains a reference list of all citations. Lastly, an appendix is provided containing the necessary supporting data that were not included in the manuscripts.

CHAPTER 1

General Introduction

Aphids are the most cosmopolitan insect pests of common wheat, *Triticum aestivum* L. Over 30 species are capable of surviving on the crop, and six species are recognized as pests of economic importance worldwide: bird cherry-oat aphid, *Rhopalosiphum padi* (L,), corn leaf aphid, *Rhopalosiphum maidis* (Fitch), greenbug, *Schizaphis graminum* (Rondani), Russian wheat aphid, *Diuraphis noxia* (Mordvilko), English grain aphid, *Sitobion avenae* (Fabricius) and rose-grass aphid, *Metopolophium dirhodum* (Walker)(Blackman & Eastop, 1984). Each spring, winged dispersers of *R. padi*, *S. avenae* and *Sc. graminum* colonize small grain crops on the northern Great Plains of the U.S.A. and the Prairies of Canada (Robinson & Hsu, 1963; Kieckhefer *et al.*, 1974; Migui, 1996). The dominant crop in the region is spring-sown wheat comprising common wheat and durum wheat, *Triticum durum* Desf. (DePauw *et al.*, 1995). These wheats are most susceptible to aphid damage from flowering through kernel formation (Johnstone & Bishop, 1987). Colonies of *S. avenae* and *R. padi* occur on spikes (Migui, 1996), where they reduce seed yield by directly competing with the filling grain for plant nutrients. In Scandinavia, *R. padi* is regularly a pest of spring cereals and causes direct crop losses of as much as 10% in an outbreak year (Sundell, 1977). Aphid feeding on wheat spikes can cause as much as 42% yield loss in western Europe (George & Gair, 1979).

For the past several decades, aphid control on wheat (here defined as any species in the genus *Triticum*) concentrated on use of chemical insecticides as the first line of defence. For example, in western Europe, the adoption of high yield wheat technology has resulted in absolute dependence on insecticides (Vereijken *et al.*, 1985), and insecticide applications begin at the onset of flowering (George & Gair, 1979). In Southern U.S.A., granular insecticides have been applied to the soil to control early aphid infestations on wheat (Cate *et al.*, 1973). The routine application of insecticides has led to the development of aphid populations exhibiting resistance to insecticides, for example, some *Sc. graminum* genotypes are resistant to organophosphate insecticides (Teetes *et al.*, 1975). Moreover, insecticides cause harmful effects on non-target organisms and the environment (Flickinger *et al.*, 1991). Because of such problems, and because wheat yield and profit margins are low in many regions of the world (Briggle & Curtis, 1987; Webster, 1990), the need for alternative approaches to control pests cannot be overemphasized. Other aphid control options include cultural practices, classical biological control, and plant resistance.

Host plant resistance is a particularly desirable method of managing aphid populations because it is compatible with other aphid control options and helps conserve the natural enemies of aphids. For example, the use of sorghum hybrids, *Sorghum bicolour* (L.) Moench, particularly resistant to *Sc. graminum* biotype C, allow the use of extremely low dosage rates of insecticides (Cate *et al.*, 1973). Cultivars resistant to *Sc. graminum* released sequentially prevented millions of dollars in crop losses and insecticide use each year in the U. S. A., even though appropriate resistance management

did not prevent development of new biotypes (Porter *et al.*, 1997, 2000). However, no evidence of relationship between resistant crops and biotype development was found (Porter *et al.*, 1997).

Plant resistance to insects is usually a relative phenomenon: the resistant plant is less damaged by the insect pest than a more susceptible plant. Where the level of resistance is not high but still potentially useful, it is referred to as partial resistance. Most previous research on resistance to cereal aphids has been conducted on winter wheat seedlings because seedlings are more easily screened than adult plants, winter wheat dominates production in Europe and the United States of America, and cereal aphids tend to attack winter wheat earlier in its development than they attack spring wheat. In the U. S. A., evaluation of seedlings of cultivated wheats for resistance to *Sc. graminum* and *D. noxia* showed low levels of resistance (Starks & Merkle, 1977; Smith *et al.*, 1991). In Canada, screening of seedling barley varieties, *Hordeum vulgare* L., for resistance to *R. padi* revealed no reliable resistance source (Hsu & Robinson, 1962, 1963). Screening of immature wheat and barley cultivars in France and Great Britain revealed low levels of resistance to *S. avenae* (Lowe 1984a; Dedryver & Di Pietro, 1986; Di Pietro & Dedryver, 1986). Some studies looked at the possibility of finding resistance to aphids in adult wheat cultivars, and again only low levels of resistance were reported (Stokes *et al.*, 1980; Lowe, 1984b; Lee, 1981, 1984; Dewar *et al.*, 1985; Riedell *et al.*, 1999). Nonetheless, some wheat cultivars have been found to exhibit resistance to aphids. Havlickova (1993) found resistance to *S. avenae* in winter wheat cultivars and associated the resistance with long awns.

The search for sources of wheat resistant to insects and pathogens has sometimes turned to the wild relatives of cultivated wheats. Five Hessian fly-resistance genes, H13, H22, H23, H24 and H26 have been transferred from *Triticum tauchii* (Coss.) Schmal. to common wheat (Raupp *et al.*, 1993; Cox & Hatchett, 1994). Two genes conferring resistance to stem rust, *Sr36* and *Sr37*, have been transferred to common wheat from *Triticum timopheevii* Zhuk. and *Sr40* has been transferred from *Triticum araraticum* Jakubz. (Allard & Shands, 1954; Dyck, 1992). In glasshouse studies, Sotherton & Van Emden (1982) demonstrated that the ancient wheat, *Triticum monococcum* L., was more resistant to *S. avenae* than modern wheat cultivars. Kazemi & van Emden (1992) reported that emmer wheat, *Triticum dicoccum* Schrank, a tetraploid, exhibited higher resistance to *R. padi* than hexaploid wheat. Harvey *et al.* (1980) identified resistance to *Sc. graminum* bioptype C in synthetic hexaploid wheats derived from *T. tauschii* var *strangulata* and *T. tauschii* var *typica*. Genes for resistance to *D. noxia*, have been found in *T. monococcum*, *T. tauschii* and *Triticum ventricosum* Ces. (Nkongolo *et al.*, 1990). Thus, wheat species throughout the genus *Triticum* might serve as potential sources of resistance to cereal aphids, although no comprehensive examination of resistance to aphids has been undertaken for the genus.

For thousands of years the genus *Triticum* has gone through a large evolutionary change, some of which is human driven. Both cultivated and wild wheats naturally occur in three ploidy levels: diploid, tetraploid and hexaploid (Bowden, 1959). There are eight distinct haploid genomes of seven chromosomes within the genus *Triticum*, named as A, B, C, D, G, M, S, U (Kimber & Sears, 1987). These haploid genomes occur in diploid

sets in the wheat species (Peterson, 1965). The primary commercial species are common wheat, *T. aestivum*, and durum wheat, *T. durum*, but other species have been grown under cultivation, particularly in the past. Common wheat is a hexaploid species with the genome AABBDD and durum is a tetraploid with the genome AADD (Kimber & Sears, 1987). The commercial wheats have evolved through domestication from wild diploid and tetraploid ancestors.

Although some potential sources of resistance have been identified, plant breeders rarely use susceptibility or tolerance to aphids as criteria for retaining superior lines of wheat. Aphids and their damage are usually cryptic and often ephemeral, which both limits the attention paid to the damage and makes resistant phenotypes difficult to identify, particularly partially resistant phenotypes. Furthermore, on the Prairies of Canada and the northern Great Plains of the USA, cereal aphids are pests of adult plants, because they disperse into these areas in late spring rather than overwintering locally (Robinson & Hsu, 1963; Irwin & Thresh, 1988). Finally, cereal aphids consist of a variety of species, representing different genera, and the species composition varies from area to area. The relative pest status of these aphids and the potential of specific resistance mechanisms to be effective against different species are poorly understood.

In this study, genetically diverse cultivated and wild wheats were used as tools for investigating the potential of crop resistance in the management of cereal aphids which are pests of adult plants of spring wheat. Because relatively little information is available on resistance to aphids in adult plants of spring cultivated wheat, the first step was to determine methods that might be used to investigate this resistance, and then to

characterize the level of resistance or susceptibility shown by these wheats (Chapter 3). The second step was to assess whether the low level of resistance generally observed in modern cultivated wheats can be attributed to domestication (Chapter 4). This question was addressed by examining the levels of adult plant resistance in diverse accessions of wheats in the genus *Triticum* to reveal patterns of change in resistance in relation to the evolution of species in the genus. The methods tested in Chapter 3 were adapted to this purpose. The patterns of resistance in *Triticum* were also used to reveal species in the genus which might provide the best sources of resistance. The third step was to focus the search for resistance to aphids in adult plants on one species in the genus *Triticum* (Chapter 5). Diverse accessions of *T. monococcum* were investigated for resistance, because this species has one of the smallest genomes in the genus, it is the progenitor of domesticated wheats, and it is suspected of being more resistant to aphids than modern wheats.

CHAPTER 2

Host relationships of cereal aphids and wheats in the genus *Triticum*: a literature review on the potential of crop resistance for aphid pests

Abstract

The current utilization of host plant resistance in cultivated wheat against aphids is reviewed. Extensive screening of cultivated wheat germplasm in North America and western Europe shows low levels of resistance to *Schizaphis graminum* and *Sitobion avenae* respectively. The occurrence of aphid genotypes that cause different reactions in the same host plant complicate the search for aphid resistant wheat germplasm. A review of the origin and evolution of wheat shows that many species within the genus *Triticum* are closely related to wheat and form fertile hybrids which facilitate transfer of useful genes from wild wheat to common wheat. A variety of wild wheats has been used as sources for resistance to pathogens and insect pests. Some primitive relatives of wheat are reported to have high levels of resistance to aphids and are considered valuable components of resistance breeding programs. Utilization of wheat cultivars with resistance to aphids would provide a desirable base to which other pest management strategies could be added.

Introduction

Wheat, *Triticum aestivum* L. (Gramineae), is the most widely grown food crop in the world, followed by rice and corn (Campbell & Shebeski, 1986). Wheat is grown in a wide range of conditions from subsistence agriculture in parts of the Near/Middle East, to high technology, extensive production in North America and Australia, and to high technology intensive production in northern Europe (Briggle, 1980). In Canada, wheat is the principal crop grown with 95% of the total production coming from the three prairie provinces, Manitoba, Sakatchewan and Alberta (Briggle & Curtis, 1987). The prairie provinces of Canada and the Northern Great Plains of the USA are characterized by long and cold winters, short and hot summers and low rainfall (Briggle & Curtis, 1987). Although the relatively low rainfall limits yield, it is an important factor in producing grain that is high in protein and high in baking quality (Briggle & Curtis, 1987).

Wheat crops are attacked by a number of arthropod pests that reduce grain yield and quality. Insect pests of wheat on the prairies include: grasshoppers, wheat midge, cutworms, wireworms, wheat stem sawfly and aphids (Olfert, 1986). Cereal aphids are usually not able to overwinter on the Canadian prairies or the northern plains of the U.S.A. (Robinson & Hsu, 1963; Irwin & Thresh, 1988) and these areas are thought to be re-invaded annually by dispersers from the south. Occasional outbreaks of aphids in these regions can result in serious yield losses (Haber, 1990; Kieckhefer & Kantack, 1980).

In the southern U.S.A., wheat is treated annually with insecticides to control Russian wheat aphid, *Diuraphis noxia* (Mordvilko), and greenbug, *Schizaphis graminum* Rondani (Flickinger *et al.*, 1991). In the northern U.S.A. and southern Canada

applications of insecticides to control aphid pests of wheat are less wide-spread and less frequent than in the southern U.S.A. Frequent use of insecticides sometimes has led to development of insecticide resistant aphid populations. For example, some greenbug populations are resistant to organophosphate insecticides (Teetes *et al.*, 1975). Moreover, insecticides cause undesirable effects on non-target organisms and the environment. For example, in the Texas Panhandle, in 1988, 200 Canada geese were killed in a wheat field due to acute toxicity of parathion sprayed to control *D. noxia* (Flickinger *et al.*, 1991). Such incidents have led to increasing awareness of the need to adopt integrated pest control schemes that minimize the use of pesticides. The use of host plant resistance is a desirable approach because resistant plants are usually associated with reduced damage by pests. For example, the sequential release of wheat cultivars resistant to *Sc. graminum*, prevented millions of dollars in crop losses and insecticide use each year, even though use of appropriate resistance management did not prevent development of new biotypes (Porter *et al.*, 1997, 2000). Where the level of resistance is not high but still potentially useful, it is referred to as partial resistance. Even partial resistance could confer considerable benefits in aphid management on wheat. This chapter reviews the current utilization of host plant resistance and explores the potential for exploiting wild relatives of wheat as sources of resistance for aphid management in cultivated wheat.

Origin of wheat

Bread, the main product from common wheat, has been a basic food for humans throughout recorded history and probably for a much longer period. The story of the

growing of wheat dates as far back as the development of civilization (Hind, 1931). The discovery of wheat in the rubbish heaps of the lake dwellings of both Switzerland and Italy by archeologists provides a clear indication that this cereal was cultivated by pre-historic humans (Buller, 1919). Wheat is thought to have originated in the Middle East, during the Old Stone Age, several hundred thousand years ago (Peterson, 1965). The oldest reported samples of wheat were carbonized spikelets from Iraq dated at approximately 6700 B.C. (Campbell & Shebeski, 1986). The carbonized spikes were identified as wild einkorn wheat, *Triticum boeoticum* Bois, wild emmer, *Triticum dicoccoides* Körn., and a species of wheat resembling emmer, *Triticum dicoccum* Schrank. Non-carbonized grains or spikelets found in containers under perpetually dry conditions in ancient Egyptian storage pits and tombs had possibly been in storage for centuries or millenia (Peterson, 1965). The diploid, wild einkorn and the tetraploids, wild emmer, emmer, and wild timopheevii, *Triticum araraticum* Jakubz., were probably taken into cultivation around the same time, about 8,000 B.C., and the hexaploid wheat, *Triticum spelta* L. around 3000 B.C. (Morris & Sears, 1967, Harlan & Zohary, 1966, Lev-Yandun *et al.*, 2000). Emmer spread rapidly displacing other cultivated wheats and remained dominant in the Near East for several thousand years (Helbaek, 1959). In China, records of wheat cultivation date back to 2700 B.C. (Buller, 1919). *Triticum durum* Desf. appeared in the Mediterranean areas of Europe, Africa and Asia about 300 B.C. (Campbell & Shebeski, 1986). Peterson (1965) suggested that *T. durum* probably arose in Egypt from emmer.

The present distribution of wild wheats may provide clues to the regions of origin and early domestication. According to Vavilov (1951), common wheat now in cultivation was derived from one or more species of wild grass that grew somewhere in Asia, its centre of origin. Based on the abundance of wild wheats, Harlan & Zohary (1966) concluded that emmer was domesticated in the upper Jordan watershed and that einkorn was domesticated in southeast Turkey. These areas lie within the region known as the Fertile Crescent, one of the cradles of civilization. Presently all the wild species of wheat are distributed in the Mediterranean basin and in southwest and central Asia with the centre of distribution being southeast Turkey (Kimber & Feldman, 1987). Climate in the area is characterized by short, mild and rainy winters and long, hot and dry summers. All the species within the genus *Triticum* have adapted to this climate by being annuals that grow in the winter and pass the hot dry summer as seed (Kimber & Feldman, 1987). The present natural distribution of the *Aegilops-Triticum-Amblyopyrum* complex occupies the region extending from Morocco to China and from Iran to Russia (Valkoun, 2001).

For many centuries, wheat growing was confined to the three old world continents of Asia, Europe and Africa. Near the end of the 15th century, wheat was taken to Australia and the Americas by explorers, traders and settlers. Wheat was brought to North America in 1493 by Christopher Columbus, and subsequently introduced to Mexico in 1510 and Canada in 1605 (Campbell & Shebeski, 1986). At present, over 20,000 modern cultivars of wheat, which are adapted to a wide range of environments, are grown in virtually all countries of the world (Feldman & Sears, 1981).

Evolution of wheat

The cultivated wheats belong to the tribe Triticeae of the family Graminae. Rye (*Secale*) and barley (*Hordeum*) also belong to Triticeae. Triticeae is divided into two sub-tribes, the Triticinae and the Hordeinae, each of which has seven genera (table 2.1). Members of different genera within these two sub-tribes occasionally form hybrids, facilitating gene flow either through crossing over or through formation of an amphiploid species, i.e., a fertile interspecific hybrid with a complete set of paired chromosomes derived from each parent species (Poehlman & Sleper, 1995).

Over the past thousands of years the genus *Triticum* has gone through large evolutionary changes, which are still proceeding in a dynamic environment. The genus *Triticum* constitutes a classic example of evolution through amphiploidy (Bowden, 1959). Both cultivated and wild wheats occur in three ploidy levels: diploid, tetraploid and hexaploid (Bowden, 1959). Polyploidy in wheat is thought to have originated when two diploid species hybridized naturally, followed by spontaneous doubling of chromosomes, giving rise to fertile individuals that existed at the tetraploid level. Similarly, hexaploid species are thought to be a product of hybridization between a tetraploid and a diploid species followed by chromosome doubling. However, interspecific hybridization at the diploid level is considered a very rare event, probably because diploids contain different genomes. For example, despite wide-spread co-occurrence of many wild diploids in Israel, interspecific hybrids were only observed between two *Triticum* species, *T. longissimum* and *T. sharonense* (Kimber & Feldman, 1987). These two species are closely related and differ from one another by a reciprocal translocation (Feldman &

Sears, 1981).

All species in the genus *Triticum* contain some multiple of the basic haploid set of seven chromosomes (Bowden, 1966). The basic set of chromosomes in a gamete is referred to as a genome. A diploid wheat has 14 chromosomes ($2n = 2 \times 7 = 14$), a tetraploid has 28 chromosomes ($2n = 4 \times 7 = 28$), and a hexaploid has 42 chromosomes ($2n = 6 \times 7 = 42$). There are eight distinct genomes in the genus *Triticum,* named as: A, B, C, D, G, M, S, U (Kimber & Sears, 1987). Diploid species contain only one of the genomes. No diploid with a genome homologous to B or G has been identified, but these two genomes occur in polyploid species. Although diploid species in the genus *Triticum* are presumed to be from a common ancestor, they have diverged considerably from one another, and there is no conclusive evidence of common ancestry (Kimber & Feldman, 1987) .

Different species resemble or differ from one another depending on their genomic constitution. Kimber & Feldman (1987) classified the species in the genus *Triticum* into three groups, based on a commonly shared genome: A-genome cluster, D-genome cluster and U-genome cluster. Table 2.2 gives a list of species in each cluster and their genomic composition. Common wheat, *T. aestivum*, is a hexaploid species and contains the genomes AABBDD (Kimber & Sears, 1987). Out of 30 species, 12 are closely related to common wheat and form successful hybrids. Out of the three clusters, the A-genome cluster is unique because it is the only one that contains species of commercial importance. Mutation in wild einkorn, *T. boeoticum*, produced the cultivated einkorn, *Triticum monococcum* L. Union between wild einkorn and an unidentified progenitor

containing the G-genome produced the tetraploid, wild timopheevii, *T. araraticum.* Union between wild einkorn, and an unidentified progenitor containing the B-genome produced the tetraploid, wild emmer, *T. dicoccoides*. Natural mutation within wild timopheevii and wild emmer populations gave rise to the cultivated timopheevii, *Triticum timopheevii* Zhuk., and emmer, *T. dicoccum*, wheats respectively. Cultivated einkorn and timopheevii naturally hybridized to produce hexaploid zhukovskyi wheat, *Triticum zhukovskyii* Men. & Er. In different outcrossing events, diploid *Triticum tauschii* Schmal. hybridized with emmer and produced three hexaploid species, *T. spelta*, *Triticum macha* Dek & Men. and *Triticum vavilovi* Jakubz. It is believed that through mutation, natural selection, and selection by early farmers *T. spelta* gave rise to *Triticum compactum* Host, *Triticum spherococcum* Percival and common wheat, *T. aestivum.*

Early farmers probably selected wheats with favourable characters, such as high yields and erect stalks. Repeated sowing and selection for specific characters led to fixation of such traits, giving rise to less diverse populations compared to the wild counterparts. Modern humans have greatly accelerated these changes through scientifically planned breeding practices that include systematic improvements in yield and quality and increased resistance to some diseases and insect pests. For the past several decades, the genetic variability of cultivated wheat has greatly diminished due to extensive breeding for cultivar uniformity. "The same practices are of course largely responsible for the present high productivity of wheat" (Feldman & Sears, 1981, p. 102). Modern cultivars, consisting of a single genotype have replaced the traditional "land races" which consisted of many different genotypes (Feldman & Sears, 1981). Erosion of

the wheat gene pool can make the crop more vulnerable to pests. It is for this reason that wild relatives of common wheat become important sources of resistance to insect pests.

Breeding for host plant resistance requires a clear understanding of the genetic relationships between wheat and its close relatives. Within the family Graminae, six genera form successful hybrids with the genus *Triticum* and 14 *Triticum* spp. are closely related to wheat (tables 2.1 and 2.2). Monte *et al.* (1993) analysed phylogenetic relationships in Triticeae using restriction fragment length polymorphisms (RFLP) and showed close associations between the R genome of *Secale* and P genome of *Agropyron.* They clustered *Secale* and *Agropyron* together with *T. monococcum*, *T. tauschii* and *Triticum speltoides* Tausch (genomes R, P, A, S and D). They also showed that rye is more closely related to wheat than to barley. Hsiao *et al.* (1995) used rDNA sequences to map genetic relationships in Triticeae and found that genomes of the grass genera *Thinopyrum* (genome J) and *Lophopyrum* (genome E) are closely related to the ABD genomes of wheat.

Broadening the genetic base of *Triticum* spp. via intergeneric hybridization and other genetic engineering techniques should provide the variability needed to greatly boost the genetic potential of wheat. Recent evidence of successful distant hybridizations involving species of allied genera and wheat indicate that the entire variation in the tribe Triticeae is potentially exploitable for wheat improvement. Diploid, tetraploid and hexaploid wheats have been crossed with species of *Aegilops*, *Agropyron*, *Secale*, *Haynaldia*, *Hordeum* and *Elymus* and intergeneric hybrids have been produced (Sharma & Gill, 1983). Furthermore, several trigenic hybrids have been produced involving

Triticum, *Hordeum*, *Aegilops*, *Agropyron*, *Haynaldia* and *Secale* (Sharma & Gill, 1983). The ease of transfer of genetic material from allied genera to wheat depends on their relative closeness and the method of transfer. In contrast to the rarity of interspecific hybrids between diploids, there is a relatively high rate of successful hybridization in the polyploids. This phenomenon is facilitated by the shared genome, which acts as a buffer. Often, there are unclear demarcations between closely and partially related species. For this reason, the genus *Triticum* should be viewed as part of a greater continuum of genetic relationships extending to many other grasses. Although new techniques of cytogenetics, genetics and molecular biology have improved wheat taxonomy, there is no consensus for a universal genetic/taxonomic unit, with divergence of opinion as to whether paraphyletic taxa developed from cladograms are allowable (Jury, 2001). "The problem lies not with the discipline of taxonomy but with our expectations of what taxonomy can and should do" (Morrison, 2001, p. 74).

Aphid pests of wheat

Over 30 species of aphids colonize wheat (Blackman & Eastop, 1984), but only six species are reported as important on cereal crops worldwide. These include the Russian wheat aphid, *D. noxia*, greenbug, *Sc. graminum*, bird cherry-oat aphid, *Rhopalosiphum padi* L., corn leaf aphid, *Rhopalosiphum maidis* (Fitch), English grain aphid, *Sitobion avenae* (Fabricius) and rose grass aphid, *Metopolophium dirhodum* (Walker) (Olsen *et al.*, 1993). Most of these species are long established pests of cereal crops. *Diuraphis noxia,* however, has become an important pest in areas where it

established recently. It was first reported in Texas in 1986 (Stoetzel, 1987), and since then has spread to many other states in the U.S.A. including North Dakota (Boeve, 1996) and the Canadian provinces of Alberta and Saskatchewan (Jones *et al*, 1989). Rapid population growth of *D. noxia* is favoured in regions with sporadic rainfall interspersed with periods of dry sunny weather (Jones *et al*, 1989). Thus, the insect is well adapted to the prairie climate particularly the western prairie, but has not yet colonized eastern Saskatchewan or Manitoba probably because it does not have a sexual cycle in North America that would produce the overwintering egg (John Burd (2002), personal communication).

Evolution of aphids

Aphids and wheat originated at different times and may have evolved at different locations. Aphids originated in the Triassic or Late Permian, about 200 million years ago, and were present before the evolution of angiosperms (Moran, 1992). The original hosts of aphids are thought to have been an extinct group of gymnosperms (Blackman & Eastop, 1984). About 4000 species of aphids are described, mostly from temperate regions (Dixon, 1987*a*). Major events in the evolution of aphids include the origin of parthenogenesis, polymorphism and adaptation to different host species. That parthenogenesis was established early in a common ancestor of the Aphidoidea is supported by its uniformity among distantly related species as well as fossil evidence (Richards, 1966). Each year, parthenogenesis enables production of several generations of offspring which are genetically identical to their parents.

Polymorphism in aphids is characterized by the occurrence of multiple, discrete phenotypes among genetically identical individuals. The phenotypes differ in several attributes which include morphology, physiology and ability to use alternative host plant taxa (Hille Ris Lambers, 1966; Dixon, 1971). The optimal phenotype depends on the particular set of conditions encountered, and there are trade-offs in aphid performance associated with each phenotype, e.g. wingless individuals have shorter developmental time and higher fecundity than winged ones (Watt, 1984; Moran, 1992; Migui, 1996).

The majority of aphids still exist on woody plants but some species have acquired additional herbaceous host plants (Blackman & Eastop, 1984). During the course of evolution, some species of aphids developed the ability to move from woody trees or shrubs (primary or over-wintering hosts) to several grasses (secondary or summer hosts) in the spring season but moved back to the primary host in the autumn. A generalized life cycle of an aphid species with primary and secondary host alternation consists of a series of parthenogenetic generations from spring through summer and a single sexual generation towards the end of the warm season. The sexual phase produces eggs that survive through winter. Wingless egg-laying females are produced on the primary host in autumn. Winged male aphids, usually produced on the secondary host, and sometimes on the primary host mate with the sexual females. Fertilized eggs are laid on the primary host where they over-winter. In the spring, the eggs hatch into the first generation of asexual (parthenogenetic) wingless females known as fundatrix. This generation gives rise to a second generation of females which in turn gives rise to a generation of winged female migrants which leave the primary host and colonize the secondary host at a time when the

nutrient status of the primary host is declining. Aphids on secondary hosts produce several generations of parthenogenetic winged and wingless females throughout the summer and their numbers can increase exponentially. Wingless aphids have high reproductive capacities (Vickerman & Wratten, 1979; Dixon, 1987*b*) and winged aphids spread infestations. Later in the season, winged migrants are produced which fly back to the primary host.

Eastop (1977) reported that only about 10% of aphid species show host alternation. In Europe, *R. padi* goes through host alternation and overwinters in the egg stage on its primary host, the bird cherry tree, *Prunus padus* L., and migrates to grasses in spring (Vickerman & Wratten, 1979). In Scandinavia this migration by *R. padi* coincides with the young growth of spring-sown cereals and the aphid frequently reaches damaging populations (ICI Agrochemicals, 1989). In the northwestern U.S.A., *R. padi* overwinters on chokecherry, *Prunus virginiana* L. (Halbert *et al.*, 1992), but aphid migration from chokecherry is not believed to be important in infestation of small grains (Kieckhefer *et al.*, 1974). Other evolutionary events in the phylogeny of aphids include, loss of host alternation and loss of the sexual phase. *Sitobion avenae* and *Sc. graminum* have lost their primary woody hosts and survive entirely on grasses (Blackman & Eastop, 1984). In Africa, the occurrence of aphids on cereals and grasses throughout the year and the absence of egg laying morphs may be an indication of complete adaptation to a different climate (S. Migui, personal observation).

Geographic distribution and host spectrum of cereal aphids

Aphids are the most cosmopolitan insect pests of wheat. *Metopolophium dirhodum, R. maidis* and *R. padi* occur on the six continents with appreciable vegetation, while *D. noxia, Sc. graminum* and *S. avenae* occur on five continents but not in Australia (Blackman & Eastop, 1984). The pest status of these aphids varies from one region to another. The most important pest species on cereal crops in various regions of the world are *R. padi* in northern Europe and southern Australia (Rautapaa, 1976; De Barro, 1992), *S. avenae* and *M. dirhodum* in western Europe and South America (Wratten, 1975; Zuniga, 1990), *D. noxia* in Kenya, South Africa and the U.S.A. (Aalbersberg *et al.*, 1988*a*; KARI-KBL 1995; Jones *et al.*, 1989), and *Sc. graminum* in North America (Kieckhefer & Kantack, 1980). In Manitoba, three of these species, *R. padi, Sc. graminum* and *S. avenae* are considered to be the most important aphid pests of wheat (Robinson & Hsu, 1963; Migui, 1996). The three species are not native to North America and were introduced from the old world (Blackman & Eastop, 1984). *Metopolophium dirhodum* is rare in Manitoba and not economically important (Robinson & Hsu, 1963).

Cereal aphids survive on a wide range of host plants and there is great overlap in their host preferences. According to Blackman & Eastop (1984), the host spectrum of the aphids *R. padi, Sc. graminum* and *S. avenae* includes: *Agropyron, Avena, Bromus, Dactylis, Eleusine, Festuca, Hordeum, Lolium, Oryza, Panicum, Poa, Sorghum, Triticum* and *Zea. Rhopalosiphum padi* is a polyphagous pest with a host range of well over 100 plant species (Kieckhefer & Gellner, 1988). Dahms *et al.* (1954) listed 78 species of grasses as hosts of *Sc. graminum.*

Different aphid species vary in their preference for certain host plants. In Finland, Rautapaa (1970) investigated the preferences of winged forms of *R. padi* and *S. avenae* on 165 cereal varieties and 59 species of Gramineae (grasses), Juncaceae (rushes) and Cyperaceae (sedges) and found that *R. padi* settled on a wider range of host plants than *S. avenae*. Rautapaa (1970) further reported that *R. padi* had almost equal preference for species of Gramineae compared to a standard oat variety, while *S. avenae* had less preference for nearly all species of Graminae, Cyperaceae and Juncaceae than for oats. Robinson and Hsu (1963) found that, out of 38 species of grasses and cereals in Manitoba, 22, 26 and 27 species were favourable hosts for *R. padi*, *Sc. graminum* and *S. avenae,* respectively. Kieckhefer *et al.* (1980) reported that *S. avenae* had similar preference for oats, wheat and barley; *R. padi* and *Sc. graminum* had greater preference for barley and wheat than oats; and oats was not a preferred host of *R. maidis*. Barley, wheat and triticale are very susceptible to damage by *D. noxia* whereas oats and rye are less susceptible (Jones *et al.*, 1989). Grass seedlings are the preferred host of *D. noxia* (John Burd (2002), personal communication). Leather & Dixon (1982) reported that *R. padi* preferred to colonize wild grasses rather than cereals. Other studies (Kieckhefer & Stoner, 1978; Kieckhefer, 1983; Kieckhefer & Lunden, 1983) indicate that certain weedy grasses may be acceptable hosts for cereal aphids at one stage of plant growth and not at another. Kieckhefer (1983) observed that *R. padi* and *Sc. graminum* were well adapted to most *Agropyron* seedlings; *S. avenae* reproduced well on mature *Agropyron* but was not well adapted to seedlings; and *Agropyron* was an unsatisfactory host for *R. maidis*.

What these broad host ranges for cereal aphids mean is that evolution of aphids is not closely linked with evolution of wheat because, in the absence of wheat, the aphids successfully survive on other grass hosts. It is likely that evolution of aphids is more closely linked to evolution of perennial wild grasses than with cultivated wheats. The ubiquitous general theory, that wide-spread use of an insect-resistant cultivar with a single, major gene for antibiosis resistance will select for new, virulent biotypes (Smith, 1989) may not be always true (Porter *et al.,* 1997). For *Sc. graminum*, the theory states that biotypes evolved as a result of the cultivation of varieties of grain resistant to it (Eisenbach & Mittler, 1987). Analysis of the history of greenbug biotypes, breeding wheat for resistance to greenbugs, and wheat resistance-greenbug biotype relationships shows no correlation between the use of resistant wheat cultivars and the development of new greenbug biotypes (Porter *et al.*, 1997). Porter *et al.* (1997) argued that virulent biotypes were already present in the fields by the time a resistant cultivar was put into field production. The conclusion of no relationship between resistant wheat cultivars and development of resistant greenbug biotypes is supported by data from molecular analysis of aphid biotypes using mitochodrial (Powers *et al.*, 1989), ribosomal (Black, 1993), and random amplified DNA (Black *et al.*, 1992), which show significant divergence among biotypes which pre-dates the cultivation of wheat (Porter *et al.*, 1997). *Schizaphis graminum* is a genetically diverse species and many new genotypes are expected to be discovered (Puterka & Peters, 1990). These conclusions are supported by the identification of interclonal variation in fecundity and weight of *Sc. graminum* from a locality in California (Wilhoit & Mittler, 1991). However, regardless of the origin of an

aphid biotype, the widespread adoption of wheat with a single resistance gene can result in an increase in frequency of the corresponding aphid biotype, leading to a breakdown of resistance.

Impact of aphids on wheat production

The direct effects of aphid feeding are variable and depend upon aphid species, the stage of growth, and condition of the host plant. Infestations by aphids on young plants lead to poor root growth and reduction in tiller number (Russell, 1978). Ortman & Painter (1960) reported that the systemic effects of the toxicogenic saliva of *Sc. graminum* can retard root growth. Both *D. noxia* and *Sc. graminum* inject toxic saliva into host tissue while feeding, causing necrosis around feeding sites. Infestation by *D. noxia* causes severe stunting, twisting of leaves and distortion of emerging spikes (Jones *et al.*, 1989). In South Africa, early and late season infestations in wheat by *D. noxia* have caused yield losses as great as 81% and 47% respectively (Aalbersberg *et al.*, 1988*b*). Thus, even small populations of *D. noxia* or *Sc. graminum* can cause considerable damage to infested plants.

Wheat is most susceptible to damage by *S. avenae* from flowering through kernel formation and even small changes in aphid populations can affect yield considerably (Johnstone & Bishop, 1987). Populations of *S. avenae* initially develop on leaves, and then gradually move to the spikes when they emerge. *Metopolophium dirhodum* feeds on leaves. Wratten (1975, 1978) found that at equivalent densities *S. avenae* causes more damage than *M. dirhodum* when infestations occur during flowering and early kernel

development. In Britain, George & Gair (1979) found that aphid feeding on spikes of wheat can reduce yield by up to 42%. In Alberta, Harper (1973) reported 8% loss in wheat kernel weight as a result of infestation by *S. avenae*.

R. padi is regularly a pest of spring cereals in Scadinavia (Weibull, 1987) and causes direct crop losses of as much as 10% in an outbreak year (Sundell, 1977). In Hungary, Papp & Mesterhazy (1993) reported yield losses of 58-63% in cultivars that were most susceptible to *R. padi*. In addition to the direct injury, cereal aphids contaminate plant surfaces with honeydew that promotes fungal growth, and also transmit plant viruses, especially barley yellow dwarf virus (Gildow, 1984).

Aphid control options

Insect control options include: chemical treatment, cultural practices, plant resistance, and classical biological control. In western Europe, application of insecticides at the onset of flowering in wheat is recommended to avoid yield reduction by aphids (George & Gair, 1979). In the southern U.S.A., granular insecticides are applied to the soil to control early aphid infestations on wheat (Cate *et al.*, 1973). Biological control organisms that attack aphids in cereal fields include: hymenopterous parasitoids, coccinellids (ladybird beetles), syrphids (hover flies), chrysopids (lacewings), staphylinid beetles, carabid beetles, spiders, mites and entomopathogens (ICI Agrochemicals, 1989). In southern South America, biological control organisms, particularly hymenopterous parasitoids, are considered to be important regulators of cereal aphids (Norambuena, 1981; Zuniga, 1990). In the prairie provinces of Canada, cultural practices such as early

sowing may sometimes help to ensure that the crop is past the critical growth stage that is most vulnerable to aphid attack by the time large aphid populations develop (Philip & Mengersen, 1989).

Plant resistance

Plant resistance to insects in wheat is associated with the relative amount of damage caused by the insects compared with damage on more susceptible varieties. Resistance mechanisms can be classified into three types, antibiosis, antixenosis and tolerance (Painter, 1951; Kogan & Ortman, 1978). Antibiosis is a resistance mechanism that adversely affects the insect's life history parameters, usually its development, growth, survival, or its fecundity when the pest feeds on the resistant plant. Antixenosis is a group of plant characters and insect responses that lead an insect away from the plant or plant part for reproduction, food, shelter or a combination of these. Tolerance allows the plant to grow and compensate injury or reproduce despite supporting a density of insects approximately equal to what would be damaging to a susceptible cultivar. The advantage of tolerance over antibiosis or antixenosis is that it does not select for pest genotypes that overcome the resistance. The disadvantage may be increased possibility of spread of a viral disease. All three mechanisms can be involved in the resistance of cereals to aphids (Starks & Merkle, 1977).

Researchers have measured resistance to aphids in many different ways. Some have used quantitative measurements, some have used semi-quantitative measurements, some have used qualitative measurements, and some have used a combination of these.

Examples include, for the aphid: developmental time, larval survival, adult survival, fecundity, population increase during infestation, intrinsic rate of increase, biomass of a nymph, biomass of an adult, production of winged morphs, host suitability (number of aphids settling/plant), characteristic probing behaviour (number of penetrations/unit time), and honey dew droplet counts; and for the plant: yield loss, 1000 kernel mass, specific impact (plant biomass lost/unit of aphid biomass gained), number of tillers, number of leaves, leaf area, leaf length, root length, stem biomass, shoot biomass, infested versus non-infested, living versus dead, infestation severity as a percentage of surface covered by aphids, leaf roll index, chlorosis (streaking) index, necrosis index, stunting index, plant height and relative turgidity of leaf (Burd *et al.*, 1993; Caillaud *et al.*, 1995; Hesler *et al.*, 1999; Miller *et al.*, 1994; Papp & Mesterhazy, 1993; Porter *et al.*, 1993; Spiller & Llewellyn, 1986; Starks & Merkle, 1977; Weibull, 1988). Although all these parameters are useful in measuring resistance under some circumstances, the qualitative and semi-quantitative measurements may only be suitable when plants with high levels of resistance to aphids are being contrasted with susceptible ones. Such methods may be unable to detect partial resistance. Because of the large number of ways resistance has been estimated, different studies are difficult to compare.

Resistance success stories

Research on host-plant resistance to Hessian fly, *Mayetiola destructor* (Say), a major pest of wheat in North America, started in the 19th century (Dunn, 1978) and over the years has encountered remarkable success. Control of the pest is effected using

resistant cultivars. Twenty-five genes for resistance of wheat to Hessian fly have been discovered (Cox & Hatchett, 1994). Among these, five genes, *H13, H22, H23, H24* and *H26* have been transferred from *T. tauchii* to common wheat (Raupp *et al.*, 1993; Cox & Hatchett, 1994). In 1978, extra yield resulting from use of resistant cultivars was estimated to be worth about 238 million U.S. dollars (Dunn, 1978). The wheat stem sawfly, *Cephus cinctus* Norton, also a major pest in North America, is controlled by use of host plant resistance. Since the 1940s over 10 resistant cultivars have been released and the resistance is primarily associated with stem solidness (Hatchett *et al.*, 1987).

Breeding disease resistant wheats has been and still is one of the outstanding accomplishments of wheat breeders. Many cultivars have been developed with genes for resistance to stem rust, leaf rust and powdery mildew. 'Hope' and 'H44' wheat cultivars, which had near immune reactions to stem rust, were responsible for one of the longest rust free periods in the U.S.A., 1938-1949, and became widely used as parents in wheat breeding (Sharma & Gill, 1983). In Canada, most rust resistance work was and still is being conducted in Winnipeg at the Dominion Rust Laboratory, now called the Cereal Research Centre of Agriculture & Agri-Food Canada. Since the inception of the Cereal Research Centre in 1925 (Agriculture Canada, 1986), more than 50 cereal varieties have been released (Agriculture and Agri-Food Canada, 2001) most of which were resistant to stem rust at the time of their release (DePauw *et al.*, 1995). There has been virtually complete control of wheat stem rust in Canada and the United States of America since 1974 (Martens & Dyck, 1989; Leonard, 2001). Sources for stem rust resistance have been diverse, with the primary ones being 'Kenya Farmer' from Kenya, 'Frontana' from Brazil

and PI170925 from South Africa (DePauw *et al.*, 1995). Resistance genes have also been valuable in protecting wheat against leaf rust. The cultivar, "Pasqua" has five genes for leaf rust resistance that were deliberately bred into it (Townley-Smith *et al.*, 1993). The example of rust resistance shows how valuable naturally occurring, genetically controlled resistance can be in crop protection.

Resistance to aphids in cultivated wheats

Breeding for insect resistance in wheat has been limited compared to breeding for disease resistance. Hsu & Robinson (1962, 1963) screened many barley varieties for resistance to *R. padi* but did not detect a reliable resistance source. The U.S.D.A. world collection of wheat was screened for resistance against *Sc. graminum* but only low levels of resistance were reported (Starks & Merkle, 1977). The possibility of exploiting inherited resistance to cereal aphid attack prompted the screening of many British cultivars, but again, only low levels of resistance were detected (Lowe, 1981; Lee, 1984). These reports suggest that cultivated wheat genotypes in North America and western Europe may not have sufficient genetic variability to provide a reliable source of resistance to aphids.

In the Czech Republic, Havlickova (1993) reported resistance to *S. avenae* in winter wheat cultivars and the resistance was associated with long awns. A similar observation was reported by Acreman & Dixon (1986), that awned wheats are self cleaning, because *S. avenae* fall off when spikes of adjacent stems brush together. Nevertheless, the predominantly awned wheats of western Canada are susceptible to *S.*

avenae (personal observation). Roberts and Foster (1983) reported that *R. padi* had reduced population growth on a pubescent wheat cultivar compared to a glabrous cultivar. Wheat cultivars with high levels of hydroxamic acids are resistant to *R. padi* and *S. avenae* at the seedling stage (Thackray *et al.*, 1990). Papp & Mesterhazy (1993) screened winter wheat genotypes for resistance against *R. padi* and found several resistant and tolerant wheat genotypes. Lamb & MacKay (1995) and MacKay & Lamb (1996) investigated the impact of aphids on the growth of seedlings of cultivated wheat and barley and reported that for each mg of aphid biomass gained, the biomass of an infested plant was reduced by about 3 mg regardless of aphid species, plant cultivar or aphid density, and therefore these cultivars were equally tolerant to aphids tested.

Although plant breeders have been successful in identifying major genes in wheat that confer high levels of resistance to *Sc. graminum*, years of painstaking research have been nullified by the ability of *Sc. graminum* genotypes to overcome the resistance. In fact, there has never been a commercially available wheat cultivar that was resistant to the *Sc. graminum* biotype prevalent at the time (Porter *et al.*, 1994, 1997). In North America, 11 biotypes of *Sc. graminum* are presently recognized, each assigned a letter A-K (Porter *et al.*, 1997). Differentiation of the aphid biotypes is based on their ability or inability to injure certain cultivars of wheat, barley and sorghum (Boeve, 1996). Useful genetic variability within cultivated wheat continues to decline as new aphid genotypes are recognized. Enrichment of the wheat gene pool may be accomplished by exploiting the abundant gene pool of the wild relatives of wheat.

Resistance to aphids in wild wheats

The wild relatives of wheat are adapted to a broad range of environments and carry a large reservoir of useful genes (Feldman & Sears, 1981). Investigations by some workers on utilization of the genetic variation present in the wild relatives have revealed their remarkable genetic diversity. Painter (1960) reported that the wheat cv. "Ponco" derived its resistance to Hessian fly from an interspecific cross with a tetraploid, *T. durum*. Resistance to wheat bulb fly was observed in diploid, tetraploid and hexaploid species of ancient wheat varieties (Lupton & Bingham, 1967).

Triticum tauschii, the donor of the D genome in common wheat, has been evaluated for a wide range of agronomically important traits, including disease and insect resistance. Gill *et al.* (1986) evaluated 66 accessions of *T. tauschii* and reported resistance (immune to moderate reactions) in 32 accessions to the leaf rust pathogen, *Puccinia recondita* Rob. ex Desm. f. sp. *tritici*; 31 to the powdery mildew pathogen, *Erysiphe graminis* DC. ex Merat f. sp. *tritici* em Marchal; 34 to the greenbug; and 24 homozygous and 16 segregating for resistance to the Hessian fly. Two genes conferring resistance to stem rust, *Puccinia gramimis* Pers. f. sp. *tritici* Erics & E. Henn., *Sr36* and *Sr37*, were transferred to common wheat from *T. timopheevii* and *Sr40* was transferred from *T. araraticum* (Allard & Shands, 1954; Dyck, 1992). Genes for resistance to powdery mildew, *Pm6*, and leaf rust, *Lr18*, also were transferred to common wheat from cultivated *T. timopheevii* (Dyck & Samborski, 1968; Jorgensen & Jensen, 1973). Disease resistance has also been transferred to wheat by intergeneric crossing with rye (Jensen & Kent, 1952).

In glasshouse studies, Sotherton & Van Emden (1982) demonstrated that some *T. monococcum* lines had an outstanding degree of antixenotic and antibiotic resistance to the aphids *M. dirhodum* and *S. avenae*. Lee (1983, 1984) and Lowe (1984*a*) reported that *T. monococcum* is more resistant to *S. avenae* than modern wheat cultivars under laboratory and field conditions and that resistance is stable against a range of clones. Kazemi & van Emden (1992) found that emmer wheat, *T. dicoccum*, a tetraploid, exhibit higher resistance to *R. padi* than hexaploid wheat.

Tremblay *et al.* (1989) tested several perennial Graminae and wheat X perennial Graminae hybrids for resistance against *R. padi* and reported significant levels of resistance in *Elymus* and *Agropyron* spp. The authors also observed that aphid population growth on the hybrids was lower than on parental wheat varieties, suggesting that the resistance trait can be transferred to cultivated wheat. Weibull (1987) screened a wide range of *Hordeum* species, comprising of diploids, tetraploids and hexaploids, for resistance against *R. padi* and observed that the most resistant species were diploids. Weibull (1987) also found that perennial barleys exhibited higher levels of resistance to *R. padi* than annuals. Similarly, interspecific barley hybrids that inherited the character of perennial life cycle showed high levels of resistance to *R. padi* (Weibull, 1987). After studying the reproduction of *R. padi* on various grasses, Villanueva & Strong (1964) placed Kentucky blue grass, *Poa pratensis* L., and seedling corn, *Zea mays* L., in the group of resistant species.

The presence of aphid biotypes which cause different reactions on the same host plant complicates the search for resistant germplasm. Biotypes likely arise via sexual

reproduction. Eleven different biotypes of *Sc. graminum* have been described in North America, with the first biotype being described at the inception of host plant resistance against the aphid pest. Breeding for *Sc. graminum* resistance began in the early 1950s when a durum wheat from North Dakota, 'Dickinson Selection 28A', resistant to biotype A , was produced commercially (Dahms *et al.* 1955). A few years later, 'Dickinson Selection 28A' was overcome by greenbug biotype B (Wood, 1961). About the same period, in Argentina, Arriaga (1954) reported greenbug resistance in rye and several varieties of *T. tauschii*. Arriaga (1956) developed a rye cultivar 'Insave F.A.' that was resistant to biotypes B and C. 'Insave F.A.' was used to develop a rye-wheat amphiploid (triticale) variety called 'Gaucho' (Wood *et al.*, 1974). 'Gaucho' was found to have a single dominant gene for resistance to greenbug (Wood *et al.*, 1974). Using X-ray technology, Sebesta & Wood (1978) transferred this resistance from rye into wheat, and in 1977 a *Sc. graminum* resistant wheat cultivar "Amigo" was released. "Amigo" germplasm was used extensively in breeding programs until the resistance was overcome by greenbug, biotype E (Porter *et al.* 1982). "Amigo" has increased hybrid vigor, increased resistance to diseases and decreased milling quality (too sticky), and is still being used in the breeding program (John Burd (2002), personal communication).

The great plains *Sc. graminum* biotype C is the most common one in North Dakota (Joppa *et al.*, 1980), and may or may not be the most common biotype in Manitoba. Harvey *et al.* (1980) identified resistance to *Sc. graminum* biotype C in synthetic hexaploid wheats derived from *T. tauschii* var *strangulata* and *T. tauschii* var *typica*. A sourse of resistance to greenbug toxin was discovered in *T. tauschii*, line "PI

268210" (Joppa *et al.*, 1980). Other wheat lines showing resistance to *Sc. graminum* have been developed, and include, "Tam 107", "Largo", "Century", "CI 17882", and "CI 17959" (Webster *et al.*, 1987; Boeve, 1996). Biotype specific resistance often does not offer durable resistance, however. Theoretically, pyramiding of unrelated genes that confer resistance against pest insects may delay pest adaptation, and prolong the life of resistant varieties (Rausher, 2001).

Biotypic variation is also reported in the Russian wheat aphid. Puterka *et al.* (1992) found a high degree of biotypic diversity within a worldwide collection of *D. noxia*, suggesting that utilization of resistant plant germplasm may have geographic limitations. However, 10 years after its introduction in North America, no biotypic variation was exhibited by the *D. noxia* populations in the U.S.A. (Shufran *et al.*, 1997) probably because *D. noxia* has not undergone sexual reproduction in North america. The highest levels of resistance to *D. noxia* have been found in triticale and oats (Webster *et al.* 1987) and in *T. monococcum* (Du Toit, 1987). Nkongolo *et al.* (1990) found genes for resistance to *D. noxia* in *T. monococcum*, *T. tauschii* and *T. ventricosum*. Formusoh *et al.* (1994) reported high levels of resistance to *D. noxia* in 23 out of 547 intergeneric hybrids of *Thinopyrum*, *Secale* and *Triticum*.

Among important aphid pests of cereal crops in the world, only *Sc. graminum* and *D. noxia* have received much attention in terms of active breeding of resistant genotypes. The reason for this may be due to the fact that the two species inject toxic saliva into host tissue, causing characteristic injury (necrosis). These symptoms allow plant breeders to make quick visual scores on test lines and enable screening of large numbers of

accessions. The other aphid pests, such as, *R. padi* and *S. avenae*, usually cause plant damage that cannot be visually scored and sometimes requires laborious measurements. Much of the information available on host plant resistance to the latter two insects are lists of possible resistance sources with little or no breeding efforts after initial screening. Although screening procedures may be tedious, it is now timely to exploit available information in directed screening and plant breeding programs. Even a slight reduction in multiplication rate of aphids may allow parasites or predators or both to contain an aphid population below the economic damage level (Zuniga, 1990). The ultimate goal is to develop cultivars with multiple mechanisms of resistance, multiple genes for resistance and multiple pest resistance. Brown-Guedira *et al.* (1996) found resistance to multiple pests in several accessions of *T. timopheevii*.

The incorporation of host plant resistance to aphids into commercial wheat has considerable potential in the integrated control of these pests. The strategy of integrated pest management (IPM) is to employ and integrate all possible control methods, the objective being to maintain pest populations below the economic injury level, with minimal adverse effects on the environment. Host plant resistance is compatible with chemical, biological and cultural control methods. For example, the use of sorghum hybrids resistant to *Sc. graminum* biotype C permitted the use of extremely low dosage rates of insecticides (Cate *et al.*, 1973). The development and utilization of a particular cultivar should be the base from which all management strategies arise. If the crop is susceptible, then chemical control is likely to be necessary. However, if a cultivar is resistant, it is inherently less damaged or less infested than comparable cultivars, and IPM

should consider this fact.

There has been virtually no screening of spring wheat germplasm of western Canada for resistance to aphids, so there is no baseline information on their susceptibility to aphids. Most work internationally on resistance in wheat to aphids is based on seedling wheat, but the problem in western Canada is on adult plants. Exploitation of the resistance reported in wild wheats must be based on adult plant resistance. As a starting point, a search for aphid resistance in *T. monococcum*, the species with the simplest genome in the genus *Triticum*, a progenitor of domesticated wheats and suspected of being more resistant to aphids than modern wheats, is recommended.

Table 2.1. Genera and number of species in the sub-tribes, Triticinae and Hordeinae.

Triticinae		Hordeinae	
Genera	Number of species	Genera	Number of species
Agropyrum *	100	*Hordeum* *	25
Hynaldia *	2	*Elymus* *	60
Secale *	6	*Asperella*	7
Heteranthelium	1	*Sitanion*	1
Henrardia	2	*Psathyrostachys*	6
Eremopyrum	5	*Crithopsis*	1
Triticum *	30	*Taeniatherum* *	2

* Genera that form successful hybrids with *Triticum* (after Feldman & Sears, 1981).

Table 2.2. The diversity of genomic compositions that occur in the genus *Triticum* and sample species showing that composition.

Species	Genome	Species	Genome
Diploids		**Polyploids (sharing DD genome)**	
T. monococcum *	AA	*T. cylindricum* *	$DDCC$
T. urartu *	AA	*T. crassum* *	$DDM^{cr}M^{cr}$
T. dischasians *	CC	*T. crassum* *	$DDD_2D_2M^{cr}M^{cr}$
T. tauschii *	DD	*T. syriacum* *	$DDM^{cr}M^{cr}S^{l}S^{l}$
T. comosum *	MM	*T. juvenale* *	$DDM^{cr}M^{cr}UU$
T. tripsacoides	$M^{t}M^{t}$	*T. ventricosum* *	$DDM^{v}M^{v}$
T. uniaristatum	$M^{u}M^{u}$		
T. speltoides	SS		
T. bicorne	$S^{b}S^{b}$	**Polyploids (sharing UU genome)**	
T. sharonensis	$S^{l}S^{l}$	*T. triunciale*	$UUCC$
T. longisimum	$S^{l}S^{l}$	*T. macrochaetum*	$UUM^{b}M^{b}$
T. searsii	$S^{s}S^{s}$	*T. columnae*	$UUM^{c}M^{c}$
T. umbelllulatum	UU	*T. triaristatum*	$UUM^{t}M^{t}$
		T. triaristatum	$UUM^{t}M^{t}M^{t2}M^{t2}$
		T. ovatum	$UUM^{o}M^{o}$
Polyploids (sharing AA genome)		*T. variabile*	$UUS^{v}S^{v}$
T. dicoccoides *	$AABB$	*T. kotschyi*	$UUS^{v}S^{v}$
T. araraticum *	$AAGG$		
T. aestivum *	$AABBDD$		

* Species that form successful hybrids with common wheat, *T. aestivum* (after Feldman & Sears, 1981).

CHAPTER 3

Susceptibility of spring wheats to three cereal aphid species in relation to crop resistance.

Abstract

The susceptibility of spring wheats, *Triticum aestivum* L. and *Triticum durum* Desf., to cereal aphids and the potential role of resistance for aphid management in these crops were investigated. Three aphid species, *Rhopalosiphum padi* (L.), *Sitobion avenae* (Fabricius) and *Schizaphis graminum* (Rondani), which are the dominant pests in the Prairies of Canada and the northern Great Plains of the USA, were considered. A genetically diverse group of Canadian wheats was used as a tool for this investigation. The objective was to clarify the need for resistance and to determine if resistance might be effective against the three aphid species and in the main classes of wheat. The relative susceptibility of these wheats to aphids was compared at different growth stages, to determine when resistance is expressed. Biomass relationships between cereal aphids and spring wheats were used to quantify antibiosis and tolerance components of crop resistance. Wheat seedlings were exposed to each of the three aphid species for six days and biomass gain by aphids and biomass loss by plants were recorded. In the field, aphids were placed on wheat in single plant and multiple plant cages at boot stage (GS 45, boots swollen, Tottman & Makepeace, 1979). After 21 days, half of the replicates were assessed for aphid biomass gain and plant biomass loss. The other half were sprayed with

an insecticide to terminate the infestations, and allowed to mature for yield assessment. Interactions between aphids and wheat differed among aphid species and between the two growth stages of the wheat plant. Seedlings were most favourable for the development and growth of *R. padi*, and exhibited a low level of antibiosis to *S. avenae* and *Sc. graminum*. Adult plants were more suitable for the development of *S. avenae* and *Sc. graminum* than *R. padi*. Tolerance levels to aphids differed among wheat classes, with seedlings being more tolerant of aphids than adult plants. Because the relative performance of the aphid species and their impact on wheat differed between seedlings and adult plants, seedling resistance to aphids cannot be used to predict adult plant resistance. Adult plants of the Canadian Western Red Spring class of wheat are more tolerant at the adult stage towards aphids than the other classes, but not sufficiently resistant to avoid economic damage.

Introduction

Host plant resistance to insects in common wheat, *Triticum aestivum* L., and durum wheat, *T. durum* Desf., has been recognized as a way to control pests and research in this area has been going on for many years. The scientific basis for host plant resistance was established as early as 1782 when the wheat cultivar "Underhill" was found to be resistant to the Hessian fly, *Mayetiola destructor* Say, in New York (Fitch, 1847). R.H. Painter, a long time advocate of host plant resistance classified resistance mechanisms into three types: antibiosis, antixenosis and tolerance (Painter, 1951; Kogan & Ortman, 1978). Antibiosis is a plant attribute which adversely affects the biology of the insect,

antixenosis leads an insect away from the plant, and tolerance allows the plant to grow and reproduce or compensate injury despite supporting a density of insects that would be damaging to a more susceptible plant. To quantify antixenosis, insect behaviour associated with host plant selection must be studied. Antixenosis requires a different experimental approach than antibiosis or tolerance and therefore, the former type of resistance will not be considered further in this study.

Researchers have estimated resistance in many different ways, some quantitative, some qualitative and some semi-qualitative (see Chapter 2 for details). Because of the diversity of ways resistance to aphids has been measured, results of different studies are difficult to compare. No one method universally describes resistance but each contributes to the understanding of aphid-wheat relationships and may vary in terms of efficiency of selection. Although the different methods are useful in estimating resistance, the qualitative and semi-quantitative measurements may only be suitable when high levels of resistance to aphids are available. They may not detect moderate levels of resistance, also described as partial resistance. A cultivar exhibiting partial resistance to aphids is less damaged than a susceptible one, but the level of resistance is not sufficient to avoid economic damage. Partial resistance is desirable because the resistance is often durable (Rajaram & Braun, 2001). A focus of this study is a screening method that quantifies partial resistance as well as high levels of resistance.

An efficient implementation of host plant resistance to aphids in wheat requires a clear understanding of the production system. Wheat is grown in a wide range of conditions from subsistence agriculture in parts of the Near/Middle East, to high

technology extensive production in North America and Australia, and to high technology intensive production in northern Europe (Briggle, 1980). Host plant resistance probably already plays an important role in agriculture where crops are grown in conditions that are ecologically similar to the natural wild wheat habitats and near the origins of wheat and its pests. Strikingly, cereal aphids are not recognized as pests in the area of origin of wheat, and cause little or no harm in the Middle East even where wheat is grown intensively, as in Israel (Way, 1988). Outside the area where wheat has been grown for centuries, and where intensive wheat production is practiced, the demand for high yielding wheat cultivars constrains the opportunities for developing host plant resistance. For example, in the Netherlands, the high yield technology has created absolute dependence on pesticides and has made other controls uneconomical (Vereijken *et al.*, 1985). In the main wheat producing areas of North America, where climatic conditions do not permit intensive wheat production, a balance between yield objectives and pest management using resistance has potential for success. For example, the sequential release of cultivars resistant to greenbug, *Schizaphis graminum* (Rondani), prevents millions of dollars in crop losses and insecticide use each year, even though deployment of each resistance gene provides protection for only a few years (Porter *et al.*, 1997, 2000).

Most breeding for resistance that has been implemented used a single major gene manifesting antibiosis (Du Toit, 1989; Baker *et al.*, 1992; Marais & Du Toit, 1993; Saidi & Quick, 1996; Porter *et al.*, 1998). Partial resistance can be a valuable component of integrated pest management, because cereal aphids are intermittent pests with populations

that often do not greatly exceed accepted economic thresholds (Wood, 1965; Hatchett *et al.*, 1987; Boeve, 1996). Antibiotic resistance that causes a slight reduction in the growth rate of aphid populations may enable natural enemies to keep aphid populations below economic levels (Zuniga, 1990). Furthermore, partial resistance is probably conferred by non-race specific polygenes with small additive genetic effects that are thought to be more durable than single, major gene resistance (Poehlman & Sleper, 1995; Rajaram & Braun, 2001). Tolerance also can be an important component of resistance, because interactions between the pest and the resistant cultivar act primarily on the plant, and therefore do not select for a response from the pest. This resistance is therefore likely to be durable (Wiseman, 1994).

Most previous research on resistance to cereal aphids has been conducted on winter wheat seedlings, because: seedlings are more easily screened than adult plants, winter wheat dominates production in Europe and North America, and cereal aphids tend to attack winter wheat earlier in its development than they attack spring wheat. In the United States, Starks & Merkle (1977) evaluated seedlings of cultivated wheats for resistance to *Sc. graminum* and reported low levels of resistance. More recent screening efforts of North American wheat cultivars and breeding lines for resistance to the Russian wheat aphid, *Diuraphis noxia* (Mordvilko), also showed low levels of resistance (Smith *et al.*, 1991). Extensive screening of seedling barley varieties, *Hordeum vulgare* L., for resistance to the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), in Manitoba revealed no reliable resistance source (Hsu & Robinson, 1962, 1963). Screening of immature wheat and barley cultivars in France and Great Britain revealed low levels of resistance to

aphids (Lowe 1984*b*; Dedryver & Di Pietro, 1986; Di Pietro & Dedryver, 1986). In seedling plants, the presence of hydroxamic acids is associated with resistance to aphids (Thackray *et al.*, 1990; Givovich *et al.*, 1994).

Some resistance research has been conducted on adult plants, mostly on winter wheat. The possibility of exploiting inherited resistance to cereal aphid attack prompted the screening of adult plants of many British winter wheat cultivars in laboratory, glasshouse and field conditions, but only low levels of resistance were detected (Stokes *et al.*, 1980; Lowe, 1984*a*; Lee, 1981, 1984; Dewar *et al.*, 1985). In the United States, infestation by *R. padi* on winter wheat caused significant yield reduction and there was no difference in responses among the varieties tested (Riedell *et al.*, 1999). In the Czech Republic, Havlickova (1993) reported resistance to the English grain aphid, *Sitobion avenae* (Fabricius), in winter wheat cultivars and the resistance was associated with long awns. Immature plants of wheat cultivars with hairy leaves were found to exhibit higher levels of resistance to *R. padi* than hairless cultivars (Roberts & Foster, 1983).

Although some potential sources of resistance have been identified, plant breeders rarely use susceptibility or tolerance to aphids as criteria for retaining superior lines of spring wheat. Aphids and their damage are usually cryptic and ephemeral, which both limits the attention paid to the damage and makes resistant phenotypes difficult to identify, particularly phenotypes with partial resistance. Furthermore, on the Prairies of Canada and the northern Great Plains of the USA, most cereal aphid species are pests of adult plants, because they disperse into these areas in late spring rather than overwintering locally (Robinson & Hsu, 1963; Irwin & Thresh, 1988). Only seedling resistance has been

investigated widely and little is known about the association between seedling and adult plant resistance. Also, the wheats grown in many areas of the world are genetically diverse, consisting of two species, *T. aestivum* and *T. durum*, a number of types or classes with different genetic backgrounds and different end uses, and many cultivars in each class of wheat. The diversity of wheats complicates the assessment of their susceptibility to aphids and the implementation of available resistance. Finally, cereal aphids consist of a variety of species, representing different genera, and the species composition varies from area to area. The relative pest status of these aphid species and the potential of specific resistance mechanisms, or partial resistance, to be effective against these different species are poorly understood.

In this study, a genetically diverse group of Canadian wheats was used as a tool for investigating the potential of crop resistance in the management of cereal aphids that are pests of adult plants of spring wheat, and for developing methods for screening such wheats for resistance. Three cereal aphid species which are the dominant pests in Prairie Canada were considered. The relative susceptibility of wheats to aphids was compared at different growth stages, to determine whether resistance already is expressed. Biomass relationships between cereal aphids and spring wheats were used to quantify the antibiosis and tolerance components of crop resistance (Lamb & MacKay, 1995; MacKay & Lamb, 1996; Gavloski & Lamb, 2000). The objectives were to clarify the need for resistance and to determine if resistance might be effective against the three aphid species and in the main classes of wheat. The following specific features of the interaction between aphid and host plant were considered, for the aphids: 1a) variation in the

performance of three aphid species on the wheats, 1b) variation in antibiosis and tolerance for clones within aphid species, 1c) the relative value of aphid numbers and biomass for quantifying antibiosis. Specific features of the interaction considered for plants were: 2a) variation in tolerance of the main wheat classes to the aphids, 2b) variation in susceptibility of cultivars within wheat classes to the aphids, 2c) the relative value of foliage and spike biomass for quantifying resistance, 2d) the predictive value of seedling resistance for adult plant resistance.

Materials and methods

Three cereal aphid species, *R. padi, Sc. graminum* and *S. avenae* which are commonly found on spring wheat in the Prairies were studied. Four clones of each of the aphid species were collected from cereal fields in southern Manitoba in 1996 with each clone established from aphids collected in a different field. A fifth clone of each species was obtained from cultures maintained for several years in the laboratory of Dr. P. A. MacKay, Department of Entomology, University of Manitoba, and originally collected from cereal fields in southern Manitoba. Commercial cultivars grown on the Canadian Prairies and belonging to two species and three classes of wheat were selected: *Triticum aestivum*, i.e. Canadian Western Red Spring (CWRS, cultivar Domain) and Canadian Prairie Spring (CPS, cultivar Foremost) and *T. durum* i.e. Canadian Western Amber Durum (CWAD, cultivar Medora). The first two are hexaploids and the third is a tetraploid wheat (Agriculture and Agri-Food Canada, 1996)

Aphids were reared in the laboratory on seedling barley, cultivar Argyle. Barley seeds were planted in Styrofoam pots (measuring 8.5 cm high by 7.3 cm in diameter) containing Metro-mix® 220 soil medium (Grace Horticultural Products, Ajax, Ontario) which was composed of: vermiculite, water, bark and related material, sphagnum peat moss, quartz, gypsum perlite and calcium carbonate. The pots were placed in a plastic container (measuring 23 cm long, 16 cm wide and 7.5 cm deep) with a perforated lid to support six pots and partially filled with Hoagland's nutrient solution (fig. 3.1). Hoagland's nutrient solution contained the following compounds (weight/50 L solution): the macronutrients, 35.42 g $Ca(NO_3)_2.4H_2O$, 10.11 g KNO_3, 24.65 g $MgSO_4.7H_2O$, 13.61 g KH_2PO_4, and 1.84 g FeEDTA, and the micronutrients, 0.05 g $CuCl_2.H_2O$, 2.5 g H_3BO_3, 0.05 g MoO_3, 1.5 g $MnCl_2.4H_2O$, and 0.1 g $ZnCl_2$. The macronutrients and the micronutrients were dissolved in distilled water in a 50 L container. The plants were placed in environmental chambers (model Conviron E8VH, Controlled Environments Ltd, Winnipeg, Manitoba) maintained at 20°C and a photoperiod of 18h:6h (light:dark). Approximately 10 days after planting, the first leaves were fully opened; only these leaves were used in aphid stock cultures. Plants were germinated at weekly intervals to produce a regular supply of leaves. Aphids were reared on 3, 4 cm pieces of barley leaf placed in 60 X 15 mm Petri dishes, which contained Hoagland's nutrient solution solidified with 1% agar, keeping the leaves turgid for 3-5 days. Aphid cultures were reared in an environmental chamber similar to the one used for plants maintained at 20°C and a photoperiod of 18h:6h (light:dark) which ensured the aphids remained asexual. Aphid clones were reared in separate dishes on racks. Within racks, aphid clones were separated

by an empty dish to lower the risk of cross contamination. Clones were maintained as uncrowded colonies by transfer of aphids at 3 day intervals onto fresh barley leaves in fresh rearing dishes. All aphid clones adapted well to the rearing conditions and provided a reliable supply of aphids of uniform age and size for use in laboratory and field experiments. Standard aphids were obtained by transferring a young adult (24-36 h after adult molt) to a fresh leaf, allowing it to produce offspring for 24 h, removing the adult, and leaving the offspring to grow to the third instar (3-4 days after birth). At this instar, offspring were transferred individually to fresh rearing dishes where they grew to the adult stage.

Resistance was estimated by assessing the amount of plant biomass lost during infestation. Initial aphid infestation was assumed to be the same because a similar number of standardized aphids were used. Both plant biomass and aphid biomass were estimated in a standard way prior to and after infestation, as described below. Resistance was based on the following equation:

Plant biomass lost = aphid biomass gained * specific impact

The specific impact is the amount plant biomass lost for each unit of aphid biomass produced (MacKay & Lamb, 1996). The measurements of plant biomass loss and aphid biomass gained, plus their relationship (specific impact) were used to reveal the presence and mechanism of resistance. Resistance is high when plant biomass loss is low; antibiosis is high when aphid biomass gain is low; and tolerance is high when specific impact is low.

Statistical tests involved analyses of variance of the dependent variables using GLM and mixed model procedures (SAS Institute Inc., 1989). A plot of mean versus variance for each dependent variable was made to determine whether transformation was required to normalize the data or stabilize variance. Where data were found to be non-normal (strong relationship between mean and variance and/or the range of variance was greater than two times the smallest variance), they were transformed by calculating natural logarithms before proceeding with statistical analysis.

Aphids on seedling plants: three wheat classes and diverse aphid clones

Interactions between aphids and wheat were first characterized in the laboratory using seedling plants. Because aphid populations occur on field crops as an assembly of clones for each species, the importance of variation among the clones was evaluated. Five clones from each aphid species were exposed to the three wheat classes, using one representative cultivar for each class: "Domain" (CWRS), "Foremost" (CPS) and "Medora" (CWAD). Because of the large number of treatments involved, the study was conducted as 18 consecutive tests. Each test lasted one week and involved five clones of one aphid species and one wheat class, replicated five times. Each test was repeated once, a week later, to give a total of 10 replications.

Seeds from each cultivar were pre-germinated in Petri dishes and individually transferred to styrofoam pots containing Metro-mix® 220 soil medium and placed in the six-pot holder plastic container and sub-irrigated with Hoagland's nutrient solution. At the two leaf stage, (GS 12, Tottman & Makepeace, 1979), healthy seedlings were selected

and their heights were measured. The plants were divided into two groups of equal numbers and equal height ranges. One group was set aside for the experiment (experimental plants); the other plants were cut at soil level and the aerial portion dried to constant moisture content at 80°C to obtain initial plant biomass (pre-experimental plants) (oven model Isotemp® 630F Fisher Scientific). A drying duration of 48 h was sufficient to ensure constant moisture content and was used as the standard drying time for both plants and aphids. Plant biomass was taken using a balance with closing doors (model Mettler AE 160, Fisher Scientific), set to read 0.0001 g.

At the beginning of each experiment, young adult aphids were selected randomly to infest plants and to estimate their initial biomass. Aphid biomass was assessed using a microbalance sensitive enough to read to 0.0001 mg level (model C-31, Cahn Instruments Inc, Cerritos, California). The initial aphid biomass was estimated by placing individuals in a drop of 95% ethanol (to kill them) in pre-weighed aluminum foil dishes, drying them, weighing them and taking the difference in weight. Each experimental plant was infested with one adult aphid and covered with a transparent, ventilated cage, which consisted of a perforated polyethylene bag 22.5 cm high by 7.4 cm diameter, with the mouth of the bag facing down and tightly secured around the pot. An uninfested control plant was also caged. The caged plants were placed in a plastic container, partially filled with Hoagland's nutrient solution and measuring 23 cm long, 16 cm wide and 7.5 cm deep, with a perforated lid to support six pots (fig. 3.2). The five aphid clones and the control were assigned randomly to the six positions in a container. One container contained one replicate, of which five were tested each week. The replicate containers were maintained

at 20°C and 18h:6h (light:dark) photoperiod. Aphids fed and multiplied on the seedlings for six days. The bag did not touch the plant at the beginning of infestation period but soon grew to the top of the cage. After six days of infestation, aphids on each plant were collected, counted and placed in a pre-weighed aluminum foil dish. The ethanol soon evaporated and aphids were dried in the oven and weighed. The plants were cut at soil level and the aerial part placed in separate pre-weighed aluminum foil dishes, dried as described earlier and weighed.

The performance of individual aphid clones on each wheat cultivar was measured as the difference between final and estimated initial aphid biomass (aphid biomass gained). The impact of aphids on wheat seedlings was estimated as the difference in biomass between control and infested plants (plant biomass lost) (Lamb & MacKay, 1995). The response of seedling plants to each aphid species was estimated by a specific impact for each cultivar, defined as the biomass reduction of plant tissue per unit biomass gained by the aphid (Lamb & MacKay, 1995; Gavloski & Lamb, 2000). A general linear model (SAS Institute Inc., 1989) was applied separately for each plant cultivar to determine if the biomass of control plants varied over time in the series of sequential tests. Control plants had similar growth patterns over the experiment ($P > 0.05$). Therefore, control plants were pooled by cultivar.

Height and biomass showed a linear relationship for pre-experiment plants ("Domain", $R^2 = 0.66$, $P \leq 0.0001$, n=84; "Foremost", $R^2 = 0.78$, $P \leq 0.0001$, n=147; "Medora", $R^2 = 0.79$, $P \leq 0.0001$, n=77). Because plant height of infested plants varied, linear regression equations derived from control plants were used to estimate expected

initial and final biomass of control plants with similar initial heights as the infested plants. The initial biomass of infested plants was estimated from plant heights using the linear regression model derived from pre-experiment plants, to solve for biomass. Initial height and final biomass of control plants were also found to be linearly related ("Domain", $R^2 = 0.59$, $P \leq 0.0001$, n=30; "Foremost", $R^2 = 0.66$, $P \leq 0.0001$, n=30; "Medora", $R^2 = 0.40$, $P \leq 0.0001$, n=30), and the respective linear equations were used to estimate the expected final biomass of a control plant with an initial height which matched an infested plant. Plant biomass loss was estimated by taking the difference between the expected final biomass of a control and actual final biomass of a matching infested plant.

Analysis of variance of the effects of wheat cultivar, aphid species and clone within aphid species on aphid numbers, aphid biomass increase and plant biomass loss after six days of seedling infestation were performed using a general linear model (SAS Institute Inc., 1989). Cultivar, aphid species and the interaction term, cultivar*aphid species, were considered fixed effects and clone within aphid species was considered a random effect. Tukey's multiple range test was used to discriminate means.

Specific impacts were calculated for aphid species and clones within aphid species, and their variances were estimated using the method of Cochran (1977, page 173). The largest and smallest specific impacts were compared among clones within each cultivar-aphid species group using a paired *t*-test. Clones did not differ from one another, except two clones of *Sc. graminum* on CPS wheat, and so clones were pooled and specific impacts were calculated for each cultivar-species combination. To test the

hypothesis that specific impacts were equal, a *t*-test was conducted using unpaired observations and unequal variances (Steel & Torrie, 1960, page 81). Differences among the three aphid species (wheat classes pooled) or among three wheat classes (aphid species pooled) were assessed by testing all possible 2-way comparisons (three comparisons each) using a *t*-test (P=0.005 for rejection of equality in a 2-way comparison gave an experimentwise error rate of 0.01). The relationships between specific impacts at different growth stages were determined by correlation (SAS Institute Inc., 1989).

Aphids on adult plants: diverse cultivars within wheat class

Three diverse cultivars of wheat (having different parentage) belonging to each wheat class (CWRS: "Domain", "Katepwa" and "Roblin"; CPS: "Foremost", "AC Karma" and "AC Vista"; and CWAD: "Medora", "Kyle" and "Plenty") were tested in the field to compare within and among class variation in the interactions between aphids and wheat. Seeds from each cultivar were germinated in the dark at room temperature (about 22°C) by placing kernels on moist filter paper in a Petri dish and covering them with an opaque plastic liner. After 48 h, seedlings with uniform root and coleoptile growth were selected and planted at the Cereal Research Centre's field plots in Winnipeg in 1 X 1 m plots spaced at 2 m intervals. The cultivars were replicated four times within each plot for a total of 36 plants/plot, in a randomized complete block design. Plants were spaced in a square grid 12 cm between rows and 12 cm within rows with 10 cm space around the block of plants so that they were not in contact with the cage initially. Two plots were sown for each aphid species along with no-aphid controls, giving eight plots. The plots

were watered to facilitate uniform seedling emergence.

Two weeks after crop emergence, plots were covered with aphid proof cages made of nylon mesh (mesh size, 13 threads/cm) measuring 1 X 1 m and 1.2 m high, anchored with steel poles at the four corners (fig. 3.3). Aphid species (one clone of one species per cage) were assigned randomly to cages when 50% of plants within a cage reached booting stage (GS 45, boots swollen, Tottman & Makepeace, 1979). A group of 10 young adult aphids from laboratory cultures were placed on each plant for a total of 360 aphids/plot and left undisturbed for 21 days. At the end of the infestation, plants in one half of the plots (whole cages) were cut at soil level, bagged individually and taken to the laboratory for further processing. Plants in the other half of the plots, were sprayed with dimethoate 480 EC at a rate of 2 ml per L of water, and left to grow to maturity for yield assessment. Cages were left in place after spraying to protect the spikes from bird damage. Out of the eight plots one control plot was lost due to colonization by wild aphids.

Aphids were collected from the bagged plants by dipping and shaking the plants in a tub of hot water. The aphid suspension was sieved and sorted to remove plant debris. Clean aphids were placed in pre-weighed aluminum dishes and weighed after being dried. The plants were cut into pieces, dried and weighed. The same balance used to weigh seedling plants was used for adult plants but material from one adult plant was sometimes subdivided into three portions for weighing.

The response of an aphid species to each plant cultivar was estimated as the dry biomass production by each aphid species during infestation. The impact of aphids on

adult plants (21 days after booting stage) was estimated as the difference in biomass between control and infested plant. The impacts of aphids on foliage biomass, spike biomass and seed biomass of mature plants (plants dry and ready for harvest) were estimated as the difference in biomass between control and infested plant.

Statistical tests involved analyses of variance of the dependent variables using GLM and mixed model procedures (SAS Institute Inc., 1989). Wheat class, aphid species and the interaction term, class*aphid species, were considered fixed effects and cultivar within class was considered a random effect. Dunnett's one tailed t-test was used to test whether an aphid species reduced plant biomass in relation to control plants.

Aphids on adult plants: three wheat classes

Field experiments involving single adult wheat plants enclosed in sleeve cages were used to investigate interactions between aphids and adult plants of three wheat classes. In the spring of 1996 and 1997, one cultivar from each of the three classes, CWRS ("Domain"), CPS ("Foremost") and CWAD ("Medora"), were planted by machine in the field using conventional seeding rates and row spacings (seeding rate of 80 kg/ha, and drill spacing of 15 cm between rows). Three weeks after crop emergence, individual plants were selected and covered with aphid-proof sleeve cages made of netting (mesh size 28 threads/cm) (fig. 3.4) to avoid infestation by wild aphids. In 1996, plants were infested at the same time but at different growth stages because different classes of wheat grew at different rates: GS 45, boots swollen for CWRS; GS 32, stem elongation and second node detectable for CPS and GS 33, stem elongation and third

node detectable for CWAD (Tottman & Makepeace, 1979). In 1997, plants of the three classes of wheat were infested at different times but the same growth stage (GS 45, boots swollen). In both years, each plant was infested with a group of 10 young adult aphids and left undisturbed for 21 days. At the end of the infestation period, half of the plots were brought to the laboratory for aphid and plant biomass measurements. The other half were sprayed with dimethoate 480 EC and allowed to grow to maturity for yield assessment.

The response of the aphids was estimated as the dry biomass production by each aphid species on each class of wheat during infestation in 1996 and 1997. The impact of aphids on adult plants each year was estimated as the difference in biomass between control and infested plants. The impacts of aphids on foliage biomass, spike biomass and seed biomass of mature plants were estimated as the difference in biomass between control and infested plant.

Statistical tests involved analyses of variance of the dependent variables using GLM procedures (SAS Institute Inc., 1989). Class of wheat, aphid species and the interaction term, class*aphid species, were considered fixed effects. Tukey's multiple range test was used to discriminate means. Specific impacts were calculated for aphid species and wheat classes using the methods of Cochran (1977) and Steel & Torrie (1960) as described above.

Results

Aphids on seedling plants: three wheat classes and diverse aphid clones

All aphid species fed and multiplied on seedling wheat. The number of offspring

produced by a wingless female during six days of infestation (wheat classes pooled) was highest for *R. padi* (71 ± 1.8, n = 149), intermediate for *Sc. graminum* (62 ± 1.6, n = 149) and lowest for *S. avenae* (29 ± 0.4, n = 149) (fig. 3.5). *Schizaphis graminum* is a smaller aphid than the other two species (table 3.1). Biomass production by *R. padi* was nearly twice that of *Sc. graminum* or *S. avenae* (fig. 3.5). Biomass production by *S. avenae* was similar to that of *Sc. graminum* because the former produced fewer but larger offspring.

All effects tested, i.e., wheat class, aphid species, aphid clone and wheat class by aphid interaction, affected aphid numbers and biomass (table 3.2). Variance components revealed that the major contributor to the total variance was aphid species (70% for aphid numbers and 74% for aphid biomass increase). Aphid clone within species contributed little to variation (variance component = 1.5% for aphid numbers and 1.1% for aphid biomass increase). Wheat class by aphid interaction was significant due to a high production of *Sc. graminum* on CPS and low production of *R. padi* on CWAD, and a high production of *S. avenae* on CWAD (fig. 3.5).

All aphid-infested wheats sustained a reduction in biomass ranging from 3-17 % compared to controls (fig. 3.6). The impact on wheat was different among the aphid species, although aphid species accounted for only 3.3% of the variation (table 3.2). *Rhopalosiphum padi* and *Sc. graminum* caused higher losses than *S. avenae.* Wheat class and aphid clone did not affect plant biomass loss, and there was no wheat class by aphid species interaction. Losses in plant biomass corresponded positively with the biomass of aphids during infestation, although the relationship explained little of the variation (aphid species pooled, $r = 0.16$, $P = 0.0008$, n = 447).

Aphids on adult plants: diverse cultivars within wheat class

When the infestation of adult plants ended, neither aphid biomass production nor plant biomass production differed among cultivars within wheat class (table 3.3) when grown together in the field in 1 X 1 m cages. The expected total degrees of freedom from the methods may seem at variance with total degrees of freedom in the results because some plants failed to establish in field cages. In most cases, only one out of the four replications of a cultivar failed to establish. The precision of aphid biomass and plant biomass was low, however, with about 90% of the variation in both variables due to differences among replications. The CWAD class ("Medora") had the highest and CWRS ("Domain") had the lowest plant biomass. The impact of aphids on wheat was more apparent at crop maturity. Foliage biomass, spike biomass and seed biomass were all affected differentially by aphid species (table 3.4). *Rhopalosiphum padi* had the lowest and *Sc. graminum* had the highest effect (table 3.5). The variance component attributable to aphid species increased three fold for plant spikes in comparison with foliage, showing that assessment of wheat spikes gave more precise estimates of the impact of aphids on wheat than assessment of foliage (table 3.4). Diverse cultivars within each class did not explain significant variation in foliage biomass, spike biomass or seed biomass. An interaction of aphid species and class of wheat affected seed biomass (table 3.4), although when the control treatment (no aphids) was removed from the analysis, the interaction term was not significant.

Aphids on adult plants: three wheat classes

In 1996, when infestations occurred at the same time but at different growth stages, aphid biomass production was affected by class of wheat; there was a class by aphid interaction but no differences attributable to the different aphid species (table 3.6). CWRS tended to have a smaller biomass of aphids than the other two classes of wheat, probably showing that *R. padi* and *Sc. graminum* develop differently on wheats of different growth stages (fig. 3.7). In 1997, when infestations were done at different times but the same growth stage, aphid-plant interactions were in reverse order, with no effects of class or class by aphid interaction. Differences in aphid biomass production were due to the different aphid species (table 3.6). The amount of rainfall during infestation differed between the two years, which may have affected aphid biomass production. In 1996, 83.5 mm of precipitation fell while all wheat classes were infested and in 1997, the precipitation was 38 mm, 29 mm and 38 mm for CWRS, CPS and CWAD respectively (Environment Canada, 1996, 1997). Because of the differences between experiments in 1996 and 1997, that is, different growth stages at infestation and different amounts of precipitation during infestation, information derived from the two data sets were considered separately. Aphid growth and development were probably less affected by factors external to the experimental objective in 1997 than in 1996. Therefore, comparisons focused on the 1997 data only.

Aphid biomass production in 1997 was affected by aphid species, with *S. avenae* and *Sc. graminum* producing the highest biomass (fig. 3.7). Biomass production by *R. padi* was about half as much as that produced by the other two species. A comparison

between the results of aphid biomass production on adult plants and on seedling plants revealed opposite trends for the three species (fig. 3.5 and fig. 3.7). Adult plants were more favourable for the growth of *S. avenae* and *Sc. graminum* populations than they were for *R. padi*, and seedling plants were most favourable for the growth of *R. padi*.

The biomass of plants at 21 days after infestation varied with aphid species and wheat class in 1996 and 1997 (table 3.7). A similar pattern of significance of influences on plant biomass was observed at maturity (table 3.8). Aphid species affected wheat yield in 1996 and 1997 but the effects of wheat class on yield were only detected in 1996 (table 3.9). Feeding by aphids reduced above ground plant biomass after 21 days of infestation by 13% to 45% compared to control (table 3.10) and reduced seed yield at maturity by 16% to 63% compared to control (table 3.11). Among the three classes of wheat tested in 1997, CPS suffered the greatest losses in foliage biomass (average 28%) and the least affected was CWAD (average 18%) (table 3.10). The greatest impact on the plants, especially on the yield, was caused by *S. avenae* and *Sc. graminum*. Aphid damage on wheat was more readily detected on wheat spikes than on the foliage (table 3.8).

Predicting adult plant resistance from seedling resistance

Where possible, resistance was partitioned into antibiosis and tolerance components.

Antibiosis

To determine whether adult antibiosis can be predicted from seedling antibiosis, aphid biomass gained on seedling plants was correlated with aphid biomass gained on

adult plants, but no significant relationships were found when individual plants were infested and caged (table 3.12). For lack of a term that describes the presence of both antibiosis and antixenosis and because the resistance of wheat in these experiments can be largely attributed to antibiosis, the resistance mechanism considered is described solely as antibiosis.

Tolerance

Estimates of plant tolerance (measured as specific impacts) ranged from 1.0 to 3.5 for seedlings and from 3.3 to 20.7 for adult plants (fig. 3.8). A unit biomass of aphids caused 1.3 to 9.3 times more damage to heading plants than to seedling plant (table 3.13). Thus, adult plants were less tolerant to aphid infestation than seedling plants on a weight for weight basis. Among aphid species, seedlings were most tolerant to *R. padi*, and adult plants were least tolerant to *R. padi* (table 3.13). The wheats exhibited similar levels of tolerance to *S. avenae* and *Sc. graminum*. Regardless of growth stage, CWRS class of wheat was more tolerant to aphids than CPS, and CWAD had intermediate tolerance. Tolerance to aphids in seedling plants was not associated with adult plant tolerance (table 3.14), although tolerance to aphids at the heading stage was associated with tolerance at maturity.

Partial resistance

Partial resistance is used to describe resistance present in cultivated wheats which, although not high enough always to provide sufficient aphid control, would usually provide acceptable yields with only an occasional application of insecticide required. The

three classes of cultivated wheats showed variable levels of partial resistance (table 3.15). All three wheats exhibited the highest levels of partial resistance to *R. padi*, with no differences among the wheats. Levels of partial resistance to *S. avenae* and *Sc. graminum* were highest for CWRS, lowest for CPS and moderate for CWAD (table 3.15).

Discussion

All the wheats tested were susceptible to aphids and the level of resistance present in these examples of the three classes of wheat was insufficient to protect the crops adequately from damage by the aphids. Even at the seedling stage where the infestation period lasted only six days, plant biomass was reduced by up to 13% compared to controls.

Interactions between aphids and wheats differed among aphid species, among wheat classes and between two growth stages of the wheat plant. Seedlings were most favourable for the development and growth of *R. padi*. Leather & Dixon (1981) also found that *R. padi* develops rapidly and has a high fecundity when fed on barley at the seedling to stem extension stages. Among five cereal aphid species common in Australia, *R. padi* also has the highest fecundity on barley seedlings (MacKay & Lamb, 1996). *Rhopalosiphum padi* may utilize seedling plants more effectively than the other two aphid species because it preferentially selects the most favourable feeding location, the stems of young wheat plants (MacKay & Lamb, 1996; Migui, 1996). As the plant develops into the adult stage, its suitability for the various aphid species changes, causing aphids to develop and reproduce at different rates than on earlier growth stages. The relative performance of

the aphid species were reversed, with adult plants becoming more suitable for the development of *S. avenae* and *Sc. graminum* than for *R. padi*. *Schizaphis graminum* prefers to feed on fully expanded leaves on the lower half of the host plant in both seedling and adult plants (Starks & Burton, 1977; Migui, 1996). Upon spike emergence, a large proportion of *S. avenae* migrates from the upper leaves to the spikes (Dean, 1974; Wratten, 1975) where its fecundity increases by up to three times (Watt, 1979). The high reproductive capacity of *S. avenae* on adult wheat was confirmed in this study. In adult plants, assimilates are relocated to the filling grain, which may become the most nutritious part of the plant. *Sitobion avenae* affects the yield of wheat by directly competing with the filling grain for plant nutrients (Wratten, 1975).

The reversal in the trend of biomass production among aphid species between the two growth stages of wheat show that some level of antibiosis to aphids is exhibited in the two growth stages. Seedling plants are susceptible to *R. padi* and exhibit antibiosis to *S. avenae* and *Sc. graminum* in comparison to adult plants, while adult plants are susceptible to *S. avenae* and *Sc. graminum* and exhibit antibiosis to *R. padi* in comparison to seedling plants. The level of antibiosis is not the same for the three aphid species, and so they need to be considered separately. The CWRS class of wheat was earlier maturing than the other two classes and supported the lowest amount of aphid biomass, probably because it grows through the critical stage that is most vulnerable to aphid attack faster than CPS or CWAD. Because aphid populations in the field increase in size as the cereal crops grow to adult stage, CWRS probably reaches the vulnerable stage when aphid populations are not as high as when CPS or CWAD reach this growth stage. By the time

CPS reaches the most susceptible stage, CWRS will have grown into a stage that is more resistant to aphids.

A greater level of resistance is required to manage aphid infestations in adult wheat. Nevertheless the wheats show variation in their susceptibility to aphids suggesting that some level of partial resistance already exists. Questions that need to be answered are: can the partial resistance be quantified, and can the partial resistance that is shown be used to identify methods for discovering other sources of partial resistance for spring wheats. Partial resistance was detected in adult plants of cultivated wheat, with the highest level of partial resistance occurring on all wheats infested with *R. padi*. On the most susceptible cultivar, "Foremost" (CPS wheat), the level of partial resistance to *R. padi* was more than double the level of partial resistance to *S. avenae* or *Sc. graminum*. These levels of partial resistance are not sufficient to avoid economic damage and need to be augmented with other control methods to give a satisfactory production level. For instance, the 59% level of partial resistance in CWAD to *R. padi* would require other control measures to further reduce the 41% difference in yield compared to the yield of uninfested controls. The literature is not clear as to which method best describes resistance. Findings from the current study demonstrate that a clear picture of host plant resistance can only be obtained by using methods which estimate responses of aphids to wheat and responses of wheats to aphids and that these assessments are conducted using the plant growth stage attacked by aphids. A superior screening method should be capable of estimating both aphid to plant and plant to aphid responses and also detect partial resistance. Measurements of aphid and plant biomass changes during infestation appear to

provide a sensitive indicator of host plant resistance.

It is clear that the plants respond differently to attacks by different aphid species, suggesting that control measures for these aphids should be considered separately. For example, for all three classes of wheat, the presence of biological control organisms in the field might provide a sufficient augmentation to partial resistance to *R. padi*, whereas, insecticide applications might be needed to control heavy infestations of *S. avenae* or *Sc. graminum*. The current recommended economic thresholds for cereal aphids on spring planted wheat in the Canadian Prairies, of 12 -15 aphids per stem until about two weeks after flowering (Manitoba Agriculture, 2001), assume aphid species have equal impact on plants, and these recommendations are not based on data collected in Canada. In light of the information obtained in this study, it is evident that to make recommendations on aphid control, the species should probably not be pooled because their impacts on the crops are different; they most likely do not occur on field crops in equal proportions, so recommendations should be based on the most abundant species. Proper assessment of economic thresholds of these aphid species in Western Canada is evidently justified. Partial resistance is useful for two reasons. First, it is useful agriculturally because it affects pest control recommendations. In spring wheat, for example, more care should be taken in making aphid control decisions for CPS wheat than CWRS, and CWAD is in between. Second, partial resistance allows examination of the resistance from a methodological point of view because it allows identification of the resistance method that best reveals partial resistance.

The occurrence of aphid populations in the field as an assortment of parthenogenetic clones casts doubt on the value of using only a single clone to assess the interaction between a wheat cultivar and aphid species. Analysis of increase in aphid numbers or aphid biomass during infestation revealed that the contribution of different clones was low and insignificant compared to the contribution of different aphid species. In other words, aphid clones belonging to the same species responded more similarly to wheat seedlings than clones of another species. The same was true for the response of the plant in terms of biomass loss. Even aphid clones that were reared in the laboratory for several years had similar effects on the plants to clones collected recently from the field. This finding is important because a single or a few clones often are used in aphid research, for practical reasons, and the observation that aphid clones in the population exhibit similar effects validates the use of a few clones for comparisons among species. Nevertheless, researchers must be alert to the problem that an initially rare, virulent clone may occur and become dominant. Such clones arise repeatedly in some aphid species and have overcome antibiotic resistance (Porter *et al.*, 1997).

Both laboratory and field studies demonstrated that all aphid species are capable of inflicting damage on wheat at seedling and adult stages, with *R. padi* having the greatest effect on seedlings, and *S. avenae* and *Sc. graminum* having the greatest effect on adult plants. The CPS class of wheat was most susceptible to *R. padi* and *S. avenae*. Interactions between aphids and wheat were similar among diverse cultivars within each class, but differed among classes. This result indicates that cultivars within each class were similarly susceptible to the aphids, which is important because it would be

impractical to test all cultivars from a given region before making a recommendation on the need for control.

All aphids feeding on adult wheat caused a higher impact on the spikes than on the foliage, and so assessment of wheat spikes alone may provide an adequate estimate of the effects of aphids on the crop. Agriculturally, the best measure of resistance, that is, plant biomass loss is seed yield loss, but for practical purposes, spike biomass loss is more closely correlated with seed yield loss than foliage biomass loss. For screening purposes resistance in adult wheat is characterized as:

Spike biomass lost = aphid biomass gained * specific impact.

Specific impacts of aphids on seedlings of cultivated wheats ranged from 1.0 to 3.5 mg of plant biomass loss for every mg gain in aphid biomass. These values are quite similar to those reported by MacKay & Lamb (1996), who found that specific impact was 3.4 mg of plant biomass lost for each mg of aphid biomass gained. Aphid-plant interactions in other systems show different specific impacts. Gavloski & Lamb (2000) reported specific impacts of two aphid species, *Lipaphis erysimi* (Kaltenbach) and *Myzus persicae* (Sulzer), on seedling canola, of 12 and 16, respectively, which are about 4 times higher than specific impacts of aphids on seedling cereal crops. Specific impacts also change with different growth stages of the same plant species. The specific impact of aphids on wheat was greater on adult than seedling plants, suggesting that on a weight for weight basis, seedlings might be more tolerant to aphids than adult plants. However, because exposure of aphids to seedlings was of much shorter duration than adult plants,

further examination of the aphid-plant relationships at different stages is needed. The similarities or differences in specific impacts may be associated with the different ways in which plants of different genetic backgrounds and different growth stages respond to aphid damage.

Assessment of aphid numbers and aphid biomass during infestation provided an estimate of antibiosis, that is, a resistance mechanism that adversely affects the aphid's life history parameters when the aphid feeds on resistant wheat. Because aphids move as they feed on plants (Mackay & Lamb, 1996, Migui, 1996), a low level of antixenosis could have occurred in multiple plant cage studies, but it is difficult to separate from antibiosis. However, the differences in aphid numbers and aphid biomass among the three wheat classes tested at the seedling and adult plant stages may be largely due to antibiosis because almost the entire aphid population in each cage was located on the plant, feeding, with few or no aphids found wandering on the sides of the cages. Despite aphid biomass measurements being not a conventional population parameter, they provide a good index for quantifying the aphid-plant interaction.

The lack of correlation between seedling resistance, either antibiosis or tolerance, and adult plant resistance shows that seedling plants cannot be used to predict resistance in adult plants. On a weight for weight basis, seedling plants exhibited higher levels of tolerance to aphids than adult plants.

The low resistance to aphids in the cultivated wheats may be associated with the many years of breeding for high yielding and disease resistant wheats with little or no effort devoted to resistance to insects. Any level of resistance that may have been present

in the early cultivars could have been lost through the breeding and selection processes. In the current study, tolerance to aphids appeared to decline with increasing age of wheat plants, as demonstrated by the rising specific impacts, which show seedling plants being as much as five times as tolerant to aphids as adult plants.

Resistance to aphids in cultivated wheats has been associated with long awns and hairy leaves (Roberts & Foster, 1983; Havlickova, 1993). A similar observation was reported in England by Acreman & Dixon (1986) that awned wheats are self cleaning, because *S. avenae* fall off when spikes of adjacent stems brush together. The CWAD and CPS wheats tested in this study had longer awns and more hairy leaves than CWRS wheat, but there was no association of these characters with manifestation of resistance. Moreover, among the three classes of wheat, CPS was found to be most susceptible to *R. padi* and *S. avenae* and suffered the greatest yield loss.

Antibiosis of wheat to aphids has been associated with the presence of allelochemicals which reach peak levels in seedlings (Thackray *et al.*, 1990; Givovich & Niemeyer, 1991). The ability of aphid species to sequester these chemicals will determine the resultant level of interaction. Rather than being limited to sequestration, aphids could (at least in theory) survive allelochemicals by detoxifying them or excreting them rapidly enough to avoid a lethal concentration. Therefore, sources of antibiosis are likely to be different for different aphid species. Tolerance may be a more general phenomenon and apply to more than one species of aphid as was the case here with little or no difference in tolerance to aphids among adult plants. The levels of antibiosis and tolerance in seedlings do not predict the levels in adult plants, and so screening for resistance to cereal aphids in

spring wheats which are infested as adult plants will have to be done on adult plants. Adult plants of Canadian wheats are susceptible to *S. avenae* and *Sc. graminum* and more attention to *S. avenae* is warranted because it is the more dominant aphid. Although the classes of wheat tested in this study are regarded as susceptible to aphids, the CWRS class shows partial resistance. Biomass transfer relationships between aphids and plants have been useful in identifying levels of partial resistance that would help protect spring wheat against these cereal aphids. This level of partial resistance can be quantified by measuring spike or seed biomass loss in adult plants. Combined partial antibiosis and tolerance might account for a considerable yield benefit for the partially resistant plant. Therefore it is worth pursuing the possibility of augmenting partial resistance for spring wheats which require resistance as adult plants. Resistance can be partitioned into antibiosis and tolerance, but in adult plants, tolerance is the most important component of resistance. The results of this study justify the need for adult plant resistance in Western Canada and define some of the methods that might be used to search for resistance.

Table 3.1. Biomass of individual wingless young, adult aphids in a controlled environment[1].

Aphid species	n	Mean biomass, mg ± SE
Rhopalosiphum padi	145	0.316 ± 0.004
Sitobion avenae	50	0.329 ± 0.010
Schizaphis graminum	80	0.190 ± 0.003

[1] Aphids ranged in age from 24 to 36 hours from the last molt, and were dried to constant weight at 80°C for 48 h.

Table 3.2. Analysis of variance of the effects of wheat class, aphid species and clone within aphid species on aphid numbers, aphid biomass increase and plant biomass loss after six days of seedling infestation.

Source of variation[1]	df	MSE	*F*	Significance level[2]	Variance component[3], %
Log_e(aphid numbers)					
CLASS	2	1.80	54.6	***	0.0
AP	2	29.85	196.7	***	69.5
CL(AP)	12	0.15	4.6	***	1.5
CLASS*AP	4	2.44	74.0	***	16.6
ERROR	426	0.03			12.4
Log_e(aphid biomass increase)					
CLASS	2	0.20	5.6	**	0.0
AP	2	23.06	227.2	***	74.1
CL(AP)	12	0.10	2.8	***	1.1
CLASS*AP	4	1.01	28.1	***	7.0
ERROR	426	0.04			17.8
Plant biomass loss					
CLASS	2	350.83	2.9	ns	0.8
AP	2	819.74	19.1	***	3.3
CL(AP)	12	42.95	0.4	ns	0.0
CLASS*AP	4	192.97	1.6	ns	1.2
ERROR	429	121.81			94.7

[1] AP = aphid species, CL = aphid clone.
[2] **, *** = significant, $P \leq 0.01$ and $P \leq 0.001$, respectively; ns = not significant, $P > 0.05$.
[3] Estimates of variance component based on a random effect ANOVA (mixed model with all effects random).

Table 3.3. Analysis of variance of the effects of aphid species, wheat class and cultivar within class on the biomass of aphids and biomass of plants at the end of the infestation period which began at boot stage and lasted for 21 days in the field (three cultivars for each of three classes of wheat).

Source of variation[1]	df	MSE	*F*	Significance level[2]	Variance component[3], %
Log_e(aphid biomass)					
AP	2	0.32	0.36	ns	0.0
CLASS	2	1.18	1.71	ns	0.0
CULT(CLASS)	6	0.69	0.79	ns	0.0
CLASS*AP	4	1.90	2.17	ns	3.9
ERROR	78	0.88			96.1
Log_e(plant biomass)					
AP	2	0.06	1.01	ns	1.1
CLASS	2	0.23	10.34	**	10.0
CULT(CLASS)	6	0.02	0.40	ns	0.0
CLASS*AP	4	0.06	1.02	ns	0.0
ERROR	78	0.06			88.9

[1] CULT = cultivar, AP = aphid species.
[2] ** = significant, $P \leq 0.01$; ns = not significant $P > 0.05$.
[3] Estimates of variance component based on a random effect ANOVA (mixed model with all effects random).

Table 3.4. Analysis of variance of the effects of aphid species, wheat class and cultivar within class on foliage biomass, spike biomass and biomass of seeds at maturity. Three cultivars for each of three classes of wheat were infested by three species of aphids for 21 days beginning at boot stage.

Source of variation[1]	df	MSE	*F*	Significance level[2]	Variance component[3], %
Log_e(foliage biomass)					
AP	3	3.41	9.91	***	23.9
CLASS	2	0.08	0.11	ns	0.0
CULT(CLASS)	6	0.70	2.04	ns	4.0
CLASS*AP	6	0.34	0.99	ns	0.0
ERROR	99	0.34			72.2
Log_e(spike biomass)					
AP	3	44.97	65.33	***	69.0
CLASS	2	0.06	0.09	ns	0.0
CULT(CLASS)	6	0.62	0.90	ns	0.0
CLASS*AP	6	1.34	1.95	ns	1.5
ERROR	99	0.69			29.5
Log_e(biomass of seeds)					
AP	3	62.2	56.83	***	65.1
CLASS	2	8.20	12.37	***	4.7
CULT(CLASS)	6	0.65	0.60	ns	0.0
CLASS*AP	6	3.54	3.23	**	7.5
ERROR	83	1.09			22.7

[1] CULT = cultivar, AP = aphid species.
[2] **, *** = significant, $P \leq 0.01$ and $P \leq 0.001$, respectively; ns = not significant, $P > 0.05$.
[3] Estimates of variance component based on a random effect ANOVA (mixed model with all effects random).

Table 3.5. Effects of three aphid species on the biomass of mature wheat (three cultivars for each of three classes).

Effect	n	Mean biomass, g ± SE	Test of significance[1]
Foliage biomass (without spikes)			
Control	28	12.9 ± 1.22	
Rhopalosiphum padi	27	9.4 ± 0.94	*
Sitobion avenae	29	8.4 ± 0.59	*
Schizaphis graminum	33	5.3 ± 0.43	*
Spike biomass			
Control	28	18.7 ± 1.83	
R. padi	27	7.1 ± 0.84	*
S. avenae	29	3.0 ± 0.41	*
Sc. graminum	33	1.2 ± 0.23	*
Biomass of seeds			
Control	28	14.6 ± 1.40	
R. padi	27	5.0 ± 0.71	*
S. avenae	24	1.0 ± 0.41	*
Sc. graminum	22	0.6 ± 0.20	*

[1]Test of whether an aphid species reduced plant biomass in relation to control plants, Dunnett's one-tailed t-test, α=0.05; * = significant.

Table 3.6. Analysis of variance of the effects of wheat class and aphid species on aphid biomass increase at the end of infestation period which began at boot stage and lasted for 21 days in the field.

Source of variation[1]	df	MSE	*F*	Significance level[2]
Log_e(aphid biomass, 1996)[3]				
CLASS	2	1.20	5.54	**
AP	2	0.39	1.79	ns
CLASS*AP	4	0.91	4.23	**
ERROR	27	0.22		
Log_e(aphid biomass, 1997)[4]				
CLASS	2	0.26	1.20	ns
AP	2	3.69	16.98	***
CLASS*AP	4	0.02	0.08	ns
ERROR	26	0.22		

[1] AP = aphid species.
[2] **, *** = significant, $P \leq 0.01$ and $P \leq 0.001$, respectively; ns = not significant, $P > 0.05$.
[3] In the 1996 season, three classes of wheat were infested with aphids at the same time but at different growth stages (when 50% of the earliest maturing class reached boot stage).
[4] In the 1997 season, three classes of wheat were infested with aphids at the same growth stage but at different times (when 50 % of the plants within a class reached boot stage).

Table 3.7. Analysis of variance of the effects of wheat class and aphid species on the biomass of plants at the end of aphid infestation period which began at boot stage and lasted for 21 days in the field.

Source of variation[1]	df	MSE	*F*	Significance level[2]
Log$_e$(plant biomass, 1996)[3]				
CLASS	2	0.46	5.33	**
AP	3	0.29	3.39	*
CLASS*AP	6	0.09	1.01	ns
ERROR	34	0.09		
Log$_e$(plant biomass, 1997)[4]				
CLASS	2	0.71	8.67	***
AP	3	0.26	3.15	*
CLASS*AP	6	0.03	0.40	ns
ERROR	35	0.08		

[1] AP = aphid species (three species and control).
[2] *, **, *** = significant, $P \leq 0.05$, $P \leq 0.01$ and $P \leq 0.001$, respectively; ns = not significant, $P > 0.05$.
[3] In the 1996 season, three classes of wheat were infested with aphids at the same time but at different growth stages (when 50% of the earliest maturing class reached boot stage).
[4] In the 1997 season, three classes of wheat were infested at the same growth stage but at different times (when 50 % of the plants within a class reached boot stage).

Table 3.8. Analysis of variance of the effects of wheat class and aphid species on foliage biomass and spike biomass at maturity after plants were infested by aphids for 21 days beginning at boot stage in the field.

Source of variation[1]	df	MSE	*F*	Significance level[2]
Log$_e$(foliage biomass) 1996				
CLASS	2	0.97	11.53	***
AP	3	0.23	2.68	ns
CLASS*AP	6	0.16	1.85	ns
ERROR	35	0.08		
Log$_e$(spike biomass) 1996				
CLASS	2	3.14	12.96	***
AP	3	1.82	7.49	***
CLASS*AP	6	0.34	1.40	ns
ERROR	35	0.24		
Log$_e$(foliage biomass) 1997				
CLASS	2	0.61	9.57	***
AP	3	0.32	5.00	**
CLASS*AP	6	0.05	0.77	ns
ERROR	34	0.06		
Log$_e$(spike biomass) 1997				
CLASS	2	1.24	5.86	**
AP	3	2.45	11.62	***
CLASS*AP	6	0.24	1.13	ns
ERROR	34	0.21		

[1] AP = aphid species. [2] **, *** = significant, $P \leq 0.01$ and $P \leq 0.001$, respectively; ns = not significant, $P > 0.05$.

Table 3.9. Analysis of variance of the effects of wheat class and aphid species on the biomass of seeds of wheat plants infested by aphids for 21 days beginning at boot stage in the field.

Source of variation[1]	df	MSE	*F*	Significance level[2]
Log_e(biomass of seeds, 1996)[3]				
CLASS	2	2.66	7.89	**
AP	3	3.76	11.16	***
CLASS*AP	6	0.50	1.47	ns
ERROR	35	0.34		
Log_e(biomass of seeds, 1997)[4]				
CLASS	2	1.07	2.65	ns
AP	3	6.13	15.25	***
CLASS*AP	6	0.25	0.61	ns
ERROR	35	0.40		

[1] AP = aphid species.
[2] **, *** = significant, $P \leq 0.01$ and $P \leq 0.001$, respectively; ns = not significant, $P > 0.05$.
[3] In the 1996 season, three classes of wheat were infested with aphids at the same time but at different growth stages (when 50% of the earliest maturing class reached boot stage).
[4] In the 1997 season, three classes of wheat were infested with aphids at the same growth stage but at different times (when 50 % of the plants within a class reached boot stage).

Table 3.10. Effects of aphid species and wheat class on the total above ground biomass of mature wheat which were individually caged in the field and infested with aphids for 21 days beginning at boot stage.

Year	Wheat class	Aphid species	n	Mean foliage biomass, g ± SE	Percent reduction
1996	Canadian Western Red Spring	Control	3	5.98 ± 0.53	0
		Rhopalosiphum padi	4	4.04 ± 0.43	33
		Sitobion avenae	4	5.10 ± 0.32	15
		Schizaphis graminum	4	4.67 ± 1.02	22
	Canadian Prairie Spring	Control	3	6.28 ± 0.99	0
		R. padi	4	5.18 ± 0.74	18
		S. avenae	4	6.83 ± 0.88	-9
		Sc. graminum	4	5.38 ± 0.61	14
	Canadian Western Amber Durum	Control	4	10.03 ± 0.70	0
		R. padi	4	6.99 ± 0.87	30
		S. avenae	4	6.35 ± 1.37	37
		Sc. graminum	4	5.47 ± 1.11	45
1997	Canadian Western Red Spring	Control	4	6.37 ± 0.47	0
		R. padi	4	5.11 ± 0.50	20
		S. avenae	4	4.70 ± 0.87	26
		Sc. graminum	4	5.51 ± 0.70	13
	Canadian Prairie Spring	Control	4	10.62 ± 1.31	0
		R. padi	4	7.74 ± 0.83	27
		S. avenae	4	6.46 ± 1.15	39
		Sc. graminum	4	8.80 ± 1.74	17
	Canadian Western Amber Durum	Control	4	8.03 ± 0.66	0
		R. padi	4	6.30 ± 1.23	21
		S. avenae	3	6.87 ± 0.34	14
		Sc. graminum	4	6.59 ± 0.80	18

Table 3.11. Effects of aphid species and wheat class on the average yield of wheat plants which were infested with aphids for 21 days beginning at boot stage.

Year	Factor	n	Mean seed biomass, g ± SE[2]	Percent reduction
1996	Aphid species			
	Control	11	4.3 ± 0.69 a[3]	0.0
	Rhopalosiphum padi	12	3.6 ± 0.60 a	16.3
	Sitobion avenae	12	3.1 ± 0.39 a	27.9
	Schizaphis graminum	12	1.6 ± 0.31 b	62.8
	Wheat class[1]			
	CWRS	12	2.0 ± 0.38 a	28.6
	CPS	12	3.7 ± 0.65 b	43.9
	CWAD	12	2.7 ± 0.36 ab	35.7
1997	Aphid species			
	Control	11	4.5 ± 0.57 a	0.0
	R. padi	12	2.5 ± 0.39 ab	44.4
	S. avenae	12	1.3 ± 0.13 bc	71.1
	Sc. graminum	12	1.1 ± 0.30 c	75.6
	Wheat class			
	CWRS	12	1.1 ± 0.16 a	65.6
	CPS	12	1.9 ± 0.43 a	66.7
	CWAD	12	1.8 ± 0.31 a	59.1

[1] CWRS = Canadian Western Red Spring, CPS = Canadian Prairie Spring, CWAD = Canadian Western Amber Durum.

[2] Means for the wheat class factor are from infested plants only.

[3] Means from the same factor in the same column within the same year followed by the same letter(s) are not significantly different from one another using Tukey's range test, $P > 0.05$.

Table 3.12. Correlation of aphid biomass gained during six days on seedlings (two leaf stage, GS 12) versus aphid biomass gained during 21 days on adult wheat (boots swollen, GS 45, Tottman & Makepiece, 1979).[1]

Aphid species	*r*	*P*	n
Rhopalosiphum padi	0.172	0.828	4
Sitobion avenae	0.013	0.987	4
Schizaphis graminum	-0.604	0.113	4

[1] Data for adult plants included all tests conducted at the same growth stage, i.e. the three classes of wheat in 1997 and CWRS in 1996.

Table 3.13. Specific impacts (mg/mg) of aphids on wheat (biomass reduction in plant per unit biomass gained by aphid) at three growth stages: seedling (growth chamber), heading (field) and mature (field). For the seed yield data, the aphid biomass gained was at heading stage and sometime before the estimated seed biomass lost.[1]

Factor	Seedling plants, six days after infestation		Adult plants at heading, 21 days after infestation		Adult plants at maturity, biomass of seeds	
	n	Mean ± SE	n	Mean ± SE	n	Mean ± SE
Aphid species						
Rhopalosiphum padi	149	1.7 ± 0.13 a[3]	12	15.5 ± 4.95 a	12	15.8 ± 3.37 c
Sitobion avenae	149	2.5 ± 0.23 b	12	7.8 ± 2.14 b	12	10.1 ± 0.95 ab
Schizaphis graminum	149	3.7 ± 0.30 c	12	4.9 ± 1.97 b	12	12.0 ± 1.51 bc
Wheat class[2]						
CWRS	150	2.1 ± 0.19 a	12	5.9 ± 1.80 a	12	10.2 ± 1.11 a
CPS	148	2.4 ± 0.19 b	12	10.4 ± 2.78 b	12	13.4 ± 1.75 b
CWAD	149	2.4 ± 0.22 b	11	6.8 ± 2.73 ab	12	11.4 ± 1.76 ab

[1] Data for specific impacts of aphids on wheat at heading and mature plant stages are from 1997 experiments only.
[2] CWRS = Canadian Western Red Spring, CPS = Canadian Prairie Spring, CWAD = Canadian Western Amber Durum.
[3] Mean specific impacts from the same factor within a column followed by the same letter(s) do not differ significantly. Differences among three aphid species (wheat classes pooled) or among three wheat classes (aphids species pooled) were assessed by testing all possible 2-way comparisons (three comparisons each) using a *t*-test ($P = 0.005$ for rejection of equality in a 2-way comparison gave an experimentwise error rate of 0.01).

Table 3.14. Correlation of specific impacts (mg/mg) of aphids on wheat (biomass reduction in plant per unit biomass gained by aphid) at different growth stages.

Growth stages	*r*	*P*	n
Seedling versus Heading	-0.54	0.137	9
Seedling versus Mature	-0.32	0.397	9
Heading versus Mature	0.84	0.005	9

Table 3.15. Partial resistance (%) of cultivated tetraploid and hexaploid wheats to three species of cereal aphids[1]

Wheat Class	Partial resistance (%)		
	Rhopalosiphum padi	*Sitobion avenae*	*Schizaphis graminum*
Canadian Prairie Spring	58	21	11
Canadian Western Red Spring	55	35	48
Canadian Western Amber Durum	59	27	27

[1] Complete resistance = 100%
Partial resistance = Control (100%) - yield loss (%)
The higer the % value, the higher the level of partial resistance

Fig. 3.1. Barley seedlings at two leaf stage (GS 12, Tottman & Makepeace, 1979) used for rearing aphids in controlled environment growth chambers.

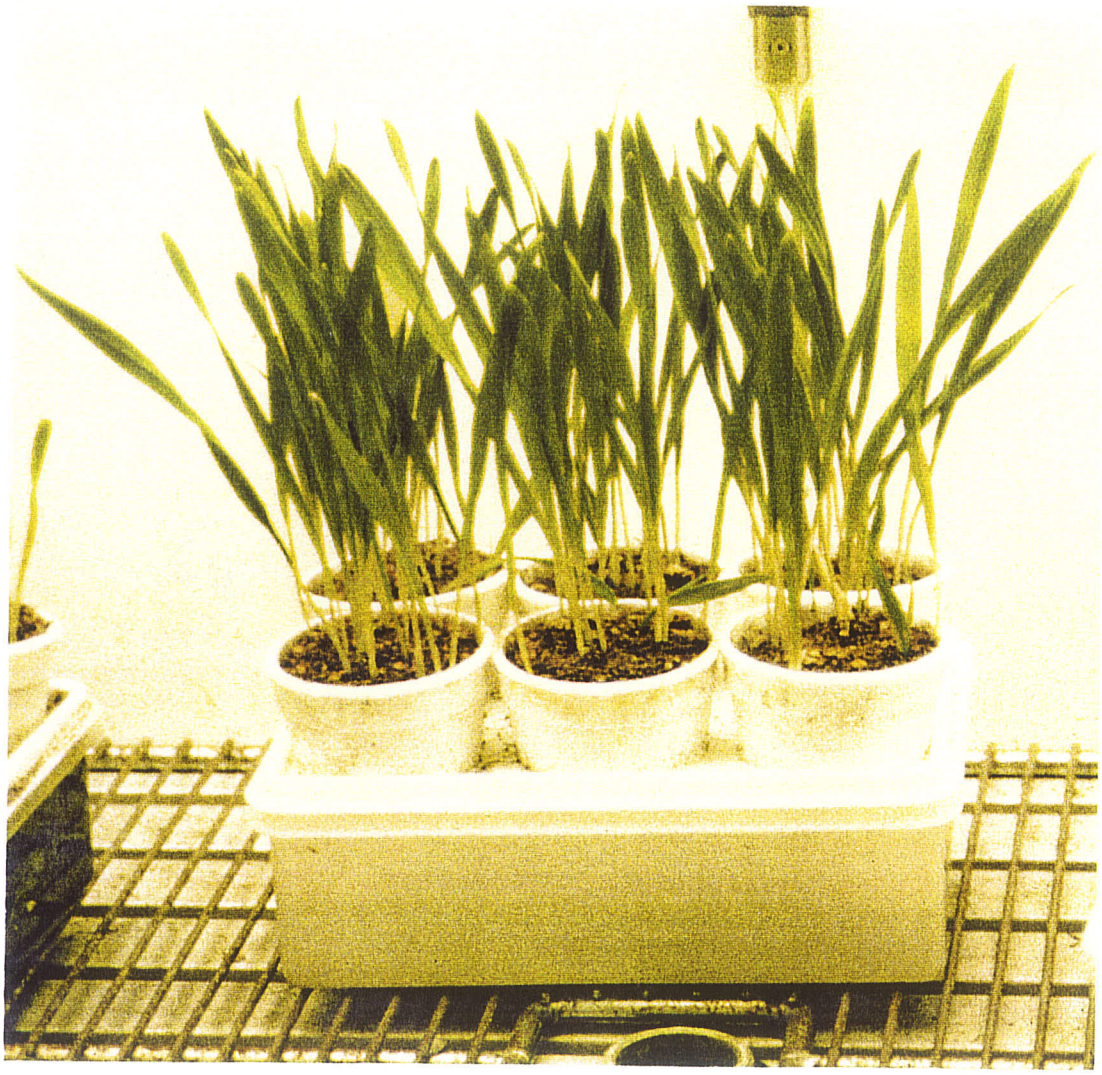


Fig. 3.2. Wheat seedlings in aphid proof cages used in the laboratory.


A-2

Fig 3.3. 1 X 1 m cages used in the investigation of resistance of adult wheat plants in the field to aphids.

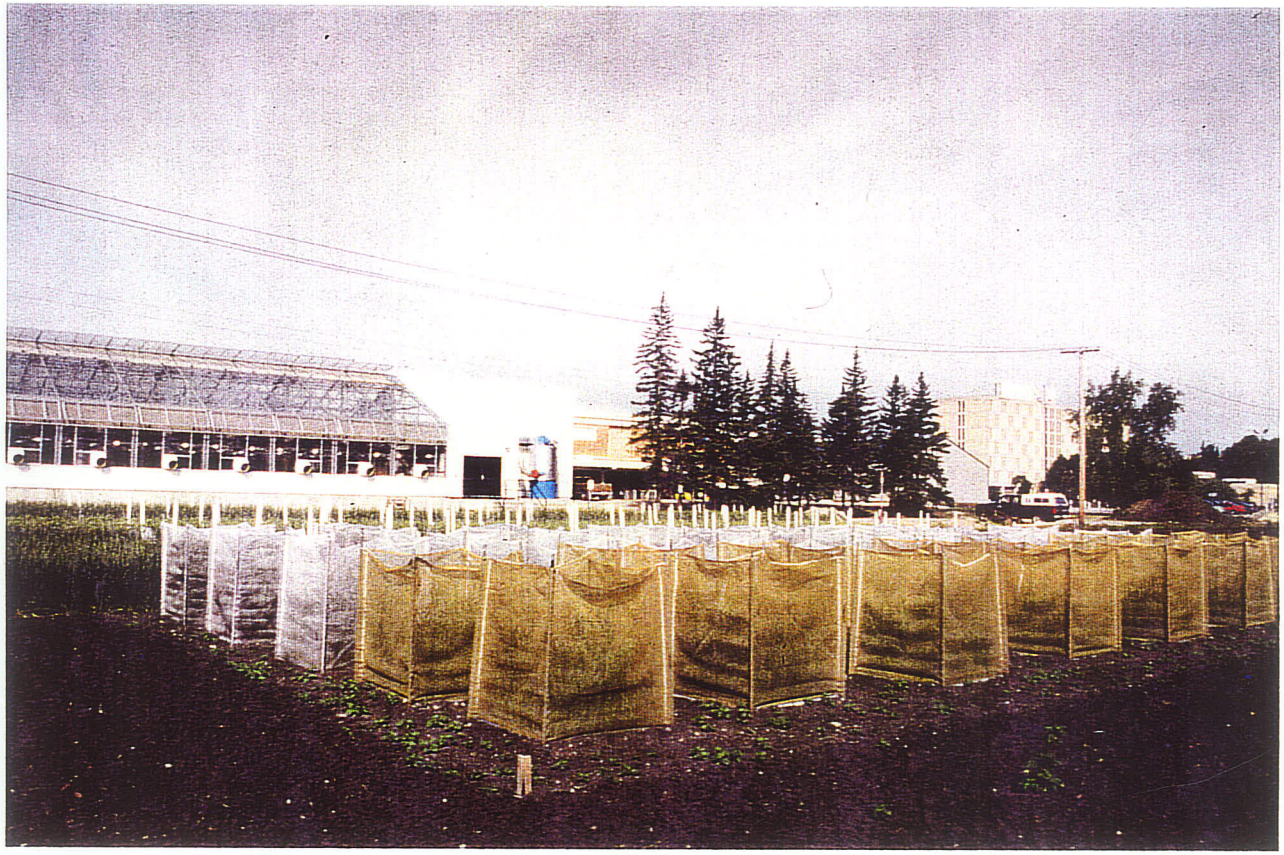
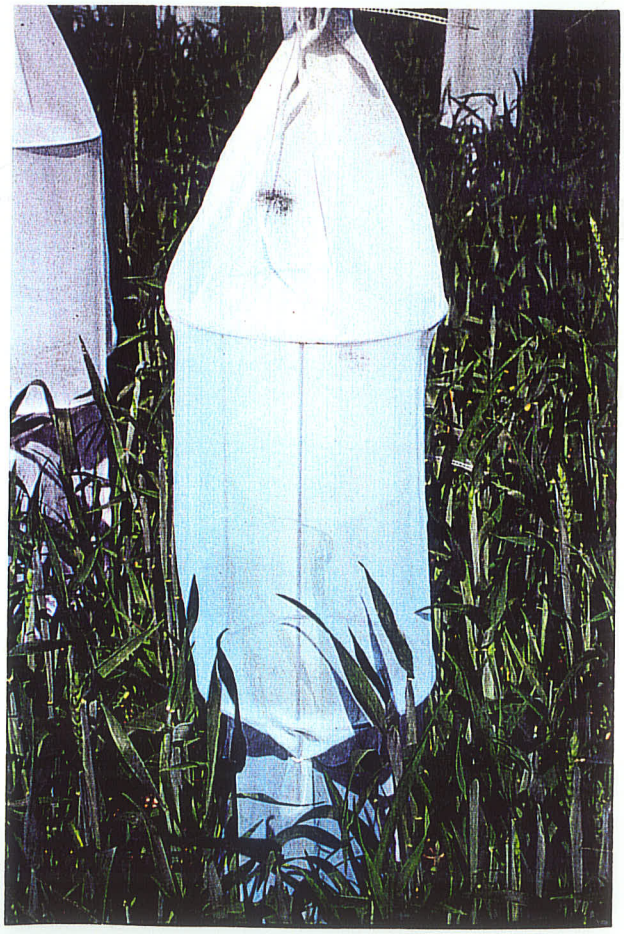


Fig. 3.4. Single adult wheat plants in sleeve cages: (a) layout in the field; and (b) a close-up of one cage.

(a)



(b)

Fig. 3.5. Mean number of aphid offspring and their biomass produced by a young, wingless adult aphid during six days on wheat seedlings.

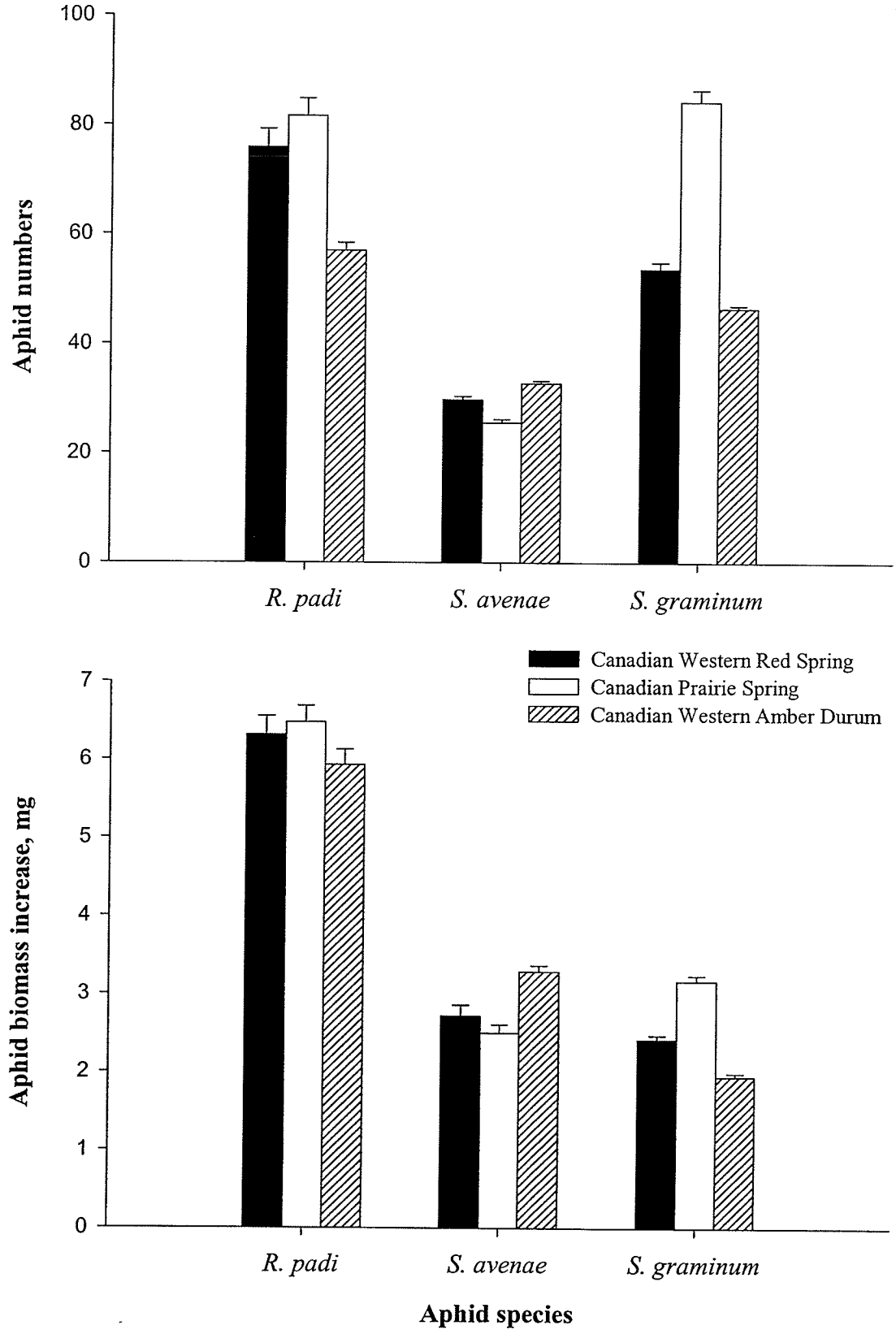

Aphid numbers
100
80
60
40
20
0
R. padi
S. avenae
S. graminum
Canadian Western Red Spring
Canadian Prairie Spring
Canadian Western Amber Durum
Aphid biomass increase, mg
7
6
5
4
3
2
1
0
R. padi
S. avenae
S. graminum
Aphid species

Fig. 3.6. Mean percent aerial biomass loss (± SE) of wheat seedlings after six days of infestation by cereal aphids in a controlled environment.

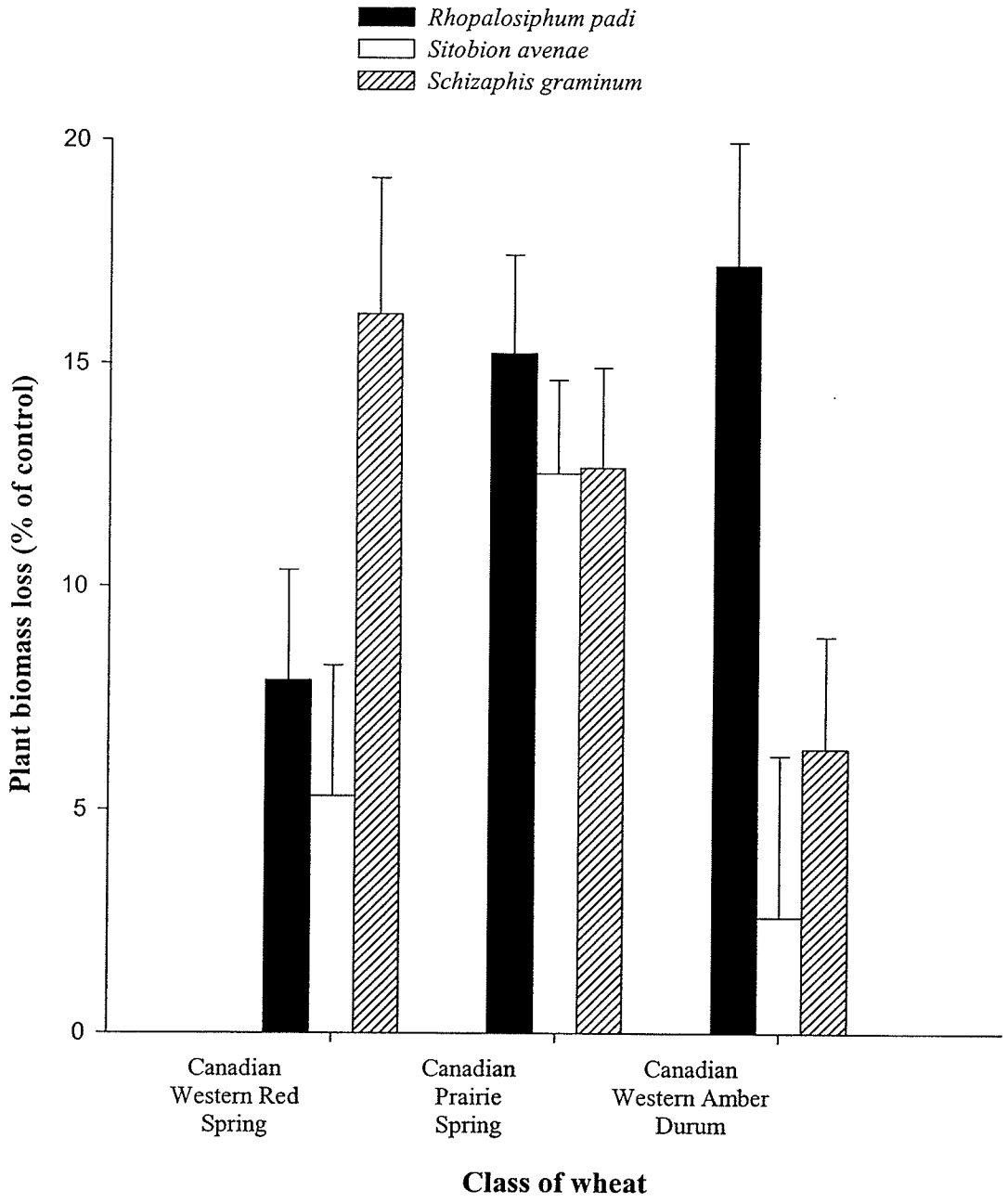

Rhopalosiphum padi
Sitobion avenae
Schizaphis graminum
20
15
10
5
0
Plant biomass loss (% of control)
Canadian Western Red Spring
Canadian Prairie Spring
Canadian Western Amber Durum
Class of wheat

Fig. 3.7 Mean biomass of cereal aphids after 21 days on wheat, from boot stage, with boots swollen (GS 45), to the milk development stage (GS 77) (Tottman & Makepeace, 1979).

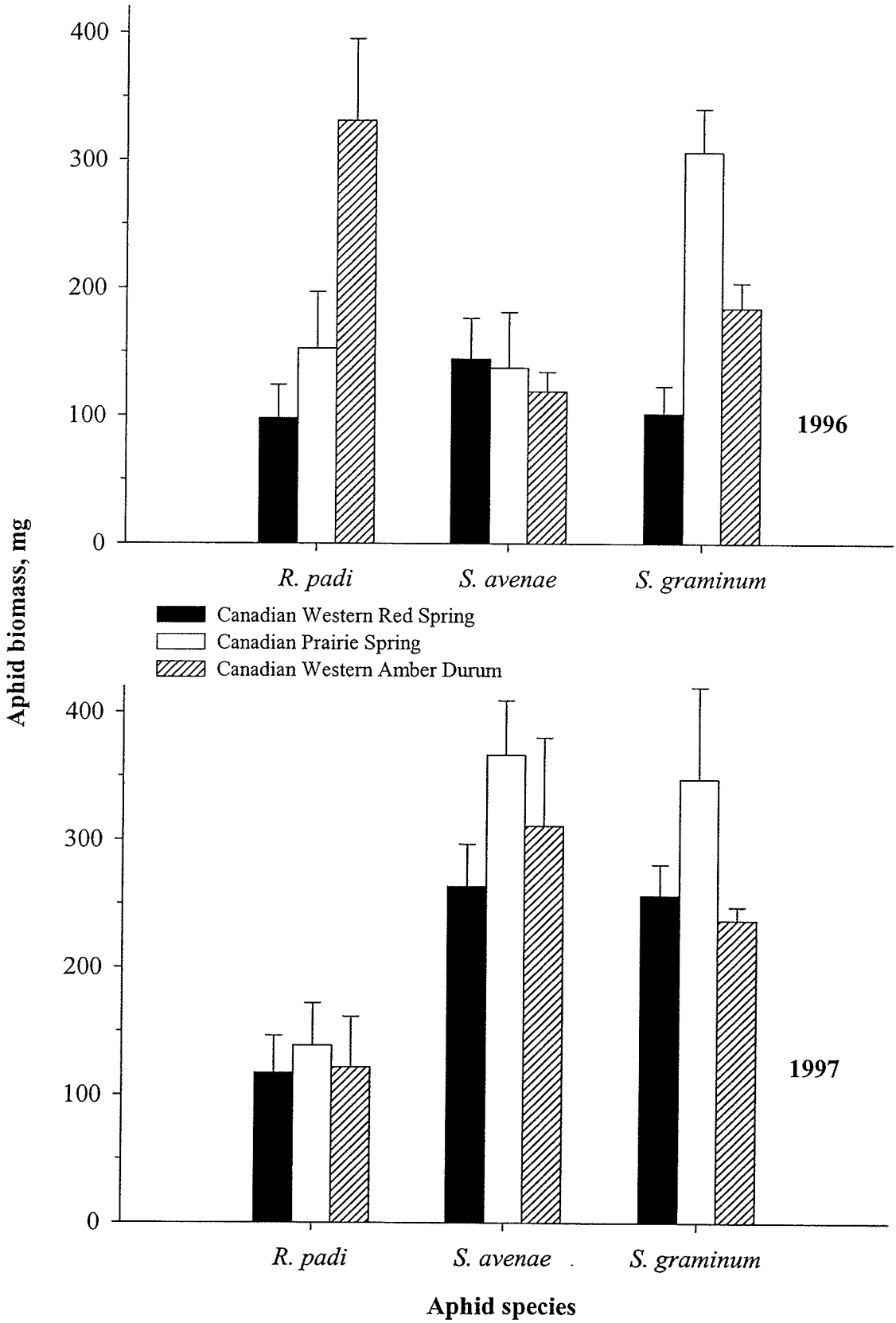
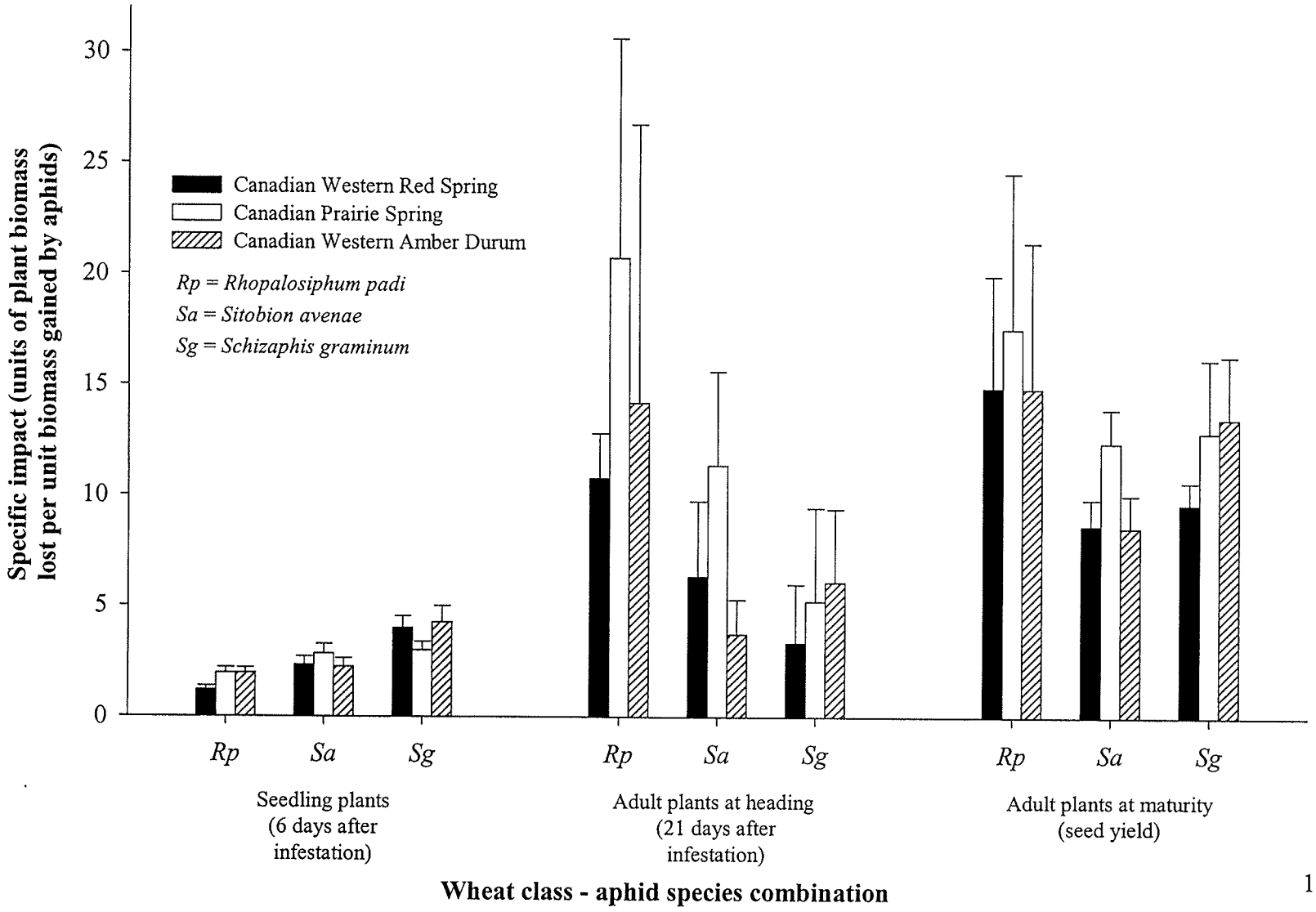

400
300
200
100
0
1996
R. padi
S. avenae
S. graminum
Canadian Western Red Spring
Canadian Prairie Spring
Canadian Western Amber Durum
Aphid biomass, mg
400
300
200
100
0
1997
R. padi
S. avenae
S. graminum
Aphid species

Fig. 3.8. Mean specific impact (± SE) measured as the biomass lost by a plant per unit biomass gained by the aphid at three growth stages: seedling, heading and mature. For the seed yield information, the aphid biomass gained was at heading stage and sometime before seed biomass loss was estimated.


Specific impact (units of plant biomass lost per unit biomass gained by aphids)
30
25
20
15
10
5
0
Canadian Western Red Spring
Canadian Prairie Spring
Canadian Western Amber Durum
Rp = Rhopalosiphum padi
Sa = Sitobion avenae
Sg = Schizaphis graminum
Rp
Sa
Sg
Rp
Sa
Sg
Rp
Sa
Sg
Seedling plants (6 days after infestation)
Adult plants at heading (21 days after infestation)
Adult plants at maturity (seed yield)
Wheat class - aphid species combination

CHAPTER 4

Host relationships of three cereal aphids and wheats in the genus *Triticum*: domestication of wheat and susceptibility to aphids

Abstract

A collection of 41 accessions of wild and cultivated wheats belonging to 19 *Triticum* species were studied to determine their suitability as hosts for three species of aphids, *Rhopalosiphum padi* L., *Sitobion avenae* Fabricius and *Schizaphis graminum* Rondani, with reference to host plant resistance. Biomass relationships between the aphids and the wheats were quantified to estimate crop resistance. Plant biomass lost due to infestation over a three week period on adult plants in the field estimated resistance. The simultaneous increase in biomass of aphids estimated the response of the aphids to the plants. All three species of aphids survived and reproduced on all wheats. Aphid biomass varied among wheat accessions with biomass of *R. padi* and *S. avenae* reduced more than that of *Sc. graminum* on the most resistant wheats. Aphids feeding on mature plants reduced foliage and spike biomass compared to uninfested controls. Spikes were more affected than foliage. Overall, increased domestication was associated with increased aphid biomass gain and increased plant biomass loss. The least domesticated diploid wheats showed the highest frequency and the most domesticated hexaploid wheats showed the lowest frequency of accessions exhibiting resistance. The wild wheats, *Triticum boeoticum* Bois, *Triticum tauschii* (Coss.) Schmal. and *Triticum araraticum*

Jakubz. consistently exhibited high levels of resistance to aphids. So also did *Triticum monococcum* which was derived from primitive, *T. boeoticum*. Although the probability of finding wheat accessions resistant to aphids was highest among primitive wheats, individual accessions with resistance occurred at all levels within the evolutionary tree of wheat, with no clear relationships between the genomic constitution of a wheat accession and its magnitude of resistance to aphids. The potential use of wild wheats in screening and plant breeding programs for resistance to aphids is discussed.

Introduction

Aphids are the most cosmopolitan insect pests of common wheat, *Triticum aestivum* L. Over 30 species can survive on the crop although only six species cause economic damage worldwide (Blackman & Eastop, 1984). These species are: Russian wheat aphid, *Diuraphis noxia* (Mordvilko), rose-grass aphid, *Metopolophium dirhodum* (Walker), bird cherry-oat aphid, *Rhopalosiphum padi* (L.), corn leaf aphid, *Rhopalosiphum maidis* (Fitch), greenbug, *Schizaphis graminum* (Rondani), and English grain aphid, *Sitobion avenae* (Fabricius). For the past several decades, chemical insecticides have been the first line of defense for control of aphids and other insect pests of wheat. In western Europe, for example, the adoption of high yield wheat technology has created absolute dependence on insecticides (Vereijken *et al.*, 1985). The consequence of routine usage of insecticides is development of insecticide resistant aphids. All greenbug biotypes can rapidly become resistant to organophosphate insecticides following widespread insecticide use (Teetes *et al.*, 1975). Moreover,

insecticides cause harmful effects on non-target organisms and the environment. For example, in the Texas Panhandle, in 1988, 200 Canada geese were killed in a wheat field due to acute toxicity of parathion sprayed to control *D. noxia* (Flickinger *et al.*, 1991). Because of such incidents, and because wheat yield and profit margins are low in many regions of the world (Briggle & Curtis, 1987; Webster, 1990), the need for alternative approaches of pest control cannot be overemphasized.

Development of cultivars with increased resistance to insect pests is gaining importance as a pest control strategy in many wheat improvement programs. In the past, attempts to screen for resistance to aphids revealed low levels of resistance in cultivated cereals (Hsu & Robinson, 1962, 1963; Starks & Merkle, 1977; Lowe, 1981; Lee, 1984). The search for sources of wheat resistant to various insect pests and diseases has now turned to wild relatives of wheat, which are becoming commonly included in screening programs. Wild wheats are adapted to a broad range of environments and carry a large reservoir of useful genes (Feldman & Sears, 1981). Investigations by several workers on utilization of the genetic variation present in the wild relatives of wheat has revealed their remarkable genetic diversity. The diploid wheat, *Triticum tauschii* (Coss.) Schmal., has a wide range of agronomically important traits, including disease and insect resistance (Gill *et al.*, 1986; Cox *et al.*, 1992). Five Hessian fly-resistance genes, *H13, H22, H23, H24* and *H26* have been transferred from *T. tauchii* to common wheat (Raupp *et al.*, 1993; Cox & Hatchett, 1994). Two genes conferring resistance to stem rust, *Sr36* and *Sr37*, were transferred to common wheat from *Triticum timopheevii* Zhuk. and *Sr40* was transferred from *Triticum araraticum* Jakubz. (Allard & Shands, 1954; Dyck, 1992). In

glasshouse studies, Sotherton & van Emden (1982) demonstrated that the ancient wheat, *Triticum monococcum* L., was more resistant to *S. avenae* than modern wheat cultivars. Kazemi & van Emden (1992) reported that emmer wheat, *Triticum dicoccum* Schrank exhibited higher resistance to *R. padi* than common wheat. Weibull (1987) screened a wide range of *Hordeum* species, comprised of diploids, tetraploids and hexaploids, for resistance against *R. padi* and observed that the most resistant species were primitive diploids. Harvey *et al.* (1980) identified resistance to *Sc. graminum* bioptype C in synthetic hexaploid wheats derived from *T. tauschii* var *strangulata* and *T. tauschii* var *typica*. Genes for resistance to *D. noxia*, have been found in *T. monococcum*, *T. tauschii* and *T. ventricosum* Ces. (Nkongolo *et al.*, 1990). Thus, a number of wheat species in the genus *Triticum* may serve as a potential source of resistance to cereal aphids.

For thousands of years the genus *Triticum* has gone through a large evolutionary change. A generalized genealogy of cultivated wheats is shown in fig. 4.1. Both cultivated and wild wheats occur in three ploidy levels, diploid, tetraploid and hexaploid (Bowden, 1959). Polyploidy in wheat is thought to have originated when two diploid species hybridized naturally, followed by spontaneous doubling of the chromosomes, giving rise to fertile individuals that existed at the tetraploid level (Kimber & Feldman, 1987). Similarly, hexaploid species are thought to be a product of hybridization between a tetraploid and a diploid, followed by chromosome doubling. However, interspecific hybridization at the diploid level is considered a rare event, probably because diploids contain different genomes (basic set of chromosomes in a gamete) (Kimber & Feldman, 1987).

All species in the genus *Triticum* contain some multiple of the basic haploid set of seven chromosomes (Bowden, 1966). A diploid wheat has 14 chromosomes (2 X 7 = 14), a tetraploid has 28 chromosomes (2 X 2 X 7 = 28), and a hexaploid has 42 chromosomes (2 X 3 X 7 = 42). There are eight distinct haploid genomes of seven chromosomes within the genus *Triticum*, named as A, B, C, D, G, M, S, U (Kimber & Sears, 1987). Kimber and Feldman (1987) classified the species in the genus *Triticum* into three groups, based on a commonly shared genome: the A-genome, D-genome, and U-genome clusters. The A-genome cluster is unique because it is the only one that contains species of commercial importance (Kimber & Feldman, 1987). The primary commercial species are common wheat, *T. aestivum*, and durum wheat, *Triticum durum* Desf. Common wheat is a hexaploid species with the genome ABD and durum is a tetraploid with the AB genome (Kimber & Sears, 1987). The commercial wheats have evolved through domestication from wild diploid and tetraploid ancestors.

On the northern Great Plains of the United States of America and the Prairies of Canada winged migrants of *R. padi*, *S. avenae* and *Sc. graminum* colonize small grain crops in the spring and early summer each year (Robinson & Hsu, 1963; Kieckhefer *et al.*, 1974). The dominant crop in the region is spring-sown wheat, which is most susceptible to aphid damage from flowering through kernel formation (Chapter 3). At this stage, colonies of *R. padi* and *S. avenae* are found on spikes (Migui, 1996), where they reduce seed yield by directly competing with the filling grain for plant nutrients. Farmers in the region rarely use insecticides to control aphids because of the narrow profit margins which make it uneconomical (personal communication, John Gavloski, Extension

Entomologist, Manitoba Agriculture). The farmers have no alternative methods of aphid control. Host plant resistance is probably the most economical, convenient and acceptable alternative method of aphid control. Lamb *et al.* (2000) have identified spring wheats with high levels of resistance to a wheat midge, *Sitodiplosis mosellana* (Géhin), which is also a major pest in the region. The resistance causes at least a 20-times difference in the level of infestation between susceptible and resistant wheats.

Chapter 3 established that aphid-plant interactions at the seedling stage differ from interactions at the adult plant stage, indicating that observed resistance to aphids on seedling plants cannot be used to predict resistance in adult plants. For this reason, development of aphid resistant cultivars for the northern Great Plains region of United States of America and Canada must be based on screening of adult plants, which represent the principal target of attack by aphids. Adult cereal crops on the northern Great Plains of the U.S.A. and the Prairies of Canada become the principle target of attack by aphids because cereal aphids are not known to overwinter in these regions (Robinson & Hsu, 1963; Irwin & Thresh, 1988), and by the time aphids from the south disperse into the northern regions, the cereal crops are close to spike emergence.

Genetically diverse species within the A-genome cluster of the genus *Triticum* were used to investigate host relationships of three common cereal aphid pests (*R. padi, S. avenae* and *Sc. graminum*) and the wheats. Biomass relationships between cereal aphids and the wheats were used to quantify crop resistance in adult plants. The objectives were to determine if there is a relationship between domestication and reaction to aphids, and identify primitive or wild wheats that provide the most promising sources

of adult plant resistance for incorporation in modern commercial cultivars of spring wheat.

Materials and Methods

Interactions between the three species of aphids and 19 species of wild and cultivated wheats were studied in the field. Seeds of wild wheat accessions were obtained from the Plant Gene Resources of Agriculture and Agri-Food Canada, the National Small Grains Research Facility of the USDA Agricultural Research Service and the Institut National de la Recherche Agronomique in France (table 4.1). The wheat species selected provided a representative sample of the species within the A-genome cluster that are reported in the evolutionary tree of *Triticum*. There were four diploid species, *T. boeoticum* Bois (=*T. aegilopoides* (Link) Bal.), *T. monococcum, Triticum speltoides* Tausch and *T. tauschii*; eight tetraploid species, *T. araraticum, Triticum carthlicum* Nevski, *Triticum dicoccoides* Körn., *T. dicoccum, T. durum, Triticum polonicum* L., *T. timopheevii*, and *Triticum turgidum* L.; and seven hexaploid species, *T. aestivum, Triticum compactum* Host, *Triticum macha* Dek & Men., *Triticum spelta* L., *Triticum sphaerococcum* Percival *Triticum vavilovii* Jakubz., and *Triticum zhukovskyii* Men. & Er. Three accessions from each species were tested except where only one or two were available, giving a total of 41 accessions. Because all species were not available in the same year, 11 species were tested in 1997, eight in 1998 and six in 1999. In each year, three cultivars, each belonging to a different class of cultivated wheat were grown as checks. These were "Domain", Canadian Western Red Spring (CWRS) (*T. aestivum*),

"Foremost", Canadian Prairie Spring (CPS) (*T. aestivum*), and "Medora", Canadian Western Amber Durum (CWAD) (*T. durum*). Although there might be cultivars which behave differently from the three checks, previous research showed that these cultivars were representative of wheats in the three classes (Chapter 3). These three cultivars are referred to as checks, and plants of each accession which were not infested with aphids are referred to as controls.

One clone from each of the three aphid species, *R. padi, S. avenae* and *Sc. graminum* was obtained from cultures maintained in the laboratory of Dr. P.A. MacKay, Department of Entomology, University of Manitoba, and originally collected from cereal fields in southern Manitoba. Previous research showed that these three clones are representative of the three species (Chapter 3). Aphid cultures were reared on a susceptible barley cultivar Argyle (*Hordeum vulgare* L.) (see Chapter 3 for details).

In order to facilitate germination of plants, especially the wild wheats, seeds were germinated in the dark at room temperature (about 22°C) by placing kernels on moist filter paper in a Petri dish covered with an opaque plastic liner. After 48 h, seedlings of wheat species suspected of exhibiting winter growth habits were vernalized by placing them in the dark in a cold room maintained at 2.5°C for 6-8 weeks. Wheat accessions with spring growth habits were germinated at the end of the vernalization period in order to synchronize the growth of plants in the field. Germinated seedlings were transferred to a greenhouse and planted in peat pots containing Metromix® soil medium (see Chapter 3 for detailed constituents of the soil medium) and sub-irrigated with tap water. After emergence, plants were sub-irrigated with 15 g of 20-20-20 All Purpose Fertilizer

solution (Plant Products Co. Ltd.) per 30 L water. The fertilizer solution was composed of: 20% total nitrogen (N), 20% available phosphoric acid (P_2O_5), 20% soluble potash (K_2O), 0.002% boron (B), 0.05% chelated copper (Cu), 0.1% chelated iron (Fe),0.05% chelated manganese (Mn), 0.0005% molybdenum (Mo), 0.05% chelated zinc (Zn) and 1% chelating agent, ethylene diamine tetraacetate (EDTA). The fertilizer solution was applied twice, first, a few days after plant emergence and second, two weeks later. Tap water was used in between the two fertilizer applications. By the second fertilizer application, the plants were well established and were transplanted into 1 X 1 m field plots. Twenty-one wheat accessions were replicated two times within each plot for a total of 42 plants/plot in 1997 and 1998, in a randomized complete block design. The plants were transplanted in a square grid with six rows and seven plants per row spaced 13 cm between rows and 11 cm within rows with about 10 cm space around the block of plants so that they were not in contact with the cage initially. In 1999, a total of 9 accessions were tested and replicated four times within each plot for a total of 36 plants/plot, in a randomized complete block design and plant spacing of 12 cm between rows and 12 cm within rows. In each of the three years, two plots were sown for each of the three aphid species along with two no-aphid controls, giving eight plots. Plots were separated by 2 m. Each plot was covered with an aphid proof cage (see Chapter 3 for details).

Aphids were introduced into the cages when 50% of plants within each cage reached boot stage (boots swollen, GS 45, Tottman & Makepeace, 1979). Aphid species were assigned randomly to the cages (one aphid species per cage). Ten young adult aphids from laboratory cultures were placed on each plant and left undisturbed for 21

days. Two cages were left uninfested to serve as controls. At the end of the infestation period, plants in one half of the plots (four whole cages, i.e. one control cage and one cage per aphid species) were cut at soil level, the aerial parts bagged individually and taken to the laboratory for further processing. The remaining plots were sprayed with dimethoate 480 E.C. at a rate of 2 ml per L of water to terminate infestation and left to grow to maturity for yield assessment. Cages were left in place to protect the spikes from bird damage. In the laboratory, aphids were collected from the bagged plants by dipping and shaking the plants in a tub of hot water. The aphid suspension was sieved and sorted to remove plant debris. Clean aphids were placed in pre-weighed aluminum dishes and dried to a constant weight at 80°C for 48 h. At crop maturity, plants in the remaining plots were cut at soil level and plant spikes and foliage were separated and dried to a constant weight at 80°C for 48 h. Spikes were used instead of seeds because most of the wild wheats had glumes tightly adhering to seeds and were difficult to thresh.

Interactions between the aphids and the wheats were quantified as changes in biomass reflecting the response of aphids to plants (antibiotic resistance) and the response of the plants to aphids (total resistance). Antibiotic resistance was estimated as the biomass accumulated by each aphid species on each accession during infestation. Aphid biomass probably mostly reflected antibiosis but a role for antixenosis cannot be ruled out, because low biomass might result, in part, from aphids leaving a less preferred plant and accumulating on a preferred one. For lack of a better terminology that describes a combination of antibiosis and antixenosis, the response of the aphids to the plants will be termed antibiosis here. Total resistance was estimated as the difference between the

biomass of infested plants and the biomass of control plants, i.e. plant biomass loss due to infestation.

Data were analysed using the procedures of SAS (SAS Institute Inc., 1989). A plot of mean versus variance for each dependent variable was made to determine whether transformation was required to normalize the data or stabilize variance. Where data were found to be non-normal, they were transformed by calculating natural logarithms before proceeding with statistical analysis. A test of the effect of year on antibiosis and resistance for the three check wheats was done using general linear model (GLM) procedures with year and class of wheat as fixed effects. The growth of aphid populations on the commercial wheat cultivars differed significantly among years, and so data were analyzed separately for each year. The effects of wheat species and accession within wheat species on the biomass of aphids accumulated during infestation and subsequent losses in foliage and spike biomass were examined using GLM procedures with both factors, wheat and accession within wheat as fixed effects. To compare results obtained from different years, standardized indices of antibiosis and resistance were computed as the amount of aphid biomass gained on a wheat accession as a proportion of the amount of biomass gained on the most susceptible commercial wheat class, CPS wheat; and the amount of plant biomass loss by a wheat accession as a proportion of the amount of biomass lost by CPS wheat, respectively. Dunnett's one-tailed t-test was used to test whether wheat accessions reduced aphid biomass or plant biomass lost in relation to the check cultivar, CPS wheat. The relationship of aphid-wheat interactions with the domestication patterns of wheat was investigated by examining the frequency of wheat

accessions with less than 50% aphid biomass gained or plant biomass lost compared to CPS wheat.

Results

Considering first the three commercial cultivars used as checks, aphid biomass increased most rapidly on CPS wheat and least on CWRS wheat for all three aphid species, although significantly so only for *Sc. graminum* (table 4.2). The relationship of year to aphid biomass production was significant, with aphid production being high in 1997, low in 1998 and high again in 1999. Because of this difference, results were analyzed separately for each year. The biomass of control plants of the check cultivars was similar among years except for CWRS which had low foliage and spike biomass at maturity in 1997 compared to the other two years (table 4.3).

The amount of aphid biomass on each commercial cultivar as a proportion of aphid biomass on CPS wheat is shown in table 4.4. The CWRS class of wheat reduced the amount of aphid biomass gain the most among the three cultivated wheats. Because CPS wheat usually was the most favourable to aphids, it was selected as the benchmark for comparing the levels of resistance among the wheat accessions.

Table 4.5 shows the ANOVA of the effects of 41 accessions of wheat on aphid biomass accumulation (estimate of antibiosis) over the three week infestation period. The wheat accessions exhibited variable levels of antibiosis to *R. padi* and *S. avenae*, but no evidence of antibiosis to *Sc. graminum* in 1997 and 1998 and near significance ($P<0.09$) for accessions tested in 1999.

Table 4.6 shows the amounts of aphid biomass on all wheat accessions as a proportion of aphid biomass on CPS wheat. Wheat accessions exhibited variable levels of antibiosis to the three species of aphids, ranging from accessions with high levels of antibiosis to accessions which were more susceptible to aphids than CPS wheat. Nine wheat accessions belonging to seven species supported significantly fewer aphids than CPS viz: *T. aegilopoides*, *T. aestivum*, *T. araraticum*, *T. dicoccum*, *T. monococcum*, *T. tauschii* and *T. zhukovskyii*, with seven out of the nine accessions producing less than 20% of the aphid biomass produced on CPS wheat.

Assessment of aerial plant biomass at maturity showed that all aphid infested plants sustained a reduction in foliage and spike biomass compared to uninfested controls. Tables 4.7 and 4.8 show the ANOVA of the effects of aphid infestation on biomass lost by foliage and spikes, respectively. The wheat accessions exhibited variable levels of resistance to all three species of aphids with the spikes being more responsive to aphid damage than foliage. This resistance could be a combination of tolerance, antibiosis and perhaps also antixenosis. Wheat accessions tested in 1997 showed greater responses (significant differences among wheat species and among accessions within wheat species) to aphid attack than either 1998 or 1999. Tables 4.9 and 4.10 show the amounts of plant biomass loss as a proportion of biomass lost by CPS wheat. Data analysis of spike biomass loss revealed five times as many resistant accessions as those produced after analysis of foliage biomass loss. An accession of *T. araraticum* exhibited the highest level of resistance, to *S. avenae*. Resistance of a wheat species to one aphid species appeared to be associated with resistance to another aphid species, particularly in 1997.

The patterns of resistance to aphids were related to the pattern of domestication or evolutionary relationships in the genus *Triticum*, but in complex ways. A 50% or greater reduction of aphid biomass or plant biomass lost compared to the susceptible check (CPS wheat) was used to define resistant accessions. Using this definition, the primitive diploid wheats usually showed the highest frequency of antibiotic resistance and total resistance followed by tetraploid wheats, and lastly, hexaploid wheats (Table 4.11). The one departure from this pattern was for accessions resistant to *R. padi*. Individual accessions exhibiting high degrees of antibiosis and/or resistance to aphids, however, were scattered throughout the evolutionary tree of wheat (Tables 4.6, 4.9 and 4.10).

Discussion

The three aphid species fed and multiplied on all wheat accessions, confirming that species in the genus *Triticum* are suitable hosts for these insects. Cereal aphids have a wide host range which includes grasses beyond the genus *Triticum*. The host spectrum of *R. padi*, *S. avenae* and *Sc. graminum*, includes species in the genera *Agropyron, Avena, Bromus, Dactylis, Eleusine, Festuca, Hordeum, Lolium, Oryza, Panicum, Poa, Sorghum, Triticum* and *Zea* (Blackman & Eastop, 1984). *Rhopalosiphum padi* is the most polyphagous pest among the three species with a host range of well over 100 species (Kieckhefer & Gellner, 1988).

Despite the large host spectrum of the aphids, their performance on the closely related species of *Triticum* varied, with primitive diploid wheats showing the highest frequency of resistant accessions and the most domesticated, hexaploid wheats showing

the lowest frequency of resistant accessions. This observation corroborates findings of other researchers on a variety of crops, that ancestral species are more resistant to insect pests than their domesticated counterparts. Holt and Birch (1984) found that ancestral species in the genus *Vicia* were the most resistant to the aphid *Aphis fabae* Scopoli, while plants with the highest degree of domestication were most susceptible. Aphid resistance in potatoes, lettuce and vetches was derived from primitive relatives of these crops (Eenink & Dieleman, 1981; Birch & Wratten, 1984; Sanford *et al.*, 1984). Wise *et al.* (2001) reported that ancestral diploid wild wheats have the lowest infestation levels of wheat midge, *S. mosellana*, compared to tetraploid and hexaploid wheats. Wild primitive wheats have been subject to sustained natural selection for resistance against insect herbivores and have evolved traits that confer resistance to aphids. In common wheat, such traits probably have been lost through thousands of years of artificial selection for productivity.

In rare cases, however, a cultivated wheat may be resistant to insects. For example, resistance to *Sc. graminum* was first identified in a cultivated durum wheat, "Dickinson Selection 28A" (Dahms *et al.*, 1955). Lamb *et al.* (2000) found high levels of antibiosis to *S. mosellana* in some cultivars of *T. aestivum*. In Morocco, field and greenhouse screening of durum wheat cultivars resulted in the identification of a durum wheat cultivar resistant to the Hessian fly, *Mayetiola destructor* (Say) (El-Bouhssini *et al.*, 1999). Thus, the possibility of finding useful resistance to aphids and other insects is present in some wheat cultivars, and suspected wheat candidates should be included in aphid resistance screening studies.

Seven accessions were identified which at the adult stage reduced the biomass of aphids. Eleven accessions were identified which sustained a reduced spike biomass loss compared to the susceptible check. Four species, *T. aegilopoides, T. aestivum, T. araraticum* and *T. tauschii* sustained reduced aphid biomass and also reduced plant biomass loss; three species, *T. dicoccum, T. monococcum,* and *T. zhukovskyi*, sustained a reduction of aphid biomass only; and seven species, *T. araraticum, T. carthlicum, T. diccoides, T. spelta, T. speltoides, T. sphaerococcum* and *T. turgidum* sustained a reduced plant biomass loss. These latter seven species exhibited resistance that was probably largely tolerance because no antibiosis was detected.

There was little association among wheats in the amounts of aphid biomass they supported. Out of the seven species which were antibiotic, three species reduced the biomass of only *S. avenae*, two reduced biomass of only *R. padi*, one species reduced biomass of *R. padi* and *S. avenae* and one species reduced the biomass of *S. avenae* and *Sc. graminum*. However, total resistance to one aphid species appeared to be related to the plant's total resistance to another aphid species. Out of the 11 species exhibiting resistance to aphids, four were resistant only to *Sc. graminum*, two were resistant only to *S. avenae*, and five were resistant to more than one aphid species. These observations, suggest that causing a reduction in aphid biomass (antibiosis) is a specific defense against a particular species, whereas total resistance which is largely tolerance is a more general defense enabling the plant to survive and reproduce despite infestation by more than one aphid species.

This study has determined that individual wheat accessions with resistance to

aphids can be found at all levels within the evolutionary tree of wheat, although more frequently among diploid ancestors than in more domesticated wheats. Other evidence for availability of some resistance to aphids in cultivated wheats is reported by Havlickova (1993) and Acreman and Dixon (1986). Thus, cultivated wheats offer a potential source of wheat resistance to aphid pests, and may need to be explored exhaustively. Nevertheless, a higher frequency of aphid resistant accessions occur among primitive wheats than in domesticated wheats. Accessions of the ancient diploid wheat, *T. monococcum*, has previously been identified as a source of resistance to *S. avenae* (Sotherton & van Emden, 1982; Caillaud *et al.*, 1994; Di Pietro *et al.*, 1998). Lee (1983, 1984) and Lowe (1984*a*) reported that *T. monococcum* was more resistant to *S. avenae* than modern wheat cultivars under laboratory and field conditions and that resistance was stable against a range of clones. Not all accessions of *T. monococcum* show resistance, however, and some are as highly susceptible as *T. aestivum*. Resistance to aphids is also reported in tetraploid progenitors of common wheat. Kazemi and van Emden (1992) found that emmer wheat, *T. dicoccum*, exhibited higher resistance to *R. padi* than hexaploid wheat.

Aphids originated in the Triassic or Late Permian, about 200 million years ago, long before the evolution of angiosperms (Moran, 1992). The original hosts of aphids are thought to have been a now-extinct group of gymnosperms (Blackman & Eastop, 1984). Wheat is thought to have originated in the Middle East, during the old stone age, several hundred thousand years ago (Peterson, 1965). The diploid, wild Einkorn, *T. boeoticum*, the tetraploids, wild emmer, *T. dicoccoides* and emmer, *T. dicoccum* were cultivated by

humans around 7000 B.C. and the hexaploid wheat, *T. spelta* around 3000 B.C. (Harlan & Zohary, 1966; Lev-Yadun *et al.*, 2000).

Cereal aphids have a more northerly origin than wheat. The primitive pattern of host use by aphids is to move seasonally to several secondary grass hosts in the spring and back to the primary host in the autumn. In Europe, *R. padi* is holocyclic, producing an egg-laying sexual generation, overwintering in the egg stage on its primary host, the bird cherry tree, *Prunus padus* L., and migrating to grasses in spring (Vickerman & Wratten, 1979). *Sitobion avenae* and *Sc. graminum* have lost their primary woody hosts and survive entirely on grasses even in regions where they continue to produce sexually and overwinter as eggs (Blackman & Eastop, 1984). Because *S. avenae* and *Sc. graminum* survive entirely on grasses, their evolutionary association with wheat might be closer than that of *R. padi*, which might help explain the lack of a clear evolutionary trend in the pattern of resistance to *R. padi* in wheats. *Rhopalosiphum padi* has a broader host range and is probably less adapted to individual cultivars. Lamb and MacKay (1995) reported that the effect of wheat cultivars containing hydroxamic acids was less on *R. padi* than on *M. dihrodum*. Dean (1973) reported that in cage tests, *R padi* colonized more host plants than either of *M. dirhodum* or *S. avenae*, and suggested that this lack of specificity by *R. padi* is a sign of less adaptation to cereal cultivars. He further suggested that the lesser adaptation of *R. padi* on cereal crops compared to *M. dirhodum* or *S. avenae* might explain why, in Britain, *R. padi* is the most common species caught in suction traps until mid-June while winged *M. dirhodum* or *S. avenae* become most abundant as the cereals mature. Porter *et al.*, (1997) demonstrated that development of *Sc. graminum* genotypes

which infest otherwise resistant wheat cultivars was not due to selection by resistant wheat, but that the aphid genotypes are opportunists which evolved on perennial non-cultivated grasses long before wheat came into cultivation. It is likely that cereal aphids, and particularly *R. padi* began using species of *Triticum* as hosts relatively recently in evolutionary time, and domesticated wheats could only have become important host plants in the past few thousand and perhaps only in the past few hundred years as wheat production spread, or as varieties were produced with less waxy surfaces and fewer hairs.

The methodology of using aphid and plant biomass measurements to estimate resistance to aphids in adult wheat allows more accurate discrimination of accessions with partial resistance than visual rating methods, especially for aphids like *R. padi* and *S. avenae*, which usually do not inflict visually identifiable damage on wheat. Wheat spikes proved to be more responsive to aphid damage than the foliage with more than five times more resistant accessions identified from spikes than foliage. Therefore, spike biomass appears to be a more effective experimental unit for conducting resistance studies in the field. Measuring the biomass of spikes alone and comparing the value for infested versus controls can provide an adequate estimate of total resistance.

This study has demonstrated that wild relatives of wheat probably carry a reservoir of useful genes which can be exploited for reducing aphid damage in wheat. Despite the mounting evidence in support of host plant resistance in wheat to aphids, little or no breeding has been undertaken after initial screening. Results of this study, show that it is now timely to exploit available information in directed screening and plant breeding programs. The seven species of wheats identified in this study exhibiting antibiotic

resistance to aphids may be good candidates for more intensive screening. Wheat researchers in the northern Great Plains of North America and the Prairies of Canada need to seriously consider screening for some level of resistance to aphids as a criterion for retaining superior lines. *Triticum monococcum* appears to be a particularly useful species to explore as a source of resistance because resistant accessions have been identified. Futhermore, its role as a direct ancestor of cultivated wheats assures that resistance genes in this species can be introgressed into commercial tetraploid and hexaploid wheats.

Table 4.1. Accession numbers and Gene Bank codes of wild and cultivated, diploid, tetraploid and hexaploid wheats evaluated in the field for resistance to cereal aphid species, *Rhopalosiphum padi* L., *Schizaphis graminum* (Rondani) and *Sitobion avenae* (Fabricius).

	Wheat species[1]	Genome	Accession no. 1		Accession no. 2		Accession no. 3	
			Code	Source	Code	Source	Code	Source
1997	*Triticum monococcum*	A	PGR0001507	Canada	PGR0001511	Canada	PGR0001514	Canada
	T. dicoccoides	AB	PGR0003982	Canada	PGR0003986	Canada	PGR0003990	Canada
	T. polonicum	AB	PGR0026495	Canada	PGR0026463	Canada	-[2]	-
	T. carthlicum	AB	PGR0003992	Canada	PGR0003999	Canada	PGR0003994	Canada
	T. durum	AB	CWAD	Canada	-	-	-	-
	T. spelta	ABD	PGR0005659	Canada	PGR0002758	Canada	-	-
	T. macha	ABD	PGR0003973	Canada	-	-	-	-
	T. vavilovii	ABD	PGR0004005	Canada	-	-	-	-
	T. compactum	ABD	CN00002674	Canada	PGR0007277	Canada	PGR0007279	Canada
	T. sphaerococcum	ABD	PGR0005661	Canada	PGR0005660	Canada	-	-
	T. aestivum	ABD	CWRS	Canada	CPS	Canada	-	-
1998	*T. aegilopoides*	A	427474	U.S.A.	RL5224	Canada	428002	U.S.A.
	T. monococcum	A	TM44	France	TM46	France	-	-
	T. speltoides	S	RL5344	Canada	609	Canada	611	Canada
	T. tauschii	D	RL5261	Canada	RL5271	Canada	RL5289	Canada
	T. timopheevii	AG	4024	Canada	4028	Canada	4040	Canada
	T. turgidum	AB	7772	U.S.A.	14795	U.S.A.	134956	U.S.A.
	T. durum	AB	CWAD	Canada	-	-	-	-
	T. aestivum	ABD	CWRS	Canada	CPS	Canada	-	-
1999	*T. monococcum*	A	TM44	France	TM46	France	-	-
	T. araraticum	AG	TA943(G2772)	Iraq	-	-	-	-
	T. dicoccum	AB	254216	U.S.A.	345471	U.S.A.	591868	U.S.A.
	T. durum	AB	CWAD	Canada	-	-	-	-
	T. zhukovskyi	AAG	355706	Canada	-	-	-	-
	T. aestivum	ABD	CWRS	Canada	CPS	Canada	-	-

[1] Wheats tested in multiple years contained a different set of accessions in each year except for the checks, *T. durum* and *T. aestivum*.
[2] Wheat accessions not available.

Table 4.2. The effects of year and class of wheat on the biomass of aphids accumulated over a three week infestation period beginning at boot stage on cultivated wheats (checks) in field cages.

Aphid species	Wheat class[1]	Mean biomass of aphids, mg ± S.E.		
		1997	1998	1999
Rhopalosiphum padi	CWRS	194.8 ± 47.07	24.4 ± 0.45	43.2 ± 16.68
	CPS	228.0 ± 59.72	39.4 ± 12.50	134.1 ± 84.57
	CWAD	138.2 ± 12.93	30.2 ± 7.05	46.3 ± 13.83
		Year:	$F_{2,17} = 17.28$,	$P = 0.0001$
		Class:	$F_{2,17} = 1.98$,	$P = 0.1691$
		Year*Class:	$F_{4,17} = 0.49$,	$P = 0.7433$
Sitobion avenae	CWRS	93.0 ± 28.59	19.4 ± 5.60	144.7 ± 69.20
	CPS	211.7 ± 33.35	32.9 ± 29.40	878.0 ± 73.22
	CWAD	122.9 ± 50.34	18.4 ± 9.50	432.7 ± 124.01
		Year:	$F_{2,18} = 25.61$,	$P = 0.0001$
		Class:	$F_{2,18} = 2.73$,	$P = 0.0919$
		Year*Class:	$F_{4,18} = 1.41$,	$P = 0.2697$
Schizaphis graminum	CWRS	53.2 ± 12.59	77.9 ± 21.80	169.3 ± 42.25
	CPS	88.3 ± 30.14	90.7 ± 6.95	371.2 ± 32.13
	CWAD	283.1 ± 116.39	-[2]	343.5 ± 97.78
		Year:	$F_{2,17} = 13.68$,	$P = 0.0003$
		Class:	$F_{2,17} = 7.06$,	$P = 0.0059$
		Year*Class:	$F_{3,17} = 1.78$,	$P = 0.1898$

[1] CWRS = Canadian Western Red Spring, CPS = Canadian Prairie Spring, CWAD = Canadian Western Amber Durum

[2] Missing data because CWAD failed to establish in the cages due to poor germination.

Table 4.3. Effect of year on the biomass of control wheat plants (no aphids) from check cultivars in field cages.

Plant part	Wheat class[1]	Mean biomass of plants, g ± SE			Effect of Year		
		1997	1998	1999	*F*	df	*P*
Total foliage at boot stage	CWRS	-[2]	22.1 ± 3.57	8.1 ± 2.48	4.40	1,3	0.1268
	CPS	-	19.8 ± 0.00	17.8 ± 5.55	0.10	1,2	0.7869
	CWAD	-	14.7 ± 3.67	14.1 ± 2.28	0.02	1,3	0.9094
Foliage at maturity (without spikes)	CWRS	3.7 ± 0.89	11.7 ± 1.27	9.0 ± 1.17	6.72	2,9	0.0164
	CPS	13.8 ± 4.75	11.7 ± 8.31	19.6 ± 4.74	0.54	2,9	0.5979
	CWAD	8.7 ± 1.65	9.6 ± 1.44	11.0 ± 2.88	0.02	2,8	0.9782
Spikes at maturity	CWRS	6.1 ± 1.24	14.7 ± 1.88	16.9 ± 1.79	14.33	2,9	0.0016
	CPS	16.9 ± 5.20	12.3 ± 9.05	29.5 ± 5.97	2.08	2,9	0.1805
	CWAD	16.8 ± 2.43	12.4 ± 1.38	21.5 ± 4.30	0.63	2,8	0.5560

[1] CWRS = Canadian Western Red Spring, CPS = Canadian Prairie Spring, CWAD = Canadian Western Amber Durum

[2] Missing data because control plants were not harvested at this growth stage (21 days after boot swollen), and were harvested at maturity.

Table 4.4. Aphid biomass on Canadian Western Red Spring (CWRS) and Canadian Western Amber Durum (CWAD) wheats as a proportion of aphid biomass on Canadian Prairie Spring wheat (CPS).

Wheat class	*Rhopalosiphum padi*	*Sitobion avenae*	*Schizaphis graminum*
CPS	1.00	1.00	1.00
CWRS 97	0.85	0.44	0.60
CWRS 98	0.62	0.59	-
CWRS 99	0.32	0.16 *	0.46
CWAD 97	0.61	0.58	3.20
CWAD 98	0.77	0.56	1.16
CWAD 99	0.34	0.49	0.93

* Aphid biomass on class of wheat is significantly smaller than aphid biomass on the check, CPS wheat, using Dunnett's one-tailed t-test, α=0.05. The ANOVA and subsequent Dunnett's test were done on log transformed data for each aphid species and year.

Table 4.5. Analysis of variance of the effect of wheat species on the biomass of aphids accummulated over a three week infestation period which began at boot stage in field cages.

Year	Aphid species[1]	Source of Variation[2]	df	MSE	*F*	*P*
		Wheat[3]	9	2.92	3.04	0.0045
	RP	Acn(wheat)	13	2.13	2.22	0.0184
		Error	63	0.96		
		Wheat	9	2.24	2.38	0.0220
1997	SA	Acn(wheat)	13	1.76	1.86	0.0525
		Error	63	0.94		
		Wheat	9	1.10	1.59	0.1362
	SG	Acn(wheat)	13	0.60	0.87	0.5880
		Error	65	0.69		
		Wheat	6	2.29	9.08	0.0001
	RP	Acn(wheat)	14	1.73	6.85	0.0001
		Error	20	0.25		
		Wheat	6	2.01	3.46	0.0155
1998	SA	Acn(wheat)	14	1.04	1.79	0.1098
		Error	21	0.58		
		Wheat	7	0.93	1.27	0.3324
	SG	Acn(wheat)	12	1.16	1.58	0.2065
		Error	14	0.73		
		Wheat	5	1.19	1.52	0.2200
	RP	Acn(wheat)	4	1.76	2.25	0.0920
		Error	25	0.78		
		Wheat	5	1.03	2.28	0.0757
1999	SA	Acn(wheat)	4	2.62	5.81	0.0018
		Error	26	0.45		
		Wheat	5	1.24	1.30	0.2929
	SG	Acn(wheat)	4	2.17	2.27	0.0885
		Error	26	0.95		

[1] RP = *Rhopalosiphum padi*, SA = *Sitobion avenae*, SG = *Schizaphis graminum*
[2] Acn(wheat) = Accession within wheat species.
[3] Wheat = wheat species

Table 4.6. Proportions of aphid biomass gained on primitive and cultivated wheats relative to the aphid biomass gained on the Canadian Prairie Spring (CPS) wheat, *Triticum aestivum*, after a three week aphid infestation period which began at boot stage in field cages (value for CPS wheat = 1.00). (Resistant plants < 1.00).

Year	Wheat species[1]	Genome	Proportions of aphid biomass relative to CPS wheat								
			Rhopalosiphum padi			*Sitobion avenae*			*Schizaphis graminum*		
			AC1[2]	AC2	AC3	AC1	AC2	AC3	AC1	AC2	AC3
1997	*Triticum monococcum*	A	0.52	0.58	2.07	0.97	2.52	0.82	1.73	1.85	1.93
	T. dicoccoides	AB	0.22	2.20	2.69	0.78	2.63	1.68	1.42	2.42	1.13
	T. polonicum	AB	0.20	0.54	-[3]	0.37	0.25	-	1.74	1.53	-
	T. carthlicum	AB	0.34	1.15	1.38	0.72	1.08	2.55	0.81	1.13	2.01
	T. durum	AB	0.61	-	-	0.58	-	-	3.20	-	-
	T. macha	ABD	2.67	-	-	1.64	-	-	3.65	-	-
	T. vavilovii	ABD	1.55	1.61	4.90	1.88	0.36	2.08	2.54	1.14	2.68
	T. compactum	ABD	1.17	1.28	1.50	1.30	2.22	0.61	3.40	1.60	1.69
	T. sphaerococcum	ABD	2.22	3.37	-	4.03	3.80	-	2.26	2.42	-
	T. aestivum	ABD	1.00	0.85	-	1.00	0.44	-	1.00	0.60	-
1998	*T. aegilopoides*	A	0.13 *	0.62	0.69	0.69	0.85	0.34	0.55	1.05	0.42
	T. monococcum	A	0.47	1.40	-	0.65	0.93	-	0.67	1.38	-
	T. speltoides	S	0.27	0.28	0.55	0.47	0.40	0.28	0.40	0.19	0.42
	T. tauschii	D	0.06 *	0.40	2.94	0.08	1.23	1.11	0.29	-	0.91
	T. timopheevii	AG	0.94	1.08	1.45	1.28	1.39	0.61	1.08	0.61	1.55
	T. turgidum	AB	1.62	2.24	2.70	1.24	3.50	1.88	4.56	1.05	2.51
	T. durum	AB	0.77	-	-	0.56	-	-	1.16	-	-
	T. aestivum	ABD	1.00	0.62	-	1.00	0.59	-	1.00	-	-
1999	*T. monococcum*	A	0.22	0.75	-	0.38	0.12 *	-	0.83	0.14 *	-
	T. araraticum	AG	0.10 *	-	-	0.13 *	-	-	0.29	-	-
	T. dicoccum	AB	0.14	0.43	0.64	0.40	0.25 *	0.46	0.56	0.27	0.87
	T. durum	AB	0.34	-	-	0.49	-	-	0.93	-	-
	T. zhukovskyi	AAG	0.31	-	-	0.32 *	-	-	0.55	-	-
	T. aestivum	ABD	1.00	0.32	-	1.00	0.16 *	-	1.00	0.46	-

[1] Wheats tested in multiple years contained a different set of accessions in each year except for the checks, *T. durum* and *T. aestivum*.
[2] AC = wheat accession. [3] Missing values due to unavailability and/or non-establishment of accession(s) in field cage experiments.
* Aphid biomass on wheat is significantly lower than on the check cultivar, CPS wheat, using Dunnett's one-tailed t-test, $\alpha = 0.05$. The ANOVA and subsequent Dunnett's test were based on log transformed aphid biomass.

Table 4.7. Analysis of variance of the effect of aphids on biomass lost by the foliage of different species of wheats at maturity after a three week infestation period which began at boot stage.

Year	Aphid species[1]	Source of Variation[2]	df	MSE	*F*	*P*
1997	RP	Wheat	10	2.01	8.82	0.0001
		Acn(wheat)	9	0.74	3.23	0.0053
		Error	38	0.23		
	SA	Wheat	10	2.00	10.26	0.0001
		Acn(wheat)	10	1.90	9.76	0.0001
		Error	36	0.19		
	SG	Wheat	10	2.46	8.32	0.0001
		Acn(wheat)	10	0.59	2.00	0.0648
		Error	34	0.30		
1998	RP	Wheat	7	1.14	2.29	0.1485
		Acn(wheat)	10	0.82	1.64	0.2620
		Error	7	0.50		
	SA	Wheat	6	1.00	4.69	0.0556
		Acn(wheat)	9	0.92	4.47	0.0570
		Error	5	0.21		
	SG	Wheat	6	0.53	1.77	0.2128
		Acn(wheat)	6	0.71	2.37	0.1184
		Error	9	0.30		
1999	RP	Wheat	5	0.83	5.54	0.0033
		Acn(wheat)	4	0.97	6.51	0.0023
		Error	17	0.15		
	SA	Wheat	5	0.91	3.03	0.0353
		Acn(wheat)	4	0.48	1.62	0.2114
		Error	19	0.30		
	SG	Wheat	5	0.41	1.18	0.3467
		Acn(wheat)	4	0.86	2.44	0.0745
		Error	24	0.35		

[1] RP = *Rhopalosiphum padi*, SA = *Sitobion avenae*, SG = *Schizaphis graminum*. [2] Acn(wheat) = Accession within wheat species.

Table 4.8. Analysis of variance of the effects of aphids on biomass lost by the spikes of different species of wheats at maturity after a three week infestation period which began at boot stage.

Year	Aphid species[1]	Source of Variation[2]	df	MSE	*F*	*P*
		Wheat	10	0.73	3.57	0.0012
	RP	Acn(wheat)	11	1.47	7.15	0.0001
		Error	52	0.21		
		Wheat	10	0.75	16.82	0.0001
1997	SA	Acn(wheat)	12	1.31	29.39	0.0001
		Error	48	0.04		
		Wheat	10	1.05	8.75	0.0001
	SG	Acn(wheat)	11	0.81	6.75	0.0001
		Error	49	0.12		
		Wheat	5	1.48	5.21	0.0259
	RP	Acn(wheat)	6	0.42	1.49	0.3049
		Error	7	0.28		
		Wheat	6	1.04	2.96	0.1064
1998	SA	Acn(wheat)	6	0.39	1.12	0.4470
		Error	6	0.35		
		Wheat	6	0.88	8.57	0.0162
	SG	Acn(wheat)	4	1.36	13.20	0.0072
		Error	5	0.10		
		Wheat	5	0.26	1.16	0.3729
	RP	Acn(wheat)	3	0.28	1.26	0.3201
		Error	16	0.22		
		Wheat	5	1.23	2.93	0.0383
1999	SA	Acn(wheat)	4	0.37	0.88	0.4935
		Error	20	0.42		
		Wheat	5	0.77	2.57	0.0549
	SG	Acn(wheat)	4	0.28	7.58	0.0001
		Error	23	0.30		

[1] RP = *Rhopalosiphum padi*, SA = *Sitobion avenae*, SG = *Schizaphis graminum*. [2] Acn(wheat) = Accession within wheat species.

Table 4.9. Proportions of foliage biomass lost by primitive and cultivated wheats relative to the foliage biomass lost by the Canadian Prairie Spring wheat (CPS), *Triticum aestivum*, after a three week aphid infestation period which began at boot stage in field cages (value for CPS wheat = 1.00). (Resistant plants > 1.00).

Year	Wheat species[1]	Genome	Proportions of plant biomass lost relative to CPS wheat								
			Rhopalosiphum padi			*Sitobion avenae*			*Schizaphis graminum*		
			AC1[2]	AC2	AC3	AC1	AC2	AC3	AC1	AC2	AC3
1997	*Triticum monococcum*	A	0.39	0.50	0.88	1.04	1.05	0.77	1.72	2.29	1.31
	T. dicoccoides	AB	2.27	4.04	-[3]	2.66	5.15	-	4.99	9.44	-
	T. polonicum	AB	0.76	0.94	-	0.42	1.15	-	1.35	1.97	-
	T. carthlicum	AB	0.72	-	0.51	1.46	0.30	0.18	2.43	0.21	0.84
	T. durum	AB		0.41	-	-	0.21	-	-	0.25	-
	T. spelta	ABD	0.17	-	-	0.17 *	1.05	-	0.06	1.03	-
	T. macha	ABD	1.36	-	-	1.64	-	-	2.21	-	-
	T. vavilovii	ABD	1.59	-	-	1.65	-	-	4.21	-	-
	T. compactum	ABD	1.13	2.47	0.75	0.35	4.55	0.56	1.77	5.59	-
	T. sphaerococcum	ABD	0.28	1.03	-	0.46	1.89	-	1.54	1.35	-
	T. aestivum	ABD	1.00	0.11 *	-	1.00	-	-	1.00	1.05	-
1998	*T. aegilopoides*	A	3.33	0.02	3.18	1.32	1.04	1.42	2.08	1.34	0.85
	T. monococcum	A	1.16	1.21	-	0.71	0.06	-	1.18	0.20	-
	T. speltoides	S	1.01	-	0.56	0.27	0.09	0.50	-	-	0.60
	T. tauschii	D	-	0.02	0.02	0.39	-	2.18	0.55	0.07	2.14
	T. timopheevii	AG	1.86	4.39	-	0.50	1.44	-	-	0.78	-
	T. turgidum	AB	0.26	0.90	0.79	-	0.10	0.64	-	-	2.19
	T. durum	AB	0.02	-	-	-	-	-	-	-	-
	T. aestivum	ABD	1.00	1.39	-	1.00	0.02	-	1.00	1.04	-
1999	*T. monococcum*	A	1.46	0.08 *	-	1.02	0.50	-	1.73	0.25	-
	T. araraticum	AG	1.42	-	-	0.19	-	-	0.85	-	-
	T. dicoccum	AB	2.33	1.32	1.41	2.84	1.46	0.75	3.22	0.99	0.90
	T. durum	AB	0.84	-	-	0.74	-	-	0.78	-	-
	T. zhukovskyi	AAG	0.97	-	-	1.08	-	-	1.27	-	-
	T. aestivum	ABD	1.00	0.35	-	1.00	0.68	-	1.00	1.02	-

[1] Wheats tested in multiple years contained a different set of accessions in each year except for the checks, *T. durum* and *T. aestivum*.
[2] AC = wheat accession. [3] Missing values due to unavailability and/or non-establishment of accession(s) in field cage experiments.
* Foliage biomass lost by wheat is significantly lower than for the check cultivar, CPS wheat, using Dunnett's one-tailed t-test, $\alpha = 0.05$.
The ANOVA and subsequent Dunnett's test were based on log transformed plant foliage biomass.

Table 4.10. Proportions of spike biomass lost by primitive and cultivated wheats relative to the spike biomass lost by the Canadian Prairie Spring wheat (CPS), *Triticum aestivum*, after a three week aphid infestation period which began at boot stage in field cages (value for CPS wheat = 1.00). (Resistant plants > 1.00).

Year	Wheat species[1]	Genome	Proportions of spike biomass lost relative to CPS wheat								
			Rhopalosiphum padi			*Sitobion avenae*			*Schizaphis graminum*		
			AC1[2]	AC2	AC3	AC1	AC2	AC3	AC1	AC2	AC3
1997	*Triticum monococcum*	A	0.67	0.75	0.79	0.82	0.71	0.75	1.09	1.27	1.07
	T. dicoccoides	AB	0.17 *	-[3]	0.75	0.10 *	1.23	0.81	-	1.76	1.25
	T. polonicum	AB	0.64	0.95	-	0.69	1.08	-	0.78	1.24	-
	T. carthlicum	AB	1.68	0.40 *	0.72	2.03	0.66	0.55 *	1.74	0.40 *	0.76
	T. durum	AB	0.79	-	-	0.68	-	-	0.95	-	-
	T. spelta	ABD	0.34 *	1.24	-	0.58 *	1.30	-	0.51	1.44	-
	T. macha	ABD	1.26	-	-	1.39	-	-	1.86	-	-
	T. vavilovii	ABD	1.81	-	-	2.04	-	-	2.92	-	-
	T. compactum	ABD	0.46	1.23	0.59	0.60 *	1.04	0.79	0.93	1.49	0.93
	T. sphaerococcum	ABD	0.27 *	0.74	-	0.28 *	0.89	-	0.40	0.89	-
	T. aestivum	ABD	1.00	0.24 *	-	1.00	0.17 *	-	1.00	0.24 *	-
1998	*T. aegilopoides*	A	0.68	-	-	0.15	-	-	0.20 *	-	-
	T. monococcum	A	1.97	1.96	-	0.45	0.05	-	1.33	0.13	-
	T. speltoides	S	0.05	0.80	0.06	-	0.19	0.02	-	0.18 *	-
	T. tauschii	D	-	-	-	0.20	-	-	0.45	0.04 *	-
	T. timopheevii	AG	2.98	6.86	-	0.68	1.49	-	-	1.45	-
	T. turgidum	AB	0.73	0.79	-	0.12	0.41	0.56	-	0.06 *	2.19
	T. aestivum	ABD	1.00	2.87	-	1.00	0.37	-	1.00	1.33	-
1999	*T. monococcum*	A	0.77	-	-	0.55	0.28	-	2.63	0.24	-
	T. araraticum	AG	0.91	-	-	0.01 *	-	-	0.33	-	-
	T. dicoccum	AB	1.23	1.29	1.09	1.32	0.74	0.67	2.96	0.89	0.70
	T. durum	AB	1.14	-	-	0.94	-	-	1.25	-	-
	T. zhukovskyi	AAG	1.08	-	-	0.72	-	-	1.56	-	-
	T. aestivum	ABD	1.00	0.37	-	1.00	0.68	-	1.00	1.45	-

[1] Wheats tested in multiple years contained a different set of accessions in each year except for the checks, *T. durum* and *T. aestivum*.
[2] AC = wheat accession. [3] Missing values due to unavailability and/or non-establishment of accession(s) in field cage experiments.
* Spike biomass lost by wheat is significantly lower than for the check cultivar, CPS wheat, using Dunnett's one-tailed t-test, $\alpha = 0.05$. The ANOVA and subsequent Dunnett's test were based on log transformed spike biomass.

Table 4.11. Frequency of antibiotic and resistant lines in diploid, tetraploid and hexaploid wheats in the genus *Triticum.*

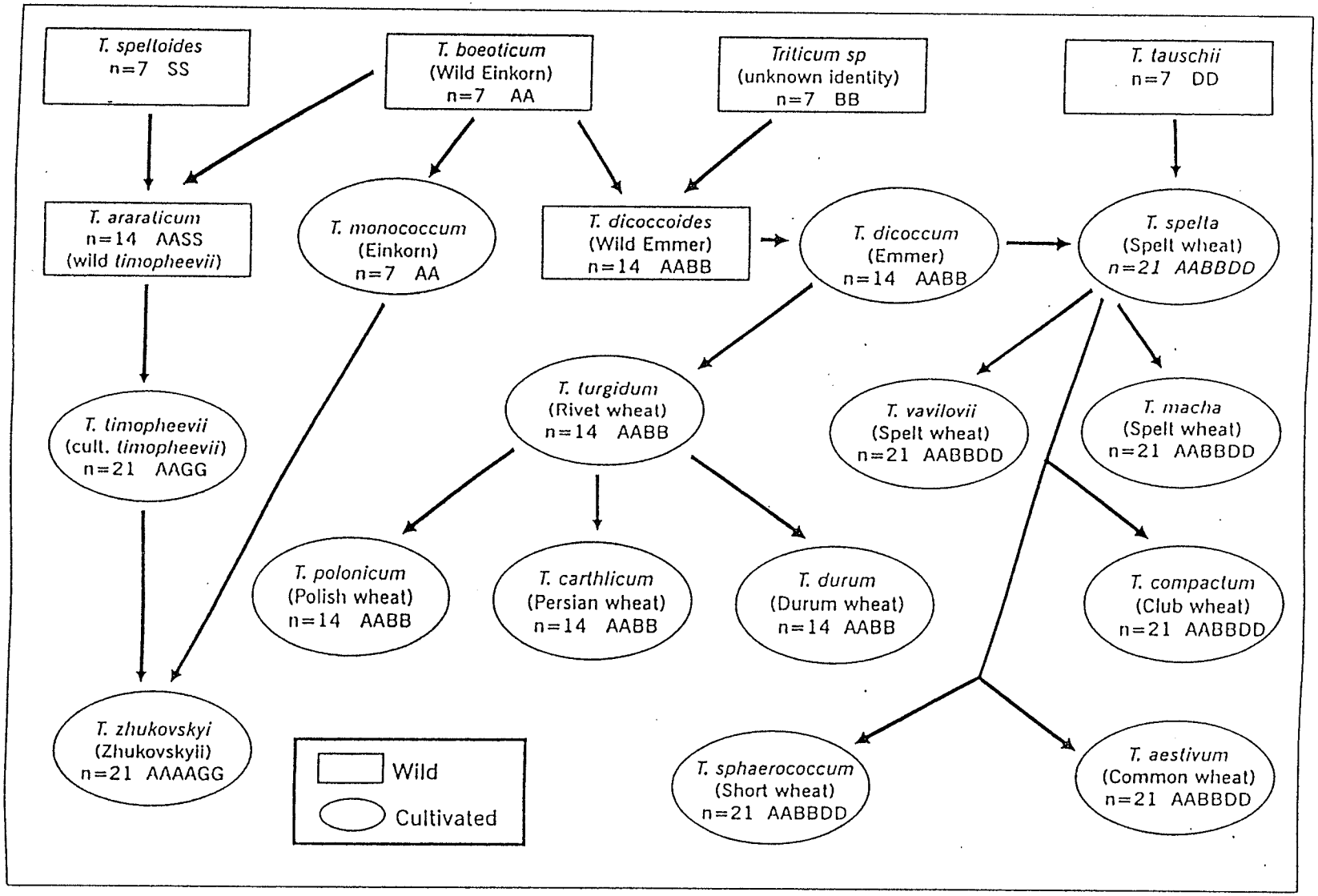
Wheat ploidy level	*Rhopalosiphum padi*			*Sitobion avenae*			*Schizaphis graminum*		
	n[1]	< 50%[2]	Frequency, %[3]	n	< 50%	Frequency, %	n	< 50%	Frequency,
a) Antibiotic resistance									
Diploid	16	7	**44**	16	7	**44**	15	6	**40**
Tetraploid	19	7	**37**	19	6	**32**	19	2	**11**
Hexaploid	12	1	**8**	12	3	**25**	12	0	**0**
b) Total resistance (spike biomass)									
Diploid	10	2	**20**	11	7	**64**	11	6	**55**
Tetraploid	17	2	**12**	18	4	**22**	15	3	**20**
Hexaploid	12	4	**33**	12	2	**17**	12	2	**17**

[1] Total number of wheat accessions (n), excluding duplicate checks in 1998 and 1999.

[2] Number of wheat accessions with less than 50% aphid biomass gained or plant biomass lost compared to the susceptible check, CPS wheat.

[3] Frequency (%) of wheat accessions with less than 50% aphid biomass gained or plant biomass lost compared to the susceptible check, CPS wheat.

Figure 4.1. A generalized genealogy of cultivated wheat species in the genus *Triticum* and their genomic constitution (after Morris and Sears, 1967; Kimber and Feldman, 1987; Gupta, 1991).


T. speltoides
n=7 SS
T. boeoticum
(Wild Einkorn)
n=7 AA
Triticum sp
(unknown identity)
n=7 BB
T. tauschii
n=7 DD
T. araraticum
n=14 AASS
(wild timopheevii)
T. monococcum
(Einkorn)
n=7 AA
T. dicoccoides
(Wild Emmer)
n=14 AABB
T. dicoccum
(Emmer)
n=14 AABB
T. spelta
(Spelt wheat)
n=21 AABBDD
T. timopheevii
(cult. timopheevii)
n=21 AAGG
T. turgidum
(Rivet wheat)
n=14 AABB
T. vavilovii
(Spelt wheat)
n=21 AABBDD
T. macha
(Spelt wheat)
n=21 AABBDD
T. polonicum
(Polish wheat)
n=14 AABB
T. carthlicum
(Persian wheat)
n=14 AABB
T. durum
(Durum wheat)
n=14 AABB
T. compactum
(Club wheat)
n=21 AABBDD
T. zhukovskyi
(Zhukovskyii)
n=21 AAAAGG
Wild
Cultivated
T. sphaerococcum
(Short wheat)
n=21 AABBDD
T. aestivum
(Common wheat)
n=21 AABBDD

CHAPTER 5

Resistance to the grain aphid, *Sitobion avenae* (Homoptera: Aphididae), among accessions of diploid wheat, *Triticum monococcum*

Abstract

The use of common wheat, *Triticum aestivum* L., and durum wheat, *Triticum durum* Desf., cultivars exhibiting resistance to aphids is a desirable method of managing aphid pests in western Canada. Cultivated wheats are susceptible to aphids or have low levels of resistance to aphids. More attention is being directed to the use of wild relatives of wheat for improved resistance in cultivated wheat to aphids. The diploid wheat, *Triticum monococcum* L., is reported to contain high levels of resistance to *Sitobion avenae* (Fabricius). Most of the reports on resistance in wheat to aphids are based on seedling studies, usually in winter wheat. Because the adult plant is the primary target of attack by *S. avenae* on the Canadian Prairies and the Northern Great Plains of the USA, a study was conducted to determine whether results of resistance to this aphid observed in seedling tests are reliable for spring wheat improvement in the region. Fourty-two accessions of *T. monococcum* and three cultivated wheats were infested with aphids for six days at the seedling stage and for 21 days at the adult stage. Antibiotic resistance was estimated from measurement of the biomass of aphids during infestation. The amount of plant biomass lost due to infestation was used to estimate total resistance. Nearly a third of the *T. monococcum* accessions exhibited moderate levels of resistance to aphids. No

relationship was found between seedling and adult plant resistance. Resistance at the seedling stage was largely due to antibiosis of plants to aphids while resistance in adult plants was largely due to tolerance. Resistance to aphids in seedling plants cannot be used to predict resistance in adult plants. Three accessions had high levels of adult plant resistance and represent promising sources of resistance to *S. avenae*, the main pest of Canadian spring wheat.

Introduction

Aphids occur on cereal crops in Manitoba every year, the most abundant species being the English grain aphid, *Sitobion avenae* (Fabricius) (Migui, 1996). These aphids infest common wheat, *Triticum aestivum* L., and durum wheat, *Triticum durum* Desf. Aphid populations initially develop on leaves and gradually move to the spikes when they emerge. Aphid populations may increase quickly and reach damaging proportions in a short period of time, especially when environmental conditions are favourable for aphid growth and development. Aphids feeding on spikes of wheat can reduce yield by up to 42% (George & Gair, 1979). In western Canada, occasional outbreaks of aphids result in serious yield losses (Haber, 1990). In addition to causing direct damage to the crop through feeding, *S. avenae* transmits viral pathogens such as barley yellow dwarf virus (Plumb, 1983).

In western Canada, wheat is the most widely grown and valuable crop although the value per unit area is low and so farmers in the region rarely use insecticides to control aphid infestations. They understand the economic constraints and are uncertain

about the damage caused by aphids. Management of the aphid populations using resistant plants is a favourable control option, because it is compatible with other aphid control options and helps conserve the natural enemies of aphids. An additional advantage of host plant resistance is that, unlike use of insecticides, aphid resistant wheat genotypes do not have negative effects on the environment.

Extensive screening of cultivated wheats for resistance to *S. avenae* has revealed only low levels of resistance (Lowe, 1981; Lee, 1984; Dedryver & Di Pietro, 1986; Di Pietro & Dedryver, 1986), and more attention is now being directed to the wild relatives of cultivated wheat. The wild relatives of cultivated wheat are adapted to a broad range of environments and probably carry a large reservoir of useful genes (Feldman & Sears, 1981). The diploid wheat, *Triticum monococcum* L., was chosen for this study because it is the most widely reported wild wheat to contain high levels of resistance to *S. avenae.* In glasshouse studies, Sotherton and van Emden (1982) showed that adult plants of some accessions of *T. monococcum* have an outstanding degree of antixenotic and antibiotic resistance to the aphids *Metopolophium dirhodum* Walker and *S. avenae*. Lee (1983, 1984) and Lowe (1984*a*) also reported that *T. monococcum* at stem elongation and flowering stages are more resistant to *S. avenae* than modern wheat cultivars and that resistance is stable against a range of clones. Di Pietro *et al.* (1998) screened a collection of 87 *T. monococcum* lines at the seedling stage and reported a high level of resistance in 17 accessions.

Most previous research on breeding wheat for resistance to aphids has concentrated on two aphid species, the greenbug, *Schizaphis graminum* Rondani, and the

Russian wheat aphid, *Diuraphis noxia* (Mordvilko), using seedling assays. Because the adult plant is the primary target of attack by aphids in western Canada, it is important to ascertain whether the resistance is also present in the adult plant before an accession expressing seedling resistance to aphids can be regarded as useful for a breeding program. The objectives of this study were: 1) to identify accessions of *T. monococcum* which express resistance to *S. avenae* at the seedling stage and/or at the adult plant stage; 2) to determine the probable mechanism of resistance at seedling and adult wheat stage; and 3) to assess the level of resistance of two *T. monococcum* lines previously reported to exhibit resistance to *S. avenae* (Di Pietro *et al.*, 1998).

Materials and Methods

Forty-two accessions of the wild diploid wheat, *T. monococcum*, and one cultivar of tetraploid wheat (*T. durum*, "Medora") and two cultivars of hexaploid wheat (*T. aestivum*, "Domain" and "Foremost") were evaluated for resistance to *S. avenae.* The commercial wheats are known to give representative responses to aphids for wheat grown in Manitoba and they served as checks. An aphid clone previously found to cause similar responses to wheat classes grown in Manitoba as other clones of *S. avenae* (Chapter 3) was selected. Tests were conducted under laboratory and field conditions. Seeds of the wild wheats were obtained from the Plant Gene Resources of Agriculture and Agri-Food Canada, the National Small Grains Research Facility of the USDA Agricultural Research Service and the Institut National de la Recherche Agronomique, France. The cultivated wheats belong to three classes: Canadian Western Red Spring (CWRS, cultivar Domain),

Canadian Prairie Spring (CPS, cultivar Foremost), and Canadian Western Amber Durum (CWAD, cultivar Medora). Total resistance was estimated by assessing the amount of plant biomass lost during infestation. Antibiotic resistance was estimated from measurement of the biomass of aphids during infestation.

Aphid rearing system

Aphids were reared in the laboratory in controlled environment chambers maintained at 18:6 L:D and 20°C on susceptible barley (*Hordeum vulgare* L., cultivar Argyle). The aphid colony comprised one clone of *S. avenae* established from cultures maintained for several years in the laboratory of Dr. P. A. MacKay, Department of Entomology, University of Manitoba. This clone was known to be representative of clones of the species in Manitoba (Chapter 3). Three environmental chambers were used in the aphid rearing system. Chamber 1 contained aphid free barley seedlings produced weekly. The barley seedlings were grown in Metromix® soil medium and watered using Hoagland nutrient solution (see Chapter 3 for details). Chamber 2 contained potted barley plants, that had been transferred from Chamber 1 and placed inside a cubical aphid rearing cage measuring 50 cm X 50 cm X 50 cm. The cage had wooden frames, with the six faces comprised of a wooden floor, clear terylene mesh on three side walls (mesh size, 28 threads/cm), a hinged wooden door and a clear transparent perspex roof. On the door was a 20.5 cm diameter circular hole centrally located on which was mounted an open ended cylindrical cotton sleeve. The cage was made completely aphid proof by tying a knot in the loose end of the cotton sleeve. Entry into the cage was by opening the door

when inserting plants and through the cloth sleeve when removing aphids. New aphid colonies were started by transferring a few aphids onto fresh plants through the cloth sleeve. Chamber 3 contained aphids which were reared on pieces of barley leaf in Petri dishes (see Chapter 3 for details). Winged aphids of uniform age and size were obtained by picking late fourth instar aphids (with wing buds) from the aphid stock culture (Chamber 2) using a fine brush and placing them individually on fresh aphid rearing dishes in Chamber 3. After molting to the adult stage the winged aphids in Petri dishes were allowed to pass through the restless teneral stage. After settling and a few hours after commencing reproduction, the adults were ready for use in laboratory and field experiments, and were referred to as standard aphids. All experiments were initiated with these young adult winged aphids, the form that would normally first infest commercial wheat.

Resistance in seedlings

Forty-five wheat accessions (table 5.1) were planted in Styrofoam cups (8.5 cm high by 7.3 cm diameter, perforated at the bottom) in Metromix® soil medium and sub-irrigated with nutrient solution. At the two leaf stage (GS 12, Tottman & Makepeace, 1979), three healthy plants, of approximately equal height, were selected for each accession. The first plant was infested with two winged adult aphids and covered with an aphid-proof cage constructed from a perforated polythene bag (see Chapter 3 for details). The second plant served as a control and was also covered with the aphid-proof bag. The control and aphid infested treatments were arranged in a completely randomized design in

a growth chamber (maintained at similar conditions to the aphid rearing chambers). The third plant was cut at soil level and weighed after being dried to estimate initial aerial plant biomass at infestation. Twenty standard aphids were placed in groups of two in 10 aluminum dishes, killed in alcohol and weighed after drying to estimate the biomass of aphids at infestation. After six days, aphids were removed from experimental plants, immobilised in alcohol, counted and weighed after drying. Both infested and control plants were cut at soil level and the aerial portion weighed after drying. The experiment was repeated each week for eight weeks to obtain sufficient replication.

Aphid biomass increase at the end of the six-day infestation period was obtained by calculating the difference between dry aphid biomass at the end and at the beginning of the experiment. Total resistance was assessed by determining the amount of aerial plant biomass lost due to infestation, by calculating the difference between the biomass of control and infested plants after aphids were removed.

Resistance in adult plants

Forty-two accessions of wheat (40 accessions of diploid *T. monococcum* and the two hexaploid *T. aestivum* cultivars, Domain and Foremost (table 5.1), as checks were germinated individually in small peat pots containing Metromix® soil medium, sub-irrigated using 20-20-20 NPK all purpose fertilizer solution, in the greenhouse. At the 3-4 leaf stage, the plants were transplanted into the field in 1 X 1 m plots and covered with 1 m high aphid proof nylon cages. Each plot contained one plant from each of the 42 accessions. The plants were laid out in a completely randomized design. Sixteen such

plots were established and caged, with 2 m between plots.

After 50% of plants within each cage reached boot stage, *S. avenae* adults (standard aphids) were introduced into eight cages by placing 10 aphids on each plant. The infestation period lasted three weeks after which half of the infested and uninfested (control) plots were sampled to assess aphid biomass increase and plant biomass loss (at this stage, the plants were referred to as adult plants at heading). Plants were cut at soil level and the aerial parts placed individually in plastic bags, taking precautions to ensure that aphids did not fall off the plants. Plants in the remaining plots were sprayed with dimethoate 480 E.C. at a rate of 2 ml per L of water which ensured adequate coverage by the insecticide to kill the aphids. The plants in these plots were allowed to grow to maturity for yield assessment (dry plants ready for harvest were referred to as adult plants at maturity).

Aphids were collected from the bagged plants by emptying the contents into a tub of hot water and shaking the plants lightly to dislodge the aphids. The plants were rinsed in another tub to ensure complete removal of aphids. The contents were sieved and sorted to separate plant debris from aphids. Clean aphids were placed in pre-weighed aluminum dishes and weighed, after being dried to constant weight at 80°C. Plant material from both aphid infested and control plots were cut into pieces and separately placed into aluminum containers and weighed after being dried to constant weight at 80°C. When the remainder of the plants in field cages reached maturity, the plants were cut at the soil surface and bagged individually. Wheat spikes and foliage of each plant were separated and weighed after being dried to constant weight at 80°C. Spikes were used instead of

seeds because the wild wheats had glumes tightly adhering to seeds and were difficult to thresh.

Two *T. monococcum* accessions (Tm44 and Tm46) reported to exhibit resistance to *S. avenae* (Di Pietro *et al.*, 1998) were tested in a separate experiment the following year along with a random selection of 10 accessions from the previous *T. monococcum* collection of 40. The wheat accessions were planted in 5 m rows (double row per accession) with a spacing of 30 cm between rows and 15 cm between plants. Three weeks after crop emergence, eight plants from each accession were randomly selected and covered with single plant sleeve cages in order to avoid infestation by wild aphids. When the plants reached boot stage, five of the caged plants for each accession were infested with 10 standard *S. avenae*. The other three plants served as controls. Aphid infestation lasted three weeks after which all the caged plants including the controls were sprayed with dimethoate 480 EC and left to grow to maturity for yield assessment. At maturity, the plants were cut at soil level and the spikes and foliage were separated and weighed after being dried to a constant weight at 80°C.

Data analysis

Data were analysed using the procedures of SAS (SAS Institute Inc., 1989) to determine differences among the wheat accessions in the amounts of aphid biomass gain and plant biomass loss. A plot of mean versus variance for each dependent variable was made to determine whether transformation was required to normalize the data or stabilize variance. Where data were found to be non-normal (strong relationship between mean

and variance and/or the range of variance was greater than two times the smallest variance), they were transformed by calculating natural logarithms before proceeding with statistical analysis. Analysis of variance tables were constructed using general linear model (GLM) procedures with wheat accession as a fixed effect and aphid biomass increase or plant biomass loss as dependent variables. Correlation tests of aphid biomass gain and plant biomass loss among different growth stages of the wheat were performed to assess the value of screening of these stages for assessing adult plant resistance. The GLM test gives a global indication of differences among at least some accessions, but does not provide a separation test for means. With 45 different sets of means, most mean separation tests give erroneous results due to lack of power. Also, most mean separation tests give overlapping and ambiguous groups of means which are difficult to interpret. This problem was overcome by performing cluster analysis using the method described by Calinski and Corsten (1985) and adopted by Di Pietro *et al.* (1998). A dendogram showing the clustering of wheat accessions was produced using the TREE procedure (SAS Institute Inc., 1989), which used standardized means, that is, lsmeans/standard error. Separation of means into non-overlapping groups provides some structure in an otherwise unstructured set of means and helps in directing attention to the emerging classes. The aim of cluster analysis in this study is not to produce a complete enumeration of all possible homogenous subsets of means but to partition the sample of means into distinct and non-overlapping subsets that may be considered internally homogeneous biologically. The probability of accepting too many homogenous groups is bounded by the risk level α (in this test, α=0.05). In the cluster analysis method, homogeneity among

means is defined as the non-rejection of equality and is by no means equivalent to equality. Treatments which belong to different homogenous groups should not be inferred as significantly different, but, treatments in the same homogenous group are not significantly different from one another (Calinski & Corsten, 1985). The maximum distance between clusters gives a measure of the degree of homogeneity among the groups, such that, two clusters with a small distance between them are more homogeneous than other groupings with larger distances between them. The normalised maximum distance between clusters is based on root mean square of sample standard deviation, so the units of distance between clusters are the same as those of the dependent variable.

Results

Resistance in seedlings

Sitobion avenae successfuly fed and multiplied on the 42 accessions of *T. monococcum* and three cultivars of wheat. Although the number of aphids produced during the six-day infestation period did not differ significantly among accessions, the biomass of aphids differed (table 5.2). The accession showing the highest level of seedling antibiosis caused a 78% reduction in aphid biomass compared to the most susceptible cultivated wheat, "Foremost" (appendix 7.1). Cluster analysis of the aphid biomass gained on the seedlings showed that accessions 41 (TM44), 20, 17, 26, 42 (TM46), 10, 27 and 19 exhibited the highest level of seedling antibiosis to *S. avenae*, with "Foremost" showing the lowest level of antibiosis (fig. 5.1; see table 5.1 for

corresponding accession names). "Domain" and "Medora" clustered in a group exhibiting susceptibility to aphids. Aphid feeding caused a 6-30% reduction in plant biomass compared to controls (appendix 7.2), but no significant differences among accessions were detected in the amounts of plant biomass loss (table 5.2). Aphid biomass and plant biomass loss on seedling plants were positively correlated ($r_p = 0.49$; $P = 0.0007$; n = 45).

Resistance in adult plants

Although aphid biomass on adult plants at heading in field cages showed five-fold variation among accessions (appendix 7.3), no significant differences among accessions were detected at the end of the 3-week infestation period (table 5.3), indicating no differential effect on the biomass of *S. avenae*. However, the aphid infestation resulted in a differential reduction in total plant biomass loss compared to controls ($P < 0.001$), and difference in biomass loss among accessions (table 5.3, appendix 7.4). Twelve accessions (32, 31, 30, 9, 23, 29, 24, 22, 38, 7, 39 and 17) showed high levels of total resistance to aphids (fig. 5.2). "Domain" clustered in the middle of the range (fig. 5.2), with a 25% biomass loss due to aphid infestation compared with 0% loss for the most resistant *T. monococcum*, accession 32 (appendix 7.4). "Foremost" clustered in the group exhibiting the lowest resistance to aphids.

Effects of the 21 day aphid infestation carried over to crop maturity, with both multiple plant and single plant cage experiments showing a reduction in foliage and spike biomass compared to controls (appendices 7.5, 7.6, 7.7, and 7.8). Foliage biomass loss and spike biomass loss differed significantly among accessions (tables 5.4 and 5.5). Spike

biomass loss and foliage biomass loss were highly correlated (fig. 5.3), showing that they provide similar information about the impact of aphids on wheat. Because wheat spikes are easier to work with than plant foliage and spike biomass is related to yield, subsequent analysis concentrated on the spikes. Figures 5.4 and 5.5 show cluster analysis of spike biomass loss at maturity in the multiple plant and single plant experiments, respectively. Accessions which clustered in the high total resistance categories included 1, 39, 30, 31, 33, 9, 15, 7, 8, 10, 3, 28, 6 and 21 for the multiple plant experiment and 41, 39, 13, 9, 36 and 18 for the single plant experiment. Again "Domain" clustered in the middle of the resistance range and "Foremost" clustered in the low resistance group. In both field experiments accessions 9 and 39 exhibited high levels of resistance to *S. avenae*.

No significant relationships were found between aphid biomass gain on seedling plants and plant biomass loss in adult plants (table 5.6). Only one accession, 41, reduced aphid biomass gain in the seedling stage and also was resistant at the adult plant stage. "Foremost" consistently showed high susceptibility to aphids at seedling and adult growth stages. Although reduction in aphid biomass gain was evident for seedlings, reduction of aphid biomass gain was not associated with adult plant resistance. Aphid biomass gain did not differ among accessions for adult plants, and adult plant resistance estimated as biomass loss was not correlated with aphid biomass gain (table 5.6). The one significant correlation between aphid biomass gain and foliage biomass loss at heading was negative, and so did not indicate that antibiosis caused the resistance. The lack of a role for antibiosis for adult plants indicates that adult plant resistance is probably due to tolerance.

Discussion

This study identified several accessions of the diploid wheat, *T. monococcum,* with high levels of resistance to *S. avenae,* both at seedling and adult plant stages. Accessions which clustered in the highest resistance categories may provide potential sources of resistance to the aphid. In both assessments of adult plant resistance, accessions 9 and 39 clustered in the highest level of resistance and may provide good sources of adult plant resistance genes. Accessions 41 and 42 are reported to possess seedling antibiosis to *S. avenae* (Di Pietro *et al.*, 1998). The antibiotic resistance of these two *T. monococcum* accessions was confirmed in the current study. Accession 41 showed both reduced aphid biomass gain on seedlings and high resistance at the adult stage and appears to be a good candidate as a source for resistance. These results corroborate earlier findings (Chapter 4) and reports by other workers, showing that *T. monococcum* contains reliable sources of resistance to *S. avenae* (Lee, 1983, 1984; Lowe, 1984*b*; Sotherton & van Emden, 1982; Di Pietro *et al.*, 1998).

The cultivar Foremost appeared to be the most susceptible among the accessions tested, confirming earlier findings which suggest that this wheat is particularly susceptible to aphids (Chapter 3). "Domain" and "Medora" also showed low levels of resistance to aphids, insufficient to avoid substantial yield losses. Because *S. avenae* occurs in Manitoba every year, it poses a constant threat to wheat production unless these highly susceptible cultivars are replaced.

Aphid biomass and plant biomass loss on seedling plants were positively correlated suggesting that seedling resistance was due primarily to antibiosis rather than

tolerance. There was no association between seedling resistance and adult plant resistance to aphids. Accessions which exhibited high resistance to aphids at the seedling stage were usually susceptible at the adult plant stage. This finding is important because research on host plant resistance to aphids has traditionally used seedling plants in screening programs and assumed that insect-plant interactions would be similar in the adult plant. Findings from this study stress the importance of screening adult plants if the intended resistance is to be useful in adult plants. Earlier findings in Chapter 3 support this conclusion. Seedlings of three cultivars, "Domain", "Foremost" and "Medora" were found to be more tolerant to aphids than adult plants. Therefore, in western Canada, where the adult wheat plant is the primary target of attack by cereal aphids, screening and breeding for resistance to aphids should be conducted based on performance of the adult plant. Likewise, seedling screening procedures are considered inadequate for corn against corn leaf aphid, *R. maidis*, and field screening is preferred (Auclair, 1989).

The use of wheat spikes for assessment of resistance to aphids in adult plants in the field is recommended because they are convenient to handle and also provide information on yield. The emerging wheat spike is also the most vulnerable part of the wheat plant to attack by *S. avenae*. Grapel (1982) reported that a short period of aphid infestation before the time of flowering caused a small yield reduction, but a similar infestation during the flowering period caused serious damage. Change in biomass of wheat spikes probably will provide a sufficient estimate of the impact of *S. avenae* on adult wheat.

This study identified two types of resistance mechanisms which influenced the resultant interactions between aphids and the wheats tested. Resistance in seedling plants was probably largely due to antibiotic properties of the wheat accessions. Aphids feeding on resistant wheat accessions accumulated less biomass than aphids feeding on susceptible accessions, implying that the resistant accessions negatively affected the biology of the aphids. The resistant accessions may have contained low amounts of important nutrients, such as amino acids essential for growth and development of the aphids. Alternatively, resistant accessions may have contained higher concentrations of toxic substances which reduce growth and slow development of the insects (Argandona *et al.*, 1983). For example, the presence of high levels of hydroxamic acids in seedlings of wheat and barley is implicated in the antibiosis of seedlings to aphids (Argandona *et al.*, 1983; Thackray *et al.*, 1990; Givovich & Niemeyer, 1995). Resistance in adult plants was largely due to tolerance because large differences in resistance were not associated with differences in aphid biomass production among wheat accessions. Furthermore, no correlation was detected between plant biomass loss and aphid biomass gain. Tolerant plants sustained low plant biomass losses as a result of infestation by aphids. Plant tolerance to aphids is difficult to breed for, because of the many factors that cause variation in the biomass of mature plants. Nonetheless tolerance is potentially a very important component of host plant resistance.

The two aphid species, *S. graminum* and *D. noxia*, which have received worldwide attention on breeding wheat cultivars resistant to the aphids, inject toxic saliva into host tissue causing chlorosis and sometimes necrosis. This characteristic injury

allows plant breeders to make quick visual scores on test lines and enables screening of large numbers of accessions. Other aphid pests, such as *S. avenae* and *R. padi* usually cause plant damage that cannot be visually scored and sometimes requires laborious measurements. Much of the information available on host plant resistance to the latter two pests are lists of possible resistance sources with little or no breeding efforts after initial screening. In the current study, use of aphid biomass and plant biomass measurements provided an efficient way of assessing the impact of resistant wheat accessions on the aphid pest. Although the screening procedure may be tedious, the available information on sources of resistance to aphids should be exploited in directed screening and plant breeding programs with the purpose of transferring the resistance to cultivated wheats.

In conclusion, these results indicate that *T. monococcum* is a remarkable source of genetic material which can be exploited to confer resistance to *S. avenae* in cultivated wheats. It is important to note that resistance observed at the seedling stage cannot be used to predict adult plant resistance. The high genetic diversity in *T. monococcum* means that accessions within this species can occur anywhere within a continuum of host resistance to aphids, including the extreme ends, i.e. high resistance and high susceptibility to aphids. Thus, there is need to use screening programs that enable efficient detection of resistant germplasm.

Table 5.1. Accession numbers and Plant Gene Resources codes of diploid wheat, *Triticum monococcum*, and cultivated tetraploid and hexaploid wheats screened for resistance to *Sitobion avenae*.

ACC No.[1]	PGR code[2]	ACC No.	PGR code	ACC No.	PGR code
1	1730	16	1751	31	1766
2	1731	17	1752	32	1767
3	1733	18	1753	33	1768
4	1734	19	1754	34	1770
5	1735	20	1755	35	1771
6	1737	21	1756	36	1772
7	1738	22	1757	37	1773
8	1739	23	1758	38	1507
9	1744	24	1759	39	1511
10	1745	25	1760	40	1514
11	1746	26	1761	41	TM 44
12	1747	27	1762	42	TM 46
13	1748	28	1763	43	DOMAIN
14	1749	29	1764	44	FOREMOST
15	1750	30	1765	45	MEDORA

[1]ACC = Accession; [2]PGR = Plant Gene Resources of Agriculture and Agri-Food Canada; TM 44 and TM 46 came from the Institut National de la Recherche Agronomique, France.

Experiment 1: Laboratory, single plant cages, seedlings; accession numbers 1-45.

Experiment 2: Field, multiple plant cages, adult plants; accession numbers 1-40, 43, 44.

Experiment 3: Field, single plant cages, adult plants; accession numbers 6, 9, 13, 18, 21, 26, 31, 34, 36, 39, 41, 42.

Table 5.2. Analysis of variance of the effects of different accessions of diploid wheat, *Triticum monococcum*, and cultivated tetraploid and hexaploid wheats on the numbers and biomass increase of *Sitobion avenae*, and plant biomass loss after sixdays of seedling infestation in a controlled environment.

Source of variation	df	MSE	*F*	*P*
Aphid numbers				
ACCESSION	44	32.88	1.31	0.0987
ERROR	304	25.04		
Log_e(aphid biomass increase)				
ACCESSION	44	0.90	4.19	< 0.0001
ERROR	304	0.21		
Log_e(plant biomass loss)				
ACCESSION	44	0.00019	0.61	0.9756
ERROR	315	0.00011		

Table 5.3. Analysis of variance of the effects of 42 accessions of diploid wheat, *Triticum monococcum*, and cultivated hexaploid wheats on the biomass of *Sitobion avenae* and plant biomass loss at the end of the infestation period.

Source of variation	df	MSE	*F*	*P*
Log_e(aphid biomass)				
ACCESSION	41	0.43	0.63	0.9521
ERROR	122	0.68		
Log_e(plant biomass loss)				
ACCESSION	41	1.46	2.22	0.0004
ERROR	122	0.66		

Table 5.4. Analysis of variance of the effects of *Sitobion avenae* infestation on foliage biomass loss and spike biomass loss of 42 accessions of diploid wheat, *Triticum monococcum*, and cultivated hexaploid wheats, at maturity.

Source of variation	df	MSE	*F*	*P*
Log_e(foliage biomass loss)				
ACCESSION	41	1.99	2.58	< 0.0001
ERROR	157	0.77		
Log_e(spike biomass loss)				
ACCESSION	41	1.83	2.11	0.0006
ERROR	157	0.87		

Table 5.5. Analysis of variance of the effects of *Sitobion avenae* on foliage biomass loss and spike biomass loss of 12 accessions of diploid wheat, *Triticum monococcum,* after a three week infestation period which began at boot stage.

Source of variation	df	MSE	*F*	*P*
Log_e(foliage biomass loss)				
ACCESSION	11	1.64	2.40	0.0182
ERROR	48	0.68		
Log_e(spike biomass loss)				
ACCESSION	11	1.39	2.31	0.0229
ERROR	48	0.60		

Table 5.6. Correlation of resistance parameters for *Sitobion avenae* on diploid *Triticum monococcum* and cultivated tetraploid and hexaploid wheats.

Resistance parameters			r_p	P	n
First variable		Second variable			
Aphid biomass on seedlings	vs	Aphid biomass on adult plants	0.10	0.5406	42
Aphid biomass on seedlings	vs	Foliage biomass loss at maturity	-0.28	0.0764	42
Aphid biomass on seedlings	vs	Spike biomass loss at maturity	-0.07	0.6523	42
Aphid biomass at heading	vs	Foliage biomass loss at heading	-0.31	0.0481	42
Aphid biomass at heading	vs	Foliage biomass loss at maturity	0.08	0.6070	42
Aphid biomass at heading	vs	Spike biomass loss at maturity	-0.02	0.8867	42

r_p = Pearson correlation

Figure 5.1. Cluster analysis of the biomass gain by *Sitobion avenae*, feeding for six days on seedlings of 45 accessions of diploid wheat, *Triticum monococcum*, and cultivated wheats in single plant cages. D ("Domain"), F ("Foremost"), and M ("Medora") are the three cultivated wheats; TM44 and TM46 were previously identified as resistant; n=8; see table 1 for accession numbers and corresponding identifier.

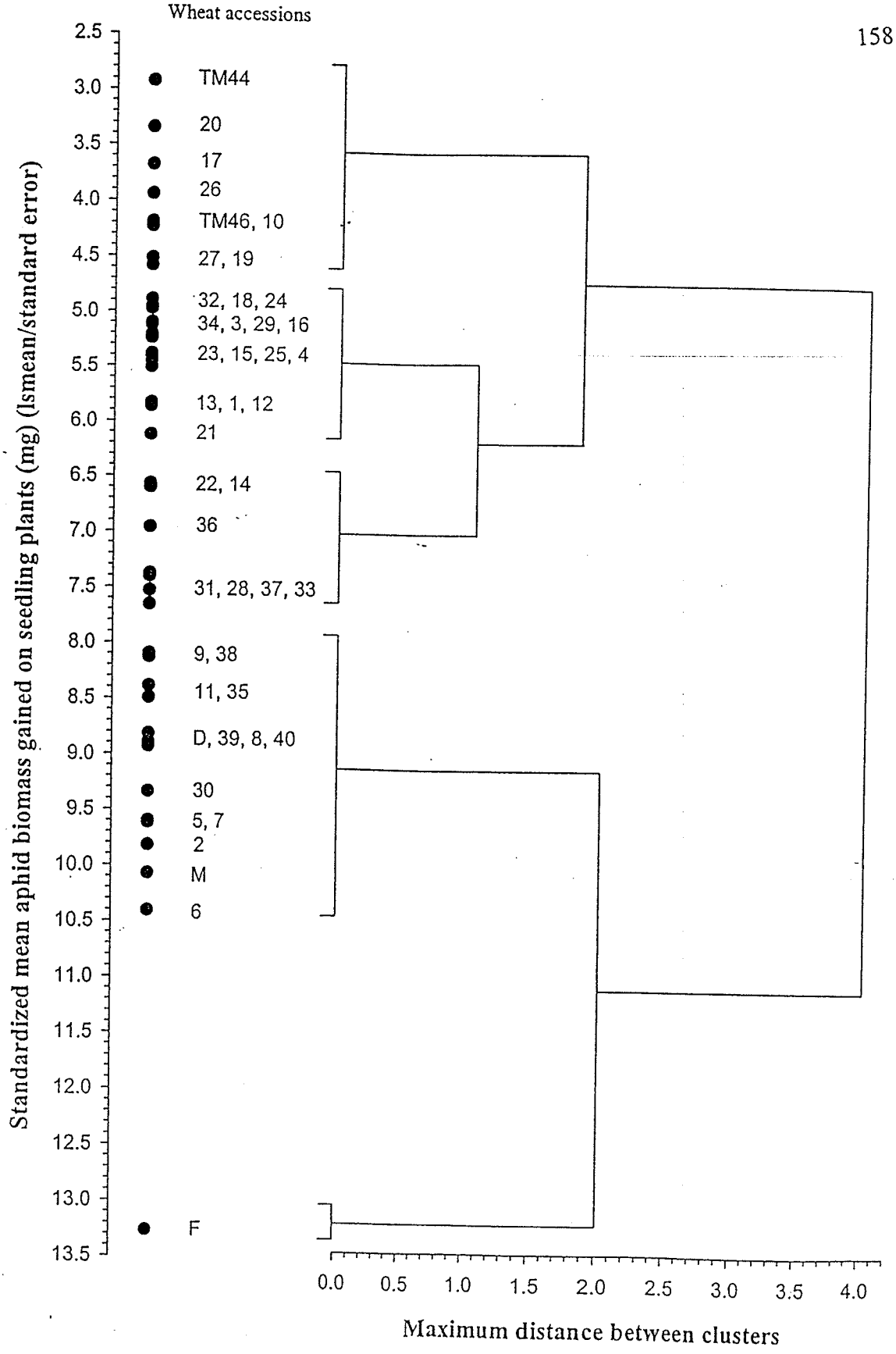

Wheat accessions
TM44
20
17
26
TM46, 10
27, 19
32, 18, 24
34, 3, 29, 16
23, 15, 25, 4
13, 1, 12
21
22, 14
36
31, 28, 37, 33
9, 38
11, 35
D, 39, 8, 40
30
5, 7
2
M
6
F
Standardized mean aphid biomass gained on seedling plants (mg) (lsmean/standard error)
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
10.0
10.5
11.0
11.5
12.0
12.5
13.0
13.5
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Maximum distance between clusters

Figure 5.2. Cluster analysis of the biomass loss by adult plants of 42 accessions of diploid wheat, *Triticum monococcum*, and cultivated hexaploid wheats, harvested green after a 21 day infestation period by *Sitobion avenae* in multiple plant cages. D ("Domain"), F ("Foremost"); n=4; see table 1 for accession numbers and corresponding identifiers.

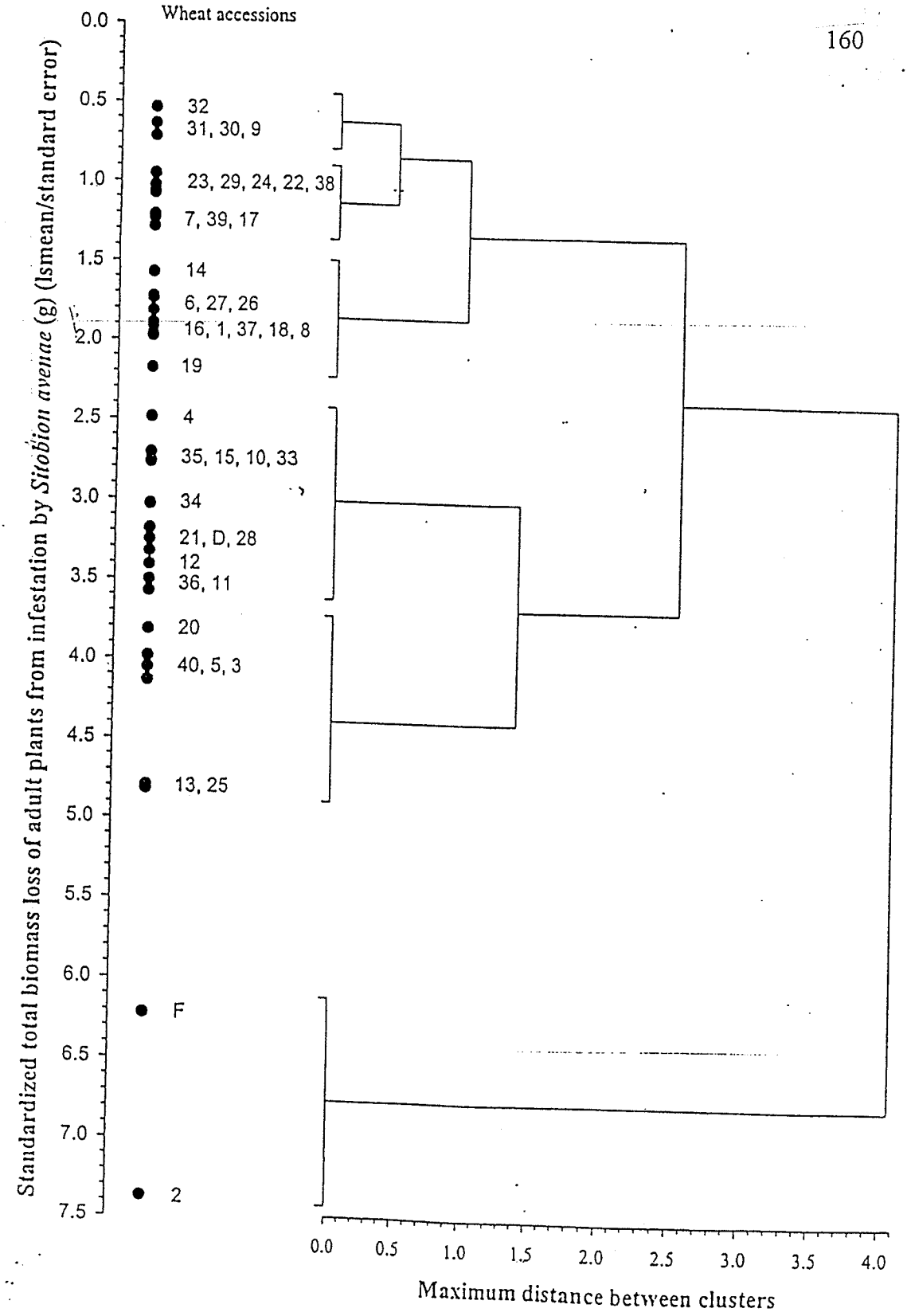
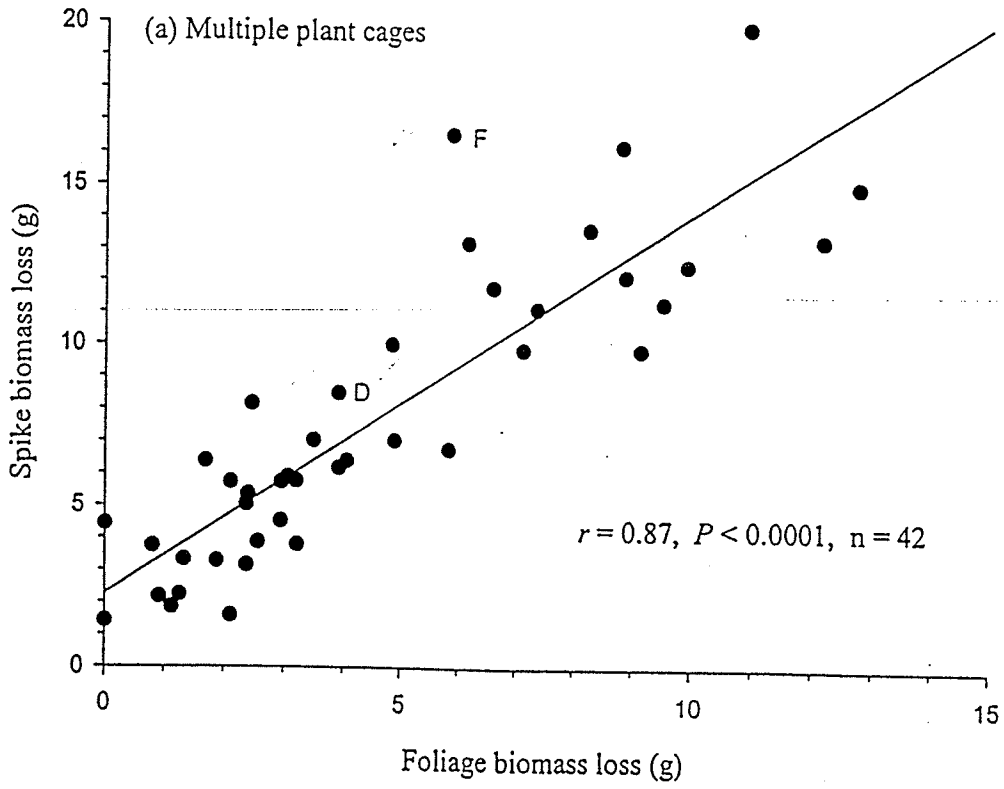

Wheat accessions
Standardized total biomass loss of adult plants from infestation by Sitobion avenae (g) (lsmean/standard error)
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
32
31, 30, 9
23, 29, 24, 22, 38
7, 39, 17
14
6, 27, 26
16, 1, 37, 18, 8
19
4
35, 15, 10, 33
34
21, D, 28
12
36, 11
20
40, 5, 3
13, 25
F
2
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
Maximum distance between clusters

Figure 5.3. Correlation of spike biomass loss with foliage biomass loss of diploid wheat, *Triticum monococcum,* and cultivated hexaploid wheats, after a 21 day infestation period by *Sitobion avenae,* beginning at boot stage in the field in multiple plant cages and single plant cages. D ("Domain"), F ("Foremost") are two cultivated hexaploids; TM44 and TM46 are *T. monococcum* accessions previously identified to exhibit seedling resistance; n=42 for multiple plant cages, and n=12 for single plant cages.


(a) Multiple plant cages
F
D
$r = 0.87$, $P < 0.0001$, n = 42
Spike biomass loss (g)
Foliage biomass loss (g)
0
5
10
15
20

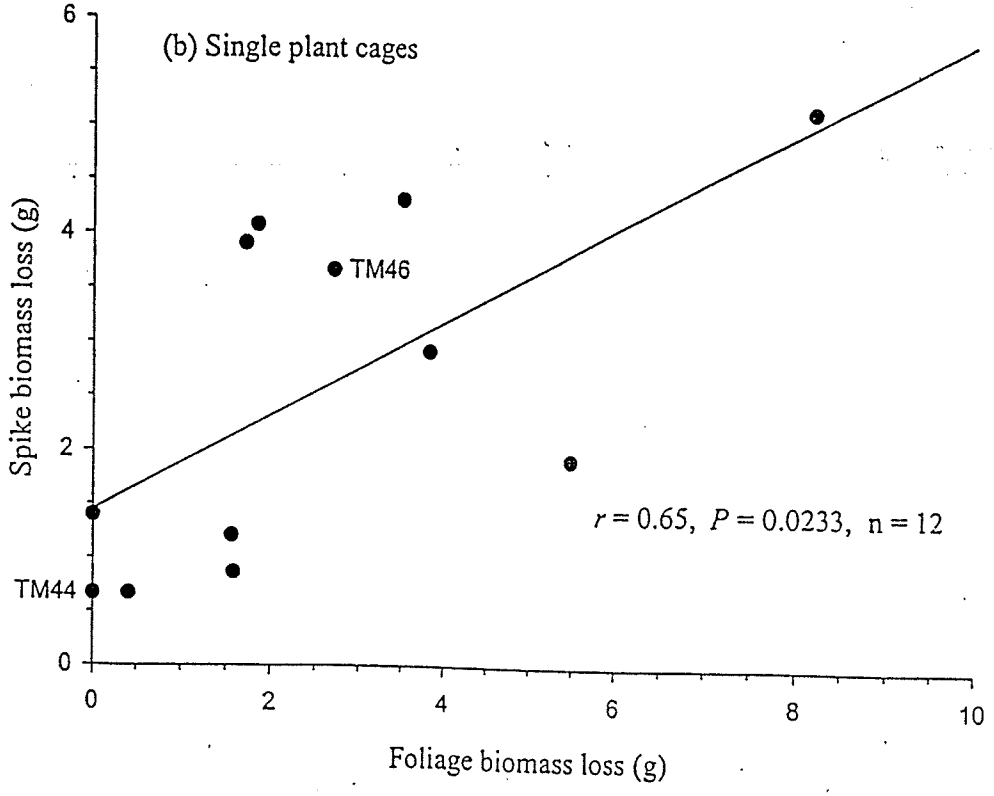

(b) Single plant cages
TM46
TM44
$r = 0.65$, $P = 0.0233$, n = 12
Spike biomass loss (g)
Foliage biomass loss (g)
0
2
4
6
8
10

Figure 5.4. Cluster analysis of the spike biomass loss by mature plants of 42 accessions of the diploid wheat, *Triticum monococcum,* and cultivated hexaploid wheats, after a 21 day infestation period by *Sitobion avenae,* which began at boot stage in multiple plant cages. D ("Domain") and F ("Foremost") are two cultivated hexaploids; n=5; see table 1 for accession numbers and corresponding identifier.

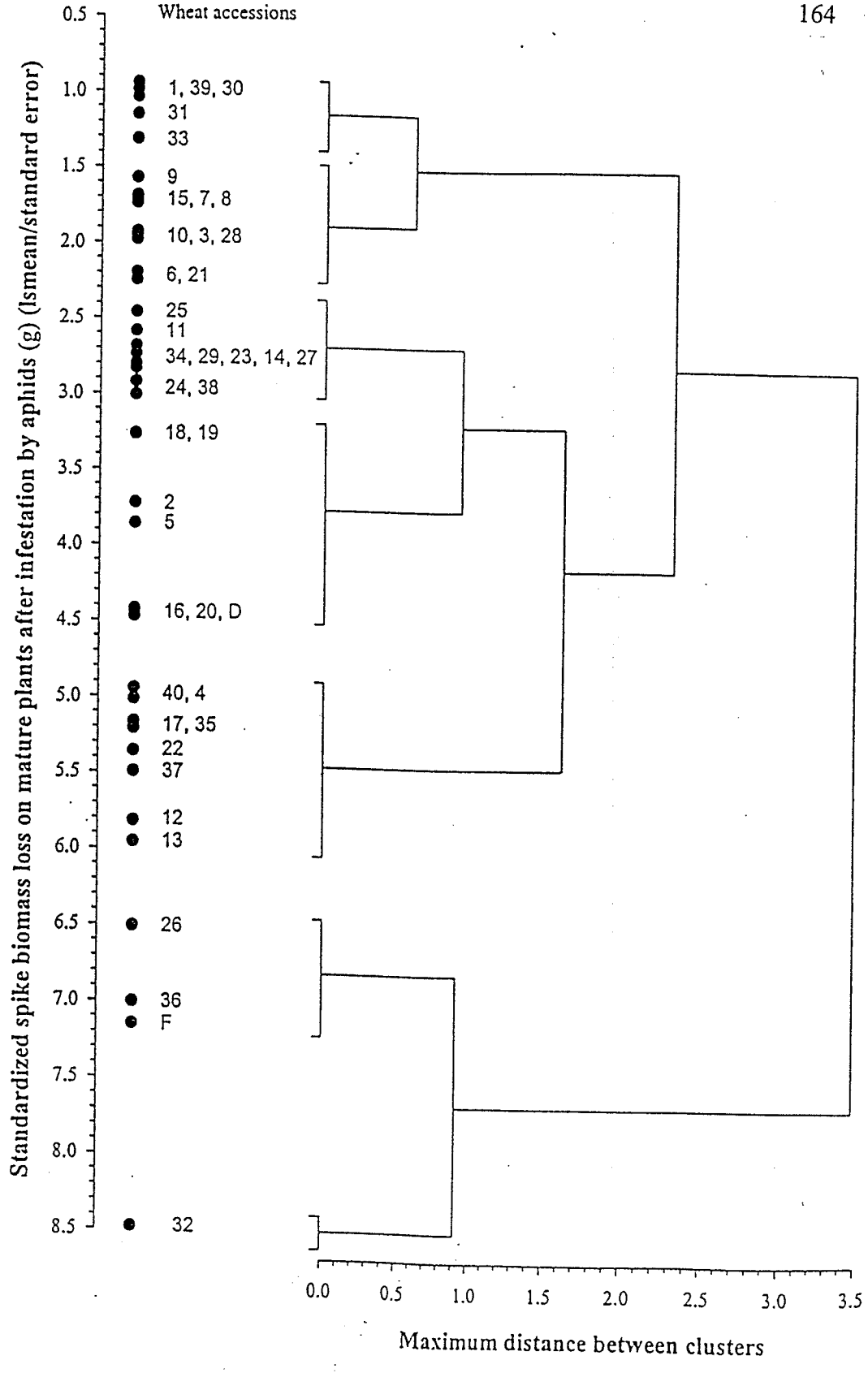
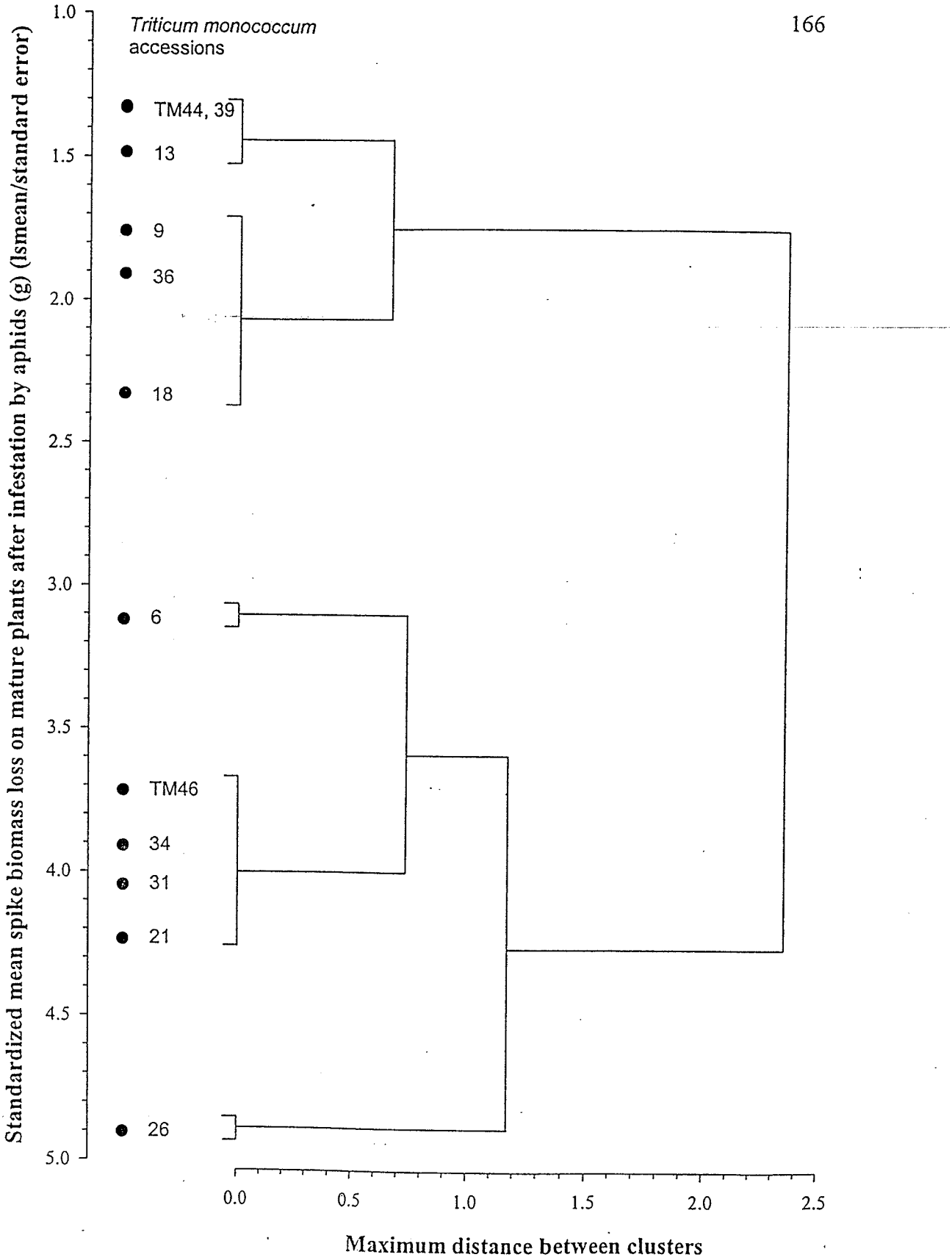

Wheat accessions
Standardized spike biomass loss on mature plants after infestation by aphids (g) (lsmean/standard error)
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
1, 39, 30
31
33
9
15, 7, 8
10, 3, 28
6, 21
25
11
34, 29, 23, 14, 27
24, 38
18, 19
2
5
16, 20, D
40, 4
17, 35
22
37
12
13
26
36
F
32
0.0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
Maximum distance between clusters

Figure 5.5. Cluster analysis of the spike biomass lost by mature plants of 12 accessions of the diploid wheat, *Triticum monococcum,* after a 21 day infestation period by the aphid, *Sitobion avenae,* which began at boot stage, in single plant cages. TM44 and TM46 were previously identified as resistant; n=5; see table 1 for accession numbers and corresponding identifier.


Triticum monococcum
accessions
TM44, 39
13
9
36
18
6
TM46
34
31
21
26
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
Standardized mean spike biomass loss on mature plants after infestation by aphids (g) (lsmean/standard error)
0.0
0.5
1.0
1.5
2.0
2.5
Maximum distance between clusters

CHAPTER 6

General Discussion

Host plant resistance is widely recognized as an important component of pest management. Its use is particularly desirable for crops with a narrow profit margin which makes other pest control options uneconomic. Production of spring wheat in the northern Great Plains of the USA and the Prairies of Canada and its association with aphid pests fits into this category. As yet, however, no wheat cultivars resistant to aphids have been developed in western Canada. This study investigated the potential of crop resistance in the management of aphid pests of adult plants of spring wheat and confirmed the feasibility for host plant resistance. Aphids inflicted heavy damage on the three classes of wheat tested, with losses in above ground biomass and yield of infested caged plants being as much as 45% and 76% respectively.

Interactions between aphids and wheat classes differed among aphid species and between two growth stages of wheat. On seedling plants, *R. padi* produced almost twice as much biomass as that produced by *S. avenae* or *Sc. graminum* showing that seedlings are most favourable for the development and growth of *R. padi.* This aphid appears to utilize seedling plants more effectively than *S. avenae* or *Sc. graminum* probably because it preferentially selects the most favourable feeding location, the stems of young wheat plants (MacKay & Lamb, 1996; Migui, 1996). As the plant develops into the adult stage, its suitability for each aphid species changes, causing aphids to develop and reproduce at different rates. The relative performance of aphids on adult plants was reversed, with the

plants becoming more suitable for the development of *S. avenae* and *Sc. graminum* than for *R. padi*. Upon spike emergence, *S. avenae* preferentially moves to the spikes, where its fecundity increases by up to three times (Watt, 1979). In the adult plant, the spike becomes the most nutritious part of the plant as assimilates are relocated to the filling grain. *Sitobion avenae* affects yield by directly competing with the filling grain for plant nutrients. The fact that aphid clones within species vary less than aphid species validates the use of a few clones for comparisons among species. Nevertheless, researchers must be alert to the problem that a rare, virulent clone may occur and become important. Such clones arise repeatedly in some aphid species and have overcome antibiotic resistance (Porter *et al.*, 1997).

Cultivars within wheat classes are more similar to each other than the classes, which is important because it would be impractical to test all cultivars in each class. The genetic similarities of wheats within classes likely assures similar resistance levels. All three classes of wheat show relatively low levels of resistance to all three aphids at both seedling and adult plant stages. Nevertheless CWRS wheat is more resistant to *S. avenae* and *Sc. graminum* than CPS with CWAD being intermediate. The partial resistance shown by CWRS, although insufficient, would be of some agricultural benefit, reducing losses in yield by as much as 15% on average compared to CPS. The differences in resistance were sufficient to allow examination of how such partial resistance might be estimated, and what the relationship is between resistance in seedlings and adult plants.

Resistance to one aphid species appeared to be associated with resistance to other aphid species in adult plants. The resistance that was observed was primarily tolerance

which could be measured by specific impact: units of biomass lost by the plant per unit of biomass gained by the aphids. Resistance in seedling plants was primarily antibiosis. Resistance due to tolerance is more general than resistance due to antibiosis. In other words, antibiosis appears to be a specific defence against a particular species, whereas tolerance is a more general defence enabling the plant to survive and reproduce despite supporting an aphid population similar to what would be damaging to a susceptible plant.

Wild primitive wheats have been subject to sustained natural selection for resistance against insect pests and may possess traits of resistance to aphids. Evaluation of a collection of 41 accessions of wild and cultivated wheats belonging to 19 species of the genus *Triticum* showed that the patterns of aphid biomass gain and plant biomass loss were related to the domestication of wheat. The ploidy level in the genus *Triticum*, which reflects some multiple of the basic set of haploid chromosomes from the progenitors of modern wheat, also represents a spectrum of the degree of domestication, with diploids corresponding to the least domesticated and the hexaploids corresponding to the most domesticated. Primitive diploid wheats carried the highest frequency of resistant accessions, and the most domesticated, hexaploid wheats carried the lowest frequency of resistant accessions. This observation, based on comprehensive examination of the genus, corroborates findings of other researchers on small numbers of species from a variety of crops, that ancestral species are more resistant to insect pests than their domesticated counterparts. Lee (1983, 1984) and Lowe (1984*a*) reported that diploid wheat, *T. monococcum* is more resistant to *S. avenae* than modern hexaploid wheat cultivars under laboratory and field conditions and that resistance was stable against a range of clones.

Kazemi & van Emden (1992) found that a tetraploid wheat, *T. dicoccum*, exhibited higher resistance to *R. padi* than hexaploid wheat. The loss of pest resistance with increased levels of domestication may be a common phenomenon in cultivated crops. Holt & Birch (1984) found that the least advanced *Vicia* species were most resistant to the aphid, *Aphis fabae* Scopoli, while plants with the highest degree of domestication and those closely related to *Vicia faba* L., and *V. faba* itself, were most susceptible. They also found that within each taxonomic group, the most domesticated species were least resistant (Holt & Birch, 1984). Thus, most cultivated crops, may have lost important genes for resistance to pests through the process of domestication.

In common wheat, resistance traits probably were lost through thousands of years of artificial selection for productivity. Nonetheless, there is a possibility of finding useful resistance to insect herbivores in some modern wheat cultivars (Dahms *et al.*, 1955; El-Bouhssini *et al.*, 1999; Lamb *et al.*, 2000), and so suspect candidate wheats identified as resistant or partly resistant should be included in aphid resistance screening programs. Evaluation of 42 accessions of *T. monococcum*, the species most often reported to contain resistance to aphids, showed that approximately half are more resistant than CWRS. A few were highly resistant to *S. avenae*. Some others were as resistant as previously identified resistant *T. monococcum* lines (Di Pietro *et al.,* 1998).

Aphid biomass and plant biomass loss on seedling plants of *T. monococcum* were positively correlated suggesting that seedling resistance was due primarily to antibiosis rather than tolerance. There was no association between seedling resistance and adult plant resistance to aphids. Furthermore, no correlation was detected between plant

biomass loss and aphid biomass gain, suggesting that adult plant resistance was primarily tolerance rather than antibiosis as observed for seedlings. Accessions which exhibited high resistance to aphids at the seedling stage were usually susceptible at the adult plant stage. This finding is important because research on host plant resistance to aphids has traditionally used seedling plants in screening programs and assumed that insect-plant interactions would be similar in the adult plant (Hsu & Robinson, 1962, 1963; Starks & Merkle, 1977; Di Pietro *et al.,* 1998; Hesler *et al.*, 1999).

Seedlings of three commercial cultivars in western Canada, each of which belongs to a different class of wheat, "Domain" (CWRS), "Foremost" (CPS) and "Medora" (CWAD) were found to be more tolerant to aphids than adult plants, i.e. a unit biomass of aphids resulted in higher plant biomass losses on adult plants than seedling plants. Therefore, in the northern parts of North America, where the adult wheat plant is the primary target of attack by cereal aphids, screening and breeding for resistance to aphids should be conducted based on performance of the adult plant. Seedling screening procedures also are considered inadequate for corn against corn leaf aphid, *R. maidis*, and field screening is preferred (Auclair, 1989).

Some research reports corroborate the findings of this study. Argadona *et al.* (1980) found young wheat plants to be more resistant than older plants to *M. dirhodhum.* On wheat and oats in the field, *S. avenae* had higher reproductive rates on the spikes than on young leaves (Watt, 1979). Using meteorological and aphid immigration data, and the numbers of natural enemies in a simulation model, Acreman & Dixon (1985) predicted the population growth of *S. avenae* on winter wheat and reported that as the wheat

developed its suitability to *S. avenae* varied, with the peak aphid population size being determined by the number of aphids at spike emergence. These changes in suitability of wheat to *S. avenae* may help explain the differences observed between laboratory and field resistance ratings (Markkula & Roukka, 1972; Dean 1973; Chapter 3 & Chapter 5 of these studies). Changes in allelochemical constituents of plants with growth stage may be the causal agents determining these interactions. Certain chemicals present in plant sap affect insect herbivores in various ways; they may be phagostimulatory, antixenotic, antibiotic or toxic (Virtanen, 1965; Beland *et al.*, 1970; Givovich & Niemeyer, 1995). Important allelochemicals commonly found in cereals are phenolic compounds (Leszczynski *et al.*, 1989).

Apparently, the observation that resistance in wheat to aphids begins as antibiosis at the seedling stage, and ends as tolerance at the adult stage is a phenomenon occurring in other pest-host situations. For example, maize seedlings are generally resistant to aphids (Villanueva & Strong, 1964). Maize seedlings contain higher levels of hydroxamic acids (phenolic compounds) than adult plants (Bing *et al.*, 1991). Long *et al.* (1977) reported a high correlation between infestation by *R. maidis* and hydroxamic acids concentration in stem tissues of corn, with mortality of *R. maidis* increasing with higher concentrations of the hydroxamic acids. Enhanced resistance to the European corn borer, *Ostrinia nubilalis* (Hübner) was attained by breeding for increased concentrations of DIMBOA (a hydroxamic acid). Despite the absence of DIBOA (another hydroxamic acid) in cultivated barley, its presence in wild barley (Barría *et al.*, 1992) is proof that these chemicals which negatively affect the performance of insect herbivores were probably

more widespread in wild plants and were probably lost through the process of domestication. So, plant resistance in the form of antibiosis in seedlings and tolerance in adult plants may be common for certain plant species and pests, and shows why resistance observed in the seedling stage cannot be used to predict resistance at adult stage and vice versa.

This study determined that individual wheat accessions with partial resistance to aphids can be found throughout the evolutionary tree of wheat, although more frequently among diploid ancestors than in more domesticated wheats. Accessions of the ancient diploid wheat, *T. monococcum*, appear to contain the most promising sources of resistance to cereal aphids because a number of researchers have identified it as a source of resistance to *S. avenae* (Sotherton & van Emden, 1982; Caillaud *et al.*, 1994; Di Pietro *et al.*, 1998). Not all accessions of *T. monococcum* show resistance, however, and some are as susceptible as *T. aestivum*. *Triticum monococcum* appears to be a particularly useful species to be included in resistance breeding programs as a source of resistance to aphids because resistant accessions have already been identified. Furthermore, its role as a direct ancestor of cultivated wheats assures that resistance genes in this species can be introgressed into commercial tetraploid and hexaploid wheats. Resistance to aphids is also reported in tetraploid progenitors of common wheat, and resistance genes in these wheats could be even more easily introgressed into cultivated wheats than those of *T. monococcum*.

The methodology of using aphid and plant biomass measurements to assess resistance to aphids in adult wheat allows more accurate discrimination of accessions

with less than complete resistance (partial resistance), which are not detectable using other types of resistance measurements such as intrinsic rate of increase (Spiller & Llewellyn, 1986), visual rating indices and aphid counts. This method is particularly suitable for aphids such as *R. padi* and *S. avenae*, which usually do not inflict visually identifiable damage on wheat.

Spike biomass more effectively estimates partial resistance than foliage biomass, either at the end of infestation or at maturity. More than five times more resistant accessions were identified using spike than foliage biomass. The spikes are convenient to handle and related to yield. Therefore, the spike appears to be a suitable experimental unit for conducting resistance studies in the field. Measuring the biomass of spikes alone and comparing the values for infested versus controls may provide a quick and adequate estimate of resistance. Plant biomass loss is easier to estimate than aphid biomass increase.

Resistance mechanisms may not always fall into the distinct theoretical categories of resistance, viz: antibiosis, antixenosis and tolerance. On one hand, antibiosis may be estimated from the accumulation of aphid biomass on plants, but the numbers that occur make the process time consuming, and may confound antibiosis and antixenosis. On the other hand, plant tolerance to aphids may be difficult to breed for, because of the many factors that cause variation in the biomass of mature plants. Nonetheless tolerance is potentially a very important component of host plant resistance.

Earlier findings (Chapter 3) suggest that cultivated wheats in western Canada should be classified as susceptible to aphids. The wheat class CPS was the most

susceptible among the classes tested. Although the low levels of resistance to aphids found in CWRS and CWAD are insufficient to avoid substantial yield losses, they are useful agriculturally because they might affect economic thresholds or the rates of insecticide applications. Sorghum hybrids, *Sorghum bicolour* (L.) Moench, resistant to *Sc. graminum* biotype C permitted the use of very low dosage rates of insecticides (Cate *et al.*, 1973). Of the three species of aphids studied, *S. avenae* is commonly the most abundant species in Manitoba, poses a constant threat to wheat production and is most likely responsible for annual crop losses.

Researchers need to develop screening and plant breeding programs to transfer useful resistance from promising sources to commercial cultivars. Use of wheat spike as the experimental unit might help speed up the screening process. Initial screening tests should involve the most resistant of the domesticated wheats. Searching for sources of resistance in *T. monococcum* should be conducted more rigorously. Crosses should be made between resistant and susceptible *T. monococcum* to study the inheritance of resistance traits. Crosses between resistant *T. monococcum* and resistant tetraploid and hexaploid wheats also are recommended. Cereal varieties resistant to aphids could be the basis of future management strategies for these important pests.

CHAPTER 7

Summary

Aphids are pests of adult wheat on the Prairies of Canada and the northern Great Plains of the USA, because they migrate into these areas in summer rather than overwintering locally. Aphids and their damage are usually cryptic and ephemeral, which limits the attention paid to them. The potential for utilization of crop resistance in the management of cereal aphids was investigated by using genetically diverse cultivated and wild wheats.

Because relatively little information is available on resistance to aphids in adult plants of spring cultivated wheat, the first step was to determine methods that might be used to investigate this resistance, and then to characterize the level of resistance or susceptibility shown by these wheats. Biomass relationships between cereal aphids and spring wheats were used to quantify total resistance and two components of resistance, antibiosis and tolerance. Seedlings were most favourable for the development and growth of *R. padi*, and exhibited a low level of antibiosis to *S. avenae* and *Sc. graminum*. Adult plants were more suitable for the development of *S. avenae* and *Sc. graminum* than *R. padi*. Tolerance levels to aphids differed among wheat classes, with seedlings being more tolerant of aphids than adult plants. Resistance to aphids in wheat seedlings was not correlated with resistance in adult plants, so seedling resistance cannot be used to predict adult plant resistance. Adult plants of the CWRS class of wheat exhibited partial

resistance, but the resistance was not sufficient to avoid economic damage.

The second step was to assess whether the low level of resistance generally observed in modern cultivated wheats can be attributed to domestication. This question was addressed by examining the levels of adult plant resistance in diverse accessions of wheats in the genus *Triticum* to reveal patterns of change in resistance in relation to the evolution of species in the genus. Resistance to aphids among genetically diverse wheat accessions was associated with domestication. The least domesticated diploid wheats showed the highest frequency and the most domesticated hexaploid wheats showed the lowest frequency of accessions exhibiting resistance. The patterns of resistance in *Triticum* were also used to reveal species in the genus which might provide the best sources of resistance. The wild wheats, *Triticum boeoticum* Bois, *Triticum monococcum* L., *Triticum tauschii* (Coss.) Schmal. and *Triticum araraticum* Jakubz. consistently exhibited high levels of resistance to aphids. Although the probability of finding wheat accessions resistant to aphids was highest among primitive wheats, individual accessions with resistance occurred at all levels within the evolutionary tree of wheat, with no clear relationships between the genomic constitution of a wheat accession and its magnitude of resistance to aphids. The potential use of wild wheats in screening and plant breeding programs for resistance to aphids is discussed.

The third step was to focus the search for resistance to aphids in adult plants on one species in the genus *Triticum*. Diverse accessions of *T. monococcum* were investigated for resistance, because this species has the simplest genome in the genus, it is the progenitor of domesticated wheats, and it is suspected of being more resistant to

aphids than modern wheats. Nearly a third of the *T. monococcum* accessions exhibited moderate levels of resistance to aphids. Three accessions had high levels of adult plant resistance and represent promising sources of resistance to *S. avenae*, the main pest of Canadian spring wheat. Results of this study stress the need for wheat researchers in Canada to begin screening for resistance to aphids and to consider retaining partially resistant phenotypes as a selection criteria.

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Appendix 7.1. Mean (± SE) biomass increase of *Sitobion avenae* on seedlings of diploid wheat, *Triticum monococcum*, and tetraploid and hexaploid wheats for six days in the laboratory in single plant cages.

ACC No.[1]	PGR code[2]	n	Mean aphid biomass increase, mg ± SE
20	1755	8	0.59 ± 0.11
41	TM 44	6	0.59 ± 0.12
17	1752	8	0.64 ± 0.10
26	1761	8	0.69 ± 0.07
42	TM 46	8	0.73 ± 0.09
10	1745	8	0.74 ± 0.15
27	1762	7	0.85 ± 0.12
32	1767	8	0.86 ± 0.11
19	1754	7	0.86 ± 0.07
18	1753	8	0.87 ± 0.13
3	1733	8	0.90 ± 0.11
29	1764	8	0.91 ± 0.16
24	1759	7	0.93 ± 0.23
23	1758	8	0.94 ± 0.10
25	1760	8	0.96 ± 0.14
34	1770	7	0.96 ± 0.13
4	1734	8	0.97 ± 0.09
16	1751	7	0.98 ± 0.19
15	1750	7	1.01 ± 0.12
13	1748	8	1.02 ± 0.16
1	1730	8	1.03 ± 0.14
21	1756	8	1.07 ± 0.11
12	1747	7	1.10 ± 0.27
22	1757	8	1.15 ± 0.15
14	1749	8	1.16 ± 0.21
36	1772	8	1.22 ± 0.09
31	1766	8	1.29 ± 0.18
28	1763	8	1.30 ± 0.13
33	1768	8	1.34 ± 0.24
37	1773	7	1.41 ± 0.17
9	1744	8	1.42 ± 0.25
38	1507	8	1.43 ± 0.16
11	1746	8	1.47 ± 0.15
35	1771	8	1.49 ± 0.18
43	DOMAIN	8	1.55 ± 0.20
39	1511	8	1.56 ± 0.19
8	1739	8	1.56 ± 0.23
40	1514	8	1.57 ± 0.24
30	1765	8	1.64 ± 0.23
5	1735	8	1.68 ± 0.19
7	1738	8	1.69 ± 0.24
45	MEDORA	8	1.77 ± 0.16
6	1737	8	1.82 ± 0.28
2	1731	7	1.84 ± 0.22
44	FOREMOST	8	2.33 ± 0.36

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.

Appendix 7.2. Mean (± SE) plant biomass loss and biomass of control plants of seedling of diploid wheat, *Triticum monococcum*, and tetraploid and hexaploid wheats after six days of infestation by *Sitobion avenae* in the laboratory in single plant cages.

CC No.	PGR code[2]	n_1	Mean plant biomass loss, mg ± SE	Mean plant biomass of controls, mg ± SE	n_2
15	1750	8	3.64 ± 1.92	58.70 ± 6.18	8
24	1759	8	4.73 ± 2.99	43.55 ± 6.60	8
9	1744	8	5.14 ± 2.75	55.08 ± 7.74	8
1	1730	8	6.04 ± 3.41	52.29 ± 5.93	8
3	1733	8	6.18 ± 2.72	48.31 ± 7.54	8
29	1764	8	7.17 ± 3.85	57.11 ± 5.14	8
19	1754	8	7.84 ± 3.89	58.31 ± 7.48	8
41	TM 44	8	7.87 ± 2.58	49.14 ± 7.95	8
42	TM 46	8	7.87 ± 3.71	60.25 ± 7.43	8
25	1760	8	8.11 ± 4.05	60.49 ± 8.75	8
11	1746	8	8.26 ± 3.29	44.61 ± 4.90	8
4	1734	8	8.37 ± 3.32	53.51 ± 6.40	9
10	1745	8	8.63 ± 3.11	55.24 ± 6.46	8
31	1766	8	8.97 ± 4.18	60.84 ± 7.12	8
32	1767	8	9.18 ± 4.60	50.73 ± 8.96	8
37	1773	8	9.18 ± 4.72	57.90 ± 6.17	8
26	1761	8	9.48 ± 4.07	59.79 ± 6.53	8
12	1747	8	9.54 ± 4.10	66.73 ± 7.04	8
28	1763	8	9.56 ± 4.26	48.15 ± 7.69	8
21	1756	8	9.60 ± 3.70	61.98 ± 7.86	8
2	1731	8	9.70 ± 4.78	54.59 ± 5.81	8
17	1752	8	10.18 ± 3.76	66.30 ± 7.02	8
36	1772	8	10.28 ± 4.65	51.58 ± 8.07	8
27	1762	8	10.62 ± 3.12	63.86 ± 7.88	8
38	1507	8	11.06 ± 5.44	63.70 ± 7.49	8
23	1758	8	11.14 ± 4.35	66.21 ± 7.44	8
7	1738	8	11.21 ± 6.00	59.29 ± 7.97	8
13	1748	8	11.24 ± 4.58	55.23 ± 6.06	8
14	1749	8	11.35 ± 4.95	66.66 ± 9.99	8
40	1514	8	11.36 ± 6.00	65.25 ± 9.21	8
18	1753	8	11.50 ± 4.36	57.04 ± 6.53	8
22	1757	8	11.64 ± 4.15	66.85 ± 9.41	8
34	1770	8	11.98 ± 5.28	53.30 ± 9.16	8
6	1737	8	12.34 ± 6.32	67.55 ± 7.33	8
33	1768	8	13.31 ± 5.12	74.34 ± 8.21	7
35	1771	8	13.73 ± 7.21	74.96 ± 9.17	8
20	1755	8	13.76 ± 4.37	79.83 ± 9.64	8
44	FOREMOST	8	14.06 ± 6.40	74.56 ± 10.73	8
16	1751	8	14.36 ± 4.47	81.46 ± 11.15	8
5	1735	8	14.52 ± 6.03	67.73 ± 7.69	8
39	1511	8	14.94 ± 7.30	78.39 ± 9.41	8
43	DOMAIN	8	15.09 ± 7.13	99.06 ± 16.30	8
30	1765	8	18.56 ± 8.79	69.34 ± 7.85	8
45	MEDORA	8	21.38 ± 7.76	71.36 ± 8.92	8
8	1739	8	22.47 ± 6.60	89.81 ± 8.00	8

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.
n_1, n_2: Number of replications for aphid infested and control plants respectively.

Appendix 7.3. Mean (± SE) biomass increase of *Sitobion avenae* after a 21 day infestation period on adult plants of diploid wheat, *Triticum monococcum*, and tetraploid and hexaploid wheats, beginning at boot stage.

ACC No.[1]	PGR code[2]	n	Mean aphid biomass increase, mg ± SE
2	1731	4	61.5 ± 17.7
29	1764	3	62.0 ± 8.5
37	1773	4	88.9 ± 11.1
3	1733	4	100.8 ± 18.7
10	1745	4	103.7 ± 34.0
13	1748	4	107.1 ± 14.5
15	1750	4	107.2 ± 46.8
4	1734	4	117.6 ± 40.7
19	1754	4	119.4 ± 47.0
7	1738	4	125.8 ± 35.6
9	1744	4	128.5 ± 35.6
17	1752	4	129.7 ± 24.2
23	1758	4	133.4 ± 21.3
40	1514	4	134.8 ± 46.2
20	1755	4	145.4 ± 67.5
1	1730	4	146.6 ± 76.2
21	1756	4	147.1 ± 39.1
44	FOREMOST	4	147.2 ± 41.2
25	1760	4	147.3 ± 49.7
38	1507	4	148.6 ± 64.1
32	1767	4	150.7 ± 53.4
34	1770	4	153.1 ± 46.9
12	1747	4	158.1 ± 59.2
31	1766	4	161.4 ± 17.7
5	1735	4	165.1 ± 13.5
43	DOMAIN	4	170.3 ± 86.5
26	1761	4	171.0 ± 123.5
18	1753	4	172.0 ± 98.1
39	1511	2	174.1 ± 9.8
33	1768	4	176.3 ± 96.9
27	1762	4	184.1 ± 94.3
6	1737	4	195.6 ± 60.7
28	1763	4	197.7 ± 101.0
35	1771	4	197.9 ± 78.9
36	1772	4	207.9 ± 78.4
14	1749	4	232.3 ± 162.1
11	1746	4	233.3 ± 89.8
30	1765	4	235.2 ± 65.7
8	1739	4	260.3 ± 66.9
16	1751	4	266.1 ± 122.7
24	1759	3	287.1 ± 94.5
22	1757	4	313.4 ± 136.4

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.

Appendix 7.4. Mean (± SE) plant biomass loss and biomass of control plants of adult plants of diploid wheat, *Triticum monococcum*, and tetraploid and hexaploid wheats after a 21 day infestation period by *Sitobion avenae* beginning at boot stage.

ACC No.[1]	PGR code[2]	n_1	Mean plant biomass loss, g ± SE	Mean plant biomass of controls, g ± SE	n_2
32	1767	4	0.00 ± 0.00	11.39 ± 7.30	2
31	1766	4	0.19 ± 0.19	15.34 ± 1.41	2
30	1765	4	0.33 ± 0.33	17.92 ± 1.56	2
9	1744	4	0.33 ± 0.20	16.79 ± 1.74	2
23	1758	4	0.78 ± 0.77	16.37 ± 5.28	2
22	1757	4	0.98 ± 0.98	19.34 ± 1.04	2
38	1507	4	1.00 ± 1.00	15.41 ± 3.32	2
29	1764	3	1.21 ± 0.80	13.12 ± 5.35	2
24	1759	3	1.21 ± 1.21	18.74 ± 1.28	2
7	1738	4	1.25 ± 1.03	21.05 -	1
17	1752	4	1.39 ± 0.24	16.56 ± 0.36	2
14	1749	4	1.93 ± 0.81	19.48 ± 5.30	2
6	1737	4	2.21 ± 1.20	19.88 ± 1.13	2
27	1762	4	2.23 ± 0.99	19.28 ± 3.27	2
39	1511	2	2.24 ± 1.63	21.56 -	1
26	1761	4	2.38 ± 1.25	14.49 ± 2.78	2
16	1751	4	2.52 ± 0.97	18.63 ± 2.00	2
1	1730	4	2.56 ± 1.17	17.15 ± 0.09	2
37	1773	4	2.66 ± 2.22	14.51 ± 1.63	2
18	1753	4	2.67 ± 0.90	18.79 ± 0.90	2
8	1739	4	2.68 ± 1.57	24.32 ± 4.07	2
19	1754	4	3.05 ± 3.05	14.02 ± 5.07	2
4	1734	4	3.63 ± 2.68	17.31 ± 1.34	2
35	1771	4	4.04 ± 1.11	24.72 ± 0.06	2
15	1750	4	4.13 ± 1.89	18.69 ± 4.74	2
10	1745	4	4.14 ± 3.26	15.55 ± 6.05	2
33	1768	4	4.15 ± 1.93	25.68 ± 3.66	2
34	1770	4	4.64 ± 1.82	23.15 ± 4.94	2
21	1756	4	4.92 ± 2.27	21.84 ± 3.86	2
41	DOMAIN	4	5.05 ± 1.69	20.30 ± 0.84	2
28	1763	4	5.19 ± 1.40	20.30 ± 0.65	2
12	1747	4	5.35 ± 2.39	22.48 ± 3.12	2
36	1772	4	5.52 ± 2.56	25.85 ± 1.28	2
11	1746	4	5.65 ± 3.20	20.77 ± 0.48	2
20	1755	4	6.10 ± 2.39	22.48 ± 3.41	2
40	1514	4	6.41 ± 2.32	19.98 ± 4.01	2
5	1735	4	6.54 ± 2.31	25.89 ± 1.08	2
3	1733	4	6.70 ± 1.33	22.47 ± 1.60	2
13	1748	4	7.92 ± 2.64	24.01 ± 1.67	2
25	1760	4	7.96 ± 0.30	23.68 ± 2.62	2
42	FOREMOST	4	10.56 ± 3.91	23.23 ± 3.36	2
2	1731	4	12.70 ± 2.84	29.07 ± 4.08	2

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.
n_1, n_2: Number of replications for aphid infested and control plants, respectively.

Appendix 7.5. Mean (± SE) foliage biomass loss and foliage biomass of control plants of adult diploid wheat, *Triticum monococcum*, and tetraploid and hexaploid wheats at maturity which were subjected to a 21 day infestation by *Sitobion avenae* beginning at boot stage in multiple plant cages.

ACC No.[1]	PGR code[2]	n_1	Mean foliage biomass loss, g ± SE	Mean foliage biomass of controls, g ± SE	n_2
7	1738	3	0.00 ± 0.00	10.21 ± 3.48	2
39	1511	5	0.00 ± 0.00	5.09 ± 1.98	2
10	1745	5	0.80 ± 0.44	12.18 ± 3.92	2
31	1766	4	0.92 ± 0.92	9.82 ± 2.88	3
30	1765	4	1.12 ± 1.12	5.58 ± 2.76	2
33	1768	5	1.25 ± 1.07	7.16 ± 5.61	3
9	1744	4	1.32 ± 0.99	14.47 ± 5.41	3
34	1770	4	1.68 ± 1.34	13.04 ± 3.26	3
8	1739	5	1.87 ± 1.18	15.28 ± 3.27	3
1	1730	4	2.11 ± 1.22	11.90 ± 1.95	3
29	1764	5	2.11 ± 0.84	7.91 ± 2.08	3
6	1737	4	2.37 ± 2.34	11.33 ± 3.23	3
15	1750	5	2.38 ± 1.15	11.00 ± 1.52	3
11	1746	5	2.40 ± 1.31	12.23 ± 3.06	3
2	1731	5	2.46 ± 1.76	15.94 ± 7.19	3
28	1763	5	2.56 ± 1.12	7.17 ± 2.31	3
21	1756	5	2.94 ± 1.26	13.87 ± 2.32	3
23	1758	5	2.95 ± 0.92	9.55 ± 1.63	3
14	1749	5	3.06 ± 1.61	16.44 ± 3.36	3
25	1760	4	3.20 ± 1.59	14.71 ± 3.72	3
3	1733	5	3.22 ± 1.57	12.57 ± 4.81	3
19	1754	5	3.49 ± 2.43	14.88 ± 8.75	3
5	1735	5	3.91 ± 1.72	12.42 ± 6.92	3
24	1759	5	3.92 ± 1.25	13.99 ± 7.15	3
38	1507	5	4.05 ± 1.53	11.04 ± 2.54	3
43	DOMAIN	5	4.83 ± 0.68	10.44 ± 4.83	3
18	1753	5	4.89 ± 1.73	14.03 ± 7.64	3
27	1762	4	5.83 ± 3.21	15.39 ± 3.82	3
44	FOREMOST	5	5.86 ± 1.65	17.55 ± 4.78	3
17	1752	4	6.15 ± 1.45	16.12 ± 6.36	3
35	1771	5	6.59 ± 2.08	18.13 ± 5.37	3
20	1755	5	7.11 ± 2.23	18.76 ± 5.75	3
40	1514	5	7.34 ± 1.86	18.23 ± 3.54	2
13	1748	5	8.25 ± 1.84	22.27 ± 8.04	3
36	1772	5	8.79 ± 3.25	19.77 ± 6.21	2
22	1757	5	8.86 ± 2.81	19.12 ± 5.84	3
16	1751	5	9.13 ± 2.08	16.95 ± 2.37	3
4	1734	5	9.51 ± 2.48	21.56 ± 7.80	3
37	1773	5	9.92 ± 3.36	21.97 ± 11.39	3
32	1767	5	10.93 ± 2.84	18.33 ± 9.23	2
12	1747	5	12.19 ± 2.40	21.79 ± 12.64	2
26	1761	5	12.77 ± 3.32	25.76 ± 10.73	2

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.
n_1, n_2: Number of replications for aphid infested and control plants, respectively.

Appendix 7.6. Mean spike biomass loss and spike biomass of control plants of adult diploid wheat, *Triticum monococcum*, and tetraploid and hexaploid wheats at maturity which were subjected to a 21 day infestation by *Sitobion avenae* beginning at boot stage.

ACC No.[1]	PGR code[2]	n_1	Mean spike biomass loss, g ± SE	Mean spike biomass of controls, g ± SE	n_2
39	1511	5	1.43 ± 0.88	4.33 ± 1.26	2
1	1730	4	1.60 ± 0.95	10.35 ± 1.50	3
30	1765	4	1.85 ± 1.36	5.96 ± 3.65	2
31	1766	4	2.17 ± 1.27	9.24 ± 3.33	3
33	1768	5	2.24 ± 1.37	6.96 ± 5.58	3
15	1750	5	3.15 ± 1.42	10.51 ± 1.76	3
8	1739	5	3.27 ± 2.04	11.74 ± 5.69	3
9	1744	4	3.32 ± 2.03	13.91 ± 5.71	3
10	1745	5	3.74 ± 1.11	13.35 ± 4.31	2
3	1733	5	3.80 ± 2.04	10.56 ± 4.42	3
28	1763	5	3.86 ± 1.31	6.79 ± 1.88	3
7	1738	3	4.43 ± 2.56	11.97 ± 5.99	2
21	1756	5	4.52 ± 2.25	14.28 ± 2.13	3
6	1737	4	5.03 ± 2.23	11.92 ± 3.44	3
11	1746	5	5.35 ± 2.35	12.97 ± 3.37	3
29	1764	5	5.72 ± 0.87	8.71 ± 2.08	3
23	1758	5	5.72 ± 1.34	10.20 ± 1.65	3
25	1760	4	5.76 ± 2.09	13.96 ± 4.48	3
14	1749	5	5.87 ± 2.63	17.45 ± 5.64	3
24	1759	5	6.17 ± 1.25	14.05 ± 7.84	3
34	1770	4	6.36 ± 3.10	13.47 ± 3.87	3
38	1507	5	6.38 ± 1.73	10.79 ± 3.62	3
27	1762	4	6.77 ± 2.57	14.47 ± 3.53	3
18	1753	5	7.01 ± 2.16	15.24 ± 8.89	3
19	1754	5	7.02 ± 2.34	15.39 ± 9.48	3
2	1731	5	8.14 ± 2.59	17.09 ± 7.81	3
5	1735	5	8.47 ± 2.20	14.69 ± 8.29	3
16	1751	5	9.85 ± 0.85	14.23 ± 1.54	3
20	1755	5	9.87 ± 2.99	18.55 ± 5.31	3
43	DOMAIN	5	9.97 ± 0.74	13.58 ± 6.02	3
40	1514	5	11.14 ± 2.47	20.31 ± 5.69	2
4	1734	5	11.30 ± 3.28	21.03 ± 6.58	3
35	1771	5	11.78 ± 3.13	19.94 ± 5.46	3
22	1757	5	12.15 ± 2.74	20.77 ± 6.63	3
37	1773	5	12.48 ± 4.13	22.94 ± 12.09	3
17	1752	4	13.17 ± 3.81	20.26 ± 8.98	3
12	1747	5	13.27 ± 2.47	20.53 ± 12.13	2
13	1748	5	13.61 ± 3.93	24.93 ± 9.86	3
26	1761	5	14.96 ± 3.53	25.85 ± 12.18	2
36	1772	5	16.18 ± 3.32	24.00 ± 7.72	2
44	FOREMOST	5	16.54 ± 4.47	26.26 ± 8.41	3
32	1767	5	19.81 ± 4.04	27.40 ± 2.28	2

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.

n_1, n_2: Number of replications for aphid infested and control plants, respectively.

Appendix 7.7. Mean foliage biomass loss and spike biomass of control plants of a random selection of 12 diploid wheats, *Triticum monococcum*, at maturity, which were subjected to a 21 day infestation by *Sitobion avenae* beginning at boot stage.

ACC No.[1]	PGR code[2]	n_1	Mean foliage biomass loss, g ± SE	Mean spike biomass of controls, g ± SE	n_2
41	TM 44	5	0.00 ± 0.00	12.57 ± 1.10	3
36	1772	5	0.00 ± 0.00	14.69 ± 3.89	3
39	1511	5	0.41 ± 0.41	17.90 ± 1.47	3
9	1744	5	1.56 ± 0.94	19.35 ± 3.35	3
13	1748	5	1.58 ± 0.97	20.31 ± 1.89	3
34	1770	5	1.71 ± 1.06	20.53 ± 4.91	3
31	1766	5	1.85 ± 0.98	24.19 ± 5.65	3
42	TM 46	5	2.71 ± 0.96	25.29 ± 6.47	3
21	1756	5	3.50 ± 2.16	26.79 ± 5.02	3
6	1737	5	3.82 ± 1.66	27.86 ± 5.51	3
18	1753	5	5.47 ± 1.85	29.58 ± 3.73	3
26	1761	5	8.19 ± 3.50	39.61 ± 5.44	3

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.
n_1, n_2: Number of replications for aphid infested and control plants, respectively.

Appendix 7.8. Mean spike biomass loss and spike biomass of control plants of a random selection of 12 diploid wheats, *Triticum monococcum*, at maturity, which were subjected to a 21 day infestation by *Sitobion avenae* beginning at boot stage.

ACC No.[1]	PGR code[2]	n_1	Mean spike biomass loss, g ± SE	Mean spike biomass of controls, g ± SE	n_2
41	TM 44	5	0.66 ± 0.65	12.10 ± 3.38	3
39	1511	5	0.67 ± 0.67	9.57 ± 0.49	3
13	1748	5	0.86 ± 0.60	15.97 ± 1.30	3
9	1744	5	1.21 ± 1.01	17.29 ± 4.76	3
36	1772	5	1.39 ± 1.39	13.91 ± 1.88	3
18	1753	5	1.92 ± 1.27	17.81 ± 3.87	3
6	1737	5	2.91 ± 1.67	18.25 ± 2.31	3
42	TM 46	5	3.66 ± 1.09	13.35 ± 3.66	3
34	1770	5	3.90 ± 1.19	26.72 ± 3.68	3
31	1766	5	4.07 ± 1.12	14.02 ± 1.16	3
21	1756	5	4.31 ± 2.19	22.92 ± 5.71	3
26	1761	5	5.15 ± 1.25	23.86 ± 4.36	3

[1]ACC = Accession; [2]PGR = Plant gene resources identifier.
n_1, n_2: Number of replications for aphid infested and control plants, respectively.