# DISSERTATION

# OVERWINTERING ECOLOGY OF THE RUSSIAN WHEAT APHID, *DIURAPHIS NOXIA* (KURDJUMOV), IN EASTERN COLORADO

Submitted by

Scott Curtis Merrill

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY SCOTT CURTIS MERRILL ENTITLED OVERWINTERING ECOLOGY OF THE RUSSIAN WHEAT APHID, *DIURAPHIS NOXIA* (KURDJUMOV), IN EASTERN COLORADO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

Frank B. Peairs

William J. Parton

N. Thompson Hobbs

Thomas O. Holtzer
Advisor

William K. Lauenroth
Department Head/Director

ABSTRACT OF DISSERTATION

# OVERWINTERING ECOLOGY OF THE RUSSIAN WHEAT APHID, *DIURAPHIS NOXIA* (KURDJUMOV), IN EASTERN COLORADO

The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), is a serious pest of small-grains throughout much of the United States. This body of work integrates many components of research directed towards elucidating overwintering RWA population dynamics. Components include: 1) a literature review, 2) meta-analyses of RWA reproductive and developmental rates as functions of temperature, 3) a RWA density model based on weather conditions, 4) a high-resolution, spatially explicit RWA density model that incorporates the techniques of Geographic Information Systems and spatial statistical modeling, 5) a cross-validation analysis that calculates prediction errors for the spatially explicit RWA density model, and 6) a study of the spatially explicit correlation between fall and spring RWA densities.

The literature review and meta-analysis chapters provide background for the formulation of hypotheses and augment our general understanding of RWA overwintering population dynamics. A spatially implicit RWA density model was developed using precipitation and temperature variables, which yielded boundary conditions on spring RWA densities. Additionally, a spatially explicit RWA density model was developed from Landsat 7 Enhanced Thematic Mapper Plus imagery, topographic variables, and soil information. Cross-validation statistics indicate that the spatially explicit RWA density model, which relies entirely on remotely sensed data, is successfully predicting RWA densities as well or better than traditional field scouting. RWA density models were used to develop spatially explicit RWA density maps, which can be used for a variety of purposes including risk assessment. Unsurprisingly, fall RWA densities explained a significant but limited amount of variation in spring RWA densities.

Spatially explicit RWA density models will enable management actions to be focused on locations and times when the risk of economic damage is high. Use of this research for forecasting spatially explicit RWA densities, as well as increasing knowledge on initial and boundary conditions, will facilitate directed scouting, precision agricultural techniques, and within-field management practices for control of RWA. Adoption of these practices and techniques has the potential to reduce pesticide inputs, allow for more judicious use of resistant cultivars (when they become available), increase natural enemy refuges, and reduce pesticide exposure to agricultural workers and consumers.

Scott C Merrill
Graduate Degree Program in Ecology
Colorado State University
Fort Collins, CO 80523
Spring 2007

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# Chapter 1

# Introduction

The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), is a pest of small grains. RWA in the United States are believed to rely solely on parthenogenesis with a telescoping generation strategy (Halbert and Stoetzel 1998), which allows for exceptionally rapid population growth (Burd et al. 1998). That is, RWA are born parthenogenically, alive and pregnant. No male RWAs have been found on this continent to date. Management tools for controlling RWA populations and the associated damage are limited. Resistant wheat cultivars were successfully developed for Biotype 1 of the RWA, but new biotypes have been found that are virulent to all commercially available winter wheat cultivars (e.g., Haley et al. 2004). Possibly because of the RWA's exceptionally high intrinsic rate of increase, biological control for the RWA has been only marginally effective in North America. That is, under many conditions natural enemy populations cannot increase quickly enough to control RWA populations. Because of the current dearth of effective management tools, management relies primarily on pesticide applications. In the first ten years after its introduction into the United States in the mid 1980's, direct and indirect costs were estimated at ca. $1 billion dollars (e.g., Morrison and Peairs 1998). Dryland wheat in Colorado has a profit potential of approximately $50 per acre (Peairs personal communications). Pesticide applications for RWA range between ca. $10 (Webster et al. 1994) and $25 per acre (Rudolph, personal communication). The obvious repercussions are that a substantial portion of profits disappears with every pesticide application. RWA that migrate into fields in the spring tend to be associated with lower crop damage levels than aphid populations that successful survived the winter in a field (Peairs et al. 2006). This is likely due to the crop phenology – aphid interactions. That is, equivalent RWA densities have been found to do less damage to later growth stages of winter wheat and barley, as compared to the earlier growth stages (e.g., Hein 1992). Densities of RWA within spring agroecosystems are known to be heterogeneous (unless populations go extinct). Many important questions arise from this heterogeneity, including: 1) Is spring heterogeneity predictable? 2) If RWA overwintering success and heterogeneity in spring RWA densities are predictable, what are the driving variables for the variation seen in the winter-wheat agroecosystem? 3) Are there important driving variables that yield boundary conditions on the heterogeneity? And 4) when does the heterogeneity found in the spring become predictable (i.e., do fall RWA densities correlate with spring densities)?

Management tools could be improved by understanding the driving variables in spring RWA densities and heterogeneity. For example, accurate RWA density models could be used to generate maps for use in directed scouting, precision application of pesticides, and more judicious use of other management tools including resistant cultivars.

This research is designed to examine RWA overwintering with the goal of understanding and predicting heterogeneity in densities of RWA within the winter wheat – fallow agroecosystem. Specifically, Chapter 2 introduces the RWA with a literature review. Chapter 3 continues creating the required background with a meta-analysis relating many RWA biological aspects to temperature. Chapter 4 is a study of large-extent (i.e. between field site) effects of temperature and precipitation on RWA overwintering success. Chapter 5 details the creation of a model that delineates within field, spatially explicit, RWA densities. Chapter 6 combines models from chapters 4 and 5 to cross-validate the spatially explicit RWA density model. Chapter 7 examines the relationship between fall RWA density surfaces and spring density surfaces, and Chapter 8 is a brief conclusion that endeavors to tie together this body of research and suggest directions for future research.

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# Chapter 2

# Literature Review of the Russian Wheat Aphid

## The Russian Wheat Aphid in Brief

The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), is a pest of small-grains that has caused economic damages in excess of a billion dollars since its introduction into the United States (Webster et al. 1994, Morrison and Peairs 1998). This is a well-studied species: As of March 2007, Colorado State University's Web of Science documented 389 peer-reviewed articles with "Russian wheat aphid" or "*Diuraphis noxia*" in the title. Entire books, technical reports, bibliographies, workshops, and conferences have been dedicated to understanding and studying this species. The following literature review is an endeavor to touch on much of this body of knowledge.

## Taxonomy and Nomenclature

Taxonomic characterization quoted primarily from Stoetzel (1987): In life, RWA are yellow-green or gray-green and often covered with wax. They are small aphids (1.3 - 2.55 mm), with a convex elongate and spindle shaped body (Mohamed 1995). Antenna are 6-segmented, the unguis is straight and 2 to 2.2-fold longer than base of last antennal segment; there is no secondary sensorial on the third antennal segment of aptera, there 4-8 on the third antennal segment, and 1-3 on the fourth antennal segment of alata. Antennal and body hairs are fine and inconspicuous. The last rostral segment is approximately 0.08 mm long. The cornicles are short, truncate, and about as long as they are wide, and are of a pale coloration. The cauda are elongate usually with two to three pairs of lateral setae and one dorsal preapical seta, also pale in color. The supracaudal process is present on the dorsum of the eighth abdominal tergite, and is about as long as the cauda in aptera but only a short knob in alata.

The Russian wheat aphid is the most frequently used "common" name for this species (Stoetzel 1987).

Synonomy quoted from Durr (1983), Stoetzel (1987) and Kovoley et al. (1991) can be found in Table 2.1. There is some controversy over the nomenclature of this species. In an exhaustive search, Durr (1983) could not find any record of publication prior to Kurdjumov's 1913 publication. However, as stated by Durr (1983), this publication gives the impression that the aphid had already been described (i.e., Kurdjumov states "The Barley Aphid (*Brachyocolus noxius* Mordvilko *korotnewi* auct.)"). However, as no previous publication describing the RWA can be discovered, and in accordance with the International Code of Zoological Nomenclature, N. V. Kurdjumov must be referred to as the author of *Diuraphis noxia* (Kovaley et al. 1991).

## History and Distribution

RWA is generally considered a palearctic species (Blackman and Eastop 1984, Kiriac et al. 1990). More specifically, it is indigenous to the Ukraine, central Asia, Iran, Afghanistan and countries bordering the Mediterranean sea (Walters et al. 1984, Aalbersberg et al. 1987b, Gonzalez et al. 1989). The earliest reports of the RWA as a pestiferous species come from the southern Ukraine between 1900 and 1914 (Gonzalez et al. 1989). From its native range, the RWA spread throughout many of the grain producing areas of Europe (Stary 1996, 1999, 2000, Stary et al. 2003). In 1978, the RWA was identified in South Africa, prompting a large body of scientific research (Walters et al. 1984). It was first reported in the new world, in Mexico in 1980 (Halbert and Stoetzel 1998). In addition to most of Eurasia, North America, and South Africa, the pest can be found in South America and other countries in Africa (Walters et al. 1984, Gonzalez et al. 1989, Halbert and Stoetzel 1998).

Although indications suggest that RWA were in the United States at least as early as 1985, they were first positively identified near Muleshoe, Texas in 1986 (Morrison 1987, Morrison and Peairs 1998). The pest spread rapidly with significant crop damages occurring as early as 1987 (Elliott et al. 1998, Morrison and Peairs 1998).

Survey work has indicated that RWA has spread to 17 states and 3 Canadian provinces (Elliott et al. 1998). RWA is a serious pest throughout small-grain producing areas west of the 100$^{th}$ meridian (Hein et al. 1990). It is unclear as to why the RWA does not reach economically damaging numbers in areas east of the 100$^{th}$ meridian but differences are likely do to moisture and climate. In essence, RWA has been found nearly everywhere wheat and barley are grown in the southern and central great plains and has been a consistent pest in the region since its initial detection (Elliott et al. 1998).

## Biology

### *Morphology (Apterous and Alate Forms)*

The RWA is polymorphic with both winged (i.e., alate) and wingless forms (apterous). Resource allocation dictates that different morphs specialize in different attributes. The alate form has increased dispersal abilities but has a reduced fecundity and development rate as compared to the apterous form (Dixon 1985, Kieckhefer and Elliott 1989).

Distinguishing between alate and apterous forms is difficult until the aphid is near maturity (Peairs et al. 2006a).

Many factors seem to affect polymorphism in aphids, with increasing alate production related to crowding, day length and host quality (Walters et al. 1984, Dixon 1985, Baugh and Phillips 1991). Although, Baugh and Phillips (1991) found no relationship between crowding and alate production in RWA, they did find a relationship between plant water potential (i.e., host quality) and RWA alate production, with an intermediately water stressed plant resulting in the peak of alate production. That is, highly stressed plants (e.g., 1.21 – 1.31 -MPa produced a mean of 4.8 alates) and plants that were not water stressed (e.g., 0.51 – 0.61 -MPa produced a mean of 8.2 alates) produced a lower proportion of alates than intermediately water stressed plants (e.g., 0.93 – 1.03 -MPa produced a mean of 16.5 alates). Some areas of low quality barley or disturbed areas that adversely affected barley quality were found to be refugium areas (i.e., hotspots) for RWA and sources of higher migrant alate populations (Stary and Lukasova 2002).

### *Reproduction, Development and Lifecycle*

From birth to adult state, the RWA has 4-6 instars or stadia (Aalbersberg et al. 1987b). They reproduce using telescoping generations and show rapid development, enabling exponential population growth (Burd et al. 1998). In simplistic terms, temperature over a certain length of time can be used to predict reproduction. And while results from various studies differ there is general agreement that RWA can reproduce and develop over a wide range of temperatures (Kieckhefer and Elliott 1989) estimated using meta-analyses data by Pike et al. (1991) to range between 5° C and 30° C. And even if temperatures rise above the developmental threshold for only a short portion of the day, some development does occur (Pike et al. 1991).

Most aphids reproduce using cyclical parthenogenesis, with several generations of parthenogenesis between each bout of sexual reproduction (Dixon 1985). Throughout the spring and summer seasons, worldwide populations of RWA reproduce parthenogenically, giving birth to live and pregnant clones (Halbert and Stoetzel 1998).

In the Palearctic region, the RWA is known to reproduce using cyclical parthenogenesis (i.e., use both anholocyclic and holocyclic life cycles) (Kiriac et al. 1990, Stary 1999). That is, they reproduce parthenogenically during the majority of the year (i.e., growing season and late summer), followed by a sexual cycle in the fall. The sexual cycle produces cold-hardy eggs for overwintering. Fundatrices emerge from their eggs in late April in Central Europe (Stary 1999).

However, there have been no males found in North America. While oviparae have been found (Kiriac et al. 1990), there is no record of any fertile eggs or males. Therefore, Russian wheat aphids in North America are believed to reproduce solely by parthenogenesis (Halbert and Stoetzel 1998). That is, they reproduce using an anholocyclic life style strategy (Butts 1992). Hence, if RWA are anholocyclic, then the population consists solely of apterous and alate adult, female RWA (Burd et al. 1998). As RWA in the United States do not appear to have a cold hardy egg laying stage, they must overwinter as adults using various attributes and cold weather survival tactics to minimize mortality. The ability of RWA to survive anholocyclically may be important because earlier and larger population increases could be expected from overwintering aphids than from spring migrants moving into the area (Harvey and Martin 1988). This will be discussed in more detail later.

There are distinct advantages and disadvantages to utilizing an anholocyclic lifecycle. Advantages include telescoping generation times and early release from mild winters. Conversely, because there is no cold hardy egg laying stage, hard winters will result in late releases or localized extinction. Another important feature is that the anholocyclic lifecycle does not have sexual genetic mixing.

### *RWA Biotypes and Evolution*

RWA biotypes are defined based on phenotypic responses (i.e., symptoms) by their host plants. Plant differentials (e.g., wheat, rye and barley cultivars) are used to differentiate between different biotypes. For example, wheat cultivars with the *Dn*4 gene are resistant to RWA Biotype 1 and therefore do not show symptoms. However, plants with the *Dn*4 gene are susceptible to RWA Biotype 2 and do show symptoms caused by RWA feeding. This differential phenotypic response to a single cultivar allows us to differentiate between these two biotypes. The Peairs lab currently uses a set of 24 different cultivars (i.e., differentials) to differentiate between known North American RWA biotypes. The phenotypic responses are heritable and show limited plasticity. This is indicative of genotypic differences between biotypes. Since the introduction of the RWA into North America, only one biotype was known to exist until the spring of 2003, when a new biotype of the Russian wheat aphid was discovered in SE Colorado (Haley et al. 2004). Since then, many additional biotypes have been discovered (e.g.,Burd et al. 2006). The mechanism behind this evolution is not yet understood. Dixon (1985) suggests that there may be multiple mechanisms for genetic recombination during parthenogenesis and these mechanisms may be responsible for the increase in genetic diversity, as seen in the increase in the number of biotypes that we are currently seeing. An alternative hypothesis is that evolution from sexual selection is occurring from an as yet undiscovered source of male RWA.

Biotype 2 seems to be expanding its current range in Colorado (See Figure 2.2). Using a Markov-Transition Matrix, it appears that Biotype 2 is supplanting Biotype 1 in Colorado (Merrill, unpublished data). However, current survey methods for determining RWA biotype in Colorado are based on a 4-cultivar differential system. This system will accurately determine if some of the sampled RWA are virulent to *Dn*4 (e.g., Biotypes 2-7). However, if the survey sample is a mix of RWA Biotype 1 and RWA Biotype 2, the sample will test as the more virulent of the biotypes (i.e., as RWA Biotype 2). That is, the current plant differential system will not determine if aphids sampled at a single location are a mix of different biotypes or a single biotype.

The expansion of RWA Biotype 2 is not readily understood. The amount of Biotype 1 resistant cultivars planted in Colorado (<25%) (USDA-NASS 2003) would not generate the striking advantage that RWA Biotype 2 seems to hold over RWA Biotype 1 (i.e., Biotype 2 population seems to be displacing Biotype 1 in Colorado). Randolph (2004) has found that RWA Biotype 2 has a slightly greater intrinsic rate of increase. The differences in intrinsic rates are more substantial over the 13-18° C temperature range. Lower temperatures have not been tested. If differences in intrinsic rates of increase continue along these trends over lower temperatures, Biotype 2 would have a dramatic advantage during the spring. An intrinsic rate of increase advantage could lead to higher population densities and earlier spring flights. Therefore, the combination of these two attributes (i.e., advantages on resistant wheat cultivars and the slightly higher intrinsic rate of increase) may explain the rapid spread of RWA Biotype 2. Less is known about the distribution of other RWA Biotypes.

## Ecology

### *Phenology*

Availability of preferred host plants play a crucial role in the seasonal history of the RWA. Populations can only build-up during periods of the year when preferred hosts, like wheat and barley are available (Walters et al. 1984). And many factors can cause population mortality including reduced host plant availability or quality and adverse weather conditions (Walters et al. 1984). Spring infestations may result from either RWA that overwintered locally or that migrated from areas where overwintering was successful. Winged aphids begin to appear in the High Plains in April and May, and flights peak during July in most wheat-producing areas of this region (Peairs et al. 2006a). RWA will infest alternate hosts during this spring flight, which will allow for survival during the oversummering period (i.e., the period from winter wheat or barley harvest until emergence of the following year's crop.) Typically movement to the newly emerged crop takes place in October and early November (Peairs 1990, Peairs et al. 2006a). RWA are known to utilize winter wheat from crop emergence to harvest (Peairs 1990, Peairs et al. 2006a). RWA are known to overwinter successfully on winter wheat (Peairs et al. 2006a), and winter barley. Some evidence exists (Messina 1993), that they may be able to overwinter on alternate hosts. However, this population is likely to be a small fraction of the overwintering RWA population. In a typical Colorado year, RWA numbers increase on recently emerged winter wheat from emergence (i.e., September or early October) through late November or early December. This is followed by a slow population decline until around the beginning of March, after which the population increases in a fairly exponential fashion until the late growth stages of winter wheat (Peairs 1990). RWA populations typically show a gradual decline in the last month or two before harvest. Needless to say, large year-to-year variation occurs in this pattern.

## ***Host Plants and Feeding***

### **The Feeding Process**

RWA are a phloem-feeding insect. Specifically, RWA feed in the phloem of the host vascular bundle, with stylets winding their way between the mesophyll cells until reaching the vascular bundle (i.e., penetration is intercellular) (Fouche et al. 1984). Enzymes secreted by RWA during feeding causes a break down in the chloroplast membrane of the host (Fouche et al. 1984, Pike et al. 1991). Salivation (i.e., the injection of the toxic enzymes into the vascular bundle) is followed by bouts of ingestion (Pike et al. 1991, Girma et al. 1992). Typically, once RWA find a good host and a good ingestion site, they will stay and feed at that site for multiple hours. For example, Girma et al. (1992) found that RWA feeding on wheat for fifteen minutes, indicating that they had found a preferred ingestion site, would likely stay for at least two hours. RWAs' preferred feeding site appears to be the base of rolled or semi-rolled leaves (Stary 1999). RWA typically aggregate on new growth, in the axils of the leaves, or within curled leaves to feed (Walters et al. 1984, Burd and Burton 1992). RWA feeding impacts protein synthesis and accumulation on a systemic basis (Porter and Webster 2000).

## Nature of damage

Visual symptoms of plant damage include: 1) streaking or chlorosis (White, Yellow or purplish streaks on leaves and stems), 2) prostrate growth, 3) leaf rolling, (actually the prevention of leaves from unrolling), 4) trapping of plant material in the convoluted rolled leaves (also known as fish hooking), 5) poorly formed or blank grains (Fouche et al. 1984, Walters et al. 1984, Webster et al. 1987b, Riedell 1989, Peairs 1990, Burd and Burton 1992). The prevention of leaf unrolling by RWA feeding results from the reduction of leaf turgor below the threshold for elongation and cell wall extensibility (Burd and Burton 1992) or from collapsed bulliform cells in the leaf epidermis (Riedell 1989). RWA feeding results in systemic protein-pattern changes that are the cell-level reflection of the characteristic leaf-streaking symptom (Porter and Webster 2000). Injection with RWA total extracts (i.e., mimicking potential aphid feeding behavior or salivation) induced leaf rolling and stunting in susceptible wheat cultivars but not in a resistant cultivar (Li et al. In Press). Leaf purpling is caused by cyanidine accumulation, which occurs after prolonged feeding (i.e., > 200 hours) (Fouche et al. 1984). Leaf purpling appears to be more pronounced and frequent on plants infested during the winter months (Hewitt et al. 1984), indicative of a potential interaction between symptoms and temperature or day length. And because RWA feeding results in changes to growth and water status of the host plant, occurrence of additional drought-stress related symptoms may occur (Riedell 1989). That is, RWA infestations did decrease the plant's ability to maintain leaf relative water content in response to drought stress (Riedell 1989). Hewitt et al. (1984) found that symptoms are not reversible with the removal of aphid feeding on all cultivars studied. For example, leaves with purple streaking turned brown and died within four weeks even if aphids were removed.

Prevention of the leaf from unrolling has pronounced benefits for RWA: Good insecticide coverage is difficult to achieve and rolled leaves reduce the ability of parasitoids and predators from successfully encountering RWA (Peairs et al. 2006a).

Interestingly, feeding damage symptoms are a light activated process (Macedo et al. 2003). That is, aphids feeding under continuous dark conditions did not appear to hinder plant metabolism, cause feeding symptoms or reduce plant growth, possibly indicative of an interaction between aphid feeding and photosynthesis. Moreover, it is suggested by Botha et al. (2006) that the ability of the host plant to maintain photosynthetic activity while under aphid feeding pressure is one of the determining mechanisms in plant resistance.

## Host Plants

RWA are polyphagous insects, feeding on many species in the Graminae. Host plants documented for RWA include 43 genera and more than 140 species of grasses (Pike et al. 1991). For example, Kindler and Springer (1989) found that RWA survived for two weeks in a greenhouse on 47 out of 48 tested cool-season grasses and 18 out of 32 tested warm-season grasses, but they did not survive on any of the tested forbs or legumes (i.e., 0 of 44 species examined).

### Preferred Hosts

Unfortunately from the farmer's perspective, wheat, barley and triticale seem to be preferred hosts for the RWA (Webster et al. 1987b). Host preference can be examined by looking at development and reproductive rates across the host feeding range of RWA. Behle and Michels (1990) found a consistently higher intrinsic rate of increase on wheat than on rye. Springer et al. (1992) found that Russian wheat aphid Biotype 1 prefer winter wheat to many available alternate hosts (i.e., *Bromus secalinus, Bromus tectorum, Bromus japonicus* Thunberg). *Sorghum* seems to show high RWA resistance with the exception of at least one exotic *sorghum* species (Harvey and Kofoid 1993). However, Harvey and Kofoid (1993) argue that it is unlikely that RWA will be come a pest of sorghum.

**Alternate Hosts**

While RWA seem to prefer winter wheat and spring barley, these crops are not available throughout the year. Because of the nature of the cropping system, RWA require an alternate host from harvest of the spring/summer crop until emergence of the fall crop (i.e., the oversummering period). The oversummering time period has been studied fairly extensively (Kindler and Springer 1989, Hammon et at. 1989, Clement et al. 1990, Armstrong et al. 1991, Brewer et al. 2000).

Moreover, alternate hosts can play an important role by providing refuges for the pest, and its natural enemies. Refuges provide migrants during the cropping season, making insecticide usage problematic, as well as maintaining populations while the crop host is unavailable (Messina et al. 1993b). The system becomes more complex when differential survival (Brewer and Noma 2002) and growth rates on alternate hosts are considered (i.e., hosts may be sources or sinks for the RWA population).

There are many known alternate hosts (e.g., Appendix A) for the RWA. Clement et al. (1990) studied 6 species in Washington, Brewer et al. (2000) studied 7 species in southern Wyoming, In Utah, Messina (1993) found RWA naturally occurring in an experimental garden on 6 species, Hammon et al. (1989) studied 19 species in Colorado, and Armstrong et al. (1991) found RWA on 20 of 25 species of grasses in Colorado, 7 of which were annuals. Pike et al. (1991) suggested that Bluebunch wheatgrass may serve as the most acceptable RWA host during the winter. Many of these alternate hosts species are commonly planted as conservation reserve grasses and are likely a large source of migrants during the fall (e.g., Washington county, Colorado had 56,000 ha of conservation reserve grasses in 1991)(Armstrong et al. 1991).

Archer and Bynum (1993) found low numbers of RWA during the fall in Texas, suggesting that oversummering may be a period of high mortality of RWA in that area. However, the mild winter temperatures permitted high overwintering success in their study.

Mowry et al. (1995) studied fecundity and survival on 25 perennial grass species and found that wheatgrasses were the best alternate hosts for RWA populations. Additionally, they found that host plant maturity past the first year did not affect RWA population growth.

### *Natural Enemies and Defense Mechanisms*

While predation and parasitism are frequent occurrences within RWA populations, their effect on population dynamics is unclear. Natural enemies of cereal aphids can play a large role in controlling aphid populations (Feng et al. 1992). And in some areas of the world this appears to be the case for RWA. For example, Chen and Hopper (1997) found that aphid predators were negatively correlated with RWA population growth in France, suggesting that predators limited RWA abundance. Over

100 species of natural enemies attack RWA worldwide (Pike et al. 1991). In Washington, Pike et al. (1997) found 13 species of parasitoids attacking small-grain aphids, including RWA. Mohamed et al. (2000) found spiders, carabids, coccinellids, syrphids, nabids, and chrysopids predating RWA in Colorado. Studies have shown that natural enemies can lower RWA populations under constrained circumstances (Mohamed et al. 2000, Kerzicnik 2002). However, studies in North America have not conclusively shown that natural enemies suppress RWA populations (Meyer and Peairs 1989, Feng et al. 1992, Wraight et al. 1993, Mohamed et al. 2000).

RWA feeding prevents many host plants from unrolling their leaves. This host plant symptom creates a barrier that insulates aphids from weather, natural enemies and some insecticides (Walters et al. 1984). Host plant leaf architecture (e.g., potential areas of refuge) significantly changed RWA predation risk by ladybeetles (Messina et al. 1997, Clark and Messina 1998) and Lacewings (Messina et al. 1997). That is, RWA successfully avoid predation by using rolled leaves when available. However, some parasitoids have been found to successfully and regularly parasitize RWA in rolled leaves (e.g., *Aphelius varipes* (Foerster) and *Diaeretiella rapae* (M'Intosh)) (Feng et al. 1992).

Alarm pheromones are used by many aphid species as a population defense mechanism (Gibson and Rice 1989). In one study, RWA responded to an aphid alarm pheromone by removing their stylets and moving to a new area (Shah et al. 1999). However, it is unclear whether or not RWA actively secrete alarm pheromones.

An additional defense mechanism, used by numerous aphids, including the RWA is the use of a dropping mechanism upon contact by a natural enemy (Clark and Messina 1998, Mohamed et al. 2000).

### *RWA as Vectors*

RWA do not appear to be good vectors for viruses in the North America. For example, research has found no transmission for barley stripe mosaic virus or barley yellow dwarf virus and very low transmission rates for brome mosaic virus (Damsteegt and Hewings 1988, Damsteegt et al. 1992). However, there is evidence that viruses are transmitted by RWA in South Africa (Von Wechmar 1984, Von Wechmar and Rybicki 1984, Walters et al. 1984).

### *Overwintering Ecology*

Knowledge of the overwintering success or failure of an insect pest precedes any management strategy (Armstrong and Nielsen 2000). In general aphids cause more damage when they survive anholocyclically than when populations rely on spring migrations (Harvey and Martin 1988, Peairs et al. 2006a). For example, greenbug is most damaging in Kansas when it survives mild winters (Harvey and Martin 1988). The extent to which anholocyclic aphid colonies survive the winter varies from year to year and is related to the severity of the weather (Dewar and Carter 1984). Studies of *Sitobian avenae* (Fabricus) and *Myzus persicae* (Sulzer) have found a negative correlation between mid-winter temperatures and timing of spring populations in areas where anholocyclic clones predominate (Walters and Dewar 1986, Harrington et al. 1990).

Although there is substantial year-to-year variability, RWA are known to overwinter successfully in many locations across North America and occasionally successfully overwinter in Canada (Thomas and Butts 1990). For example, RWA typically survive most winters in SE Colorado (e.g., this study) but do not typically survive most winters in Northern Utah (Messina 1993). Moreover, even at a small scale (e.g., within-field) overwintering mortality is heterogeneous (Armstrong and Peairs 1996). Although much research has focused on temperature effects for determining overwintering mortality and population dynamics, many other variables are essential for determining overwintering success.

RWA are generally thought to be one of the more cold-hardy species of aphid pest on the Great Plains (Harvey and Martin 1988, Archer and Bynum 1993). For example, Harvey and Martin (1988) found that RWA is better adapted to survive winters than the greenbug (*Schizaphis graminum* Rondani). The RWA's ability to survive under harsh winter conditions using an anholocyclic life cycle strategy is one of the primary reasons that they are one of the most damaging pests of small-grain cultivars in the United States. However, because RWA do not have a cold-hardy egg laying stage in North America, weather conditions can cause complete localized extinction. For example, Armstrong and Peairs (1996) estimated that at approximately 3000 degree-hours below zero complete mortality of RWA populations would occur. Moreover, Armstrong and Peairs (1996) argue that differences in weather conditions between years explain up to 64% of the variation in survival of RWA on winter wheat. And Butts and Schaalje (1997) found that exposure to epigeal temperatures below - 10° C will cause catastrophic declines in RWA populations.

**<u>Supercooling</u>**

The Russian wheat aphid is a freeze intolerant insect, meaning that the formation of ice crystals in the fluids of the aphid results in mortality. To survive freezing temperatures, many insects supercool. The melting point of water is 0° C but when a sample is cooled it will not normally freeze at its melting point but will remain unfrozen until cooled to lower temperatures (Leather et al. 1995). Liquids that remain unfrozen at temperatures below their melting point are considered supercooled. The supercooling point is defined as the temperature at which spontaneous freezing occurs and many freeze intolerant insect species use supercooling as a form of protection against low temperatures (Salt 1961, Somme 1982). The supercooling point is widely used (and perhaps incorrectly used) as a comparative index of cold hardiness for freezing intolerant species (Knight et al. 1986). Supercooling is maximized when ice-nucleating agents in the gut are minimized (e.g., phloem sap is relatively free of nucleating agents compared to woody plants) (Odoherty and Ring 1987, Armstrong and Nielsen 2000).

Because RWA in North America use an anholocyclic reproduction strategy, they must be able to survive sub-zero temperatures. Many aphids, including RWA, are able to supercool well below freezing, thus survive cold winter temperatures. Mean supercooling temperatures have been measured at -26.8° C in first instars RWA, -24.9° C in adults (Butts 1992), and -27.6° C in adults (Armstrong and Nielsen 2000). This is a relatively low supercooling point compared to many aphid species that are pests of small-grains on the Great Plains (e.g., Knight et al. 1986).

## Damage and Mortality from Temperatures above the Supercooling Point

Although many aphids supercool to extremely low temperatures, damage and mortality to aphids from cold temperatures can be caused before supercooling points are reached (Knight et al. 1986, Duman et al. 1991, Hutchinson and Bale 1994, Butts et al. 1997b). Aphids, including the RWA may be susceptible to lethal "chill coma". For example, *Sitobian avenae* were found to supercool to -24.2° C but have an $LT_{50}$ (i.e., temperature causing 50% mortality) of -8.1° C (Knight et al. 1986). Field populations of RWA decreased at temperatures much higher than the supercooling points for RWA morphs, indicating that the supercooling point may not be useful for forecasting cold tolerance (Butts 1992). Chill coma can result from problems in secondary adaptations such as maintenance of neural function, changes in membrane lipids, adaptation of enzymes and other macromolecules to function at low temperatures, behavioral adaptations or desiccation resistance (Duman et al. 1991). As temperatures decrease below 0° C, aphids mortality increases, and surviving individuals may incur damage that could subsequently affect aphid population dynamics (Knight et al. 1986, Hutchinson and Bale 1994). Hutchinson and Bale (1994) reported reduced development, fecundity, and survivorship of adult *Rhopalosiphum padi* L. that had been exposed to -5 and -7.5° C.

In association with the chill coma concept, Hutchinson and Bale (1994) found that the offspring of the grain aphid, *Rhopalosiphum padi*, were less fit (i.e., reduced fecundity and lifespan) when the parent was exposed to cold temperatures. This has broad implications for degree-day models and models that forecast population growth without calculating the effects of reduced population fitness following a cold spell.

## Developmental Temperature Threshold

While supercooling and lethal thresholds can account for many of the differences in overwintering ability between RWA and other small-grain aphid pests, another difference may be in the developmental temperature threshold (i.e., the temperature threshold is the temperature above which development is possible). Decreases in aphid population numbers while the temperature remains above lethal cold temperatures may occur because aphids are not being replaced by reproduction unless temperatures are above the developmental threshold (Butts and Schaalje 1997). For example, Campbell et al. (1974) quantified developmental temperature thresholds for 5 aphids species and found temperature thresholds ranging from 1.7° C – 8.3° C. The RWA developmental temperature threshold has been estimated at 4.1° C (Kieckhefer and Elliott 1989), 0.54° C (Aalbersberg et al. 1987a), 5.2° C (Nowierski et al. 1995) and -1.57° C (Girma et al. 1990) (the mean of these temperature development threshold values is 2.07° C). Most of these temperature estimates would be considered low or below the scale developed by Campbell et al. (1974).

## Secondary Effects of Temperature and the Environment on Overwintering RWA Populations

### Host Plants

RWA mortality may be due to effects of temperature on the plant host rather than the direct effect of temperature on the aphid (Butts 1992). RWA and their hosts may have different supercooling properties. Generally speaking, RWA hosts have supercooling points well above the RWA supercooling point. Powell (1974) found significant correlation between food source and supercooling point in aphids. That is, aphids that were feeding had supercooling points rise, approaching their food source's supercooling point. Therefore, Powell (1974) suggested that the governing factor in aphid overwintering survival is the supercooling properties of the host. For example winter wheat was found to supercool to approximately - 6° C (± 3° C) (Armstrong and Nielsen 2000). Therefore, feeding RWA would have a higher supercooling temperature than their non-feeding counterparts.

Moreover, even if RWA survive cold temperatures, they may lack a food source when subzero temperatures are prolonged, or in more extreme cases they may face starvation if the phloem completely freezes, plant cells lyse, and the host dies (Armstrong and Nielson 2000). Butts (1992) hypothesized that RWA overwintering mortality well above the supercooling point (e.g., 0° C to -5° C) may be due to starvation rather than direct effects of temperature.

Plant quality likely has significant effects on aphid overwintering mortality. Butts et al. (1997a) found that aphid mortality decreased with exposure to intact plants as opposed to excised leaves or being off the plant, suggesting that higher plant quality should enhance overwintering survival. Thomas and Butts (1990) found that microtopography (i.e., within field locations with increased cold stress or snow buildup) and previous feeding by RWA were both strong factors in creation of differential and spatially heterogeneous mortality of winter wheat. Therefore, a spatial gradient in host quality for the RWA should exist. Hence, overwintering success of the RWA should be spatially heterogeneous based on plant host quality, as well as factors that more directly affect RWA mortality.

Grass architecture, because of differences in insulation and protection from natural enemies, is likely to be highly correlated to overwintering success. Tiller density was significantly correlated to overwintering success in winter wheat (Merrill, unpublished data). And tussock density was suggested by Messina (1993) as likely to be positively correlated with overwintering survival of RWA on range grasses. Other aphid species have been known to crawl into dense tussocks for protection from cold conditions

(Dean 1974). Insulative properties in overwintering sites have been correlated with survival in a large variety of insect species (Baust 1976).

**Snow Cover**

Microclimatic or microtopographic changes can influence the ability of RWA to survive winters (Hammon and Peairs 1992). Even small changes in the weather or topography can radically alter the local environment (e.g., by the creation of snowdrifts or wind scoured surfaces). Armstrong and Peairs (1996) demonstrated that snow cover can be beneficial or harmful to RWA populations. Extended time spent under snow cover prevents RWA from rising above the developmental threshold and can increase mortality (i.e., > 40 days under snow cover appears to result in 100% mortality). However, snow cover also insulates populations from temperature extremes and fast moving cold fronts. That is, 15-20 cm of low-density snow can provide insulation sufficient to completely dampen daily air fluctuations (Marchand 1982). However, wetter, denser snow would have less insulative properties for the same thickness, indicating that warm, wet snows followed by cold snaps would be more detrimental than low-density snowfalls followed by the equivalent cold period.

**Overwintering Natural Enemies**

Overwintering weather conditions can influence the abundance and distribution of microbial and arthropod natural enemies (Dreistadt and Dahlsten 1991, Bernal and Gonzalez 1993, 1995, Leather et al. 1995, Tenhumberg and Poehling 1995, Bernal and Gonzalez 1996). The parasite, predator or parasitoid population cannot establish before the prey population has established (Campbell et al. 1974). And given the variance in overwintering success of the RWA found in Colorado (Armstrong and Peairs 1996, Merrill, this publication), many of the diapausing obligate predators and parasitoids of small-grain aphids likely would emerge from diapause after populations of the RWA have successfully established (i.e., population survival would be enhanced by the presence of adequate prey numbers at emergence). This is less critical for generalist predators or parasitoids that can utilize a variety of other food sources.

Because aphid populations can grow exponentially, natural enemies that start predating or parasitizing the aphids earlier would have a greater impact than those arriving later. If conditions are favorable for aphid population growth, a time lag of only a few days could be responsible for failure of biological control (Tenhumberg and Poehling 1995).

## Overwintering on Alternate Hosts

Some evidence exists that RWA may be able to overwinter on alternate hosts. However, this population is likely to be a small fraction of the overwintering RWA population. Messina (1993a) completed a study that demonstrated differential overwintering success of RWA on different species of range grasses in northern Utah. Unfortunately, he did not have the opportunity to directly compare the six grass species to winter wheat. In this study, he found 6 species of range grasses infested with RWA in northern Utah during the late fall, which he monitored monthly from October until April. Interestingly, Crested wheatgrass (*Agropyron cristatum*) had live aphids into March. However, all aphids had died off by the April sampling date. Unlike much of the natural range of Crested wheatgrass, Northern Utah typically shows an absence of aphids in the spring, which suggests that fall RWA populations are eliminated during most winters.

Crested wheatgrass, which hosted RWA for the majority of the winter in northern Utah is found in approximately 12.4 million acres in the United States and an additional 800 thousand acres in Canada (Rogler and Lorenz 1983). Much of this acreage is in more hospitable climates, possibly allowing RWA overwintering success on Crested wheatgrass.

### ***Other Factors Effecting RWA Population Dynamics***

Crop stress arising from a number of factors seems to favor RWA population growth (Peairs 1990, Peairs et al. 2006a).

#### **Ozone and Pollution**

Summers et al. (1994) analyzed the effects of air pollution on RWA. They found that increased ozone levels increased the growth rate of individuals, but also in some cases caused plant stress or injury. For example, a 72 hour exposure to the highest ozone level tested, ca. 0.1 μl per liter (i.e., ca. 2*ambient levels at their study site in California) increased the mean relative growth rate of RWA individuals by 43%. It is hard to determine the relationship between ozone and RWA due to the confounding effects of ozone on the host plant. The effect of ozone may be just another indicator that stressed plants are better hosts for RWA than non-stressed hosts. While the exact nature of the effect of ozone is unclear, it is fairly clear that increased levels of ozone pollutants will be beneficial to the aphid pests.

## Water Stress

Archer et al. (1995) found that water stressed plants had higher numbers of RWA. Researchers (Walters et al. 1984, Archer et al. 1995) have found that RWA population densities are higher on water-stressed plants as compared to unstressed plants. Therefore, dry growing seasons will likely result in higher RWA populations (although temperature effects can confound results).

## Fertilizers

Previous research has indicated that response to fertilizer is not consistent between aphid species (Archer et al. 1995). Results for Nitrogen fertilizer additions on RWA population dynamics have been mixed (Riedell 1990, Archer et al. 1995, Moon et al. 1995). Effects of nitrogen additions likely have more of an indirect effect on RWA populations, through a direct effect on host plant quality.

## Topography and Furrow Direction

Hammon and Peairs (1992) found that the south side of east-west facing irrigation ditches accumulated more degree-days than the north side of the irrigation ditch or either side of the north-south facing irrigation ditches and consequently the south facing side had higher infestations of RWA in the spring. Additionally, they found that fields with a tall, steep slope associated with irrigation furrows had higher infestations than fields with shorter or shallower slopes.

# Economics and Integrated Pest Management

## *Damage and Economics*

The RWA is widely considered one of the most economically damaging pests of wheat in the world. RWA was recognized as a pest as early as 1900 (Gonzalez et al. 1989) and having a serious pestiferous outbreak as early as 1912 in the Republic of Moldova and the southern Ukraine where harvest was reduced by as much as 75% (Halbert and Stoetzel 1998). Damages in South Africa have been reported with up to 60% yield loss (Webster et al. 1987a).

### Direct and Indirect Costs

Losses to the United States cereal industry from 1987 to 1993 were estimated at \$893.1 million (Webster et al. 1994, Morrison and Peairs 1998). The highest total costs were in 1988, losses of \$274.1 million dollars (Morrison and Peairs 1998). Total costs are based on both direct and indirect costs. Direct costs include costs for insecticides, biocontrol agents and their applications. Indirect costs represent the estimate of losses sustained by the regional economy due to reduction in yields (e.g., producers with less money will reduce purchases of goods within their communities resulting in a decrease in tax dollars and employment)(Morrison and Peairs 1998). From its introduction to 1998, crop losses to wheat and barley in the United States were in excess of 102 million bushels (Souza 1998). In Colorado, average direct losses have averaged above \$11 million from 1987 – 1999 (Peairs, unpublished data). Harvest acres of barley in Colorado dropped from approximately 360,000 acres per year before the introduction of RWA (i.e., 1985) to approximately 60,000 acres at present (Colorado Agricultural Statistics, http://151.121.3.33:8080/QuickStats/Create_Federal_Indv.jsp). Large differences in aphid abundance and economic impact have been observed between years. In Colorado, for example, RWA caused an estimated $0.5 million in 1996 but an estimated $14.3 million dollars damage in 1997 (Figure 2.1, Peairs, unpublished data).

From 1986-1991, 17.5 million pounds of insecticides were used nationally for RWA control, with a direct cost of over $70 million to the American farmer, plus indirect costs to the water quality, human health, food safety, non-target organisms, and general environmental quality (Peairs, unpublished data).

## Wheat Yield

Total biomass is reduced on RWA infested wheat plants (Fouche et al. 1984, Burd and Burton 1992, Girma et al. 1993). Fouche et al. (1984) found that RWA does not seem to effect seed quality (i.e., Percent Nitrogen, total protein, phosphorous, potassium or magnesium content). However, Girma et al. (1993) found that not only was overall yield reduced by RWA feeding, the quality and protein content of the seed were also reduced. Girma et al. (1993) found that infestations of 3 or more RWA per plant in growth stages before heading caused significant reduction in plant height and yield.

### Fall Infestation Effects on Yield

Butts et al. (1997) found that RWA densities in the fall were not significantly correlated with yield. However, they found that aphid densities were related to plant stand density, which is correlated with yield. Heavy fall infestations of RWA will decrease cold-hardiness and therefore increase winterkill of winter wheat (Thomas and Butts 1990). Similarly, Girma et al. (1993) and Archer et al. (1998a) found that sensitivity of wheat yield components to fall infestations is less than spring infestations. Thus, there is substantial agreement that a RWA population in the fall will cause less damage than the equivalent population size in the spring, assuming that the fall population dies off during the winter.

**Effects of Infestation at Different Plant Growth Stages**

Hein (1992) found that more damage occurred when the RWA infestation occurred during the earlier growth stages in winter wheat (i.e., 2-3 leaf and early post-vernalization). When RWA do not overwinter successfully damages to crops tends to be greatly reduced (Peairs et al. 2006a). If overwintering does not occur, arrival from dispersing RWA (i.e., the Spring Flight) into small-grain fields typically occurs at a later and more tolerant growth stage in winter wheat. In association with increasing damage, Girma et al. (1990) found the highest reproduction rates in the jointing stage of wheat growth and Hein (1992) found a large reduction in reproduction on late tillering and early heading stages, when compared to earlier wheat growth stages. Kieckhefer et al. (1995) found that the vulnerability of plants to aphid damage declines with advances in growth stage of the plant. And Chander et al. (2006) modeled RWA effects and found greater damage occurring in the earlier growth stages of winter wheat as compared to late tillering and heading.

**Economic Injury Levels, Economic Thresholds, and Crop Losses**

Increasing an insect pest population and/or increasing the duration of the infestation are factors generally expected to increase crop losses (Ruppel 1983). To estimate crop losses Ruppel (1983) suggests a formula for calculating Insect Days. That is, a quantifiable measurement of the pest population numbers combined with duration of time spent on the crop. This measurement can be used to quantify the quality of control measures or to estimate crop losses if pest numbers are known across time. And more cereal aphids feeding for a longer period of time will increase the yield loss (Kieckhefer et al. 1995).

While Insect Days is a valuable concept, it is not very practical, as a producer would need precise knowledge of pest density over time. Of more realistic use are the concepts relating damage by the pest at different population levels to cost of controlling for the pest: the Economic Injury Level (EIL) and the Economic Threshold (ET). The EIL is the minimum pest population density that causes economic damages to the crop (Stern et al. 1959, Du Toit 1986, Chander et al. 2006). The economic injury level can be determined by the following formula (e.g., Girma et al. 1993):

$$EIL = CC / MV*D$$

where CC is the cost of a control unit (e.g., a pesticide application per acre), MV is the market value per production unit (e.g., $5 / bushel of hard red winter wheat), D is the injury or damage per pest (e.g., bushels per acre / pest). With regard to pest management, the EIL is generally in the form of density of pests, or incidence of pests (e.g., aphids per unit area or percentage of infested tillers).

The ET is the level of infestation at which control measures should be applied to prevent an increasing pest population from reaching the EIL (Stern et al. 1959, Du Toit 1986). The ET is always lower than the EIL to permit sufficient time for the initiation of control measures and time for the control measures to take effect (Stern et al. 1959). The ET is also referred to as the action threshold, and is of more practical value than the EIL.

A study (Du Toit 1986) of winter wheat in South Africa estimated an EIL of 14% infested tillers at growth stage 59 (ear clear of leaf sheath) and an Economic Threshold of 3.6 - 6.4 % of tillers infested at growth stage 31 (one node). Archer and Bynum (1992) calculated a 0.46% yield loss per 1 % damaged tillers and a 0.48 yield loss for 1 % infested tillers. Peairs et al. (2006a) suggests a 0.5% yield loss per percentage of infested tillers.

Girma et al. (1993) found a strong relationship between aphid density per tiller and percentage of infested tillers. Not only was overall yield reduced by RWA feeding, the quality and protein content of the seed were also reduced. Additionally, they found that infestations of 3 or more RWA per plant in growth stages before heading caused economic damage (i.e., 3 or more RWA per plant exceeds the EIL). Additionally, Girma et al. (1993) calculated a density based EIL of 2.2 and 4.0 aphids per 7 plants for fall infestation in Kansas for the years 1988 and 1989 respectively.

Archer et al. (1998b) used a measure of aphid density over time (e.g., aphid days similar to Ruppel's (1983) Insect Days) to calculate an economic loss factor. Their loss factor ranged from 0.01 % to 0.15 % of bulk weight per aphid day. Loss factors increase with latitude in North America with the coldest states and Canada having loss factors approximately 1.5 to 3 times the loss factors in Texas (Archer et al. 1998b).

## *Forecasting and Modeling*

### Forecasting Flights and Outbreaks

Dewar and Carter (1984) found that the most important factors for determining aphid summer outbreak of *Sitobian avenae* were fall infestation levels (i.e., density of fall flight), winter severity, spring densities of natural enemies, crop planting date, and size of the spring infestation or spring migration. Additionally, they found that the number of degree-days below zero was correlated to summer outbreaks.

Two studies (Turl 1980, Walters and Dewar 1986) found that degree-days above zero subtracted from the number of degree-days below zero showed a strong correlation with spring migration flight date in some cereal aphids.

## Modeling Population Dynamics and Spatial Distributions

Legg and Brewer (1995) used cumulative RWA aphid-days regressed against heat units and rainfall from first detection to predict population growth, with cumulative RWA aphid-days positively affecting population growth and rainfall negatively affecting population growth.

The spatial distribution of RWA in fall populations was found to be highly aggregated, especially at low aphid densities (Butts and Schaalje 1994). This heterogeneity may match up with winterkill of wheat (Butts 1992), hotspots in the spring, and yield loss at harvest.

## Sampling

Schaalje and Butts (1992) developed a good model for translating binomial (i.e., presence / absence) sampling to RWA densities. And Archer and Bynum (1993) found a strong correlation between infested plants and aphid density. Using metadata and methodology from Hein et al. (1995), the following formula can be used to translate between percentage of tillers infested and RWA density:

$$\log_e m = 2.17 + 1.15 \log_e [ -\log_e (1-p) ]$$

where $m$ is the mean number of RWA per tiller and p is the proportion of infested tillers. The intercept and slope are developed from metadata collected by Hein et al. (1995).

Therefore, scouting could use either density measurements or incidence measurements.

### *Management Strategies and Factors*

As per integrated pest management guidelines, RWA populations should be managed using multiple tactics to prevent populations from overcoming any one tactic. Modifications in date of planting, fertilization, weed management, crop selection, and grazing have all been observed to have some influence on RWA incidence (Walters et al. 1984, Peairs 1990, Peairs et al. 2006a). Resistant wheat cultivars are not currently available for use in an integrated pest management plan, but are expected to be commercially viable within 3-8 years (Haley, personal communications). Unfortunately, knowledge for use in development of an integrated pest management strategy is not being utilized. For example, in North America, chemical control is the primary means of control for the RWA.

#### **Chemical Control (Insecticides)**

While insecticides provide good control of RWA, it is crucial to remember the financial perspective. That is, with the low profit margins seen in small-grain production, reducing inputs (e.g., insecticide applications) needs to be stressed to make the crop economically viable (Peairs 1990). Current costs of pesticide application average around \$10 per acre (Webster et al. 1994), but in some areas cost as much as \$25 per acre

(Peairs, personal communication), which equates to approximately 20-50 % profit loss per application (i.e., based on a profit potential of ca. $50 / acre of winter wheat.)

Chemical control of RWA can be achieved with systemic insecticides applied to the seed furrow at planting or with foliar systemic and contact insecticides applied with aerial or ground equipment (Peairs 1990). Lorsban, Mustang Max, Di Syston, dimethoate, Penn Cap M, Thiodan, Warrior and Lannate have all been used for control of RWA in the Great Plains since 1986 (Peairs et al. 2006b). Currently, control efforts primarily use foliar contact insecticides (Rudolph personal communications). Furadan 4F, Gaucho (several formulations), Cruiser 5FS, Baythroid XL, Chlorpyrifos 4E, Dimethoate, Lamda cyhalothrin, Mustang Max, Penn Cap M, and Proaxis are recommended for chemical control of the RWA in Colorado (Peairs et al. 2006a). 25% of the United States cumulative total acres of wheat treated with insecticide for RWA are in Colorado, although Colorado grows only 6% of the actual wheat that is infested with RWA (Kerzicnik 2002). Spraying can be detrimental if strong resurgence is likely. Trumper and Holt (1998) modeled potential for resurgence after insecticide usage. They found that resurgence was strongest when natural enemies have a strong effect on the population dynamics the prey (pest). Contrary to evidence that natural enemies are strongly linked to RWA populations in Europe (Chen and Hopper 1997), this does not seem to be the case in the United States (Randolph et al. 2002, Lee et al. 2005). Although, Lee et al. (2005) did find a correlation between summer populations of predators and RWA population growth later in the growing season and therefore suggests that predation may play a more controlling role in oversummering population dynamics.

If RWA fail to overwinter, economic infestations occur later in the spring, reducing the need for insecticide applications (Armstrong and Peairs 1996)

## Fungus Treatments

Wang and Knudson (1993) found that the pathogen *Beauveria bassiana* significantly increased mortality of RWA. Applications of Fungal insecticides worked for control of RWA under favorable conditions (Vandenberg et al. 2001). However, for good control to occur using fungus treatments, humidity levels need to be higher than seen in non-irrigated cropping systems.

## Planting Date

RWA infestation levels tend to be higher on earlier planted winter wheat (Hammon et al. 1996, Peairs et al. 2006a). Hammon et al. (1996) found that planting dates as little as 12 days apart significantly effected yield (i.e., the later planting date showed significantly higher yield). Planting date effects are due to greater activity early in the fall in early-planted fields, and to greater susceptibility to aphids on early growth stages in the spring (e.g., Hammon et al. 1996).

## Biological Controls and Natural Enemies

Biological control is the action of parasites, predators or pathogens on a host or prey population which produces a lower general equilibrium position than would prevail in the absence of these agents (Stern et al. 1959). Because the RWA is an introduced species, substantial effort has been placed on classical biological control (Gonzalez et al. 1989, Mohamed 1995, Mohamed et al. 2000). Several geographic collections of at least 25 species of natural enemies were introduced from 20 countries and released against the

RWA (Mohamed et al. 2000). More than 15.5 million natural enemies have been released for control of RWA (Prokrym et al. 1998). In Colorado alone, Elliott et al. (1995) released 1.6 million parasitoids in SE Colorado over a three year period.

Unfortunately, it does not appear that introduced species are having a suppressive effect on RWA populations and biocontrol additions do not seem to be economically viable. For example, Randolph et al. (2002) did not find cost effective control of RWA using releases of two biocontrol agents. And Meyer and Peairs (1989) did not see a reduction in RWA populations after the addition of green lacewings. However, cumulative effects of a wide range of natural enemies and biological control agents on RWA populations would be difficult to measure.

## Mulches and Powders

Research has demonstrated that alate aphids respond to soil color. Colors such as orange-green-yellow seem to attract alate migrants, white or reflective coloration appear to discourage migrants (Loebenstein and Raccah 1980, Gibson and Rice 1989, Doring et al. 2004). This makes it possible to influence host-seeking behavior by altering the visible soil substrate by the addition of reflective mulches, powders or fertilizers (Gibson and Rice 1989). Unfortunately, foliage seems to partially block the effects of reflective mulches (Loebenstein and Raccah 1980). Using many color-based techniques for attracting (e.g., color traps) and repelling (e.g., reflective mulches) aphids would not be cost effective for controlling RWA in large acreage small grain fields.

## Grazing

Perennial grass hosts of the RWA that had been clipped had higher populations that unclipped grasses, which has implications for grazing grasses during the oversummering period (Messina et al. 1993a).

## Volunteer Grains

Hewitt et al. (1984) indicated that volunteer wheat plants are problematic in that they serve as an important primary source of infestation of newly emerged crops and as an important oversummering host. Armstrong and Rudolph (1988) found large populations of oversummering RWA on both volunteer wheat and barley. Volunteer grains appears to be one of the most important source of oversummering RWA, and hence control of volunteer small grains prior to planting has been recommended (Peairs 1990).

## Plant Resistance and Resistant Cultivars

### Plant Resistance Background

There are three types of plant resistance:

Antibiosis: a plant defensive mechanism, which reduces fecundity, development, and/or survival. Antibiosis resistance negatively effects insect biology.

Tolerance: Insect survival and fecundity are not effected, yet damage per insect sustained by the plant is less than on susceptible varieties.

Antixenosis (i.e., non-preference) Antixenosis resistance is considered to be something that affects the behavior of the insect, benefiting a resistant plant as compared to a susceptible plant. Generally antixenosis refers to the suppression of feeding or oviposition.

Some confusion exists between antixenosis and antibiosis resistance mechanisms. Plant resistance can be a combination of these two mechanisms, which makes determination of the "type of resistance" difficult. However, the degree of antixenosis present is usually indicated by the plant-insect interaction, where negative insect reactions are expressed at or from the moment of first encounter with the resistant plant (Lake 1989). If non-preference is expressed only after feeding or after prolonged exposure to the plant, after initial acceptance as a suitable host, then the resistance is likely antibiosis.

Antibiosis is a strong source of potential resistance given the RWA preference for prolonged feeding at a single location. Therefore, feeding time may be a quick determinant of potential resistant cultivars (Girma et al. 1992). Porter and Webster (2000) argue that feeding alters the protein patterns necessary for normal metabolic functions in susceptible cultivars and that these changes have strong implications for understanding antibiotic resistance mechanisms.

**Resistance Mechanisms**

Wheat plants that are resistant to fungi show a hypersensitive response to fungal infection. In some cases this response (i.e., hypersensitive cell death) lignifies cells around the infected cell. This lignification may prevent or reduce the spread of the rust (Moerschbacher et al. 1990). Martinelli et al. (1993) suggests that the hypersensitive cell-death reaction appears to be correlated with induced resistance to pathogens (e.g., barley-powdery mildew). Symptoms similar to the pathogen-generated hypersensitive cell death appear in association with RWA feeding on resistant wheat varieties (i.e., collapsed autofluorescent cells). These symptoms appear to result from chloroplast and cell membrane disintegration (Fouche et al. 1984). Resistant barley cultivars produce significantly more collapsed autofluorescent cells than susceptible varieties (Belefant-Miller et al. 1994). Belefant-Miller et al. (1994) hypothesize that these cells are somehow less palatable and may result in the aphid moving to a new feeding site. Li et al. (In Press) suggest that the collapsed autofluorescent cells are a one-to-one gene plant response to proteins injected by the RWA. Moreover, Li et al. (In Press) have found significant increases of defense-related enzymes in resistance cultivars when injected with RWA proteins (i.e., as would be seen by feeding), indicating that at least some resistance mechanisms are elicited responses to RWA feeding.

Miller et al. (2003) found that plant resistance generally increased with plant age.

**Resistance Cultivars**

Before 1998, over 25,000 accessions of cereal grains were tested for resistance to RWA Biotype 1 (Souza 1998), and approximately 27,000 additional accessions have been tested since, with ca. 12,000 tested for RWA Biotype 2 resistance (Rudolph, Peairs, personal communications). Many studies highlight the value of resistant cultivars for the reduction in pesticide usage and increasing yield. For example, Randolph et al. (2003) found decreasing yield with increasing infestation numbers on a susceptible wheat cultivar. However, under high RWA infestation pressure, yield loss on a resistant line was only 1% (Cultivar: RWA-E1, Randolph et al. 2003). Resistant genes characterized so far include *Dn*1 through *Dn*9 (Collins et al. 2005b), as well as provisional designations based on two other sources assumed to be different genes based on chromosomal location (*Dnx*, Liu et al. 2001) or geographic origin (*Dny*, Smith et al. 2004).

There are many differences between small grain crops. Rice and Oats both have resistance to RWA (Peairs et al. 2006a). Triticale has moderate resistance to RWA (Peairs et al. 2006a). Barley and winter wheat lines resistant to all known RWA biotypes in North America have been found and are currently being developed for commercial use (Peairs, Rudolph, personal communications).

*Dn*4 has been the most widely adopted of the resistant genes for winter wheat. And wheat cultivars that incorporated the *Dn*4 resistance were used in approximately 24% of all dryland winter wheat acres grown in Colorado during 2003 (USDA-NASS 2003). Unfortunately, recently discovered biotypes (e.g., Biotype 2) are virulent to the *Dn*4 source of resistance.

With the advent of the new RWA biotypes in the United States, there are no currently available commercial winter wheat cultivars that are resistant to all known biotypes. However promising research is underway to develop resistant lines. For example, Collins et al. (2005a) identified forty-four germplasm accessions as having high to moderate levels of resistance to RWA Biotype 2. Approximately 3-8 more years is the current estimated time for the development of commercially viable wheat cultivars with resistance to Biotype 2 (Haley, personal communications).

Currently, the Peairs Lab, in conjunction with S. Haley, is considering cultivars with antixenosis properties (e.g., plants with large trichomes or thick pubescence), antibiosis properties and combinations of the two. Leaf structure including leaf trichomes has been associated with antixenotic properties of wheat hosts to RWA (Ni and Quisenberry 1997).

Ideally, future cultivars will have stacked or pyramid resistance genes to decrease the likelihood of mutation in the aphid leading to virulence in new cultivars. Stacked or pyramid resistance factors conceptually refer to breeding multiple different sources of resistance (i.e., a stack or a pyramid of resistant sources) into a single cultivar. To overcome the multiple sources of resistance the aphid must adapt to each of the resistance sources. That is, mutation at a single gene locus will not result in selective advantage and therefore should radically increase the length of time until the aphids overcome the resistance.

Figure 2.1: Direct economic impact of RWA and pesticide usage for control of RWA from 1986 through 1998 in Colorado (F. B. Peairs, unpublished data).

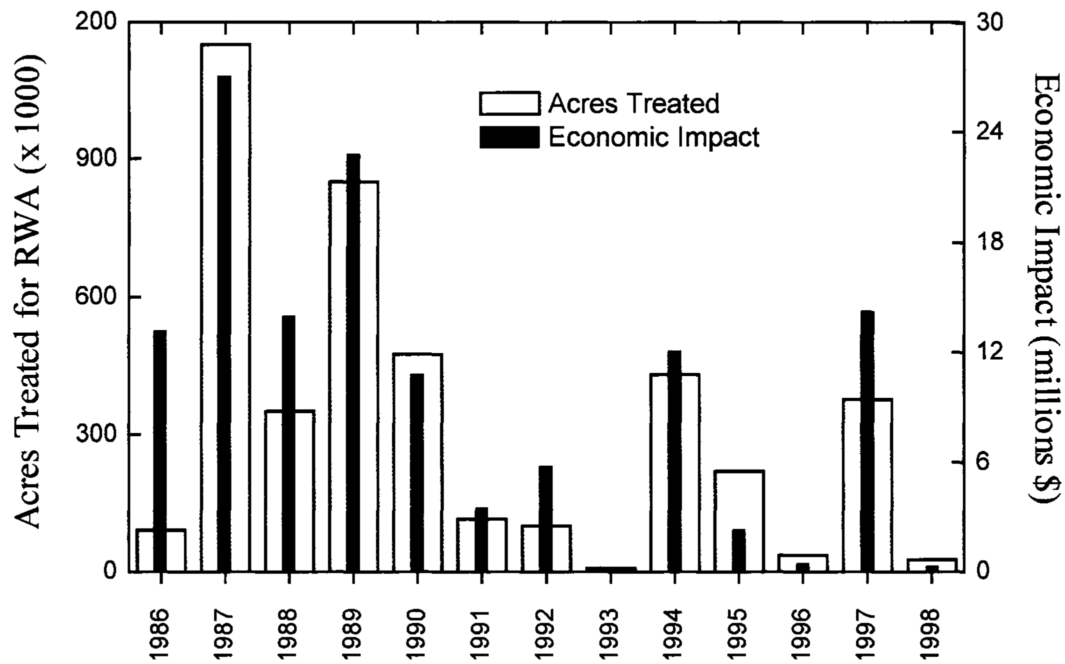

Figure 2.2: RWA Biotype Survey Maps for Colorado 2004, 2005 and 2006

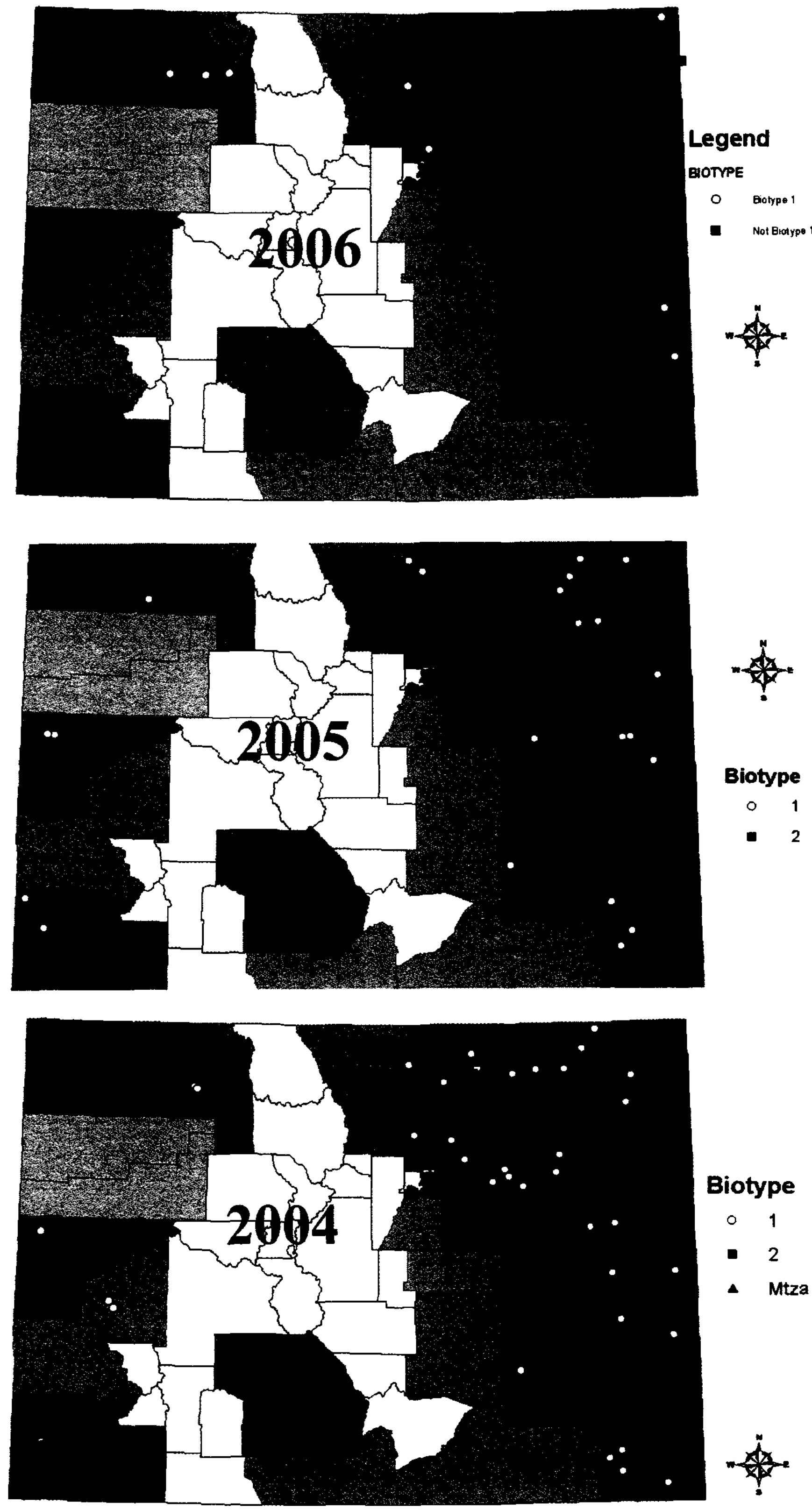

Table 2.1: RWA Synonomy

| Genus Species | Authority |
|---|---|
| *Diuraphis noxia* | Mordvilko |
| *Diuraphis noxia* | Kurdjumov |
| *Diuraphis noxia* | Mordvilko ex Kurdjumov |
| *Brachycolus noxius* | Mordvilko ex Kurdjumov |
| *Cavahyalopterus graminarium* | Mimeur |
| *Cavahyalopterus noxius* | Mordvilko |
| *Cuernavaca noxia* | Mordvilko |

*Notes:* Synonomy quoted from Durr (1983), Stoetzel (1987) and Kovoley et al. (1991). Kurdyumov is an alternate spelling of Kurdjumov, and is seen in some publications (e.g., Durr 1983).

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# Chapter 3

# Meta-Analysis of Russian Wheat Aphid Reproduction and Development Related to Temperature

## Abstract

The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), is a significant pest of small grains in the United States and worldwide. Understanding basic biological traits allows for the development of hypothesis regarding Russian wheat aphid interactions with the ecosystem. Metadata were used to develop relationships between temperature and reproductive and developmental traits of the RWA. Specifically, functions were developed between temperature and the following traits: lifespan, fecundity, reproductive rate, pre-nymphipositional period, and reproductive period. Upper and lower temperature reproductive thresholds were calculated as 2.6° C and 34.4° C. The lower temperature developmental threshold was calculated as 2.0° C. Modeled longevity reached its maximum around at about 96 days. Meta-analysis indicates a maximum fecundity occurring at approximately 18.5° C, with a maximum fecundity rate of ca. 2.1 nymphs per day. The calculated maximum total fecundity is ca. 57 nymphs per female. Reproductive period is modeled with a gaussian approximation and reaches its maximum at 31.8 days.

## Introduction

RWA is generally considered a palearctic species (Blackman and Eastop 1984, Kiriac et al. 1990). Although indications suggest that RWA were in the United States at least as early as 1985, they were first positively identified near Muleshoe, Texas in 1986 (Morrison 1987, Morrison and Peairs 1998). The pest spread rapidly with crop damage occurring as early as 1987 (Elliott et al. 1998, Morrison and Peairs 1998). Since its introduction into the United States, RWA have caused losses of over $1 billion to the small-grain industry (Webster et al. 1994, Morrison and Peairs 1998). Constructing basic models and hypothesis about developmental and reproductive rates is essential for understanding and managing this pest. Meta-data provide a robust source of information and can be used to develop mathematical relationships between important biological variables. This study uses meta-data from numerous studies to explore relationships between temperature and population dynamics.

The influence of temperature, weather and climate on RWA biology has been well studied (e.g., Webster and Starks 1987). Temperature appears to be a dominant factor influencing reproductive and development rates (e.g., Aalbersberg et al. 1987). However, many other variables play strong roles. Examples of factors influencing reproductive and developmental rates include host plant growth stage (e.g., Girma et al. 1990), host quality (e.g., Merrill et al, unpublished data), aphid bioytpe (e.g., Randolph and Peairs, unpublished data), population density (Michaud et al. 2006), feeding site (e.g., Stary 1999). Although much more variation could be understood if all of these covariates were used, this was not done because of inconsistencies among studies (e.g., growth stage), or data were not adequately reported, or were too varied (e.g., cultivar effects) to analyze. Rather, this meta-analysis concentrates on temperature effects and ignores the variability associated with many of these important covariates (e.g., host quality). Standard errors and measures of central tendencies were not universally reported making weighting data points by their standard errors impossible.

My goal was to determine basic rates and boundary conditions (e.g., estimated maximum longevity) for development and reproduction to elucidate population dynamics during the cool winter months (i.e., understand the effects of temperature).

## Methods

The following references were used for data development: Aalbersberg et al. (1987), Webster and Starks (1987), Michels and Behle (1988, 1989), Kieckhefer and Elliott (1989), Behle and Michels (1990), Girma et al. (1990), Webster et al. (1993), Nowierski et al. (1995), Butts and Schaalje (1997), Haile et al. (1999), Hawley et al. (2003), Miller et al. (2003), Randolph and Peairs (Unpublished data), and Merrill et al. (Unpublished data) (See Table 3.1).

Parameters for development and reproduction variables were extracted from each of the aforementioned research papers by temperature. Variables of interest were longevity, total fecundity, daily fecundity rate, reproductive period (or nymphipositional period), and pre-nymphipositional period (i.e., the number of days before giving birth for the first time). If multiple temperatures were studied within a single research paper, each temperature was considered a data point (For number of data points per citation see Table 3.1). When average temperature was held constant and other factors were varied (e.g., growth stage) parameters were averaged to obtain a single data point. For example, Michels and Behle (1989) examined three different temperature regimes and therefore had three data points included in this meta-analysis. Conversely, Girma et al. (1990) were studying reproduction and development rates across five growth stages using three temperature regimes. Instead of using 15 data points from this study (i.e., 3 temperatures * 5 growth stages), the tillering through heading growth stages were averaged within each temperature regime for a total of 3 data points. Mathematical relationships were developed based on fitting simple mathematical models (i.e., linear, $2^{nd}$ order polynomial, gaussian, or exponential curves).

## Results

### *Fecundity and Temperature*

Temperature has a dramatic effect on lifetime fecundity, defined as the total number of nymphs produced over the lifetime of an aphid. Exceptionally high and low temperatures result in no reproduction. Following a pre-analysis maximum fecundity was estimated to occur at approximately 20° C. Given the pattern in the data, I assumed that the fecundity – temperature relationship was either approximately gaussian or a $2^{nd}$ order polynomial. The gaussian curve had a lower mean squared error (gaussian MSE = 262, $2^{nd}$ order polynomial MSE = 267) with the same number of parameters as the $2^{nd}$ order polynomial and therefore the gaussian curve was assumed to be a better model. Figure 3.1 depicts lifetime fecundity at various temperatures (red squares). A gaussian curve (blue line in Figure 3.1) was fit to the data using a least mean squares error approach and is calculated by the formula:

$$\text{Formula \# 1:} \quad \text{Nymphs / Female} = 57.11\ e^{-(\text{Temperature} - 18.48)\text{\^{}}2/129.61}$$

The gaussian approximation calculates a maximum fecundity of approximately 57 nymphs (at 18.48° C), which is well under the maximum reported average of 81.46 nymphs (at 17.25° C) (Aalbersberg et al. 1987). However, the curve does supply a general trend that can be used to generate hypotheses. A minimum reported fecundity was an average of 4.67 nymphs per female (at 30° C) reported by Michels and Behle (1988).

Fecundity rate (Figure 3.2), defined as the average number of nymphs per reproductive day, has a very similar relationship with temperature as average lifetime fecundity. Reproductive rate is modeled using a gaussian approximation using a least squares approach (The blue line in Figure 3.2). The reproductive rate curve can be calculated by:

$$\text{Formula \# 2:} \quad \text{Reproductive rate} = 2.06\, e^{-(\text{Temperature} - 20.87)^{\wedge}2/142}$$

This formula calculates a maximum of 2.06 nymphs per day (at 20.87° C) during the reproductive period. The maximum reported average nymphs per day was 6.0 at 26.5° C (Haile et al. 1999). However, this data point was removed as an outlier from the analysis, resulting in a maximum of 2.47 nymphs per day at 19.7° C (Girma et al. 1990). The minimum reported average daily fecundity was 0.40 nymphs per day at 5° C (Michels and Behle 1988).

### *Temperature Reproduction and Development Thresholds*

The temperature reproduction thresholds are defined as the upper and lower temperature limits where reproduction occurs. These thresholds were calculated in a linear fashion using number of nymphs per female data below 20° C for the minimum reproduction temperature threshold (Figure 3.3) and data above 20° C (inclusive) for the maximum reproduction temperature threshold (See Figure 3.4). The minimum temperature threshold for reproduction to occur was calculated at 2.6° C with a maximum temperature of 34.4° C.

The temperature development threshold, defined as the lowest temperature where development occurs, has been calculated for RWA in numerous studies: Aalbersberg et al. (1987) calculated a developmental threshold of 0.54° C. Girma et al. (1990) calculated a lower temperature threshold for development at -1.57° C. Kieckhefer and Elliott (1989) found a lower developmental threshold limit of 4.1° C for development of immature RWA. Nowierski et al. (1995) found a development threshold of 5.2 on excised barley leaves. These four studies averaged 2.06° C as a lower developmental threshold.

For this meta-analysis, the temperature development threshold (Figure 3.5) was calculated by linearly regressing the inverse of developmental time from birth to adult against temperature for all data points (Aalbersberg et al. 1987, Kieckhefer and Elliott 1989, Girma et al. 1990). The developmental threshold calculated using metadata was 1.98° C, which compares favorably to the 2.06° C lower developmental threshold calculated by averaging the aforementioned studies.

### *Longevity and Temperature*

Longevity is modeled as a linear function of temperature (Figure 3.6). Modeled longevity reaches its maximum at around approximately 96 days or just over 3 months, with longevity increasing as temperature decreases towards the developmental threshold.

### *Reproductive period and Temperature*

Reproductive period, or the nymphipositional period is defined as the number of days from the first to last birth per mother aphid. These data (Figure 3.7) are quite variable and a pattern is less easily discerned. However, if we assume that temperatures below the reproduction threshold result in zero births then these data can be modeled as approximately gaussian, with a maximum of 34.42 days around 14.5° C. The gaussian approximation (i.e., the blue line in Figure 3.7) to the reproductive period – temperature relationship is given by the following formula:

Formula # 3: $\text{Reproductive period} = 34.42\ e^{-(\text{Temperature} - 14.57)^{\wedge}2/154.37}$

The minimum average reproductive period reported was 5.3 days (Michels and Behle 1988) at their highest temperature regime, 30° C, with the maximum reproductive period reported at 56.44 days at 13° C (Aalbersberg et al. 1987).

### *Pre-nymphipositional Period and Temperature*

Pre-nymphipositional period is defined as the number of days from birth of an aphid to the birth of its first offspring. Pre-nymphipositional period is a powerful and necessary statistic for understanding the intrinsic rate of increase in RWA populations. That is, the delay between birth and the potential for the newly born aphid to give birth yields valuable information about generational time. Data appear to indicate that the number of days until first birth increases exponentially as temperature decreases (Figure 3.8). Pre-nymphipositional period was modeled using the following power function:

Formula # 4: $\text{Pre-nymphipositional period} = 429.56 * \text{Temperature}^{(-1.2334)}$

Interestingly, if one models pre-nymphipositional period as a power function (the blue line in Figure 3.8, Formula 4), the resulting formula yields a second estimate of the reproduction threshold. That is, if it is assumed that a maximum lifespan is around 90 to 100 days then when the pre-nymphipositional period is equal to the maximum lifespan, no reproduction can occur. Using Formula 5, a second reproduction threshold is calculated to be 1.56° C (± 0.1) when lifespan is 90 to 100 days. This value (1.56° C) has good concurrence with the reproduction threshold (2.57° C) calculated earlier using a linear regression of reproduction data at temperatures under 20° C.

Formula # 5: Pre-nymphipositional period = Lifespan = 429.56 * Temperature $^{(-1.2334)}$

## Conclusions

Trends indicate that a basic slowing of metabolic functions occur with deceasing temperature, which supports assertions by Howe (1967) and Campbell et al. (1974) In this study, longevity is increased as temperatures decrease towards the developmental threshold, under which damage may occur to the aphid (e.g., chill coma (Knight et al. 1986)). However, as longevity increases, a reproductive penalty is incurred. That is, fecundity decreases as longevity increases. This analysis indicates that RWA populations must give birth during the winter months to successfully overwinter.

Logan et al. (1976) argue effectively that many of the curves developed for describing arthropods temperature dependent rates are not symmetric around an optimum. For example, high temperatures may create a rapidly declining curve, possibly attributed to enzyme denaturization or desiccation, in many temperature related functions (Logan et al. 1976). Pike et al. (1991) used $4^{th}$ order polynomial curves to describe lifespan – temperature and development – temperature relationships, likely overfitting the data. Campbell (1974) suggested that many relationships between temperature and aphid developmental rates followed a sigmoid curve from low temperatures upwards to a maximum. Similar relationships have been found between temperature and developmental, and reproduction rates for many of the important aphid pests of small grains in the Great Plains. For example, Acreman and Dixon (1989) found temperature dependent rates in *Sitobion avenae*, indicated by decreasing intrinsic rates of increase and decreasing mean relative growth rates with decreasing temperatures (below approximately 25° C). And Walgenbach et al. (1988) found a lower reproduction threshold of ca. 6° C with developmental rates increasing by a sigmoid function towards a maximum fecundity for *Schizaphis graminum* at ca. 21° C. Nyaanga et al. (2005) found consistantly higher intrinsic rates of increase *Rhopalosiphum padi* compared to *S. graminum* at a range of temperatures, with both species development rates increasing as temperature regimes increased. More research should be done to examine fitting curves to meta-analysis data, specifically the longevity – temperature relationship, the reproductive rate – temperature relationship, and the fecundity – temperature relationship. All of these relationships may be better fit to a non-symmetric curve around an optimal value. However, until RWA data collection is more uniform across studies a parsimonious approach may be warranted. That is, assuming symmetry until variability in data collection across studies is reduced.

Although not formally quantified in this study, RWA reproductive and development rates appear to optimize at lower temperatures as compared to other important small-grain aphid pests on the Great Plains. Therefore, typical conditions in the early spring (cooler temperatures) should favor RWA population development over many other aphid pests (e.g., Harvey and Martin 1988).

Additional meta-analysis of important aphid pests of small-grains on the Great Plains would be valuable for developing further understanding of aphid population responses to different temperature regimes with implications for global climate change and pest forecasting.

Figure 3.1: Data from studies in Table 3.1 for the average number of nymphs produced per female at temperatures from 5° - 30° C (red squares). The blue line depicts a gaussian approximation to the data.

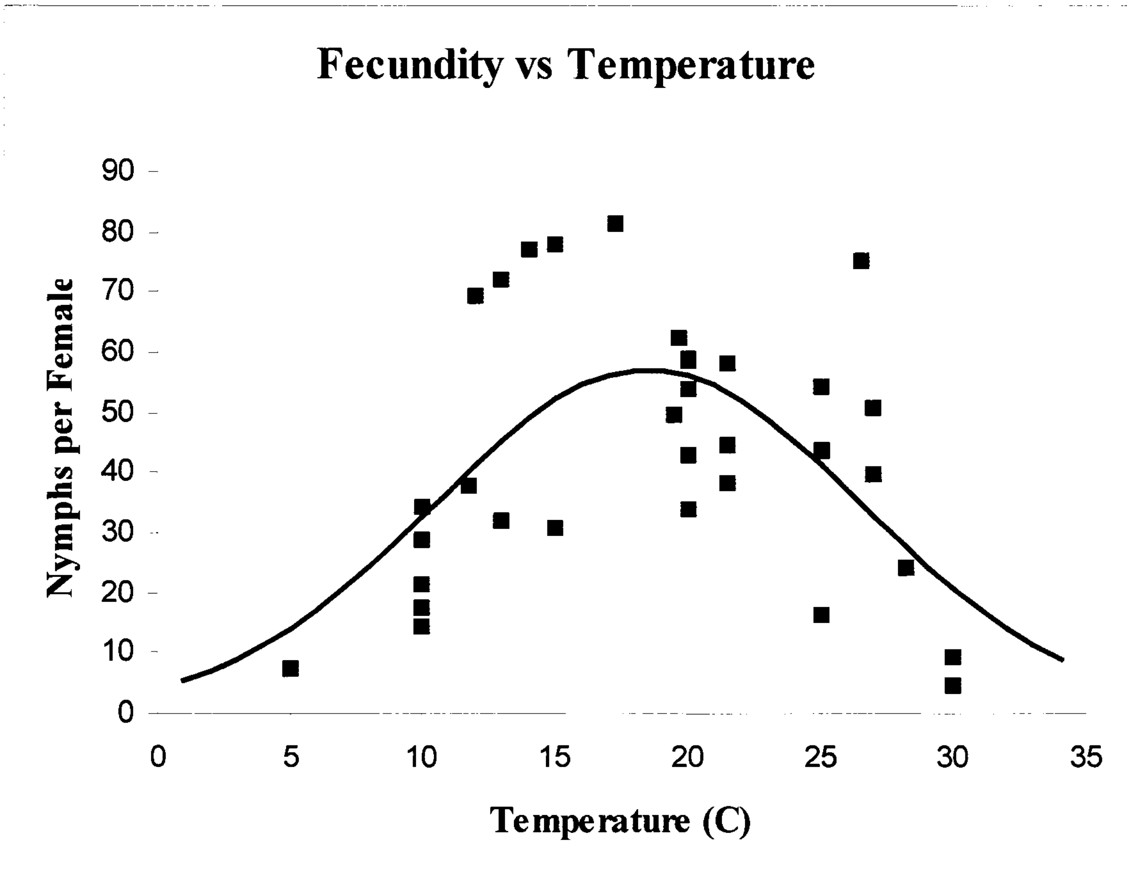


Figure 3.2: Data from studies in Table 3.1 for the average number of nymphs produced per female per day during the reproductive period at temperatures from 5° - 30° C (red squares). The blue line depicts a gaussian approximation to the data.

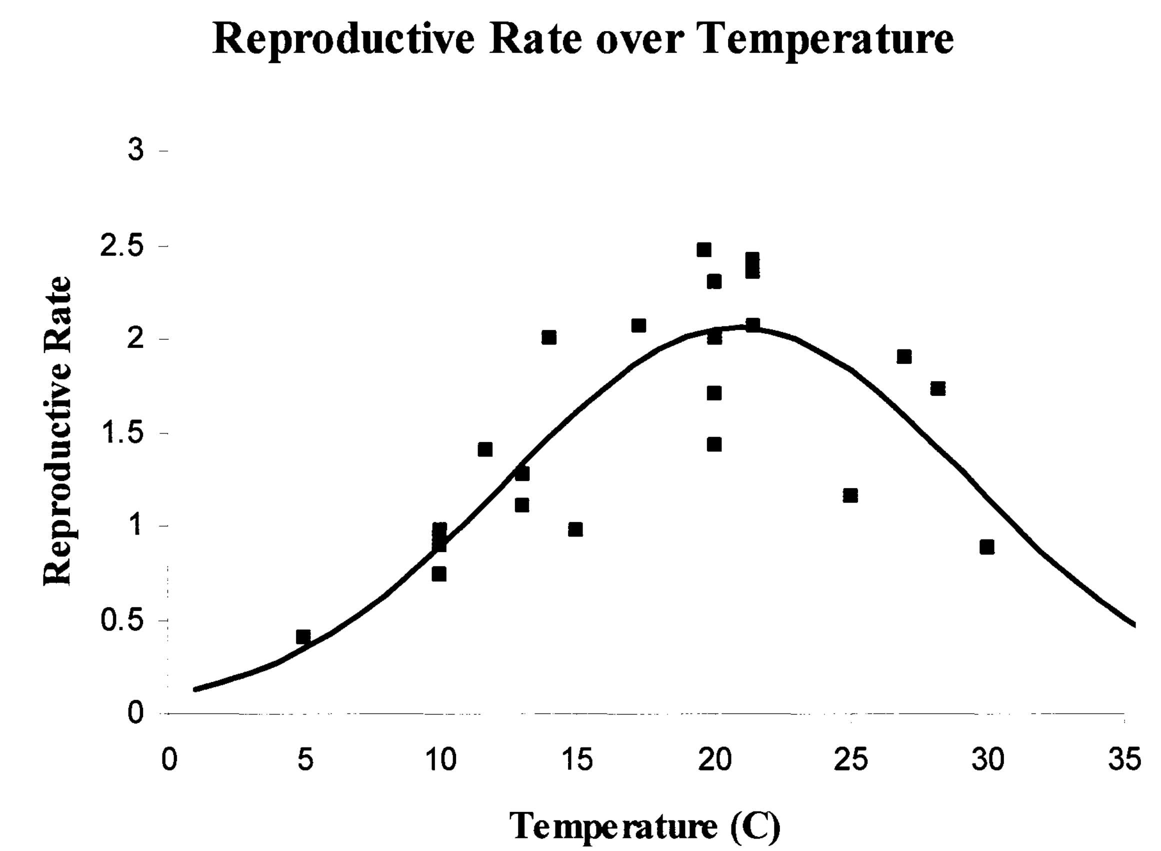


Figure 3.3: Fecundity and temperature data from studies in Table 3.1 were used to linearly regress temperature against fecundity to calculate a minimum reproduction threshold using temperature data from 5° - 20° C.

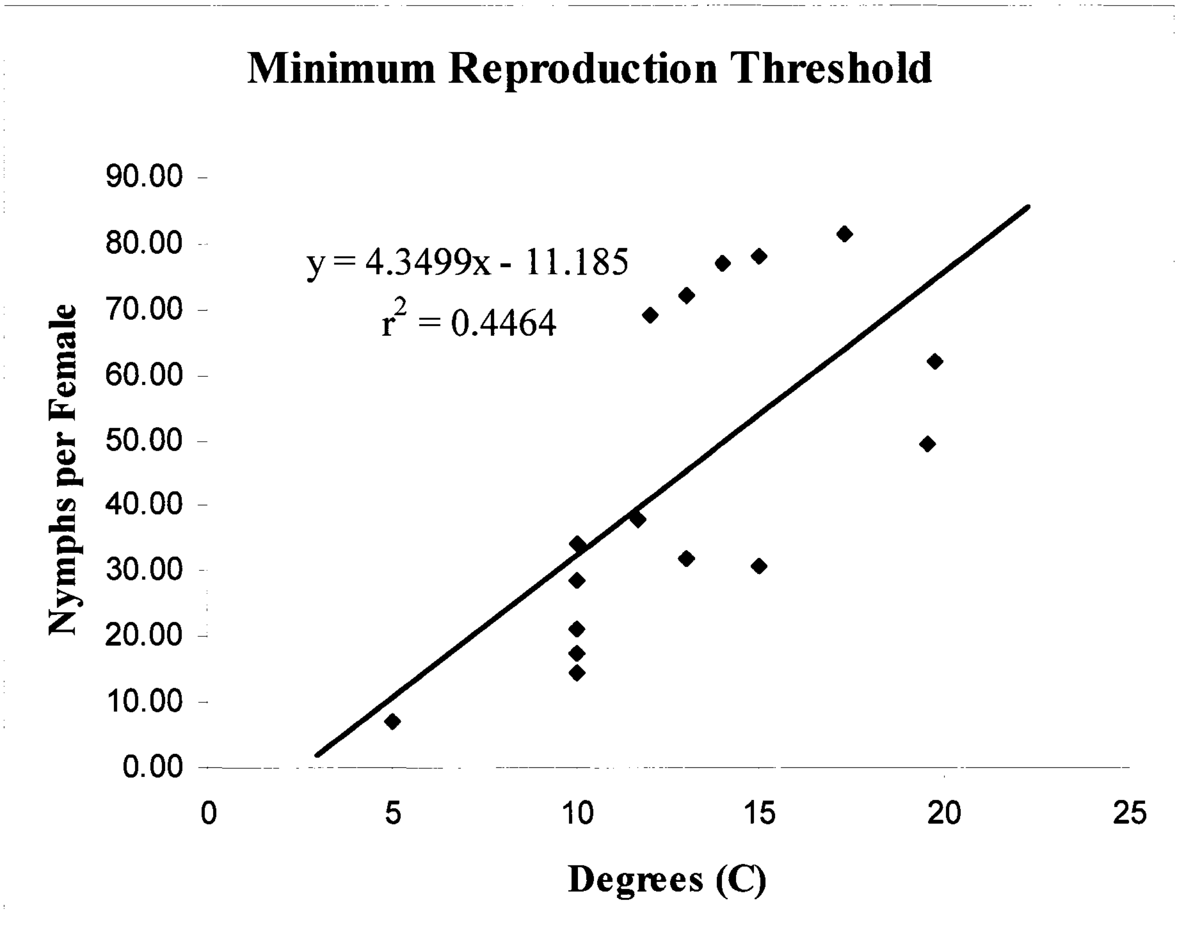


Figure 3.4: Fecundity and temperature data from studies in Table 3.1 were used to linearly regress temperature against fecundity to calculate a maximum reproduction threshold using temperature data from 20° to 30° C.

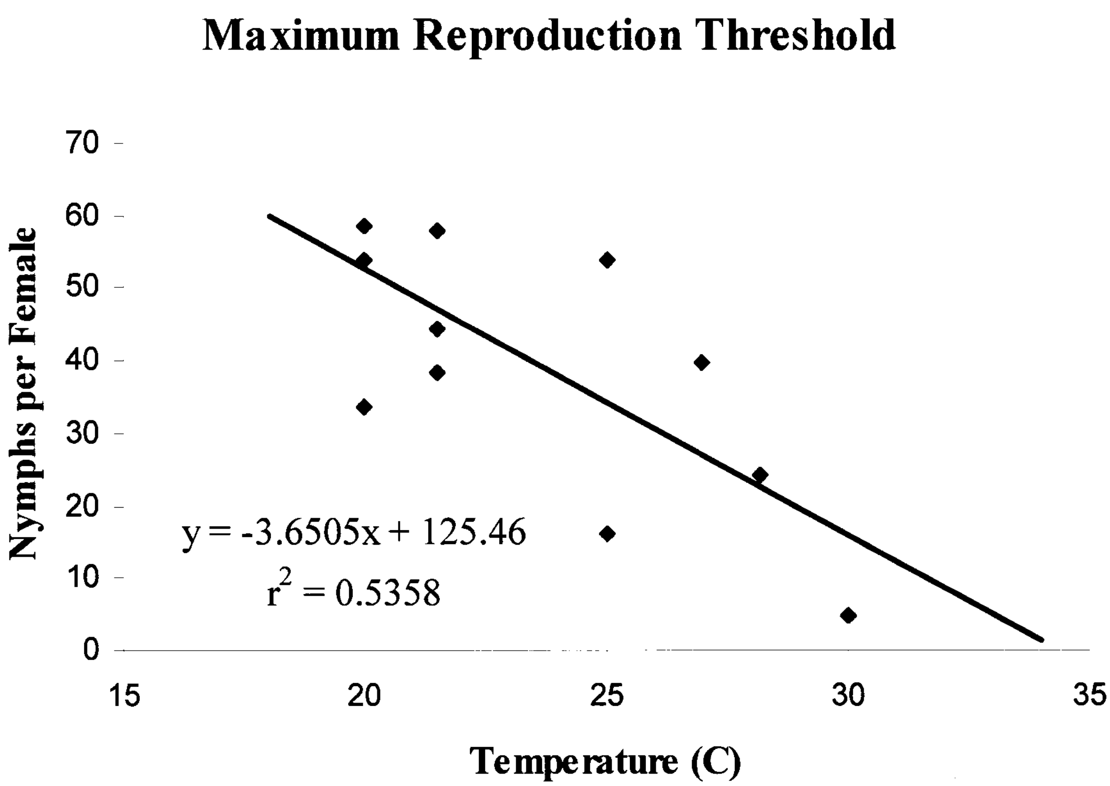


Figure 3.5: Temperature Development Threshold data extracted from studies in Table 3.1. A temperature development threshold was calculated by linearly regressing the inverse of the pre-nymphipositional time against temperature.

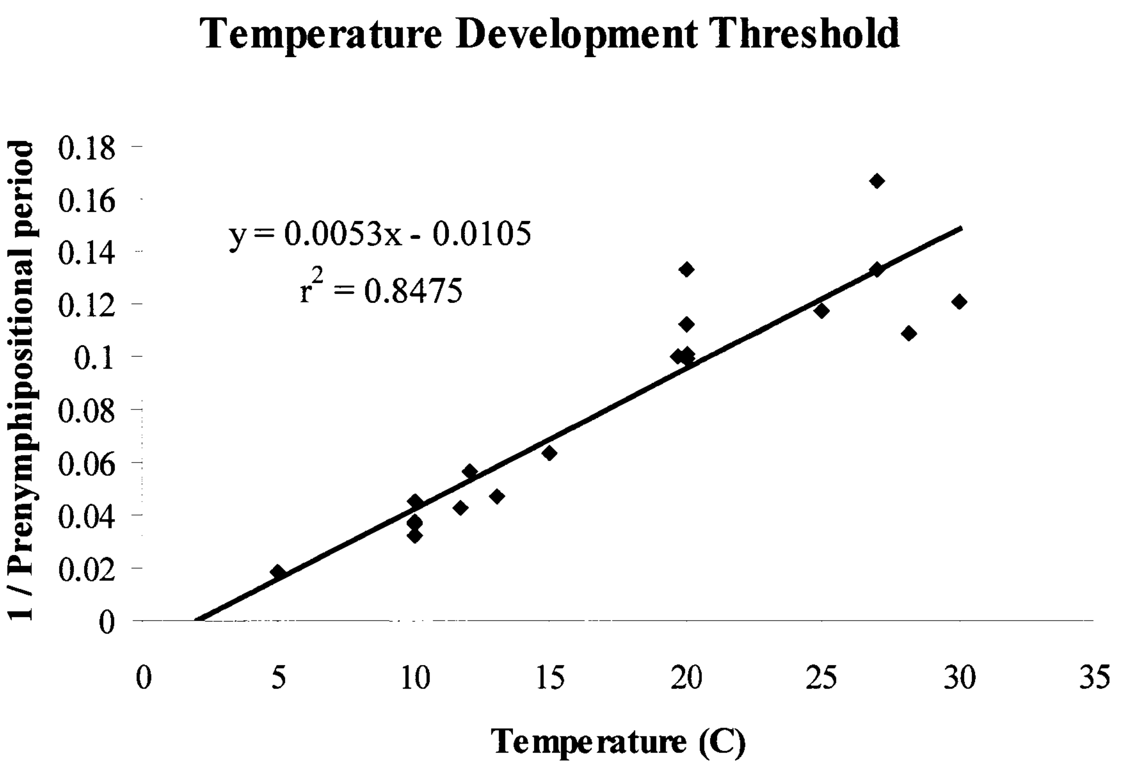


Figure 3.6: Longevity and temperature data extracted from studies in Table 3.1 are used to depict average longevity over temperature. Maximum longevity is approximately 96° C.

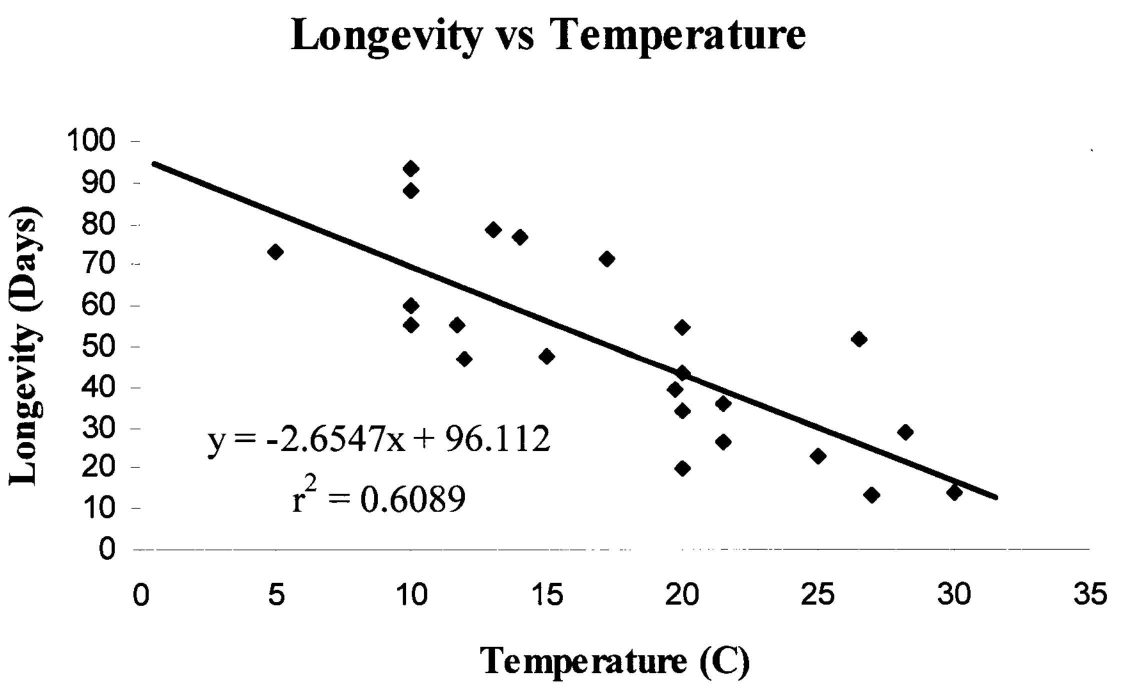
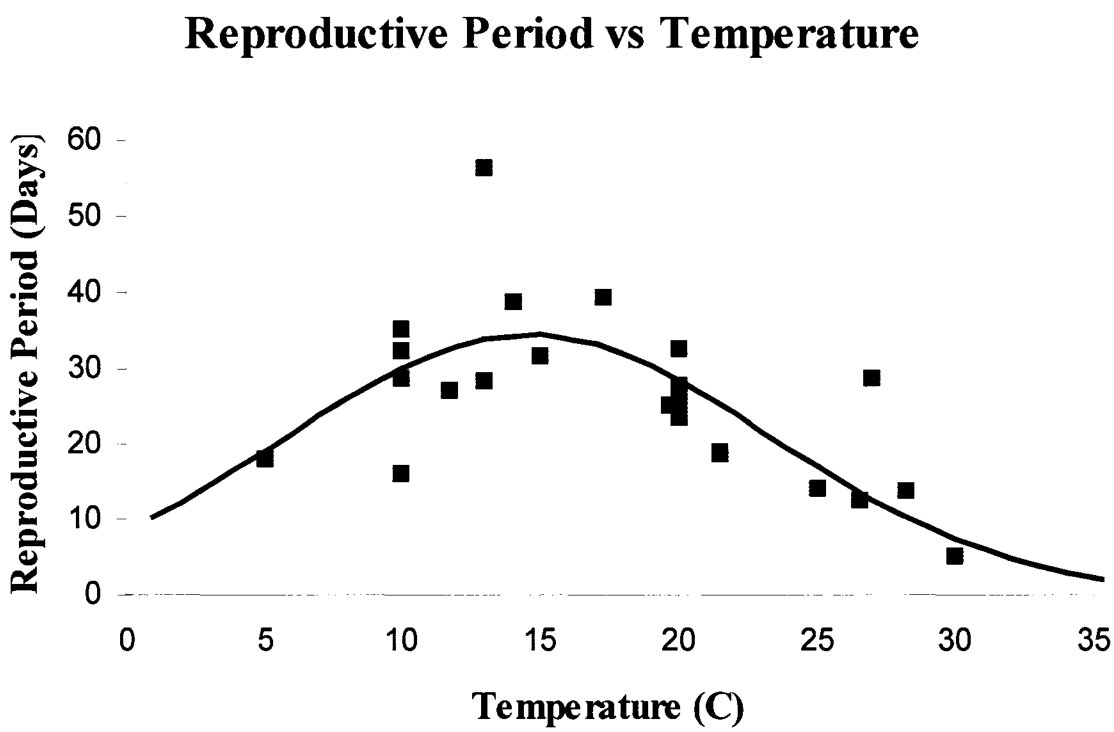


Figure 3.7: Length of the RWA Reproductive Period in Days versus Temperature. Reproductive period and temperature data were extracted from studies in Table 3.1. Pattern in the Reproductive period data is difficult to discern. However, data appears to be approximately gaussian (i.e., the




blue line).

Figure 3.8: Pre-nymphipositional period and temperature data were extracted from studies in Table 3.1 and used to graph the number of days until first birth across various temperatures. This data fits an exponential curve (i.e., the blue line) very well as captured by the formula and $r^2$ in the upper right hand corner.

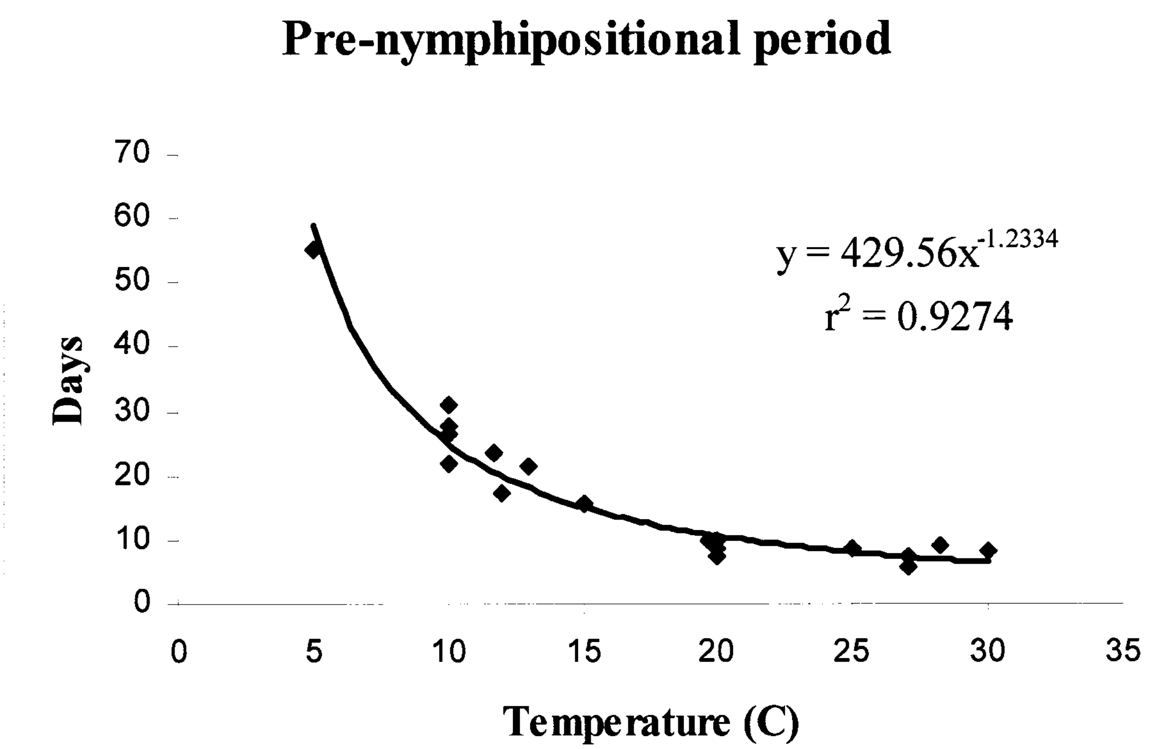


Table 3.1: Citations used in meta-analysis, year of publication and number of data points extracted from each citation

| Authors | Year | Data Points |
|---|---|---|
| Webster and Starks | 1987 | 3 |
| Aalbersberg et al. | 1987 | 3 |
| Michels and Behle | 1988 | 6 |
| Michels and Behle | 1989 | 3 |
| Kieckhefer and Elliott | 1989 | 3 |
| Girma et al. | 1990 | 3 |
| Behle and Michels | 1990 | 1 |
| Webster et al. | 1993 | 2 |
| Nowierski et al. | 1995 | 4 |
| Butts and Schaalje | 1997 | 5 |
| Haile et al. | 1999 | 1 |
| Hawley et al. | 2003 | 1 |
| Miller et al. | 2004 | 1 |
| Randolph and Peairs | Unpublished | 1 |
| Merrill et al. | Unpublished | 1 |

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# Chapter 4

# Using Weather Data to Generate Estimates of Russian Wheat Aphid Overwintering Success


## Abstract

The Russian wheat aphid (RWA), *Diuraphis noxia*, (Kurdjumov) is a significant pest of small grain crops. Since their invasion into the United States around two decades ago, total damage is estimated in the hundreds of millions of dollars. However, aphid abundances, and associated crop damage, vary radically from year-to-year. Crop damage is typically much higher from aphid populations that successfully overwinter in a location, rather than from aphids that migrate to a given location in the spring. Therefore, much of the year-to-year variation in crop damage is associated with overwintering mortality. Based on previous studies, it is hypothesized that the magnitude of three weather related variables affects overwintering mortality of the Russian wheat aphid in the following ways: 1) increased snowfall or precipitation decreases overwintering mortality, 2) increased degree-days below 0° C increases overwintering mortality, and 3) increased degree-days above 0° C increases RWA densities. Data collected over three years, at two sites in eastern Colorado were used to develop a model for overwintering success of the Russian wheat aphid. An information theoretic approach yielded four models with support in the data. A model-averaged procedure of these four models explained 81 % of the variation ($r^2 = 0.81$) in RWA densities using weather data.

## Introduction

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) is a significant pest of small grain crops. Since their invasion into the United States around two decades ago, damages are estimated in the hundreds of millions of dollars (Webster et al. 1994, Morrison and Peairs 1998). However, aphid abundances vary radically from year-to-year. For example, in the early years following the introduction of the RWA, total losses varied from $274 million in 1988 to $12 million in 1991 (Webster and Treat 1997). Understanding the ecological factors that determine the year-to-year variation in RWA population densities and associated crop damage would be of significant value for developing a more comprehensive integrated pest management strategy for RWA. One important factor in determining crop damage in the spring is the density of RWA that successful overwinter. That is, when RWA do not overwinter successfully, recolonization must occur in the spring, and damage to crops tends to be greatly reduced (Peairs et al. 2006). Unlike many aphid species, RWA in North America do not have a diapausing egg stage. Thus, it is especially important to examine the ecology of adult RWA during the winter season to determine important variables for governing overwintering survival. Overwintering success has been shown in other anholocyclic aphids to be directly related to climate and to the severity of winter weather (Dewar and Carter 1984).

Undoubtedly linked to climate, significant spatial heterogeneity in RWA overwintering mortality exists across North America. In many areas of Canada, complete winter mortality of RWA populations is commonly observed and re-establishment must occur from areas where populations successfully overwintered (Butts 1992). Even in milder, more southern areas such as Idaho, Montana, and northern Utah, RWA populations survive only in warmer winters (Feng and Nowierski 1992, Messina 1993, Elliott et al. 1998). On the other hand, RWA have a high probably of overwintering success in areas of northern Texas, southeastern Colorado, eastern New Mexico and the Oklahoma panhandle (Elliott et al. 1998). The inability of RWA to survive in less hospitable climates, or under difficult winter conditions is likely related to the fact that populations in North America are anholocyclic, without the range of overwintering strategies (e.g., a cold-hardy egg stage) available to sexually producing species.

Much research has examined the ecological relationship between adult RWA and environmental conditions that could impact RWA populations during the overwintering period (e.g., Campbell et al. 1974, Powell 1974, Turl 1980, Dewar and Carter 1984, Dixon 1985, Knight et al. 1986, Walters and Dewar 1986, Aalbersberg et al. 1987, Odoherty and Ring 1987, Webster and Starks 1987, Harvey and Martin 1988, Kieckhefer and Elliott 1989, Michels and Behle 1989, Behle and Michels 1990, Girma et al. 1990, Harrington et al. 1990, Thomas and Butts 1990, Butts 1992, Archer and Bynum 1993, Messina 1993, Messina et al. 1993b, Hutchinson and Bale 1994, Armstrong and Peairs 1996, Butts et al. 1997a, Butts and Schaalje 1997, Butts et al. 1997b, Archer et al. 1998, Burd et al. 1998, Armstrong and Nielsen 2000, Stary and Lukasova 2002). In general, RWA are considered one of the more winter-hardy aphid pests of small-grains on the Great Plains (Harvey and Martin 1988, Archer and Bynum 1993). Although RWA can withstand exceptionally cold temperatures, their expected lifespan and fecundity decrease with increasing time spent below 0° C (Knight et al. 1986, Hutchinson and Bale 1994, Butts and Schaalje 1997).

Armstrong and Peairs (1996) indicated that 64% of the variation in overwintering survival of RWA in Colorado was due to variation in weather conditions. They modeled winter mortality of RWA using two weather variables, temperature and precipitation (i.e. snow cover). Specifically, they found a strong relationship between overwintering survival and snow cover. Snow cover provided insulation from colder temperatures and therefore decreasing mortality. Moreover, they demonstrated that overwintering mortality was linearly related to winter temperatures, with 100 % population mortality occurring at ca. 125 degree days below zero. (A degree-day below 0° C (DD-0°) is the equivalent of 1° C below zero for one day. DD-0° accumulate with any combination of decreasing temperature during the day or increasing the time spent at temperatures. For example, 10 DD-0° could be accumulated by a temperature of -10° C for 1 day or -1° C for 10 days.) Research by Armstrong and Peairs (1996) suggests that warm and wet winters should result in strong overwintering survival. Conversely, cold and dry winters should have high RWA overwintering mortality.

Another important factor influencing overwintering mortality is the longevity of RWA. Meta-analysis data (See Chapter 3 for details) suggests that the maximum average RWA lifespan is approximately three months (Figure 4.1). Therefore, reproduction must occur during the winter months for RWA populations to survive. For development and reproduction to occur, it is essential that aphids have temperatures above freezing (Chapter 3, Meta-analysis results). The results plotted in Figure 4.2 show a relatively linear increase in fecundity from an average daily temperature of 0° C to an average daily temperature of 20° C. The RWA developmental temperature threshold has been estimated at 4.1° C (Kieckhefer and Elliott 1989), 0.54° C (Aalbersberg et al. 1987), 5.2° C

(Nowierski et al. 1995) and -1.57° C (Girma et al. 1990). Pike et al (1991) showed that if temperatures rise above the developmental threshold for only a short portion of the day, some development does occur. For the purposes of my modeling efforts, 0° C was assumed to be the temperature threshold above which development occurs and conversely, below which mortality increases. Meta-analysis indicates this assumption is reasonable, and it has the benefit of reducing model complexity. Additional time at higher temperatures (up to approximately 20° C) positively affects development and reproduction. Degree-days above 0° C (DD0°) are used to quantify developmental units (a combination of temperature and time spent at the temperature). Similar to DD-0°, a DD0° is the equivalent of 1° C above zero for one day. Degree-days accumulate with any combination of temperature or time spent at temperatures above 0° C. Meta-analysis data (Chapter 3) indicate that increases in temperature, which lead to greater degree-day accumulation, also result in increased fecundity for temperatures between 0° C and 20° C (Figure 4.2). Given the aforementioned considerations, three weather-mediated mechanisms are suggested that could affect overwintering success of RWA populations:

1. Greater snow cover (or as a surrogate, precipitation) increases overwintering success due to increased longevity.
2. Greater DD-0° decreases overwintering success because it decreases longevity.
3. Greater DD0° increases overwintering success because the increase in fecundity more than offsets the decrease in longevity.

I hypothesize that much of the variation seen in RWA overwintering success can be explained through the effects of these three weather related variables. The winter and spring seasons are time periods of dynamic change in RWA population densities. A diagrammatic representation of the RWA population density during these time periods and throughout the rest of the year is depicted in Figure 4.3. My research focused on creating a log linear model to estimate the population change in the spring (i.e., the period depicted by the blocked green zone in Figure 4.3) based upon winter and spring weather conditions. Accurate prediction of RWA population density in the spring would be a valuable tool for pest management, and would allow for timely field scouting and pesticide applications.

## Methods

Sites were chosen to represent widely differing climates from among eastern Colorado's wheat growing areas (Last Chance Site: 39°44' N 103°48' W, Lamar Site: 37°58' N 102°30' W).

Plots were infested using a Davis Inoculator (Davis and Oswalt 1979) in the late fall (primarily in November) with Biotype 1 RWA (For more details regarding infestations see Appendix B). The sampling design was intended to obtain samples over three years at two sites with two sampling dates per site per year (the unit of one sample date per site per year will henceforth be referred to as a sample set or SS). However, one SS in Year Two was not obtained for logistical reasons. Therefore, there were 11 SS (i.e., 2 sites x 3 years x 2 sample periods per year, minus one SS). For wheat variety and planting details see Appendix B. Additionally, RWA density on infested wheat was measured in early winter to determine if infestation was successful. To determine RWA densities, tillers were removed from subplots during each sampling period. Sampling design was for tillers to be removed at a rate of six tillers per subplot. If tiller density was low (e.g., from low emergence), tillers were removed to maximize tillers obtained over both SSs. For example, if only six tillers existed on a subplot during the first SS, half of the tillers were removed allowing the second set of three tillers to remain for sampling during the second SS. Tillers were clipped from each subplot, placed into ziplock bags, and transported to Colorado State University's Agricultural Research Development and Education Center (ARDEC). Tillers were then removed from the ziplock bags and placed into Berlese devices. Berlese devices heated the wheat tillers, causing any aphids on the plant material to retreat to cooler areas and hence causing aphids to fall into a Berlese cup containing a 70/30 alcohol/water mixture. From the alcohol/water mixture, RWA were counted under a dissecting microscope. RWA density per subplot was calculated as the number of aphids per sample divided by the number of tillers per sample. Subplot densities were averaged to obtain a plot average. Mean RWA density per SS was calculated by the mean of the plot averages per SS and a log transformation ( ln(mean RWA density) + 0.1) per SS was used to normalize the data. Each SS mean RWA density was calculated from approximately 58 RWA plot density averages. SS mean RWA densities were used as the dependent variable in the following model development and analysis.

Temperature and precipitation data were obtained from the Colorado Agricultural Meteorological network (CoAgMet) Stations on or near each field site. CoAgMet stations provide high and low temperature and precipitation on a daily basis. (For more details on the CoAgMet network see: http://ccc.atmos.colostate.edu/~coagmet/index.php.) Degree-days above and below 0° C are calculated for all days between December 1st and the sampling date, if the average daily temperature (i.e. [high temperature – low temperature] / 2) was greater than 0° C, that temperature was added to the DD0° total. And conversely, if the average daily temperature was below 0° C, that temperature was added to the DD-0° total.

### *Model Development and Selection*

A set of a priori models was developed using all subsets of the variables of interest (i.e., precipitation, DD-0° and DD0° and their interaction terms). All variables were normalized between 0 and 1. Normalization allows for comparisons of the magnitude of the effect size between predictor variables. Normalization for precipitation (max =5.49, min = 0.11), DD0° (max = 771.81, min = 208.28), and DD-0° (max = 243.94, min = 120.05) were calculated by: $(X_i - X_{min}) / (X_{max} - X_{min})$.

Pearson's Correlations Coefficients were calculated for each of the independent variables. DD0° and precipitation were highly correlated (r = 0.73). Instead of removing one of these variables or risking losing information if only one variable was allowed during model selection procedures, an index (PD Index) was created by averaging the normalized values for precipitation and DD0°. The PD Index predictor variable was added to the candidate variable set. Therefore, four variables (DD0°, DD-0°, Precipitation, and the PD Index) were used. However because precipitation, DD0°, and the PD Index were highly correlated, models with more than one of these variables were discarded. Models were compared using an information theoretic approach (Burnham and Anderson 2002, 2004). The information theoretic approach is based on parsimony, which is the trade-off between model fit and the number of parameters in the model, and favors the model with the least number of parameters that adequately describes the variation in the data (Burnham and Anderson 2002, Adair 2005). Models were ranked based on Akaike's Information Criterion (AIC) (Akaike 1973, 1981, Burnham and Anderson 2002, 2004). As is recommended for small sample sets (e.g., this sample set with $n = 11$) a correction to AIC was used (AICc). AICc values were calculated for all models in the model data set and were used to select the models that would best approximate RWA densities (see Table 4.1). AICc values, ΔAICc, and AICc weights (Burnham and Anderson 2002, 2004) were calculated for each model. These statistics can be used to quantify the strength of evidence supporting each of the models.

ΔAICc values are calculated as the difference between the model of interest and the model with the lowest AICc value (i.e., the best approximating model). The ΔAICc for the best approximating model is therefore 0. Models with ΔAICc values from 0-3 are considered to have strong support in the data for being selected as the best approximating model using a different data set developed under similar processes and under similar conditions. Values from 4-7 are considered to have increasingly less support. Models with ΔAICc values above 7 are not considered to have much support for their being the best approximating model for the data (Burnham and Anderson 2002).

AICc weights ($w_r$) were assigned to each of the models based on their distance from the model with the lowest AICc. $w_r$ is a measure of model selection uncertainty and can be interpreted as the likelihood that a model will be chosen as the best approximating model, given a similar set of data (Burnham and Anderson 2002, 2004). If no single model distinguishes itself as the best approximating model ($w_r > 0.9$) (Burnham and

Anderson 2002), model averaging can be used to reduce model selection bias. Model selection bias is the bias associated with the selection of a single model or a small set of models, to the exclusion of other models that also have support in the data for prediction of the dependent variable. Many model selection techniques (e.g., stepwise selection) select a single best model without examining whether other models or other predictor variables approximate the data well. That is, many model selection techniques do not provide information about how much better the selected model is as compared to the rejected models. Moreover, once the model is selected, all inference between predictor variables and dependent variables is based on the selected model, ignoring all bias associated with the selection and ignoring any predictions generated by other models. Methods used in this effort were chosen to overcome these weaknesses.

### *Examining Important Variables*

AICc weights are used to assess the relative importance of each predictor variable (e.g., DD0°) in explaining variation in the dependent variable (Adair 2005). Variable relative importance weight, $w_{+(i)}$, is the sum of the AICc weights for predictor variable $i$ over all models in which predictor variable $i$ occurs (Burnham and Anderson 2002). The resulting $w_{+(i)}$ can range from 0 to 1, with the more important variables having higher values (i.e., close to 1). The $w_{+(i)}$s allow the predictor variables to be ranked (known as Variable Ranking) based on their strength of support in the data. Because $w_{+(i)}$s are derived from AICc weights ($w_r$), their interpretation can be similar. That is, $w_{+(i)}$ can be interpreted as the likelihood of predictor $i$ being an important predictor variable for understanding variation in the system. ($w_{+(i)}$ refers to AICc variable weights, whereas $w_r$ refers to AICc model weights.)

### *Parameter Estimates*

Weighted average parameter estimates ($\beta_{+(i)}$) are calculated by using $w_r$s in conjunction with parameter estimates from each model in the model selection set:

$$\text{Formula \# 1: } \beta_{+(i)} = \sum w_r * \beta_{r(i)} \ldots \text{ for all models } r = 1 \text{ to R}$$

where $w_r$ is the AICc weight for model $r$ and $\beta_{r(i)}$ is the parameter estimate for variable $i$ in model $r$.

DD0°, DD-0°, precipitation and the PD Index were normalized as described above. Because these variables were normalized, parameter estimates for each variable yield the magnitude of the variables' effect size and the direction of its effect on RWA densities.

## Results

### *Model Selection and Model Averaging*

No single model distinguished itself as the best approximating model. The model with the lowest AICc (DD0°, DD-0°, and interaction terms) had an AICc $w_r$ of 0.739 ($\Delta$AICc = 0), the second best approximating model (DD0°) had an AICc $w_r$ of 0.111 ($\Delta$AICc = 3.79), the third best approximating model (PD Index) had an AICc $w_r$ of 0.095 ($\Delta$AICc = 4.11), and the fourth best approximating model (DD0° & DD-0°) had an AICc $w_r$ of 0.055 ($\Delta$AICc = 5.19). All other models had $\Delta$AICc values greater than 7. Model selection results are detailed in Table 4.1. Because several models had support in the data for being the best approximating model, a model-averaged result was calculated using the four models with ΔAICc values less than 7. To do so, AICc weights were normalized over the four models selected for the model averaging procedure (See Table 4.2). These models were averaged using their respective AICc $w_r$s to form the following model-averaged result:

$$\ln(\text{RWA density} + 0.1) = -0.595 + 0.241 * (\text{PD Index}) + 4.315 * (\text{DD}0°) + 0.344 * (\text{DD-}0°) + (-5.837) * (\text{DD}0°) * (\text{DD-}0°)$$

The model-averaged result explains 81 % of the variance in RWA density ($r^2 = 0.81$).

## *Variable Importance and Variable Ranking*

Each of the predictor variables was examined to elucidate its strength and importance as a predictor variable for RWA densities. DD0° had the highest variable rank and $w_{+(i)}$ ($w_{\text{DD0°}} = 0.905$), with a large positive effect (DD0° effect size = 4.315). Additionally, DD-0° and the DD-0° * DD0° interaction term were both strong indicators of RWA densities ($w_{\text{DD-0°}} = 0.794$, $w_{\text{DD0°*DD-0°}} = 0.739$). DD-0° had a small positive effect (DD-0° effect size = 0.344) and the DD0°*DD-0° interaction term had a large negative effect (DD0°*DD-0° effect size = -5.837). The PD Index had the lowest rank and $w_i$ of the included variables ($w_{\text{PDIndex}} = 0.095$), indicting a relative low likelihood of this variable elucidating variation in the system. The PD Index had a small but positive effect size (PD Index effect size = 0.241). Table 4.3 depicts the variable weight, ranking, parameter estimates (effect size), and direction of the effect. In this case, because of the strength of the best approximating model ($w_r = 0.739$), weight of parameter estimates (effect size and direction) from variables included in all other models are relatively diminished. In this study, parameter estimates from variables included in the best approximating model have approximately 3 times the weight of parameter estimates from all of the other models combined (AICc weight ratio of the best approximating model to the remaining models is 0.739 / 0.271 = 2.83). This leads to an unexpected result; specifically, the positive direction of the DD-0° effect. The positive direction of the DD-0° effect results from the way model-averaged parameter estimates are calculated. Parameter estimates, which give effect size and direction, are calculated using a weighted average of the parameter estimates from each model selected for model averaging. If one model has a large weight, model-averaged parameter estimates are heavily weighted towards estimates from that model. In this case, the best approximating model includes an interaction term between DD-0° and DD0°. The interaction term is strongly negative, and the model parameterizes DD-0° in a positive direction to best fit the data and correct for the strongly negative interaction term. That is, this positive effect is an artifact of its inclusion with its interaction term in the best approximating model. In models where the interaction term was not included, the effect direction of DD-0° was always negative.

### *Trend Surfaces and RWA Density Surfaces*

The model-averaged result can be used in conjunction with weather data to develop a RWA density surface. As an example, I developed trend surfaces for DD0°, DD-0°, and the PD Index using CoAgMet 2001-2002 weather data from December 1$^{st}$ 2001 through March 31$^{st}$ 2002 (See Appendix C for details). Figure 4.4 depicts a RWA density surface for March 31$^{st}$ 2002 calculated using the model-averaged result.

## Discussion

This research corroborates previous research, agreeing that the number of degree days spent under the developmental threshold, precipitation and the number of degree days spent above the temperature threshold all influence overwintering survival. The degree-day variables (DD0° and DD-0°) both had strong AICc weights, with DD0° being slightly more likely to influence overwintering mortality of RWA.

The variables DD0° and precipitation were highly correlated, as was the index created to collapse these two variables (PD Index). All of these variables have positive effects on RWA overwintering success (Table 4.3). In contrast, the variable DD-0° has a negative effect (where not included with an interaction term) on RWA densities and is associated with increasing mortality. Although many (e.g., Messina et al. 1993a, Armstrong and Peairs 1996) have suggested that cold winters are responsible for RWA mortality, data reported here suggest that the cold temperatures are only one factor linked with overwintering mortality. Apparently, the negative effects of cold temperatures combined with the positive effects from increasing degree-days above the developmental threshold are both important variables. Precipitation was not selected as an important variable during the model selection process. And while the PD Index was included, its AICc weight was low (i.e., $w_{(PD\ Index)} = 0.095$). Based on previous research, precipitation was expected to be an important variable for understanding RWA overwintering population dynamics. There are many possible reasons for the exclusion of the precipitation variable from the model and the low weight of the PD Index including: 1) Precipitation was not a strong indicator of RWA overwintering mortality. 2) Precipitation was not a good surrogate for snow cover, which was found to be a strong predictor of

RWA mortality by Armstrong and Peairs (1996). And 3) the resolution or scale of the precipitation data did not capture the influence of precipitation on RWA mortality. In addition there may be other, unknown reasons that the data used in this study did not capture the signal generated by precipitation. This study used only a small number of sample sets and additional data might support precipitation as a stronger variable.

DD0°, which is assumed to be a direct driver of population growth, might be expected to show a stronger effect than DD-0°. When conditions allow, exponential population growth rates in aphids can lead to exceptionally rapid density increases. For example, at 20° C a RWA can give birth to 8 nymphs per day (Merrill, unpublished data). A high rate of population increase could have swamped effects from variables with more linear effects (e.g., DD-0° were modeled to linearly decrease populations of RWA by Armstrong and Peairs 1996). Precipitation would not be expected to directly increase population growth. However, snow cover and its insulative properties should allow existing populations to persist during colder periods, especially during cold snaps. Cold snaps (e.g., short duration, relative extreme negative temperatures such as -25°C) have drastic negative affects on RWA populations if the populations were not insulated (Knight et al. 1986, Armstrong and Peairs 1996). However, Armstrong and Peairs (1996) found that prolonged exposure to snow cover (i.e., greater than 40 days) appeared to have negative effects on RWA survival, even though the temperature to which they were exposed may have been relatively mild. These negative effects may be because feeding behavior was inhibited at these temperatures.

## Conclusions

Modeling results indicate that temperature variables are more important than precipitation variables. This study suggests that the number of warm days and the temperature of those days are essential variables for determining overwintering success. This contrasts with the more conventional view centered around aphid mortality resulting primarily from cold temperatures. The models developed here treat temperatures in a fairly simplistic framework and extreme weather events are outside of the variation explained. For example, a severe cold snap could cause complete localized extinction of RWA populations, even if the rest of the winter is mild. Prolonged snow cover (e.g., greater than 40 days) will likely have dramatically negative effects on RWA populations (Armstrong and Peairs 1996). More studies should be undertaken to determine if increasing the number of samples and changing the geographic region of study would allow for the elucidation of other real signals in overwintering RWA density data.

The variability explained by this RWA density model was very high ($r^2 = 0.81$) and shows good promise for future development of RWA management tools. Unfortunately, obtaining high-resolution temperature and precipitation data would be costly. And this high cost may reduce the utility of spatially explicit modeling of variation in RWA densities with these variables. Moreover, this model was parameterized for winter wheat that had been infested at a high rate with RWA. Populations outside of the study areas, different RWA infestation levels, or RWA on alternate crops may show different population dynamics. Additionally, many biological factors are likely to be important such as natural enemies and the condition of the crop. The large-extent RWA density trend surface for March 31st 2002 (Figure 4.4) is an example of the predictive capacity of the model. However, this trend surface cannot be considered adequate for management purposes until validation has been completed. Additionally, inputs (i.e., precipitation, DD0°, and DD-0° layers) of higher resolution and accuracy are needed to build a realistic RWA density prediction surface across the extent depicted in Figure 4.4.

Figure 4.1: Meta-analysis data used to develop a relationship between temperature and RWA longevity feeding on wheat (Data from Aalbersberg et al. 1987, Michels and Behle 1988, Kieckhefer and Elliott 1989, Michels and Behle 1989, Behle and Michels 1990, Girma et al. 1990, Webster et al. 1993, Butts et al. 1997a, Hawley et al. 2003, Miller et al. 2003, Randolph and Peairs unpublished data)

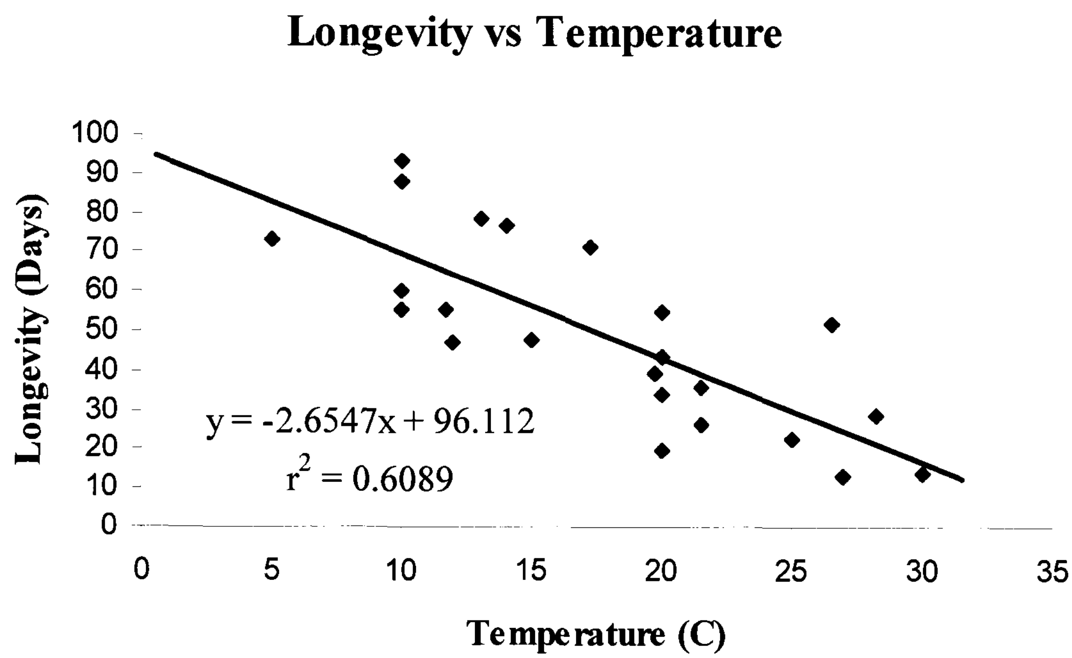

Figure 4.2: Meta-Analysis data used to develop a relationship between temperature and the number of nymphs produced per female over her reproductive period feeding on wheat (Data from Aalbersberg et al. 1987, Webster and Starks 1987, Michels and Behle 1988, Kieckhefer and Elliott 1989, Michels and Behle 1989, Behle and Michels 1990, Girma et al. 1990, Webster et al. 1993, Nowierski et al. 1995, Butts et al. 1997a, Hawley et al. 2003, Miller et al. 2003, Randolph and Peairs unpublished data).

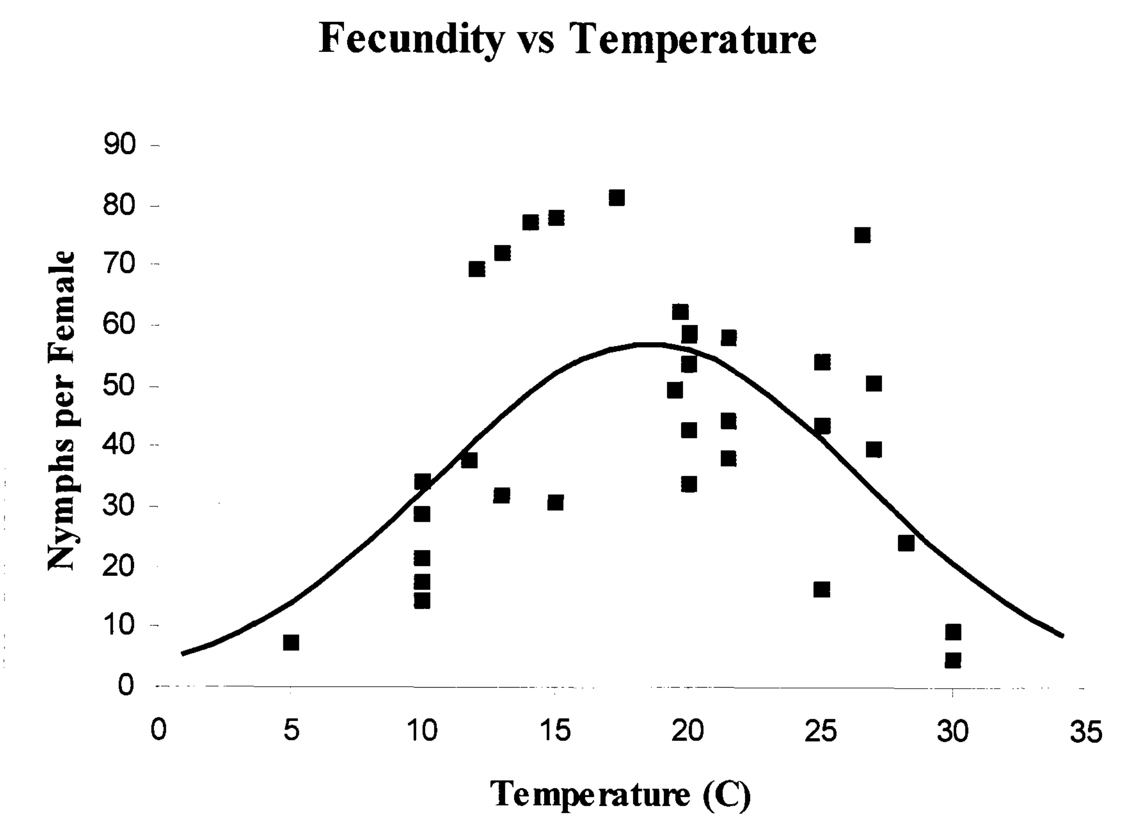

Figure 4.3: A simplistic representation of the likely RWA population density over time. The blocked green zone represents the time period modeled by the large-extent RWA density model. The y-axis represents relative RWA densities and is not scaled due to typically large year-to-year variance. For example, densities in 2010 could be ten fold greater than densities seen in 2004, but the both 2004 and 2010 population density patterns should follow that depicted by the diagram.

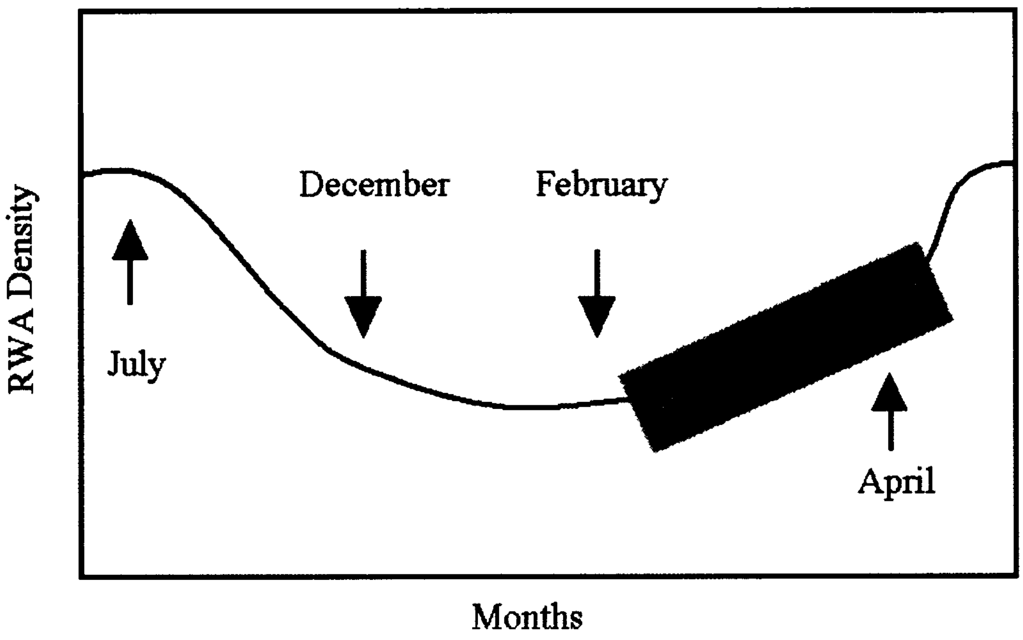

Figure 4.4: Large-extent RWA density trend surface using data from December 1st 2001 – March 31st 2002. The expected RWA density surface from March 31st 2002 is depicted. Areas in green have low densities of RWA whereas areas in red have relatively high RWA density. The model generated high RWA densities in mountainous regions. This is an artifact created by the importance placed on elevation as a predictor variable in the weather variable models (Appendix C).

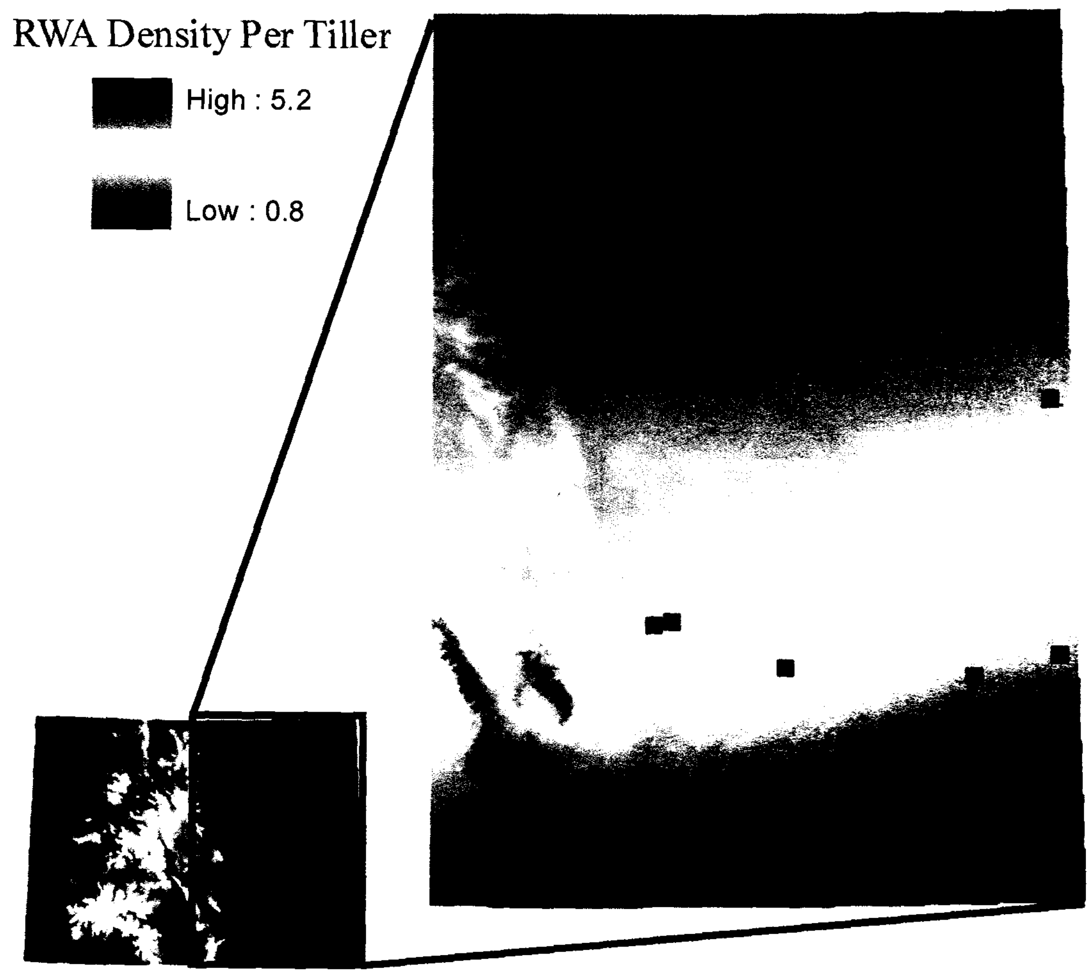

Table 4.1: Candidate Models.

| Model | $K$ | MSE | AICc | ΔAICc | $\mathcal{L}$($g_i$/data) | AICc Weight ($w_r$) |
|---|---|---|---|---|---|---|
| DD0° & DD-0° with Interaction terms | 5 | 0.111 | -8.316 | 0.000 | 1 | 0.732 |
| DD0° | 3 | 0.161 | -4.528 | 3.788 | 0.150 | 0.110 |
| PD Index | 3 | 0.189 | -4.208 | 4.109 | 0.128 | 0.094 |
| PD Index & DD-0° with interaction terms | 5 | 0.184 | -3.895 | 4.701 | 0.080 | 0.006 |
| DD0° & DD-0° | 4 | 0.174 | -3.125 | 5.191 | 0.075 | 0.055 |
| PD Index & DD-0° | 4 | 0.208 | -2.452 | 11.670 | 0.003 | 0.002 |
| Precipitation | 3 | 0.295 | -0.302 | 13.820 | 0.001 | 0.001 |
| Precipitation & DD-0° | 4 | 0.325 | 1.815 | 15.937 | 0.000 | 0.000 |
| Precipitation & DD-0° with interaction terms | 5 | | 3.604 | 17.726 | 0.000 | 0.000 |
| DD-0° | 3 | 0.470 | 4.667 | 18.789 | 0.000 | 0.000 |

*Notes:* $K$ is the number of estimated parameters in the model. Akaike's Information Criterion for small sample sizes (AICc), and AICc weights ($w_r$) quantify the support in the data for each of the models (Burnham and Anderson 2002). $\mathcal{L}$($g_i$/data) is the likelihood of the model ($g_i$) given the data and is also a measure of the support in the data for model ($g_i$).

Table 4.2: Parameter Estimates, Intercepts, Renormalized AICc $w_r$, and $r^2$ for all models with ΔAIC < 7.

| **Model: ln (RWA density + 0.1) =** | **AICc $w_r$ Renormalized** | **$r^2$** |
|---|---|---|
| (DD0°) * 5.33 + (DD-0°) * 0.53 + (DD0°) * (DD-0°) * (-7.90) - 0.60 | 0.739 | 0.849047 |
| (DD0°) * 2.28 - 0.75 | 0.111 | 0.608285 |
| (PD Index) * 2.54 - 0.54 | 0.095 | 0.596866 |
| (DD0°) * 2.19 + (DD-0°) * (-0.85) - 0.27 | 0.055 | 0.669975 |

*Notes:* AICc weights were renormalized using all models with AICc < 7.

Table 4.3: Variable Importance and Parameterization.

| Rank | Variable | AIC$_c$ Variable Weight ($w_{+(i)}$) | Parameter Estimate | Direction |
|---|---|---|---|---|
| 1 | DD0° | 0.905 | 4.315 | + |
| 2 | DD-0° | 0.794 | 0.344 | + |
| 3 | DD0° * DD-0° | 0.739 | -5.837 | - |
| 4 | PD Index | 0.095 | 0.241 | + |
| X | Intercept | | -0.595 | - |

*Notes:* Variable Rank is an indicator of the likelihood of the variable being an important predictor variable as compared to other variables in the procedure and is quantified by its AICc weight ($w_{+(i)}$). Because the variables have been normalized the parameter estimate yields the magnitude of the variables' effect size and the direction of its effect. Variables in the green section have large weights and a strong likelihood for being important variables for prediction of RWA densities. The PD Index, which is shaded in blue, has a low AICc $w_{+(i)}$. Therefore it has a low probability for being chosen again as an important variable and has a small relative effect on RWA densities in the model.

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# Chapter 5

# Modeling Spatial Variation of Russian Wheat Aphid Overwintering Population Densities Within a Colorado Cropping System


## Abstract

Russian wheat aphids (RWA), *Diuraphis noxia* (Kurdjumov), are pests of wheat and barley and have caused hundreds of millions of dollars of damage to small grain crops since their introduction into the United States in the mid-1980s. Much is known about RWA population dynamics during the time period when most of the crop damage occurs (i.e., during the spring and early summer). However, very little is known about the system proceeding this time period (i.e., the overwintering period). If RWA do not survive the overwintering period and rely on migration from areas where overwintering was successful, then they are found to do substantially less crop damage as compared to areas where overwintering was successful. Limiting early control efforts to locations where RWA successfully overwintered would benefit both the agroecosystem and the producer (i.e., reduced pesticide inputs would result in reduced environmental contamination, reduced costs to the producer, better insecticide resistance management, and would allow refuges for natural enemies).

To build an understanding of RWA density variability in this agroecosystem, a small-scale (i.e., 30-meter grid), within-field RWA density model was developed to

explain spatial and temporal variation of RWA densities during the late winter - early spring period (i.e., late February through April). Collection of RWA density data was undertaken over three years at two sites in eastern Colorado. The model incorporates georeferenced data from soil surveys, topography, and satellite imagery as predictor variables. From the data, a spatially explicit RWA density model was developed using an information theoretic approach. The model was used to create trend surfaces depicting RWA density across winter wheat / fallow cropping systems. The model explained approximately 29% ($r^2 = 0.29$) of the variability in the RWA density data.

## Introduction

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) is a pest of wheat and barley. Damage estimates are in the hundreds of millions of dollars since their invasion into the United States (Webster et al. 1994, Morrison and Peairs 1998). There has been extensive research into elucidating the population dynamics during the growing season, when most of the crop damage occurs to the small grain crops (i.e., spring and early summer). However, very little is known about RWA population dynamics in the time period immediately proceeding the growing season (i.e., the overwintering period) (e.g., Messina et al. 1993, Armstrong 1994, Armstrong and Peairs 1996).

RWA overwinter within the winter wheat agroecosystem (i.e., the ecosystem associated with the winter wheat / fallow cropping system) as adult females. During this time period RWA are relatively dormant but will be seen moving and feeding when conditions permit (Merrill, personal observations). Because RWA reproduce parthenogenically, using a telescoping generation strategy (i.e., RWA are born alive and pregnant) population growth can be exceptionally rapid (Burd et al. 1998). Despite numerous and extensive efforts to establish and enhance various biological control agents, biological control has not been shown to be a major factor influencing natural RWA infestations in North America (Meyer and Peairs 1989, Feng et al. 1992, Wraight et al. 1993, Mohamed et al. 2000). Some ecological manipulations have been shown to help reduce infestation levels (e.g., planting date (Hammon et al. 1996, Peairs et al. 2006)), but most do not adequately protect yield. Resistant wheat cultivars do provide excellent crop protection, but with the advent of numerous new RWA biotypes (e.g., Haley et al. 2004) all commercially available winter wheat cultivars are currently susceptible to RWA feeding damage and associated yield losses. New wheat cultivars resistant to known RWA biotypes will take at least 4-7 additional years to become commercially viable (Haley, personal communications). And if we rely on resistant cultivars as our dominant RWA management tactic, cultivar resistance will likely be overcome by the pest (Souza 1998). Due to the dearth of effective RWA control tactics, insecticides have become the key tactic in use on all Colorado wheat varieties. Current management practices recommend for the crop to be scouted and treated with an insecticide if economic thresholds are exceeded (McDonald et al. 2003). However, a single pesticide application costs between $10 and $25 per acre (Webster et al. 1994, Peairs, personal communications), which drastically reduces the profit margin typically seen in dryland winter wheat (i.e., expected profit potential of winter wheat in Colorado is ca. $50 / acre).

One management system that is currently being under-utilized is the combined use of directed scouting and precision agriculture. Precision agriculture assumes that not all areas of the agroecosystem are homogeneous; and therefore, delineated areas could be managed differently, depending upon management goals (e.g., managing fertilization based on expected yield or spraying pesticides on areas of the field that are experiencing or at risk for a pest outbreak, while leaving the rest of the field unsprayed). Site-specific spraying has greatly reduced pesticide usage in some areas (Inoue 2003). For example, to control the Colorado potato beetle in Pennsylvania, Weisz et al. (1996) either treated potato fields with whole-field insecticide applications or treated subsections of a field with insecticide applications. Treating only the infested portions of the field reduced the amount of pesticides needed to control the Colorado potato beetle by 30-40% (Weisz et al. 1996).

A spatially explicit model of RWA densities is necessary for the development of tactics such as site-specific pesticide spraying, directed scouting or precision management of RWA. There has been success in correlating remotely sensed reflectance data, topography data and soil data to aphid incidence (e.g., Loebenstein and Raccah 1980, Hammon and Peairs 1992, Riedell and Blackmer 1999). The present research focuses on developing a spatially explicit RWA density model that will delineate RWA densities within the winter wheat agroecosystem. If found to be robust, this model could be applied to generate risk assessment maps, which would delineate areas at risk for high RWA densities during the early spring. I hypothesized that some of the within-field variation in overwintering success may be predictable based on satellite imagery, topography, and soil characteristics. Application of a spatially explicit RWA density model would have numerous benefits to the agroecosystem and to the producer including: 1) reducing pesticide inputs and associated costs, 2) reducing environmental contamination, 3) improving pesticide resistance management, 4) providing for more judicious use of resistant wheat cultivars when they become available, and 5) preserving refuges for natural enemies. The development of the spatially explicit RWA density model used accessible data inputs with repeatable methods allowing for further model reparameterization and application. Since the overwintering time period for this agroecosystem is not well understood, much of the work is exploratory, and model validation (e.g., Chapter 6) should be completed before acceptance as a management tool.

### *Background*

The RWA is widely considered one of the most economically damaging pests of wheat in the world. RWA were recognized as having a serious pestiferous outbreak as early as 1912 in the Republic of Moldova and the southern Ukraine where harvest was reduced by as much as 75% (Halbert and Stoetzel 1998). This pest is generally considered a palearctic species (Blackman and Eastop 1984, Kiriac et al. 1990) and was first reported in the new world, in Mexico in 1980 (Halbert and Stoetzel 1998). RWA were first positively identified in the United States in 1986 (Morrison 1987, Morrison and Peairs 1998). Since its introduction the RWA has spread to 17 states and 3 Canadian provinces (Elliott et al. 1998).

Losses to the United States cereal industry from 1987 to 1993 were estimated at ca. $900 million (Webster et al. 1994, Morrison and Peairs 1998). The highest total yearly cost to date was $274 million dollars in 1988 (Morrison and Peairs 1998). Although there is exceptionally high year-to-year variation (e.g., total losses varied from $12 million in 1991 to $274 million in 1988 (Webster and Treat 1997)), it appears that losses were decreasing with the adoption of resistant wheat cultivars. However, with the advent of many new biotypes (e.g., Haley et al. 2004), conventional insecticide treatment will once again be the primary control method (McDonald et al. 2003) and costs are expected to resurge, approaching levels seen before the deployment of resistant wheat cultivars.

## Reproduction and Development of the RWA

RWA reproduce using telescoping generations and show rapid development, enabling exponential population growth (Burd et al. 1998). There are many factors that are likely to affect RWA population densities including plant growth stage, host condition (e.g., water stress), temperature and weather conditions, and topography (e.g., Walters et al. 1984, Hammon and Peairs 1992, Hein 1992, Archer et al. 1995, Armstrong and Peairs 1996).

Aphid stress is caused by over-exploitation of their host plants and/or upon natural host plant senescence (Halbert et al. 1992). Stress leads to the production of alate (winged) RWA forms and results in increased dispersal. One peak in RWA dispersal occurs in the spring (the spring flight). The spring flight allows dispersal to areas where RWA populations were absent (e.g., from complete overwintering mortality). However, by the time of most spring flights, wheat is typically at a late growth stage (Peairs, personal communication). When RWA infest later growth stages they have been found to do substantially less crop damage as compared to infestations occurring on early growth stages (Peairs et al. 2006). Therefore, reduction of early season RWA densities should prove more beneficial than controls undertaken at a later date.

## Geographic Information Systems, Satellite Imagery and Remotely Sensed Data

**Geospatial data:** Geographic Information Systems (GIS), remote sensing, Global Positioning Systems (GPS) and spatial statistical analysis are being integrated with existing non-spatial models for use in basic and applied sciences. In addition, these advances are leading to innovative technologies such as GPS-guided tractors. Remote sensing methods are a powerful tool for providing within- or between-field spatial information (Inoue 2003). GIS has been used extensively for studying agroecosystems, addressing pest management questions, and is the basis for the burgeoning field of precision agriculture.

**Reflective Imagery:** Remotely sensed imagery, or reflective bands (i.e., detected emissions within a range of wavelengths) have broad applicability to insect landscape ecology and specific applicability for use in determining aphid presence. For example, in a greenhouse experiment Riedell and Blackmer (1999) found excellent correlation between remotely sensed wavelengths and RWA feeding. Additionally, they found an increase in both the 350-750 nm range and the 850-1000 nm range correlated with an increase in RWA damage at the leaf scale. They hypothesized that increases in the 350-750 nm range were due to decreased total chlorophyll, whereas increases in detection over the 850-1000 nm range were due to a lower water content or drought stress symptoms. Unfortunately, Riedell and Blackmer (1999) suggest that scaling up from the scale of the leaf to the canopy level may be very difficult because of the addition of light scatter, soil reflectance, etc. Mirik et al. (2004) used a hyperspectral ground spectrometer to remotely sense RWA stress and incidence, giving credence to remotely sensed reflective signals yielding information about aphid incidence, especially in the 750 – 900 nm region (i.e., Wavelengths detected by Landsat 7 Enhanced Thematic Mapper PLUS (ETM+) Band 4). Specific to RWA, Dvorak et al. (2004) used aircraft based remotely sensed data to create vegetation indices, which were correlated with the presence of RWA in field plots.

Detecting differential species-specific insect/plant damage signatures may be difficult from imagery at the 30-meter grid scale (i.e., the scale of this study). However, general plant vigor and pest presence should be attainable. For example, healthy plants reflect highly in the near infrared region likely due to a high intercellular space to cell ratio (Riedell and Blackmer 1999).

This study utilizes USGS Landsat 7 ETM+ Imagery. The USGS Landsat 7 satellite was launched in April of 1999 (USGS 2003) to detect wavelength bands from the earth's surface. These remotely sensed data are georeferenced and then delivered as a package of bands called ETM + imagery (Figure 5.1). These high-resolution data have been used by government, commercial, industrial, civilian, military, and educational communities in the United States and worldwide (USGS 2003). More specifically, Landsat data have been used as predictor variables to detect plant condition for use in insect abundance modeling. For example, Hurley et al. (2004) used Landsat 7 ETM+ imagery to detect defoliation associated with gypsy moth damage, and thereby determined likely locations for Gypsy Moth egg masses in Ohio. Hunt and Rock (1989) used remotely sensed wavelengths (i.e., near infrared and middle infrared bands) to detect changes in leaf water content caused by drought stress. Hunt and Rock's (1989) research may be applicable because many symptoms caused by RWA feeding are difficult to distinguish from drought stress (e.g., Riedell 1989). Using remote sensing to detect symptoms generally identified with drought stress may indicate locations where the apparent drought related symptoms are actually caused by aphid feeding damage.

**Spectral Vegetation Indices:** One of the most important discoveries of the Landsat project was the universal generality of spectral vegetation indices, which are derived by considering contrasts between visible and near infrared spectral reflectances (Goward and Williams 1997). Typically, green vegetation foliage produces a stepped reflectance, a result of pigment absorption in the visible range and strong light scatter from the cell walls in the near infrared (Woolley 1971, Tucker 1979). Other land surfaces such as bare soil and litter generally record slowly increasing reflectance between visible and near infrared (Goward and Williams 1997). Therefore, vegetation indices (e.g., Normalized Difference Vegetation Index) are designed to distinguish between surface vegetation cover types.

## Topography

Aspect and slope have both been found to influence RWA population dynamics. For example, Hammon and Peairs (1992) found that the south side of east-west facing irrigation ditches accumulated more degree-days than the north side of the irrigation ditch or either side of the north-south facing irrigation ditches and consequently the south facing side had higher infestations of RWA in the spring. Moreover, they found that fields with irrigation furrows with steep slopes had higher infestations than fields with irrigation furrows with more gradual slopes. Additionally, Thomas and Butts (1990) found that microtopography (i.e., within-field locations with increased cold stress or snow buildup) and previous feeding by RWA were both strong factors in creation of differential and spatially heterogeneous mortality of winter wheat. Therefore, a spatial gradient in overwintering host quality based on topography should exist.

**Soil Characteristics**

Soil properties are likely to affect aphid overwintering mortality. Aphid – soil interactions have been shown to be very complex. For example, aphids are known to affect soil chemistry by the production of honeydew (Stadler et al. 1998). Aphid dispersal is affected by soil color (Loebenstein and Raccah 1980, Gibson and Rice 1989, Doring et al. 2004). The interaction between overwintering aphid mortality and soil properties is an area that has seen limited, if any research. However, one could hypothesis that soil properties should play an important role in overwintering mortality. For example, soil texture could affect moisture availability and desiccation, as well as directly affecting aphids through wind movement (e.g., dust buffering). Soil color and its albedo effects could create microclimatic temperature differences, which could in turn affect snow accumulation, as well as change the degree-days above and below the aphid's developmental temperature threshold. Increased snow cover has been shown to decrease overwintering mortality (Armstrong and Peairs 1996). Much improvement could be made to future modeling efforts through improved understanding of the soil attributes that affect aphid survival.

## Methods

### *Sampling Design*

Two field sites, the Last Chance field site (39°44' N 103°48' W) and the Lamar field site (37°58' N 102°30' W), were established based disparate topographic and climatic variables and were located representatively for Colorado dryland wheat harvested acreage.

Each year ca. 80 plots were established at each field site. All plots were georeferenced using a GPS device (Garmin GPSmap76S). For the first two years plots were selected based on a stratified random grid design. The third year was stratified across soil type as early analysis indicated that soil type was an important variable. Plots consisted of three consecutive rows (subplots) of dryland winter wheat. For more planting details see Appendix B.

Subplots were infested in late fall with RWA from the RWA Biotype 1 colony at Colorado State University (For more details regarding infestations see Appendix B). The sample design was intended to obtain samples over three years at two sites with two sampling periods per site per year. However, one sampling period was not obtained in Year Two for logistical reasons. Therefore, there were 11 sampling sets (SS) (i.e., 2 sites x 3 years x 2 sample periods per year, minus one SS). Additionally, RWA density on infested wheat was measured in early winter to determine if infestation was successful. To determine RWA densities, tillers were removed from subplots on two sample dates per site per spring, with the exception of Year Two at the Lamar field site (i.e., only one sample set was obtained from Lamar in the spring of 2003). Sample design was for tillers to be removed at a rate of six tillers per subplot. If tiller density was low (e.g., from low emergence), tillers were removed to maximize tillers obtained over both sample periods. For example, if only six tillers existed on a subplot during the first sample period, half of the tillers were removed allowing the second set of three tillers to remain for sampling during the second sample period. Tillers were clipped at each subplot, placed into ziplock bags, and transported to Colorado State University's Agricultural Research Development and Education Center (ARDEC). Tillers were then removed from the ziplock bags and placed into Berlese devices. Berlese devices heated the wheat tillers, causing any aphids on the plant material to retreat to cooler areas and hence causing aphids to fall into a Berlese cup containing a 70/30 alcohol/water mixture. From the alcohol/water mixture, RWA were counted under a dissecting microscope. RWA densities were calculated per tiller. Subplot densities were averaged to obtain a plot average. RWA density averages at the plot level were right skewed and a log transformation (i.e., ln (RWA Density + 0.1)) was used to approximate normal data.

## Geographic Information System (GIS) and Data Layers

36 predictor variables were developed for use in modeling RWA densities. All GIS data layers (i.e., data layers associated with the predictor variables) were projected to the NAD 84 (North American Datum of 1984) projection. For each site, GIS data layers were developed for all of the following predictor variables:

### Topography Layers

Topography layers were developed from a United States Geological Survey 30-meter digital elevation map (DEM). All topography data layers were generated with a 30-meter grid resolution.

**Relative Elevation:** Relative elevation is the measure of the elevational distance (in meters) from the mean elevation at the field site. This variable was included instead of elevation because elevation differences would highlight between-site variation instead of within-site variation. This variable is similar to Landshape (see below) except it quantifies differences between points at the extent of the field site.

**Slope:** Slope is measured in degrees and was derived from the USGS 30-meter DEM using the ArcGIS 9.1 (ESRI 1995-2007) slope tool.

**Aspect:** Aspect is measured in degrees from 0° to 360° and was derived from the USGS 30-meter DEM using the ArcGIS 9.1 (ESRI 1995-2007) aspect tool.

**North-South Aspect:** The North-South Aspect data layer was derived from the Aspect data layer using the Raster Calculator function in ArcGIS 9.1 (ESRI 1995-2007). The inputted function was Float(Abs(180-[Aspect])). This creates a continuous variable from 0-180 with 0 directly north and 180 directly south. All east-west variation is lost by the use of this function but it removes the incongruity that is created by cyclical nature of degree measurements ranging between 0° and 360° (e.g., the angle distance between 1° and 359° is 2°). Other publications have referred to this variable as Absolute Aspect.

**Landshape:** The Landshape data layer was created by the ArcGIS 9.1 (ESRI 1995-2007) Raster Calculator function using the function: Focalmean ([DEM],Circle,3,nodata) – [DEM]. This function calculates the mean elevation value (i.e., from the DEM) in a circle with a 3-cell (90 meter) radius around the georeferenced plot, then subtracts that value from the elevation at the plot. The resulting value describes the relative elevation of the georeferenced plot to its surroundings. That is, this layer provides a quantitative description of the shape of the landscape surrounding the plot (e.g., small valleys). I choose the 90-meter radius, based on personal experience, as representative of much of the variation in elevation that occurred within site. Other scales besides the 90-meter radius and the site scale (i.e., the Relative Elevation predictor variable) may be more relevant to insect overwintering and could be examined in future research.

**Soil Layers**

Soil data were obtained from a Colorado county soil survey paper copies and digitized into a GIS for each site. Developing soil characteristic variables was difficult due to the scale of variability seen in the field. That is, soil characteristics appeared to change at a smaller scale than was depicted on soil survey maps. Moreover, the soil types characterized by the USDA-NRCS frequently showed high soil characteristic variability within soil type. For example, the Baca series A horizon in Baca County, Colorado ranged between 13.7% sand to 26.2 % sand depending upon the pedon sampled (USDA-NRCS 2006). Originally, I examined percent clay as a continuous variable but did not find good correlation with RWA density. Because of the high spatial variability, the high variability within soil type characteristics reported by the USDA-NRCS, and the lack of correlation between RWA densities and the a priori continuous variable, I decided against using continuous variables to describe soil characteristics. Therefore, soil series or types based on the soil Musyms (i.e., Map unit symbol) were used as categorical surface grid layers. The following soil series (USDA-NRCS 2006) were used in this study:

**Wiley Series:** (ca. 5000 acres on sites)

The Wiley series consists of very deep, well drained, moderately slowly permeable soils formed in thick, calcareous loess. Wiley soils are on hills, plains, ridges, terraces, and valley side slopes. Taxonomic class: Fine-silty, mixed, superactive, mesic Aridic Haplustalfs.

**Weld Series:** (ca. 300 acres on sites)

The Weld series consists of very deep, well drained soils that formed in thick calcareous loess, or from silty uniform alluvium or outwash. Weld soils are on hills, uplands, or smooth plains and interfluves. Taxonomic class: Fine, smectitic, mesic Aridic Argiustolls.

**Shingle Series:** (ca. 500 acres on sites)

The Shingle series consists of well drained soils that are very shallow or shallow to bedrock. They formed in residuum and colluvium derived from interbedded shale and sandstone or in alluvium from mudstone. Shingle soils are on bedrock controlled hillslopes and ridges. Taxonomic class: Loamy, mixed, superactive, calcareous, mesic, shallow Ustic Torriorthents.

**Samsil Series:** (ca. 1000 acres on sites)

The Samsil series consists of shallow, well drained soils formed in alluvium or residuum weathered from shale. Permeability is slow. Taxonomic class: Clayey, smectitic, calcareous, mesic, shallow Aridic Ustorthents.

**Colby Series:** (ca. 300 acres on sites)

The Colby series consists of very deep, well drained and somewhat excessively drained, moderately permeable soils formed in calcareous loess. Taxonomic class: Fine-silty, mixed, superactive, calcareous, mesic Aridic Ustorthents.

**Baca Series:** (ca. 400 acres on sites)

The Baca series consists of very deep, well drained soils that formed in mixed material from Tertiary pedisediments modified by wind. Baca soils are on plains and uplands. Taxonomic class: Fine, smectitic, mesic Aridic Haplustalfs.

**Arvada Series:** (ca. 200 acres on sites)

The Arvada series consists of very deep, well drained soils formed in alluvium and colluvium derived from sodic shale. Arvada soils are on alluvial fans, fan remnants, fan terraces and hillslopes. Taxonomic class: Fine, smectitic, mesic Ustertic Natrargids.

**Adena Series:** (ca. 900 acres on sites)

The Adena series consists of moderately deep, poorly drained soils over a duripan that formed in mixed alluvium. Adena soils are in flood plains or alluvial fans. Taxonomic class: Fine-loamy, mixed, superactive, frigid Aquic Haplodurids.

**Soil Type: Gullied Land:** (ca. 124 acres on sites)

**Soil Type: Loamy Alluvial Land:** (ca. 660 acres on sites)

**Soil Type: Alluvial Land Complex:** (ca. 39 acres on sites)

**Satellite Imagery**

Unfortunately, satellite imagery that provides data with both high spatial resolution and high temporal resolution do not yet exist (e.g., Nouvellon et al. 2001). Many of the processes that occur in winter wheat during the overwintering period are temporally dynamic (e.g., growth of winter wheat over time). To examine some of the spatial and temporal processes in the winter wheat agroecosystem, two sets of Landsat 7 ETM + images per year at each site were obtained, one in the spring between sampling periods, and one in the early winter (e.g., typically around December 15$^{th}$). Image date was variable due to the frequency of the satellite overpass timing and the necessity of cloud-free imagery over the field site. Landsat ETM+ 7 bands from the spring will be denoted with a (S), while bands obtained during the winter (W).

Landsat 7 collects nine bandwidths of data per ETM+ image package (each image is approximately 185 km on a side). The following reflective bandwidths are detected:

**Band 1 (Blue-Green):** Band 1 (Wavelengths: 450-515 nm, Resolution: 30-meters) senses reflectance in visual light, roughly blue/green. Band 1 is useful for bathymetric mapping and distinguishing soil from vegetation and deciduous from coniferous vegetation (USGS 2003).

**Band 2 (Green):** Band 2 (Wavelengths: 525 - 605 nm, Resolution: 30-meters) senses reflectance in visual light, roughly green/yellow. Band 2 emphasizes peak vegetation, which is useful for assessing plant vigor (USGS 2003).

**Band 3 (Red):** Band 3 (Wavelengths: 630 - 690 nm, Resolution: 30-meters) senses reflectance in visual light, the reds. Band 3 discriminates vegetation slopes. (USGS 2003). This band detects chlorophyll absorption in vegetation (thus low reflection) (Noorbergen 2004).

**Band 4 (Reflected Infrared, Near Infrared):** Band 4 (Wavelengths: 750 - 900 nm, Resolution: 30-meters) senses near infrared light. This is associated with many vegetation indexes (e.g., Normalized Difference Vegetation Index). Band 4 emphasizes biomass content and shorelines (USGS 2003). The high reflectance peak from vegetation is detected, enabling discrimination of numerous vegetation types and land-water content (Noorbergen 2004). For example, Leaf Area Index was found to be strongly correlated with near infrared reflectance as well as the Normalized Difference Vegetation Index (e.g., Kodani et al. 2002). Chlorophyll content is a linear function of green or near infrared reflectance (Kodani et al. 2002).

**Band 5 (Reflected Infrared, Short Wave Infrared):** Band 5 (Wavelengths: 1500 - 1750 nm, Resolution: 30-meters) senses wavelengths in the short wave infrared spectrum. Band 5 penetrates thin clouds and discriminates moisture content of soil and vegetation (USGS 2003). This band features high water absorption, thus enabling detection of very thin water layers (less than 1 cm), as well as variations in ferric iron ($Fe_2O_3$) content in rocks and soils (i.e., higher reflections with higher contents) (Noorbergen 2004).

**Bands 6.1 and Band 6.2 (Thermal Infrared):** Bands 6.1 and 6.2 (Wavelengths: 10400 - 12500 nm, Resolution: 60-meters) sense thermal reflectance or heat. An important characteristic of these bands is that they have lower resolution than other bands in this system. These bands are useful for thermal mapping and estimated soil moisture (USGS 2003). Inoue (1991) found that physiologically stressed wheat showed much higher thermal infrared temperatures.

**Band 7 (Reflected Infrared, Short wave infrared):** Band 7 (Wavelengths: 2090 - 2950 nm, Resolution: 30-meters) senses reflectance in visual light, roughly blue/green. Band 7 is useful for mapping hydrothermally altered rocks associated with mineral deposits (USGS 2003). Band 7 can also be used to detect heat sources (Noorbergen 2004).

**Band 8 (Panchromatic, Visible through Near Infrared):** The Panchromatic Band (Wavelengths: 520 - 900 nm, Resolution: 15-meters) senses a broad range of visible to near infrared wavelengths, but at a higher resolution. The grid layer created by the panchromatic band is at a resolution of 15 meters and is used for "sharpening" of multispectral images (USGS 2003).

**Normalize Difference Vegetation Index (NDVI) (Function of Band 3 and Band 4: NDVI = [Band 4-Band 3]/[Bands 3 + 4]):** NDVI (Resolution: 30-meters) senses vegetative cover, highlighting chlorophyll absorption. The seasonal NDVI pattern has been shown to have a convex shape in grass species with increasing followed by decreasing values (Kodani et al. 2002). NDVI has been found to predict yield in some crops (e.g., sorghum and millet) when obtained during the proper growth stage (e.g., heading) (Inoue 2003). However, models must be parameterized based on crop, variety, location, and other variables (Inoue 2003).

### *Data and Model Development*

In association with the Euclidean plot coordinates (GPS coordinates) for each RWA density sample, data were extracted from the GIS data layer associated with each predictor variable. All GIS layers were normalized between 0 and 1. Normalization allows for comparisons of the magnitude of the effect size between predictor variables. For example, assume two variables, relative elevation and Landsat ETM+ Band 4, are selected for inclusion in a model. After normalization, Relative Elevation is parameterized to have a large slope, and Landsat ETM + Band 4 is parameterized to have a small slope. In this case, a ten percent change in Relative Elevation would have a much larger effect on RWA densities than a ten percent change in Landsat ETM + Band 4. Therefore, the size of the parameter estimate yields information on the effect size of that variable on the dependent variable.

All Landsat imagery was normalized within image capture date (i.e., within ETM+ package) to observe relatively high and low emission data within-field instead of between fields. That is, the range of emissivity values per Landsat band can change between images captured, which requires normalization within each capture date instead of across the set of captured images (e.g., thermal band emissions can change depending upon the daily temperature). All other GIS layers were normalized across all data using the standard formula ($X_i$ – Minimum(X) / (MaximumX – MinimumX) ) for all data points i (See Appendix D for normalization parameters).

Because within-field, small extent knowledge was our goal, each sampling date per site per year (SS) was considered as a categorical variable. The SS categorical variable was included in every model in the candidate model set.

All subsets of the predictor variables were linearly regressed against the dependent variable:

$$\ln(\text{RWA density} + 0.1) = \text{Intercept} + \sum \beta_i X_i \; \ldots \; \text{for } i = 1 \text{ to n}$$

where $X_i$ is the $i$th predictor variable, and $\beta_i$ is the parameter estimate associated with the $i$th variable.

**Developing the Model Set Using an Information Theoretic Approach**

Chamberlin (1965- originally published in 1890) over a century ago advocated the following:

> ...the effort is to bring up into view every rational explanation of the phenomenon in hand and to develop every tenable hypothesis relative to its nature, cause or origin, and to give all of these as impartially as possible a working form and a due place in the investigation. (The researcher) proceeds ... knowing well that some of (his/her)

> intellectual children (i.e., the hypotheses) must needs perish before maturity, but yet with the hope that several of them may survive the ordeal of crucial research.... Honors must often be divided between (surviving) hypothesis.... But an adequate explanation often involves the coordination of several causes.... Several agencies may participate, not only one, but their proportions and importance may vary from instance to instance in the same field.

In this spirit, I have endeavored to analyze and compare numerous possible models and hypotheses to elucidate a system that is very poorly understood – overwintering survival of Russian wheat aphids. Therefore, I decided against using traditional hypothesis testing (e.g., generating p-values), or building statistics based on a null model, because it does not allow for comparisons of models. Hoeting et al. (1999) argue that p-values should not be used to contrast models, as is frequently seen with the terminology $p = 0.05$ significant and $p = 0.01$ highly significant, because they do not take model uncertainty (i.e., the uncertainty or bias associated with choosing one model over others) into account. p-values arguably overstate the evidence for an effect even when there is no model uncertainty.

## The Information Theoretic Approach and Akaike's Information Criterion

An Information Theoretic approach allows for the comparison of multiple hypothesis or models. All models in the model set (i.e., models selected for comparison or the candidate models) were ranked using Akaike's Information Criterion with a correction for small sample sizes (i.e., AICc) (Burnham and Anderson 2002, 2004). AICc is the appropriate information criterion when sample size is small relative to the number of parameters (Burnham and Anderson 2002) and produces more conservative estimates of strength of evidence in high dimensional models (Twombly et al. in press). Each model $r$ has an associated $\Delta AICc_r$, which is defined as difference between the model with the lowest (i.e., best) AICc value and model $r$. The ΔAICc value for the $r$th model can be used to determine the likelihood that the $r$th model would be chosen as the best approximating model given another independent set of data generated under the same process and under similar conditions. This likelihood can be calculated by: exp (-$\Delta AICc_r/2$), which provides the relative likelihood of the model $r$ given the data (i.e., $\mathcal{L}$ ($g_r$ |data)) (Burnham and Anderson 2004) and is known as the AICc weight ($w_r$). When normalized, $w_r$s can be interpreted as the weight of evidence in favor of a model ($g_r$ (·|data)) being the best approximating model in the model set or $w_r$s can be interpreted as the probability that the $r$th model would be chosen as the best approximating model given another independent set of data generated under the same process and under similar conditions (Burnham and Anderson 2002, 2004). Models with a ΔAICc between 0-3 have considerable evidence supporting them (i.e., a high likelihood of being chosen as the best approximating model given another similar data set). Models with ΔAICc between 4-7 have some support in the data. Models with ΔAICc less than 7 are considered not to have a strong likelihood of being chosen as the best approximating model (Burnham and Anderson 2002). ΔAICc values therefore allow for quantification of the strength of evidence, or weight of evidence supporting each model as the best approximating model.

**Model Selection Uncertainty and Bias**

Model Selection Uncertainty is the likelihood that model $r$ would be chosen as the best model with a similar, independent set of data obtained under nearly identical conditions (e.g., Burnham and Anderson 2002). Model selection bias is conditional on the model selected to generate the predictions. That is, if there are multiple competing candidate models with support in the data for prediction of the dependent variable, the choice of one model creates bias. For example, assume there are two good models with substantial support in the data. Both models have disparate predictions, but on average, both elucidate variance in the dependent variable. Each model generates predictions and associated errors for the dependent variable. If one model is selected as the "best" approximating model (e.g., selected based on best AICc etc.), then the error associated with the "best" approximating model predictions does not include the uncertainty associated with selecting that model (and its associated predictions). Any predictions made by the second best approximating model, even if it is virtually identical in quality, are ignored. The goal is to produce a prediction that is as unconditional on model selection as possible, thereby reducing model selection bias. Model selection bias can be reduced by using model averaging. However, even if all the candidate models in the model set are used, there still exists some model selection bias based on any models not included in the original candidate model set (e.g., there may be a model that would be better than any tested models that hasn't even been considered). Therefore, model selection bias can never be completely eliminated but it is important to be aware of its existence and reduce this bias when possible (Burnham and Anderson 2004).

## Model Averaging

Model averaging is considered superior to making model predictions and inferences about variable importance based only on one best approximating model when alternate models are nearly as well supported as the best approximating model (Burnham and Anderson 2004). Model averaging takes a weighted average of candidate models using AICc weights ($w_r$) (i.e., models that have a higher probability of being the model that best approximates that data are given more weight). While model selection bias would be reduced by averaging over all models in the model selection set, in this situation (i.e., high dimensional modeling of RWA densities) it is logistically difficult. Therefore, a cutoff was chosen at ΔAICc less than 7, because models with a ΔAICc greater than 7 have virtually no support of evidence (i.e., a very low likelihood) for being the best approximating model (Burnham and Anderson 2002). A model-averaged result is developed simply by multiplying each model $r$ prediction by its associated $w_r$ for all the models selected for model averaging and calculating the sum of the results. That is:

Formula # 2: $\text{RWA} = \sum w_r$ *(Model $r$ prediction) … for all models $r$ = 1 to R.

Model averaging produces a model-stabilized inference (Burnham and Anderson 2002) and can reduce overall prediction error.

**Variable Weighting ($w_{+(i)}$) and Variable Ranking**

AICc weights are used to assess the relative importance of each predictor variable in explaining variation in the dependent variable (Adair 2005). Variable relative importance weight $w_{+(i)}$ is the sum of the AICc weights for predictor variable $i$ over all models in which predictor variable $i$ occurs (Burnham and Anderson 2002). The resulting $w_{+(i)}$ can range from 0 to 1, with the more important variables having higher values (i.e., close to 1). $w_{+(i)}$s allow predictor variables to be ranked (known as Variable Ranking) based on their strength of support in the data. Because $w_{+(i)}$s are derived from AICc weights, their interpretation can be similar. That is, $w_{+(i)}$ can be interpreted as the likelihood of predictor $i$ being an important predictor variable for understanding variation in the system.

## Parameter Estimates and Confidence Intervals

Weighted average parameter estimates ($\beta_{+(i)}$) are calculated by using AICc $w_r$s in conjunction with parameter estimates from each model in the model selection set:

$$\text{Formula \# 3:} \quad \beta_{+(i)} = \sum w_r * \beta_{r(i)} \ldots \text{ for all models } r = 1 \text{ to R}$$

where $w_r$ is the AICc weight for model $r$ and $\beta_{r(i)}$ is the parameter estimate for variable $i$ in model $r$.

In a similar fashion to determining a weighted parameter estimate, upper and lower confidence limits are developed. These weighted confidence limits create unconditional confidence intervals as described by Burnham and Anderson (2002).

## Model Selection

The ideal approach to reduce model selection bias is to generate candidate models from all possible combinations of the predictor variables (i.e., all-subsets). However, creating candidate models from all-subsets across 36 variables (as is the case with this work) would require 6.87 E +10 models (i.e., $2^{36}$-1). Obviously computing statistics over that many models is logistically very difficult. Reducing the number of models increases the model selection bias because a potentially biased choice needs to be made as to which models should be removed.

To reduce the number of models to a reasonable level, I followed a criterion-based, forward selection procedure for model selection (Faraway 2005, Twombly et al. In

Press). SS categorical variables were included in every model as elucidation of within-field variance was the goal. Variance Inflation Factors (VIF) and Pearson's pairwise correlation coefficients were calculated for all predictor variables to test for colinearity (i.e., test for independence) (Proc Corr, (SAS 2002-2003)). During the forward selection procedure, no variable was considered for inclusion if it was highly correlated to a variable already included in the model. To be more explicit, when modeling for prediction purposes, the goal is to have parameter estimates that are accurate and uninflated. If the predictor variables are highly intercorrelated and only one is actually correlated with the dependent variable, then the estimates of the regression coefficients will likely be substantially biased away from 0 (i.e., inflated) in the subset of models where the associated predictor variable is selected (Burnham and Anderson 2002). Colinearity can be measured by Pearson's pairwise correlation coefficients. Therefore, potential variables to be added during the forward selection procedure were limited to those without substantial colinearity (i.e., models including any variables with a Pearson's pairwise correlation coefficient greater than 0.6 were discarded).

I used a criterion based, forward selection procedure for model selection (Twombly et al. In Press). Specifically, I added each of the 36 variables to the null model (i.e., the model with only the SS categorical variables) to build 36 single-variable models. These were fit to measured field density data using SAS 9.1, Proc GLM (SAS 2002-2003), and AICc values were computed for each single-variable model. If the $\Delta$AICc value of the single-variable models was greater then 2.0 compared to the null model, model selection was finished. Otherwise, I selected all models with $\Delta$AICc less than 2.0 as the best single-variable model or models (BSVM). Then I iteratively added each of the remaining 35 variables to the BSVM(s) to build 35 two-variable models for each BSVM model, excluding any variables with high colinearity. If the ΔAICc value of the two-variable models was greater then 2.0 compared to the BSVM, model selection was finished. Otherwise, I obtained all candidate models with a ΔAICc less than 2.0 in the best two-variable model or models (BTVM). I then proceeded by iteratively adding each of the remaining 34 variables to the BTVM(s) to build candidate three-variable models. This process was repeated to build four-variable models, five-variable models, etc., by adding any of the remaining variables until ΔAICc values were greater than 2.0 compared to the candidate model with the lowest overall AICc. After which, candidate model selection was finished. All models selected as candidate models during the forward selection procedure were considered in the candidate model set.

After candidate models were selected, each model was examined for exclusion from the candidate model set based on the following criterion: Removal of a candidate model from consideration was based on the confidence intervals (CI) of parameterized variables in the each of the models. If any variable was parameterized with 0 included in its 95 % CI, the model was discarded. That is, candidate models were removed if they included a variable parameterized such that the direction of its effect was in question (i.e., if the parameter value associated with a variable included both positive and negative values in its 95 % CI, then its effect on RWA density could either be positive or negative). Candidate models with a ΔAICc less than 7 were selected for model averaging.

### *Trend Surfaces*

Trend surfaces are spatial explicit representations of mathematical formulas or models, in this case in a GIS format. The Raster Calculator function in ArcGIS 9.1 (ESRI

1995-2007) was used to create trend surfaces spatially delineating RWA densities at the site level, using model-averaged results.

## Results

During the study, 1767 subplot densities (RWA / tiller) were collected (See Table 5.1). Subplot RWA densities were averaged to obtain a whole plot average RWA density. With subplot averaging, 641 spring densities were obtained over three years at the two sites.

The density data were log transformation as previously mentioned. These data were treated as the dependent variable.

Upon generation of the complete data set, there were 36 predictor variables (i.e., Landshape, Slope, Relative Elevation, Aspect, North-South Aspect, imagery from spring and winter Landsat 7 ETM+ imagery [Bands 1, 2, 3, 4, 5, 6.1, 6.2, 7, 8, the vegetation indices NDVI (S), NDVI (W)], and the soil types [Shingle, Arvada, Samsil, LAL, Colby, Baca, Weld, Wiley, Break, Gullied, and Adena]).

Mean squared error (MSE) was generated using SAS 9.1, Proc GLM (SAS 2002-2003) for all of the models selected by the forward selection procedure. MSE and the number of parameters were used to calculate AICc statistics, including AICc values, AICc $w_r$s, and ΔAICc. Additionally, parameter estimates (effect size), direction of the effect, AICc $w_{+(i)}$s, variable ranking, and 95 % CI were calculated for every variable in each model.

### *Model Selection and Model Averaging*

After running the forward stepwise procedure and removing models based on the above criteria, 11 models (see Table 5.2) had support for being the best approximating model (i.e., $\Delta$AICc < 7.) These models were then averaged using a weighted average based on their associated $w_r$. For example, the model estimate from Model # 1 had a $w_1$ of 0.34, Model # 2's estimate had a $w_2$ of 0.30. Akaike weights ($w_r$s) were multiplied by the model RWA density estimate (or log linear approximation) and summed together. This sum, or the weighted average is the estimated RWA density. By this method, all 11 models were weighted and summed, resulting in a final model-averaged result. After simplifying algebraically the final model-averaged formula is:

$$\ln(RWA + 0.1) = -0.850 * SS1 - 1.348 * SS2 - 0.477 * SS3 - 1.374 * SS4 - 0.501 * SS5 - 0.42 * SS6 - 1.401 * SS7 + 0.285 * SS8 - 0.00 * SS9 - 0.691 * SS10 - 0.282 * SS11 + 1.502 * NDVI(S) + 0.708 * Band3(S) + 0.278 * Band8(W) + 0.019 * Band2(W) - 0.019 * Band5(W) + 0.204 * Band3(W) + 0.797 * Baca + 0.51 * LAL + 1.312 * Slope - 0.597 * R\_Elevation - 1.159$$

where $SS_n$ is the categorical variable associated with the nth sampling date per site per year, and R_Elevation is the relative elevation.

### *Variable Importance Results*

Variable ranking and $w_{+(i)}$ are indicative of the predictor variable's importance in determining the dependent variable. Because all of the variables have been normalized between zero and one, they can be used to compare the relative magnitude of the effect size of each predictor variable. Five variables have large weights and positive effects on RWA density: Slope ($w_{+(Slope)} = 1$), NDVI (S) ($w_{+(NDVI\_S)} = 1$), Band 3 (S) ($w_{+(Band3S)} = 1$), and the soil types LAL ($w_{+(LAL)} = 0.977$) and Baca ($w_{+(Baca)} = 0.809$). Relative Elevation ($w_{+(R\_Elevation)} = 0.928$) has a negative effect. That is, areas of the field that are relatively high (e.g., ridge tops) support lower RWA densities. Band 8 (W) ($w_{+(Band8W)} = 0.448$) and Band 3 (W) ($w_{+(Band3W)} = 0.342$) both have small relative weights with a positive effect on RWA densities. Band 5 (W) ($w_{+(Band5W)} = 0.034$) and Band 2 (W) ($w_{+(Band2W)} = 0.033$) have very low relative weights, making their effects negligible. Table 5.3 provides the variable weight, ranking, parameter estimates (effect size), direction of the effect and the upper and lower confidence limits for all predictor variables. There seems to be natural breaks between the six highest ranked variables (i.e., NDVI (S), Slope, Band 3 (S), Relative Elevation, and the soil types: LAL and Baca) being included in most or all of the models with larger weights, the middle two variables (i.e., Band 8 (W) and Band 3 (W)) included in a couple of the models with larger weights, and the bottom two variables (i.e., Band 5 (W) and Band 2 (W)) were each included in only one low weight model. The highest ranked variables (shaded green in Table 5.3) have high probabilities of being chosen as good predictor variables with a similar data set. The middle variables (shaded yellow in Table 5.3) have some support, whereas, the bottom variables (shaded blue in Table 5.3) have virtually no support in the data for being important predictors of RWA densities.

### *Generating RWA Density Trend Surfaces from Model-Averaged Results*

The model-averaged results for each sampling period were entered into the Raster Calculator Function (ArcGIS 9.1, ESRI 1995-2007) to create RWA density trend surfaces using GIS layers associated with the important predictor variables. RWA density trend surfaces can be depicted in a variety of ways. Figures 2 and 3 depict two different continuous RWA density surfaces for the Last Chance field site based on conditions from 2002 and 2003. Figure 5.2 is the based on data from April 25$^{th}$ 2003 and Figure 5.3 is based on data from March 23$^{rd}$ 2002. RWA density surfaces can be used to develop risk assessment maps, which are maps that indicate areas that are at high and conversely low risk for aphid population blooms with associated yield damages. Figure 5.4 is a risk assessment map based on data from the April 6$^{th}$ 2002 sampling date at the Last Chance field site. Maps can explicitly delineate areas above and below the Economic Threshold, which would allow for management decisions on pesticide usage. Figure 5.5 is an economic status map based on data from April 11$^{th}$ 2003 at the Lamar field site.

### *Uncertainty Maps*

Parameter estimation and variability around parameter estimates can be used to depict differential precision of model predictions (i.e., uncertainty maps). Because of the variance of the input variables, there is less confidence in predictions of RWA densities on some areas of the field than predictions on other areas. As an example, a GIS depiction of the uncertainty around predictions was calculated by the following procedure: 1) A trend surface depicting upper confidence limits for RWA density predictions was calculated using the upper confidence limit value for each of the important predictor variables (Table 5.3) using the ArcGIS 9.1 (ESRI 1995-2007) Raster Calculator function. 2) Similarly, a trend surface depicting lower confidence limits of RWA density predictions was calculated using lower confidence limits (Table 5.3) for each variable selected as an important predictor variable. And 3) the lower confidence limit RWA density trend surface was subtracted from the upper confidence limit RWA density trend surface. The resulting GIS surface (Figure 5.6) spatially depicts areas with differential uncertainty in model predictions. Uncertainty in model predictions can be used in numerous ways: 1) If the model predictions were used for directed scouting, scouting efforts should be concentrated on areas of the field with the lowest uncertainty. Thus, map predictions could be verified with fewer scouting inputs. And 2) to improve future model predictions, directed sampling efforts should concentrate on areas of the field with the highest uncertainty because high uncertainty could be indicative of important, and unexplained factors affecting RWA densities. Thus, directed sampling using uncertainty maps could potentially reduce unexplained variation in modeled RWA densities.

## Discussion and Conclusions

The variable weights and variable ranking results indicate that six variables are likely to elucidate variation in RWA densities: Slope, Band 3 (S), NDVI (S), relative elevation, and the soil types LAL and Baca. Other variables have limited support in the data.

Increasing the slope decreases aphid mortality. This finding supports work by Hammon and Peairs (1992) who found that fields with a tall, steep slope associated with irrigation furrows had higher infestations than fields with shorter or flatter slopes. More research should be undertaken to determine the physiological components behind the effect's of this variable.

Both NDVI (S) and Band 3 (S) detect aspects of vegetation. Band 3 (S) could be detecting differences in chlorophyll absorption directly relating to symptomatic changes caused by aphid feeding (e.g., streaking or chlorosis (e.g., Fouche et al. 1984)). Or Band 3 (S) and NDVI (S) may simply describe areas where aphid hosts are located and hence, could and conversely could not survive (e.g., winter wheat vs. bare soil).

Relative elevation could be a strong predictor for many reasons. For example, low lying areas likely would experience shelter from wind effects. Areas of low relative elevation may have increased snow accumulation, which has been correlated to overwintering success (Armstrong and Peairs 1996). Increased moisture availability in low-lying areas (e.g., from snow deposition or surface flow) may decrease deaths caused by desiccation.

Similarly soil types, with their associated differences in soil color and texture could affect snow accumulation (i.e., albedo affects), soil moisture availability, and temperature on a microclimatic scale.

Seven out of the top eleven models included at least one of the Landsat 7 ETM + winter bands. Most of these bands are highly correlated (i.e., the lowest Pearson's pairwise correlation of $r = 0.29$ is seen between Band 5 (W) and Band 8 (W), with an pairwise average between winter Bands 2, 3, 5, and 8 of $r = 0.57$). Of the included winter Landsat imagery Band 5 (W) is the only emissive band with a negative effect. However, Band 5 (W) is only included in a single model, which also includes Band 8 (W). In this model, Band 8 has a stronger positive effect than Band 5 (W)'s negative effect. Therefore, it appears that an increase in emissivity during the winter detected by many of the bands is indicative of a positive effect on RWA densities. The ecological factors and their effects on RWA, which are being detected by an increase in emissivity across a broad range of winter imagery, are unclear.

Surprisingly, some of the predictor variables (e.g., Aspect) that were thought to have the strongest support from previous research (e.g., Hammon and Peairs 1992) were not supported as quality predictors during this model selection process. Variables may not have been selected or have a low weight due to a number of possible reasons: 1) The scale at which they were measured (i.e., Aspect was measured on at a 30-meter grain size) did not correspond to the scale at which they affect the dependent variable. 2) The natural signal that related the predictor variable to RWA density was detected more strongly by another variable (using the model framework, this correlation may have removed one of the variables from the data set). 3) The predictor variable was not a good indicator of RWA densities. And 4) the data was biased, reducing the effect size of the variable.

While temperature and precipitation (Armstrong 1994, Armstrong and Peairs 1996, Merrill Chapter 3) have been shown to be important variables in broad-scale patterns of overwintering success, many of the factors that could influence RWA abundance and density on a smaller-scale had not previously been explored.

Variables with $w_{+(i)}$ values close to 1 should be considered as good predictors of RWA density and can be used delineate areas of differential RWA population densities.

Important variables were used in conjunction with a GIS to build RWA density maps on a 30-meter grid scale. These maps could be used for a variety of functions such as for use in directed scouting. If model predictions were shown to be accurate, limiting pesticide applications to areas of the agroecosystem delineated as having high RWA densities (e.g., above the Economic Threshold) would reduce pesticide usage with all of the associated benefits.

This model estimates significant variation across sampled field sites. However, data were collected from winter wheat fields that were heavily infested at a uniform rate. Different infestation rates (e.g., natural infestations), different crops, and environmental conditions outside of the range tested in this study would likely alter results. Chapter 6 develops prediction errors using cross-validation of the spatially explicit RWA density model developed in this chapter and Chapter 4's large-extent RWA density model.

Figure 5.1: Two presentations of Landsat 7 ETM+ Band Range.

Figure 5.1A: Visual Depiction from the USGS site (USGS 2003).

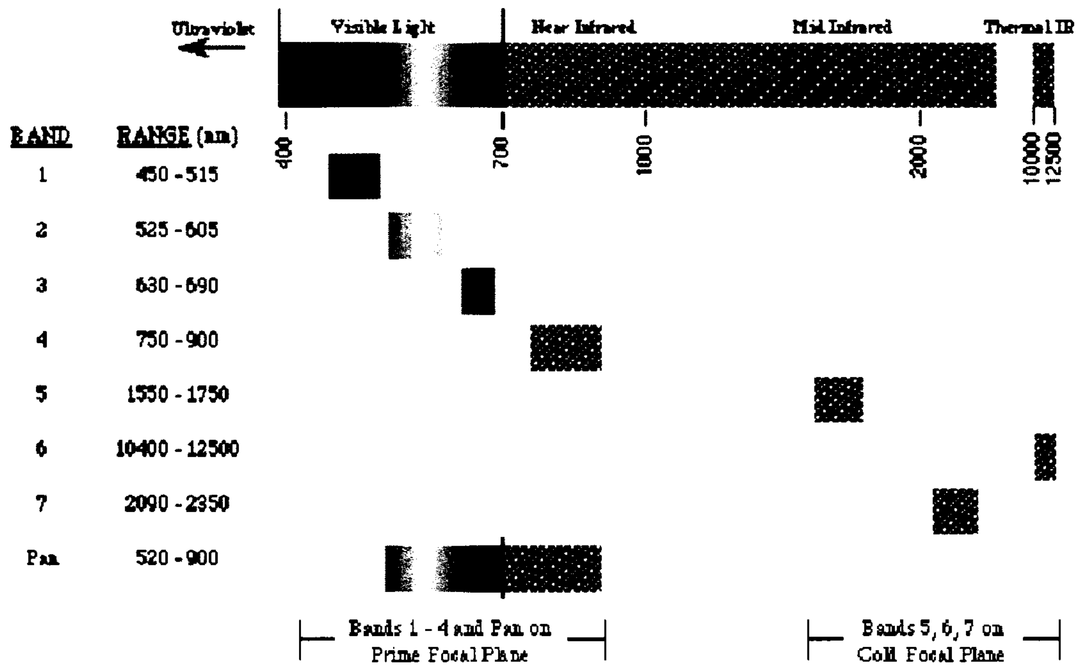


Figure 5.1B: Depiction from NRL Space – Remote Sensing website (Noorbergen 2004):

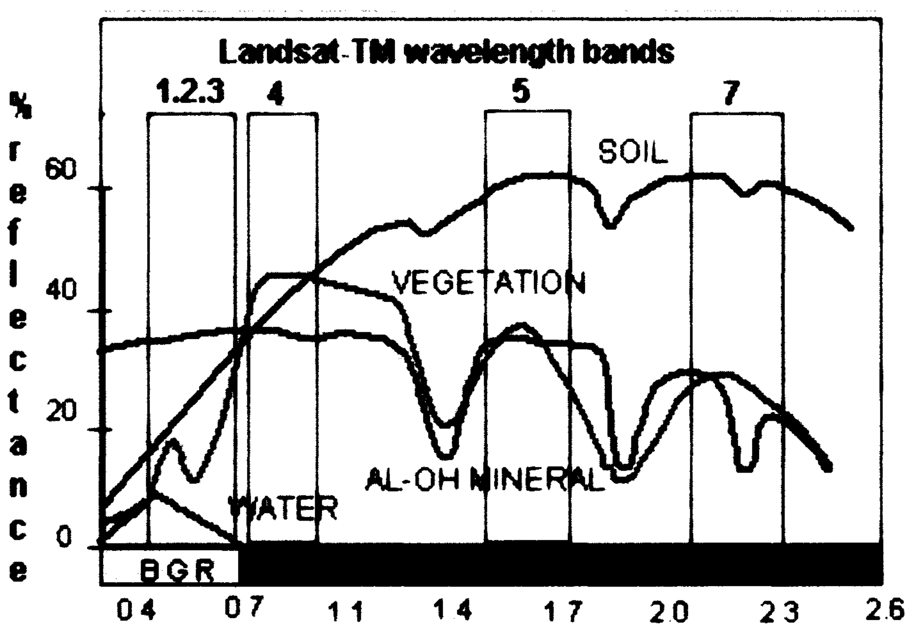

Figure 5.2: The modeled RWA density trend surface for the Last Chance Field Site, April 25th 2003 sampling date. Blue dots represent plot locations.

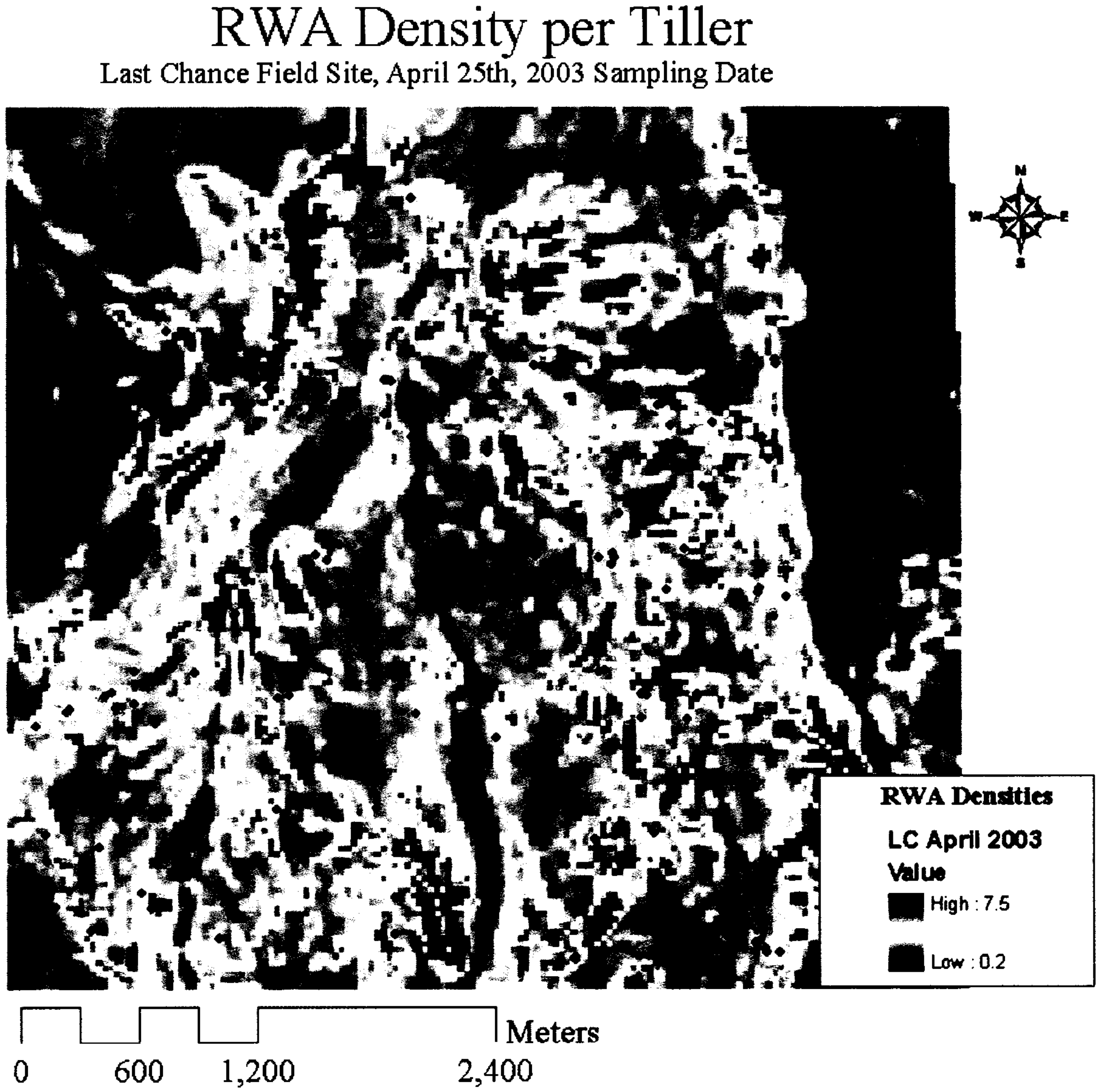

Figure 5.3: The modeled RWA density trend surface for the Last Chance Field Site, March 23rd 2002 sampling date. Blue dots represent plot locations.

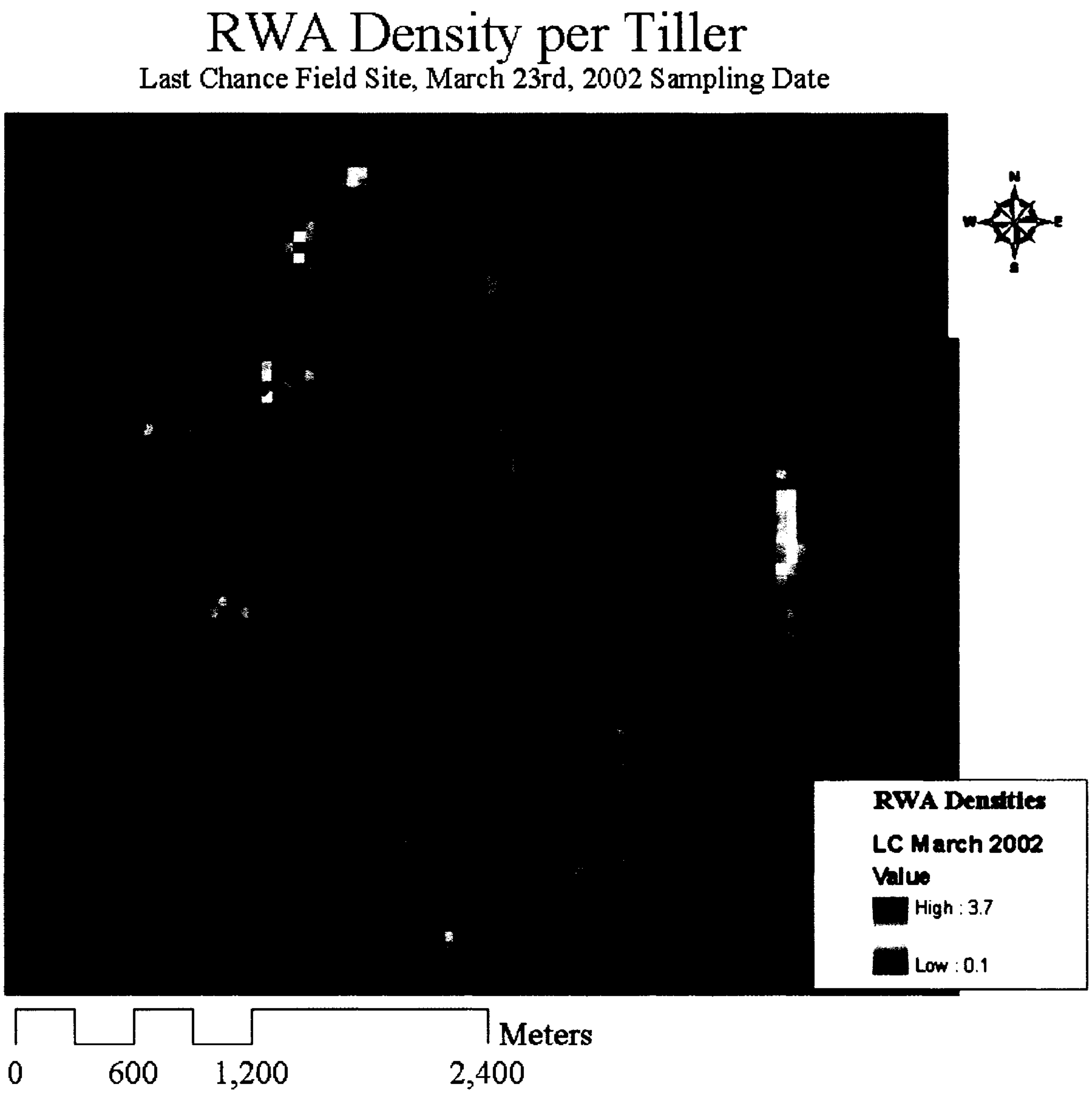

Figure 5.4: A risk assessment map based on the RWA density trend surface for the Last Chance Field Site, April 6th 2002 sampling date. Blue dots represent plot locations.

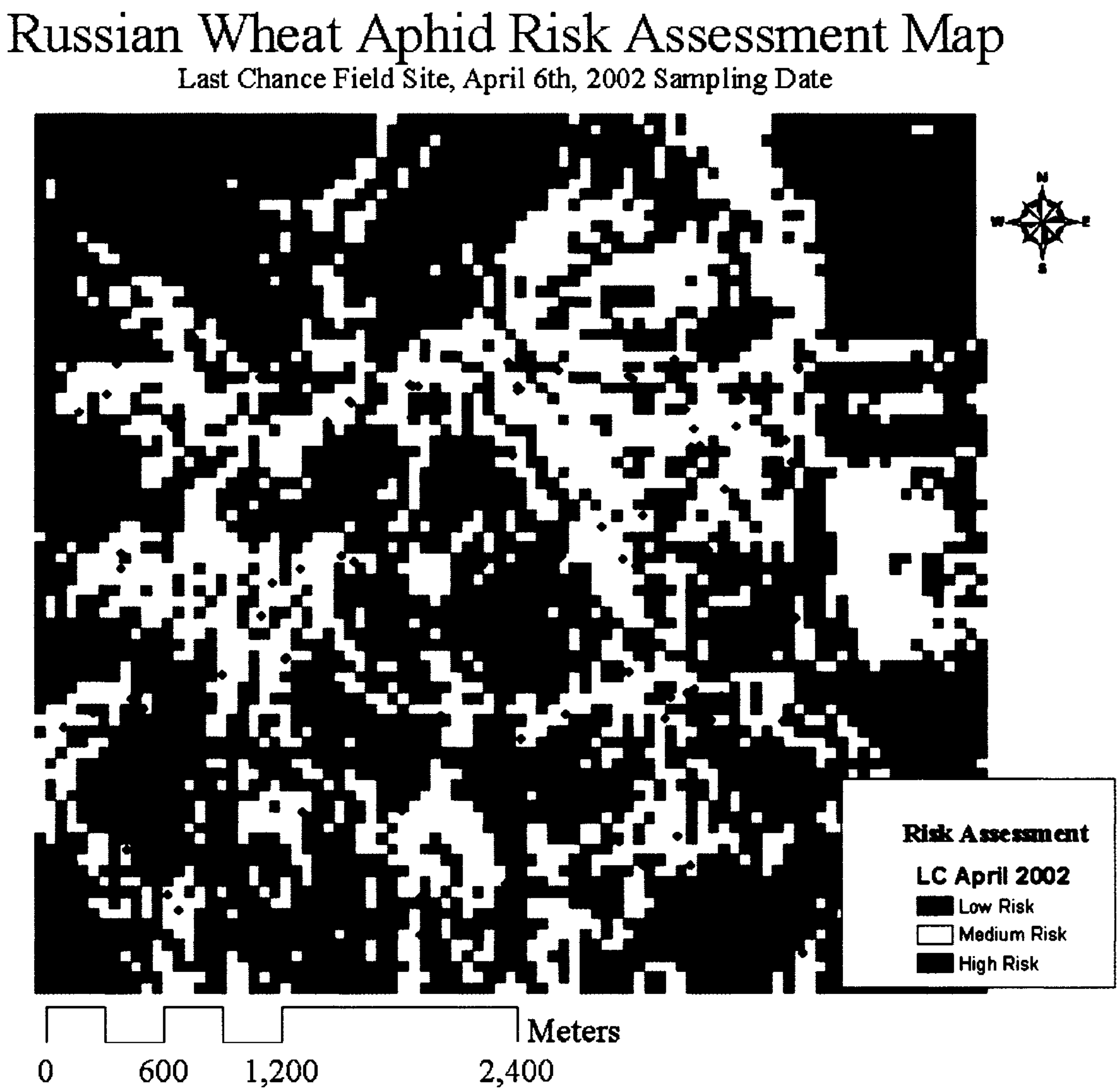

Figure 5.5: An economic status map for the Lamar Field site for April 11th 2003, including three different levels of economic danger. Areas shaded red are above the economic injury level of 3 RWA per tiller (Girma et al. 1993), defined in this case by the density of RWA per plant that result in economic losses greater than the cost of controlling for the pest. Green areas are below the economic threshold, which is defined as the RWA density where control efforts should be initiated to prevent RWA from reaching the economic injury level (chosen arbitrarily to be 2 RWA per plant). The areas in yellow depict RWA densities that are above the economic threshold but below the economic injury level.

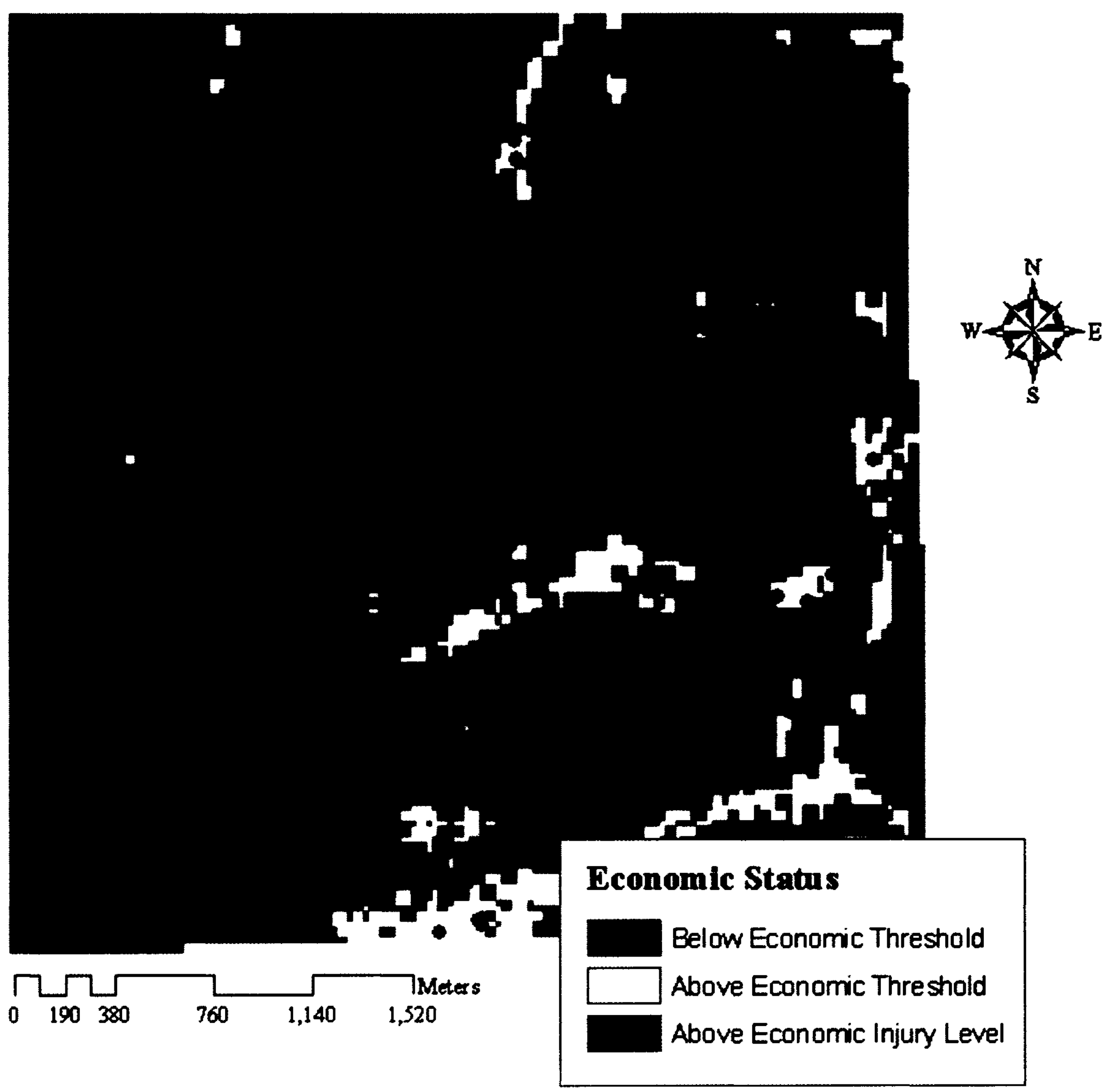

Figure 5.6. An uncertainty map for the Lamar Field site for April 11th 2003. The uncertainty map is calculated by subtracting the upper and lower confidence interval maps, and is indicative of areas of the field with differential variability in modeled predictions. Areas in red have higher uncertainty of correctly predicting aphid densities. Areas in green have higher precision in model predictions.

Table 5.1: Sample numbers, sampling date, and location.

| **Last Chance Field Site:** | |
|---|---|
| **Samples** | **Sampling Date** |
| 158 samples (subplot level) | March 23, 2002 |
| 175 samples (subplot level) | April 6, 2002 |
| 190 samples (subplot level) | March 30, 2003 |
| 119 samples (subplot level) | April 25, 2003 |
| 153 samples (subplot level) | April 13, 2004 |
| 173 samples (subplot level) | March 19, 2004 |
| **Lamar Field Site:** | |
| **Samples** | **Sampling Date** |
| 187 samples (subplot level) | February 23, 2002 |
| 175 samples (subplot level) | April 12, 2002 |
| 183 samples (subplot level) | April 11, 2003 |
| 140 samples (subplot level) | March 25, 2004 |
| 114 samples (subplot level) | April 25, 2004 |

Table 5.2: Models included in the Model Averaging Procedure, where SS is the categorical variable sampling date per site per year.

| Model # | Variables | AICc | ΔAICc | $\mathcal{L}(g_r/\text{data})$ | AICc $w_r$ Normalized |
|---|---|---|---|---|---|
| # 1 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca, Band 8 (W) | 341.86 | 0.0000 | 1.0000 | 0.340 |
| # 2 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca, Band 3 (W) | 342.08 | 0.2186 | 0.8964 | 0.304 |
| # 3 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca | 343.92 | 2.0577 | 0.3574 | 0.121 |
| # 4 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Band 8 (W) | 345.4 | 3.5449 | 0.1699 | 0.058 |
| # 5 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Band 3 (W) | 346.26 | 4.4023 | 0.1107 | 0.038 |
| # 6 | SS, NDVI (S), Band 3 (S), Slope, Band 8 (W), Band 5 (W), LAL | 346.44 | 4.5793 | 0.1013 | 0.034 |
| # 7 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Band 2 (W) | 346.54 | 4.6832 | 0.0962 | 0.033 |
| # 8 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, Baca | 347.28 | 5.4270 | 0.0663 | 0.023 |
| # 9 | SS, NDVI (S), Band 3 (S), Slope, Baca, LAL | 347.42 | 5.5598 | 0.0620 | 0.021 |
| # 10 | SS, NDVI (S), Band 3 (S), Slope, Band 8 (W), LAL | 347.91 | 6.0519 | 0.0485 | 0.016 |
| # 11 | SS, NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL | 348.53 | 6.6730 | 0.0356 | 0.012 |

*Notes:* Akaike's Information Criterion for small sample sizes (AICc), and AICc weights ($w_r$) quantify support in the data for each of the models (Burnham and Anderson 2002). $\mathcal{L}(g_r/\text{data})$ is the likelihood of the model ($g_r$) given the data.

Table 5.3: Variable Importance and Parameterization.

| Rank | Variable | AIC$_c$ Variable Weight ($w_{+(i)}$) | Parameter Estimate | Direction | LCL | UCL |
|---|---|---|---|---|---|---|
| T1 | NDVI (S) | 1.000 | 1.502 | + | 0.937 | 2.067 |
| T1 | Band 3 (S) | 1.000 | 0.708 | + | 0.176 | 1.240 |
| T1 | Slope | 1.000 | 1.312 | + | 0.712 | 1.912 |
| 4 | LAL | 0.977 | 0.510 | + | 0.152 | 0.868 |
| 5 | R_Elevation | 0.928 | -0.597 | - | -1.054 | -0.141 |
| 6 | Baca | 0.809 | 0.797 | + | 0.199 | 1.395 |
| 7 | Band 8 (W) | 0.448 | 0.278 | + | 0.045 | 0.510 |
| 8 | Band 3 (W) | 0.342 | 0.204 | + | 0.021 | 0.387 |
| 9 | Band 5 (W) | 0.034 | -0.019 | - | -0.037 | -0.001 |
| 10 | Band 2 (W) | 0.033 | 0.019 | + | 0.002 | 0.036 |
| X | Intercept | | -1.159 | - | -1.796 | -0.522 |

*Notes:* Variable Rank, which is an indicator of the likelihood of the variable being an important predictor variable as compared to other variables in the procedure and is quantified by its AICc weight ($w_{-(i)}$). Because the variables have been normalized the parameter estimate yields the magnitude of the variables' effect size and the direction of its effect. Also included are the upper (UCL) and lower confidence limits (LCL) for the parameter estimates. Variables in the green section have large weights and a strong likelihood for being important variables for prediction of RWA densities. Variables in the yellow section have medium weights, indicating that they were in some of the important models for elucidating RWA densities. And variables shaded in blue have low AICc weights, have a low probability for being chosen again as important variables, and therefore, have small effects on RWA densities in the model.

## References to Chapter 5

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# Chapter 6

# Using Cross-Validation to Generate Prediction Errors for a Russian Wheat Aphid Density Model Including Parameter Estimation of Unsampled Initial Conditions

## Abstract

Since its invasion into North America, the Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), has caused hundreds of millions of dollars of damage to small grain crops. Accurate prediction of the spatial and temporal distribution of RWA populations would allow for a reduction in control inputs (e.g., pesticides and scouting inputs). RWA density models from Chapters 4 & 5 have value for estimating early spring RWA densities. However, these models have not been validated for prediction of unsampled sites or years. To address this, a modified version of Chapter 5's spatially explicit RWA density model was developed in this chapter for cross-validation. To create unique RWA density surfaces for each of the unsampled periods or locations, initial conditions for the RWA density surfaces need to be estimated. Parameter estimates for initial conditions were calculated using two techniques: 1) initial conditions were calculated with Chapter 4's large-extent RWA density model, and 2) initial conditions were fit by minimizing the difference between modeled RWA density surfaces and measured data. Cross-validation prediction errors were smaller than or equivalent to the within-field, within-sample date variability using Chapter 4's large-extent RWA density

model to generate initial conditions. Moreover, prediction errors were substantially lower than within-field, within-sample date variability using fitted initial conditions. From a management perspective, cross-validation results yielded confidence that Chapter 5's spatially explicit RWA density model will generate model predictions (using a model which relies solely on remotely sensed data) that are more accurate than data obtained by a field scout traveling to a field to obtain RWA density measurements.

## Introduction

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov) (Homoptera: Aphididae) has been a major pest of small grains since its invasion of the western United States (Morrison and Peairs 1998). Losses to the cereal industry since the aphid's introduction are measured in the hundreds of millions of dollars (Webster et al. 1994, Morrison and Peairs 1998). RWA reproduce parthenogenically with an exceptionally high intrinsic rate of increase under optimal conditions (Burd et al. 1998, Merrill unpublished data). A predictive model for spatial delineation of RWA population densities would allow producers to manage the pests with significantly fewer inputs. For example, information from a spatially explicit RWA density model could be used to reduce pesticide applications and focus field scouting efforts, thus reducing input costs for the producer and reducing indirect costs such as improving pesticide resistance management, reducing environmental damage, and increasing refuges for natural enemies.

Cross-validation can be used to generate prediction errors to determine the value of the RWA density models for prediction of RWA densities in winter wheat cropping systems. Cross-validation removes data from the model data set and refits the model based on the remaining data (e.g., Hevesi et al. 1992). Then, the refit model is used to generate predictions for the removed data. Prediction errors are calculated by using the difference between predicted values from the refit model and the removed data values. An important characteristic of this cross-validation method is that "removed" is synonymous with "unsampled" because the removed data were not used to generate parameter estimates.

Simple cross-validation typically removes a small portion of the data (frequently ten percent of the data), refits the model based on the remaining data, then tests model predictions against the removed data. However, data that are spatially or temporally close (e.g., data from a single field or data from a single sampling date) are unlikely to be independent. Therefore, because of the probable lack of independence in the data, simple cross-validation can lead to elevated confidence in cross-validation results (i.e., error around predictions would be reduced with dependent data). To reduce the likelihood of dependence in the data, the minimum data removed during this procedure was all the data from a site for an entire year (about 1/6 of the data). Unfortunately, by removing data in this fashion, generating initial conditions for the removed data becomes complex. A positive aspect of cross-validation procedures that results from removing large portions of potentially dependent data is the applicability to more real world scenarios. For example, using this approach allows for examination of model predictions for both unsampled sites and unsampled years.

## Methods

### *Developing Models for Cross-Validation*

Chapter 5's spatially explicit RWA density model (henceforth known as the SERD model) generates RWA density surfaces based on a model-averaged result from 11 models. (A table of acronyms (Table 6.1) is included at the end of this chapter.) The SERD model, if found to be robust, could be used to predict spatially explicit RWA density surfaces. The SERD model, which delineates within-field variation in RWA densities, can be used as input for management decisions. Specifically, managers could use the SERD model to target control efforts at specified locations (e.g., using precision agriculture or directed scouting).

Unfortunately, manipulation of the SERD model for cross-validation was structurally and computationally complex. Complexity arose because each SERD model prediction was generated using a weighted-average of 11 candidate models (i.e., candidate models with ΔAICc less than seven). To reduce complexity, a simplified version of the SERD model was developed for use in this cross-validation chapter (henceforth known as the S-model). The S-model reduced complexity yet retained enough of the SERD model structure to allow confidence that the S-model would generate similar predictions and prediction errors to those made by the SERD model. The S-model uses a weighted average of all the candidate models from Chapter 5 with a ΔAICc less than 3 (i.e., models that have substantial support for being the best approximating model (Burnham and Anderson 2002)). Given a similar data set, included models have a combined AICc weight ($w_r$) of approximately 0.77, and therefore, have a very strong combined likelihood of elucidating RWA densities as compared to the other candidate models examined in Chapter 5. Three candidate models from Chapter 5 met the criteria and were selected for use in developing the S-model. The three models selected are listed in Table 6.2. Because of the combined AICc weight of these three models (i.e., $w_r = 0.77$) the predictions made by the S-model are expected to be very similar to those of the SERD model.

## *Data and Cross-Validation Design*

The sampling design was intended to obtain samples over three years at two sites with two sampling dates per site per year (One sample date per site per year is referred to as a sample set or SS). However, one SS in Year Two was not obtained for logistical reasons. Therefore, there were 11 SSs (i.e., 2 sites x 3 years x 2 sample dates per year, minus one sample set) Data collected during each SS consists of approximately 58 samples with a total data set of 641 samples. Each sample includes RWA density data and all associated predictor variables (e.g., satellite imagery, soils data, topography, etc.). As in Chapters 4 and 5, a log transformation of RWA density data (ln (RWA density +0.1) was used for all S-model and L-model calculations. Data were back-transformed to obtain RWA density estimates. Data and data collection are described in more detail in Chapters 4 and 5.

Data collected at two sites over three years create six year by site combinations (3 years * 2 sites = 6 year by site combinations). For example, one of the site by year combinations is data from the Lamar field site for 2002, a second of the site by year combinations is the data from the Last Chance field site for 2003. Cross-validation procedures will obtain predictions for three categories of data: cross-validation by site, cross-validation by year and cross-validation of the site by year combinations.

Cross-validation of the site by year combinations entails removal of data from one of the six site by year combinations (e.g., removing all data from the Last Chance field site for 2002), then refitting the S-model to the remaining five site by year combinations. Then iteratively repeating this process for the remaining five site by year combinations. That is, removing first data from Lamar 2002, refitting the S-model with data from all five remaining site by year combinations, and generating prediction errors. Then replacing the Lamar 2002 data, removing a different site by year combination, Lamar 2003, refitting the S-model with data from the remaining five site by year combinations and generating prediction errors. After this process has been reiterated for all site by year combinations, prediction errors are averaged.

Cross-validation by site entails removal of all data from one of the sites (i.e., three of the site by year combinations), then refitting the model and generating prediction errors from the refit model predictions to the removed data. The following specific steps serve as an example: 1) Remove all data collected at the Last Chance field site. 2) Refit the S-model using only the data collected at the Lamar field site. 3) Generate prediction errors between the refitted model and the Last Chance field site data. 4) Replace the Last Chance field site data into the data set. 5) Remove all of the data collected at the Lamar field site. 6) Refit the S-model to all of the remaining data (i.e., data from the Last Chance field site). 7) Generate prediction errors from the fitted model to the removed data (i.e., data from the Lamar field site.) And 8) average prediction errors from both sites.

Cross-validation by year follows a similar design as the other two cross-validation processes. Cross-validation by year removes an entire year of data (i.e., two of the year by site combinations) and refits the S-model based on the remaining two years of data. Afterwards, the refit S-model is used to generate predictions, and prediction errors between the predictions and the removed year's data. This process is reiterated for all three years. Prediction errors for all three years are then averaged to generate cross-validation by year prediction errors.

S-model cross-validation was developed to answer the following questions:

1. How well does the S-model predict unsampled sites (simulated by cross-validation by site)?
2. How well does the S-model predict unsampled years (simulated by cross-validation by year)?
3. How well does the S-model predict an unsampled site by year combination (simulated by cross-validation of the site by year combination)?

### *Prediction Errors*

There are many ways to view the structure of the error distribution between model predictions and field measured data. Two measures of prediction error were used to characterize the structure of the error distribution. These two measures of prediction error generate a more robust framework for examining potential problems in the S-model.

The first measure of prediction error used is the Mean Absolute Error (MAE) between field measurements and model predictions:

Formula # 1: $\text{MAE} = (\sum |\text{ observed } (x) - \text{predicted } (x)\ |) / n$

MAE was chosen as a predictor variable for two reasons: (1) MAE quantifies the mean difference between field measurements of density and predictions (in units of RWA

/ tiller), and (2) MAE does not assume a normal distribution of errors in the error structure.

The second prediction error was the variance (VAR) associated with the difference between the log transformed measured data and the log transformed predictions:

Formula # 2: $\mathrm{VAR} = \sum (\ln(\text{observed}) - \ln(\text{predicted}))^2 / (n-1)$

VAR was chosen as a prediction error for two reasons: 1) VAR assumes normally distributed data, which the log transformation was intended to provided and 2) VAR gives more weight to outlying or extreme values on a per plot measurement basis (e.g., VAR would give more weight to RWA density hotspots).

### *Field Variability*

Field variability is described in two ways in this study. The first measure of field variability is the mean within-field, within-sample date difference (MFD). MFD is calculated as the difference between individual within-field, within-sample date plot measurements and the field mean of the within-field, within-sample date plot measurements:

Formula # 3: $\mathrm{MFD} = \sum |(x - \text{mean}(x)| / n$ … for each SS

MFD is comparable to MAE. If MFD is greater than MAE then the model predictions are more accurately predicting variability than would be described by the measured field mean.

The second measure of field variability is the within-field, within-sample date variance (FVAR). FVAR is calculated as the variance of the log transformed data within-field, within-sample date:

Formula # 4: FVAR = $\sum$ ( ln (observed) – mean (ln (observed)))^2 / (n-1)

FVAR can be compared directly to VAR. If FVAR is greater than VAR then the model predictions are more accurately predicting variance within-field, within-sample date than would be described by the within-field, within-site variance of the log transformed measured data.

These comparisons (i.e., comparing FVAR to VAR and comparing MFD to MAE) were selected to mimic comparisons between information gathered by a field scout and model-predicted RWA density surfaces. That is, if model predictions are more accurately predicting field variability (using a model which relies on remotely sensed data) than a field scout traveling to a field to obtain RWA density measurements, then the model would have substantial economic value. Specifically, model predictions could be used to focus scouting efforts to limited areas of the field, reducing cost associated with scouting. Moreover, if managers decided to apply pesticides, applications could be limited to areas of the field where RWA densities warranted control. Thus, using a robust and accurate prediction model would result in limiting pesticide application costs, limiting environmental costs, reducing potential risks to non-target organisms, and allowing for better management of pesticide resistance.

### *Generating Initial Conditions for Unsampled RWA Density Surfaces*

To generate a RWA density surface, an initial condition (IC) is required. Conceptually, the IC is the intercept or the anchor for a density surface that, without an IC, could shift up and down. The S-model can be used to quantify the IC for any SS included in the data. However, if all data from one SS are removed, the S-model cannot fit the IC for that SS. In a mathematical sense, once data have been removed there is not enough remaining information in the model data set to create a unique solution (i.e., prediction). Simulating unsampled sites or unsampled years requires the removal of data for an entire site or year. That is, all data from a fraction of the SSs are removed, making fitting of the IC impossible. Without an IC there cannot be a fixed RWA density surface, and hence there cannot be a prediction (or prediction errors) for the RWA value on a field at a point in time. That is, an IC is necessary to generate a prediction, and to generate prediction errors. There are two solutions to the problem of generating ICs for data from unsampled or removed SSs: One solution to developing an IC is to calculate the best fit for the IC. A second approach is to add information so that an IC can be estimated. Each of these approaches provides useful information and is analyzed below.

### *Generating a Best Fit IC*

The S-model without an IC can be used to generate a relative RWA density surface, which predicts relative RWA densities at each point in the field. That is, the S-model describes areas of the RWA density surface that have relatively high and relatively low densities. Varying the IC shifts the surface upwards or downwards. Therefore, varying the IC to minimize the difference between predictions and measured data (i.e., minimize each of the prediction errors – MAE and VAR) quantifies the maximum variation explained by the predicted RWA density surface as compared to the measured data. The IC associated with the minimized prediction errors is called the fitted IC. If model prediction errors (MAE and VAR) using the fitted IC are greater than the MFD and FVAR respectively, then the S-model fails to predict spatial variability.

### *Generating an Estimated IC with Additional Information*

An alternate approach to generating an IC for unsampled or removed data is to generate an estimate of the IC with additional information. The large-extent RWA density model created in Chapter 4 was used to obtain estimates of RWA overwintering densities using weather variables. This model, henceforth known as the L-model (Large-extent RWA density model) regresses the log transformed mean RWA density for data from each SS (there are 11 SSs (combinations of site, year and sampling date) in the L-model) against a combination of temperature and precipitation variables (See Chapter 4 for details). The L-model and the S-model both provide RWA density estimates. However, there are important differences between them. Because of the resolution in the weather data, the L-model does not explicitly explain any of the spatial, within-field variation; it only estimates an average RWA density per SS. The L-model generates estimates of mean RWA densities. A correction to the mean RWA densities generated by the L-model is needed to obtain an IC for that SS.

Therefore, to estimate an IC for unsampled or removed RWA surfaces, the L-model is used to generate a mean RWA density measurement. Then a correction term is applied to the L-model RWA density measurement. The resulting value, after the correction is applied, is an estimate of the IC for that SS. The correction is calculated using data that have not been removed from the data set. The S-model generates ICs for data from each SS remaining in the data set. Additionally, the L-model generates mean RWA densities for data from each SS. The correction is calculated by the mean difference (MD) between the mean RWA densities generated by the L-model and the S-model ICs:

Formula # 5: MD = $\sum$(L-model mean density) - (S-model IC) for all SS = 1 to 11

Once the MD (i.e., the correction term) has been calculated then estimates for ICs at unsampled or removed SSs can be estimated. That is, use the L-model to generate a mean RWA density for the unsampled or removed date and subtract the correction term:

Formula # 6: L-model mean RWA density – MD = Estimated IC

For example, assume the L-model estimated a mean density of 1.5 RWA per tiller for the Lamar Field Site on April 4th 2002. Also, assume the S-model calculated an IC for that SS equal to 0.8 RWA per tiller. The difference between the mean RWA density estimated by the L-model and the calculated S-model IC for that SS is a correction of 0.7 RWA per tiller (1.5 (L-model mean RWA density estimate) – 0.8 (S-model calculated IC) = 0.7). If differences were calculated for all SSs included in the data set, and the resulting mean difference (MD) would be the correction term for that data set. ICs are estimated by subtracting the correction term, MD, from the L-model mean RWA density estimates from each SS.

Table 6.3 is included as an example of the calculations used to obtain estimates of ICs, as well as parameter estimates for all of the other important variables, for the Last Chance field site data (6 SSs) using Lamar data. This table generates parameter estimates (including ICs) for one half of the cross-validation by site procedure. Parameter estimates are then used to build predicted RWA density surfaces.

## Results

Using the described methods, MFD was calculated to be 1.990 RWA / tiller. FVAR was calculated at 2.450. Therefore, if MAE is less than 1.990 RWA / tiller the model is accurately predicting RWA densities on an across-field basis. And if VAR is less than 2.450, the model surfaces are explaining spatial variability with more weight given to correctly predicting extreme RWA density values.

### *Cross-Validation Using Fitted ICs*

Across all cross-validation procedures, RWA density surfaces calculated using fitted ICs generated prediction errors that ranged from 1.815 to 1.824 for the MAE and 2.03 to 2.09 for VAR. These values were less than MFD and FVAR respectively (Table 6.3). The lowest MAE was generated between the surfaces with fitted ICs calculated from cross-validation by site (MAE = 1.815). MAE was 0.175 aphids / tiller less than MFD. MAE for surfaces calculated using fitted ICs for both cross-validation by year and cross-validation of the site by year combinations were both similarly lower as compared to the MFD (Table 6.3). The lowest VAR also was seen in the RWA density surface associated with a fitted IC during the cross-validation by site procedure (VAR = 2.030 as compared FVAR = 2.450).

### *Cross-Validation Using Estimated ICs*

Cross-validation prediction errors calculated from surfaces using estimated ICs were lower than the field variability in both cross-validation by site and cross-validation of the site by year combinations (Table 6.5) and approximately equal for cross-validation by year. MAE for the cross-validation by site using an estimated IC was substantially less than MFD (1.990 – 1.858 = 0.132 aphids / tiller). VAR was likewise lower at 2.175, which is 0.275 less than FVAR. Prediction errors for cross-validation of the site by year combinations were less than field variability (MAE = 1.908 or 0.088 fewer aphids per tiller than MFD; VAR = 2.255 or 0.195 lower than FVAR). Prediction errors for cross-validation by year using surfaces calculated using estimated ICs were approximately equal to the field variability (i.e., MAE = 1.990 RWA/tiller = MFD; VAR = 2.462, slightly higher than FVAR; 2.462[VAR] - 2.450[FVAR] = 0.012) (See Table 6.4).

## Discussion

Cross-validation results indicate that the fitted surfaces have smaller prediction errors, for all cross-validated sets, than the variability derived from field sampling. Moreover, the calculated surfaces from the S-model generated using estimated ICs performed well for unsampled sites and the site by year combinations. The S-model RWA density surfaces calculated for removed years using estimated ICs were approximately equal to variability derived from field sampling. For cross-validation by year, there was a large difference between the prediction errors generated using an estimated IC as compared to the fitted IC. This difference suggests that errors exist in the L-model RWA mean density predictions between years. Large year-to-year variability may exist that is not being captured adequately by the L-model. Additional data for more accurate parameterization of the L-model may shrink the error between estimated and fitted ICs.

Using the S-model, which relies solely on remotely sensed data, will yield predictions with errors that are equal to or smaller than errors associated with field variability. The S-model uses a selection of the models with greater probabilities of being good models for approximating RWA densities. Therefore, model selection bias (see Chapter 5 for details on model selection bias) is higher in the S-model than the SERD model. Although predictions are likely to be very similar between the SERD and the S-model, and because the SERD model has less model selection bias, predictions by the SERD model are likely to be more accurate.

### *Parameterizing Soil Characteristics*

Model predictions for unsampled sites would be expected to improve if soil characteristics are accurately parameterized. Neither the S-model nor the SERD model can parameterize unsampled soil types. Many of the soil types, including the soil types Baca and LAL (i.e., the soil types found to be important variables in the SERD model), that are found at one site may not be found at the other locations and therefore, are not estimable. Data used to develop the SERD model suggest that some soil types significantly affect RWA overwintering densities. However, the model will parameterize the excluded soil type data as having zero effect. Therefore, if soil types are not included in the model data set, the model will not explain variance arising from differences in the effects of those soil types. If the model were expanded to include other non-sampled locations any new soil types would be parameterized as having zero effect. Because soil characteristics are among the most important variables for predicting RWA densities (see Chapter 5 for details), future studies of important soil characteristics (e.g., percent sand) that affect RWA would be of more value than attempting to categorically parameterize effects of the myriad of soil types.

### *Using the SERD Model as a Relative RWA Density Surface*

Predicted RWA density surfaces, even if the ICs were unknown, would be of value to crop managers. In that situation, managers could use the model-generated RWA surfaces to predict relative densities. That is, SERD model RWA density surfaces predict areas of the site that should have relatively high or low densities. If the SERD model were found to be robust (through development and testing with additional data collected across a greater variety of initial conditions) density maps generated by the model would be a valuable tool for RWA management. For example, RWA density maps could be used for directed scouting, where scouting efforts are limited to small areas of the field and then extrapolated to the rest of the field. Risk assessment maps, which delineate areas of the field were economic damage was likely to occur, could be used in a precision agriculture framework to direct pesticide applications to high risk areas, thereby limiting pesticide inputs, their associated costs, and reducing potential environmental contamination.

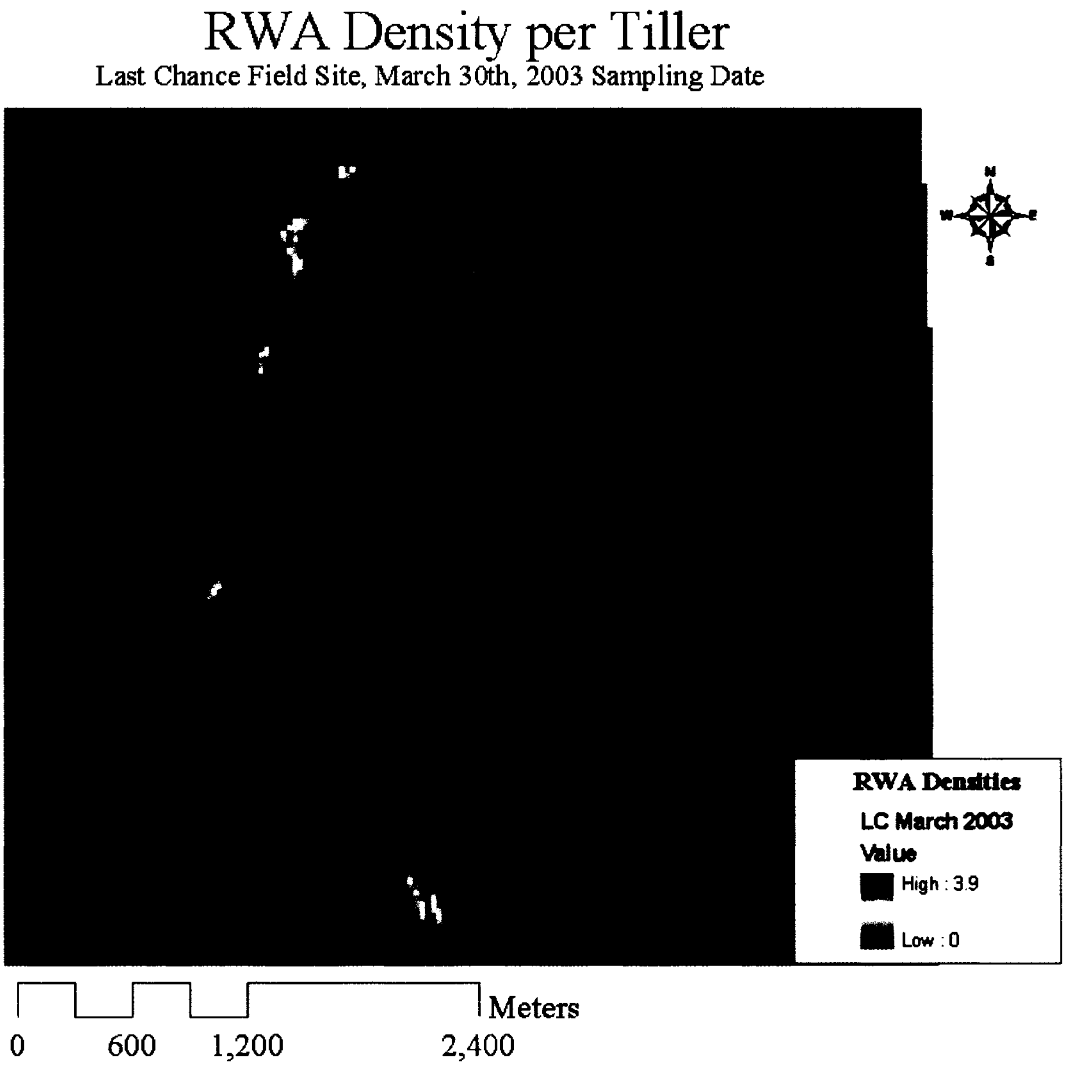
## Conclusions

All of the above cross-validation results paint an optimistic picture of the usefulness of the SERD model. The SERD model parameterized important variables using all of the collected data (e.g., all soil types included in the data set were parameterized); and therefore, it could be argued that the parameterization for future predictions would be better than indicated by cross-validation procedures where large portions of the data set have been removed. If more data become available, allowing for more accurate modeling and a better understanding of RWA population dynamics, the difference between the estimated ICs and the fitted ICs will shrink. These results indicate that it would be advantageous to use the SERD model compared to going directly to the field site and taking an average density per tiller to describe the RWA density surface. Therefore, the model could provide valuable information to crop managers and have a direct economic impact.

However, the constraints and assumptions should be reexamined before accepting all SERD model predictions. There are several reasons for caution: First, data were generated from plots that had been infested with RWA in the late fall at a uniform, and fairly high infestation rate (e.g., ca. 60 RWA / row meter). If an actual fall flight was not uniform or low levels of infestation occurred, results might be different. Second, model performance is uncertain outside of the range of variability analyzed with this data set. Periods closer to harvest may have more variation in aphid density than can be accurately predicted by the model. Third, it is unclear how well these density models will predict early winter (e.g., January) population densities because densities in this time period typically are decreasing.

While additional data would enable direct testing of the predictions of this model in the field, the cross-validation statistics create confidence that the SERD model is accurately modeling variation in this agroecosystem. When examining a system with high-dimensionality in the predictor variables there is always a concern that the model is over-parameterizing the data or modeling random noise. Cross-validation statistics provide a check to this concern. Results developed in this chapter provide evidence that the SERD model is detecting a real and predictable pattern in RWA densities.

Figure 6.1: The SS density surface for the Last Chance Field Site, March 30th 2002, Sample Period # 1. Blue dots represent RWA density sample locations.



# Tables

Table 6.1: Acronyms

| Acronym | Definition |
|---|---|
| RWA | Russian wheat aphid |
| SERD model | Chapter 5's spatially explicit RWA density model |
| S-model | Simplified version of Chapter 5's spatially explicit RWA density model (SERD Model) |
| L-model | Chapter 4's large-extent RWA density model |
| SS | The set of data from one sample date at one site during one year |
| IC | Initial condition - analogous to an intercept |
| AICc | Akaike's Information Criterion for small sample sizes (See Chapters 4 and 5 for details) |
| ΔAICc | Change in Akaike's Information Criterion for small sample sizes (see Chapters 4 and 5 for details). Denotes distance from the model with the lowest AICc value. |
| $w_r$ | AICc weight or Akaike weight (see Chapters 4 and 5 for details) |
| MAE | Mean absolute error between measured as the absolute difference between predicted and measured values |
| MFD | Mean difference between the mean RWA within-field, within-sample date density and the within-field, within-sample date plot measurements |
| VAR | The modeled variance measured as the sum of squared error between predicted and measured values of the log transformed data divided by n-1 |
| FVAR | Variance of the log transformed, within-field, within-sample date plot measurements |
| MD | Mean Distance: The distance between S-model IC per SS and L-model mean RWA density |

Table 6.2: Models, which were originally developed in Chapter 5, that are averaged by AICc weight to generate the S-model.

| Model # | Variables | AICc | ΔAICc | AICc $w_{+(i)}$ | AICc $w_{+(i)}$ Renormalized |
|---|---|---|---|---|---|
| # 1 | NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca, Band 8 (W) | 341.86 | 0.0000 | 1.0000 | 0.44 |
| # 2 | NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca, Band 3 (W) | 342.08 | 0.2186 | 0.8964 | 0.40 |
| # 3 | NDVI (S), Band 3 (S), Slope, Relative Elevation, LAL, Baca | 343.92 | 2.0577 | 0.3574 | 0.16 |

Table 6.3: This table is an example of the calculations used to derive parameter estimates for variables in a cross-validation procedure. In this procedure, all data collected at the Last Chance field site for all years has been removed. Remaining data is used to develop parameter estimates for all of the variables in the S-model. These parameterized variables will be used to develop predictive RWA density surfaces for the Last Chance field site for all three years (i.e., 6 SSs). Prediction errors are generated between data collected at the Last Chance field site and the RWA surfaces generated by parameterized values generated here.

Table 6.3a: Using Lamar data to generate weighted average values for variable parameters (orange column) as part of the cross-validation by site. All Last Chance data have been removed.

| **Variables Included in the S-Model** | **Parameter Estimates for the Three Models That Make Up the S-Model** | | | **Parameterized Values * Renormalized AICc Weights** | | | **Weighted Average of the Parameter Estimates** |
|---|---|---|---|---|---|---|---|
| | **Model 1** | **Model 2** | **Model 3** | **Model 1** | **Model 2** | **Model 3** | |
| Intercept | -1.0170 | -1.3063 | -0.9558 | -0.4512 | -0.5196 | -0.1516 | -1.1224 |
| SS 1 | | | | | | | |
| SS 2 | | | | | | | |
| SS 3 | | | | | | | |
| SS 4 | -1.4940 | -1.4028 | -1.4583 | -0.6629 | -0.5579 | -0.2313 | -1.4521 |
| SS 5 | | | | | | | |
| SS 6 | -0.5276 | -0.5495 | -0.5367 | -0.2341 | -0.2185 | -0.0851 | -0.5377 |
| SS 7 | | | | | | | |
| SS 8 | 0.1522 | 0.2517 | 0.1842 | 0.0675 | 0.1001 | 0.0292 | 0.1969 |
| SS 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| SS 10 | | | | | | | |
| SS 11 | 0.1407 | 0.1271 | 0.1372 | 0.0624 | 0.0505 | 0.0218 | 0.1347 |
| Band 3 (S) | 0.9385 | 1.0166 | 1.2399 | 0.4164 | 0.4043 | 0.1966 | 1.0174 |
| Band 3 (W) | | 0.5564 | | | 0.2213 | | 0.2213 |
| Slope | 1.1760 | 1.1533 | 1.0638 | 0.5218 | 0.4587 | 0.1687 | 1.1492 |
| LAL | 0 | 0 | 0 | 0 | 0 | 0 | 0.0000 |
| Baca | 0.8605 | 0.8871 | 0.9050 | 0.3818 | 0.3528 | 0.1435 | 0.8781 |
| Relative Elevation | -1.1278 | -1.1782 | -1.2374 | -0.5004 | -0.4686 | -0.1962 | -1.1652 |
| NDVI (S) | 1.7138 | 2.1456 | 1.8853 | 0.7604 | 0.8534 | 0.2990 | 1.9127 |
| Band 8 (W) | 0.4837 | | | 0.2146 | | | 0.2146 |

| | **Model 1** | **Model 2** | **Model 3** |
|---|---|---|---|
| **AICc Weights Renormalized (Using models with ΔAICc < 3)** | 0.4437 | 0.3977 | 0.1586 |

*Notes:* The S-model is a model-averaged result of three models. The yellow cells in Table 6.3a are the AICc weights for each model. Data remaining in the data set are used to parameterize variables (SAS 9.1 Proc GLM (SAS 2002-2003)), which are listed in the green columns, for each of the three models in the S-model. AICc weights (Table 6.3a, yellow cells) are multiplied by the parameter values (Table 6.3a, green cells) to calculate weighted parameter estimates (Table 6.3a, blue column). Weighted parameter estimates (Table 6.3a blue column) are summed to obtain weighted averages for variable parameter estimates (Table 6.3a, orange column).

Table 6.3b. Calculations for generating IC estimates by subtracting L-model RWA density

| Samples | L-Model RWA Density Estimate | Variables in the S-Model | Weighted Average of the Parameter Estimates | Difference Between S-Model IC and L-Model RWA Density Estimate | IC Estimates (L-Model RWA Density Estimates - MD) = 1.0733 |
|---|---|---|---|---|---|
| | | Intercept | -1.1224 | | |
| SS 1 | -0.3790 | SS 1 | | | -1.4523 |
| SS 2 | -0.1190 | SS 2 | | | -1.1923 |
| SS 3 | -0.6190 | SS 3 | | | -1.6923 |
| SS 4 | -0.5925 | SS 4 | -1.4521 | 0.8596 | |
| SS 5 | 0.4045 | SS 5 | | | -0.6688 |
| SS 6 | 0.5279 | SS 6 | -0.5377 | 1.0656 | |
| SS 7 | 0.1284 | SS 7 | | | -0.9449 |
| SS 8 | 1.3336 | SS 8 | 0.1969 | 1.1367 | |
| SS 9 | 0.4471 | SS 9 | 0.0000 | 0.4471 | |
| SS 10 | 0.7357 | SS 10 | | | -0.3376 |
| SS 11 | 1.9923 | SS 11 | 0.1347 | 1.8575 | |
| | | Band 3 (S) | 1.0174 | | |
| | | Band 3 (W) | 0.2213 | | |
| | | Slope | 1.1492 | | |
| | | LAL | 0.0000 | | |
| | | Baca | 0.8781 | | |
| | | Relative Elevation | -1.1652 | | |
| | | NDVI (S) | 1.9127 | | |
| | | Band 8 (W) | 0.2146 | | |

| | |
|---|---|
| **Mean Difference (MD):** The Average of the Yellow Cells | 1.0733 |

*Notes:* The L-model is used to calculate mean RWA densities per SS (Table 6.3b, green columns). Differences between L-model RWA densities and ICs parameterized by the S-model (Table 6.3b, yellow cells) are calculated (i.e., the differences are calculated by the L-model RWA densities minus the S-model ICs). A correction term (Table 6.3b, orange cells), the mean difference (MD), is calculated by taking the average of the yellow cells. Estimated ICs (Table 6.3b, blue column) are calculated by subtracting the MD from the mean RWA densities calculated by the L-model.

Table 6.3c: Parameter estimates for all variables in the S-model, including estimated ICs (blue cells) and values directly parameterized by the S-model (green cells).

| Variables in the S-model | Parameter Estimates |
|---|---|
| Intercept | -0.4402 |
| SS1 | -1.4523 |
| SS2 | -1.1923 |
| SS3 | -1.6923 |
| SS4 | -0.0039 |
| SS5 | -0.6688 |
| SS6 | 0.7455 |
| SS7 | -0.9449 |
| SS8 | 1.2549 |
| SS9 | 0.4471 |
| SS10 | -0.3376 |
| SS11 | 1.9375 |
| Band 3 (S) | 0.4313 |
| Band 3 (W) | 0.0707 |
| Slope | 0.4580 |
| LAL | 0 |
| Baca | 0.3580 |
| Relative Elevation | -0.4782 |
| NDVI (S) | 0.7725 |
| Band 8 (W) | 0.0681 |

*Notes:* The parameterized values for all of the variables in the S-model (Table 6.3c, green columns) for this iteration of the cross-validation procedure are a combination of the directly parameterized values from the S-model model averaging procedure (Table 6.3a, orange cells) and the estimated ICs (Table 6.3b, blue cells). The soil type LAL was parameterized as having zero effect because there are no LAL soil types in the Lamar data.

Table 6.4: Cross-validation using a fitted IC. Cross-validation statistics (MAE and VAR) are compared to field variability (MFD and FVAR).

| Prediction Errors | Removed Site (Fitted IC) | Removed Year (Fitted IC) | Site by Year Combinations (Fitted IC) | Field Variability |
|---|---|---|---|---|
| Best MAE | 1.815 | 1.824 | 1.817 | MFD = 1.990 |
| Best VAR | 2.030 | 2.090 | 2.054 | FVAR = 2.450 |

*Notes:* Because data are not perfectly normal, the minimizing MAE does not minimize VAR. That is, the best MAE does not coincide with the best VAR.

Table 6.5: Cross-validation results using an estimated IC.

| Prediction Errors | Removed Site (Estimated IC) | Removed Year (Estimated IC) | Site by Year Combinations (Estimated IC) | Field Variability |
|---|---|---|---|---|
| MAE | 1.858 | 1.990 | 1.908 | MFD = 1.990 |
| VAR | 2.175 | 2.462 | 2.255 | FVAR = 2.450 |

*Notes:* Cross-validation statistics (MAE and VAR) are compared to the field variability statistics MFD and FVAR.

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# Chapter 7

# Examining Spatial Correlation Between Successful Fall Infestations and Spring Population Densities of the Russian Wheat Aphid

## Abstract

The Russian wheat aphid (RWA), *Diuraphis noxia* (Kurdjumov), is a serious pest of small grain production with damage estimated in excess of a billion dollars since its introduction into the United States in the mid-1980s. In continued efforts to decrease management inputs and increase our understanding of RWA population dynamics, research was initiated to study the time period prior to spring growth of winter wheat. This time period is crucial to understanding variability of RWA population dynamics. RWA densities decrease in the winter time period, resulting in densities being low or locally extinct by the early spring. Low RWA density levels may be manageable with fewer inputs, using precise pesticide applications on areas where RWA densities are potentially harmful, while leaving other areas untreated. That is, managing RWA populations before they are allowed to become sources of infestation for nearby crops or have a chance to cause substantial crop damages. My research goal was to determine if spatial heterogeneity in RWA fall infestation success directly correlated to spatially explicit spring RWA densities. Analysis revealed that fall densities correlated significantly with spring densities ($p < 0.0001$, F-statistic 23.69). However, the total variation in spring densities explained by the relationship with fall density data was low

($r^2 = 0.038$) indicating a need for study of alternative models and variables that could influence overwintering success or failure of RWA.

## Introduction and Background

The Russian wheat aphid, *Diuraphis noxia* (Kurdjumov), is a serious pest of small grain production in areas west of the 100th meridian with crop damages estimates in the hundreds of millions of dollars (Webster et al. 1994, Morrison and Peairs 1998) The RWA was likely introduced in 1985 and was first positively identified in the United States in 1986 (Morrison 1987, Morrison and Peairs 1998). Resistant wheat cultivars were developed for RWA biotype 1 and effectively eliminate the need for pesticide applications. However, since 2003 many new biotypes have been discovered (e.g., Haley et al. 2004) that are virulent to all commercially available winter wheat cultivars. It is estimated that an additional 4-7 years (Haley, personal communications) will be needed to develop winter wheat cultivars resistant to the known biotypes. Effective management practices for control of the RWA are limited and rely primarily on pesticide application. Greater understanding of spatial and temporal RWA population dynamics within small-grain agroecosystems would be beneficial for limiting direct (e.g., pesticide inputs) and indirect (e.g., pesticide resistance management and environmental contamination from pesticide usage) costs associated with RWA management.

Past research suggests that many factors in fall infestation levels affect spring aphid abundances and crop damage. For example, Dewar and Carter (1984) found that the most important factors for determining aphid summer outbreak of *Sitobian avanae* were fall infestation levels (i.e., density of fall flight), winter severity, spring densities of natural enemies, crop planting date, and size of the spring infestation or spring migration.

Fall infestations can result in increased winterkill of damaged plants (Thomas and Butts 1990). Butts et al. (1997) did not find a direct correlation between fall RWA abundances and yield loss. However, they did find an indirect correlation between fall infestations and yield loss. Specifically, RWA densities were correlated with plant stand density, which was correlated with yield.

The spatial distribution of RWA in fall populations was found to be highly aggregated, especially where aphid densities were low (Butts and Schaalje 1994). This heterogeneity may correlate with winterkill of wheat (Butts 1992), RWA hotspots or areas with a high degree of positive spatially autocorrelation in aphid population densities and associated yield losses in the spring, and yield loss at harvest.

Conversely, fall RWA density and variations in density may be of limited importance in predicting spring RWA density and yield. For example, Girma et al. (1993) and Archer et al. (1998) found that sensitivity of wheat yield components to fall infestations is less than to spring infestations. Therefore, if fall densities are not strongly correlated with spring densities, determining the factors influencing successful fall infestations would be of low importance from a management perspective.

As previously mentioned, studies (e.g., Chapter 5) have found that spring RWA densities are spatially heterogeneous within many agroecosystems. The primary objective of this study was to determine if spatially explicit fall infestation densities are correlated with heterogeneity in spring RWA densities within a wheat-fallow agroecosystem. That is, research was initiated to determine if spatial heterogeneity that exists after initial fall infestations predict the spatial heterogeneity that will exist the following spring.

# Methods

## *Sampling Design*

Two field sites, the Last Chance field site (39°44' N 103°48' W) and the Lamar field site (37°58' N 102°30' W), were established based on disparate topographic and climatic variables and were located representatively for Colorado dryland wheat harvested acreage.

Each year ca. 80 plots were established at each field site. All plots were georeferenced using a GPS device (Garmin GPSmap76S). For the first two years, plots were selected based on a stratified random grid design. The third year was stratified across soil type because preliminary analysis indicated that soil type was an important variable for determining spring abundances. Plots consisted of three consecutive rows (subplots) of dryland winter wheat. For more planting details see Appendix B.

Subplots were infested in late fall (ca. November 15$^{th}$) with RWA from the RWA Biotype 1 colony at Colorado State University (For more details regarding infestations see Appendix B). RWA densities were measured once in the early winter (ca. December 10$^{th}$) and measured twice the following spring. Winter and spring data were collected at both sites for three overwintering periods (i.e., the winters of 2001-2002, 2002-2003, and 2003-2004). Weather factors prohibited winter sampling at the Lamar field site during December 2002. To determine RWA densities, wheat tillers were removed from subplots. Sample design was for tillers to be removed at a rate of six tillers per subplot. If tiller density was low (e.g., from low wheat emergence) tillers were removed to maximize tillers obtained over both sample periods. For example, if only six tillers existed on a subplot during the first sample period, half of the tillers would be removed allowing the second three tillers to be removed during the second sample period. Tillers were clipped at each subplot, placed into ziplock bags, and transported to Colorado State University's Agricultural Research Development and Education Center (ARDEC). Tillers were then removed from the ziplock bags and placed into berlese devices using a 70/30 - alcohol/water mixture. Berlese devices heat the wheat tillers, causing any aphids on the plant material to retreat to cooler areas and hence aphids fall into a berlese cup containing the alcohol/water mixture. From the alcohol/water mixture, RWA were counted under a dissecting microscope and expressed on a per tiller basis. Subplot densities were averaged to obtain a plot average. The distribution of RWA density averages at the plot level was right skewed. Therefore, a log transformation (ln (RWA density + 0.1)) was used to approximate a normal distribution.

### *Geographic Information System (GIS) and Data Layers*

26 predictor variables were developed for use in developing fall RWA density trend surfaces. All GIS data layers (i.e., data layers associated with the predictor variables) were projected to the NAD 84 (North American Datum of 1984) projection. The data layers used were Landsat 7 ETM+ Band imagery from images taken ca. December 15$^{th}$ of each winter (i.e., Nine data layers: Bands 1-5, Thermal Bands 6.1 and 6.2, Band 7, and the panchromatic Band 8), categorical soil data layers (Nine layers including the soil types: Weld Series, Wiley Series, Baca Series, Colby Series, Samsil Series, Arvada Series, Shingle Series, Adena Series, Loamy Alluvial Lands, and Gullied Land), topographic data layers (Five layers including Relative elevation, Landshape,

Aspect, North-South aspect, and Slope). See Chapter 5 for details regarding GIS layer development.

### *Data and Model Development*

Data values were extracted for each predictor variable (i.e., from the GIS data layer developed for each predictor variable) in association with the GPS coordinates for each RWA density measurement. All predictor variables were normalized. All Landsat imagery was normalized within image capture date to observe relatively high and low emission data within-field instead of between fields. For example, emissivity detected by the thermal bands can change depending upon the daily temperature. If the Landsat bands were not normalized within capture date, then emissivity detected between capture dates could mask variation seen within capture date. Relative elevation was normalized by site to correct for the large relative elevation differences between sites. All other GIS layers were normalized across all data using the standard formula ($X_i$ – Minimum(X) / (MaximumX – MinimumX) ) for all data points i (See Appendix D for normalization parameters).

#### **Model development**

The goal of this study was to determine if spatially explicit RWA fall densities correlated with spring densities. To develop fall RWA density surfaces, I analyzed and parameterize variance components associated with both the large-scale covariance structure (i.e., the trend surfaces) and the small-scale variance associated with the error structure (i.e., the residuals). Trend surface analyses were used to determine large-scale variance with extensive efforts made to analyze accessible covariates (Cressie 1993).

Variance associated with the covariance structure residuals was examined for additional patterns including spatial autocorrelation. If additional signals, besides signals in the covariance structure, were detected, they were used to develop a more accurate interpolated density surface (i.e., reduced prediction errors between the model and observed data.)

Spatial autocorrelation (i.e., spatial dependence) between data points or residuals was tested for using Moran's contiguity ratio (1948) (also known as Moran's I). If spatial autocorrelation was found, it was quantified using a variogram. The variogram was used to develop an interpolated surface (kriged surface) between spatially delineated points. Residuals from the trend surface analysis were analyzed for spatial dependence, kriged, and added to the trend surface as a GIS layer if spatial dependence was detected.

Kriging of residuals for use as a GIS layer should not be used to determine the causes or effects of the interpolated density surface. That is, a kriged residual surface is built from an analysis of the structure in the residuals and does not have explicit biological or ecological meaning. However, this study did not intend to determine the dominant ecological factors for understanding fall RWA density surfaces. The goal of this study was to determine if spatial heterogeneity of RWA fall densities correlates to RWA spring densities (i.e., surface to surface analysis). Therefore, development of the best trend surface for fall RWA densities was necessary, as compared to understanding the factors underlying the characteristics of the surface.

Fall RWA density interpolated surfaces were developed for each overwintering period at each site (i.e., trend surfaces plus kriged surfaces). Data values were extracted from the fall interpolated density surfaces in association with the GPS positions of the

RWA spring density data. Because prediction of future fall density surfaces was not the goal, the best possible RWA density surface from each site for each year was used to depict fall densities (i.e., model selection bias was ignored).

## Trend Surfaces and the Covariance Structure

An information theoretic approach for model selection using Akaike's Information Criterion (AIC) with an adjustment for small sample sizes (AICc) was used to analyze the support of evidence for each of the candidate models. Candidate models were generated using an AICc (e.g., Burnham and Anderson 2002, Burnham and Anderson 2004) based, forward selection procedure (e.g., Chapter 4, Twombly et al. In Press). All models were formed by linearly regressing the predictor variables (i.e., GIS data layers) against the fall RWA density data:

$$\ln(\text{RWA density} + 0.1) = \text{Intercept} + \sum \beta_i X_i \ldots \text{ for } i = 1 \text{ to n}$$

where $X_i$ is the *i*th predictor variable, and the $\beta_i$ is the parameter estimates associated with the *i*th variable. AICc based, forward selection was undertaken as follows (Twombly et al. In Press): At each step of the model selection process, I computed the AICc (e.g., Burnham and Anderson 2002, Burnham and Anderson 2004) of the candidate model as compared to the lowest AICc from any previous steps. Specifically, I added each of the 26 predictor variables to the null model (i.e. intercept only) to build 26 single-variable models. These were fit to measured winter RWA density data using SAS Proc GLM (SAS 2002-2003), and AICc values were computed for each single-variable model. If the AICc values for every single-variable model were greater than the AICc of the null model, model selection was finished. Otherwise, I selected the model with the lowest

AICc as the best single-variable model (BSVM). Then, I iteratively added each of the remaining 25 predictor variables to the BSVM to build 25 two-variable models. If the AICc values of the two-variable models were greater than the BSVM then model selection was finished. If not, I obtained the best candidate model (i.e., the model with the lowest AICc) as the best two-variable model (BTVM). After which, I iteratively added each of the remaining 24 predictor variables to the BTVM to build candidate three-variable models. This process was repeated to build four-variable models, etc., until all AICc values were greater if any of the remaining variables were added to the candidate model with the lowest overall AICc. The model with the lowest AICc was selected as the best approximating model. The best approximating model was used to develop a GIS-based trend surface for each of the five fall data sets (see Figure 7.1 for an example).

## Examining Residuals and Kriging

Residuals (i.e., the remaining error between the observed and predicted values from the initial regression equations) from each of the best approximating models were analyzed for spatial autocorrelation using Moran's I (1948) (S-Plus 2005, spatial library functions developed by Robin Reich), Spatial library functions developed by Robin Reich). If spatial autocorrelation was detected, residuals were kriged (Cressie 1993) (S-Plus 2005, spatial library functions developed by Robin Reich) and added as a layer to the trend surface (see Figure 7.1 for an example).

Therefore, the final interpolated surface for each of the five data sets was generated by a combination of known covariates (i.e., the best approximating model of the tested linear regression models) and where significant, the kriged residuals, which were derived from the additional spatial autocorrelation structure in the data. The biological and ecological factors that control the kriged surfaces are unknown and make interpretation of the interpolated grid surface ill advised.

## Results and Discussion

Linear models were developed using the AICc based, forward selection (Twombly et al. In Press), with a single best approximating model selected (i.e. the model with the lowest AICc). The variables selected by the criterion based, forward selection procedure for each fall regression equation are listed in Table 7.1. Interpolated surfaces of RWA densities were developed for each fall data set. Residuals from the best approximating model were tested for spatial autocorrelation. Only data from the Last Chance field site during the 2001-2002 winter were spatially autocorrelated (i.e., significant Moran's I at $p = 0.08$). Therefore, residuals from the fall period for the 2001-2002 winter data were kriged and added to the associated regression equation (Figure 7.1). Data were extracted from each interpolated density surface from the spatial location (i.e., the global positioning system coordinates) associated with spring density measurements. Fall interpolated surface density data were then regressed against spring density measurements (Proc GLM, SAS 2002-2003).

Fall densities were found to be significantly associated with spring densities ($p < 0.0001$, F-statistic = 23.69), elucidating approximately 4 % of the variation in spring densities (Table 7.2). Fall surfaces predicted more variance in the spring surfaces during the early spring (i.e., the first sample period, which was in late February or March) ($r^2 = 0.061$ for Period 1) as compared to the late spring (i.e., the second sample period was typically in April) ($r^2 = 0.034$ for Period 2). However, $r^2$ results are difficult to compare because within field variance during Period 2 sharply increases. That is, the later spring density measurements have more variation than measurements taken earlier in the spring.

## Conclusion

As expected, RWA fall density distributions significantly correlated to spring density distributions. Continued research into the factors influencing successful fall infestation would therefore have merit. However, the amount of variance explained ($r^2$ ca. 4 %) is low. Indicating that fall infestation level is an important variable but that other variables are likely much more valuable for elucidating spring population structures. For example, topographic variables such as slope could greatly influence overwintering survival, masking and overwhelming any affects of initial fall infestation levels.

Figure 7.1 (A-C): Interpolated RWA density surface development for the winter 2001-2002 Last Chance Field Site.

Figure 7.1A: A trend surface was developed from the best approximating model to the Last Chance Winter 2001-2002 fall RWA density data. Green dots are spring density measurements.

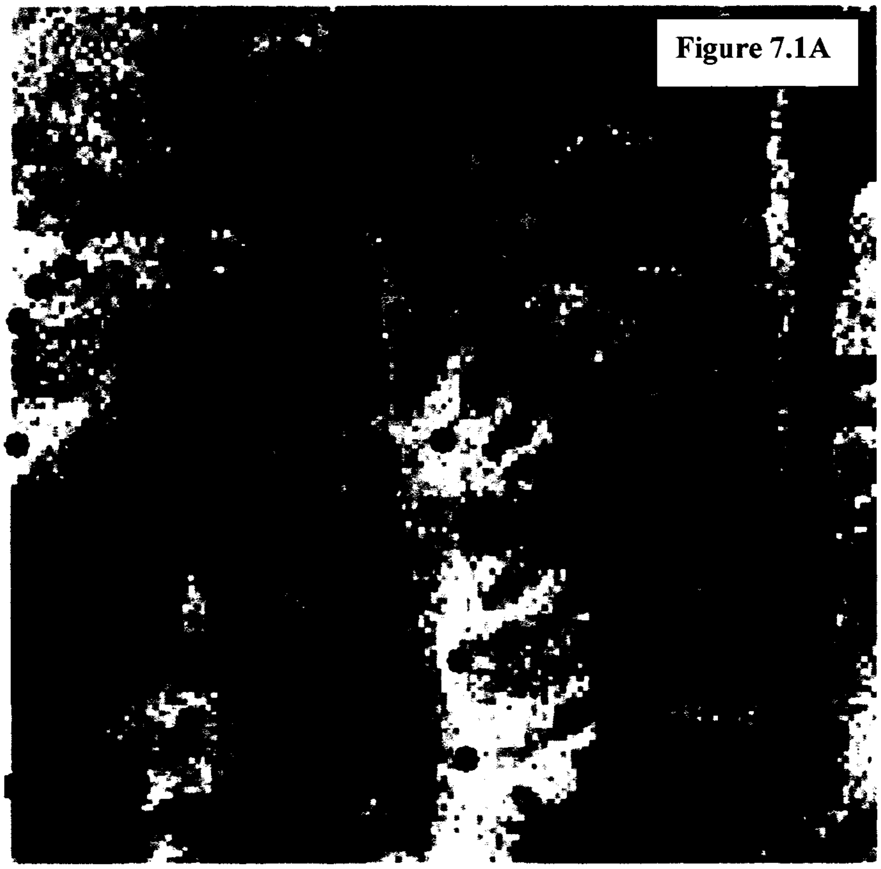

Figure 7.1B: Residuals showed positive spatial autocorrelation and were kriged. Green dots are spring density measurements.

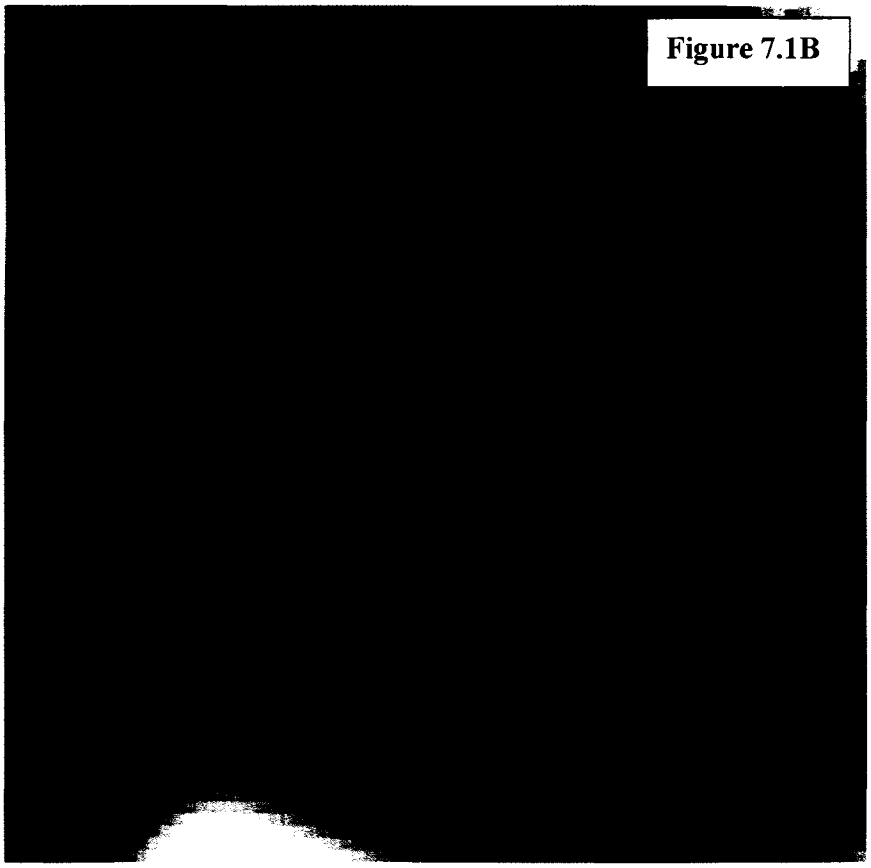

Figure 7.1C: Kriged surfaces (i.e., the surface created from the structure in the residuals) were added to the trend surfaces to develop a final interpolated density surfaces. Green dots are spring density measurements. Data were extracted from the interpolated RWA fall density surfaces (e.g., this figure) at each georeferenced spring plot and regressed against the spring RWA density measurement data for that plot.

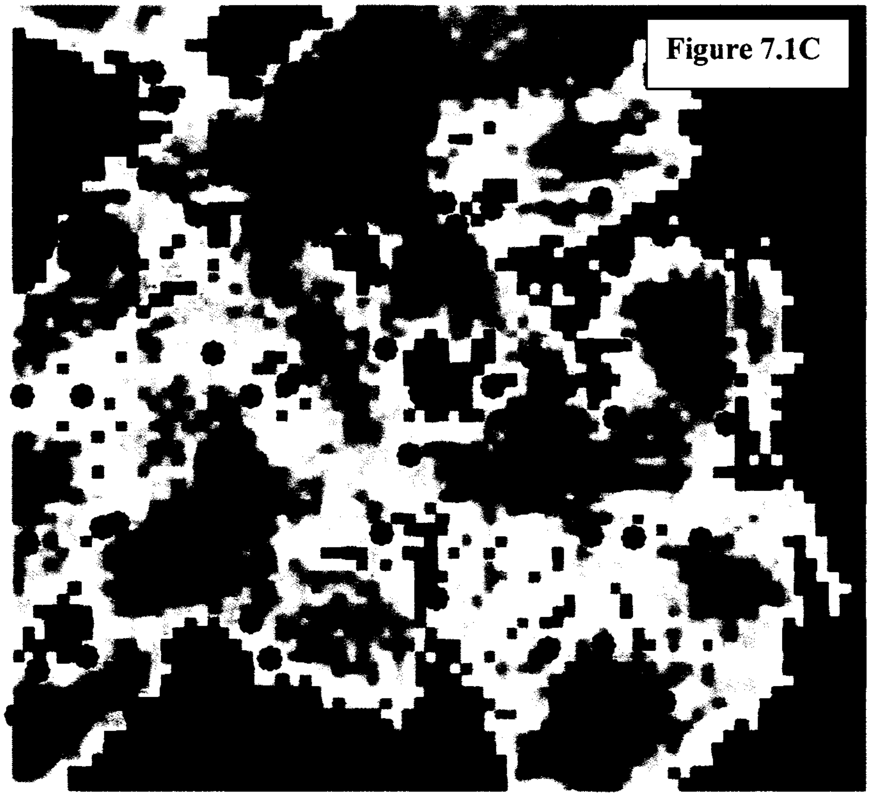

Table 7.1: Table of data layers for interpolated surfaces for each winter period.

| Site | Winter Date | Variables in Trend Surface | Moran's i Spatial Autocorrelation | Kriged Residual Layer added? |
|---|---|---|---|---|
| Last Chance | 2001 Winter | Band 6.2, Relative Elevation, Band 1, Band 3, Landshape, Soil types: Wiley, LAL, AcC, Weld, Adena, Kriged Residual Surface layer | $p = 0.08$ | Yes |
| Last Chance | 2002 Winter | Relative Elevation, Band 1, Band 2, Band 3, and the soil types Samsil and Wiley | $p = 0.664$ | No |
| Last Chance | 2003 Winter | Slope, North-South Aspect, Band 2, Band 8 and the soil type Weld | $p = 0.667$ | No |
| Lamar | 2001 Winter | Band 3, Band 4, and the soil type Baca | $p = 0.32$ | No |
| Lamar | 2003 Winter | Relative Elevation, Slope, North-South Aspect, Band 1, Band 6.1, Band 7 and the soil type Baca | $p = 0.17$ | No |

Table 7.2: Regression statistics for fall interpolated density surfaces regressed against spring density data.

| | **F-stat** | **p-value** | **$r^2$** |
|---|---|---|---|
| Full Model | 23.69 | < 0.0001 | 0.038 |
| Period 1 | 20.26 | < 0.0001 | 0.061 |
| Period 2 | 9.91 | 0.0018 | 0.034 |

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# Chapter 8

# Conclusion

This body of work integrates many components of research directed towards gaining an understanding of overwintering population dynamics of the Russian wheat aphid (RWA). Components include: 1) a literature review, 2) generating the basic biological building blocks for developing a population model, 3) building and parameterizing a large-extent, between-site and between-year model based on weather conditions, 4) building and parameterizing a high resolution, within-site model that incorporates the techniques of Geographic Information Systems and spatial statistical modeling, 5) generating prediction errors for the small-scale, spatially explicit RWA density model using validation techniques, and 6) studies of spatially explicit effects of fall infestation on spatially explicit, spring RWA densities.

Evidence has been developed to help answer many of the questions that guided this research. Spring heterogeneity does seem to be predictable, at the scale of this analysis. Many variables in the winter-wheat agroecosystem have been explored, some of which appear to elucidate variation in spring RWA densities. Some of the important weather variables that yield boundary conditions on heterogeneity have been confirmed as driving variables. And fall RWA densities do provide information, albeit limited, on spring densities.

This research has been designed to be a building block for creating applications that will be used by farm managers. That is, the integrated model (i.e., the model cross-validated in Chapter 6) has been designed to generate spatially explicit RWA density predictions and, in association with loss functions, Risk Assessment Maps (i.e., maps which delineate economic risk). Collecting data on variables needed for generating RWA density surfaces and Risk Assessment Maps are relatively inexpensive, providing an incentive for adopting this model as a management tool.

Chapter 4 and 5's RWA density models will enable management actions to be focused on locations and times when the risk of economic damage is high. Future work should concentrate on continued validation of the RWA density models. If these models are found to be robust, they will enhance opportunities to develop a management system that makes more effective and judicious use of available management tools. Given the loss of efficacy of previously resistant cultivars due to the new RWA biotype, I expect this research to have broad applicability in RWA management in the Great Plains.

Further research should continue validation of Chapter 4 and Chapter 5's RWA density models for alternate cropping systems, and across a wider range of conditions. Additional research in other ecosystems that have a potential for supporting RWA populations during the winter should be undertaken. For example, if grasses on Conservation Reserve Program (CRP) lands were found to have high densities of overwintering RWA, movement into nearby small-grain fields could create pronounced edge effects in the crop. If CRP lands were found to be sources of local small-scale migration, an additional GIS layer could be introduced to increase RWA densities in locations bounded by CRP lands.

Forecasting spatially explicit RWA densities, as well as increasing knowledge on initial and boundary conditions, will enable directed scouting, precision agricultural techniques, and within-field management practices for control of RWA. Adoption of these practices and techniques has the potential to reduce pesticide inputs, allow for more judicious use of resistant cultivars (when they become available), increase natural enemy refuges, and reduce pesticide exposure to agricultural workers and consumers.

# Appendix A

# Examples of Alternate Host Species Lists for the Russian wheat aphid

## Species Lists

### *Alternate Host Species Studied by Hammon et al. (1989)*

1. Jointed Goatgrass (*Aegilops cylindrical* Host)
2. Crested Wheatgrass (*Agropyron cristatum* L.)
3. Western Wheatgrass (*Agropyron smithi* Rydb)
4. Threeawn (*Aristida* sp.)
5. Wild Oats (*Avena fatua* L.)
6. Side-oat Gramma (*Bouteloua curipendula* Michx.)
7. Blue Gramma (*Bouteloua gracilis* (HBK))
8. Canada Wildrye (*Elymus Canadensis* L.)
9. Bottlebrush Squirreltail (*Elymus Elymoides* (Raf.)
10. Russian Wildrye (*Elymus iunceus* Fisch)
11. Bearded Wheatgrass (*Elymus subsecundus* (Link.))
12. Slender Wheatgrass (*Elymus trachycalus* (Link.))
13. Intermediate wheatgrass (*Elytrigia Intermedia* (Host.))
14. Pubescent Wheatgrass (*Elytrigia intermedia barbulato* (Schur.))
15. Stinkgrass (*Eragrostis cilianesis* (All.))

16. Jointed Goatgrass (*Hordeum iubatum* L.)

17. Sand Dropseed (*Sporobolus cryptandrus* (Torr.))

18. Annual Wheatgrass (*Eremopyron triticum* (Gaertn.))

19. Tall Wheatgrass (*Elytrigia pontica* (Podp.))

### *Alternate host species studied by Messina (1993)*

1. Crested Wheatgrass (*Agropyron cristatum* L.)
2. Snake River Wheatgrass (*Elymus lanceolatus*)
3. Great Basin Wildrye (*Leymus cinereus*)
4. Indian Ricegrass (*Oryzopsis hymenoides*)
5. Blue Bunch Wheatgrass (*Pseudoregneria spicata*)
6. Intermediate Pubescent Wheatgrass (*Thinopyrum intermedium*)

### *Alternate host species studied by Armstrong et al. (1991)*

1. Crested Wheatgrass (*Agropyron cristatum* L.)
2. Canada Wildrye (*Elymus Canadensis* L.)
3. Barnyardgrass (*Echinochloa crusgalli* L. Beauv)
4. Green Foxtail (*Setaria viridis* L.)
5. Witchgrass (*Panicum capillare* L.)
6. Sand Dropseed (*Sporobolus cyrptandrus* Torr. Agrax)
7. Intermediate wheatgrass (*Elytrigia Intermedia* (Host.))

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# Appendix B

# Planting and Infestation Details

## Planting and Watering Protocol

Three subplots were planted for each plot. Wheat planted by the farmer was removed with a hoe. TAM 107 was planted at a rate of 2.45 grams/meter row. Water was added to offset soil disturbance and to increase emergence likelihood. Water was added at a rate of 1 liter per subplot (except at the Last Chance Field site in 2001, which received 2 liters per subplot). Because of the extremely dry conditions that occurred during this study subplot length was reduced from 1 meter in the first overwintering season to 0.33 meters in the 2nd and 3rd seasons to maximize the logistically available water. Specifically, this allowed the amount of water per meter row to triple, ideally resulting in increased emergence. Emergence in the first year was approximately 50% even with the extra water received by the Last Chance field site. Where wheat emerged, tiller density did not seem to be limiting. That is, with emergence sample and infesting could occur, even with a reduced subplot length. Therefore, by reducing subplot length, water per subplot could be increased three-fold. In summary, subplots were three times as long (i.e., 1 meter / subplot) in season 1, receiving 1 liter per subplot. Subplots in seasons 2 and 3 were 0.33 meters long and received 1 liter per subplot. Emergence in seasons 2 and 3 increased to approximately 70%.

## Farmer Planted Wheat Varieties

In Years Two and Three, low emergence of planted TAM 107 seed at the Lamar field site necessitated the use of winter wheat planted by the farmer. Approximately 40% of plots at the Lamar site Years Two and Three were planted to Prowers (old). Cultivar type had no statistical effect on RWA densities.

## Infestation Notes

All RWA used for infestations were from Colorado State University's Biotype 1 colony. All subplots were infested with using a Davis Inoculator (Davis and Oswalt 1979).

### *Last Chance Field Site: Winter 2001-2002*

94 plots were infested with ca. 315 RWA per subplot on October 14th 2001.

### *Lamar Field Site: Winter 2001-2002*

88 plots were infested with ca. 135 RWA per subplot on November 3rd 2001

### *Last Chance Field Site: Winter 2002-2003*

88 plots infested on November 10th 2002 with ca. 79 RWA per subplot.

### *Lamar Field Site: Winter 2002-2003*

62 plots were infested with ca. 102 RWA per subplot on January 6th 2003

### *Last Chance Field Site: Winter 2003-2004*

72 plots infested on November 8th 2003 with ca. 114 RWA per subplot.

### *Lamar Field Site: Winter 2003-2004*

89 plots were infested at ca. 154 RWA per subplot on November 15th 2003.

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# Appendix C

# Developing Weather Related Variable Models and Trend Surface Layers

## Introduction

Chapter 4's large-extent RWA density model was developed for predicting RWA densities using weather variables. This model can be used to develop a RWA density trend surface using a Geographic Information System (GIS) framework. To do so, GIS layers need to be developed for each of the important variables from the large-extent RWA density model (i.e., degree days above zero (DD0°), degree days below zero (DD-0°), and the precipitation – degree day above zero index (PD Index)). The goal of this appendix is to develop an example of a spatially explicit RWA density map for eastern Colorado using Chapter 4's large-extent RWA density model. An important consideration is that any errors in the underlying GIS layers will compound error from the large-extent RWA density model. Twenty-four Colorado Agricultural Meteorological (CoAgMet) (See http://ccc.atmos.colostate.edu/~coagmet/ for details) stations were used to collect weather data for eastern Colorado.

## Methods

Modeling methods similar to those used for developing the Chapter 4's large-extent RWA density model were used to develop weather variable models for each of the important variables in the large-extent RWA density model. That is, weather variable models were created for the PD Index (See Chapter 4 for details), degree-days above zero (DD0°), and degree-days below zero (DD-0°). Each weather variable model was developed from the linear statistical model with the lowest AICc (Akaike's Information Criteria adjusted for small sample sizes, see Chapters 4 or 5 for information on using AICc). From the three weather variable models, trend surface layers were calculated using ArcGIS 9.1 (ESRI 1995-2007). Data for the dependent variables (DD0°, DD-0°, and the PD Index) were collected using weather data collected from December 1st 2001 through March 31st 2002 by CoAgMet stations. Specifically, temperature data, and precipitation data were extracted from 24 CoAgMet weather stations over the 2001-2002 winter season. Predictor variables used for weather variable model development were CoAgMet Station Elevation, and it's normalized Euclidean coordinates (UTM-x and UTM-y) and interaction terms (i.e., combinations of all subsets of the predictor variables). These variables were chosen because weather related variables would be expected to change with latitudinal, longitudinal and elevational changes. The UTM-x and UTM-y GIS layers were generated using the $$xmap and $$ymap functions in ArcGIS 9.1 Raster Calculator (ESRI 1995-2007). A 30-meter grid, USGS Digital Elevation Map of Colorado was used as the elevation GIS layer. Data were extracted from predictor variable layers in association with each CoAgMet weather station. GIS layers were transformed from 30-meter grid surfaces to 100-meter grid surfaces to reduce the necessary computational load.

## Results

### *DD0 ° Trend Surface Development*

The normalized Euclidian coordinates (i.e. UTM-x and UTM-y) were found to be the best linear predictors of DD0°. UTM-x and UTM-y variables were parameterized using standard linear regressions (Proc GLM, SAS 2002-2003):

$$DD0° = 0.0864 * UTM\_x - 0.372 * UTM\_y + 0.307$$

Figure C.1 depicts a trend surface (i.e., the graphical representation of the statistical linear regression model) modeling DD0° in eastern Colorado, created using the Raster Calculator function in ArcGIS 9.1 (ESRI 1995-2007).

### *DD-0 ° Trend Surface Development*

The Elevation and UTM-y (i.e., north – south coordinates) were found to be the best linear predictors of DD-0°. Elevation and UTM-y variables were parameterized using standard linear regressions (Proc GLM, SAS 2002-2003):

$$DD\text{-}0° = 0.423 * Elevation + 1.118 * UTM\_y + 0.310$$

Figure C.2 depicts the trend surface modeling DD-0° in eastern Colorado, created using the Raster Calculator function in ArcGIS 9.1 (ESRI 1995-2007).

### *PD Index Trend Surface Development*

UTM-y (i.e., north – south coordinates) was found to be the best linear predictor of the PD Index. The UTM-y variable was parameterized using standard linear regressions (Proc GLM, SAS 2002-2003):

$$\text{PD Index} = -0.119 * \text{UTM\_y} + 0.207$$

Figure C.3 depicts the trend surface modeling PD Index in eastern Colorado, created using the Raster Calculator function in ArcGIS 9.1 (ESRI 1995-2007).

### *Using Weather Related Trend Surfaces with Chapter 4's Large-Extent RWA Density Model*

Chapter 4's large-extent RWA density model is given by the following function:

$$\ln(\text{RWA Density} + 0.1) = -0.595 + 0.241 * (\text{PD Index}) + 4.315 * (\text{DD}0°) + 0.344 * (\text{DD-}0°) + (-5.837) * (\text{DD}0°) * (\text{DD-}0°)$$

Using the trend surfaces that were created for each of the weather related variables (i.e., PD Index, DD0°, DD-0°, and the DD0°*DD-0° interaction term), a large-extent RWA density map was created. That is, the trend surfaces became the predictor variables for the large-extent RWA density model. The large-extent RWA density surface was calculated using the Raster Calculator function in ArcGIS 9.1 (ESRI 1995-2007). The resulting surface is the RWA density surface for March 1st 2002 based on weather data from December 1st 2001 to March 1st 2002. This surface is depicted in Figure C.4.

Figure C.1: DD0° trend surface model of eastern Colorado based on data collected from December 1st 2001 through March 31st 2002 from CoAgMet weather stations (Green Squares). Southeastern areas of the state (red) have the highest number of DD0°, while the northwest portion of the Colorado plains (near Fort Collins) have the lowest DD0° (blue).

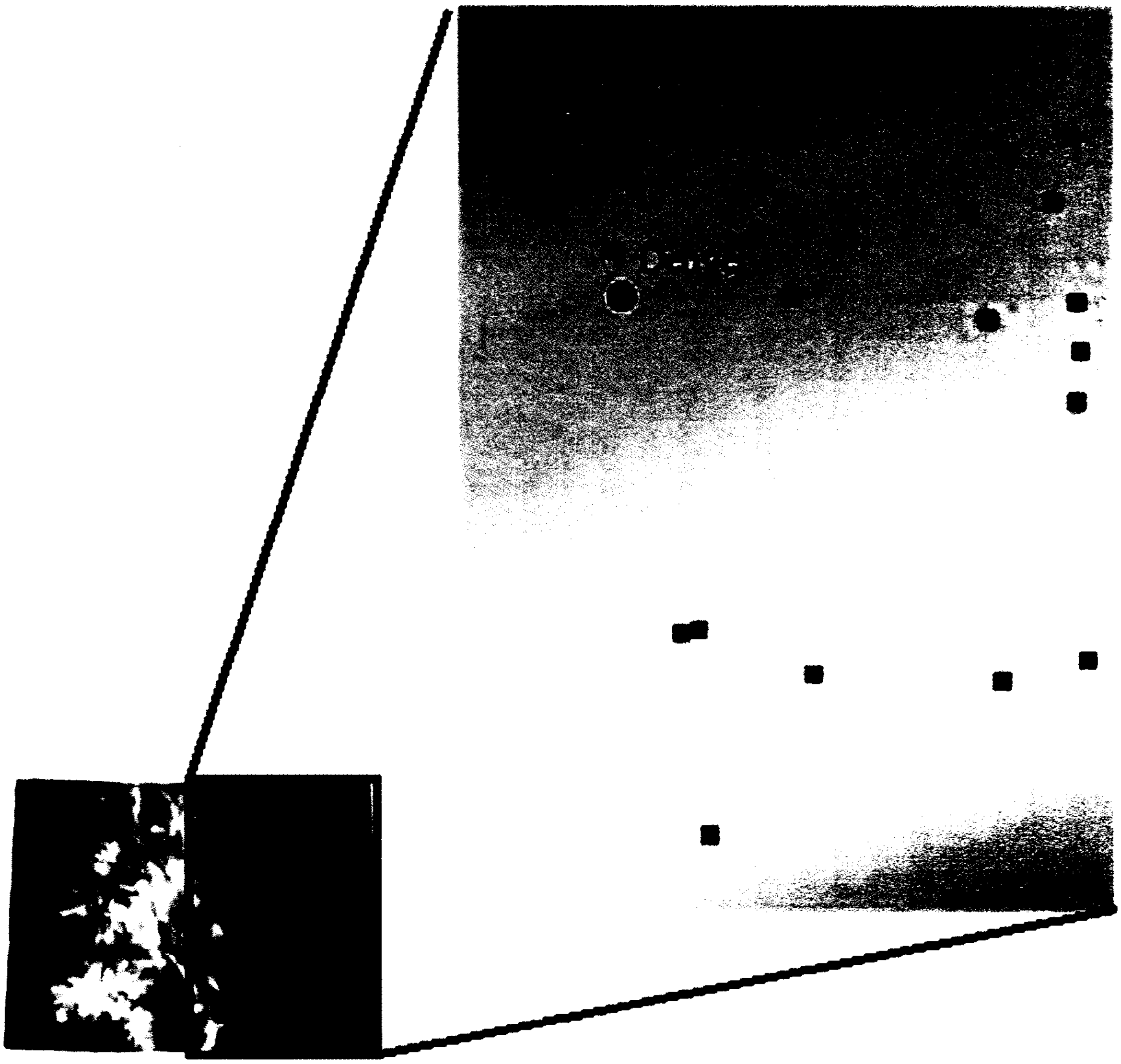


Figure C.2: DD-0°C trend surface model of eastern Colorado based on data collected from December 1st 2001 through March 31st 2002 from CoAgMet weather stations (Green squares). Areas in blue have more DD-0° (i.e., colder for longer) than areas in red.

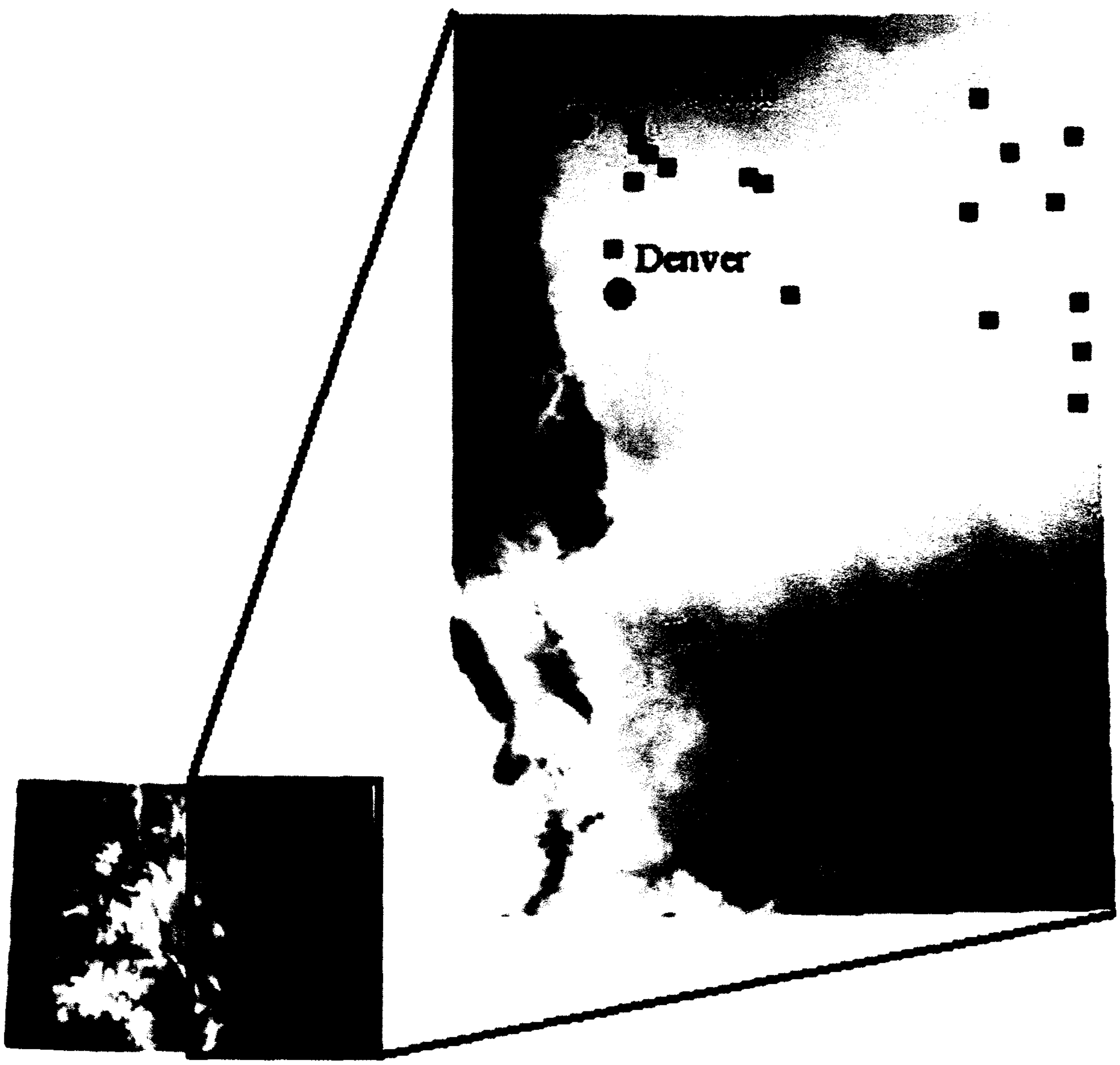


Figure C.3: PD Index of eastern Colorado based on data collected from December 1st 2001 through March 31st 2002 from CoAgMet weather stations (Green Squares). Highest PD Index values are in the southern area of the Colorado plains.

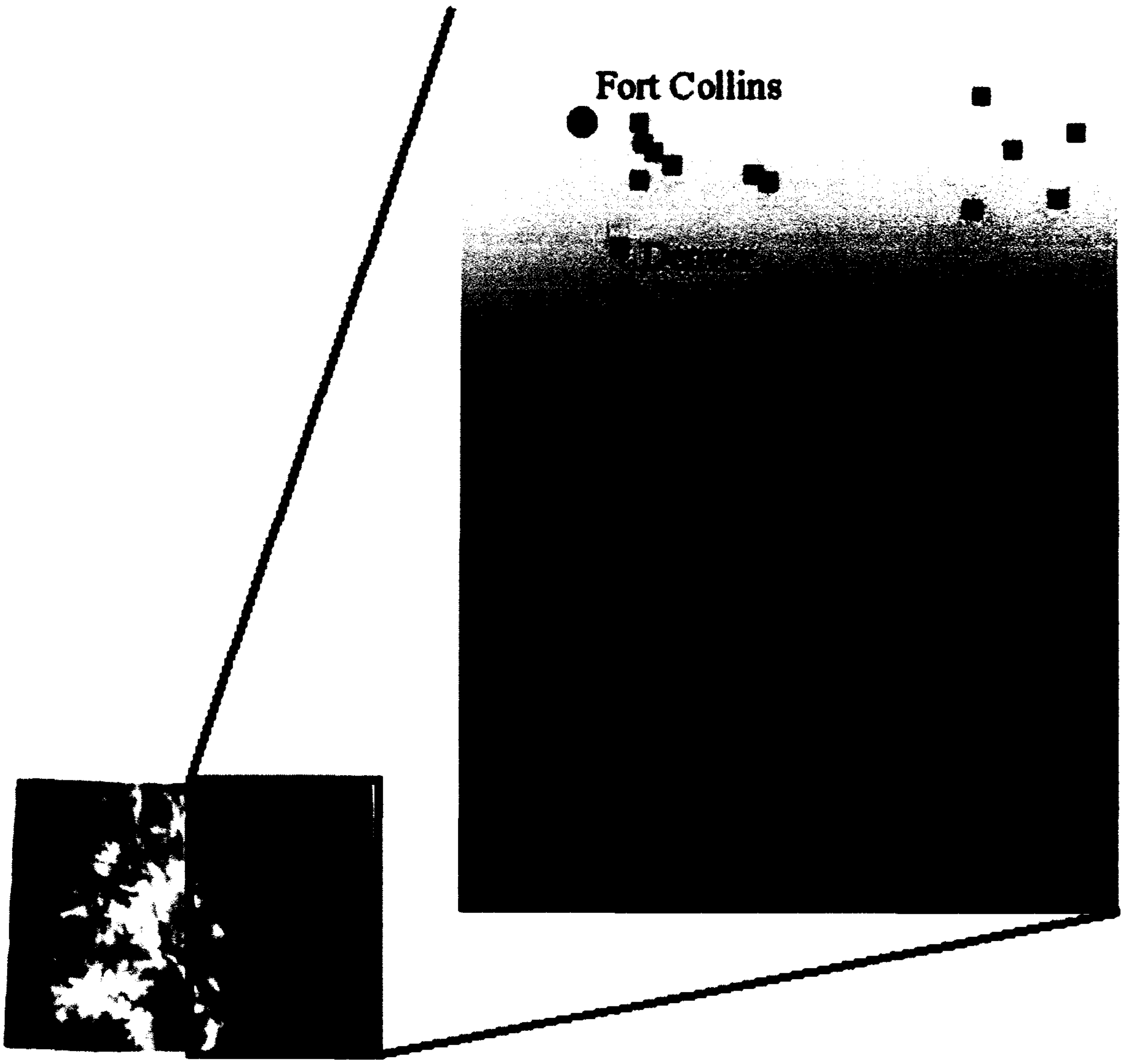
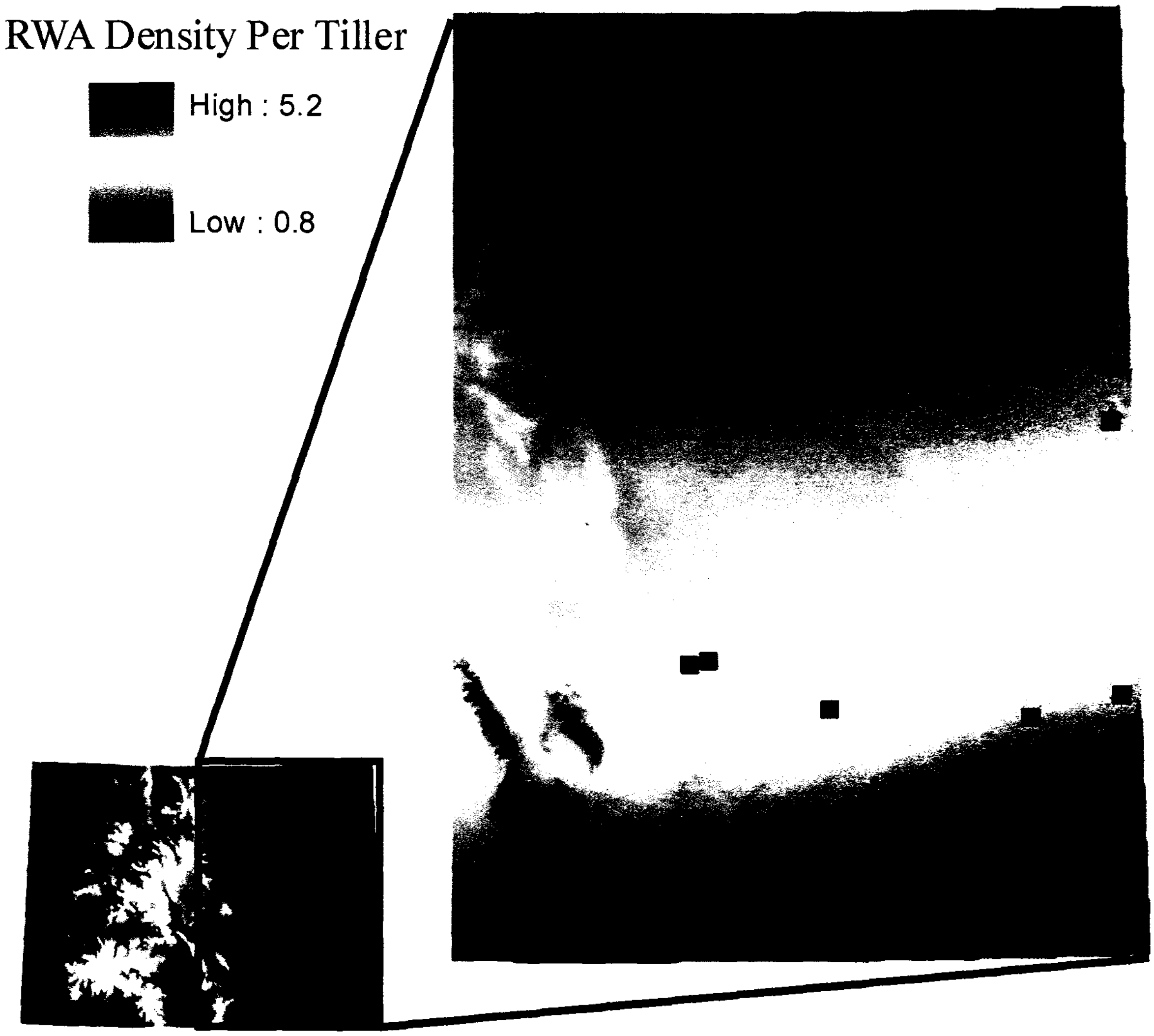


Figure C.4: Large-extent RWA density trend surface model of eastern Colorado based on modeled weather related variable trend surfaces, using weather data collected from December 1st 2001 through March 31st 2002 from CoAgMet weather stations (Green squares).



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# Appendix D

# Normalization of Variables Including Maximums and Minimums

Variables were normalized by the following formula:

Formula # 1: $(x_i - \min(x)) / (\text{Maximum}(x) - \text{Minimum}(x))$ for all data i = 1 to n

The following variables were normalized across both sites:

Aspect (Maximum: 359.748, Minimum: 0.418)

North-South Aspect (Maximum: 179.748, Minimum: 0.418)

Slope (Maximum: 6.253, Minimum: 0.149)

Landshape (Maximum: 2.081, Minimum: –2.408)

Relative Elevation (Maximum: 38.41, Minimum: -28.35) was calculated by the elevation distance from the mean elevation at each site. Relative elevation was then normalized across both sites. The Last Chance field site's mean elevation was 1487.12 meters, and the Lamar field sites mean elevation was 1176.8 meters.

Soil variables were categorical (i.e., binary or presence-absence) and therefore held either a zero or a one value.

Landsat 7 ETM+ Imagery was normalized by image to allow for analysis of within image differences. For example, thermal emissivity can change from day to day, or image to image. Normalization within image allows for detection of differences within image instead of between images. Maximum and minimum values used for normalization of Landsat imagery are in Table D.1.

Table D.1: Maximum and Minimum values for Landsat imagery.

| Lamar 2002 | Band 1 (W) | Band 2 (W) | Band 3 (W) | Band 4 (W) | NDVI (W) |
|---|---|---|---|---|---|
| Maximum | 71 | 65 | 79 | 79 | 0.106 |
| Minimum | 61 | 53 | 62 | 57 | -0.080 |
| | **Band 5 (W)** | **Band 6.1 (W)** | **Band 6.2 (W)** | **Band 7 (W)** | **Band 8 (W)** |
| Maximum | 103 | 107 | 106 | 85 | 51 |
| Minimum | 78 | 103 | 98 | 60 | 38 |
| | **Band 1 (S)** | **Band 2 (S)** | **Band 3 (S)** | **Band 4 (S)** | **NDVI (S)** |
| Maximum | 107 | 102 | 130 | 118 | 0.000 |
| Minimum | 94 | 87 | 107 | 91 | -0.102 |
| | **Band 5 (S)** | **Band 6.1 (S)** | **Band 6.2 (S)** | **Band 7 (S)** | **Band 8 (S)** |
| Maximum | 172 | 132 | 151 | 155 | 80 |
| Minimum | 136 | 125 | 137 | 105 | 62 |
| **Last Chance 2002** | **Band 1 (W)** | **Band 2 (W)** | **Band 3 (W)** | **Band 4 (W)** | **NDVI (W)** |
| Maximum | 70 | 63 | 82 | 85 | 0.339 |
| Minimum | 52 | 41 | 42 | 45 | -0.096 |
| | **Band 5 (W)** | **Band 6.1 (W)** | **Band 6.2 (W)** | **Band 7 (W)** | **Band 8 (W)** |
| Maximum | 84 | 115 | 121 | 63 | 53 |
| Minimum | 52 | 93 | 80 | 37 | 28 |
| | **Band 1 (S)** | **Band 2 (S)** | **Band 3 (S)** | **Band 4 (S)** | **NDVI (S)** |
| Maximum | 159 | 164 | 226 | 189 | 0.015 |
| Minimum | 106 | 99 | 119 | 102 | -0.993 |
| | **Band 5 (S)** | **Band 6.1 (S)** | **Band 6.2 (S)** | **Band 7 (S)** | **Band 8 (S)** |
| Maximum | 235 | 171 | 224 | 218 | 131 |
| Minimum | 146 | 158 | 199 | 120 | 75 |
| **Lamar 2003** | **Band 1 (W)** | **Band 2 (W)** | **Band 3 (W)** | **Band 4 (W)** | **NDVI (W)** |
| Maximum | 70 | 62 | 77 | 86 | 0.246 |
| Minimum | 56 | 46 | 49 | 54 | -0.062 |

| Lamar 2003 (cont.) | Band 5 (W) | Band 6.1 (W) | Band 6.2 (W) | Band 7 (W) | Band 8 (W) |
|---|---|---|---|---|---|
| Maximum | 90 | 101 | 95 | 76 | 49 |
| Minimum | 65 | 98 | 90 | 40 | 35 |
| | **Band 1 (S)** | **Band 2 (S)** | **Band 3 (S)** | **Band 4 (S)** | **NDVI (S)** |
| Maximum | 141 | 147 | 190 | 107 | 0.151 |
| Minimum | 84 | 76 | 76 | 86 | -0.279 |
| | **Band 5 (S)** | **Band 6.1 (S)** | **Band 6.2 (S)** | **Band 7 (S)** | **Band 8 (S)** |
| Maximum | 221 | 139 | 165 | 205 | 112 |
| Minimum | 123 | 135 | 157 | 86 | 74 |
| **Last Chance 2003** | **Band 1 (W)** | **Band 2 (W)** | **Band 3 (W)** | **Band 4 (W)** | **NDVI (W)** |
| Maximum | 64 | 58 | 73 | 64 | -0.029 |
| Minimum | 54 | 45 | 52 | 42 | -0.118 |
| | **Band 5 (W)** | **Band 6.1 (W)** | **Band 6.2 (W)** | **Band 7 (W)** | **Band 8 (W)** |
| Maximum | 90 | 119 | 128 | 75 | 43 |
| Minimum | 62 | 110 | 113 | 54 | 29 |
| | **Band 1 (S)** | **Band 2 (S)** | **Band 3 (S)** | **Band 4 (S)** | **NDVI (S)** |
| Maximum | 126 | 133 | 167 | 93 | -0.207 |
| Minimum | 97 | 89 | 105 | 67 | -0.321 |
| | **Band 5 (S)** | **Band 6.1 (S)** | **Band 6.2 (S)** | **Band 7 (S)** | **Band 8 (S)** |
| Maximum | 194 | 166 | 213 | 173 | 105 |
| Minimum | 144 | 151 | 184 | 115 | 67 |
| **Lamar 2004** | **Band 1 (W)** | **Band 2 (W)** | **Band 3 (W)** | **Band 4 (W)** | **NDVI (W)** |
| Maximum | 72 | 64 | 78 | 87 | 0.200 |
| Minimum | 60 | 52 | 53 | 52 | -0.071 |
| | **Band 5 (W)** | **Band 6.1 (W)** | **Band 6.2 (W)** | **Band 7 (W)** | **Band 8 (W)** |
| Maximum | 101 | 109 | 108 | 85 | 53 |
| Minimum | 82 | 102 | 97 | 56 | 38 |

| Lamar 2004 (cont.) | Band 1 (S) | Band 2 (S) | Band 3 (S) | Band 4 (S) | NDVI (S) |
|---|---|---|---|---|---|
| Maximum | 111 | 106 | 135 | 87 | -0.140 |
| Minimum | 82 | 71 | 88 | 56 | -0.301 |
| | **Band 5 (S)** | **Band 6.1 (S)** | **Band 6.2 (S)** | **Band 7 (S)** | **Band 8 (S)** |
| Maximum | 165 | 148 | 179 | 142 | 85 |
| Minimum | 130 | 126 | 169 | 96 | 54 |

| Last Chance 2004 | Band 1 (W) | Band 2 (W) | Band 3 (W) | Band 4 (W) | NDVI (W) |
|---|---|---|---|---|---|
| Maximum | 76 | 71 | 93 | 89 | 0.119 |
| Minimum | 59 | 49 | 58 | 57 | -0.113 |
| | **Band 5 (W)** | **Band 6.1 (W)** | **Band 6.2 (W)** | **Band 7 (W)** | **Band 8 (W)** |
| Maximum | 98 | 128 | 144 | 81 | 57 |
| Minimum | 68 | 86 | 70 | 45 | 36 |
| | **Band 1 (S)** | **Band 2 (S)** | **Band 3 (S)** | **Band 4 (S)** | **NDVI (S)** |
| Maximum | 107 | 111 | 146 | 102 | 0.085 |
| Minimum | 84 | 76 | 86 | 49 | -0.347 |
| | **Band 5 (S)** | **Band 6.1 (S)** | **Band 6.2 (S)** | **Band 7 (S)** | **Band 8 (S)** |
| Maximum | 165 | 154 | 191 | 146 | 82 |
| Minimum | 114 | 136 | 158 | 70 | 66 |