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THESIS


December 4, 2009

RUSSIAN WHEAT APHID, *Diuraphis noxia* (Kurdjumov), ECOLOGY AND
REPRODUCTION ON FIVE NONCULTIVATED GRASS HOSTS IN HIGH
ELEVATION ENVIRONMENTS
ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

Submitted by

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In partial fulfillment of the requirements

For the Degree of Master of Science


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Spring 2010

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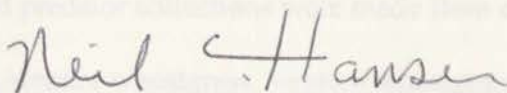
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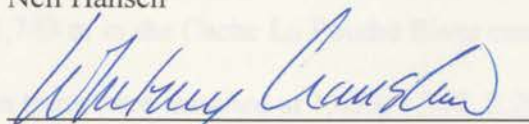
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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY SHERRI F. PUCHERELLI ENTITLED, RUSSIAN WHEAT APHID, *Diuraphis noxia* (Kurdjumov), ECOLOGY AND REPRODUCTION ON FIVE NONCULTIVATED GRASS HOSTS IN HIGH ELEVATION ENVIRONMENTS, BE ACCEPTED AS FULFILLING IN PART REQUIEREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

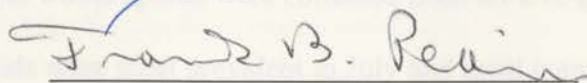
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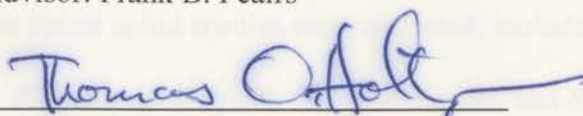
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ABSTRACT OF THESIS

RUSSIAN WHEAT APHID, *Diuraphis noxia* (Kurdjumov), ECOLOGY AND REPRODUCTION ON FIVE NONCULTIVATED GRASS HOSTS IN HIGH ELEVATION ENVIRONMENTS

Russian wheat aphid ecology, occurrence, movement, and reproduction on five noncultivated grass hosts was examined in high elevation environments. The objectives of the first study were to: 1) identify Russian wheat aphid occurrence and abundance on five common grass hosts at elevations between 1,829- 2,743 m during June-October; 2) monitor Russian wheat aphid movement and flight patterns between 1,524- 2,743 m, with the use of suction traps; 3) describe the predator and competitor assemblages encountered by the Russian wheat aphid in high elevation environments; and 4) confirm Russian wheat aphid holocycly in North America by collecting sexual forms and eggs.

Weekly aphid and predator collections were made from crested wheatgrass, intermediate wheatgrass, slender wheatgrass, western wheatgrass, and foxtail barley at 23 sites, between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado. Four suction traps were installed at 1,655, 1,992, 2,206, and 2,372 m to collect alate aphids. Russian wheat aphids were collected from all five grass hosts sampled. Russian wheat aphids were most prevalent in July and most commonly collected from crested wheatgrass. Other cereal aphid species were collected, including *Diuraphis frequens*, *Sipha elegans*, *Rhopalosiphum padi*, *Sitobion avenae*, and *Schizaphis graminum*. *Sipha elegans* was the most abundant aphid collected.

The most Russian wheat aphids were collected in June in the trap at 1,655 m, coinciding with peak captures in nearby wheat production. Trap captures declined with increasing elevation. Russian wheat aphid populations in the Cache La Poudre canyon are likely maintained by both immigrant aphids and from local metapopulations within the canyon. Environmental conditions in high elevation environments could prompt the production of novel biotypes.

The second study determined Russian wheat aphid biotype RWA2 reproductive and development rates on the same five noncultivated grass hosts to gain information about host quality, potential refuges and sources of selection pressure. Russian wheat aphid reproductive and development rates were measured at 18-24°C, on the five grass hosts sampled in the first study, and at 24-29°C, and 13-18°C on intermediate and crested wheatgrass.

The intrinsic rates of increase for all five hosts were lower than those reported for susceptible and resistant wheats. Aphids feeding on crested and intermediate wheatgrass at the 13-18°C temperature had lower fecundity, fewer nymph production days, longer generational times, and lower intrinsic rate of increase than aphids feeding at the 18-24°C temperature regime. Poor hosts pose greater selection pressures. The five noncultivated hosts tested were poor hosts in comparison to wheat, and their greater selection pressure might promote Russian wheat aphid genetic variability.

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Spring 2010

ACKNOWLEDGEMENTS

I would like to thank my advisor, Frank Peairs, for providing me the opportunity to complete my masters degree, and for guiding me through the research and writing process. Thanks also to Whitney Cranshaw and Neil Hansen for serving on my committee and providing valuable input to this research.

Thank you to my Insectary friends, Terri, Laurie, Scott, and Jeff. All of whom were always there to tech me, and provide advice. I would also like to thank Sam Thomason, Lucas Rael, Anthony Longo-Peairs, Marie Stiles, Tyler Keck, and Dylan Walker for helping me with field work. I was lucky to meet Pam Woodward, Cathy Revis, and Greg Venette, who were enthusiastic about my research and allowed me to install unsightly suction traps on their private property. A special thank you to Bill Goettlicher, with the U.S. Department of the Interior, Bureau of Reclamation, for being a great friend and helping me learn to make maps!

I would have not survived without the support and guidance of my family and boyfriend, Alex Stephens. Without them my life would have been nothing but graduate school!

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LITERATURE REVIEW

Diuraphis noxia (Kurdjumov) (Hemiptera: Aphididae), commonly known as the Russian wheat aphid, has a small, 1.3-2.55 mm convex, elongate, and spindle shaped body, which is yellow-green or gray-green and covered with wax (Stoetzel 1987, Walters et al. 1984). It has six segmented antennae, which are less than half the length of the body. Their siphunculi (cornicles) are short and as long as they are wide, while the supracaudal process is about half the length of the cauda (Walters et al. 1984). The Russian wheat aphid completes five instars from birth to maturity (Aalbersberg et al. 1987b). Mature aphids are polymorphic with winged (alate) and wingless (apterous) forms.

The Russian wheat aphid is a significant crop pest. Feeding and damage occurs when the aphid injects saliva and siphons phloem contents from the plant. Aphid feeding also prevents leaves from unrolling, which provides protection from insecticides and natural enemies. Infested leaves have long purple, white, and yellowish streaks. Best control of Russian wheat aphid results from an integrated pest management approach utilizing resistant cultivars, insecticides, and cultural control (Peairs 1998). The Russian wheat aphid has been extensively studied and literature was compiled and presented as a response model for the pest published by Quisenberry and Peairs (1998). This literature review will focus on Russian wheat aphid use of and movement to alternative hosts, modes of reproduction, sources of selection pressure, and natural enemies. Focusing on

these aspects of the Russian wheat aphid's life history in areas of agronomic production can be applied in understanding the aphid's biology in high elevation environments.

World Wide Importance, Spread, and Distribution

The Russian wheat aphid is a small grains pest of worldwide economic importance and is considered one of the most economically damaging pests of wheat, *Triticum aestivum* L., worldwide. Without management, this pest is capable of devastating dryland wheat and barley, *Hordium vulgare* L., production. In Moldova and southern Ukraine cereal harvests were reduced by 75% in 1912 (Halbert and Stoetzel 1998). In the first twelve years of Russian wheat aphid occurrence in the United States one hundred and two million bushels of wheat and barley crops were lost (Souza 1998). Accordingly, the United States cereal industry lost \$893.1 million dollars due to reduced production and increased costs (Morrison and Peairs 1998).

The Russian wheat aphid is indigenous to southern Russia, central Asia, Iran, Afghanistan, and countries bordering the Mediterranean Sea (Blackman and Eastop 1984, Kiriac et al. 1990, Walters et al. 1984). It was recognized as an important pest to small grain production in the early 1900s with outbreaks in Moldova and Ukraine (Poprawski et al. 1992, Miller et al. 2005). The pest's range expanded in the latter part of the twentieth century to include grain producing areas of Europe such as Hungary and the Czech Republic (Stary 1999, Stary et al. 2003). Populations were detected in 1978 in South Africa (Walters et al. 1984), 1980 in Mexico (Gilchrist et al. 1984, Stoetzel 1987), Chile in 1988, and Argentina in 1992 (Ortego and Delfino 1994).

Russian wheat aphid populations spread from Mexico to the United States through prevailing wind currents (Stoetzel 1987). The aphid was first identified near

Muleshoe, Texas in 1986, and crop damage was widespread by 1987 (Morrison and Peairs 1998). The aphid has spread rapidly throughout the western United States and into three Canadian provinces. In North America it can be found in 17 states including Arizona, California, Colorado, Idaho, Kansas, Montana, Nebraska, Nevada, New Mexico, North Dakota, Oklahoma, Oregon, South Dakota, Texas, Utah, Washington, and Wyoming (Elliott et al. 1998).

Host Plant Cycle

While the Russian wheat aphid is polyphagous, its preferred host plants are wheat, barley, and triticale, *Triticale hexaploide* Lart. (Webster et al. 1987). The aphid will also colonize other cereal grains such as rye (*Secale cereale*), oat (*Avena sativa*), and non-cultivated cool season grasses (Burd et al. 1998, Peairs 1998). In North America the Russian wheat aphid colonizes newly emerged grains in October and early November. Viviparous females overwinter on the crop, causing the most damage in the spring (Peairs 1998). Russian wheat aphid is one of the more cold-hardy aphid pests, as they can survive freezing temperatures in the nymph and adult stages (Harvey and Martin 1988).

When host plants are stressed and unfavorable, alate forms are produced (Walters et al. 1984). When winter grains are harvested in the summer the aphid moves to later maturing winter wheat, spring grains, and non-cultivated hosts. The Russian wheat aphid will oversummer on the non-cultivated hosts and return to fall crops (Burd et al. 1998, Peairs 1998).

Alternate Hosts

Since the Russian wheat aphid reproduces parthenogenetically in North America adults must survive year round on green plants. The Russian wheat aphid requires

alternate hosts between the harvest of the spring/summer crop and emergence of the fall crop, called the overwintering period. The aphid's economic impact is partially dependent upon its ability to utilize several hosts for overwintering in order to be present in the fall when the new wheat crop emerges (Kindler and Hays 1999). Alternate hosts, such as cool season perennial wheatgrasses (Poacea: Triticeae), contribute to successful overwintering (Donahue et al. 2000). One hundred and forty grass species in forty genera have been documented as potential hosts for the Russian wheat aphid, but most appear to be poor in comparison to wheat and barley (Kindler and Springer 1989, Pike et al. 1991). Many grasses the aphid utilizes are abundant as they are planted in the Conservation Reserve Program (Armstrong et al. 1991).

In South Africa, Russian wheat aphid overwinters on rescue grass (*Bromus willdenowii*, Kunth) and *Agrotriticum* surrounding wheat fields (Walters et al. 1984). In an Oklahoma greenhouse study, Russian wheat aphid survived on 47 of 48 cool season grasses, 18 of 32 warm season grasses, and no legumes or forbs. Of the grasses tested, the aphid survived best on jointed goatgrass (*Aegilops cylindrica* L.), barley, European dunegrass (*Elymus arenarius* L.) and little barley (*Hordeum pusillum* Nutt.) (Kindler and Springer 1989).

Many of the grass species Russian wheat aphid utilizes are subject to grazing. Messina et al. (1993) studied how grazing affects host suitability of rangeland grasses. Defoliation increased plant nitrogen and water content, making grasses more nutritious to the Russian wheat aphid. Thus spring grazing did not control insect populations.

In a field survey of twenty five grass species in northeastern Colorado, aphids were found on a wider range of hosts in the early summer in comparison to the later

summer months when grasses began to senesce. Crested wheatgrass (*Agropyron cristatum*, (L.) Gaertn) and Canada wildrye (*Elymus canadensis* L.) were considered the best hosts (Armstrong et al. 1991). Weiland et al. (2008) sampled non-cultivated grass hosts in Colorado during the fall and spring. Russian wheat aphids were collected from crested wheatgrass, downy brome (*Bromus tectorum* L.), volunteer wheat, Canada wildrye and intermediate wheatgrass (*Elytrigia intermedia*, (Host) Nevski)) at most locations. Aphids were found less frequently on bottlebrush squirreltail (*Elymus multisetus*, M.E. Jones), green foxtail (*Setaria viridis*, (L.) Beauv), smooth brome (*Bromus inermis*, Leyss), and barnyard grass (*Echinochloa crusgalli*, (L.) Beauv).

Wheatgrass as an Alternate Host

Several genera of Triticeae (the wheatgrass tribe) are known to be common perennial hosts of the Russian wheat aphid. In general, *Hordeum* and *Thinopyrum* are susceptible, *Agropyron*, *Elymus*, *Pseudorogneria*, and *Pascopyrum* are moderately susceptible, and *Leymus* and *Elytrigia* are moderately resistant (Kindler et al. 1993). Wheatgrasses are commonly planted in Department of Agriculture land conservation programs. Crested wheatgrass, in particular, may be an important host for the Russian wheat aphid, as it is growing on 12.4 million acres in the western United States, including several million acres of idled cropland in the Conservation Reserve Program (Rogler and Lorenz 1983).

The fecundity and survival of the Russian wheat aphid was studied on twenty five perennial grass species in Idaho over two years of growth. During both years, wheatgrasses were found to be the best alternative hosts, and plant age did not affect Russian wheat aphid population growth (Mowry et al. 1995). Similarly, in a Colorado

survey done by Hammon et al. (1997), wheatgrasses and wildryes were the most common and suitable hosts for the Russian wheat aphid.

While wheatgrasses appear to be suitable hosts for the Russian wheat aphid, factors such as plant age and condition may influence suitability for overwintering. Aphid populations were monitored in Wyoming on intermediate, slender (*Elymus trachycaulus*, (Link) Gould ex Shinners), thickspike (*Elymus lanceolatus*, Scribn. and J.G. Sm.) Gould), and crested wheatgrasses during the first and fifth year of growth. Species and age did affect aphid abundance on wheatgrass. Overall, crested wheatgrass supported the most aphids with more found on fifth year growth. Intermediate wheatgrass supported more aphids during first year growth (Brewer and Noma 2002). To the contrary, Brewer et al. (2000) found crested wheatgrass sustained the greatest aphid densities during the first year of growth, but after vernalization aphid densities were similar on all non-cultivated hosts tested (crested, intermediate, thickspike, slender, and bluebunch wheatgrasses (*Agropyron spicatum*, (Pursh.) Scribn. and J.G. Sm.), smooth brome, spring barley, mammoth, and Russian wildrye (*Psathyrostachys junceus* (Fischer) Nevski).

Determination of Suitable Hosts

It is still unclear which cool season grass species are suitable hosts for the Russian wheat aphid, and whether large differences in suitability exist among species (Donahue et al. 2000). In order to determine which alternative hosts are most suitable, it is useful to calculate growth rate parameters, such as the intrinsic rate of increase. The intrinsic rate of increase is the rate of increase, under specified physical conditions in an unlimited environment, where the effects of increasing density are not considered (Birch 1948). The

calculation is composed of factors which contribute to population growth, including net reproductive rate, immature development rates, and generation time.

Calculating aphid life statistics and intrinsic rate of increase on a plant is difficult and time consuming because the environment must remain static and a single aphid needs to be evaluated for the duration of her life. Typically, several aphids are caged on the plant of interest until they give birth. The newly born aphid becomes the aphid of interest and is monitored every twenty four hours to count and remove all progeny. Removing the newly born aphids provides an unlimited environment (Hawley et al. 2003).

Intrinsic rate of increase calculations are useful in determining host quality because they can quantify the aphid's reproductive potential on a host. Typically, selection pressure increases with decreasing host quality, so determining poor hosts can help assess potential refuges and sources of selection pressure (Merrill et al. 2008). Furthermore, changes in an aphid's intrinsic rate of increase could result in expanded geographic range, or altered distribution (Randolph et al. 2008). Aphid rates of increase on alternative hosts can be compared to those on the aphid's preferred hosts. Values reported for susceptible wheat are 0.31 (Merrill et al. 2008), 0.29 (Hawley et al. 2003), and 0.28 (Randolph et al. 2008). Values for resistant wheat are 0.21 (Merrill et al. 2008), 0.23 (Hawley et al. 2003), and 0.27 (Randolph et al. 2008). Several other studies have been done to test Russian wheat aphid reproduction and development under different environmental conditions and plant growth stages (Webster et al. 1987, Aalbersberg et al. 1987a, Michels and Behle 1988, 1989, Kieckhefer and Elliott 1989, Girma et al. 1990, Behle and Michels 1990, Schotzko and Smith 1991, Webster et al. 1993,

Nowierski et al. 1995, Butts and Schaalje 1997, Haile et al. 1999, Miller et al. 2003, Michaud et al. 2006).

Intrinsic rate of increase is influenced by plant growth stage and quality, temperature, moisture, aphid biotype, and feeding site. All factors must remain constant to determine the most accurate intrinsic rate of increase (Girma et al. 1990).

Reproduction and development values are also variable because of different calculation methods. Several methods have been developed to calculate the intrinsic rate of increase; most are derived from methods set out by Birch (1948). The Birch (1948) method is time consuming and requires complicated calculations, but is thought to be accurate. Since Birch, others such as Howe (1953) and Laughlin (1965) have tried to simplify this method (Wyatt and White 1977). An approach devised by Wyatt and White (1977), simplifies the process and calculation, but only follows part of the aphid's reproductive life. This approach works well for aphids that produce offspring constantly over their lifespan and less well for aphids with reproduction skewed towards early adulthood. It is still unknown if the different approaches provide comparable outcomes.

Physiological and biochemical changes occur within a plant as it matures, and these changes may also affect the aphid's development and reproduction. Fecundity may vary with leaf age, plant part, and growth stage of the plant attacked (Havlickova 1987). The effects of plant growth stage and temperature did significantly affect the Russian wheat aphid reproductive life span and production of nymphs per female in a study done by Girma et al. (1990). The highest intrinsic rate of increase was recorded at 18-21°C during the jointing stage of wheat. As ambient temperature and plant age increased, the aphid's reproductive lifespan and developmental time decreased. Furthermore, aphid

mortality rate accelerated as temperature and plant age increased, a trend also described by Michels and Behle (1988). During the coldest temperature regime (10-13°C) aphids reproduced for a significantly longer period of time.

Evaluation of reproductive potential is also affected by preconditioning. Preconditioning is defined as the abiotic and biotic conditions that experimental subjects experience before experimentation (Schotzko and Smith 1991). They preconditioned Russian wheat aphids on wheat and oat, and found that the host on which the first generation developed influenced the population development in the second generation. Aphids reared on oat produced significantly fewer adults and nymphs than those reared on wheat. Aphids reared on wheat, rather than oat, produced more nymphs after transfer to oat or wheat.

Vernalization, preconditioning, and plant age affected Russian wheat aphid increase on six alternate hosts in Wyoming (Donahue et al. 2000). Aphids preconditioned on wheat increased more quickly than those preconditioned on grasses (crested, thickspike, slender, and intermediate wheatgrasses, and mammoth and Russian wildrye). These effects persisted into later generations. When plants were vernalized, nymph counts were significantly higher than those on un-vernalized plants. Aphid counts on un-vernalized crested wheatgrass were not different than counts on vernalized plants.

Randolph et al. (2008) compared the reproductive rates of Russian wheat aphid biotypes RWA1 and RWA2 at three temperature regimes on resistant and susceptible wheat. For both biotypes the intrinsic rate of increase was higher at the 18-24°C and 24-29°C regimes than at the 13-18°C regime. Overall, RWA2 had a higher intrinsic rate of

increase and fecundity than RWA1, and this difference was greater at the lowest temperature regime of 13-18°C.

There are few reports of Russian wheat aphid intrinsic rate of increase on grass hosts. These may support reproduction and development, but over time act as population sinks (Merrill et al. 2008). Non-cultivated grasses may provide selective pressures and resistance by means of antibiosis or antixenosis. Antixenosis is expressed differently in plants with variation in leaf trichome size, leaf epicuticular structure, or tiller density. For example, western wheatgrass (*Pascopyrum smithi*, (Rydb.) A. Löve) and intermediate wheatgrass have strongly ribbed leaves covered with a waxy powder. Grasses with reddish colored leaves, such as crested and slender wheatgrass, may be antixenotic during host selection process (Ni and Quisenberry 1997).

To gain insight into selection pressures exerted by alternative hosts, Merrill et al. (2008) compared Russian wheat aphid development and reproduction rates on crested wheatgrass, intermediate wheatgrass, susceptible wheat, and resistant wheat. The Russian wheat aphid had a positive intrinsic rate of increase on all four hosts tested, indicating all would support the aphid. As expected, highest fecundity (58.5 nymphs), longevity (54.7 days), and intrinsic rate of increase (0.311) were expressed on susceptible wheat. Aphids on intermediate wheatgrass had the lowest intrinsic rate of increase (0.133), suggesting the aphids encountered greatest selective pressure on this host.

Russian Wheat Aphid Biotypes

An insect biotype is a population of insects that are able to damage host plants that were previously resistant to that specific insect species (Puterka et al. 1988). Russian wheat aphid have been monitored for biotypic diversity, because new biotypes can

potentially disrupt the progress of plant breeding programs that have developed resistance. Biotypes are determined by exposing aphid populations to plant differentials (wheat, rye, and barley cultivars). Aphids that are avirulent to specific cultivars will not damage those plants. New biotypes are described when previously resistant plants become susceptible.

To better understand world wide biotypic diversity eight Russian wheat aphid isolates from Jordan, Syria, Turkey, France, USSR, and the United States were screened on plant differentials. Seven of the eight isolates had unique biotype profiles. Two unique biotypes were discovered in the USSR and France, locations where the Russian wheat aphid has been long established. This finding suggested Russian wheat aphid biotypes could develop over time (Puterka et al. 1992).

In North America only one Russian wheat aphid biotype was described until the spring of 2003 when a new biotype was discovered in southeastern Colorado (Haley et al. 2004). Russian wheat aphids were observed causing damage to Dn4 resistant winter wheat cultivar Prairie Red. Wheat cultivars with the Dn4 gene are resistant to RWA1 and will not show symptoms. The same plants with the Dn4 gene are susceptible to RWA2 and do show feeding symptoms. The southeastern Colorado population was virulent to all plants containing the Dn4 and Dny resistance genes, confirming the presence in Colorado of the biotype now referred to as RWA2.

Several other North American biotypes have since been described. Burd et al. (2006) surveyed Kansas, Nebraska, Texas, and Wyoming for Russian wheat aphid biotypic diversity. They described three new Russian wheat aphid biotypes (RWA3, RWA4, and RWA5) from cultivated wheat and barley. An isolate from Montezuma

County, CO had a unique virulence profile and was designated as RWA6. Biotype RWA7 was collected from Canada wildrye and intermediate wheatgrass and RWA8 from crested wheatgrass and smooth brome (Weiland et al. 2008).

Mechanism behind Biotype Development

There may be multiple mechanisms for genetic recombination during parthenogenesis (Dixon 1985). Aphid parthenogenesis is apomictic and can facilitate mutation. Aphids have holocentric chromosomes, with no localized centromeres so centromeric activity is spread along the entire length of the chromosome. Holocentric chromosomes can fragment along their lengths to easily create chromosomal rearrangement. Asexual aphids also commonly generate variation through non-random mutation that creates variation visible to selection (Wilson et al. 2003).

An alternative hypothesis for Russian wheat aphid biotypic diversity in North America involves evolution resulting from sexual selection resulting from holocycly. Support for this hypothesis comes from the discovery of oviparae in North America (Kiriak et al. 1990). Biotype diversity could also result from selective pressures exerted by resistant cultivars (Merrill et al. 2008). Porter et al. (1997) studied greenbug, *Schizaphis graminum* (Rondani), biotype development and suggested that non-cultivated grass hosts could be a reservoir for aphid biotypes. Since this theory was suggested several unique greenbug biotypes have been found on non-cultivated hosts (Anstead et al. 2003, Burd and Porter 2006). Similarly, Weiland et al. (2008) found two new Russian wheat aphid biotypes on noncultivated grasses.

Reproduction and Sexual Morphology

The Russian wheat aphid is capable of sexual reproduction and parthenogenesis. Parthenogenesis is the main mode of reproduction, and allows exponential population growth. Russian wheat aphid is holocyclic in its native range where several generations are parthenogenetic, and in autumn, a sexual generation occurs consisting of males and oviparae. Sexual morphs produce hardy overwintering eggs in response to environmental conditions such as short day length and low temperatures (Burd et al. 1998). Males and eggs have not yet been documented in South Africa and North America so aphids are thought to be anholocyclic, reproducing through year round parthenogenesis and surviving the winter as viviparous females (Burd et al. 1998, Halbert and Stoetzel 1998). Overwintering anholocyclic populations are typically responsible for earlier and larger population increases in comparison to spring migrants, but hard winters could result in late release or localized extinction (Harvey and Martin 1988). Furthermore, anholocyclic populations do not receive the evolutionary benefits that sexual genetic mixing provides.

Male aphids can be alate or apterous, and are distinguished by a sclerotized genital structure. Males have smaller and uniquely sclerotized abdomens, longer antenna, and shorter cauda than females. Oviparous females are differentiated from viviparous females by swollen hind tibia, more numerous setae on the genital plate, and shorter antenna, legs, siphunculi, and cauda (Miyazaki 1987). No key has been published specifically for Russian wheat aphid sexuales.

A survey of Russian wheat aphid morphs was conducted in North America and Soviet Union by Kiriac et al. (1990). The Russian wheat aphid is largely holocyclic in the Soviet Union, and oviparae were found to constitute more than half of the Moldavian and Crimean collections, and about nine percent of the collections from Odessa and

Kherson Ukraine. Males were collected only from the Crimean peninsula. While there were no previous reports of sexual morphs in North America, six oviparae were found in Treasure Valley and the Palouse in Idaho and Oregon.

According to Kiriac et al. (1990), the winter in the Pacific Northwest, previous to these collections, was unusually harsh. Such conditions could have created a heavy selective advantage for holocyclic populations, thus making oviparae detectable in sampling. Sexual morphs represented less than one percent of the total collections in North America. Given the rarity of males in their native Soviet Union range they may have been overlooked in North America. Conversely, some populations of *Myzus persicae* (Sulzer) occasionally produce males, but never oviparae, and these populations are called androcyclic (Blackman 1974). Thus, some North American Russian wheat aphid populations could be gynocyclic, occasionally producing oviparae but never males (Kiriac et al. 1990).

Sexual morphs of three other *Diuraphis* species, *D. nodulus* (Richards), *D. tritici* (Gillette), and *D. frequens* (Walker), have been collected in North America (Stoetzel 1992). *Diuraphis tritici* was first described on Colorado blue-stem in Fort Collins Colorado, and was thought to be a major pest to wheat in Montana (Gillette 1911). Males and oviparae first appeared in October and egg laying continued to December. Sexual forms of both *D. nodulus* and *D. tritici* were collected on mountain brome (*Bromus marginatus*) in Meeker Colorado. These are the only recorded *D. nodulus* sexual and egg collections. There has been only one *D. frequens* male discovered in the United States, which was identified in February 1990 in a laboratory colony originally collected in Idaho (Stoetzel 1992).

Investment in sexual reproduction may be maintained by harsh winter conditions at high altitudes, or heterogeneous environments (Frantz et al. 2006). Sexual morphs of Aphididae typically occur in the fall when temperatures decrease, indicating the need to produce hardy eggs for winter survival. In general, holocyclic lineages occupy higher latitudes while anholocyclic lineages occupy lower latitudes. Holocyclic lineages are favored in regions with regular harsh winters because they produce cold-resistant eggs, while aphids in areas with mild winters benefit from the faster multiplication rates of asexual reproduction. However, holocyclic populations do occur in temperate regions where the winter climate is mild. The genetic variability resulting from sexual reproduction allows sexual populations to overcome environmental variability and inhabit a broader geographical range (Frantz et al. 2006).

Frantz et al. (2006) induced pea aphid sexual production on annual and perennial hosts in western France. In *Acyrtosiphon pisum* (Harris) lineages holocycly was more common on annual hosts than on perennial hosts. Annual crops are completely harvested in the summer or fall so aphids must colonize other available hosts. Host temporal heterogeneity presents selective pressures, which may explain the higher investment in sexual reproduction.

Laboratory Induction of Holocyclic and Anholocyclic Populations

In Tacheng, Xinjiang in northwest China, the Russian wheat aphid has a holocyclic life cycle. Researchers there hypothesized that the life cycle of the Russian wheat aphid could easily be changed from holocyclic to anholocyclic under the correct environmental conditions. Under laboratory conditions of 14 h/d photophase and temperature not lower than 15°C researchers were able to induce an anholocyclic

population from one originally holocyclic. After 81 generations oviparae only appeared occasionally and no eggs occurred for overwintering (Zhang et al. 2001).

Kiriac et al. (1990) attempted to induce sexual morphs from a collection of Moldavian viviparous females. Under 6:18 (L:D) photoperiod at 10°C and 20°C Moldavian Russian wheat aphids, which are commonly holocyclic, readily produced sexual morphs. Under the same laboratory conditions Syrian, French, Turkish, Jordanian, and Kirghizian populations did not produce sexual morphs. Similarly, North American populations remained anholocyclic under these laboratory conditions.

The distribution and occurrence of Russian wheat aphid sexual morphs in Chile and Argentina was described by Clua et al. (2004). In Chile the aphid was uncommon in the Central Valley and close to the Pacific Ocean, but abundant above an altitude of 1,000 m., where rainfall is greater. In Chile, aphids were found up to 2,400 m above sea level. In Argentina, the aphid was found between 400 to 1,200 m. To induce sexual morph production, aphids from locations in Chile and Argentina were placed in field cages near La Plata, Argentina, from March through November for four years. Only 20% of the Russian wheat aphid clones produced sexuals. Production of sexual forms was not related to the host, period of year, or region from which they were collected. Low production of sexuals was likely related to the warm temperature and extreme short day conditions of La Plata, because in the field at Mendoza, which is at the base of the Andes and cooler, the Russian wheat aphid readily produced sexuals.

Aphid Flight and Suction Traps

Winged aphids are typically produced in response to overcrowding or host quality deterioration (Robert 1987). When seasonal trends in host quality are predictable aphids

produce obligate migrants. Light is required to initiate, maintain, and orient flight. Aphids are weak fliers but they are capable of traveling long distances on low-level jet streams. However, an aphid would have to continue flying to be maintained in the jet stream because there is little convective lift. While wind currents may direct movement, aphids are capable of detecting light, preferring short-wavelengths. Thus, aphids can distinguish between plants and the sky. When an aphid lands on a plant it will probe to determine suitability. If the host is inappropriate the aphid can fly to a new plant (Robert 1987). Short distance movement is most common, but long distance movement can be achieved by the accidental riding of low-level jet streams (Dixon 1985).

Monitoring aphid migrations is important for predicting extent and severity of infestations. Suction traps capture winged aphids during flight and can give insight into timing of peak migrations. Suction trap data were used to determine that aphid immigration is associated with low-level jet winds (Kieckhefer et al. 1974). Loxdale et al. (1993) utilized suction trap data to determine that long range movement (>100 km) occurs but is infrequent. Halbert et al. (1990) used suction trap catches to define a safe planting date for small grains in the Pacific Northwest. Russian wheat aphid flight patterns are currently monitored with a network of suction traps located in small grain producing regions of Colorado (Hammon et al. 1999).

There is a similar network of suction traps in the United Kingdom. *Myzus persicae* (Sulzer) is a common pest in United Kingdom agriculture. *Myzus persicae* collections in the suction trap network have been analyzed for insecticide resistance via biochemical analysis. This data has been distributed to growers in resistance bulletins (Anstead et al. 2008). This same network was used to collect *Sitobion avenae* (F.) during

spring wheat colonization. Using genetic methods, collections were used to assess the relative contribution of local and transient migrants into the wheat field (Vialatte et al. 2007). Furthermore, forty years of data from European suction traps was used to correlate aphid flight phenology to climate change data. The date of first recorded aphid species in suction traps is thought to advance as average temperatures increase (Harrington et al. 2007). Hulle et al. (1994) used trap collections to relate aphid flight patterns to holocycly and anholocycly reproduction. The annual variability of patterns in flight phenologies decreased with increasing prevalence of holocycly. Temperature was more important in flight pattern prediction of anholocyclic populations.

Interpretation of suction trap data is based on early, peak and late season captures (Hammon et al. 1999). Early captures result from overwintering success and can help predict early season abundance, and local movement. Peak captures occur as the crop matures and aphids migrate to alternative hosts, and can approximate overall aphid population. Relating the peak capture to aphids in the field can indicate infestation severity. Late season captures can predict fall infestation levels. Relating suction trap data to climate data can suggest how aphid movement is affected by environmental conditions (Hammon et al. 1999).

Natural Predators

Cereal aphids have a variety of naturally occurring enemies, including specialized, oligophagous and polyphagous predators (Greenstone 2000). Specialized aphidophagous predators rely on aphids for reproduction, whereas generalist predators survive on a variety of prey. Therefore, generalists are preventive, while specialists may suppress an ongoing outbreak. Coccinellid beetles, syrphid flies, lacewings, and

heteropteran bugs are considered polyphagous, but usually have a close association with aphids. Aphid generalist predators include carabid and staphylinid beetles, spiders, and harvestmen. Specialists are mainly parasitic wasps (Toft 2005).

Specialist predators have specific search patterns defined by visual and chemical cues, and show little predatory behavior towards their prey. Generalist predators respond to many different prey items, if they move and are of correct size. Specialists are selective before prey capture, whereas generalists are initially unselective but with experience and learned preferences may become selective. Commonly, aphids are considered low quality prey for generalist species. In locations where aphid outbreaks are frequent, generalist predators may experience genetic variation allowing tolerance to an aphid diet (Toft 2005).

Over 100 species of natural enemies attack the Russian wheat aphid worldwide (Pike et al. 1991). After the appearance of the Russian wheat aphid in the United States, research showed naturally occurring predators were inefficient at controlling the pest. On the contrary, natural enemies in the aphid's native range were capable of suppression (Lee et al. 2005). Rapid spread of the Russian wheat aphid prompted a biological control effort from 1987-1994. More than fifteen million parasitoids and predators were released in eighteen states and two Canadian provinces (Prokrym et al. 1998).

In North America, natural enemies have not successfully suppressed Russian wheat aphid populations (Meyer and Peairs 1989, Feng et al. 1992, Mohamed et al. 2000). The effects of augmentative biological control releases were assessed in a cage exclusion study by Randolph et al. (2002). The release of *Hippodamia convergens* (Guerin- Meneville) and *Chrysoperla rufilabris* (Burmeister) did not have a measurable

economic benefit. Field surveys were completed by Wraight et al. (1993) to determine the existing natural enemy complex in Colorado. Parasitism rates in all surveyed fields were less than five percent, and the most common parasitoid was *Diaeretiella rapae* (McIntosh). The most constantly found predator was the syrphid larvae, but densities were overall low. Later, Mohamed et al. (2000), observed 41 species of natural enemies in Colorado. The most common predators found were coccinellids and nabids, and the only parasitoid noted in the four year study was *D. rapae*. Three species of pathogenic fungi were found, but all had low prevalence in dryland fields. A study of natural enemy impact on the Russian wheat aphid in southeastern Colorado found that coccinellid and nabid species were the most abundant predators, but did not substantially reduce aphid numbers. Parasitoids collected in this location, mainly *Lysiphlebus testaceipes* (Cresson), did not increase aphid mortality (Lee et al. 2005).

Russian wheat aphid feeding prevents leaf unrolling, providing the aphid shelter from weather, natural enemies and insecticides within the rolled leaf (Walters et al. 1984). Leaf rolling reduces predation risk from coccinellids and chrysopids (Messina et al. 1997). Some parasitoids, such as *Aphelinus varipes* (Foerster) and *D. rapae*, can parasitize the Russian wheat aphid while in the rolled leaf (Feng et al. 1992). Other defenses utilized by the Russian wheat aphid include alarm pheromones, and dropping mechanisms, where the aphid drops to the ground after coming in contact with a predator (Gibson and Rice 1989, Mohamed et al. 2000).

Effectiveness of natural enemies can depend on the herbivore's host plant. Predator searching ability may be influenced by plant architecture traits like stem and leaf dimensions and surface complexity. Clark and Messina (1998) compared the predatory

behavior of the coccinellid, *Propylea quatuordecimpunctata* (L.) towards the Russian wheat aphid on crested wheatgrass and Indian ricegrass (*Sorghastrum nutans* (L.) Nash). Crested wheatgrass has flat broad leaves, while Indian ricegrass has slender and tightly rolled leaves. In the absence of prey, *P. quatuordecimpunctata* adults and larvae had similar time budgets on the two hosts. When aphids were present, the beetles captured aphids at higher rates on Indian ricegrass than on crested wheatgrass. Indian ricegrass leaf architecture caused more aphids to feed in exposed locations, making them easier prey. Since Russian wheat aphid tends to feed in concealed locations, a plant's architecture may be an important component in predation risk.

Spiders as Aphid Predators

Spiders are generalist predators, and are capable of subsisting on many prey types. Spiders are one of the most abundant arthropods in agroecosystems, and cereal aphids constitute a substantial portion of their diet (Alderweireldt 1994). As generalist predators, spider population dynamics are independent of aphids, so at the onset of aphid colonization these predators are already present. Therefore, spiders are thought to efficiently suppress aphid populations during the early colonization stages, while more time is required for specialist parasitoids to move in (Chiverton 1986).

While spiders do consume aphids, laboratory experiments suggest that cereal aphids are low quality or even toxic for many generalist predators. Of the generalist predators, spiders have lower tolerance for aphids than carabid and staphylinid beetles (Toft 2005). The quality of prey depends on its contents, including nutrients and noxious substances. Assessment of prey value can be accomplished by measuring predator growth rate parameters such as fecundity, egg production, growth rates, and survival (Marcussen

et al. 1999). According to optimal foraging theory, low quality prey should be rejected by a predator, if better quality prey is available (Stephens and Krebs 1986).

Linyphiid spiders are commonly found in agroecosystems. Bilde and Toft (2001) assessed the food value of cereal aphids (*Metopolophium dirhodum* (Walker), *Sitobion avenae* (Fabricius), and *Rhopalsiphum padi* (L.)) to this spider family. Spiders were fed pure aphid diets, mixed aphid diets, aphids mixed with fruit flies, and pure fruit fly diets. Prey value was indicated by spider fecundity, egg production, hatching success, and offspring size. All pure aphid diets were low in value to spiders, in comparison to fruit fly diets, causing decline in egg production and poor juvenile growth.

In contrast, gut content analysis has shown that aphids constitute a significant portion of many web-building and cursorial spiders' diets in the field (Harwood et al. 2004, Harwood et al. 2005). Monoclonal antibodies have enhanced the knowledge of trophic interactions and can quantify predation on specific species. Tetragnathid spiders are not as common in the field as linyphiids, but are typically larger and may consume more aphids. Tetragnathid spiders were collected from winter wheat fields in the United Kingdom, and assayed by ELISA for aphid proteins. Tetragnathid spiders were found to consume greater quantities of aphids than linyphiid spiders. Tetragnathids may have overcome aphid toxins, making them a better quality food item. Although less abundant, these hunting spiders are capable of consuming larger numbers of aphids, suggesting that they may be an important part of the predatory complex (Harwood et al. 2005).

The presence of alternative prey may affect spider predation. To determine if alternative prey influenced linyphiid predation on aphids Harwood et al. (2004) examined the quantity of different prey proteins in gut contents. When high quality prey, such as

collembola, were at higher densities, the spiders ate fewer aphids. Conversely, low collembola populations led to higher consumption of aphids. Non-aphid prey maintain spiders in the field, which can affect aphid predation.

Cursorial and web building spiders utilize different techniques in prey capture. Birkhofer et al. (2008) compared how the differing techniques affected *S. avenae* abundance in a wheat field. Species specific aphid consumption was determined through a molecular approach. During the study, aphid densities were well below economic threshold levels. Web building spiders did not affect aphid population growth, while cursorial spiders retarded aphid growth even at low densities. Thomisids and lycosids consumed the most aphids. Differences in hunting technique may play a role in which spiders are most effective at reducing aphid populations.

Spider species presence is dependent on the environment. Spider diversity in United States wheat cropping systems is not well known. Greenstone (2000) sampled the diversity and density of spiders in a typical United States Great Plains winter wheat habitat. Spiders were sampled by vacuum, insect net, and hand searching techniques. Results showed that spider densities were lower, and fauna was more evenly dispersed over families than in other parts of the world. The most abundant families found were Linyphiidae (one quarter of individuals), Lycosidae 14%, Thomisidae, Gnaphosidae, Tetriginathidae, and Theridiidae (10% each). In total, eleven families were found including Araneidae, Dictinidae, Oxyopidae, Philodromidae, and Salticidae. Linyphiids are even more abundant in winter wheat fields in the United Kingdom (71-100%). Given the overall low densities of spiders, un-manipulated populations may not be effective biological control agents against cereal aphids.

Harvestmen as Aphid Predators

Harvestmen (Opiliones) are omnivores, but prey mainly on small soft-bodied invertebrates. Many species are opportunistic scavengers, but records of harvestmen feeding habits are scarce. Though considered generalists, opiliones have strongly preferred food types. Of the harvestmen's reported food items, aphids were specifically listed in the sub-order Eupnoi for seven species in the families Phalangiidae and Oligophinae, and for one species in the sub-order Dyspnoi (Pinto-Da-Rocha et al 2007).

Harvestmen have received increasing attention as potential agents of biological control in agroecosystems due to their polyphagous habits, broad distributions, and overall abundance. Currently, *Phalangium opilio* (L.) is a preferred species of study due to their great abundance and known consumption of aphids (Bristowe 1949). In New Zealand, harvestmen are thought to be responsible for 31.5% of the total arthropod predation on the lepidopteron pest, *Pieris rapae* (L.), in cabbage crops. This level of predation is significantly greater than that of most spiders. The lycosid spider was only responsible for 2% of predation. This may be due to the fact that harvestmen readily climb plants in search of prey, and the lycosid was never found on plants and showed little climbing ability (Pinto-Da-Rocha et al 2007).

Dixon and McKinlay (1989) examined the enteric contents of harvestmen species inhabiting potato fields in Scotland. Six species contained aphid remains. *Phalangium opilio* was the dominant species in the field and 54% had eaten live aphids. Harvestmen alone are unable to keep pest populations under control, but as part of a generalist complex they may help keep pest densities low.

The quality of harvestmen diets was assessed by Havam and Toft (2005). The harvestmen *Oligolophus tridens* (C.L. Koch) was reared on six diets, and quality was assessed by comparing fitness measures such as survivorship, growth, and development. The diets represented ordinary harvestmen prey including fruit flies, Collembola, two aphids (*S. avenae* and *R. padi*) and a mixture of all. The aphids comprised low quality diets, the mixture was of intermediate quality, and the collembolan and fruit fly diets were highest quality. None of the harvestmen fed pure aphid diets developed past the fourth instar. Thus *O. tridens* may not be as effective at biological control as other opilionid species.

Madsen et al. (2004) analyzed the capability of six generalist predators, including spiders, carabid beetles, and harvestmen to suppress *R. padi* populations in the presence and absence of alternative prey. In the absence of alternative prey, all predators except the carabid beetle were able to significantly reduce aphid population, in comparison to predator free controls. The harvestmen were the most efficient predators, reducing aphid numbers by more than 90%, with success independent of alternative prey availability. The harvestmen's success may be attributed to a metabolic rate 2-4 times higher than other arachnids. While only a few studies have addressed the harvestmen's ability to suppress aphids, all suggest they may be successful control agents. Opiliones may be overlooked because they are largely absent from tilled fields. Therefore they may have greater predatory potential in grassland systems or reduced tillage systems.

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sampling has occurred at lower elevations where wheat is produced. Typically,
holocyclic aphid populations occupy higher elevations, as these environments provide

**ECOLOGY, OCCURRENCE, AND MOVEMENT OF THE RUSSIAN WHEAT
APHID, *Diuraphis noxia* (Kurdjumov) (Hemiptera: Aphididae) ALONG
ELEVATIONAL GRADIENTS ON FIVE NONCULTIVATED GRASS HOSTS IN
COLORADO**

that may promote heliothy. Heliothy is wheat producing areas at

INTRODUCTION

Since its North American introduction in 1986, the Russian wheat aphid,
Diuraphis noxia (Kurdjumov), has spread rapidly throughout the small grain producing
regions. The aphid caused more than \$893.1 million in crop loss in the first decade of its
North American occurrence (Morrison and Peairs 1998). The aphid damages crops such
as wheat (*Triticum aestivum* L.), barley (*Hordium vulgare* L.), and triticale (*Triticale
hexaploide* Lart.), but requires noncultivated hosts for year round survival. Russian wheat
aphid populations have been effectively managed with resistant cultivars, but emerging
biotypic diversity has disrupted plant breeding progress. Eight Russian wheat aphid
biotypes have been identified in the United States, and understanding sources of selection
pressure will benefit management efforts (Haley et al 2004, Burd et al. 2006, Weiland et
al. 2008).

Biotype development can result from genetic recombination during sexual
reproduction (Dixon 1985). While Russian wheat aphid oviparae have been found in
North America, males and eggs have not been reported (Kiriac et al. 1990). Therefore,
North American Russian wheat aphid populations have been thought to be exclusively
anholocyclic, reproducing through year round parthenogenesis and surviving the winter
as viviparous females (Burd et al. 1998, Halbert and Stoetzel 1998). Holocyclic Russian

wheat aphid populations may have gone undiscovered in North America because most sampling has occurred at lower elevations where wheat is produced. Typically, holocyclic aphid populations occupy higher elevations, as these environments provide host heterogeneity and regular harsh winter conditions (Frantz et al. 2006). Russian wheat aphid populations occurring at higher altitudes encounter more extreme winter conditions that may promote holocycly. However, aphids overwintering in wheat producing areas at lower elevations may not be exposed to such harsh conditions and, thus, can successfully overwinter as viviparous adults.

Biotype development can also result from selective pressures such as antibiosis and antixenosis expressed by resistant cultivars and noncultivated grass hosts. Porter et al. (1997) studied greenbug, *Schizaphis graminum* (Rondani), biotype development and suggested that non-cultivated grass hosts could be a reservoir for aphid biotypes. Since this theory was suggested, several unique greenbug biotypes have been found on non-cultivated hosts (Anstead et al. 2003, Burd and Porter 2006). Similarly, Weiland et al. (2008) found two new Russian wheat aphid biotypes on noncultivated grasses. Porter et al. (1997) suggested that noncultivated hosts play an important role in maintaining aphid genetic diversity, and that exposure to selective pressures on grasses provides aphids with the genetic diversity needed to exploit resistant cultivars.

The Russian wheat aphid can feed on over 140 grass species and has been commonly found on wheatgrasses (Kindler and Springer 1989, Pike et al. 1991). Russian wheat aphid is especially dependent on alternative hosts during the oversummering period after winter grains are harvested. By mid-summer, noncultivated grasses at lower

elevations typically have senesced, while grasses at higher elevations are still in vegetative and early reproductive stages.

Winged aphids are typically produced in response to overcrowding or host quality deterioration (Robert 1987). Monitoring winged aphid dispersal is done with suction traps which capture alates during flight (Allison and Pike 1988). Russian wheat aphid movement from areas of wheat production to higher elevations during the summer months is undocumented.

Russian wheat aphid has been found on eighteen different grass species at all elevations between 1,524 m and 3,048 m in Colorado (Randolph et al. unpublished data). The most common hosts harboring Russian wheat aphid at high elevations were crested wheatgrass (*Agropyron cristatum*, (L.) Gaertn.), intermediate wheatgrass (*Elytrigia intermedia*, (Host) Nevski), slender wheatgrass (*Elymus trachycaulus*, (Link) Gould ex Shinnery), western wheatgrass (*Pascopyrum smithi*, (Rydb.) A. Löve), and foxtail barley (*Hordeum jubatum*, (L.) Teskey) (Randolph et al. unpublished data).

Russian wheat aphids at higher elevations are exposed to harsher winter conditions than those in a wheat field in eastern Colorado. Similarly, the aphids may be exposed to different complexes of predators and competitors. Cereal aphids have a variety of naturally occurring enemies. In Colorado wheat fields, the aphid's most common parasitoid was *Diaeretiella rapae* (McIntosh), while the most commonly found predators were syrphid larvae, coccinellids, and nabids (Wright et al. 1993, Mohamed et al. 2000). Spiders also are aphid generalist predators common in wheat fields. The most abundant spider families in a survey of Colorado winter wheat were Linyphiidae, Lycosidae, Thomisidae, Gnaphosidae, Tetrignathidae, and Theridiidae (Greenstone

2000). While all of these predators are widespread in Colorado wheat production environments it is possible that aphid predator diversity may differ in high elevation environments.

Little research has focused on the ecology of the Russian wheat aphid at elevations higher than the Western High Plains production (i.e., >1800m). Aphids surviving in these heterogeneous environments may be encountering different selection pressures, predators, and competitors than they do in an agricultural setting. Understanding the aphid's high elevation ecology may provide a more complete picture of the pest's agronomic ecology and occurrence of holocycly. The objectives of this study were to: 1) identify Russian wheat aphid occurrence and abundance on five common grass hosts at elevations between 1,829- 2,743 m during June-October; 2) monitor Russian wheat aphid movement and flight patterns between 1,524- 2,743 m, with the use of suction traps; 3) describe the predator and competitor assemblages encountered by the Russian wheat aphid in high elevation environments; and 4) attempt to confirm Russian wheat aphid holocycly in North America by collecting sexual forms and eggs.

Figure 1. Map of Russian wheat aphid noncultivated host collection (red dots) and map locations along Highway 14 in the Cache La Poudre River Canyon, Larimer County, Colorado, 2007-2008.

MATERIALS AND METHODS

Noncultivated Host Site Selection

Sites were selected along Highway 14 through the Cache La Poudre River Canyon, west of Fort Collins, in Larimer County Colorado. All sites were located along elevational gradients ranging from 1,829-2,743 m on Roosevelt National Forest land (Figure 1). Sites were selected for accessibility and for occurring at elevations higher than eastern Colorado wheat production. In August 2007, 23 sites with large patches of crested wheatgrass, intermediate wheatgrass, slender wheatgrass, western wheatgrass, or foxtail barley were selected (Table 1). The distance between sites can be seen in Figure 2. Grass patches needed to be large enough to provide enough tillers to be sampled weekly for five months. Grass species selected for this study are known noncultivated hosts of the Russian wheat aphid (Armstrong et al. 1991) and were the most common hosts in a Colorado high elevation survey conducted by Randolph et al. (unpublished data). Grasses were field identified and then verified using an illustrated key to the grasses of Colorado by Wingate (1994).

This study was designed as a survey. To increase the probability of finding Russian wheat aphids, all adequate sites found were used for sampling. If there were more than one grass species at a site, the patches were considered different samples from the same site. At each site a GPS (global positioning system) device was used to identify elevation and UTM coordinates. Sites were preliminarily sampled from August-October

Figure 1. Map of Russian wheat aphid noncultivated host collection sites, and suction trap locations along Highway 14 in the Cache La Poudre River Canyon, Larimer County, Colorado, 2007-2009.

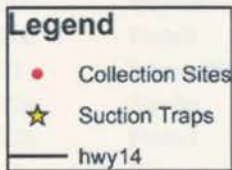
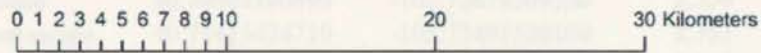
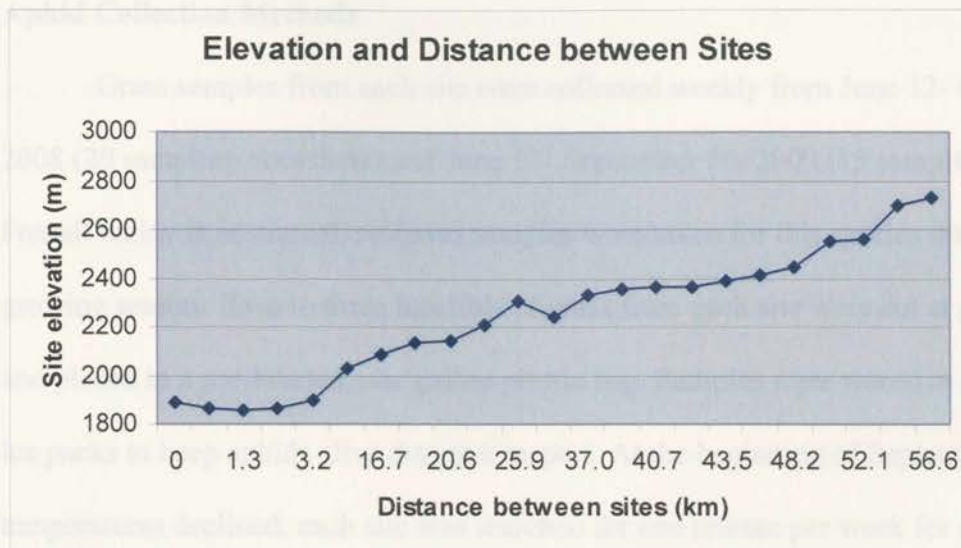


Table 1. Description of Russian wheat aphid noncultivated host and predator collection sites in the Cache La Poudre River Canyon, Larimer County, Colorado, 2007-2009.

Site	Grass Species	Site Coordinates		
		Latitude (N)	Longitude (W)	Elevation (m)
1	Slender	40.67693300530	-105.38817461800	1,891
2	Intermediate	40.68278086310	-105.39314323400	1,867
3	Crested	40.68358580910	-105.39747918400	1,860
4a	Western	40.68242158430	-105.40840663300	1,868
4b	Slender	40.68237620720	-105.40827046700	1,868
5	Intermediate	40.67782443780	-105.41422403500	1,896
6	Intermediate	40.68406828690	-105.46600098300	2,031
7	Crested	40.69072544180	-105.49841656800	2,087
8a	Crested	40.69577324240	-105.52617424400	2,138
8b	Western	40.69596465980	-105.52679556600	2,138
9	Western	40.69817280960	-105.54105974500	2,145
10a	Intermediate	40.70257231410	-105.58472745400	2,209
10b	Western	40.70280118010	-105.58460093300	2,209
11a	Slender	40.71175989150	-105.58851338700	2,306
11b	Foxtail	40.71159433700	-105.58837145400	2,306
12a	Crested	40.69830740790	-105.62333627800	2,239
12b	Slender	40.69837891920	-105.62329012900	2,239
13	Crested	40.69778915390	-105.68763846600	2,333
14	Crested	40.70902100490	-105.72619309500	2,356
15	Intermediate	40.71415474710	-105.73491520100	2,363
16	Crested	40.70561565350	-105.75430621900	2,367
17	Crested	40.68277156030	-105.77311266700	2,391
18	Crested	40.67346867590	-105.78468340400	2,412
19	Crested	40.66552477510	-105.80923344900	2,445
20a	Crested	40.63865179700	-105.80594524900	2,551
20b	Slender	40.63890456340	-105.80638730300	2,551
20c	Intermediate	40.63865752640	-105.80637185200	2,551
20d	Foxtail	40.63899930620	-105.80643211700	2,551
21	Intermediate	40.63422634590	-105.80699888900	2,558
22a	Slender	40.61265198910	-105.82716641100	2,698
22b	Foxtail	40.61208992740	-105.82675938100	2,698
23	Western	40.60419770130	-105.83649435000	2,730

Figure 2. Elevation and distance between Russian wheat aphid noncultivated host collection sites in the Cache La Poudre River Canyon, Larimer County, Colorado, 2007-2009.



Aphid Sample Processing and Identification

— Samples were brought to the Colorado State University Agricultural Research and Development Center (ARDC) where they were placed on moist paper towels inside a plastic bag for 24 hours to extract aphids. One filter, with an insect vial head, from each sample was brought back to the laboratory where identification was verified. All living specimens were collected from larvae through to a bag filled with 70% ethanol. After 24 hours, plant material was removed from the bag, weighed, and discarded. Preserved organisms were brought back to the lab where they were counted, identified, and a list of the collection sites was compiled specifically for Russian wheat aphid, and their sexual morphs. Other grass aphids, specifically: *Diuraphis sparsa* (Fallon), *Diuraphis arvensis* (Fallon) (winter wheat aphid), *Diuraphis viciae* (Fallon), *Rhopalosiphum elaeagni* (Fallon) (yellow sugarcane aphid), *Rhopalosiphum padi* (L.) (barley yellow net aphid), *Rhopalosiphum rufum* (Fallon) (corn leaf aphid),

2007, to refine site selection and sampling methods. During each sampling, both grass samples and predator samples were collected from the same sites.

Aphid Collection Methods

Grass samples from each site were collected weekly from June 12- October 30 2008 (20 sampling occasions) and June 17- September 30, 2009 (15 sampling occasions). Foxtail barley is an annual, so fewer samples were taken for this species due to its limited growing season. Two to three handfuls of grass from each site were cut at ground level and placed in a pre-labeled, one gallon plastic bag. Samples were stored in a cooler with ice packs to keep aphids alive during transport. At the beginning of September, or when temperatures declined, each site was searched for one minute per week for aphid eggs.

Aphid Sample Processing and Identification

Samples were brought to the Colorado State University Agricultural Research and Development Center (ARDEC) where they were placed on sheet metal Berlese funnels for 24 hours to extract arthropods. One tiller, with an intact seed head, from each sample was brought back to the laboratory where its identification was verified. All living organisms were collected from Berlese funnels in a cup filled with 75% ethanol. After 24 hours, plant material was removed from the funnel, weighed, and discarded. Preserved organisms were brought back to the lab where they were counted and identified under a dissecting microscope. Samples were scanned specifically for Russian wheat aphids, and their sexual morphs. Other grass aphids, specifically, *Diuraphis frequens* (Walker), *Diuraphis tritici* (Gillette) (western wheat aphid), *Diuraphis nodulus* (Richards), *Sipha elegans* (del Guercio), *Sipha flava* (Forbes) (yellow sugarcane aphid), *Rhopalosiphum padi* (L.) (bird-cherry oat aphid), *Rhopalosiphum maidis* (Fitch) (corn leaf aphid),

Sitobion avenae (F.) (English grain aphid), *Schizaphis graminum* (Rondani) (greenbug), and *Metopolophium dirhodum* (Walker) (rose grass aphid), were also counted and identified using a key to small grain aphids by Pike et al. (1991). Furthermore, all thrips and mites were counted and saved for future reference. The most common thrips collected were identified by Linda Mahaffey in the Bioagricultural Sciences and Pest Management department at Colorado State University.

Suction Trap Construction and Site Selection

To assess the movement of alate aphids, suction traps were placed along Colorado Highway 14 through the Cache La Poudre River canyon, west of Fort Collins, in Larimer County, Colorado. Four suction traps were placed at elevations of 1,655, 1,992, 2,206, and 2,372 m (Figure 1). When possible, traps were placed on private property, as permitted by owners, to prevent theft (Table 2). The distance between traps can be seen in Figure 3. The suction trap at 1,655m, at the base of the "Front Slope" required an electrical source and was placed on the property at 6309 N. Co. Rd. 29C, Bellvue, CO. This trap was constructed to the specifications of Allison and Pike (1988). The trap stood 8.5 m tall, with an opening diameter of 30 cm. An electric fan pulls air and passing insects into the trap, where insects are funneled through into a plastic jar containing a 50:50 mixture of ethylene glycol and 95% ethanol, which kills and preserves the catch.

Smaller, solar-powered traps were placed at the higher elevations. These stood 0.9 m tall and used a smaller electric fan to pull in air and funnel insects into a 50:50 mixture of ethylene glycol and 95% ethanol for preservation. The 0.9 m suction trap is mounted on a metal fence post, holding the trap opening at about 1.5 m above the ground. The electric fan is powered by a portable solar electric unit built specifically for the trap by

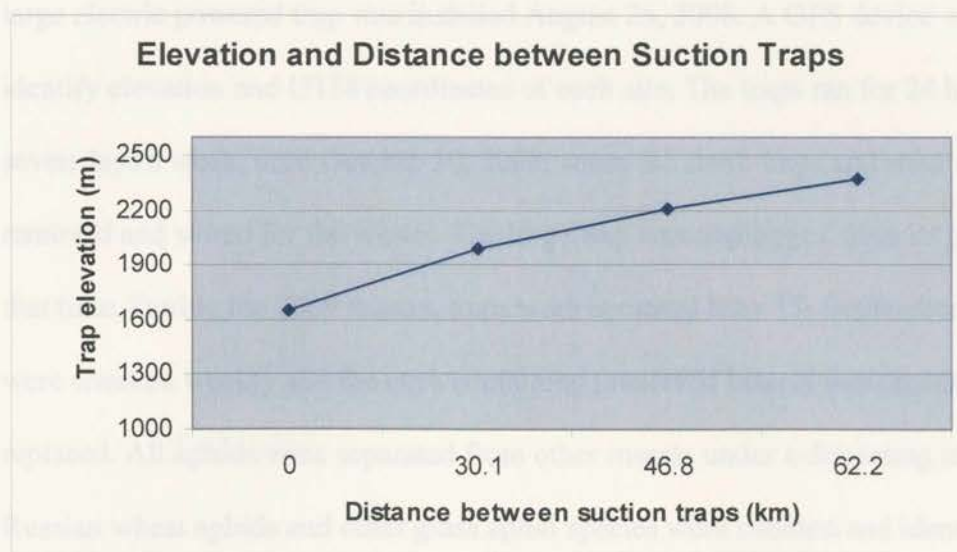
Table 2. Description of suction trap locations in the Cache La Poudre River Canyon, Larimer County, Colorado, 2008-2009.

Address	Suction Trap Elevation (m)	Site Coordinates	
		Latitude (N)	Longitude (W)
6309 N. Co. Rd. 29C ¹	1,655	40.67858246	-105.217565
Dutch George, mile marker 101 Roosevelt National Forest ²	1,992	40.69831289	-105.4438971
57 Rustic Rd. ²	2,206	40.69644698	-105.5921393
42087 Poudre Canyon Hwy ²	2,372	40.7027915	-105.7579998

¹ Full-size 8.5 m Allison-Pike suction trap

² 1.5 m solar-powered trap

Figure 3. Elevation and distance between suction trap sites in the Cache La Poudre River Canyon, Larimer County, Colorado, 2008-2009.



Solar Solutions, Inc. of Fort Collins, CO. The major components of each solar unit include one 65 watt photovoltaic collector (Kyocera Solar Inc., Scottsdale, AZ) mounted on top of a custom built ventilated battery box containing a C12 charge controller (Xantrex, Vancouver, Canada), connected to a AGM 12 volt, 100 amp hr battery with a 15 amp inline battery fuse and 2 amp in-line fan fuse (Deka, Manchester, NH). These traps were modeled after a solar powered suction trap designed by Belding et al. (1991).

The suction trap at 1,992 m was installed on Roosevelt National Forest land, near Dutch George and mile marker 101 on Highway 14. Since this trap was not on private property, the portable solar electric unit was chained and locked to a nearby tree. The trap at 2,206 m was placed at 57 Rustic Rd., in Rustic. The trap at 2,372 m was at 42087 Poudre Canyon Hwy, near Kinnikinnik. This trap was lower than the desired 2,438 m because there were no private properties or safe flat locations at higher elevations.

Suction Trap Sample Collection and Processing

The three solar powered suction traps were first installed on July 30, 2008. The large electric powered trap was installed August 26, 2008. A GPS device was used to identify elevation and UTM coordinates of each site. The traps ran for 24 hours a day, seven days a week, until October 30, 2008, when the small traps and solar units were removed and stored for the winter. The large trap was unplugged from its power source at that time. During the 2009 season, traps were operated May 15- September 30. Traps were checked weekly and the cups containing preserved insects were removed and replaced. All aphids were separated from other insects under a dissecting microscope. Russian wheat aphids and other grass aphid species were counted and identified using the key of Pike et al. (1991).

Predator Collection Methods

Predator sampling occurred weekly at the same grass sampling sites. Predators were collected prior to grass samples, so predators were not disturbed prior to collection. Predators were collected with a Stihl Model SH85 D leaf blower-vacuum (Stihl Inc., Virginia Beach, VA), modified with a handmade, mesh collection bag (Burd and Porter 2006) inserted and attached to the outlet of the vacuum tube. Five clumps of each grass species at each site were vacuumed for ten seconds each. During the ten seconds the vacuum tube was placed over a clump of grass and moved up and down making sure the ground surrounding the plant was also sampled. After five clumps were sampled, the mesh collection bag was covered, removed, and emptied into a one gallon plastic bag, which was sealed and stored in a cooler for transport. In the laboratory all predator samples were placed in a freezer for 24 hours to kill and preserve specimens for identification and counting.

Predator Sample Processing and Identification

After being frozen for at least 24 hours, each sample was emptied into a metal tray and sorted with a paintbrush. All potential aphid predators were separated and pin mounted or placed in alcohol. Predators were identified to family, using several references (Borrer and White 1970, Ubick et al. 2005, and Pinto-Da-Rocha et al. 2007).

Data Analysis

All tables and graphs were created in Microsoft Excel. Site maps were created in ArcMap 9.2 (ESRI 2009).

Table 3. Total aphid density weekly collections, 13 August-11 October 2007, from five grasses per month locations, 2,391-2,510 m in the Cache la Poudre River canyon, Larimer County, Colorado.

Aphid Species	Individual aphids per month (2007)		
	August	September	October

RESULTS

Aphid Collections (2007)

Preliminary data were collected weekly from 13 August to 11 October 2007. During this time collection methods were refined and sites were located. Only one Russian wheat aphid was collected, from crested wheatgrass at 2,391 m on 20 September. This experience suggested the best approach to study Russian wheat aphid abundance and movement in higher elevation environments was to sample numerous sites containing good hosts rather than intensive sampling of fewer, more diverse sites.

Sipha elegans, the most abundant species, was collected equally at all elevations, but most commonly on intermediate, slender, and western wheatgrass (Tables 3-5). Four *R. padi* (bird-cherry oat aphids) also were collected on intermediate and western wheatgrass (Tables 3-5). Thrips and mites were equally abundant during this collection period. The most common mites collected were Banks grass mites (*Oligonychus pratensis* (Banks)), twospotted spider mites (*Tetranychus urticae* (Koch)), and eriophyid mites (Family: Eriophyidae) (Tables 3-5). The most common thrips were *Aptinothrips stylifer* (Trybom) and *Chirothrips aculeatus* (Bagnall).

Aphid Collections (2008 and 2009)

Russian wheat aphid

In 2008, weekly collections were made from 12 June- 30 October. A total of 141 Russian wheat aphids were collected during this sampling season, and Russian wheat aphids were found on all five grass species collected (Table 6). In 2009, weekly

Table 3. Total aphids from weekly collections, 13 August- 11 October 2007, from five grasses per month between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per month (2007)			
	August	September	October	Total
<i>Diuraphis noxia</i>	0	1	0	1
<i>Sipha elegans</i>	383	605	349	1,337
<i>Rhopalosiphum padi</i>	1	3	0	4
Other Arthropods				
Thrips	2,419	1,259	649	4,327
Mites	2,531	1,533	627	4,691

¹Aphid species surveyed but not found: *Diuraphis frequens*, *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Sitobion avenae*, *Schizaphis graminum*, *Metopolophium dirhodum*

Table 4. Total aphids from weekly collections, 13 August- 11 October 2007, per grass species between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per grass species (2007)					Total
	Crested	Intermediate	Foxtail	Western	Slender	
<i>Diuraphis noxia</i>	1	0	0	0	0	1
<i>Sipha elegans</i>	52	474	16	377	418	1,337
<i>Rhopalosiphum padi</i>	0	1	0	3	0	4
Other Arthropods						
Thrips	2,574	516	7	705	525	4,327
Mites	1,248	1,816	2	1,101	524	4,691

¹Aphid species surveyed but not found: *Diuraphis frequens*, *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Sitobion avenae*, *Schizaphis graminum*, *Metopolophium dirhodum*

Table 5. Total aphids from weekly collections, 13 August- 11 October 2007, from five grasses per elevational interval between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per elevation (2007)			Total
	(1,891- 2,087m)	(2,138- 2,412m)	(2,445- 2,730m)	
<i>Diuraphis noxia</i>	0	1	0	1
<i>Sipha elegans</i>	385	519	433	1,337
<i>Rhopalosiphum padi</i>	1	0	3	4
Other Arthropods				
Thrips	1,294	1,518	1,515	4,327
Mites	990	1,372	2,329	4,691

¹Aphid species surveyed but not found- *Diuraphis frequens*, *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Sitobion avenae*, *Schizaphis graminum*, *Metopolophium dirhodum*

Table 6. Total aphids collected, per site (weekly collection from June 12- October 30, 2008) from five grass species between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Site	Grass Species	Elevation (m)	Total aphids per site (June-October 2008) ¹					Other		
			<i>Diuraphis noxia</i>	<i>Diuraphis frequens</i>	<i>Sipha elegans</i> (males)	<i>Rhopalosiphum padi</i>	<i>Sitobion avenae</i>	<i>Schizaphis graminum</i>	Thrips	Mites
1	Slender	1,891	9	0	142 (1)	13	1	0	2,190	423
2	Intermediate	1,867	1	0	605 (10)	1	0	0	1,390	1,418
3	Crested	1,860	11	0	7	28	1	2	3,434	474
4a	Western	1,868	2	2	434	2	1	0	1,008	960
4b	Slender	1,868	2	0	869 (1)	4	1	1	1,177	370
5	Intermediate	1,896	6	0	264 (4)	2	0	0	1,205	1,359
6	Intermediate	2,031	0	0	13	0	5	0	506	897
7	Crested	2,087	44	0	24	0	1	0	3,122	122
8a	Crested	2,138	2	0	5	0	0	0	3,107	30
8b	Western	2,138	0	0	0	0	1	0	1,250	103
9	Western	2,145	0	0	76	0	1	0	1,128	225
10a	Intermediate	2,209	0	0	374 (1)	3	3	0	1,481	380
10b	Western	2,209	3	0	351	0	2	0	1,439	515
11a	Slender	2,306	0	0	289	1	11	0	1,472	438
11b	Foxtail	2,306	6	0	279	0	3	0	483	27
12a	Crested	2,239	4	0	33	0	2	0	6,579	179
12b	Slender	2,239	1	0	9,613 (14)	1	1	0	998	309
13	Crested	2,333	3	0	2	0	2	0	4,283	414
14	Crested	2,356	2	0	0	0	0	0	3,350	186
15	Intermediate	2,363	0	0	0	0	0	0	1,113	228
16	Crested	2,367	10	0	1,144 (13)	0	0	0	4,723	169
17	Crested	2,391	12	0	0	0	0	0	2,563	181
18	Crested	2,412	5	0	2	2	0	0	7,048	314
19	Crested	2,445	1	0	4	17	1	0	2,132	185
20a	Crested	2,551	2	0	0	8	1	0	4,473	251
20b	Slender	2,551	0	0	704	0	0	0	847	888
20c	Intermediate	2,551	0	0	6	3	1	0	729	1,330
20d	Foxtail	2,551	0	33	13	0	7	0	155	73
21	Intermediate	2,558	0	0	171	0	0	0	1,371	1,089
22a	Slender	2,698	0	0	2,330 (16)	3	0	0	342	488
22b	Foxtail	2,698	15	0	0	0	0	0	238	50
23	Western	2,730	0	0	51	2	1	1	685	55
		Total	141	35	17,805	90	47	4	66,021	14,130

¹Aphid species surveyed but not found: *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Metopolophium dirhodum*

Sites where aphid eggs were found- 10a, 11a, 12b, 22a

collection occurred from 17 June- 30 September. In 2009, a total of 1,537 Russian wheat aphids were collected on all grass species except foxtail barley (Table 7). Russian wheat aphids collected near Rustic at 2,209 m on intermediate wheatgrass, in September, accounted for 1,326 of the total.

Russian wheat aphids were most commonly collected on crested wheatgrass in both 2008 and 2009 (Tables 6 and 7). Crested wheatgrass is widely distributed in the Cache La Poudre River Canyon and was present at more sites than the other hosts, which may account for the large amounts of aphids collected (Figure 4).

After crested wheatgrass, Russian wheat aphid, in 2008, was most commonly found on foxtail barley, followed in order by slender wheatgrass, intermediate wheatgrass, and western wheatgrass (Tables 6 and 8). In 2009 many Russian wheat aphids were found on intermediate wheatgrass, however, 98.7% of these were collected at one site. No Russian wheat aphids were collected from foxtail barley in 2009 (Tables 7 and 8).

Russian wheat aphids were collected June-October in 2008, and June- September in 2009. More Russian wheat aphids were collected in July than in other months in 2008. In 2009, the most aphids were collected in September, due in part to the very large sample on intermediate wheatgrass at one location (Table 9).

In 2008 and 2009, Russian wheat aphids were not found at all sites, but they were found within each of the three 305 m elevational intervals sampled (Table 10). Eight samples were collected weekly between 1,829- 2,134 m, 15 between 2,134- 2,438 m, and nine between 2,438-2,743 m. Although the fewest samples were collected between 1,829- 2,134 m, more Russian wheat aphids were collected there in both 2008 and 2009. The

Table 7. Total aphids collected, per site (weekly collection from June 17- September 30, 2009) from five grass species between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Site	Grass Species	Elevation (m)	Total aphids per site (June-September 2009) ¹					Other		
			<i>Diuraphis noxia</i>	<i>Diuraphis frequens</i>	<i>Sipha elegans</i> (males)	<i>Rhopalosiphum padi</i>	<i>Sitobion avenae</i>	<i>Schizaphis graminum</i>	Thrips	Mites
1	Slender	1,891	21	0	2,463 (1)	34	1	0	1,816	312
2	Intermediate	1,867	2	0	135 (1)	1	0	0	1,573	792
3	Crested	1,860	34	0	3	2	0	0	3,398	403
4a	Western	1,868	2	0	166	3	1	1	406	790
4b	Slender	1,868	1	0	218 (2)	28	1	0	784	81
5	Intermediate	1,896	6	0	353 (1)	1	0	1	1,466	455
6	Intermediate	2,031	1	0	303	1	0	0	461	1,054
7	Crested	2,087	42	0	4	1	0	0	3,090	129
8a	Crested	2,138	37	0	1	7	1	0	2,181	14
8b	Western	2,138	0	0	27	0	0	0	1,119	16
9	Western	2,145	0	0	323	0	0	0	668	123
10a	Intermediate	2,209	1,327	2	2,528 (6)	117	117	26	2,595	243
10b	Western	2,209	3	0	388 (1)	11	8	0	972	106
11a	Slender	2,306	2	0	326	14	2	0	2,731	166
11b	Foxtail	2,306	0	0	101	0	1	0	284	6
12a	Crested	2,239	30	0	599	14	1	0	8,371	89
12b	Slender	2,239	0	0	2,794 (3)	0	1	0	1,082	1,212
13	Crested	2,333	2	0	40	1	1	0	3,279	20
14	Crested	2,356	12	0	2	8	0	0	2,844	39
15	Intermediate	2,363	8	0	30	0	0	0	562	265
16	Crested	2,367	1	0	933	0	2	0	3,091	38
17	Crested	2,391	0	0	0	0	1	0	1,779	48
18	Crested	2,412	0	0	0	35	0	0	7,805	101
19	Crested	2,445	0	0	17	10	0	0	2,952	35
20a	Crested	2,551	6	0	12	2	0	0	3,515	99
20b	Slender	2,551	0	0	898	3	0	1	398	74
20c	Intermediate	2,551	0	0	109	0	0	0	737	1,094
20d	Foxtail	2,551	0	0	52	0	0	0	122	1
21	Intermediate	2,558	0	1	1,293 (1)	1	3	3	1,237	174
22a	Slender	2,698	0	0	594	1	0	0	124	25
22b	Foxtail	2,698	0	0	1	0	0	0	242	16
23	Western	2,730	0	1	0	1	6	0	556	14
Total			1,537	4	14,713	296	147	32	62,240	8,034

¹Aphid species surveyed but not found- *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Metopolophium dirhodum*

Sites where aphid eggs were found- 10a, 12b

Figure 4. Total number of grass samples collected, per grass species (weekly collection from June 12- October 30, 2008 and June 17- September 30, 2009) between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

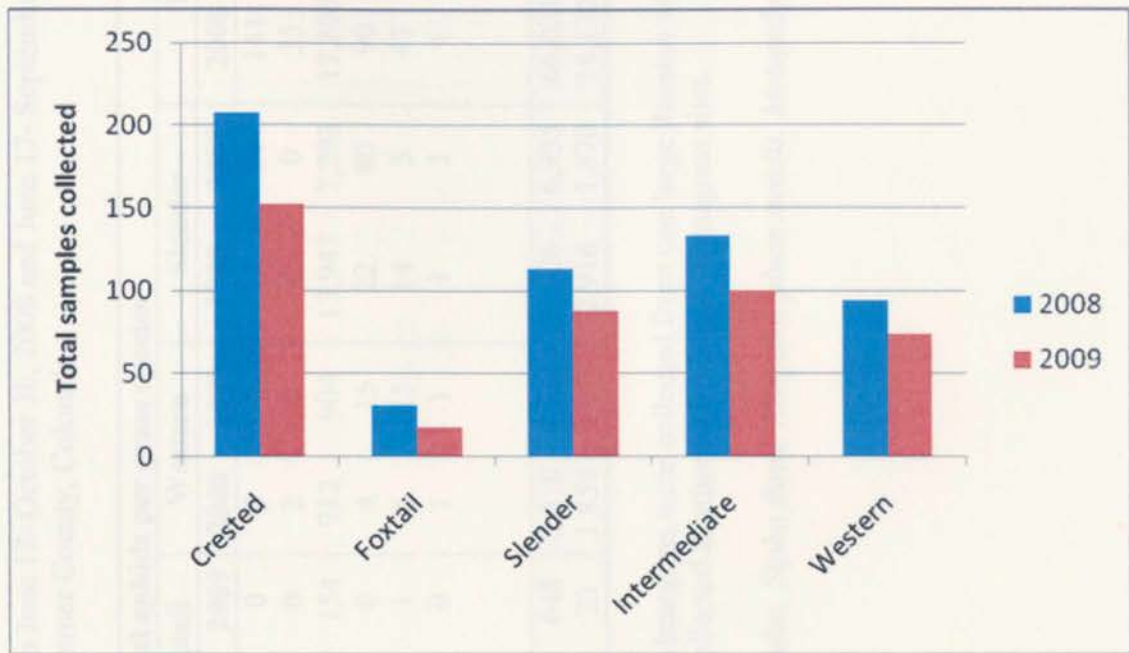


Table 8. Total samples collected per grass species (weekly collection from June 12- October 30, 2008 and June 17- September 30, 2009) between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Grass Species	Crested		Intermediate		Foxtail		Slender		Intermediate		Western	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
<i>Chrysopsis acuta</i>	50	164	7	1,307	21	0	0	0	0	0	0	0
<i>Dicentra spicata</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Lepidosiphon</i>	1,223	1,911	1,493	4,733	292	154	0	0	0	0	0	0
<i>Stipa capensis</i>	35	80	9	121	0	0	0	0	0	0	0	0
<i>Stipa capensis</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Stipa capensis</i>	2	0	0	0	0	0	0	0	0	0	0	0
Total	4,314	4,056	7,299	11,161	312	154	0	0	0	0	0	0
Mean	2,157	2,028	3,649	5,580	156	77	0	0	0	0	0	0

Table 8. Total aphids collected per grass species (weekly collection from June 12- October 30, 2008 and June 17- September 30, 2009) between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per grass species											
	Crested		Intermediate		Foxtail		Western		Slender		Total	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
<i>Diuraphis noxia</i>	96	164	7	1,344*	21	0	5	5	12	24	141	1,537
<i>Diuraphis frequens</i>	0	0	0	3	33	0	2	1	0	0	35	4
<i>Sipha elegans</i>	1,221	1,611	1,433	4,751	292	154	912	904	13,947	7,293	17,805	14,713
<i>Rhopalosiphum padi</i>	55	80	9	121	0	0	4	15	22	80	90	296
<i>Sitobion avenae</i>	8	6	9	120	10	1	6	15	14	5	47	147
<i>Schizaphis graminum</i>	2	0	0	30	0	0	1	1	1	1	4	32
Other Arthropods												
Thrips	44,814	42,305	7,795	8,631	876	648	5,510	3,721	7,026	6,935	66,021	62,240
Mites	2,505	1,015	6,701	4,077	150	23	1,858	1,049	2,916	1,870	14,130	8,034

* 1,326 of the 1,344 Russian wheat aphids collected from intermediate wheatgrass were collected from one large Russian wheat aphid population found at 2,209 m. The 18 other Russian wheat aphids were collected at other intermediate wheatgrass sites.

¹Aphid species surveyed but not found- *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Metopolophium dirhodum*

Table 9. Total aphids collected per month (weekly collection from June 12- October 30, 2008 and June 17- September 30, 2009) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per month											
	June		July		August		September		October		Total	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
<i>Diuraphis noxia</i>	5	29	52	59	25	78	44	1,371*	15	-	141	1,537
<i>Diuraphis frequens</i>	0	0	0	0	33	0	0	4	2	-	35	4
<i>Sipha elegans</i>	366	629	6,641	4,383	4,862	4,218	4,040	5,483	1,896	-	17,805	14,713
<i>Rhopalosiphum padi</i>	54	119	3	47	6	5	6	125	21	-	90	296
<i>Sitobion avenae</i>	8	8	28	17	8	5	1	117	2	-	47	147
<i>Schizaphis graminum</i>	2	3	0	0	0	0	0	29	2	-	4	32
Other Arthropods												
Thrips	23,672	12,819	26,539	34,130	9,116	10,830	4,330	4,461	2,364	-	66,021	62,240
Mites	2,197	900	4,250	2,876	3,643	1,426	2,881	2,832	1,159	-	14,130	8,034

* 1,326 of the 1,371 Russian wheat aphids collected in September 2009 were collected from one large Russian wheat aphid population found at 2,209 m on intermediate wheatgrass. The 45 other Russian wheat aphids were collected at other sites in September.

¹Aphid species surveyed but not found- *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Metopolophium dirhodum*

Table 10. Total aphids collected per elevation (weekly collection from June 12- October 30, 2008 and June 17- September 30, 2009) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per elevation							
	(1,891- 2,087m)		(2,138- 2,412m)		(2,445- 2,730m)		Total	
	2008	2009	2008	2009	2008	2009	2008	2009
<i>Diuraphis noxia</i>	75	109	48	1,422*	18	6	141	1,537
<i>Diuraphis frequens</i>	2	0	0	2	33	2	35	4
<i>Sipha elegans</i>	2,358	3,645	12,168	8,092	3,279	2,976	17,805	14,713
<i>Rhopalosiphum padi</i>	50	71	7	207	33	18	90	296
<i>Sitobion avenae</i>	10	3	26	135	11	9	47	147
<i>Schizaphis graminum</i>	3	2	0	26	1	4	4	32
Other Arthropods								
Thrips	14,032	12,994	41,017	39,363	10,972	9,883	66,021	62,240
Mites	6,023	4,016	3,698	2,486	4,409	1,532	14,130	8,034

* 1,326 of the 1,422 Russian wheat aphids collected between 2,138- 2,412 m were collected from one large Russian wheat aphid population found at 2,209 m. The 96 other Russian wheat aphids were collected at other sites between 2,138- 2,412 m.

¹Aphid species surveyed but not found- *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*, *Rhopalosiphum maidis*, *Metopolophium dirhodum*

least Russian wheat aphids were found between 2,438-2,743 m. In both years, Russian wheat aphids were found throughout the sampling period at lower elevations and at higher elevations only during the latter part of the sampling period (Figures 5-8).

All Russian wheat aphid samples collected in 2008 and 2009 were examined for the presence of sexual morphs, and when temperatures began to cool, all sites were searched for eggs. No Russian wheat aphid sexual morphs or eggs were found in 2008 or during the planned 2009 samples. However, given the large number of Russian wheat aphids found on intermediate wheatgrass at the 10a site (Table 7), this location was searched for aphid eggs several additional times in October and November.

On 6 October, 2009 the first aphid eggs were found at the site. However, *S. elegans*, *R. padi*, *S. avenae*, and *S. graminum* also were present so eggs were collected for DNA comparisons, as well as storage, hatching and rearing. Some of the eggs collected were individually placed in an Eppendorf tube with 15 µl of DNAzol® genomic DNA isolation reagent, then were frozen at 20°C for later genomic analysis. All Russian wheat aphids collected at the site were scanned for sexual morphs.

Other Aphids

Other than Russian wheat aphids, samples were also examined for the presence of *D. frequens*, *D. tritici*, *D. nodulus*, *S. elegans*, *S. flava*, *R. padi*, *R. maidis*, *S. avenae*, *S. graminum*, and *M. dirhodum*. *Diuraphis tritici*, *D. nodulus*, *S. flava*, *R. maidis*, and *M. dirhodum* were not found.

The most common species collected in this study was *S. elegans* (Table 6 and 7). It was most abundant on slender wheatgrass in both 2008 and 2009 (Table 8). Fewer *S. elegans* were collected in June and October, but it was abundant during July-September

Figure 5. Total Russian wheat aphids at 305 m elevational intervals, per month (weekly collection from June 12- October 30, 2008) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

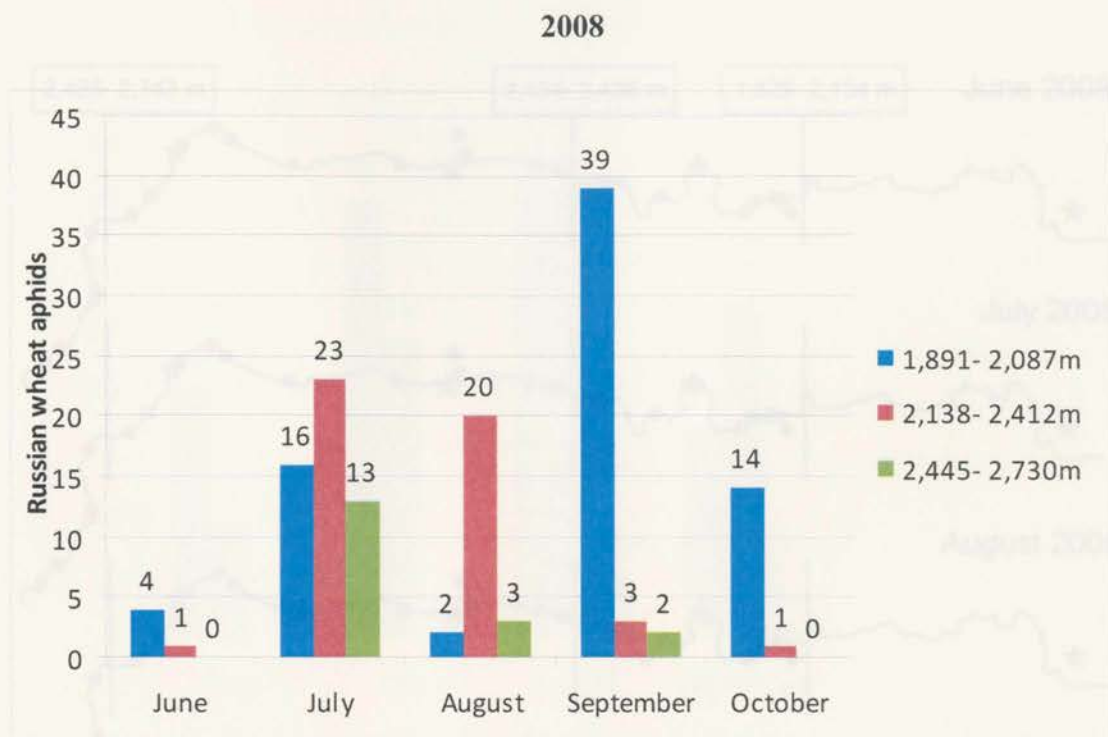


Figure 6. Monthly presence or absence of Russian wheat aphid per site and suction trap (weekly site collection from June 12- October 30, 2008, weekly suction trap samples from July 30- October 30, 2008) in the Cache La Poudre River canyon, Larimer County, Colorado.

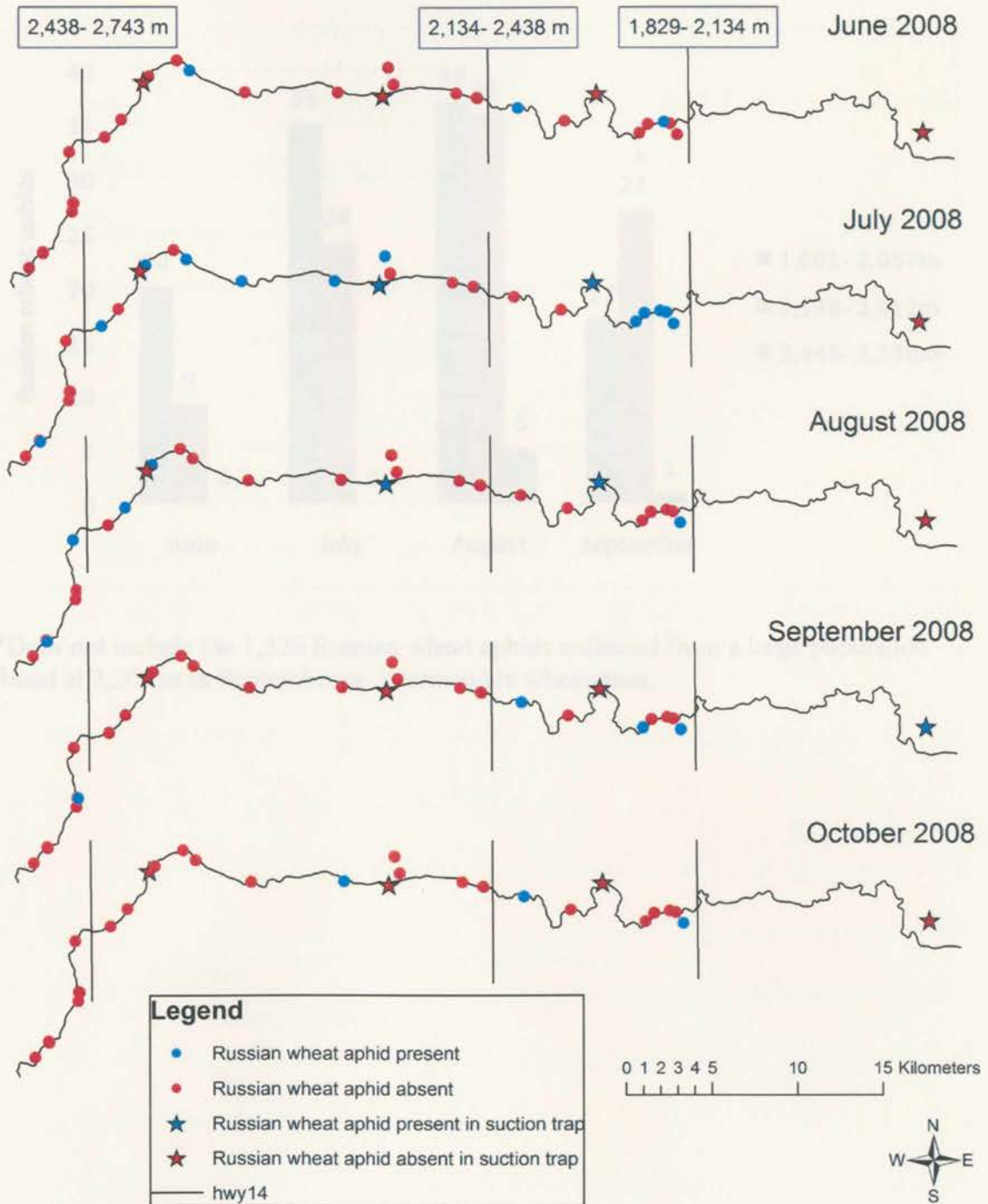
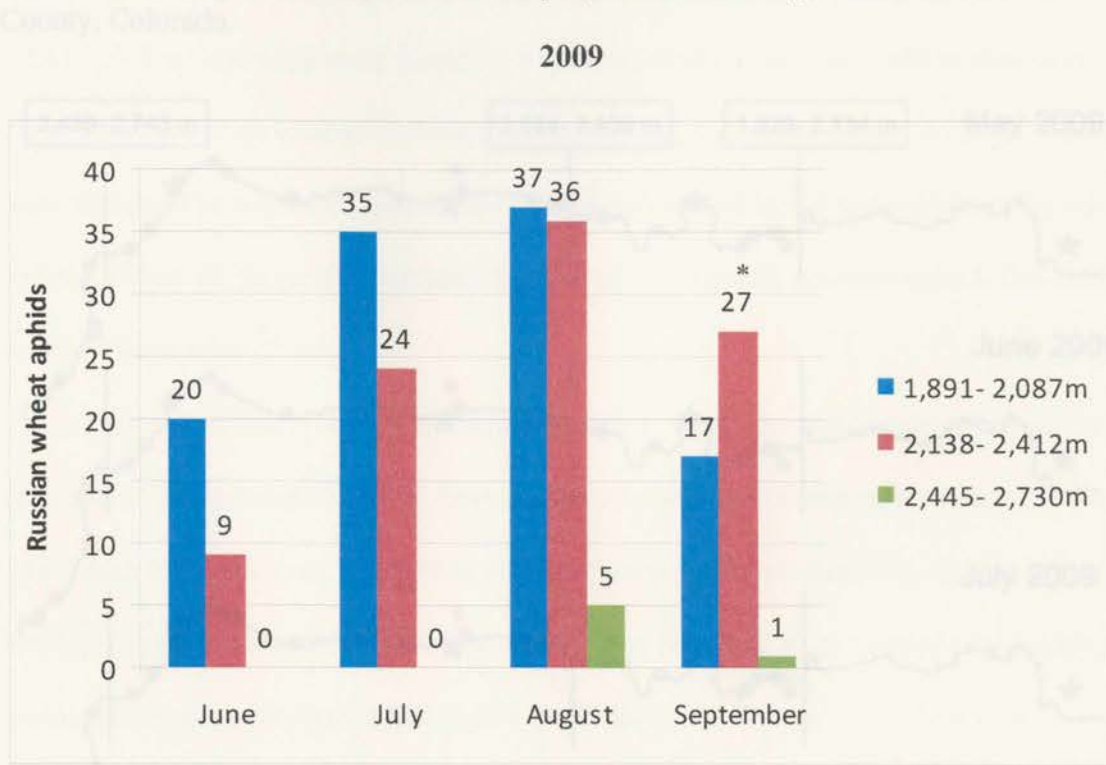
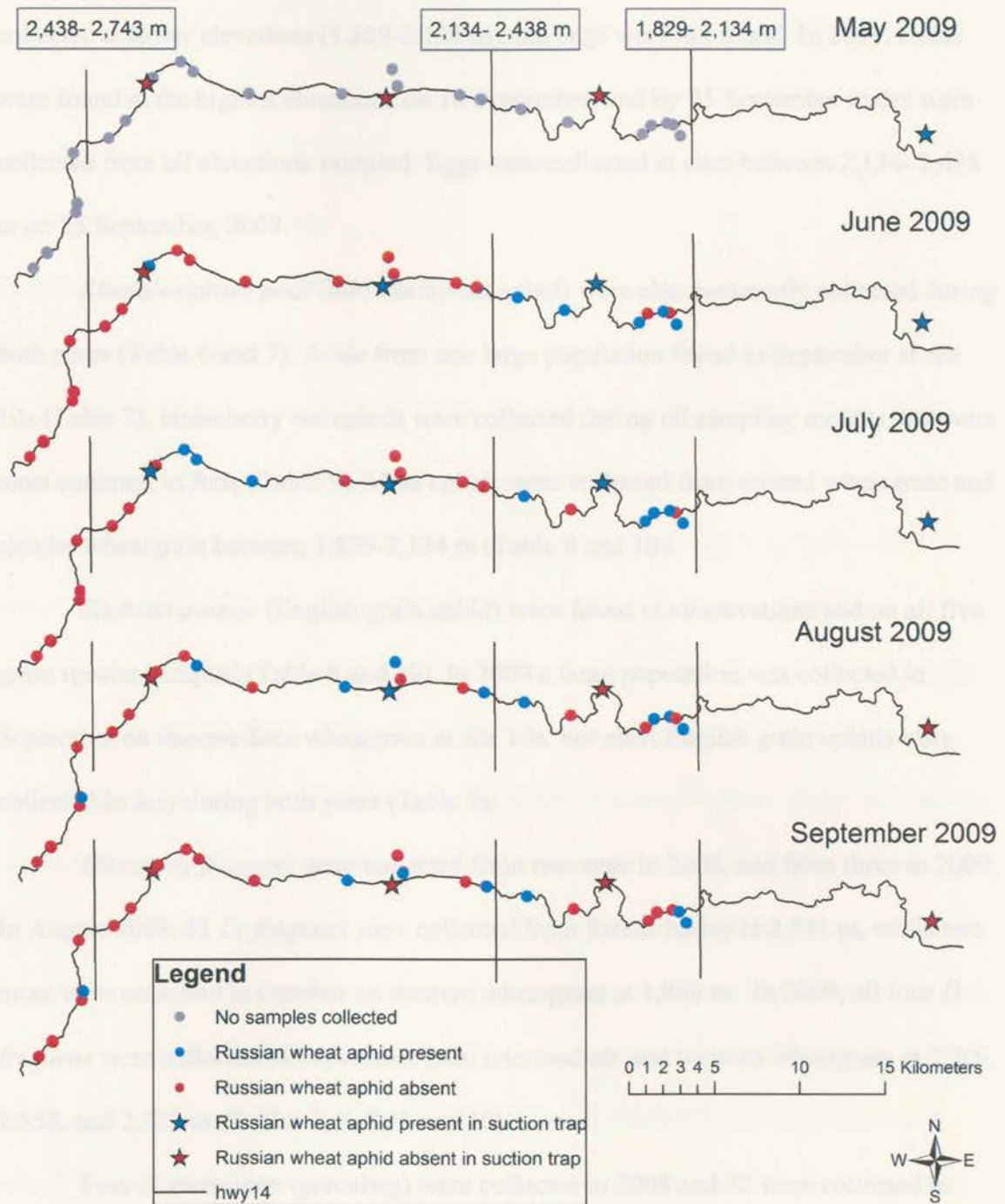


Figure 7. Total Russian wheat aphids at 305 m elevational intervals, per month (weekly collection from June 17- September 30, 2009) from five grass species between 1,829-2,743 m in the Cache La Poudre River canyon, Larimer County, Colorado.



*Does not include the 1,326 Russian wheat aphids collected from a large population found at 2,209 m in September on intermediate wheatgrass.

Figure 8. Monthly presence or absence of Russian wheat aphid per site and suction trap (weekly site collection from June 17- September 30, 2009, weekly suction trap samples from May 15- September 30, 2009) in the Cache La Poudre River canyon, Larimer County, Colorado.



(Table 9). *Sipha elegans* sexual morphs and eggs were collected in 2008 and 2009 (Tables 6 and 7). In 2008, the first males were collected on 25 September, between 2,134-2,743 m, and eggs were found on 9 October at the same sites. Males also were collected at lower elevations (1,829-2,134 m), but eggs were not found. In 2009, males were found at the highest elevations on 10 September, and by 25 September males were collected from all elevations sampled. Eggs were collected at sites between 2,134- 2,438 m on 25 September, 2009.

Rhopalosiphum padi (bird-cherry oat aphid) were also commonly collected during both years (Table 6 and 7). Aside from one large population found in September at site 10a (Table 7), bird-cherry oat aphids were collected during all sampling months, but were most common in June (Table 9). Most aphids were collected from crested wheatgrass and slender wheatgrass between 1,829-2,134 m (Table 8 and 10).

Sitobion avenae (English grain aphid) were found at all elevations and on all five grass species sampled (Table 8 and 10). In 2009 a large population was collected in September on intermediate wheatgrass at site 10a, but most English grain aphids were collected in July during both years (Table 9).

Diuraphis frequens were collected from two sites in 2008, and from three in 2009. In August 2008, 33 *D. frequens* were collected from foxtail barley at 2,551 m, while two more were collected in October on western wheatgrass at 1,868 m. In 2009, all four *D. frequens* were collected in September from intermediate and western wheatgrass at 2,209, 2,558, and 2,730 m (Tables 6, 7, 8, 9, and 10).

Four *S. graminum* (greenbug) were collected in 2008 and 32 were collected in 2009. Aside from one large population at site 10a in September 2009, greenbug were

mainly collected in June, September, and October. Greenbug were collected from all five grass hosts, and were mainly found between 1,829-2,134 m and 2,438- 2,743 m (Tables 6, 7, 8, 9, and 10).

Thrips were the most abundant arthropod collected in 2008 and 2009, but mites also were numerous (Table 6 and 7). The most common thrips collected were *A. stylifer* and *C. aculeatus*. The most common mites collected were *O. pratensis*, *T. urticae*, and eriophyid mites (Tables 8-10).

Suction Trap Collections (2008 and 2009)

Russian wheat aphid

Alate aphids were collected with four suction traps at 1,655 m, 1,992 m, 2,206 m, and 2,372 m. Suction trap samples were examined for the same aphid species as in the grass samples. Ten Russian wheat aphids were collected in the traps in 2008, and 206 were collected in 2009. Russian wheat aphids were found in the traps from May-September, but none were found in October (Table 11). The most Russian wheat aphids were collected in June (Table 11), and in the lowest trap at 1,655m (Table 12). As the traps increased in elevation, less Russian wheat aphids were collected. Only one Russian wheat aphid was collected from the trap at the highest elevation (Table 12).

In July and August 2008, Russian wheat aphids were collected only in the 1,992 and 2,206 m traps. In September 2008, the only capture was in the lowest trap at 1,655 m (Figure 9). In May 2009, Russian wheat aphids were collected at 1,655m, but by June aphids were collected at 1,655, 1,992, and 2,206 m. In July 2009, less Russian wheat aphids were collected from each trap than the previous month. The only Russian wheat aphid collected from the 2,372 m suction trap was collected on 8 July, 2009. By August

Table 11. Monthly aphid collections, July- October 2008 and May- September 2009, from four suction traps at elevations 1,655, 1,992, 2,206, and 2,372 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species ¹	Individual aphids per month													
	May		June		July		August		September		October		Total	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
<i>Diuraphis noxia</i>	-	15	-	171	2	19	7	1	1	0	0	-	10	206
<i>Diuraphis frequens</i>	-	0	-	0	0	2	0	0	0	0	0	-	0	2
<i>Sipha elegans</i>	-	0	-	0	0	0	0	1	0	1	0	-	0	2
<i>Rhopalosiphum padi</i>	-	22	-	714	1	67	99	91	448	301	83	-	631	1,195
<i>Rhopalosiphum maidis</i>	-	3	-	15	0	15	41	54	69	43	12	-	122	130
<i>Sitobion avenae</i>	-	0	-	14	0	3	1	12	24	7	4	-	29	36
<i>Schizaphis graminum</i>	-	0	-	54	0	0	0	3	0	2	3	-	3	59
<i>Metopolophium dirhodum</i>	-	1	-	20	0	1	5	0	4	0	0	-	9	22

The 1,655m suction trap was 8.5 m tall and weekly collection occurred from August 26- October 30, 2008 and May 15- September 30, 2009.

The 1,992, 2,206, and 2,372 m suction traps were 1.5 m tall and weekly collection occurred from July 30- October 30, 2008 and May 15- September 30, 2009.

¹Aphid species surveyed but not found- *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*

Table 12. Total aphids collected per suction trap in the Cache La Poudre River canyon, Larimer County, Colorado.

Aphid Species*	Individual aphids per suction trap									
	1,655 m ¹		1,992 m ²		2,206 m ²		2,372 m ²		Total	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
<i>Diuraphis noxia</i>	1	145	7	41	2	19	0	1	10	206
<i>Diuraphis frequens</i>	0	0	0	0	0	0	0	2	0	2
<i>Sipha elegans</i>	0	1	0	0	0	1	0	0	0	2
<i>Rhopalosiphum padi</i>	237	537	111	148	163	348	120	162	631	1,195
<i>Rhopalosiphum maidis</i>	32	30	35	67	30	23	25	10	122	130
<i>Sitobion avenae</i>	20	20	2	3	4	6	3	7	29	36
<i>Schizaphis graminum</i>	3	44	0	6	0	8	0	1	3	59
<i>Metopolophium dirhodum</i>	2	9	0	8	4	3	3	2	9	22

¹ The 1,655m suction trap was 8.5 m tall and weekly collection occurred from August 26- October 30, 2008 and May 15- September 30, 2009.

² The 1,992, 2,206, and 2,372 m suction traps were 1.5 m tall and weekly collection occurred from July 30- October 30, 2008 and May 15- September 30, 2009.

*Aphid species surveyed but not found- *Diuraphis tritici*, *Diuraphis nodulus*, *Sipha flava*

Figure 9. Total Russian wheat aphids, collected per suction trap, per month, in the Cache La Poudre River canyon, Larimer County, Colorado.



The 1,655m trap was 8.5 m tall and weekly collection occurred from August 26- October 30, 2008.

The traps at 1,992, 2,206, and 2,372 m were 1.5 m tall and weekly collection occurred July 30- October 30, 2008.

2009 only one aphid was collected, and it was found in the 2,206 m trap. No Russian wheat aphids were collected in any suction trap in September (Figure 10).

Other Aphids

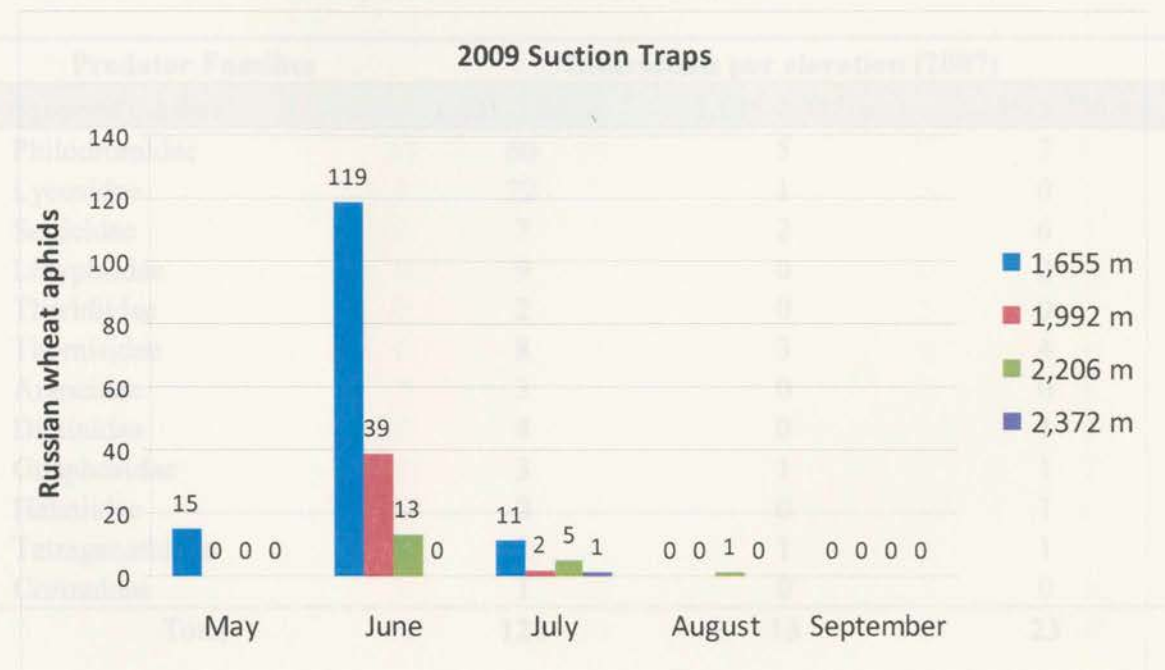
Rhopalosiphum padi was the most commonly collected aphid in all four traps, but was most prevalent in the lowest, 1,655m trap. *Rhopalosiphum maidis* were also prevalent in all four traps, especially in August and September. *Sitobion avenae*, *S. graminum*, *M. dirhodum* were collected from all four traps in 2008 and 2009, but most were found in the 1,655 m trap. The most *S. graminum* and *M. dirhodum* were captured in June (Tables 11 and 12).

Diuraphis frequens and *S. elegans* were only collected in 2009. *Sipha elegans* was the most common aphid collected from the grass samples in both 2008 and 2009, but only two were collected in the suction traps in 2009. One aphid was collected in August at 2,206 m, and the other was collected in September, at 1,655 m. Only two *D. frequens* were collected in 2009, both were found in July at 2,372 m (Tables 11 and 12).

Predator Collections (2007)

In 2007, aphid predators were collected from 23 August- 13 September to refine sampling methods. Aphid predators such as spiders, harvestmen, and insects were collected with a vacuum sampler, and identified to the family level. No parasitoids were sampled, because aphid populations were not large enough to collect and place in emergence canisters. Spiders were the most abundant predator group in 2007, as twelve spider families were collected. The most common spider families were Philodromidae and Lycosidae (Tables 13-15). Spider individuals were most abundant between 1,829-2,134 m (Table 13). One harvestmen family was collected, including 14 individuals, 12

Figure 10. Total Russian wheat aphids, collected per suction trap, per month, in the Cache La Poudre River canyon, Larimer County, Colorado.



The 1,655m trap was 8.5 m tall, and traps at 1,992, 2,206, and 2,372 m were 1.5 m tall. Collection occurred from May 15- September 30, 2009.

Family	1,655 m	1,992 m	2,206 m	2,372 m
Lygellidae	2	3	0	0
Certhidae	10	0	1	0
Coccinellidae	3	3	1	0
Nabidae	1	1	3	0
Psephenidae	2	0	0	0
Syrphidae	0	0	1	0
Total	18	7	5	0

Table 13. Total predators collected per family and elevation (weekly collection from August 23- September 13, 2007) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Predator Families	Individuals per elevation (2007)		
	1,891-2,087m	2,138-2,412m	2,445-2,730m
Spider Families			
Philodromidae	60	5	7
Lycosidae	22	1	0
Salticidae	7	2	6
Linyphiidae	9	0	2
Theridiidae	2	0	0
Thomisidae	8	3	4
Araneidae	3	0	0
Dictinidae	4	0	1
Gnaphosidae	3	1	1
Hahniidae	0	0	1
Tetraganathidae	2	1	1
Corinnidae	1	0	0
Total	121	13	23
Harvestmen Family			
Phalangidae	1	1	12
Insect Families			
Lygaeidae	2	5	0
Carabidae	10	0	8
Coccinellidae	3	3	1
Nabidae	1	1	5
Reduviidae	2	0	0
Syrphidae	0	0	1
Total	18	9	15

Table 14. Total predators collected per family and grass species (weekly collection from August 23- September 13, 2007) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Predator Families		Individuals per grass species (2007)				
Spider Families	Crested	Intermediate	Foxtail	Slender	Western	
Philodromidae	13	11	0	27	21	
Lycosidae	9	3	0	6	5	
Salticidae	3	5	0	2	5	
Linyphiidae	0	5	0	0	6	
Theridiidae	0	0	0	2	0	
Thomisidae	2	3	0	4	6	
Araneidae	2	0	0	1	0	
Dictinidae	0	1	0	1	3	
Gnaphosidae	0	2	0	1	2	
Hahniidae	0	1	0	0	0	
Tetraganathidae	1	0	0	2	1	
Corinnidae	0	0	0	1	0	
Total	30	31	0	47	49	
Harvestmen Family						
Phalangidae	1	10	0	1	2	
Insect Families						
Lygaeidae	3	0	0	2	2	
Carabidae	10	6	0	2	0	
Coccinellidae	3	1	0	1	2	
Nabidae	1	4	0	2	0	
Reduviidae	1	0	0	1	0	
Syrphidae	1	0	0	0	0	
Total	19	11	0	8	4	

Table 15. Total predators collected per family and month (weekly collection from August 23- September 13, 2007) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, in Larimer County, Colorado.

Predator Families	Individuals per month (2007)	
	August	September
Spider Families		
Philodromidae	56	16
Lycosidae	15	8
Salticidae	13	2
Linyphiidae	7	4
Theridiidae	0	2
Thomisidae	11	4
Araneidae	3	0
Dictinidae	5	0
Gnaphosidae	5	0
Hahniidae	0	1
Tetraganathidae	2	2
Corinnidae	1	0
Total	118	39
Harvestmen Family		
Phalangiidae	10	4
Insect Families		
Lygaeidae	5	2
Carabidae	16	2
Coccinellidae	6	1
Nabidae	5	2
Reduviidae	1	1
Syrphidae	1	0
Total	34	8

of which were collected between 2,438- 2,743 m (Table 13). Eight predatory insect families were collected, the most abundant was Carabidae.

Predator Collections (2008 and 2009)

In 2008, aphid predators were collected from 12 June- 30 October. The five most abundant predators were the spider families Philodromidae, Lycosidae, the insect family Lygaeidae (subfamily: Geocorinae), the harvestmen family Phalangidae, and the spider family Salticidae (Tables 16 and 17).

In 2009, predators were collected from 17 June- 30 September. The five most abundant predators in 2009 included the spider families Philodromidae, Lycosidae, and Linyphiidae, the insect family Carabidae, and the spider family Araneidae (Tables 18-19).

Spiders were the most abundant aphid predator collected during both years. Fifteen spider families were collected, including 873 individuals in 2008, and 921 individuals in 2009. More spider individuals were collected between 1,829-2,134 m than at higher elevations (Table 20). Spiders also were more abundant in August and September (Table 21).

Harvestmen were also common, but Phalangidae was the only family collected. Harvestmen were equally abundant June- August, with less collected in September- October (Table 21). Harvestmen were collected at all elevations sampled, but more were found between 2,134- 2,743 m (Table 20).

Eleven insect predator families were collected (Tables 17 and 19). The most common families were Lygaeidae, Carabidae, Coccinellidae, Nabidae, and Staphylinidae. More insect predators were collected between 1,829- 2,134 m than at higher elevations (Table 20).

Table 16. Total spiders and harvestmen collected per family and site (weekly collection from June 12- October 30, 2008) from five grass species, between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Site	Grass Species	Elevation (m)	Total spiders per family and site (June-October 2008)															Harvestmen
			Philodromidae	Lycosidae	Salticidae	Linyphiidae	Theridiidae	Thomisidae	Araneidae	Dicrinidae	Graphosidae	Hahniidae	Tetragnathidae	Agelenidae	Pisauridae	Corinnidae	Oxyopidae	Phalangidae
1	Slender	1,891	24	7	1	7	0	0	2	1	0	1	0	0	0	1	0	3
2	Intermediate	1,867	79	1	11	1	2	3	1	0	0	0	0	0	0	0	0	2
3	Crested	1,860	11	26	6	3	1	5	2	2	1	0	0	0	0	0	0	
4a	Western	1,868	57	24	5	19	17	5	2	0	0	1	0	0	1	0	0	2
4b	Slender	1,868	20	24	1	10	9	4	5	1	1	2	1	0	1	0	0	4
5	Intermediate	1,896	9	2	5	1	1	0	3	0	0	0	0	0	0	0	0	1
6	Intermediate	2,031	14	0	3	2	2	1	2	2	2	0	1	0	0	0	0	0
7	Crested	2,087	22	0	1	0	1	2	0	1	2	0	0	0	0	0	0	3
8a	Crested	2,138	10	2	3	0	0	0	0	0	2	0	0	0	0	0	0	0
8b	Western	2,138	2	0	1	0	0	2	1	2	1	0	0	0	0	0	0	0
9	Western	2,145	3	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
10a	Intermediate	2,209	11	2	2	1	2	1	2	1	0	0	0	0	0	0	0	5
10b	Western	2,209	14	5	0	2	0	0	2	0	0	0	0	0	0	0	0	11
11a	Slender	2,306	1	0	0	0	6	1	0	0	0	1	0	0	0	0	0	2
11b	Foxtail	2,306	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	1
12a	Crested	2,239	27	2	3	1	0	0	0	1	1	0	0	0	0	0	0	1
12b	Slender	2,239	43	6	7	0	0	0	0	1	2	0	0	0	0	0	0	1
13	Crested	2,333	23	3	2	1	0	0	0	4	1	0	0	0	0	0	0	0
14	Crested	2,356	3	3	2	1	0	2	0	0	0	0	0	0	0	0	0	1
15	Intermediate	2,363	9	0	0	0	0	0	2	3	0	0	0	0	0	0	0	1
16	Crested	2,367	4	0	2	0	0	0	0	1	0	0	0	0	0	0	1	0
17	Crested	2,391	15	9	2	0	0	3	4	0	7	0	0	1	0	0	0	3
18	Crested	2,412	17	7	1	0	1	3	0	1	0	0	0	0	0	0	0	2
19	Crested	2,445	4	1	0	0	0	0	0	0	1	0	0	0	0	0	0	3
20a	Crested	2,551	3	1	3	2	2	1	0	1	0	0	0	0	0	0	0	2
20b	Slender	2,551	1	0	2	0	0	0	0	1	0	0	0	0	0	0	0	1
20c	Intermediate	2,551	10	0	2	1	0	0	0	0	1	0	0	0	0	0	0	0
20d	Foxtail	2,551	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
21	Intermediate	2,558	6	0	1	0	0	2	0	1	0	0	0	0	0	0	0	5
22a	Slender	2,698	3	0	0	1	1	1	0	1	2	0	1	0	0	0	0	2
22b	Foxtail	2,698	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	Western	2,730	0	0	0	0	1	0	0	1	1	0	0	1	0	0	0	10
	Total		450	125	67	53	46	37	30	26	25	5	3	2	2	1	1	68

Table 17. Total insect predators collected per family and site (weekly collection from June 12- October 30, 2008) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, in Larimer County, Colorado.

Site	Grass Species	Elevation (m)	Total insects per family and site (June-October 2008)										
			Lygaeidae	Carabidae	Coccinellidae	Nabidae	Reduviidae	Syrphidae	Hemeroptera	Chrysopidae	Staphylinidae	Anthocoridae	Neuroptera
1	Slender	1,891	0	1	0	1	0	0	0	0	0	0	0
2	Intermediate	1,867	6	3	3	1	2	0	1	0	0	0	0
3	Crested	1,860	13	10	3	0	1	2	2	0	0	0	0
4a	Western	1,868	16	4	1	0	2	0	0	0	0	0	0
4b	Slender	1,868	7	3	6	0	0	0	0	0	0	0	0
5	Intermediate	1,896	2	0	1	0	0	0	0	0	0	0	0
6	Intermediate	2,031	1	2	0	0	0	0	0	0	0	0	0
7	Crested	2,087	6	0	0	1	1	0	0	0	0	0	0
8a	Crested	2,138	10	0	0	2	0	0	0	0	0	0	0
8b	Western	2,138	10	1	0	6	0	0	0	0	0	0	0
9	Western	2,145	0	0	0	1	0	0	0	0	0	0	0
10a	Intermediate	2,209	0	0	3	4	0	1	0	0	0	0	0
10b	Western	2,209	0	0	0	1	0	0	0	0	0	0	0
11a	Slender	2,306	2	2	2	10	0	0	0	1	0	0	0
11b	Foxtail	2,306	0	0	1	0	0	0	0	0	0	0	0
12a	Crested	2,239	5	1	2	0	0	0	0	0	0	0	0
12b	Slender	2,239	10	0	5	2	0	1	0	0	0	0	0
13	Crested	2,333	2	1	0	0	0	0	0	0	0	0	0
14	Crested	2,356	2	0	1	0	0	0	0	0	0	0	0
15	Intermediate	2,363	0	0	1	0	0	0	0	0	0	0	0
16	Crested	2,367	1	1	0	0	0	0	0	0	0	0	0
17	Crested	2,391	0	4	1	0	0	0	0	0	0	0	0
18	Crested	2,412	2	7	0	0	0	0	0	0	0	0	0
19	Crested	2,445	1	0	1	1	0	0	0	0	0	0	0
20a	Crested	2,551	0	1	1	0	0	0	0	0	0	0	0
20b	Slender	2,551	0	0	0	0	0	0	0	0	0	0	0
20c	Intermediate	2,551	0	0	0	0	0	0	0	0	0	0	0
20d	Foxtail	2,551	0	0	0	0	0	0	0	0	0	0	0
21	Intermediate	2,558	0	1	1	0	0	0	0	0	0	0	0
22a	Slender	2,698	0	0	2	0	0	0	0	0	0	0	0
22b	Foxtail	2,698	0	0	0	0	0	0	0	0	0	0	0
23	Western	2,730	0	0	0	0	0	0	0	0	0	0	0
	Total		96	42	35	30	6	4	3	1	0	0	0

Table 18. Total spiders and harvestmen collected per family and site (weekly collection from June 17- September 30, 2009) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Site	Grass Species	Elevation (m)	Total spiders per family and site (June-September 2009)															Harvestmen
			Philodromidae	Lycosidae	Salticidae	Linyphiidae	Theridiidae	Thomisidae	Araneidae	Dictynidae	Gnaphosidae	Hahniidae	Tetragnathidae	Agelenidae	Pisauridae	Corinnidae	Oxyopidae	Phalangidae
1	Slender	1,891	16	6	0	46	2	1	14	1	0	0	1	1	1	0	0	1
2	Intermediate	1,867	63	3	3	3	3	4	4	1	0	0	1	0	0	0	0	1
3	Crested	1,860	31	63	5	8	2	5	13	2	1	0	0	0	1	0	0	6
4a	Western	1,868	24	41	2	53	32	4	13	0	2	0	4	0	0	0	0	3
4b	Slender	1,868	19	8	1	10	1	1	4	0	1	0	0	0	0	0	0	2
5	Intermediate	1,896	20	1	2	0	4	3	2	14	0	0	1	0	0	0	0	0
6	Intermediate	2,031	14	4	2	8	0	1	0	2	0	0	0	0	0	1	0	0
7	Crested	2,087	5	2	2	2	2	1	2	1	0	0	0	1	0	1	0	3
8a	Crested	2,138	12	2	0	0	0	1	0	0	1	0	0	0	0	0	0	0
8b	Western	2,138	10	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
9	Western	2,145	6	2	1	0	1	0	0	1	1	0	0	0	0	0	0	1
10a	Intermediate	2,209	5	2	2	2	0	0	1	1	2	0	0	0	0	0	0	0
10b	Western	2,209	5	6	2	4	1	0	2	1	1	0	2	0	0	0	0	3
11a	Slender	2,306	3	9	0	5	4	1	4	2	0	4	0	0	0	0	0	6
11b	Foxtail	2,306	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
12a	Crested	2,239	13	0	6	0	0	1	2	0	0	0	0	0	1	0	0	1
12b	Slender	2,239	8	0	2	1	0	0	0	0	1	0	0	0	0	1	0	1
13	Crested	2,333	7	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0
14	Crested	2,356	2	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
15	Intermediate	2,363	9	1	2	0	1	0	1	0	0	0	0	0	0	0	0	1
16	Crested	2,367	2	4	2	0	0	0	1	2	0	0	0	0	0	0	0	0
17	Crested	2,391	9	18	3	0	1	1	3	0	1	0	0	0	0	0	0	1
18	Crested	2,412	3	10	1	0	0	1	0	0	2	0	0	0	0	0	0	4
19	Crested	2,445	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	3
20a	Crested	2,551	4	0	3	0	0	0	0	0	0	0	0	0	0	0	0	4
20b	Slender	2,551	4	0	2	0	0	1	0	0	0	0	0	0	0	0	0	3
20c	Intermediate	2,551	3	0	1	0	0	0	0	0	0	1	0	0	0	0	0	2
20d	Foxtail	2,551	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
21	Intermediate	2,558	2	0	0	0	0	0	0	0	0	1	0	0	0	0	0	4
22a	Slender	2,698	2	0	1	1	0	1	1	1	0	0	0	0	0	0	0	2
22b	Foxtail	2,698	0	0	1	0	0	1	2	0	0	0	0	0	0	0	0	0
23	Western	2,730	0	0	0	4	0	0	10	0	4	2	0	0	0	0	0	15
	Total		302	183	48	148	55	29	80	31	18	8	9	2	2	4	0	69

Table 19. Total insect predators collected per family and site (weekly collection from June 17- September 30, 2009) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Site	Grass Species	Elevation (m)	Total insects per family and site (June-September 2009)										
			Lygaeidae	Carabidae	Coccinellidae	Nabidae	Reduviidae	Syrphidae	Hemerobiidae	Chrysopidae	Staphylinidae	Anthocoridae	Neuroptera
1	Slender	1,891	0	4	0	5	0	0	0	0	0	0	0
2	Intermediate	1,867	4	5	2	0	0	0	0	0	1	0	0
3	Crested	1,860	3	7	0	3	3	1	0	0	6	1	0
4a	Western	1,868	7	15	4	5	1	0	0	0	14	0	0
4b	Slender	1,868	4	13	1	3	0	0	0	0	4	0	0
5	Intermediate	1,896	0	2	0	0	0	0	0	1	0	0	0
6	Intermediate	2,031	0	6	0	1	0	0	0	0	1	0	0
7	Crested	2,087	5	7	2	1	0	0	0	0	0	0	0
8a	Crested	2,138	5	0	0	1	0	0	0	0	0	0	0
8b	Western	2,138	2	2	1	0	1	0	0	0	0	0	0
9	Western	2,145	5	11	0	1	0	0	0	0	1	0	0
10a	Intermediate	2,209	0	4	0	1	0	0	0	0	2	0	0
10b	Western	2,209	0	4	1	1	0	0	0	0	2	0	0
11a	Slender	2,306	2	6	1	6	0	0	1	1	0	0	0
11b	Foxtail	2,306	0	1	0	0	0	0	0	0	0	0	0
12a	Crested	2,239	6	2	5	1	0	0	0	0	0	0	0
12b	Slender	2,239	7	0	5	2	0	0	0	0	0	0	0
13	Crested	2,333	0	0	0	0	0	0	0	0	0	0	0
14	Crested	2,356	0	0	0	1	1	0	0	0	0	0	1
15	Intermediate	2,363	0	1	0	0	0	0	0	0	1	0	0
16	Crested	2,367	0	0	2	0	0	0	0	0	0	0	0
17	Crested	2,391	2	1	1	4	0	0	0	0	0	0	0
18	Crested	2,412	2	3	0	1	0	0	0	0	0	0	0
19	Crested	2,445	0	2	0	0	0	0	0	0	0	1	0
20a	Crested	2,551	2	0	0	3	0	0	0	0	0	0	0
20b	Slender	2,551	1	0	0	1	0	0	0	0	1	0	0
20c	Intermediate	2,551	0	1	0	0	0	0	0	0	0	0	0
20d	Foxtail	2,551	0	2	0	0	0	0	0	0	0	0	0
21	Intermediate	2,558	0	1	0	0	0	0	0	0	0	0	0
22a	Slender	2,698	0	1	0	0	0	0	0	0	0	0	0
22b	Foxtail	2,698	1	1	2	0	0	0	0	0	0	0	0
23	Western	2,730	0	0	1	0	0	0	0	0	0	0	0
	Total		58	102	28	41	6	1	1	2	33	2	1

Table 20. Total predators collected per family and elevation (weekly collection from June 12- October 30, 2008, and June 17- September 30, 2009) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Predator Families	Individuals per elevation					
	1,891-2,087m		2,138-2,412m		2,445-2,730m	
Spider Families	2008	2009	2008	2009	2008	2009
Philodromidae	236	192	182	94	32	16
Lycosidae	84	128	39	55	2	0
Salticidae	33	17	26	22	8	9
Linyphiidae	43	130	6	13	4	5
Theridiidae	33	46	9	11	4	0
Thomisidae	20	20	13	5	4	4
Araneidae	17	52	13	15	0	13
Dictinidae	7	21	14	9	5	1
Gnaphosidae	6	4	14	10	5	4
Hahniidae	4	0	1	4	0	4
Tetraganathidae	2	7	0	2	1	0
Agelenidae	0	2	1	0	1	0
Pisauridae	2	1	0	1	0	0
Corinnidae	1	3	0	1	0	0
Oxyopidae	0	0	1	0	0	0
Total	488	623	319	242	66	56
Harvestmen Family						
Phalangidae	15	16	28	19	25	34
Insect Families						
Lygaeidae	51	23	44	31	1	4
Carabidae	23	59	17	35	2	8
Coccinellidae	14	9	16	16	5	3
Nabidae	3	18	26	19	1	4
Reduviidae	6	4	0	2	0	0
Syrphidae	2	1	2	0	0	0
Hemerobiidae	3	0	0	1	0	0
Chrysopidae	0	1	1	1	0	0
Anthocoridae	0	1	0	0	0	1
Staphylinidae	0	26	0	6	0	1
Neuroptera	0	0	0	1	0	0
Total	102	142	106	112	9	21

Table 21. Total predators collected per family and month (weekly collection from June 12- October 30, 2008, and June 17- September 30, 2009) from five grass species between 1,829-2,743 m, in the Cache La Poudre River canyon, Larimer County, Colorado.

Predator Families	Individuals per month									
	June		July		August		September		October	
	2008	2009	2008	2009	2008	2009	2008	2009	2008	2009
Spider Families										
Philodromidae	52	26	92	59	131	59	127	158	48	-
Lycosidae	23	36	14	21	21	60	46	66	21	-
Salticidae	10	10	16	10	28	11	11	17	2	-
Linyphiidae	13	16	13	10	4	31	20	91	3	-
Theridiidae	5	8	7	10	14	14	13	25	7	-
Thomisidae	8	6	5	12	9	7	12	4	3	-
Araneidae	9	4	10	4	5	25	5	47	1	-
Dictinidae	8	7	10	6	4	12	3	6	1	-
Gnaphosidae	6	1	6	5	7	9	5	3	1	-
Hahniidae	1	0	1	3	0	1	2	4	1	-
Tetraganathidae	0	0	1	2	1	5	1	2	0	-
Agelenidae	1	0	0	1	0	0	0	1	1	-
Pisauridae	0	1	0	1	0	0	1	0	1	-
Corinnidae	0	2	0	2	0	0	1	0	0	-
Oxyopidae	0	0	0	0	0	0	1	0	0	-
Total	136	117	175	146	224	234	248	424	90	-
Harvestmen Family										
Phalangidae	20	10	15	28	18	26	12	5	3	-
Insect Families										
Lygaeidae	12	7	15	17	27	16	33	18	9	-
Carabidae	1	4	32	32	7	29	2	37	0	-
Coccinellidae	6	4	15	19	5	5	6	0	3	-
Nabidae	1	3	6	11	6	10	10	17	7	-
Reduviidae	2	3	0	1	1	2	1	0	2	-
Syrphidae	3	0	1	1	0	0	0	0	0	-
Hemerobiidae	0	1	0	0	1	0	1	0	1	-
Chrysopidae	0	0	0	1	0	1	0	0	1	-
Anthocoridae	0	1	0	0	0	1	0	0	0	-
Staphylinidae	0	2	0	8	0	16	0	7	0	-
Neuroptera	0	0	0	0	0	1	0	0	0	-
Total	25	25	69	90	47	81	53	79	23	-

DISCUSSION

While the Russian wheat aphid is a pest of wheat, its ability to colonize noncultivated grass hosts has long been a concern to managers. The aphid's economic impact is partially dependent upon its ability to utilize several hosts for overwintering (Kindler and Hays 1999). Grass hosts may also provide selective pressures and resistance by means of antibiosis or antixenosis (Ni and Quisenberry 1997). Furthermore, the Russian wheat aphid's ability to utilize several hosts may facilitate long distance movement of the pest. Long distance movement away from wheat fields would require the Russian wheat aphid to survive in more heterogeneous environments, which could present further selective pressures.

The Russian wheat aphid has been found at elevations up to 3,452 m in Colorado (Randolph et al. unpublished data). This study was designed to elucidate Russian wheat aphid occurrence, movement, and holocycle in high elevation environments. In 2008, a total of 141 Russian wheat aphids were collected from June through October, and in 2009, 1,537 total Russian wheat aphids were collected, including one large population. Russian wheat aphid populations fluctuate from year to year and, in 2008, only four Russian wheat aphids were collected in a suction trap on the High Plains near Briggsdale, Colorado suggesting aphid populations were relatively low (Peairs et al. 2009). In 2009, high Russian wheat aphid densities were seen throughout the Colorado wheat producing regions (Frank Peairs, Department of Bioagricultural Sciences and Pest Management, Colorado State University, personal communication).

More aphids may have been collected during the summer of 2009 because of a large number of immigrants from wheat producing areas to the east, or because local environmental conditions were more favorable than in 2008. The study location received more rain in the early summer of 2009 than in 2008, and subsequently the grasses stayed succulent for a longer period. The study location received only a small amount of rain in 2008, and grasses began to senesce by July. During this time, Russian wheat aphids were found at the highest elevations (2,438-2,743 m) by July (Figure 5 and 6). It is possible that aphids moved to higher elevations to find grasses in early vegetative states. In 2009, fewer aphids were found at the highest elevations, and they were not collected there until August (Figure 7 and 8). Better host quality at the lower elevations sampled may have delayed movement to higher elevations.

The large Russian wheat aphid population discovered in September 2009 at site 10a was found inhabiting a healthy, green patch of intermediate wheatgrass, on the west facing slope, next to a small stream along N. County Road 69 near Rustic. This aphid population was probably present throughout the summer, but was not detected until 10 September. Another large Russian wheat aphid population was discovered in the Cache la Poudre River Canyon at 2,239 m on crested wheatgrass during a 2006 survey conducted by Randolph et al. (unpublished data). Both crested and intermediate wheatgrass are favorable and common hosts utilized by the Russian wheat aphid (Armstrong et al. 1991, Mowry et al. 1995, Hammon et al. 1997). Russian wheat aphid is capable of considerable reproduction on these two hosts in high elevation environments.

Five of the Russian wheat aphid's preferred grass hosts were intensely sampled at 23 sites during this study. The Russian wheat aphid was found on each of the five hosts

sampled, indicating that these hosts are capable of supporting the aphid. Crested wheatgrass, the most commonly encountered species in the Cache La Poudre River canyon, harbored the most Russian wheat aphids. This may be due to the greater abundance of crested wheatgrass rather than the greater suitability as a Russian wheat aphid host.

The fewest Russian wheat aphids were collected from western wheatgrass, which may be a result of antixenosis. Kindler et al. (1993) found the western wheatgrass genera, *Pascopyrum*, to be tolerant to moderately susceptible to Russian wheat aphid feeding. Western wheatgrass has strongly ribbed leaves, covered by a waxy powder, which may make it difficult for the aphids to move and feed. Aphids may select grass hosts based on abundance, appearance, physical condition, and surrounding environmental conditions. The Russian wheat aphid can utilize many hosts, and may be able to generate significant reproduction on any of these grass species if the environmental conditions are appropriate.

The Russian wheat aphid is capable of surviving and reproducing in high elevation environments during the summer months. Aphids were found in June, the first month of sampling, but more aphids were collected during July and August, and by September and October aphids were less prevalent. It is difficult to say if the aphids collected in these locations are local or immigrants from lower elevations.

Russian wheat aphid may move from areas of wheat production during the summer as wheat hosts deteriorate, and as local alternative grass hosts begin to senesce. Alate aphids could catch wind currents that would deposit them at higher elevations where hosts are more favorable due to delayed phenology. Aphids are capable of long distance movement

when lifted high enough by convection to reach low-level jet streams (Dixon 1985).

While long-range movement (>100 km) does occur, Loxdale et al. (1993) suggest that it is infrequent, and short-range dispersal (<20 km) is much more common.

This study presents some support for this scenario. Winter wheat crops in Colorado typically begin to dry down in June and July, and during this time Russian wheat aphids begin to produce alate morphs. Peak Russian wheat aphid flight time is usually from June through July (Hammon et al. 1999). Interestingly, the peak Russian wheat aphid flights at the 1,655, 1,992, and 2,206 m suction traps all occurred in June, when wheat plants were beginning to mature.

The most aphids were collected in the 1,655 m trap which was at the mouth of the Cache la Poudre River canyon near the foothills. This trap was also the tallest trap, standing at 8.5 m, and had the most powerful fan. This trap is about 27 km away from any wheat production, and collecting so many Russian wheat aphids at this site during the typical summer flight time suggests that Russian wheat aphids can move from surrounding wheat fields towards the foothills.

In 2009, the peak flights at the 1,992 m and 2,206 m traps were also in June. Since there were many aphids flying around at lower elevations, it is possible that some of the aphids got caught in low-level jet streams and were moved over 47 km from wheat producing areas to the trap locations. This distance is not unheard of, as aphids have been known to move over 100 km (Loxdale et al. 1993). But Halbert et al. (1998) suggest that suction trap captures usually reflect aphid flight activity within a 30 km radius of the trap. The smaller solar powered traps were designed to detect local movement (Belding et al. 1991), so the captures seen at 1,992 m and 2,206 m were probably a result of movement

from more local populations. But if these were local migrants it is unclear why the Russian wheat aphids would be producing winged morphs at this time of the year. Typically, alate aphids are produced in response to overcrowding or poor host quality (Hulle et al. 1994), and during June, grasses at high elevations are in early vegetative states, and aphid overcrowding is rarely an issue. It may be that the aphids were dispersing from oviposition sites, where eggs had hatched in the spring.

It is also possible that local Russian wheat aphid populations reproduce throughout the growing season in high elevation environments. The aphids may be able to overwinter as viviparous adults, or more likely, in the cold-tolerant egg stage. Holocyclic aphid populations typically occupy higher elevations as these environments provide host heterogeneity and regular harsh winter conditions (Frantz et al. 2006).

This study also provides some support for the possibility of year round survival at high elevations. There were a few sites from which Russian wheat aphids were regularly collected during both years. The consistent occurrence of aphids at these sites suggests that there may be a Russian wheat aphid metapopulation (Levins, 1969) at these higher elevations. The sites where aphids were consistently collected may represent source populations that expand under favorable conditions. Most Russian wheat aphids were collected between 1,829- 2,134 m (Table 10), and the three sites with regular collections were at 1,891, 1,860, and 2,087 m. These sites may favor permanent colonization and may serve as sources for aphids colonizing additional sites during the growing season.

It is likely that Russian wheat aphid populations in the Cache La Poudre River canyon are maintained by both immigrant aphids and from local metapopulations within the canyon. Russian wheat aphid populations appear to exist year-round in high elevation

environments. Due to the complexity of the landscape and variable host quality, the aphids may encounter selective pressures different from those experienced in a wheat field.

Temperatures are lower at higher elevations, and Russian wheat aphid populations may require holocycly for year round survival. Male Russian wheat aphids have not been found in North America, but six oviparae were found in Treasure Valley and the Palouse in Idaho and Oregon. According to Kiriac et al. (1990), the winter in the Pacific Northwest, prior to these collections, was unusually harsh. Such conditions could have induced holocycly. Sexual morphs represented less than one percent of the total collections. Kiriac et al. (1990) also found males to be rare in their native Soviet Union range, suggesting males could be overlooked in North America. North American populations of Russian wheat aphid also might be gynocyclic, occasionally producing oviparae but never males (Kiriac et al. 1990).

This study provided no concrete evidence of Russian wheat aphid holocycly. Evidence of sexual reproduction would most likely be found in a large Russian wheat aphid population at high elevation during the fall or early winter. Such a population was found in September 2009, and was sampled throughout the fall, and through several snow events. Several eggs were found within curled leaves surrounded only by Russian wheat aphids. Aphid eggs were collected, but have not been identified. The eggs collected either were preserved for genetic identification or saved so hatching can be induced in the spring. *Sipha elegans* was present at this location, and its eggs cannot be distinguished morphologically from Russian wheat aphid eggs.

Other Aphids

No key describing Russian wheat aphid sexual morphs has been published. Generally, male aphids have a sclerotized genital structure, smaller abdomens, longer antenna, and shorter cauda than females (Miyazaki 1987). Male aphid genitalia are diagnostic, especially after being preserved in alcohol. Two immature alate aphids collected from the large Russian wheat aphid site had a unique genital structure similar to a male, and will be further examined. While sorting live aphids from the large population, one female Russian wheat aphid was found with what looked like an egg exiting her body. The aphid was saved, but later was found dead.

Although holocyclic Russian wheat aphid populations were not confirmed during this study, most aphid species developing in heterogeneous environments do benefit from sexual reproduction. Genetic variability resulting from sexual reproduction allows sexual populations to overcome environmental variability and inhabit a broader geographic range (Frantz et al. 2006). If Russian wheat aphid populations living in the Cache La Poudre River Canyon are holocyclic, or are encountering selective pressures from their hosts or environment, it is possible that new biotypes could be generated. Recently, two new Russian wheat aphid biotypes have been discovered in Colorado on noncultivated grass hosts (Weiland et al. 2008).

Russian wheat aphid biotype diversity is a significant management concern. This study shows that Russian wheat aphid populations exist in high elevation environments and that long distance movement is possible. Environmental conditions could prompt the production of novel biotypes and these aphids could disperse by wind currents to cereal producing regions.

Other Aphids

Of the 11 aphid species collected in this survey, *S. elegans* was the most abundant. While *S. elegans* was collected from all five grass species, it was predominantly collected from slender wheatgrass. Dense *S. elegans* populations were often found inhabiting a single leaf. Because so many *S. elegans* were found on the grasses in this study it is surprising that the aphid is not more commonly seen in cereals along the Front Range. This aphid has been known to occur on various *Poaceae* species, including wheat (Blackman and Eastop 1984). *Sipha elegans* was first described at the beginning of the century on *Hordeum murinum* in Italy, then in the early twenties on wheat in southern Russia (Mordvilko 1922). According to Havlickova et al. (1996) *S. elegans* is a common aphid in the Czech Republic and Slovakia on various species of wild grasses. The preferred feeding site of *S. elegans* is the flag leaf, on which feeding produces clear cut yellow patches. In a wheat field, this damage could reduce grain mass (Havlickova et al. 1996). Blackman and Eastop (1984) also propose this aphid is a potential disease vector because it is a monoecious holocyclic aphid species that attacks both wild grass and cultivated cereal crops. No information on the economic damage caused by *S. elegans* on cereal crops is available.

Because *S. elegans* and Russian wheat aphid utilize the same noncultivated grass hosts, interspecific competition may occur. *Sipha elegans* was much more abundant than Russian wheat aphids during this study, and thus may be better adapted, and able to outcompete Russian wheat aphid on high elevation roadside grasses. On wheat plants, *S. elegans* have been commonly found in the center of bird-cherry oat aphid colonies, suggesting an interspecific interaction. Havlickova et al. (1986) suggests that chemical

changes in the wheat plants induced by bird-cherry oat aphids could increase *S. elegans* attraction to the leaf site.

Sipha elegans holocycle may help outcompete Russian wheat aphid at higher elevations. *Sipha elegans* males and eggs were collected at the end of September into October. The ability to successfully overwinter in the egg stage may allow *S. elegans* populations to easily establish in the spring and dramatically multiply throughout the summer. During the first month of sampling, in June 2008 and 2009, 366 and 629 *S. elegans* were collected respectively. In comparison, only 5 and 29 Russian wheat aphids were collected. Readily producing eggs should allow aphids to easily establish the following spring.

Large populations of *S. elegans* were collected from the same sites each year. This suggests that *S. elegans* may be functioning as a metapopulation (Levins, 1969), and these sites could represent source populations that disperse to additional sites during the growing season. While *S. elegans* was the most abundant aphid species collected during this study, only two aphids were captured in the suction traps during both years of operation. It is possible that *S. elegans* fly earlier in the season, when the suction traps were not in operation.

It is unclear why this abundant aphid was so infrequently collected in the traps. Little is known about the aphid's flight and migration patterns. Many *S. elegans* collected from the grasses did have wing pads. Three *S. elegans* were collected in the Briggsdale suction trap in 2008 (Randolph, Department of Bioagricultural Sciences and Pest Management, Colorado State University, personal communication). It is possible that the

aphid does not need to travel long distances in high elevation environments because it does so well on a variety of grass species and at high densities.

Bird-cherry oat aphids were the most common aphid collected in the suction traps and were also commonly found on grass samples. They were collected from grass samples during all sampling months, but were most common in June. The bird-cherry oat aphid flight peaked in June and September. This aphid has been commonly collected in the suction trap network in the grain producing regions of Colorado. Historical suction trap data from 1988 to 1999 show the aphid's peak flights are typically in June, as the wheat crop matures, and in September as corn matures (Hammon et al. 1999). The same peak flights were seen in the 2008 Briggsdale suction trap (Randolph, Department of Bioagricultural Sciences and Pest Management, Colorado State University, personal communication).

Bird-cherry oat aphids have several life cycle phenotypes. Some populations are holocyclic and host-alternating, while others are permanently anholocyclic. Heteroecious holocyclic forms migrate to *Prunus* in the fall where they produce eggs (Hammon et al. 1999). Movement to *Prunus* from grass hosts may account for the large numbers of bird-cherry oat aphids seen in the high elevation suction traps in September. These eggs hatch in the spring, and after a couple generations on *Prunus* they move to wheat or other grasses. During the late summer they infest corn and other grass hosts (Hammon et al. 1999).

In the high elevation suction traps, peak flights also were seen in June for the English grain aphid, greenbug, and rose grass aphid. All of these grain aphids overwinter on noncultivated grass hosts, and in June they are probably moving from

late maturing grains to early maturing grasses. The English grain aphid had another peak flight in September. This aphid may have been returning to grain hosts, as they are known to lay eggs on grains in the fall. The peak corn leaf aphid flight was in August and September. This aphid is not known to produce eggs so they may have been moving to lower elevations and hosts better fit for overwintering as viviparous females. More corn leaf aphids are generally seen in corn in late August and early September (Randolph, Department of Bioagricultural Sciences and Pest Management, Colorado State University, personal communication).

Aphid Predator Collections

Over 100 species of natural enemies attack the Russian wheat aphid worldwide (Pike et al. 1991). The goal of this predator survey was to document aphid predator families at high elevations. Spiders are generalist predators and one of the most abundant arthropod groups in agroecosystems. Cereal aphids constitute a substantial portion of their diet (Alderweireldt 1994). Spiders were the most abundant predators collected here, with fifteen families found. The most common were Philodromidae, Lycosidae, and Linyphiidae.

Spider abundance is dependent on the environment. Spider densities were lower, and fauna was more evenly dispersed over families in a typical United States Great Plains winter wheat habitat than in other parts of the world (Greenstone 2000). The most abundant families were Linyphiidae (one quarter of individuals), Lycosidae 14%, Thomisidae, Gnaphosidae, Tetriginathidae, and Theridiidae (10% each). Linyphiids are even more abundant in winter wheat fields in the United Kingdom (71-100%). In total,

eleven families were found including Araneidae, Dictynidae, Oxyopidae, Philodromidae, and Salticidae (Greenstone 2000).

The same families found by Greenstone (2000) also were found in this study. High elevation environments may support more spider family diversity than a typical agroecosystem. Spiders appeared to be the most prevalent generalist predators in this study, however, predators were collected only by vacuuming so many predator groups could have been missed.

Harvestmen were also common predators found in this survey, but only the family Phalangidae was collected. Harvestmen were collected at all elevations sampled, but unlike the spiders and insects they were more abundant between 2,134-2,743 m.

Harvestmen are generalist predators, but they have family specific food preferences. The family Phalangidae has been reported to feed on aphids (Pinto-Da-Rocha et al. 2007).

Dixon and McKinlay (1989) examined the enteric contents of harvestmen species in a potato field in Scotland. Six species contained aphid remains, and 54% of the most abundant harvestmen species, *Phalangium opilio* (L.), had eaten live aphids. Madsen et al. (2004) analyzed the capability of six generalist predators, including spiders, carabid beetles, and harvestmen to suppress *R. padi* populations in the presence and absence of alternative prey. The harvestmen were the most efficient predators, reducing aphid numbers by more than 90%, with success independent of alternative prey availability. The harvestmen's success may be attributed to a metabolic rate 2-4 times higher than other arachnids. Harvestmen may have been overlooked as an aphid control agent because they are largely absent from tilled fields. Therefore, they may have greater predatory potential in grassland systems or reduced tillage systems (Madsen et al. 2004).

Eleven insect predator families were collected, most commonly Lygaeidae (subfamily: Geocorinae), Carabidae, Coccinellidae, Nabidae, and Staphylinidae. No sampling for parasitoids was conducted. However parasitized Russian wheat aphids were observed at site 10a. Aphid predators are clearly abundant in high elevation environments. During both years more spider and insect predator individuals were collected between 1,829-2,134 m than at higher elevations. Predator numbers may be lower at the higher elevations since aphids occur here later in the season and for shorter amounts of time. As aphids move to higher elevations during the summer, it is possible that the higher they move the less predation they experience.

**RUSSIAN WHEAT APHID *Diuraphis noxia* (Kurdjumov) (Hemiptera: Aphididae)
REPRODUCTION AND DEVELOPMENT ON FIVE NONCULTIVATED GRASS
HOSTS**

INTRODUCTION

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), is an important small grains pest considered one of the most economically damaging pests of wheat (*Triticum aestivum* L.) worldwide (Morrison and Peairs 1998). Development of resistant cultivars has been one of the most successful management techniques for control of Russian wheat aphid. The presence of Russian wheat aphid biotypic diversity can disrupt the progress of plant breeding programs. For example, a new Russian wheat aphid biotype (designated as RWA2) was discovered in Colorado in 2004. This new biotype is virulent to many advanced wheat lines, which were developed to manage RWA1 within the United States and Canada (Haley et al. 2004).

Biotype development can result from selective pressures such as antibiosis and antixenosis expressed by resistant cultivars and noncultivated grass hosts. Porter et al. (1997) studied greenbug, *Schizaphis graminum* (Rondani), biotype development and suggested that noncultivated grass hosts could be a reservoir for aphid biotypes. Since this theory was suggested, several unique greenbug biotypes have been found on noncultivated hosts (Anstead et al. 2003, Burd and Porter 2006). Similarly, Weiland et al. (2008) found two new Russian wheat aphid biotypes on noncultivated grasses. Porter et al. (1997) suggested that noncultivated hosts play an important role in maintaining aphid

genetic diversity, and that exposure to selective pressures on grasses allows for additional diversity that may be needed to exploit resistant cultivars.

The Russian wheat aphid is polyphagous, feeding on winter wheat and barley during the winter and spring, and surviving on noncultivated grass hosts during the summer months (Burd et al. 1998). It is still unclear which cool season grass species are suitable hosts for the Russian wheat aphid, and whether large differences in suitability exist among species (Donahue et al. 2000). In order to determine which alternative hosts are most suitable, it is useful to calculate growth rate parameters, such as the intrinsic rate of increase. The intrinsic rate of increase is the rate of increase, under specified physical conditions in an unlimited environment, where the effects of increasing density are not considered (Birch 1948). The calculation is composed of factors which contribute to population growth, including net reproductive rate, immature development rates, and generation time. An aphid's intrinsic rate of increase is influenced by plant growth stage and quality, temperature, moisture, aphid biotype, and feeding site (Girma et al. 1990). Intrinsic rate of increase calculations are useful in determining host quality because they quantify the aphid's reproductive potential on a host. Typically, selection pressure increases with decreasing host quality, so determining poor hosts can help assess potential refuges and sources of selection pressure (Merrill et al. 2008). Furthermore, changes in an aphid's intrinsic rate of increase could result in expanded geographic range or altered distribution (Randolph et al. 2008).

Noncultivated grass hosts provide the Russian wheat aphid with summer refuges. However, grasses at lower elevations often have senesced by midsummer so aphids may seek grasses at higher elevations that are still in vegetative and early reproductive stages.

Russian wheat aphids have been found on eighteen different grass species at all elevations between 1,524 m and 3,048 m in Colorado (Randolph et al. unpublished data). Grasses found in high elevation environments may be important for year round aphid survival. Few studies have focused on the Russian wheat aphid's reproduction and development on noncultivated hosts, especially those hosts most commonly encountered in high elevation environments.

The first objective of this study was to determine Russian wheat aphid reproductive and development rates, at optimum temperature, on five common noncultivated grass hosts utilized by the aphids at elevations higher than most Colorado wheat production. These hosts included crested wheatgrass (*Agropyron cristatum*, (L.) Gaertn.), intermediate wheatgrass (*Elytrigia intermedia*, (Host) Nevski), slender wheatgrass (*Elymus trachycaulus*, (Link) Gould ex Shinnars), western wheatgrass (*Pascopyrum smithi*, (Rydb.) A. Löve), and foxtail barley (*Hordeum jubatum*, (L.) Tesky). The second objective was to compare Russian wheat aphid reproduction and development under high, optimum, and low temperature regimes on intermediate and crested wheatgrass. Understanding the Russian wheat aphid's population dynamics on these common alternative hosts can help elucidate host quality and potential refuges and sources of selection pressure.

MATERIALS AND METHODS

Separate intrinsic rate of increase studies were conducted under three different temperature regimes. All experiments were conducted in the same growth chamber with a photoperiod of 14:10 (L:D) h. The first experiment included five hosts (intermediate wheatgrass, crested wheatgrass, western wheatgrass, slender wheatgrass, and foxtail barley), and was conducted at a temperature regime of 18-24°C, which is the optimum temperature for reproduction according to Girma et al. (1990) and Randolph et al. (2008). These hosts were selected because they commonly harbor Russian wheat aphids at high elevations (Randolph et al. unpublished data). The second experiment examined two of the five hosts (intermediate and crested wheatgrass) using two temperature regimes (high: 24-29°C, and low: 13-18°C) in addition to the optimum temperature regime examined in the first experiment.

Host Preparation

The hosts used for these experiments included intermediate wheatgrass ('Oahe', Sharp Brothers Seed Company, Healy, Kansas), crested wheatgrass ('Hycrest', Sharp Brothers Seed Company, Healy, Kansas), western wheatgrass ('Native', Pawnee Buttes Seed Inc. Greeley, Colorado), slender wheatgrass ('San Luis', Pawnee Buttes Seed Inc. Greeley, Colorado), and foxtail barley (unknown variety, seed collected from CSU campus). Seeds were germinated in Petri dishes lined with moistened disc style coffee filters. Seeds were planted in 13cm pots containing 3 parts soil, 2 parts peat moss potting soil mixture, and 1 part perlite. Grasses were grown in a greenhouse, and covered with

organza sleeve cages to protect them from natural infestation and predation. All grasses used in this experiment were 2-6 months of age; Feekes stages 2-10.5 (tillering to heading).

Data Collection

Experimentation began when eight pots of each plant species had matured to the same age and growth stage. One clip cage, similar to those described by Hawley et al. (2003), was placed on the youngest leaf on each of the eight plants. Three 3rd-4th instar RWA2, from the Colorado State University colony (aphids from the CSU RWA2 colony were reared on a winter wheat mixture), were placed in each cage. Aphids were moved in and out of the clip cages with a size 0000 sable/synthetic horsehair brush. Experiments were performed in an Environmental Growth Chamber (Model G10, Environmental Growth Chambers, Chagrin Falls, OH) under the appropriately programmed temperature regime (13-18°C, 18-24°C, or 24-29°C). Plants were checked every other day, and watered as needed.

The three aphids in each clip cage were monitored daily until two or three nymphs were born on the same day. At this time, all three original aphids were removed from the cage, leaving the newly born aphids. This date was recorded as the birth date of the aphid of interest. When these aphids reached approximately third instar all but one were removed. The remaining aphid became the aphid of interest. This process insured that the aphid of interest had completed her whole life cycle on the specific grass species to reduce maternal effects. The aphid was monitored every 24 hours for the duration of her life, and all aphids born to her were removed and recorded daily. When the aphid and clip

cage had to be moved due to leaf senescence, they were moved to the youngest unrolled leaf on the same plant.

Statistical Analysis

All statistical analysis was carried out using SAS v. 9.1, Proc GLM and Proc Mixed LSMeans (SAS Institute 2005). Nine life statistic parameters were calculated for each aphid of interest. Life statistics were recorded as described by Hawley et al. (2003) and include pre-nymphipositional period (the number of days until first birth), nymphipositional period (the days lapsed from first birth to last for a given mother), number of nymphs produced per day of nymphipositional period, number of nymph production days (number of days on which the aphid mother actually gave birth), maximum number of nymphs produced in a 24 hour period, longevity (the days between an aphid mothers birth and death), and fecundity (total nymphs produced by each aphid mother). All fecundity data were transformed by the square root method prior to analysis, with original means reported in the results.

Mean generation time (G) was calculated as described by Behle and Michels (1990) using the following formula:

$$G = \sum l_x m_x x / R_o$$

where l_x is the probability of being alive on day x . l_x was generated by first calculating the probability of death on each day. To do so, the probnorm was calculated by subtracting day x by average longevity and dividing by its standard deviation. This number was inserted into SAS (probnorm) to achieve the probability of death on each day. To find the probability of being alive on day x (l_x), the probability of death was subtracted from one. The variable m_x is the average birth rate on day x , and was generated

by averaging the births of all eight mothers on a single day. The variable R_o is fecundity (i.e., total nymphs produced by each mother).

Mean generational time and intrinsic rate of increase (Birch 1948) were calculated using a fitted least mean square approach; therefore statistics about the central tendencies of the means were not calculated. The intrinsic rate of increase (r) was calculated using the following formula:

$$\sum e^{-rx} (l_x m_x) = 1$$

where x is the time increment (experimental day), l_x is the probability of being alive on day x , m_x is the average birth rate on day x , and r is the intrinsic rate of increase.

Another method for calculating the intrinsic rate of increase, described by Wyatt and White (1977), was calculated as a comparison to the Birch method, and to allow statistical analysis. The following formula takes into account the aphid's pre-nymphositional period (d) and the number of young produced during d -days of the reproductive period (m_d).

$$r_m = .738(\log_e(m_d)) / d$$

This method assumes that progeny produced during the first days (m_d) of the reproductive period is relatively constant and then falls gradually over time. The rate of progeny produced early in the reproductive period should influence the intrinsic rate of increase value more than later progeny (Wyatt and White 1977).

RESULTS

Experiment 1: Russian wheat aphid reproduction on five non-cultivated hosts at 18-24°C

When comparing RWA2 reproduction and development on crested wheatgrass, intermediate wheatgrass, foxtail barley, slender wheatgrass, and western wheatgrass at the temperature regime of 18-24°C and 14:10 (L:D) h photoperiod, reproductive differences were observed for most parameters (Table 22). Significant differences were not observed among hosts for pre-nymphositional period ($F = 0.78$; $df = 4$; $P = 0.5482$) and number of nymphs produced per day of nymphositional period ($F = 1.92$; $df = 4$; $P = 0.1297$).

Differences in nymphositional period were observed among hosts ($F = 5.43$; $df = 4$; $P = 0.0017$). Aphids feeding on crested wheatgrass had a longer nymphositional period (34.3 ± 3.1 days) than those on foxtail barley (24.1 ± 4.4 days), slender wheatgrass (18.3 ± 2.6 days), and western wheatgrass (19.3 ± 2.4 days). Aphids on intermediate wheatgrass had a longer nymphositional period (33.4 ± 3.5 days) than those on slender and western wheatgrass.

Aphids feeding on different hosts varied in the number of days on which nymph production occurred ($F = 5.94$; $df = 4$; $P = 0.0009$). Aphids on crested and intermediate wheatgrass had more nymph production days (23.9 ± 2.9 days and 23.1 ± 3.7 days, respectively) than those on foxtail barley (15.1 ± 2.7 days), western wheatgrass (10.1 ± 1.5 days), and slender wheatgrass (12.0 ± 1.8 days). Similarly, aphids on crested and

Table 22. Reproduction and development of Russian wheat aphid biotype RWA2 on five noncultivated hosts at 18-24°C and 14:10 (L:D) photoperiod.

Host	PNympP ^a (days)	NympP ^a (days)	NpDNP ^a (nymphs)	NPD ^a (days)	Max ^a (nymphs)	Longevity (days)	Fecundity (nymphs)
Crested wheatgrass	12.1 ± 1.1a	34.3 ± 3.1a	1.2 ± 0.2a	23.9 ± 2.9a	3.4 ± 0.3a	48.8 ± 2.7a	42.3 ± 6.9a
Intermediate wheatgrass	9.5 ± 1.2a	33.4 ± 3.5ab	1.3 ± 0.3a	23.1 ± 3.7a	4.1 ± 0.9a	43.9 ± 3.0ab	46.6 ± 15.2a
Foxtail barley	11.0 ± 0.6a	24.1 ± 4.4bc	0.9 ± 0.1a	15.1 ± 2.7b	2.9 ± 0.4ab	41.9 ± 3.5ab	23.4 ± 4.8ab
Western wheatgrass	11.3 ± 1.1a	19.3 ± 2.4c	0.6 ± 0.1a	10.1 ± 1.5b	1.8 ± 0.3b	39.9 ± 2.1bc	12.5 ± 2.5b
Slender wheatgrass	11.4 ± 1.3a	18.3 ± 2.6c	1.1 ± 0.2a	12.0 ± 1.8b	2.8 ± 0.5ab	32.1 ± 3.6c	20.4 ± 4.3b

Means in the same column followed by the same letter are not statistically different from each other ($\alpha = 0.05$; LSMeans). Fecundity data transformed by the square root method, original means presented.

^a PNympP, pre-nymphipositional period; NympP, nymphipositional period; NpDNP number of nymphs produced per day of nymphipositional period; NPD, number of nymph production days; Max, maximal number of nymphs produced in a 24-h period.

intermediate wheatgrass hosts produced more nymphs in a 24 hour period than aphids on western wheatgrass ($F = 2.93$; $df = 4$; $P = 0.0342$).

Aphid longevity on the five hosts was variable ($F = 4.08$; $df = 4$; $P = 0.0081$). Aphids feeding on crested wheatgrass lived longer (48.8 ± 2.7 days) than those on slender (32.1 ± 3.6 days) and western wheatgrass (39.9 ± 2.1 days). Also, aphids feeding on intermediate wheatgrass and foxtail barley lived longer than aphids on slender wheatgrass. Aphid fecundity also varied among hosts ($F = 4.22$; $df = 4$; $P = 0.0068$). Russian wheat aphids feeding on crested and intermediate wheatgrass produced more nymphs during their lifetime (42.3 ± 6.9 nymphs and 46.6 ± 15.2 nymphs, respectively) than aphids on western and slender wheatgrass (12.5 ± 2.5 nymphs and 20.4 ± 4.3 nymphs, respectively).

Mean generational time was calculated using a fitted least mean square approach, therefore, statistics about the central tendencies of the means were not calculated (Table 23). Mean generational time was longest for aphids feeding on crested wheatgrass (29.4 days), followed by intermediate wheatgrass (27.8 days), foxtail barley (23.9 days), western wheatgrass (21.0 days), and slender wheatgrass (19.9 days).

Intrinsic rate of increase calculations, as described by Birch (1948), also do not allow for calculation of the central tendencies of the means, while Wyatt and White (1977) calculations are appropriate for statistical analysis (Table 23). Using the Birch (1948) method, Russian wheat aphids feeding on intermediate wheatgrass had the greatest intrinsic rate of increase ($r_m = 0.199$), followed by slender wheatgrass ($r_m = 0.183$), crested wheatgrass ($r_m = 0.170$), foxtail barley ($r_m = 0.166$), and western wheatgrass ($r_m = 0.141$). The Wyatt and White (1977) method produced different values,

Table 23. Mean generation time, intrinsic rate of increase of Russian wheat aphid biotype RWA2 on five noncultivated hosts at 18-24°C and 14:10 (L:D) photoperiod.

Host	Mean Generation Time	Intrinsic Rate of Increase (Birch)	Intrinsic Rate of Increase (Wyatt and White)
Crested wheatgrass	29.4	0.170	0.176 ± 0.01a
Intermediate wheatgrass	27.8	0.199	0.176 ± 0.02a
Foxtail barley	23.9	0.166	0.162 ± 0.01a
Western wheatgrass	21.0	0.141	0.139 ± 0.02a
Slender wheatgrass	19.9	0.183	0.164 ± 0.03a

Mean generation time and intrinsic rate of increase (Birch 1948) values were fitted (i.e., optimized) using fitted least mean square approach; therefore, statistical information about the central tendencies of the means were not calculated.

Means in the Wyatt and White (1977) column followed by the same letter are not statistically different ($\alpha = 0.05$; LSMeans).

and significant differences were not observed among hosts for this calculation ($F = 0.66$; $df = 4$; $P = 0.6247$). Both crested and intermediate wheatgrass had the greatest intrinsic rate of increase value ($r_m = 0.176 \pm 0.01$ and $r_m = 0.176 \pm 0.02$, respectively), followed by slender wheatgrass ($r_m = 0.164 \pm 0.03$), foxtail barley ($r_m = 0.162 \pm 0.01$), and western wheatgrass ($r_m = 0.139 \pm 0.02$).

Experiment 2: Russian wheat aphid reproduction on crested and intermediate wheatgrass at 13-18°C, 18-24°C, and 24-29°C

Temperature changes resulted in RWA2 reproduction and development differences between crested and intermediate wheatgrasses (Table 24). Aphids did not survive long enough to reproduce at the 24-29°C temperature regime, therefore no data were collected. There were more nymph production days at 18-24°C than at 13-18°C for aphids feeding on crested wheatgrass ($t = -2.60$; $df = 21$; $P = 0.0168$), and intermediate wheatgrass ($t = -4.27$; $df = 21$; $P = 0.0003$).

Russian wheat aphids on intermediate wheatgrass have a longer pre-nymphipositional period at 13-18°C than at 18-24°C ($t = 3.10$; $df = 21$; $P = 0.0054$). Aphids produced more nymphs per day during the nymphipositional period at 18-24°C than at 13-18°C on intermediate wheatgrass ($t = -2.38$; $df = 21$; $P = 0.0270$).

The maximum number of nymphs produced in a 24 hour period was lower for aphids feeding on intermediate wheatgrass at 13-18°C than at 18-24°C ($t = -3.94$; $df = 21$; $P = 0.0008$). Aphids feeding on intermediate wheatgrass at the 13-18°C temperature also had a lower maximum number of nymphs produced in a 24 hour period than aphids did on crested wheatgrass at the same temperature ($t = 2.33$; $df = 21$; $P = 0.0301$).

Fecundity differed between temperature regimes for both grass species. Lower fecundity was found at 13-18°C than at 18-24°C for aphids feeding on crested wheatgrass

Table 24. Reproduction and development of Russian wheat aphid biotype RWA2 on crested and intermediate wheatgrass at 13-18°C, 18-24°C, and 24-29°C at 14:10 (L:D) photoperiod.

Test parameter	Crested wheatgrass			Intermediate wheatgrass		
	13-18°C	18-24°C	24-29°C ^b	13-18°C	18-24°C	24-29°C ^b
PNympP (days) ^a	17.3 ± 2.3ab	12.1 ± 1.1b	—	22.5 ± 5.2a	9.5 ± 1.2b	—
NympP (days) ^a	32.6 ± 6.5ab	34.3 ± 3.1a	—	17.6 ± 7.3b	33.4 ± 3.5ab	—
NpDNP (nymphs) ^a	1.2 ± 0.5ab	1.2 ± 0.2a	—	0.4 ± 0.1b	1.3 ± 0.3a	—
NPD (days) ^a	13.4 ± 2.3b	23.9 ± 2.7a	—	5.9 ± 2.5b	23.1 ± 3.7 a	—
Max (nymphs) ^a	3.0 ± 0a	3.4 ± 0.3a	—	1.4 ± 0.4b	4.1 ± 0.9a	—
Longevity (days)	45.9 ± 6.2a	48.8 ± 2.7a	—	44.0 ± 8.6a	43.9 ± 3.0a	—
Fecundity (nymphs)	19.1 ± 3.0b	42.3 ± 6.9a	—	7.6 ± 3.3c	46.6 ± 15.2a	—

Means in the same row followed by the same letter are not statistically different from each other ($\alpha = 0.05$; LSMeans). Fecundity data were analyzed using the square root method, original means presented.

^a PNymP, pre-nymphositional period; NymP, nymphositional period; NpDNP number of nymphs produced per day of nymphositional period; NPD, number of nymph production days; Max, maximal number of nymphs produced in a 24-h period.

^b Aphids did not survive long enough to reproduce at 24-29°C.

($t = -2.15$; $df = 21$; $P = 0.0431$), and intermediate wheatgrass ($t = -4.31$; $df = 21$; $P = 0.0003$). Fecundity was also greater on crested wheatgrass than on intermediate wheatgrass at 13-18°C ($t = 2.20$; $df = 21$; $P = 0.0389$).

Mean generational time was calculated using a fitted least mean square approach; therefore statistics about the central tendencies of the means were not calculated (Table 25). Mean generational times were longer at the lower temperature regime (13-18°C) for aphids on both crested (30.9 days) and intermediate wheatgrass (37.6 days). Generational times were slightly lower for crested (29.4 days) and intermediate wheatgrass (27.8 days) at 18-24°C.

Intrinsic rate of increase calculations as described by Birch (1948) also do not allow for calculation of the central tendencies of the means, while Wyatt and White (1977) calculations are appropriate for statistical analysis (Table 25). Using the Birch (1948) method, Russian wheat aphids feeding at the higher temperature regime (18-24°C) on intermediate wheatgrass had the greatest intrinsic rate of increase ($r_m = 0.199$), followed by aphids feeding on crested wheatgrass at 18-24°C ($r_m = 0.170$), crested wheatgrass at 13-18°C ($r_m = 0.120$), and intermediate at 13-18°C ($r_m = 0.055$).

The Wyatt and White (1977) method produced different values than the Birch method, and significant differences were observed between hosts at the different temperature regimes. Aphids on both crested ($t = -2.83$; $df = 21$; $P = 0.0100$) and intermediate wheatgrass ($t = -6.49$; $df = 21$; $P < 0.0001$) had a higher intrinsic rate of increase at 18-24°C than at 13-18°C. Also, aphids feeding at 13-18°C had a lower intrinsic rate of increase on intermediate wheatgrass than aphids feeding on crested wheatgrass ($t = 3.64$; $df = 21$; $P = 0.0015$).

Table 25. Mean generation time, intrinsic rate of increase of Russian wheat aphid biotype RWA2 on crested and intermediate wheatgrass at 13-18 °C, 18-24°C, and 24-29 °C at 14:10 (L:D) photoperiod.

Test parameter	Crested wheatgrass			Intermediate wheatgrass		
	13-18°C	18-24°C	24-29°C ^a	13-18°C	18-24°C	24-29°C ^a
Mean generation time	30.9	29.4	—	37.6	27.8	—
Intrinsic Rate of Increase (Birch 1948)	0.120	0.170	—	0.055	0.199	—
Intrinsic Rate of Increase (Wyatt and White 1977)	0.114 ± 0.01b	0.176 ± 0.01a	—	0.035 ± 0.01c	0.176 ± 0.02a	—

Mean generation time and intrinsic rate of increase (Birch 1948) values were fitted (i.e., optimized) using fitted least mean square approach; therefore, statistical information about the central tendencies of the means were not calculated. Means in the intrinsic rate of increase (Wyatt and White 1977) row followed by the same letter are not statistically different ($\alpha = 0.05$; LSMeans).

^a Aphids did not survive long enough to reproduce at 24-29°C.

DISCUSSION

Experiment 1: Russian wheat aphid reproduction on five non-cultivated hosts at 18-24°C

Intrinsic rate of increase values are useful in determining host quality because they can quantify an aphid's reproductive potential on a host. Typically, selection pressure increases with decreasing host quality, so identifying poor hosts (or poor aphid reproductive ability) can help assess potential refuges and sources of selection pressure (Merrill et al. 2008).

At a temperature regime of 18-24°C, RWA2 had a positive intrinsic rate of increase on all five hosts tested, suggesting that each would support population growth at an optimal temperature. The intrinsic rate of increase values reported for these five non-cultivated hosts are lower than those reported for both susceptible and resistant wheats. For example, some intrinsic rate of increase values reported for RWA2 on susceptible wheat are 0.31 (Merrill et al. 2008), 0.28 (Randolph et al. 2008), and 0.29 (Hawley et al. 2003). Values reported for wheats with the *Dn4* resistance gene are 0.21 (Merrill et al. 2008), 0.27 (Randolph et al. 2008), and 0.23 (Hawley et al. 2003).

In this study, Russian wheat aphids feeding on intermediate wheatgrass had the highest intrinsic rate of increase (Birch 1948) ($r_m = 0.199$), followed by slender wheatgrass ($r_m = 0.183$), crested wheatgrass ($r_m = 0.170$), foxtail barley ($r_m = 0.166$), and western wheatgrass ($r_m = 0.141$). Merrill et al. (2008) conducted the same experiment with crested and intermediate wheatgrass at a temperature of 20°C ± 0.5 °C with a photoperiod 16:8 (L:D)h. A higher intrinsic rate of increase was found on crested

wheatgrass ($r_m = 0.220$) and a lower rate for intermediate wheatgrass ($r_m = 0.133$). The different temperatures and photoperiods under which the two experiments were conducted may have resulted in the dissimilar outcomes.

Russian wheat aphids feeding on crested wheatgrass, intermediate wheatgrass, and foxtail barley had longer nymphipositional periods, longevity, and greater fecundity than aphids feeding on slender and western wheatgrass. Since aphids on these hosts had the longest generation times, their intrinsic rates of increase were lower. Typically, aphids that have shorter generation times have higher rates of increase because it takes less time to complete a generation. Aphids feeding on western and slender wheatgrass had lower fecundity, but their generation times were much faster, resulting in intrinsic rates of increase similar to aphids with greater fecundity.

Although the differences between the aphid's intrinsic rates of increase on these five alternative hosts seem small, they can result in exponential population growth rate differences. For example, using results from this research, an initial population of 100 Russian wheat aphids on intermediate wheatgrass, under optimum conditions, would increase to 19,309 after 30 days. Under the same conditions, a population of 100 Russian wheat aphids on western wheatgrass would increase to only 4,584 after 30 days.

The two intrinsic rate of increase calculations as described by Birch (1948) and Wyatt and White (1977) did not produce the same results. According to the Birch method, aphids on intermediate wheatgrass had an intrinsic rate of increase of 0.199, whereas the Wyatt and White method was used to calculate an intrinsic rate of increase of 0.176. If two Russian wheat aphid populations of 100 were to increase at these rates they would grow to 19,309, and 11,010 respectively. Over time these growth rates could result

in large differences. The Birch method requires reproductive data from the aphid's entire life span, while the Wyatt and White method is based on the aphid's pre-nymphositional period and early adulthood fecundity. Wyatt and White (1977) assumes that aphid reproduction rises quickly at first then remains constant over the first days of reproduction then falls gradually over the remainder of the aphid's life. Mathematically, early progeny are more important than later progeny. Because many of the Birch rates in this study were higher than the Wyatt and White rates, it is likely that the Russian wheat aphid progeny-time curve is not constant while feeding on alternative hosts. Variability in reproduction and progeny produced latter in life may have a greater impact on the intrinsic rate of increase than suggested by the Wyatt and White method.

The five non-cultivated hosts tested in this study would support Russian wheat aphid reproduction, but all are relatively poor hosts in comparison to susceptible and resistant wheat. Poor hosts typically present greater selection pressures (Merrill et al. 2008). Non-cultivated grasses may provide selective pressures and resistance by means of antibiosis or antixenosis. Antixenosis is expressed differently in plants with variation in leaf trichome size, leaf epicuticular structure, or tiller density. For example, western and intermediate wheatgrass have strongly ribbed leaves covered with a waxy powder. Grasses with reddish colored leaves, such as crested and slender wheatgrass may be antixenotic during the host selection process (Ni and Quisenberry 1997).

Overcoming these selection pressures to obtain a greater rate of increase would result in significant adaptive advantages. Porter et al. (1997) suggested that non-cultivated hosts play an important role in greenbug genetic diversity. Furthermore, deploying genetically different sorghum hybrids may allow for exploitation by these

genetically diverse greenbug reservoirs. Similarly, the Russian wheat aphid depends on non-cultivated hosts for survival between wheat crops. The five hosts tested in this study are abundant, and regular exposure to their selection pressures may result in genetic variability within North American Russian wheat aphid populations.

Experiment 2: Russian wheat aphid reproduction on crested and intermediate wheatgrass at 13-18°C, 18-24°C, and 24-29°C

An aphid's intrinsic rate of increase can be greatly affected by temperature, but little research has been done to determine how temperature affects reproduction potential on alternate hosts. In this study, RWA2, were exposed to three temperature regimes as they fed on crested and intermediate wheatgrass.

At the highest temperature regime (24-29°C), aphids feeding on both crested and intermediate wheatgrass did not survive long enough to reproduce. Randolph et al. (2008) and Girma et al. (1990) conducted a similar study on wheat and found longevity and reproductive rates were reduced under this same temperature regime. Merrill et al. (2009) found that Russian wheat aphid mortality increased as temperatures increased above 18.4°C. Crested and intermediate wheatgrass hosts may be too low quality to support the Russian wheat aphid under consistently extreme environmental conditions. It is also possible that a microclimate could have been created within the clip cage, due to reduced air flow, leading to temperatures warmer than the surrounding growth chamber. According to the results of this study the Russian wheat aphid would not be able to effectively reproduce on crested and intermediate wheatgrass at consistently warm temperatures.

Russian wheat aphids at the lowest temperature regime (13-18°C) had a lower fecundity, less nymph production days, and longer generational times on both hosts than

aphids at the intermediate temperature regime (18-24°C). The outcomes of the two intrinsic rate of increase calculation methods were not the same, but both calculations suggest aphids on both hosts had a lower intrinsic rate of increase at the lowest temperature regime (13-18°C). Similar observations were made by Randolph et al. (2008) on wheat, where aphids feeding on the wheat line TAM 107 had an intrinsic rate of increase of 0.20 at 13-18°C, and 0.28 at 18-24°C. On the wheat line Prairie Red (which carries *Dn4* aphid resistance gene) aphids had an intrinsic rate of increase of 0.19 at 13-18°C, and 0.27 at 18-24°C.

Russian wheat aphid intrinsic rates of increase were lower on crested and intermediate wheatgrass than on susceptible and resistant wheat at both temperature regimes. This study suggests that temperatures consistently cooler and warmer than optimum would result in decreased reproductive ability by the Russian wheat aphid on crested and intermediate wheatgrass. When an aphid is feeding on a low quality host, unfavorable changes in environmental conditions may decrease reproductive ability more than if the aphid was feeding on a better quality host. Overcoming the pressures that low quality hosts present would allow aphids to better utilize non-cultivated hosts in more variable environments. Russian wheat aphids are known to utilize non-cultivated hosts in high elevation environments, where they can experience extreme temperature variability. If these aphids were able to overcome host selective pressures by genetic mutation or recombination, reproduction could be maximized resulting in a large adaptive advantage. Russian wheat aphid biotypic diversity is problematic for plant breeding programs. Non-cultivated hosts in agricultural and high elevation environments may play an important roll in maintaining Russian wheat aphid genetic diversity.

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