

**Local and regional approaches to studying the phenology
and biological control of the soybean aphid**

by

Nicholas Patrick Schmidt

A dissertation submitted to the graduate faculty

in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Entomology

Program of Study Committee:

Matthew E. O'Neal, Major Professor

Paul F. Anderson

Marlin E. Rice

Thomas W. Sappington

Lisa A. Schulte

Iowa State University

Ames, Iowa

2010

Copyright © Nicholas Patrick Schmidt, 2010. All right reserved.

Table of Contents

Abstract	iv
Chapter 1. General introduction and literature review	
Dissertation Organization	1
Introduction and Literature Review	1
<i>Aphis glycines</i> biology and ecology	2
<i>Rhamnus cathartica</i> biology and ecology	5
Aphidophagous natural enemies	5
Current state of agroecosystems	7
Objectives and Hypotheses	8
References Cited	10
Chapter 2. Effects of grassland habitat and plant nutrients on soybean aphid and natural enemy populations	16
Abstract	16
Introduction	17
Materials and Methods	19
Results	24
Discussion	26
Acknowledgments	30
References Cited	31
Tables	37
Figure Legends	43
Figures	44
Chapter 3. How does proximity to prairie affect the abundance of soybean aphids and aphidophagous natural enemies in soybean?	52
Abstract	52
Introduction	53
Materials and Methods	54
Results	58
Discussion	61
Acknowledgments	65
References Cited	66
Tables	70
Figure Legends	77
Figures	78
Chapter 4. Spatial distributions of soybean aphids: A summary of the suction trap network	89
Abstract	89
Introduction	90
Materials and Methods	92
Results	96

Discussion	98
Acknowledgments	101
References Cited	102
Tables	105
Figure Legends	113
Figures	114
Chapter 5. Predicting overwintering sites of <i>Aphis glycines</i> and <i>Harmonia axyridis</i> based on supercooling temperatures	126
Abstract	126
Introduction	127
Materials and Methods	129
Results and Discussion	130
Acknowledgments	133
References Cited	134
Tables	138
Figure Legends	141
Figures	142
Chapter 6. General Conclusions	149
Recommendations	151
References Cited	153
Acknowledgments	154

Abstract

Soybean aphids *Aphis glycines* Matsumura (Hemiptera: Aphididae) are an economic pest of soybean *Glycine max* (L.) Merr. in much of the United States and parts of Canada. Some crucial phenological information of *A. glycines* is unknown, specifically source-sink dynamics between and within host plants and factors guiding aphid migrations. In addition, there are discrepancies in the literature on the importance of food webs and how local landscape effects can alter *A. glycines* populations. Increasing our understanding of *A. glycines* population dynamics may improve predictions of aphid outbreaks and integrated pest management efforts. The first objective was to determine how landscape composition and heterogeneity impact *A. glycines* and their natural predator community. This study was centered in and around the Neal Smith National Wildlife Refuge located in Jasper County, Iowa. A second objective was to determine how prairie plantings adjacent to soybean impact *A. glycines* and natural enemy populations. To accomplish this, four study sites in central Iowa, transects were established up to 200 m in both soybean and prairie. A third objective was to describe *A. glycines* movement patterns on a regional scale. We monitored winged aphids (alates) using a suction trap network established at 42 locations over 10 states. Alates were correlated with northern latitudes which led to the last objective which was to predict *A. glycines* using low temperature data from the Midwest US and determine whether temperatures have reached *A. glycines* supercooling point (-34°C).

Chapter 1

General Introduction and Literature Review

Dissertation Organization

The scope of this research encompasses field, landscape, and regional studies, and is organized into six chapters. Chapter one contains a general introduction, which includes research objectives, and a literature review of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), *A. glycines* movement, *A. glycines* supercooling, *A. glycines* overwintering host common buckthorn, *Rhamnus cathartica* L. (Rhamnaceae), and conservation of aphidophagous natural enemies. Chapter two determines how landscape metrics and plant nutrients impact *A. glycines* and natural enemy populations. Chapter three determines how an adjacent remnant or reconstructed prairie impact aphidophagous natural enemies and *A. glycines*. Chapter four summarizes *A. glycines* migrations from data collected by the suction trap network. Chapter five determines if *A. glycines* supercooling point can predict first alate capture in the suction trap network. Chapter six provides a list of general conclusions from this research, followed by acknowledgments.

Introduction and Literature Review

Due to *A. glycines* recent introduction to the United States, a limited amount of phenological information is known. For example, the mechanism(s) guiding *A. glycines* and aphidophagous natural enemy population dynamics are limited, and a better understanding may improve management efforts and prediction of outbreaks. In an attempt to increase our understanding and predictive ability, *A. glycines* were sampled at multiple scales in soybean and a regional suction trap network in various habitats, whereas aphidophagous natural enemies were sampled in soybean and remnant and reconstructed prairies.

***Aphis glycines* biology and ecology**

Prior to the arrival of the soybean aphid, *Aphis glycines*, in North America, soybean *Glycine max* (L.) Merr. had escaped insect pests and diseases associated with its native country Asia, as a result, soybean producers in the United States had a limited need for pest management interventions (Fernandez-Cornejo and Jans 1999). First discovered in the US in July of 2000 in Wisconsin, *A. glycines* has been found in 22 US states and parts of Canada (Venette and Ragsdale 2004). Herbivory from *A. glycines* has resulted in soybean yield reductions exceeding 40% (Ragsdale et al. 2007), and it has been estimated that producers will save between \$949 million and \$1.623 billion by controlling *A. glycines* over the next 10 years (Kim et al. 2008).

Life cycle. *Aphis glycines* has a heteroecious holocyclic (alternates hosts and reproduces sexually during parts of its life cycle) life cycle where eggs hatch on buckthorn, *Rhamnus* spp. in spring after bud break, giving rise to wingless fundatrices and reproduce asexually up to four generations (Ragsdale et al. 2004). Dependent on spring conditions, generation three and/or four produces alates (winged aphids) and emigrate in search of their secondary host, soybean (Ragsdale et al. 2004). Under favorable conditions, *A. glycines* is capable of doubling its population in as little as 1.5 days resulting in up to 15 – 18 overlapping generations of aphids (both apterous and alate morphs) on soybean (McCornack et al. 2004). Later in the growing season, a reduction in photoperiod and temperature triggers the production of gynoparae (winged females) and later males, which migrate in search of *Rhamnus* spp., primarily common buckthorn *R. cathartica* L. (Ragsdale et al. 2004). When gynoparae locate *R. cathartica* they feed and produce nymphs that develop into oviparae; later males emigrate from soybean searching for oviparae to mate with (Ragsdale et al. 2004). Mated females lay and deposit eggs on *R. cathartica*, typically at the base of the bud where they overwinter (Ragsdale et al. 2004, Wu et al. 2004, McCornack et al. 2005, Voegtlin et al. 2005). In addition, Voegtlin et al. (2005) has identified *A. glycines* ability to survive on native *R. alnifolia* L'Hér., and *R. lanceolata* Pursh.

Integrated pest management. Current integrated pest management strategies of *A. glycines* in soybean consist of both preventative and therapeutic practices. Preventative practices are pest management approaches that aim to reduce or eliminate problems before the pest reaches economic populations, and therapeutic practices are management approaches that attempt to manage economic pest populations (Pedigo and Rice 2009). In soybean, preventative practices consist of host plant resistance and biological control. Host plant resistance is the use of a heritable plant trait(s) that reduces the damage to a plant by a pest (Pedigo and Rice 2009). Three genes *Rag1*, *Rag2* (Kim et al. 2008), and *Rag3* (Zhang et al. 2010) have been identified that exhibit some resistance to *A. glycines*. However, commercial soybean varieties are slow to release due to known biotypes, Illinois and Ohio isolates, which are resistant to one or more of the *Rag* genes (Kim et al. 2008). Biological control is the use of a biological agent to manage a pest (Pedigo and Rice 2009). A single classical biological control agent, *Binodoxys communis* (Gahan), (Hymenoptera: Braconidae), has been approved for released in the US (Rice et al. 2007). An endemic natural enemy community also exists in the Midwest US and will be discussed more in depth below. In soybean, therapeutic practices consist of insecticides and its usage is ideally based on an economic injury level (EIL) or the minimum pest density that causes economic damage, and economic threshold (ET) or pest density that triggers management intervention (Pedigo and Rice 2009). For *A. glycines*, the EIL is 674 ± 95 with an ET of 273 ± 38 aphids/plant (Ragsdale et al. 2007).

Movement. Due to an aphid's small size, studies have shown, in order to get above the surface boundary layer, air currents are needed to carry them (Loxdale and Lushai 1999, Isard and Gage 2001). Loxdale and Lushai (1999) observed small insects dispersing at random with wind direction influencing their distribution. Assisting the spread of *A. glycines* across North America is its capacity for movement aided by migration. Development of alates is prompted by various stimuli (photoperiod, temperature, over-crowding, and host plant quality; Dingle 1996); furthermore, studies have reported some aphid species capable of traveling great distances ($> 1,000$ km) from their nearest possible source (Kring 1972). Using a flight chamber Kennedy and Booth (1963) found that the black bean aphid, *Aphis*

fabae Scop. exhibited a positive phototaxis before take off with three flight phases. First, alates demonstrated a brief “erratic” phase with both vertical and horizontal movement; typically reaching the maximum rate of climb within the first minute. Second, a “cruising” flight, lasting minutes or hours, was maintained in the horizontal plane. Finally, alates terminate flight with erratic declining movements displaying negative phototaxis (Kennedy and Booth 1963). Little information is known about the elements assisting *A. glycines* migrations and the potential for movement across landscapes. Hodgson et al. (2005a) tested the relationship between alate production and photoperiod with *A. glycines*; they found in both years increased alate production was explained by decreased photoperiod. Alate colonizing patterns across Minnesota were also described, 2002 alates were first observed at R1 (initial flowering stage; Pederson 2004), whereas in 2003 alates were observed approximately two weeks prior to vegetative stages and before flowering (Hodgson et al. 2005a). Furthermore, alate production peaked in both 2002 and 2003 at R5 (beginning of seed set; Pederson 2004) (Hodgson et al. 2005a). In a similar study, Hodgson et al. (2005b) evaluated the distribution of alates in soybean field using pan traps. Results suggest direction and distance from field edge did not affect trap catches (Hodgson et al. 2005b). Using an aphid flight mill, Zhang et al. (2008) studied the flight potential of *A. glycines* reared on soybean. Alates at the age of 12 – 24 hours (0 being the day of adult molt) produced the strongest flight potential, with flight times averaging 3.3 – 4.1 h (corresponding to 4.6 – 5.1 km), and with optimum flight temperatures from 16 – 28°C and a relative humidity of 75% (Zhang et al. 2008).

Plant nutrients. Three important plant macronutrients, nitrogen (N), phosphorus (P), and potassium (K), are also thought to have an influence on herbivores. In a review, Awmack and Leather (2002) identified multiple aphid species that achieved increased growth rates and fecundity due to increased plant N. Noma et al. (2010) found *A. glycines* was positively correlated with plant N, and negatively correlated with plant K. In contrast, Myers and Gratton (2006) found *A. glycines* had reduced growth rates on K deficient plants. Jansson and Ekbom (2002), found adult aphid weight was positively correlated with P. Varied responses have occurred between studies, and one explanation may be related Jansson and

Ekbom (2002); which found ratios of nutrients to better explain aphid performance rather than a single nutrient level.

Supercooling point. Insects have the ability to survive cold temperatures by supercooling, which decreases the freezing point of bodily fluids (McCornack et al. 2005). The overwintering stage of *A. glycines* is an egg and its supercooling point (SCP), the temperature at where spontaneous freezing occurs, is -34°C (McCornack et al. 2005). Using historical temperature data from the previous 75+ years, McCornack et al. (2005) estimated the probability of nine Midwest states reaching -34°C . In general, the probabilities were over 50% in 56% of Minnesota, 20% of Wisconsin, and 6% of Michigan.

***Rhamnus cathartica* biology and ecology**

Rhamnus cathartica is native to Eurasia and was first introduced to North America in the 1800's where it was used as an ornamental shrub (Knight et al. 2007). *Rhamnus cathartica* was selected for its hardiness and ability to survive in many soil and light conditions (Knight et al. 2007). Since its introduction, *R. cathartica* has become naturalized through much of the Midwest, northeastern US, and parts of Canada (Knight et al. 2007, Kurylo et al. 2007). Its invasive attributes include high fecundity, high germination rates, bird-dispersed fruit, and the ability to survive in disturbed environments with a range of soil characteristics (Knight et al. 2007). Once established, *R. cathartica* can alter ecosystems by modifying soil characteristics, specifically increasing soil N and an increased removal of leaf litter (Knight et al. 2007).

Aphidophagous natural enemies

In Asia, *A. glycines* are held below EIL's by an array of natural enemies (Liu et al. 2004, Miao et al. 2007). In North America, Rutledge et al. (2004) found *A. glycines* was attacked by over 30 species of predators, eight species of parasitoids and several species of fungal pathogens. Donaldson et al. (2007) found the endemic natural enemy community in the US capable of eliciting a density-dependent response to an increased abundance of *A. glycines*. Specifically, *Harmonia axyridis* (Pallas), *Coccinella septempunctata* L.

(Coleoptera: Coccinellidae), and *Orius insidiosus* (Say) (Hemiptera: Anthracoridae) dominate the foliar predator community (Rutledge et al. 2004, Schmidt et al. 2007, Schmidt et al. 2008), and in their absence *A. glycines* populations have increased 3-7 fold (Fox et al. 2004, Schmidt et al. 2007, Miao et al. 2007, Gardiner et al. 2009a). Despite evidence for biological control of *A. glycines*, aphid populations have continually reached EIL for many growers across the north central US, resulting in an increased need for foliar insecticides to maintain yields (Johnson et al. 2008, Johnson et al. 2009).

Nutrients. Natural enemies can be affected by the nutrient composition from which their prey feed. Mayntz and Toft (2001) found the wolf spider, *Pardosa amentata* (Clerk) (Araneae: Lycosidae) had increased weight and survival when fed fruit flies, *Drosophila melanogaster* Meigen (Diptera: Drosophilidae), with increased amino acids and fatty acids. In cotton, *Gossypium hirsutum* L., Chen and Ruberson (2008) found herbivorous insects and predaceous spiders and *Geocoris* spp. were positively correlated with N. In apple trees, *Pyrus malus* (Rosaceae), biological control of the phytophagous mite *Panonychus ulmi* (Acari: Tetranychidae) by predaceous mites, *Typhlodromus pyri* (Acari: Phytoseiidae) and *Zetzellia mali* (Acari: Eriophyidae) was negatively correlated with low N in trees (Walde 1995).

Conservation and management. There is an increasing body of evidence indicating landscape structure is paramount for determining the abundance, community structure and effectiveness of predator and parasitoid communities in agricultural landscapes (Marino & Landis 1996, Dyer & Landis 1997, Menalled et al. 1999, Thies & Tscharntke 1999, Elliott et al. 2002, Menalled et al. 2003, Thies et al. 2003, Thies et al. 2005). Parasitism tends to be lower in simple agricultural landscapes compared to more diversified landscapes that incorporate alternate hosts, adult feeding sites and overwintering habitats (Menalled et al. 1999, Thies et al. 2005). Gardiner et al. (2009a), found more diverse landscapes composed of forest and grassland increased biological control of *A. glycines*. Furthermore, native coccinellidae were associated to low-diversity landscapes with increased grassland, whereas exotic coccinellidae were associated with increased forest (Gardiner et al. 2009b). Multiple

forms of habitat management are used to increase the abundance and diversity of insect natural enemy communities. For example, variations of conservation strips are used to enhance biological control of Hemipteran pests (Janice et al. 1996, Bowie et al. 1999, Collins et al. 2002, Weiser et al. 2003), some are as simple as enhancing field borders with a perennial flower (Janice et al. 1996), and others incorporate strips or “beetle banks” at set distances throughout the field (Bowie et al. 1999, Collins et al. 2002, Weiser et al. 2003).

Current state of agroecosystems

The development of large-scale agroecosystems in Iowa and other states comprising the Midwest US has been accompanied by a profound loss of biological diversity (Landis et al. 2008). Before Euro-Americans settled Iowa in 1833, the landscape was approximately 79.5% prairie, 11.7% forest, 6.7% savanna, and 1.4% wetland (Smith 1998). Today two crops, corn, *Zea mays* L., and soybean dominate Iowa’s landscapes comprising ~62.8% of the land area (USDA 2007), whereas the native prairie plant species corn and soybean replaced, occupy < 0.1% of this area (Smith 1998). This decrease in native biodiversity may have resulted in a reduction in the ability to moderate hydrologic flows and protect water quality, in addition to several other important ecosystem functions, including natural control of insect pests and weeds (Kreuss and Tscharntke 1994, Thies and Tscharntke 1999, Elliott et al. 2002, Menalled et al. 2003). Diversification of agroecosystems may improve natural control of pests provided by beneficial insects and other indigenous pest control agents (Menalled et al. 2003, Kremen et al. 2002, Lee et al. 2001, Landis et al. 2008). Habitat management has been found to be an effective approach for conserving natural enemies, resulting in more sustainable integrated pest management in some agroecosystems (Gurr and Wratten 1999, Landis et al. 2000, Fiedler et al. 2008).

Objectives and Hypotheses

Chapter two

- Determine the affects of landscape composition, diversity, and plant nutrients (N, P, and K) on *A. glycines* and natural enemies.
 - I hypothesize that soybean fields in landscapes with an abundance of reconstructed prairie will increase the abundance of natural enemies by providing habitat and alternative prey; a greater abundance of natural enemies would then reduce the abundance of *A. glycines*.
 - I hypothesize that both *A. glycines* and natural enemies will be more abundant on soybean plants with higher N and less abundant on plants with lower P and K.

Chapter three

- Determine if the abundance and diversity of the aphidophagous community in soybean is affected by the nearby presence of remnant and reconstructed prairie.
 - I hypothesize that the abundance of natural enemies in soybean is greater near prairie.
 - I hypothesize that the abundance of *A. glycines* is correspondingly reduced near prairie.

Chapter four

- Summarize regional suction trap data based on trap captures from 2005 – 2008, determine if there were directional trends and spatial autocorrelation between suction trap sites
 - I hypothesize that *A. glycines* alate captures will be greater in the north, presumably due to a greater abundance of *R. cathartica*, and that trap catches will not be spatially dependent on neighboring locations.

Chapter five

- Determine if temperatures in the Midwest US have reached *A. glycines* supercooling point (-34°C).
- Determine if low temperatures can predict first alate capture of *A. glycines* from the suction trap network.
- I hypothesize the supercooling point will be reached in northern regions of the study area but will occur minimally in much of the central and southern regions.
- I hypothesize low temperatures will predict first alate capture of *A. glycines* from the suction trap network.

References Cited

- Awmack, C. S., and S. R. Leather. 2002.** Host plant quality and fecundity in herbivorous insects. *Annu. Rev. Entomol.* 47: 817-844.
- Bowie, M. H., G. M. Gurr, Z. Hossain, L. R. Baggen, and C. M. Frampton. 1999.** Effects of distance from field edge on aphidophagous insects in a wheat crop and observations on trap design and placement. *Int. J. Pest Manage.* 45: 69-73.
- Chen, Y., and J. R. Ruberson. 2008.** Impact of variable nitrogen fertilization on arthropods in cotton in Georgia, USA. *Agric. Ecosyst. Environ.* 126: 281-288.
- Collins, K. L., N. D. Boatman, A. Wilcox, J. M. Holland, and K. Chaney. 2002.** Influence of beetle banks on cereal, aphid predation in winter wheat. *Agric. Ecosyst. Environ.* 93: 337-350.
- Donaldson, J. R., S. W. Myers, and C. Gratton. 2007.** Density-dependent responses of soybean aphid (*Aphis glycines* Matsumura) populations to generalist predators in mid to late season soybean fields. *Biol. Control* 43: 111-118.
- Dyer, L. E., and D. A. Landis. 1997.** Influence of noncrop habitats on the distribution of *Eriborus terebrans* (Hymenoptera: Ichneumonidae) in cornfields. *Environ. Entomol.* 26: 924-932.
- Elliott, N. C., R. W. Kiekefer, G. J. Michaels, and K. L. Giles. 2002.** Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. *Environ. Entomol.* 31: 253-260.
- Fernandez-Cornejo, J., and S. Jans. 1999.** Pest management in U.S. Agriculture. Resource Economics Division, Economic Research Service, U.S. Department of Agriculture. Agriculture Handbook No 717.
- Fiedler, A. K., D. A. Landis, and S. D. Wratten. 2008.** Maximizing ecosystem services from conservation biological control: The role of habitat management. *Biol. Control* 45: 254-271.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004.** Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33: 608-618.

- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. Chacon, M. Wayo, N. P. Schmidt, E. Mueller, and G. E. Heimpel. 2009a.** Landscape diversity enhances the biological control of an introduced crop pest in the north-central US. *Ecol. Applic.* 19: 143-154.
- Gardiner, M. M., D. A. Landis, C. Gratton, N. P. Schmidt, M. O'Neal, E. Mueller, J. Chacon, G. E. Heimpel, and C. D. DiFonzo. 2009b.** Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity Distrib.* 15: 554-564.
- Gurr, G. M., and S. D. Wratten. 1999.** 'Integrated biological control': a proposal for enhancing success in biological control. *Int. J. Pest Manage.* 45: 81-84.
- Hodgson, E. W., R. C. Venette, M. Abrahamson, and D. W. Ragsdale. 2005a.** Alate production of soybean aphid (Homoptera: Aphididae) in Minnesota. *Environ. Entomol.* 34: 1456-1463.
- Hodgson, E. W., R. L. Koch, and D. W. Ragsdale. 2005b.** Pan trapping for soybean aphid (Homoptera: Aphididae) in Minnesota soybean fields. *J. Entomol. Sci.* 40: 409-419.
- Isard, S. A., and S. H. Gage. 2001.** Flow of life in the atmosphere: An airscape approach to understanding invasive organisms. Michigan State University Press, East Lansing.
- Janice, M. H., and S. D. W. 1996.** Use of *Phacelia tanacetifolia* strips to enhance biological control of aphids by hoverfly larvae in cereal fields. *J. Econ. Entomol.* 89: 832-840.
- Jansson, J., and B. Ekbom. 2002.** The effect of different plant nutrient regimes on the aphid *Macrosiphum euphorbiae* growing on petunia. *Entomol. Exp. Appl.* 109: 109-116.
- Johnson, K. D., M. E. O'Neal, J. D. Bradshaw, and M. E. Rice. 2008.** Is preventative, concurrent management of the soybean aphid (Hemiptera: Aphididae) and bean leaf beetle (Coleoptera: Chrysomelidae) possible? *J. Econ. Entomol.* 101: 801-809.
- Johnson, K. D., M. E. O'Neal, D. W. Ragsdale, C. D. Difonzo, S. M. Swinton, P. M. Dixon, B. D. Potter, E. W. Hodgson, and A. C. Costamagna. 2009.** Probability of cost-effective management of soybean aphid (Hemiptera: Aphididae) in North America. *J. Econ. Entomol.* 102: 2101-2108.

- Kennedy, J. S., and C. O. Booth. 1963.** Free flight of aphids in the laboratory. *J. Exp. Biol.* 40: 67-85.
- Kim, C. S. G. Schaible, L. Garret, R. Lubowski, and D. Lee. 2008.** Economic impacts of the U.S. soybean aphid infestations: A multi-regional competitive dynamic analysis. *Agri. Res. Econ. Rev.* 27: 227-242.
- Kim, K. S., C. B. Hill, G. L. Hartman, M. A. R. Mian, and B. W. Diers. 2008.** Discovery of soybean aphid biotypes. *Crop Sci.* 48: 923-928.
- Knight, K. S., J. S. Kurylo, A. G. Endres, J. R. Stewart, and P. B. Reich. 2007.** Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): A review. *Biol. Invasions* 9: 925-937.
- Kremen, C., N.M. Williams, and R.W. Thorp. 2002.** Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA.* 99: 16812-16816.
- Kreuss, A., and T. Tschardt. 1994.** Habitat fragmentation, species loss, and biological control. *Science* 264: 1581-1584.
- Kring, J. B. 1972.** Flight behaviour of aphids. *Annu. Rev. Entomol.* 17: 461-492.
- Kurylo, J. S., K. S. Knight, J. R. Stewart, and A. G. Endress. 2007.** *Rhamnus cathartica*: Native and naturalized distribution and habitat preferences. *J. Torrey Bot. Soc.* 134: 420-430.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000.** Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175-201.
- Landis, D. A., M. M. Gardiner, W. Van Der Werf, and S. M. Swinton. 2008.** Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proc. Nat. Acad. Sci. USA.* 105: 20552-20557.
- Lee, J. C., F. D. Menalled, and D. A. Landis. 2001.** Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *J. Appl. Ecol.* 38: 472-483.
- Liu, J., K. M. Wu, K. R. Hopper, and K. J. Zhao. 2004.** Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. *Ann. Entomol. Soc. Am.* 97: 235-239.
- Loxdale, H. D., and G. Lushai. 1999.** Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Phil. Trans. R. Soc.*

Lond. 354: 1479-1495.

- Marino, P. C., and D. A. Landis. 1996.** Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecol. Appl.* 6: 276-284.
- Mayntz, D., and S. Toft. 2001.** Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* 127: 207-213.
- McCornack, B. P., D. W. Ragsdale, and R. C. Venette. 2004.** Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. *J. Econ. Entomol.* 97: 854-861.
- McCornack, B. P., M. A. Carrillo, R. C. Venette, and D. W. Ragsdale. 2005.** Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). *Environ. Entomol.* 34: 235-240.
- Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999.** Does agricultural landscape structure affect parasitism and parasitoid diversity? *Ecol. Appl.* 9: 634-641.
- Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. 2003.** Temporal variation in the response of parasitoids to agricultural landscape structure. *Agric. Ecosys. Environ.* 96: 29-35.
- Miao, J., K. Wu, K. R. Hopper, and G. Li. 2007.** Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and impact of natural enemies in northern China. *Environ. Entomol.* 36: 840-848.
- Myers, S. W., and C. Gratton. 2006.** Influence of potassium fertility on soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), population dynamics at a field and regional scale. *Environ. Entomol.* 35: 219-227.
- Noma, T., C. Gratton, M. Colunga-Garcia, M. J. Brewer, E. E. Mueller, K. G. Wyckhuys, G. E. Heimpel, and M. E. O'Neal. 2010.** Relationship of soybean aphid (Hemiptera: Aphididae) to soybean plant nutrients, landscape structure, and natural enemies. *Environ. Entomol.* 39: 31-41.
- Pederson, P. 2004.** Soybean growth and development. Iowa State University Extension.
- Pedigo, L. P., and M. E. Rice. 2009.** Entomology and pest management, 6th edition. Pearson Prentice Hall, Upper Saddle River, NJ and Columbus, OH.

- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004.** Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97: 204-208.
- Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter, I. V. Macrae, E. W. Hodgson, M. E. O'Neal, K. D. Johnson, R. J. O'Neil, C. D. Difonzo, T. E. Hunt, P. A. Glogoza, and E. M. Cullen. 2007.** Economic threshold for soybean aphid (Hemiptera: Aphididae). *J. Econ. Entomol.* 100: 1258-1267.
- Rice, M. E., M. E. O'Neal, and P. Pederson. 2007.** Soybean aphids in Iowa-2007. Iowa State University Extension. SP 247.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004.** Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240-248.
- Schmidt, N. P., M. E. O'Neal, and J. W. Singer. 2007.** Alfalfa living mulch advances biological control of soybean aphid. *Environ. Entomol.* 36: 416-424.
- Schmidt, N.P., M. E. O'Neal, and P. M. Dixon. 2008.** Aphidophagous predators in Iowa soybean: A community comparison across multiple years and sampling methods. *Ann. Entomol. Soc. Am.* 101: 341-350.
- Smith, D. D. 1998.** Iowa prairie: Original extent and loss, preservation and recovery attempts. *J. Iowa Acad. Sci.* 105: 94-108.
- Thies, C. I., and T. Tscharntke. 1999.** Landscape structure and biological control in agroecosystems. *Science* 285: 893-895.
- Thies, C. I. Steffan-Dewenter, and T. Tscharntke. 2003.** Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101: 18-25.
- Thies, C., I. Indra Roschewitz, and T. Tscharntke. 2005.** The landscape context of cereal aphid-parasitoid interactions. *Proc. R. Soc. B.* 272: 203-210.
- United States Department of Agriculture (USDA). 2007.** National Agricultural Research Service. 2007 census of agriculture report, Vol. 1, U.S. summary and state reports (Table 26). Washington, D.C.
- Venette, R. C., and D. W. Ragsdale. 2004.** Assessing the invasion by soybean aphid (Homoptera: Aphididae): Where will it end? *Ann. Entomol. Soc. Am.* 97: 219-226.
- Voegtlin, D. J., R. J. O'Neil, W. R. Graves, D. Lagos, and H. J. S. Yoo. 2005.** Potential winter hosts of soybean aphid. *Ann. Entomol. Soc. Am.* 98: 690-693.

- Walde, S. J. 1995.** How quality of host plant affects a predator-prey interaction in biological control. *Ecol.* 76: 1206-1219.
- Weiser, L. A., J. J. Obrycki, and K. L. Giles. 2003.** Within-field manipulation of potato leafhopper (Homoptera: Cicadellidae) and insect predator populations using an uncut alfalfa strip. *J. Econ. Entomol.* 96: 1184-1192.
- Wu, Z. S., D. Schenk-Hamlin, W. Y. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004.** The soybean aphid in China: A historical review. *Ann. Entomol. Soc. Am.* 97: 209-218.
- Zhang, G., C. Gu, and D. Wang. 2010.** A novel locus for soybean aphid resistance. *Theor. Appl. Genet.* 120: 1183-1191.
- Zhang, Y., L. Wang, K. Wu, K. A. Wyckhuys, and G. E. Heimpel. 2008.** Flight performance of the soybean aphid, *Aphis glycines* (Hemiptera: Aphididae) under different temperature and humidity regimens. *Environ. Entomol.* 37: 301-306.

Chapter 2

Effects of grassland habitat and plant nutrients on soybean aphid and natural enemy populations

A paper to be submitted to *Environmental Entomology*

Nicholas P. Schmidt, Matthew E. O'Neal, and Lisa A. Schulte¹

Department of Entomology, ¹Natural Resource Ecology and Management,
Iowa State University,
Ames, IA 50011-3140

Abstract

The soybean aphid *Aphis glycines* Matsumura (Hemiptera: Aphididae) is an invasive and economic pest of soybean *Glycine max* (L.) Merr., in the United States. Research has shown the endemic natural enemy community in the US is capable of suppressing *A. glycines* below economic injury levels. However, biological control is inconsistent, especially in simple agricultural landscapes. In the course of a three-year project (2006 – 2008) from June – August, we sought to determine the affects of landscape composition, configuration, and plant macronutrients (N, P, and K) on *A. glycines* and aphidophagous natural enemy abundance; we specifically aimed to test the role nearby grassland habitat may play in the suppression of *A. glycines* through biological control. The study site was located around the Neal Smith National Wildlife Refuge (NSNWR), which has > 2,000 ha of reconstructed tallgrass prairie, located in the southwest corner of Jasper County, Iowa. We sampled *A. glycines*, natural enemies, and plant nutrients in 100 soybean fields while characterizing the landscape surrounding each field. The abundance of *A. glycines* was lowest in 2006, whereas aphids reached economically damaging populations in 2007 and 2008. The response of natural enemies to increased *A. glycines* abundance decreased in each year of our study (2006 > 2007 > 2008). Variation in *A. glycines* and their natural enemies was best explained by year and to a lesser extent, by plant nutrient levels (N, P, and K). *Aphis glycines* had a significant positive relationship with plant nutrients (N and P), but no significant effect was observed with landscape parameters. The response of natural enemies varied with taxon, with many significant positive and negative relationships with the abundance of alfalfa, corn,

soybean, N, and P. Results suggest a reduction in natural enemy abundance may be producing larger immigration events of *A. glycines* and outbreaks in Iowa.

KEYWORDS: Biological control, tritrophic interaction, ecosystem service

Introduction

Soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is an invasive economic pest of soybean, *Glycine max* (L.) Merr., in the United States. Before *A. glycines* arrived in 2000, soybean in the north central region of the US had escaped many of the pests and diseases with which it was associated in Asia (Kogan and Turnipseed 1987). In Asia, natural enemies suppress *A. glycines* below economic injury levels (Liu et al. 2004, Miao et al. 2007), and the impact of generalist natural enemies, composed of > 30 predator species and eight parasitoids, in north-central US soybean agroecosystems is important (Rutledge et al. 2004). The generalist natural enemy community, when present, can reduce *A. glycines* populations by 3-7 fold (Fox et al. 2004, Schmidt et al. 2007, Miao et al. 2007, Gardiner et al. 2009a). Despite evidence for this biological control of *A. glycines*, economic populations are encountered by many growers across the north-central US, resulting in an increased use of foliar insecticides to maintain optimal yields (Johnson et al. 2009).

The development of large-scale agricultural systems in Iowa and other states comprising the US Corn Belt has been accompanied by a profound loss of native biological diversity (Smith 1998). Before the arrival of Euro-Americans in 1833, land in Iowa was composed of approximately 79.5% prairie, 11.7% forest, 6.7% savanna, and 1.4% wetland (Smith 1998). Today two crops, Corn, *Zea mays* L., and soybean dominate Iowa's landscapes comprising ~62.8% of the land cover (USDA 2007), whereas native prairies occupy < 0.1% of this area (Smith 1998). Several perennial forbs commonly found in prairies are highly attractive to natural enemies of herbivorous pests (Fiedler and Landis 2009). This loss of native biodiversity may negatively affect ecosystem services, specifically biological control of insect pests (Kreuss and Tscharntke 1994, Thies and Tscharntke 1999, Elliott et al. 2002, Menalled et al. 2003). Habitat management can improve the delivery of ecosystem services lost by intensified agricultural practices, such as pest suppression, by conserving endemic populations of natural enemies (Gurr and Wratten 1999, Landis et al. 2000).

In general, diversification of agroecosystems may improve ecosystem services delivered by beneficial insects, including biological control of pests (Menalled et al. 2003, Kremen et al. 2002, Lee et al. 2001). An insect's ability to move in landscapes is dependent on variables such as composition and structure of surrounding agroecosystems, and can affect biological control services provided by natural enemies (Marino and Landis 1996, Elliott et al. 1999, Thies et al. 2003, and Tschardt et al. 2005). Landscape structure is a key factor in determining the abundance, community structure and effectiveness of predator and parasitoid communities in agricultural landscapes (Marino & Landis 1996, Dyer and Landis 1997, Menalled et al. 1999, Thies & Tschardt 1999, Elliott et al. 2002, Menalled et al. 2003, Thies et al. 2003, Thies et al. 2005). Parasitism in a field cropping system is reduced in simplified agricultural landscapes compared to more diversified landscapes that include potential alternate hosts, adult feeding sites and overwintering habitats (Menalled et al. 1999, Thies et al. 2005).

Adding to spatial variability in a landscape are abiotic factors such as plant macronutrients (N, P, and K) that can influence the growth rates of herbivorous pests. Myers and Gratton (2006) observed an increase in *A. glycines* population growth rates on K deficient plants grown on K deficient soils. Walter and DiFonzo (2007) suggested that the nutritional quality of soybeans for *A. glycines* is improved when the plant is K-deficient. Noma et al. (2010) observed that *A. glycines* abundance had a significant positive correlation with concentration of N in leaves, and a significant negative correlation with the concentration of leaf K. Moving up a trophic level, natural enemies can also be affected by the nutrient composition of the plants on which their prey or hosts feed (Mayntz and Toft 2001, Walker et al. 2008). Mayntz and Toft (2001) observed increased growth rates and survivorship of wolf spiders *Pardosa amentata* (Cl.) when fed more nutritious food items, and Walker et al. (2008) observed greater parasitism of the tephritid fly *Xyphosia miliaria* (Schrank) on fertilized thistles.

Previous studies have observed an affect of landscape composition and diversity on *A. glycines* abundance (Gardiner et al. 2009a, Noma et al. 2010) and natural enemy diversity and abundance (Gardiner et al. 2009b, Noma et al. 2010). These studies suggest that the biological control of *A. glycines* is positively influenced by non-crop habitat surrounding

soybean fields. Based on these findings and the lack of non-crop habitat in Iowa, our goal was to determine the effect of landscape composition, configuration, and plant nutrients on *A. glycines* and natural enemy abundance. We hypothesized that soybean fields in landscapes with an abundance of grassland habitat would harbor an increased abundance of natural enemies by providing habitat and alternative prey. In turn, we expected that a greater abundance of natural enemies would reduce the abundance of *A. glycines*. Since prairie was once the dominant land cover in Iowa (Smith 1998), we anticipated the response of natural enemies to be more evident than results from Gardiner et al. (2009b) and Noma et al. (2010). To account for possible nutritional effects on *A. glycines* and natural enemy abundance, we also measured plant macronutrients (N, P, and K). We hypothesized that *A. glycines* and natural enemies will be more abundant on soybean plants with higher N and less abundant on plants with lower P and K.

Materials and Methods

Experimental Design. Over the course of this three-year study, 100 conventionally managed soybean fields (30, 36, and 34 in 2006, 2007, and 2008 respectively) were monitored around the Neal Smith National Wildlife Refuge (NSNWR; Figure 1). NSNWR consists of > 2,000 ha of reconstructed tallgrass prairie planted with more than 200 species of forbs and grasses. The land around NSNWR is dominated by corn – soybean crop rotations with patchy fragments of deciduous forests, pasture, and alfalfa. All soybean fields used in this study were planted in 38 cm rows, followed a corn rotation, and were managed with minimum or no-tillage. An herbicide (typically glyphosate) was applied to soybean about one month after planting to control weeds.

In each year, fields were initially selected based on our ability to gain access. The final selection criteria were: distance from NSNWR (grassland), field size, and distance from nearest selected field. Field size ranged from 4 – 70 ha, and averaged 20.7, 17.3, and 17.6 ha in 2006, 2007, and 2008 respectively. A distance of approximately 1.0 km was used to select fields (mean distance between two field's centers was ~2.5 km). Because fields were rotated, there was no overlap between fields in consecutive years; however, three fields were used in both 2006 and 2008. Within each field, four sample locations were randomly selected using a

geographic information system, with a minimum distance between two sample locations set to 20 m, and a minimum distance from field edge set to 10 m and stored in global position systems (GPS) for field use (ESRI 2007).

Soybean Aphid and Natural Enemy Sampling. The dependent (response) variables for this study include the abundance of *A. glycines* and natural enemies. All soybean fields were sampled once per week for *A. glycines* and natural enemies. To focus our sampling effort on natural enemies that were aphidophagous and most likely to respond to *A. glycines*, field-counts, sweep-nets, and yellow-sticky cards were used (Schmidt et al. 2008). *Aphis glycines* and natural enemy abundance was determined by counting all aphids and natural enemies (adult and immature) on 20 consecutive plants at four locations per field using (*in situ*) field-counts from June – August. The abundance of *A. glycines* was averaged across field by date and summarized by calculating cumulative aphid days (CAD; are like degree days and are a measure of the seasonal exposure of plants to *A. glycines*; Hanafi et al. 1989). Natural enemies were collected using 20 continuous pendulum sweeps from a single location in each field, and one unbaited yellow-sticky card, 27 by 45 cm folded in half so it was sticky on both sides, at four sample locations per field (Pherocon AM, Trécé, Inc. Adair, OK). Yellow-sticky cards were mounted on a wooden stake and the height of the card was adjusted each week to keep it immediately above the soybean canopy. The abundance of individual natural enemy taxa was summarized for June, July, and August.

Natural enemies obtained from sweep-net and yellow-sticky card samples were bagged and stored at -20°C. All natural enemies collected were sorted and identified to at least the family level except for *O. insidiosus* (insidious flower bug), *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), and all Coccinellidae, which were identified to species. Both adult and immature stages of natural enemies were counted and voucher specimens were deposited in the Department of Entomology insect collection at Iowa State University, Ames, IA.

The precision of a sampling method varies by natural enemy taxon; therefore, data from a single sampling method were used to represent an individual taxon (Schmidt et al. 2008). In previous studies, we found that, field-counts were the most precise method for

collecting *O. insidiosus*, sweep-net samples for *Nabis* spp. (Hemiptera: Nabidae) and Araneae, and yellow-sticky cards for all coccinellids, syrphids, *Chrysoperla* spp. (Neuroptera: Chrysopidae), and parasitic wasps (Braconidae and Ichneumonidae) (Schmidt et al. 2008). A principal component analysis (PCA) was used to determine which natural enemies explained most of the variability in abundance using R statistical packages (Oksanen et al. 2010, R Development Core Team 2009). The covariance matrix was created using weekly count data to determine the variance of species, and the degree to which species were correlated.

Plant Nutrient Sampling. Soybean plant nutrients were quantified at the end of July when plants were in the R4 stage (pod growth; Pederson 2004). The single uppermost trifoliolate was removed from five plants at each of the four sample locations per field (20 trifoliolates per field). Samples were allowed to dry in paper bags at room temperature for a minimum of two months, and sent to a private laboratory (Agvise Laboratories, Northwood, ND) for analysis. N, P, and K content were each expressed as a percent of total dry mass.

Landscape Measurements. From 2006 – 2008, all land cover elements within 2.5 km of the field center were summarized at a 15-m resolution using land cover maps. Common Land Unit (USDA FSA 2006) and National Land Cover Dataset data (NLCD 2001) were initially used to create maps, but all land cover elements were confirmed through an on-the-ground survey.

In preliminary analyses, we divided the land cover data into multiple, non-overlapping concentric rings to determine whether there was an effect of distance on *A. glycines* or natural enemy community response to land cover (Thies et al. 2005, Gardiner et al. 2009a, Gardiner et al. 2009b). However, we detected no effect and indeed little change in composition, diversity, or configuration of the landscape at different distances from the surveyed fields, all landscover data were combined into a single 0-2.0 km dataset centered on each field in all subsequent analyses. Measures of surrounding landscape composition, diversity, and contagion (spatial configuration) were calculated for each field on rasterized layers of land cover.

Approximately 97% of all landscape composition included alfalfa, corn, forest, grassland, residential, roads, soybean, and water. Using methods from Gardiner et al. (2009a, 2009b), landscape diversity was measured with Simpson's index, $(1 - D)$, calculated using R statistical packages (Oksanen et al. 2010, R Development Core Team 2009). The value of D ranges between 0 and 1 with zero corresponding to simple and one corresponding diverse landscapes (Magurran 2004). Simpson's index is typically used to summarize species diversity, but here it was used to summarize landscape diversity. A contagion index (Li and Reynolds 1993) was calculated from a simplified land cover layer, in which all vegetation types were reclassified as either perennial or annual, using Fragstats (McGarigal et al. 2002). Contagion measures the extent to which landscape patches, or raster "cells", are clumped or dispersed (McGarigal and Marks 1995). A large contagion value suggests a landscape contained a few large contiguous patches, whereas a small value suggests the landscape contained many small dispersed patches (McGarigal and Marks 1995).

Data Analysis. To determine whether sampled soybean fields were independent of one another, Moran's I , a test for spatial autocorrelation, was conducted on response variables (CAD and natural enemy data) using R statistical packages (Bivand et al. 2010, R Development Core Team 2008). We did not detect spatial autocorrelation in peak CAD or pooled natural enemy data (all field and distance combinations; $P > 0.07$). Because growers treated *A. glycines* populations at varying times in all three years, all analyses were conducted on aphid data through the second week of August.

To determine which plant nutrients and landscape metrics explained most of the variability in the response variables, CAD and natural enemies were analyzed using multidimensional scaling (MDS) with the Bray-Curtis distance measure (Bray and Curtis 1957). MDS is a multivariate statistical technique that summarizes relationships between response and explanatory variables accordingly to their distances in multidimensional space, so the closer two points are the more similar they are (Kenkel and Orlóci 1986). Pairwise correlations were assessed with the intent of selecting a subset of independent explanatory variables to include in the analysis and thus reducing multicollinearity in the dataset (Weisberg 1985). All pairwise correlations were below $r = 0.70$ so all variables were

included in the MDS analysis. Preliminary analyses were run with up to six ordination axes, and based on levels of stress the final analysis was run with two. The specifications of the final MDS model included two axes and a random starting configuration with both real and random data. The final solution had a stress of 14.28 and a final instability of 0.00001 based on 91 iterations. The amount of variation explained by two axes produced an $R^2 = 0.90$ and the level of stress in the final solution was satisfactory for ecological community data (McCune and Grace 2002). All response variables were graphed as points and independent variables were graphed as vectors using PC-ORD on MDS plots (McCune and Mefford 1999). Vectors indicate the direction and strength of correlations among CAD and natural enemies, year, plant nutrients and landscape variables. Pearson correlations were used to assess the importance of independent and response variables. This analysis was initially conducted for individual years; however, due to weak correlations in these data, all years were combined and year was included as an explanatory variable.

We used multiple linear regression analysis and Akaike's Information Criterion for model selection, adjusted for sample size (AIC_c ; Burnham and Anderson 2002), to determine which variables (year, plant nutrients and/or landscape metrics) best explain CAD and individual natural enemy abundance. Eleven variables were compared: year (categorical variable), N, P, K, alfalfa, corn, forest, grassland, soybean, Simpson's D , and contagion. For each analysis, we present the number of variables in a model (K), and several parameters associated with that model including; AIC_c value, AIC_c differences (ΔAIC_c), Akaike weight (w_i) and adjusted R^2 value. For each response variable, we present the "best-fit" model, which had the minimum AIC_c value, and "competing" models, which had a ΔAIC_c difference of less than two and showed strong support for the response variable (Burnham and Anderson 2002). The AIC_c analysis was conducted and adjusted R^2 were calculated using JMP (SAS Institute 2009). We used linear regression analysis to determine the relationship between response and explanatory variables identified by both best-fit and competing models using JMP (SAS Institute 2009).

To determine the relationship between *A. glycines* and natural enemies, the mean abundance of natural enemies, pooled across seven taxa, and *A. glycines* was calculated for each week during 2006, 2007, and 2008. The abundance of *A. glycines* and natural enemies

was transformed ($\ln + 1$) to meet the assumptions of ANOVA (Sokal and Rohlf 1995). The values used for natural enemies were based on a mean pooled across seven taxa collected from their corresponding sampling method(s): *O. insidiosus*, *Nabis* spp., native and exotic coccinellids, *Chrysoperla* spp., syrphids, and Araneae. These generalist natural enemies are known predators of *A. glycines*. Although adult *Chrysoperla* spp. and syrphids are not predaceous, an increase in their abundance could indicate a numerical response to increased *A. glycines* populations. Using an analysis of covariance (ANCOVA) in JMP (SAS Institute 2009), we tested the hypothesis that slopes between years are equal. We predicted that an increase in *A. glycines* would elicit an increase in natural enemies, therefore, slopes would increase. The response variable in the ANCOVA model was natural enemy and covariates were *A. glycines*, year, and the interaction between aphids and year. Slopes were compared between years using contrast statements.

Results

Soybean Aphid and Natural Enemy Populations. Peak populations of *A. glycines* averaged 170 aphids per plant (256 CAD) in 2006; 370 aphids per plant (3,472 CAD) in 2007; and 993 aphids per plant, (7,653 CAD) in 2008 (Figure 2). *Aphis glycines* populations peaked in late August in 2006 and 2008, and the second week of August in 2007 (Figure 2).

A total of 17,601 natural enemies (adult and immature) were collected, which included 7 orders and 17 families for 2006 – 2008 (Table 1). The ranking of natural enemy abundance by year was 2007 > 2008 > 2006 (Table 1). Native coccinellids consisted of nine species (Table 1) and made up 36% of all coccinellids collected, whereas the remaining 64% consisted of two exotic coccinellids, *H. axyridis* and *C. septempunctata* (Table 1). We used a PCA to determine which natural enemies explained the greatest variability within the larger community and eight taxa were identified: *O. insidiosus*, *Nabis* spp., exotic coccinellids, native coccinellids, *Chrysoperla* spp., parasitic wasps, syrphids, and Araneae (N.P.S. unpublished data).

We summarized the mean abundance of eight natural enemies, collected in June, July, and August in 2006, 2007, and 2008 (Figures 3A, 3B, 3C). In 2006, parasitic wasps were most abundant in June, and *Chrysoperla* spp. in July and August (Figure 3A). In 2007, both

parasitic wasps and syrphids were most abundant in June, syrphids in July, and *Nabis* spp. in August (Figure 3B). In 2008, syrphids were the most abundant natural enemy in June, July, and August (Figure 3C).

Landscape Measurements. The study site was located in a landscape ranging from simple (up to 95% arable, Simpson's $D = 0.56$, and contagion = 77.96) to complex (21% arable, Simpson's $D = 0.81$, and contagion = 37.86). Land cover around a given soybean field did not vary much among the three years of this study (Figures 4A, 4B, 4C). Land cover was similar among all radii except at 0.5 km where a decreased amount of soybean existed (Figures 4A, 4B, 4C). The final MDS solution included a 2-dimensional axis, which explained ~90.2% of the variability in these data, with 11 explanatory and 9 response variables (Figure 5). On both axes variables year and plant nutrients (N, P, and K) explained the majority of the variability in both CAD and natural enemies (Table 2).

Model Comparisons. All best-fit and competing models were significant at $P < 0.01$ (Table 3). For all response variables we have listed the explanatory variables from best-fit and competing models. Only the significantly correlated response and explanatory variables are described below.

Cumulative aphid days were best predicted by year, grassland, forest, P, and K, and competing models included N and contagion (Table 3). CAD had a significant positive relationship with year ($R^2 = 0.87$; $F_{2,99} = 326.89$; $P < 0.0001$), P ($R^2 = 0.35$; $F_{1,99} = 51.77$; $P < 0.001$), and N ($R^2 = 0.30$; $F_{1,99} = 42.52$; $P < 0.001$). Syrphids were best predicted by year, grassland, Simpson's D , and corn, and competing models included forest, contagion, soybean, alfalfa, and P (Table 3). Syrphids had a significant positive relationship with year ($R^2 = 0.67$; $F_{2,99} = 97.20$; $P < 0.0001$), corn ($R^2 = 0.07$; $F_{1,99} = 6.94$; $P < 0.01$), and P ($R^2 = 0.22$; $F_{1,99} = 27.62$; $P < 0.001$), and a significant negative relationship with soybean ($R^2 = 0.05$; $F_{1,99} = 5.23$; $P = 0.02$) and alfalfa ($R^2 = 0.07$; $F_{1,99} = 6.87$; $P = 0.01$). Parasitic wasps were best predicted by year, contagion, and corn, and competing models included N, soybean, and forest (Table 3). Parasitic wasps had a significant positive relationship with corn ($R^2 = 0.05$; $F_{1,99} = 5.21$; $P = 0.02$), and N ($R^2 = 0.05$; $F_{1,99} = 5.57$; $P = 0.02$).

Chrysoperla spp. were best predicted by year and alfalfa, and competing models included alfalfa, N, P, K, grassland, and corn (Table 3). *Chrysoperla* spp. had a significant positive relationship with soybean ($R^2 = 0.04$; $F_{1,99} = 4.00$; $P < 0.05$), and a significant negative relationship with year ($R^2 = 0.45$; $F_{2,99} = 40.52$; $P < 0.0001$), N ($R^2 = 0.20$; $F_{1,99} = 24.65$; $P < 0.001$), P ($R^2 = 0.09$; $F_{1,99} = 10.18$; $P < 0.01$), and K ($R^2 = 0.04$; $F_{1,99} = 4.42$; $P = 0.04$). Native coccinellids was best predicted by year, and competing models included N, P, K, alfalfa, and Simpson's *D* (Table 3). Native coccinellids had a significant negative relationship with year ($R^2 = 0.19$; $F_{2,99} = 11.35$; $P < 0.0001$), N ($R^2 = 0.08$; $F_{1,99} = 8.08$; $P < 0.01$), and P ($R^2 = 0.04$; $F_{1,99} = 4.57$; $P = 0.04$). Exotic coccinellids was best predicted by year, grassland, and forest, and competing models included corn, Simpson's *D*, alfalfa, contagion, soybean, and N (Table 3). Exotic coccinellids had a significant positive relationship with alfalfa ($R^2 = 0.04$; $F_{1,99} = 4.28$; $P = 0.04$), and a significant negative relationship with year ($R^2 = 0.50$; $F_{2,99} = 48.77$; $P < 0.0001$) and N ($R^2 = 0.24$; $F_{1,99} = 30.72$; $P < 0.001$). Araneae was best predicted by year, forest, alfalfa, and corn, and competing models included grassland, K, Simpson's *D*, and contagion (Table 3). Araneae had a significant positive relationship with forest ($R^2 = 0.10$; $F_{1,99} = 10.37$; $P < 0.01$) and alfalfa ($R^2 = 0.24$; $F_{1,99} = 11.52$; $P < 0.001$), and a significant negative relationship with year ($R^2 = 0.19$; $F_{2,99} = 22.41$; $P < 0.0001$) and corn ($R^2 = 0.11$; $F_{1,99} = 17.39$; $P < 0.001$). *Orius insidiosus* was best predicted by year and forest, and competing models included Simpson's *D*, P, grassland, and contagion (Table 3). *Orius insidiosus* had a significant negative relationship with year ($R^2 = 0.09$; $F_{2,99} = 9.66$; $P < 0.01$). *Nabis* spp. were best predicted by year and alfalfa, and competing models included forest, corn, contagion, grassland, Simpson's *D*, N, and P (Table 3). *Nabis* spp. had a significant positive relationship with alfalfa ($R^2 = 0.04$; $F_{1,99} = 3.87$; $P = 0.05$).

Relationship of Natural Enemies to Soybean Aphids. To determine the relationship between *A. glycines* and natural enemies we tested the hypothesis that slopes between years are equal. Slopes between 2006 – 2007 were not significant ($F_{1,21} = 0.23$; $P = 0.64$); but slopes were significant between 2006 – 2008 ($F_{1,21} = 9.4$; $P < 0.01$) and 2007 – 2008 ($F_{1,21} = 6.4$; $P = 0.01$; Figure 6). A greater positive slope in 2006 suggests that natural enemies

exhibited a numerical response with increased *A. glycines* abundance compared to 2007 and 2008 where closer to zero and/or negative.

Discussion

In our initial hypothesis, we stated that soybean fields in landscapes with an abundance of reconstructed prairie would harbor an increased abundance of natural enemies. and reduce the abundance of *A. glycines*. Our analyses suggest landscape composition, diversity and contagion explained little of the variation in both response variables at our study site. Over the course of this three-year study, we found no significant correlation between the amount of grassland habitat within 2 km of soybean fields and *A. glycines* or natural enemies. Instead, most variation in abundance of *A. glycines* was explained by an effect of year and to a lesser extent by plant nutrients (N and P; Table 2). Similarly, variation in the abundance of eight natural enemy taxa was best explained by the year effect, and to a lesser extent landscape composition and plant nutrients (Table 2).

Aphis glycines populations have been known to fluctuate across the north central US between years, with high populations typically observed in odd years and low populations in even years (Myers and Gratton 2006). In this study we observed low *A. glycines* populations in 2006 and high populations that exceeded the economic threshold (250 aphids per plant; Ragsdale et al. 2007) in 2007 and 2008. Natural enemies respond to an increased abundance of *A. glycines* in a density-dependent way (Donaldson et al. 2007, Schmidt et al. 2007). However, in our study the response of natural enemies to *A. glycines* abundance decreased over time (Figure 6). One likely explanation may be substantial variation in immigration rates of alate *A. glycines* experienced in Iowa during this study. In 2008, > 3,500 alates (3-times more than 2007 and 3-orders of magnitude more than 2006; Figure 7) were collected during August in a suction trap approximately 64 km from the center of our study site. Alate *A. glycines* counts in suction traps were positively associated with the abundance of aphids on soybean plants (Rhainds et al. 2010), although this relationship was only examined within 10 km of suction traps and the spatial extent of this relationship is not known. Therefore, assuming our study area received a greater immigration of alates in 2008, *A. glycines* may have escaped the functional and numerical response of natural enemies (Figure 2). *Aphis*

glycines overwinters on *R. cathartica*, however, each year we walked the perimeter of each soybean field, in addition to woodlots in the NSNWR and local parks, and found none (N.P.S. Unpublished data).

A second explanation for the decline in the response of natural enemies to *A. glycines* may be due to a reduction in their abundance. In 2008 5,260 individual natural enemies were collected; however, 69.7% of this community was represented primarily by adult syrphids (Table 1). Also in 2008, the abundance of native and exotic coccinellids, *O. insidiosus*, and *Chrysoperla* spp. was much lower than 2006 (Figure 3A, 3B, 3C). The decline of these predatory taxa is more worrisome because they have been shown to cause significant aphid mortality (Fox et al. 2004, Schmidt et al. 2007, Miao et al. 2007, Gardiner et al. 2009a). In 2008 we observed reduced natural enemy populations (Figure 3), and if we assume this trend was consistent throughout the north-central US in 2008, it would be easier for *A. glycines* populations to increase and immigrate to new areas without mortality from predators. Other explanations may include weather events from the previous year and insecticide usage.

Plant nutrients helped explain much of the variation in *A. glycines* abundance. There is a documented relationship between plant nutrients and *A. glycines* population growth. Myers and Gratton (2006) found similar results where peak *A. glycines* populations were positively correlated with N, P, and K, while at the same time aphid growth rates were negatively correlated with N, P, and K. In addition, Noma et al. (2010) found *A. glycines* populations were positively correlated with N, and negatively correlated with K. Increased nutrient levels in our study, may be related to the no tillage and minimum tillage practices used. Over an eight-year study in south-central Texas, soil nutrients P and K, and extractable P and K, were in greater concentrations at depths of 0 – 0.05 m in no-till compared to conventionally tilled sorghum *Sorghum bicolor* (L.), wheat *Triticum aestivum* L. and soybean fields (Franzluebbers and Hons 1996).

Gardiner et al. (2009a) found increased biological control of *A. glycines* in more diverse landscapes that included forest and grassland. Furthermore, the abundance of native coccinellids was positively correlated with landscapes consisting of low-diversity and increased grassland, whereas the abundance of exotic coccinellids was correlated with increased forest (Gardiner et al. 2009b). In our study, native coccinellids were affected by

year and negatively correlated with reduced plant N and P, whereas exotic coccinellids were affected by year, and positively correlated with increased alfalfa, and negatively correlated with reduced plant N (Table 3). Overall, landscape metrics explained little variation in our natural enemy data compared to previous research. One explanation may be provided by Hodgson et al. (2009), who observed at the landscape level, habitat quality for the butterfly *Plebejus argus* L. (Lepidoptera: Lycaenidae) appeared less important at greater abundances. Hodgson et al. (2009) suggests the varying levels of disturbance and succession in a landscape affected habitat quality and indirectly the ability to detect the abundance of *P. argus*. The NSNWR was established in 1990 and managers add new prairie plantings each year. Management of grasslands at NSNWR consists of mowing and fire, which both disturbs the landscape and alters succession. In addition, natural enemies can be indirectly affected by the nutrient composition of the plants on which their prey feed (Mayntz and Toft 2001), and can result in increased parasitism (Walker et al. 2008). Gratton and Denno (2003) suggest plant N can mediate the affects of natural enemies on herbivore populations; specifically spiders in the family Lycosidae were 440% more abundant in plots with increased N.

Our results suggest that variability in the abundance of *A. glycines* was affected most by year, likely due to year-to-year variation in immigration rates of *A. glycines* given the lack of overwintering sites in our study area. Year explained 87% of the variation in *A. glycines* and 19 – 67% of the variation in natural enemy abundance, suggesting other unmeasured abiotic and/or biotic factors may be as or more influential than our measured variables on *A. glycines* and natural enemies. In discussing soybean production practices with growers in our study area, we found that most seed planted in recent years was treated with an insecticide. Generalist predators have been observed in soybean early in the growing season feeding on thrips or plants. Carnivorous species sometimes feed on plant tissue, and such zoophytophagy is commonly observed with *O. insidiosus* and more recently *H. axyridis* and *Coleomegilla maculata* DeGeer (Moser et al. 2008). Moser and Obrycki (2009) found a significant reduction in *H. axyridis* larvae that fed on corn seedlings treated with neonicotinoids. Extrapolating these findings to soybean agroecosystems may explain the general decline in predators that was observed over the three years of this study. Future

research is needed to discern the effects of alate *A. glycines* immigration in soybean and the impacts of non-target effects of seed treatments in soybean agroecosystems.

Acknowledgments

We thank Mike Gannon of the Heartland City Co-op., all landowners who allowed us to collect data on their property, graduate students Kevin Johnson and Mike McCarville, and hourly workers Dustin Paulson, Daniel Stull, Robert Moore, Finn Pillsbury, Matt Maher, Nathan Johnson, and Andrew Thraenert, and Todd Hanson, Bonnie Jan, and Anna MacDonald for assistance with digitizing. This work was funded by the Leopold Center for Sustainable Agriculture (Title: The Impact of Biodiversity Services in Rowcrop Production in Annual versus Perennial Landscapes; grant E2006-13). In addition, this journal paper of the Iowa Agriculture and Home Economics Experiment Station, Ames, Iowa, Project No. 5032, was supported by Hatch Act and State of Iowa funds.

References Cited

- Bivand, R., L. Anselin, R. Assunção, O. Berke, A. Bernat, E. Blankmeyer, M. Carvalho, Y. Chun, B. Christensen, C. Dormann, S. Dray, R. Halbersma, E. Krainski, N. Lewin-Koh, H. Li, J. Ma, G. Millo, W. Mueller, H. Ono, P. Peres-Neto, G. Piras, M. Reder, M. Tiefelsdorf, and D. Yu. 2010.** Spdep: Spatial dependence: Weighting schemes, statistics and models. R package version 0.5-4.
<http://CRAN.Rproject.org/package=spdep>
- Bray, J. R., and J. T. Curtis. 1957.** An ordination of the upland forest communities of southern Wisconsin. Ecol. Monogr. 27: 325-349.
- Burnham, K. P., and D. R. Anderson. 2002.** Model selection and multimodel inference: A practical information-theoretic approach. 2nd Edition. Springer-Verlag, New York, New York.
- Donaldson, J. R., S. W. Myers, and C. Gratton. 2007.** Density-dependent responses of soybean aphid (*Aphis glycines* Matsumura) populations to generalist predators in mid to late season soybean fields. Biol. Control 43: 111-118.
- Dyer, L. E., and D. A. Landis. 1997.** Influence of noncrop habitats on the distribution of *Eriborus terebrans* (Hymenoptera: Ichneumonidae) in cornfields. Environ. Entomol. 26: 924-932.
- Elliott, N. C., R. W. Kieckhefer, J. H. Lee, and B. W. French. 1999.** Influence of within-field and landscape factors on aphid predator populations in wheat. Landscape Ecol. 14: 239-252.
- Elliott, N. C., R. W. Kieckhefer, G. J. Michaels, and K. L. Giles. 2002.** Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. Environ. Entomol. 31: 253-260.
- Environmental Systems Research Institute (ESRI). 2007.** ArcGIS 9.2. www.esri.com
- Fiedler, A. K., and D. A. Landis. 2009.** Which plants are best?
<http://nativeplants.msu.edu/results.htm>; last visited 1 May, 2010
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004.** Predators suppress *Aphis glycines* Matsumura population growth in soybean. Environ. Entomol. 33: 608-618.

- Franzluebbers, A. J., and F. M. Hons. 1996.** Soil-profile distribution of primary and secondary plant-available nutrients under conventional and no tillage. *Soil Tillage Res.* 39: 229-239.
- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. Chacon, M. Wayo, N. P. Schmidt, E. Mueller, and G. E. Heimpel. 2009a.** Landscape diversity enhances the biological control of an introduced crop pest in the north-central US. *Ecol. Applic.* 19: 143-154.
- Gardiner, M. M., D. A. Landis, C. Gratton, N. P. Schmidt, M. O'Neal, E. Mueller, J. Chacon, G. E. Heimpel, and C. D. DiFonzo. 2009b.** Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity Distrib.* 15: 554-564.
- Gurr, G. M., and S. D. Wratten. 1999.** 'Integrated biological control': A proposal for enhancing success in biological control. *Int. J. Pest Manage.* 45: 81-84.
- Hanafi, A., E. B. Radcliffe, and D. W. Ragsdale. 1989.** Spread and control of potato leafroll virus in Minnesota. *J. Econ. Entomol.* 82: 1201-1206.
- Hodgson, E. W., R. L. Koch, and D. W. Ragsdale. 2005.** Pan trapping for soybean aphid (Homoptera: Aphididae) in Minnesota soybean fields. *J. Entomol. Sci.* 40: 409-419.
- Hodgson, J. A., A. Moilanen, and C. D. Thomas. 2009.** Metapopulation responses to patch connectivity and quality are marked by successional habitat dynamics. *Ecol.* 90: 1608-1619.
- Isard, S. A., and S. H. Gage. 2001.** Flow of life in the atmosphere: An airscape approach to understanding invasive organisms. Michigan State University Press, East Lansing, MI.
- Johnson, K. D., M. E. O'Neal, D. W. Ragsdale, C. D. Difonzo, S. M. Swinton, P. M. Dixon, B. D. Potter, E. W. Hodgson, and A. C. Costamagna. 2009.** Probability of cost-effective management of soybean aphid (Hemiptera: Aphididae) in North America. *J. Econ. Entomol.* 102: 2101-2108.
- Kenkel, N. C., and L. Orlóci. 1986.** Applying metric and nonmetric multidimensional scaling to ecological studies: Some new results. *Ecol.* 67: 919-928.

- Kogan, M., and S. G. Turnipseed. 1987.** Ecology and management of soybean arthropods. *Ann. Rev. Entomol.* 32: 507-538.
- Kremen, C., N. M. Williams, and R. W. Thorp. 2002.** Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci. USA.* 99: 16812-16816.
- Kreuss, A., and T. Tscharntke. 1994.** Habitat fragmentation, species loss, and biological control. *Science* 264: 1581-1584.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000.** Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175-201.
- Lee J. C., F. D. Menalled, and D. A. Landis. 2001.** Refuge habitats modify impact of insecticide disturbance on carabid beetle communities. *J. Appl. Ecol.* 38: 472-483.
- Li, H., and J. F. Reynolds. 1993.** A new contagion index to quantify spatial patterns of landscapes. *Landscape Ecol.* 8: 155-162.
- Liu, J., K. M. Wu, K. R. Hopper, and K. J. Zhao. 2004.** Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. *Ann. Entomol. Soc. Am.* 97: 235-239.
- Magurran, A. E. 2004.** Measuring biological diversity. Blackwell publishing, Malden, MA.
- Marino, P. C., and D. A. Landis. 1996.** Effect of landscape structure on parasitoid diversity and parasitism in agroecosystems. *Ecol. Appl.* 6:276-284.
- Mayntz, D., and S. Toft. 2001.** Nutrient composition of the prey's diet affects growth and survivorship of a generalist predator. *Oecologia* 127: 207-213.
- McCune, B., and J. Grace. 2002.** Analysis of ecological communities. MjM Software Design, Gleneden Beach, OR.
- McCune, B., and M. J. Mefford. 1999.** Multivariate analysis of ecological data. Version 4.25. MjM Software, Gleneden Beach, Oregon, U.S.A. (PC-ORD).
- McGarigal, K., and B. J. Marks. 1995.** Fragstats: Spatial pattern analysis program for quantifying landscape structure. USDA For. Serv. Gen. Tech. Rep. PNW-351.
- McGarigal, K., S. A. Cushman, M. C. Neel, and E. Ene. 2002.** Fragstats: Spatial pattern analysis program for categorical maps. Computer software program produced by the authors at the University of Massachusetts, Amherst.
www.umass.edu/landeco/research/fragstats/fragstats.html

- Menalled, F. D., P. C. Marino, S. H. Gage, and D. A. Landis. 1999.** Does agricultural landscape structure affect parasitism and parasitoid diversity? *Ecol. Appl.* 9: 634-641.
- Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. 2003.** Temporal variation in the response of parasitoids to agricultural landscape structure. *Agric. Ecosys. Environ.* 96: 29-35.
- Miao, J., K. Wu, K. R. Hopper, and G. Li. 2007.** Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and impact of natural enemies in northern China. *Environ. Entomol.* 36: 840-848.
- Moser, S. E., J. D. Harwood, and J. J. Obrycki. 2008.** Larval feeding on *Bt* hybrid and non-*Bt* corn seedlings by *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 37: 525-533.
- Moser, S. E., and J. J. Obrycki. 2009.** Non-target effects of neonicotinoid seed treatments; mortality of coccinellid larvae to zoophytophagy. *Biol. Control* 51: 487-492.
- Myers, S. W., and C. Gratton. 2006.** Influence of potassium fertility on soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), population dynamics at a field and regional scale. *Environ. Entomol.* 35: 219-227.
- National Land Cover Database (NLCD). 2001. MRLC Consortium.** 17 April, 2006.
<http://gisdata.usgs.net/website/MRLC/>
- Noma, T., C. Gratton, M. Colunga-Garcia, M. J. Brewer, E. E. Mueller, K. G. Wyckhuys, G. E. Heimpel, and M. E. O'Neal. 2010.** Relationship of soybean aphid (Hemiptera: Aphididae) to soybean plant nutrients, landscape structure, and natural enemies. *Environ. Entomol.* 39: 31-41.
- Oksanen, J. F., G. Blanchet, R. Kindt, P. Legendre, R. G. O'Hara, G. L. Simpson, P. M, Solymos, H. H. Stevens, and H. Wagner. 2010.** *Vegan: Community Ecology Package.* R package version 1.17-0. <http://CRAN.R-project.org/package=vegan>
- Pederson, P. 2004.** Soybean growth and development. Iowa State University Extension.
- R Development Core Team. 2009.** R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>

- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004.** Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97: 204-208.
- Rhainds, M., H. J. S. Yoo, K. L. Steffey, D. J. Voegtlin, C. S. Sadof, S. Yaninek, and R. J. O'Neil. 2010.** Potential of suction traps as a monitoring tool for *Aphis glycines* (Hemiptera: Aphididae) in soybean fields. *J. Econ. Entomol.* 103: 186-189.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004.** Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240-248.
- SAS Institute Inc. 2009.** JMP, Version 8.0. SAS Institute Inc. Cary, NC.
- Schmidt, N. P., M. E. O'Neal, and J. W. Singer. 2007.** Alfalfa living mulch advances biological control of soybean aphid. *Environ. Entomol.* 36: 416-424.
- Schmidt, N.P., M. E. O'Neal, and P. M. Dixon. 2008.** Aphidophagous predators in Iowa soybean: A community comparison across multiple years and sampling methods. *Ann. Entomol. Soc. Am.* 101: 341-350.
- Smith, D. D. 1998.** Iowa prairie: Original extent and loss, preservation and recovery attempts. *J. Iowa Acad. Sci.* 105: 94-108.
- Sokal, R. R., and F. J. Rohlf. 1995.** Biometry: The principles and practice of statistics in biological research. 3rd edition. W. H. Freeman and Co.: New York.
- Thies, C., and T. Tscharntke. 1999.** Landscape structure and biological control in agroecosystems. *Science* 285: 893-895.
- Thies, C., I. Steffan-Dewenter and T. Tscharntke. 2003.** Effects of landscape context on herbivory and parasitism at different spatial scales. *Oikos* 101: 18-25.
- Thies, C., I. Indra Roschewitz and T. Tscharntke. 2005.** The landscape context of cereal aphid-parasitoid interactions. *Proc. R. Soc. B.* 272: 203-210.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005.** Landscape perspectives on agricultural intensification and biodiversity: Ecosystem service management. *Ecol. Lett.* 8: 857-874.
- United States Department of Agriculture Farm Service Agency (USDA FSA). 2006.** Aerial photography field office. Common land unit.
<http://www.igsb.uiowa.edu/nrgislibx/>

- United States Department of Agriculture (USDA). 2007.** National Agricultural Research Service. 2007 census of agriculture report, Vol. 1, U.S. summary and state reports (Table 26). Washington, D.C.
- Walker, M., S. E. Hartley, and T. H. Jones. 2008.** The relative importance of resources and natural enemies in determining herbivore abundance: Thistles, tephritids and parasitoids. *J. Anim. Ecol.* 77: 1063-1071.
- Walter, A. J., and C. D. DiFonzo. 2007.** Soil potassium deficiency affects soybean phloem nitrogen and soybean aphid populations. *Environ. Entomol.* 36: 26-33.
- Weisberg, S. 1985.** Applied linear regression, 2nd ed. John Wiley and Sons, New York.

Table 1. Total natural enemies collected from Iowa soybean fields in 2006, 2007, and 2008

Taxon Collected	Total Abundance ^a		
	2006	2007	2008
Order Hemiptera			
Anthocoridae ^b			
<i>Orius insidiosus</i> (Say)	329	723	157
Nabidae ^b			
<i>Nabis</i> spp.	80	288	88
Pentatomidae ^c			
<i>Podisus maculiventris</i> (Say)	78	11	3
Order Coleoptera			
Coccinellidae ^d			
<i>Brachiacantha ursina</i> F.	4	50	6
<i>Coccinella hieroglyphica</i> L.	0	0	14
<i>Coccinella septempunctata</i> L.	345	423	113
<i>Coleomegilla maculata</i> (DeGeer)	51	21	11
<i>Cycloneda munda</i> (Say)	56	150	179
<i>Harmonia axyridis</i> (Pallas)	464	286	64
<i>Hippodamia convergens</i> Guerin-Meneville	219	37	13
<i>Hippodamia parenthesis</i> Say	45	91	9
<i>Hippodamia tredecimpunctata</i> L.	2	4	6
<i>Hippodamia variegata</i> (Goeze)	2	0	0
Order Neuroptera			
Chrysopidae ^d			
<i>Chrysoperla</i> spp.	1,499	1,229	284
Hemerobiidae ^d	34	8	31
Order Hymenoptera ^e			
Parasitic wasps (Braconidae and Ichneumonidae)	654	1,639	528
Order Diptera ^d			
Syrphidae	818	2,521	3,667
Order Araneae ^f			
Agelenidae	1	2	7
Araneidae	2	3	0
Linyphiidae	0	1	1
Lycosidae	5	2	13
Oxyopidae	15	6	0
Salticidae	11	17	0
Tetragnathidae	18	42	45
Thomisidae	22	10	15
Order Opiliones ^f	4	19	6
Total	4,758	7,583	5,260

Table 1. Continued

^a Direct comparisons between years cannot be made because the number of fields varied between 2006, 2007, and 2008 (30, 36, and 34).

^b Adults and nymphs collected from field-counts.

^c Adults and nymphs collected from sweep-nets and field-counts.

^d Adults and larvae collected from yellow-sticky cards and field-counts.

^e Adults collected from yellow-sticky cards.

^f Adults and nymphs collected from sweep-nets.

Table 2. Pearson correlations of explanatory and response variables with multidimensional scaling axis 1 and 2, which explain 23.2% and 64.8% of the variation respectively and have 69.8% orthogonality

Variables	<i>r</i> - values	
	Axis 1	Axis 2
Explanatory		
Year	0.63	0.94
N	0.41	0.69
P	0.34	0.54
K	0.17	0.39
Alfalfa	-0.02	-0.25
Soybean	-0.32	-0.23
Corn	0.16	0.15
Forest	0.06	-0.01
Grassland	0.05	-0.02
Contagion	-0.20	0.04
Simpson's <i>D</i>	0.02	-0.05
Response		
<i>Aphis glycines</i> ^a	0.67	0.76
Syrphidae	0.59	0.87
<i>Chrysoperla</i> spp.	-0.79	-0.62
Exotic coccinellids ^b	-0.51	-0.73
Araneae	-0.48	-0.46
Native coccinellids ^c	-0.33	-0.42
<i>Orius insidiosus</i>	-0.05	-0.37
Parasitic wasps	0.27	-0.19
<i>Nabis</i> spp.	0.01	-0.06

^a Cumulative aphid days (ln +1).

^b *Harmonia axyridis* and *Coccinella septempunctata* comprised 64% of all coccinellids collected.

^c Eight species of native coccinellids were collected and comprised 36% of all coccinellids collected.

Table 3. Best-fit and competing models for *Aphis glycines* and natural enemy abundance in relation to landscape parameters for 2006 – 2008 significant at $P < 0.01$

Response Variable	K	AIC _c	ΔAIC _c	w_i	Adj. R ²	Variables ^a in Model
<i>Aphis glycines</i> ^b	5	262.75	0.00	0.32	0.90	Year, Grass, Forest, P, K
	4	262.86	0.12	0.30	0.90	Year, Grass, Forest, K
	6	264.62	1.87	0.13	0.90	Year, Grass, Forest, N, P, K
	5	264.66	1.91	0.12	0.90	Year, Grass, Forest, K, Contag
	5	264.71	1.96	0.12	0.90	Year, Grass, Forest, P, K, Contag
Syrphidae	4	897.13	0.00	0.13	0.73	Year, Grass, Simp, Corn
	3	897.43	0.30	0.11	0.73	Year, Grass, Corn
	5	897.64	0.52	0.10	0.74	Year, Grass, Forest, Simp, Corn
	4	897.84	0.71	0.10	0.73	Year, Forest, Contag, Corn
	4	898.03	0.90	0.08	0.73	Year, Grass, Contag, Corn
	5	898.21	1.08	0.07	0.73	Year, Grass, Simp, Corn, Soy
	4	898.46	1.33	0.07	0.73	Year, Alfalfa, Contag, Corn
	5	898.47	1.34	0.07	0.73	Year, Forest, Alfalfa, Contag, Corn
	5	898.51	1.38	0.06	0.73	Year, Grass, Alfalfa, Simp, Corn
	5	898.62	1.49	0.06	0.73	Year, Grass, Simp, Corn, P
	4	898.85	1.72	0.05	0.73	Year, Grass, Corn, P
	4	898.88	1.75	0.05	0.73	Year, Grass, Forest, Contag, Corn
Parasitic wasp	3	899.11	1.98	0.05	0.72	Year, Contag, Corn
	3	790.20	0.00	0.28	0.53	Year, Contag, Corn
	4	791.16	0.95	0.17	0.53	Year, Contag, Corn, N
	4	791.38	1.18	0.15	0.53	Year, Contag, Corn, Soy
	3	791.40	1.20	0.15	0.53	Year, Cornag, Soy
	3	791.56	1.36	0.14	0.52	Year, Contag, Corn
	4	792.13	1.93	0.11	0.53	Year, Forest, Corn
<i>Chrysoperla</i> spp.	2	863.96	0.00	0.26	0.46	Year, Alfalfa
	1	865.13	1.17	0.14	0.44	Year
	3	865.13	1.17	0.14	0.46	Year, Alfalfa, N
	3	865.19	1.23	0.14	0.46	Year, Alfalfa, P
	3	865.51	1.55	0.12	0.46	Year, Grass, Alfalfa,
	3	865.68	1.72	0.11	0.45	Year, Alfalfa, K
	3	865.91	1.95	0.10	0.45	Year, Alfalfa, Corn
Native	1	597.89	0.00	0.33	0.17	Year
Coccinellidae	2	599.65	1.75	0.13	0.17	Year, K
	2	599.66	1.76	0.14	0.17	Year, N
	2	599.67	1.78	0.14	0.17	Year, P
	2	599.75	1.86	0.13	0.17	Year, Alfalfa
	2	599.82	1.92	0.13	0.17	Year, Simp

Table 3. Continued

Response Variable	K	AIC _c	Δ AIC _c	w_i	Adj. R ²	Variables ^a in Model
Exotic	4	717.13	0.00	0.09	0.51	Year, Grass, Forest
Coccinellidae	2	717.35	0.22	0.08	0.50	Year, Corn
	2	717.50	0.37	0.08	0.50	Year, Grass
	2	717.70	0.57	0.07	0.50	Year, Forest
	3	717.76	0.63	0.07	0.50	Year, Forest, Simp
	5	718.11	0.98	0.06	0.52	Year, Grass, Forest, Alfalfa, Contag
	1	718.15	1.02	0.06	0.50	Year
	3	718.17	1.04	0.05	0.50	Year, Grass, Forest
	3	718.18	1.05	0.05	0.50	Year, Grass, Alfalfa
	2	718.23	1.10	0.05	0.50	Year, Soy
	4	718.58	1.45	0.04	0.51	Year, Forest, Simp, Corn
	3	718.80	1.67	0.04	0.50	Year, Corn, N
	3	718.85	1.72	0.04	0.50	Year, Corn, Soy
	3	718.94	1.81	0.04	0.50	Year, Simp, Corn
	3	718.97	1.84	0.04	0.50	Year, Forest, Corn
	4	718.98	1.85	0.04	0.51	Year, Grass, Forest, Simp
	3	719.07	1.94	0.03	0.50	Year, Alfalfa, Corn
	5	719.08	1.95	0.03	0.51	Year, Grass, Forest, Contag, N
	3	719.13	1.99	0.03	0.50	Year, Grass, Corn
Araneae	4	408.64	0.00	0.15	0.42	Year, Forest, Alfalfa, Corn
	3	408.99	0.35	0.13	0.41	Year, Alfalfa, Corn
	4	409.54	0.90	0.10	0.41	Year, Grass, Alfalfa, Corn
	4	409.71	1.07	0.09	0.41	Year, Alfalfa, Corn, K
	5	409.77	1.12	0.09	0.42	Year, Forest, Alfalfa, Corn, Soy
	5	409.77	1.13	0.08	0.42	Year, Forest, Alfalfa, Corn, K
	5	409.82	1.18	0.08	0.42	Year, Grass, Forest, Alfalfa, Corn
	4	409.04	1.30	0.08	0.41	Year, Alfalfa, Simp, Corn
	5	409.05	1.31	0.08	0.42	Year, Grass, Alfalfa, Corn, K
	5	410.24	1.60	0.07	0.41	Year, Forest, Alfalfa, Contag, Corn
	5	410.29	1.65	0.07	0.41	Year, Forest, Alfalfa, Corn, N
<i>Orius insidiosus</i>	2	660.51	0.00	0.26	0.49	Year, Forest
	3	661.15	0.64	0.19	0.50	Year, Forest, Corn
	2	661.73	1.22	0.14	0.49	Year, Simp
	3	662.20	1.69	0.11	0.49	Year, Forest, P
	3	662.32	1.81	0.10	0.49	Year, Grass, Forest
	2	662.33	1.82	0.10	0.49	Year, Contag
	4	662.36	1.85	0.10	0.50	Year, Forest, Corn, P

Table 3. Continued

Response Variable	K	AIC _c	Δ AIC _c	w_i	Adj. R ²	Variables ^a in Model
<i>Nabis</i> spp.	2	480.98	0.00	0.10	0.30	Year, Alfalfa
	1	481.10	0.11	0.10	0.29	Year
	2	481.16	0.17	0.09	0.30	Year, Forest
	3	481.87	0.89	0.07	0.30	Year, Forest, Corn
	3	482.04	1.06	0.06	0.30	Year, Forest, Contag
	3	482.11	1.13	0.06	0.30	Year, Forest, Alfalfa
	3	482.24	1.26	0.05	0.30	Year, Grass, Forest
	2	482.37	1.39	0.05	0.29	Year, Simp
	3	482.43	1.44	0.05	0.30	Year, Alfalfa, N
	2	482.67	1.69	0.04	0.29	Year, Soy
	3	482.77	1.79	0.04	0.30	Year, Alfalfa, Soy
	4	482.81	1.83	0.04	0.31	Year, Forest, Alfalfa, Corn
	3	482.82	1.83	0.04	0.30	Year, Grass, Soy
	2	482.82	1.88	0.04	0.29	Year, Grass
	2	482.88	1.89	0.04	0.29	Year, N
	3	482.94	1.95	0.04	0.30	Year, Alfalfa, P
	3	482.96	1.97	0.04	0.30	Year, Alfalfa, Corn
	4	482.97	1.98	0.04	0.30	Year, Forest, Alfalfa, Contag

Notes: Bold indicates best-fit model. Competing models are any with Δ AIC_c < 2.

^a Variables abbreviated: Grass = grassland, Simp = Simpson's index (1 - *D*), contag = contagion, soy = soybean, N = soybean plant nitrogen, P = soybean plant phosphorus, and K = soybean plant potassium.

^b Cumulative aphid days (ln + 1).

Figure Legends

- Figure 1. Study site located around Neal Smith National Wildlife Refuge (NSWR) in southeast Jasper County, Iowa (30 km east of Des Moines); inset shows study site location in U.S.
- Figure 2. Mean soybean aphids per plant and week in 2006 – 2008.
- Figure 3. Mean natural enemies collected per sample unit (varied with taxon) and month in 2006 (A), 2007 (B), and 2008 (C).
- Figure 4. Percent land cover at 0.5, 1.0, 1.5, and 2.0 km from the center of all soybean fields in 2006 (A), 2007 (B), and 2008 (C).
- Figure 5. Multidimensional scaling (MDS) analysis showing variation in *A. glycines* (CAD) and natural enemies among sites (A), variation and cluster among *A. glycines* (CAD) and natural enemies (B), and explanatory variables: year, plant nutrients, and landscape parameters (C). The length and direction of vectors indicates the strength and direction of the correlation, and only explanatory variables significant at $P < 0.05$ are shown. Axis one and two explained 75.2% and 15.0% of the variation in the data respectively.
- Figure 6. Relationship between *Aphis glycines* and natural enemies (averaged across seven taxa: *O. insidiosus*, *Nabis* spp., exotic coccinellids, native coccinellids, *Chrysoperla* spp., syrphids, and Araneae) in 2006 – 2008. Weekly aphid and natural enemy abundance data were transformed ($\ln + 1$). Lines associated with the same letters do not have significantly different slopes ($P > 0.05$).
- Figure 7. Alate *A. glycines* counts from a suction trap located in Boone County, Iowa for 2006 – 2008. This was the nearest trap to our study sites (~64 km north).

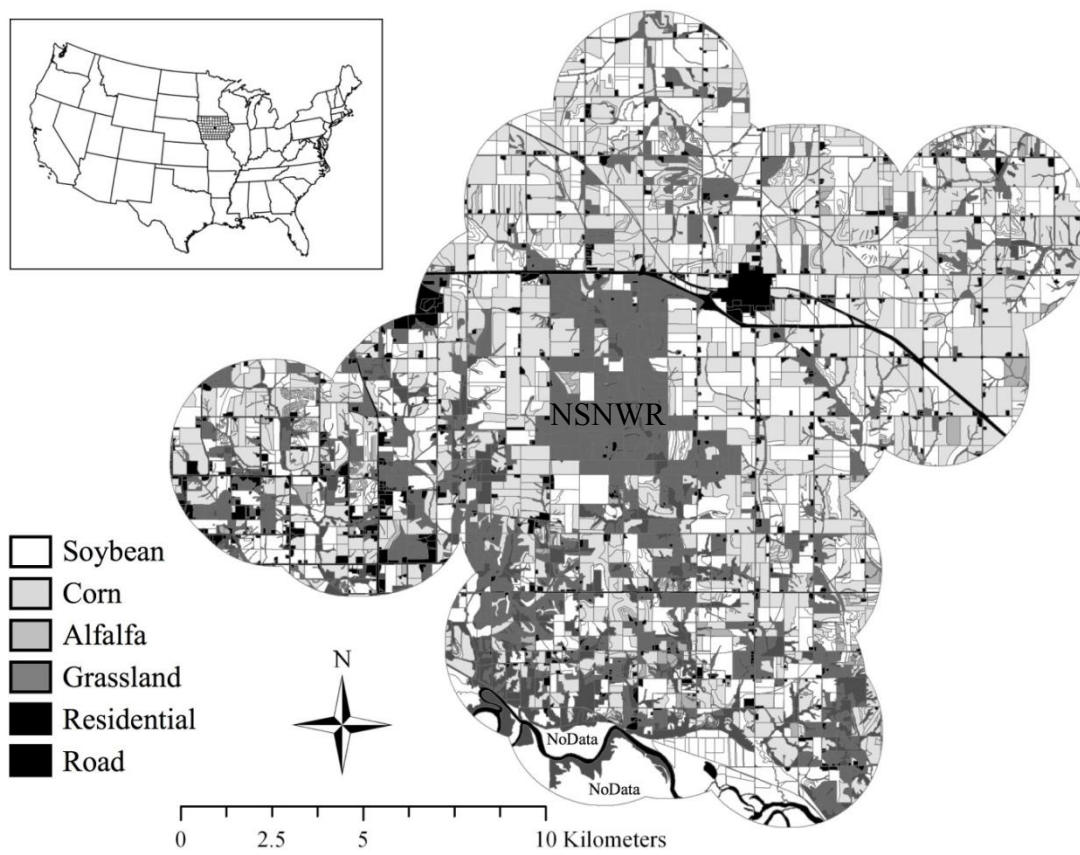


Fig. 1

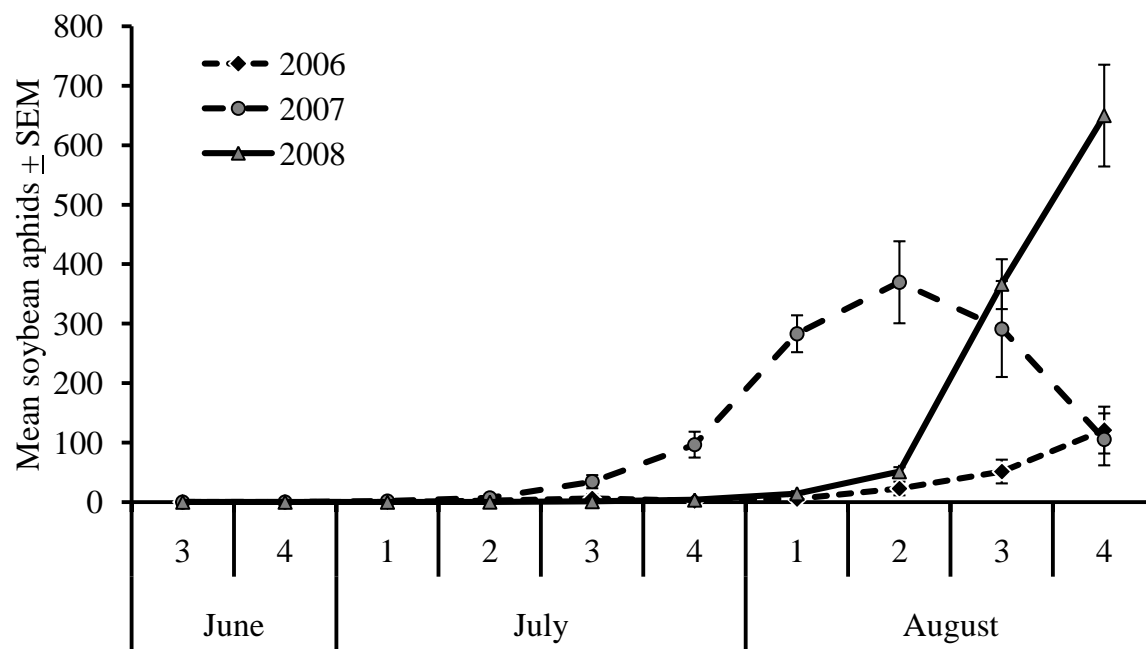


Fig. 2

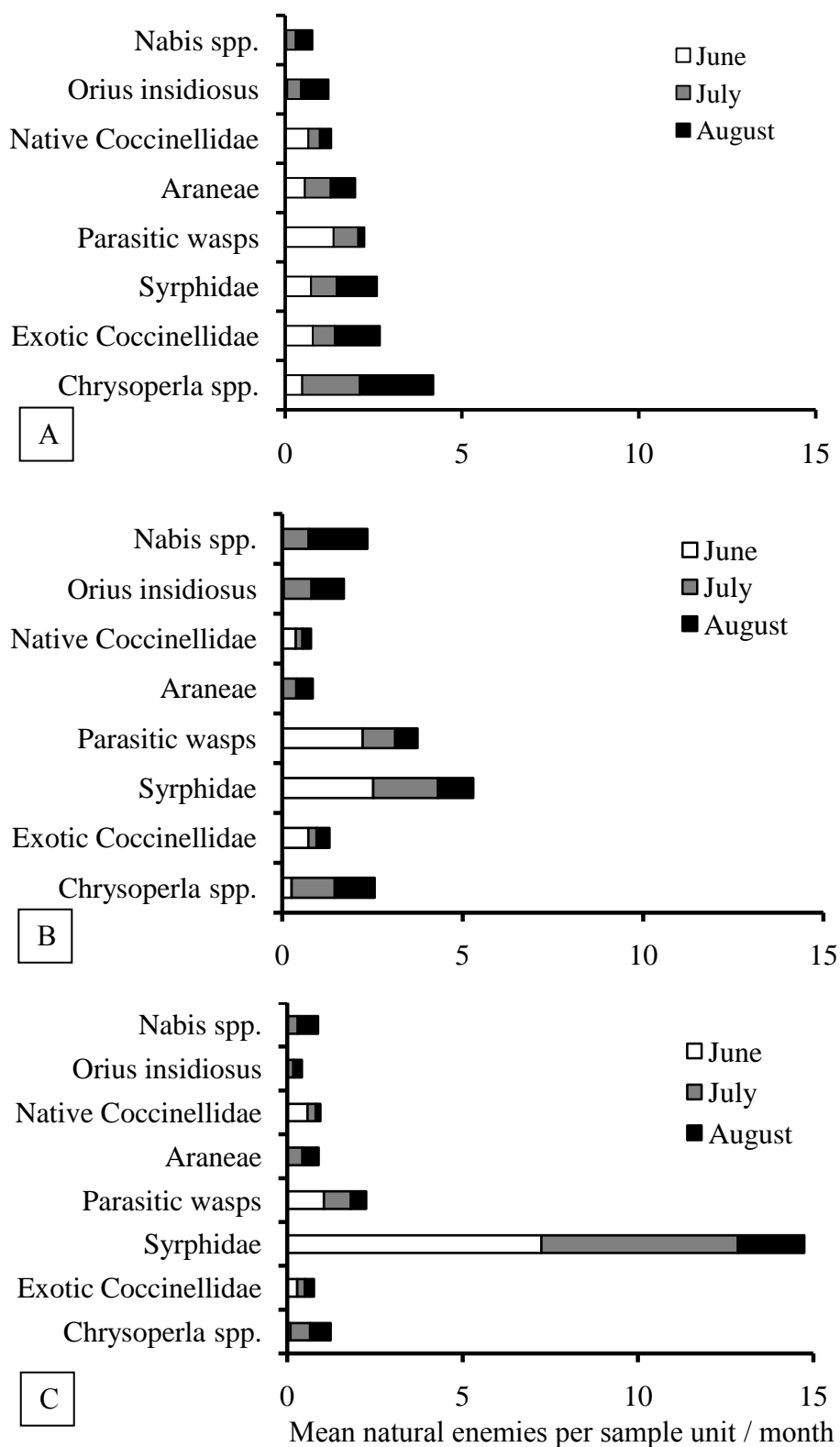


Fig. 3

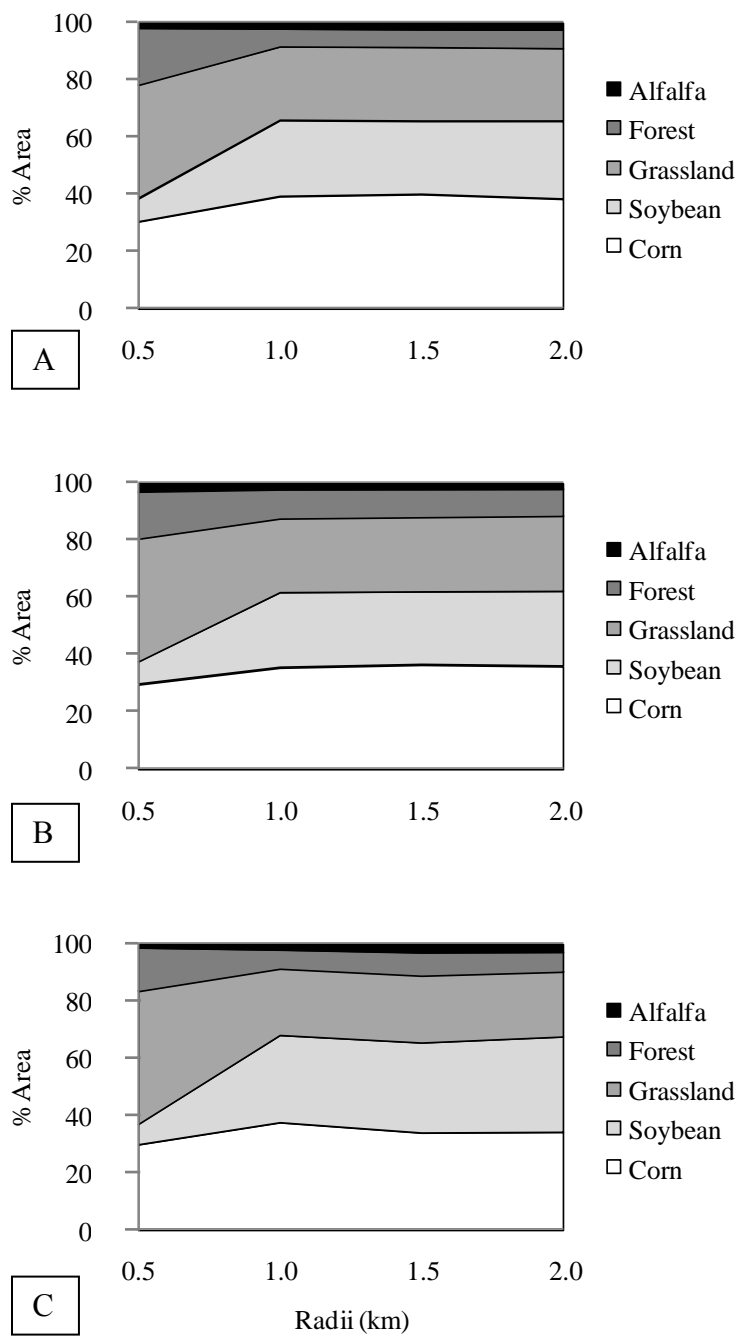


Fig. 4

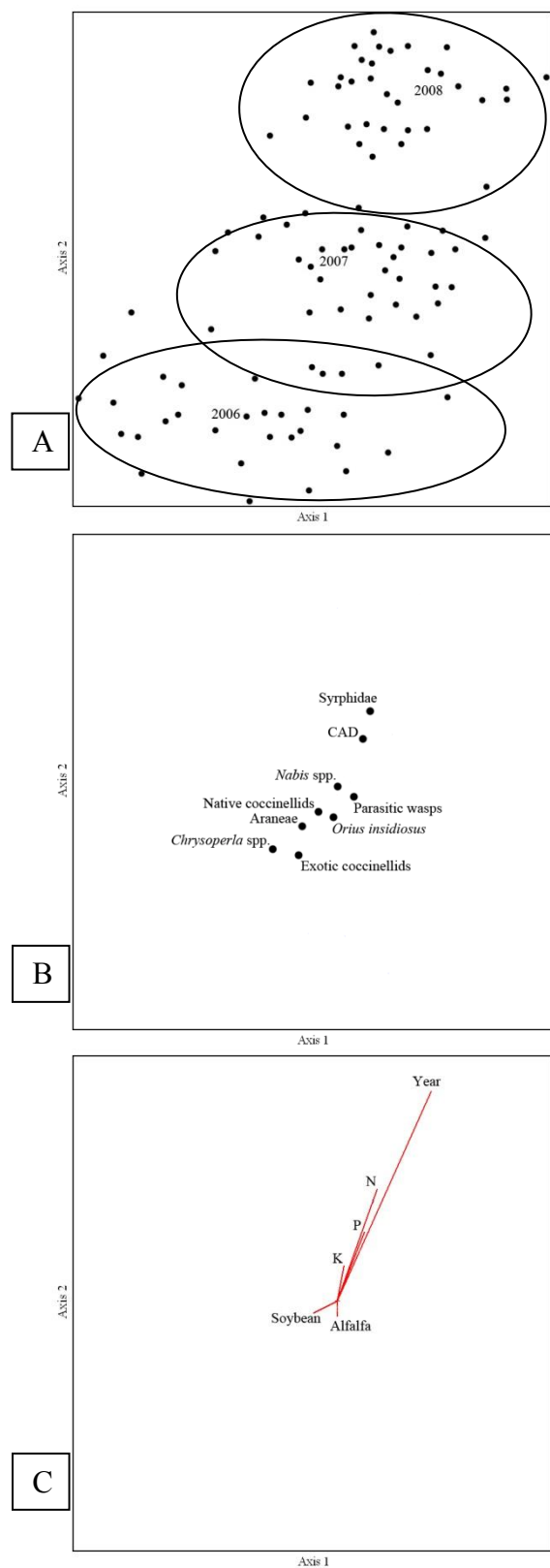


Fig. 5

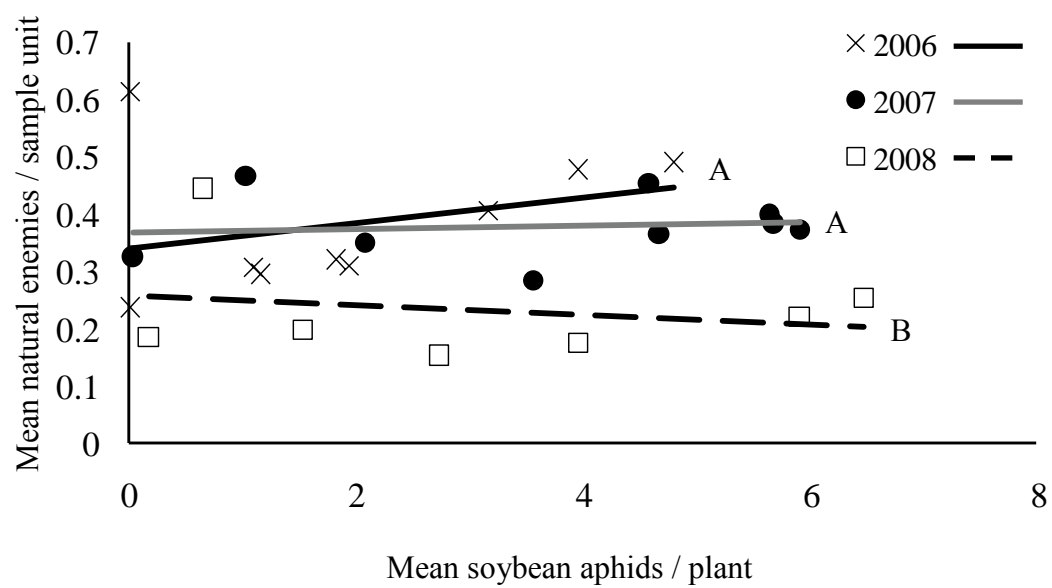


Fig. 6

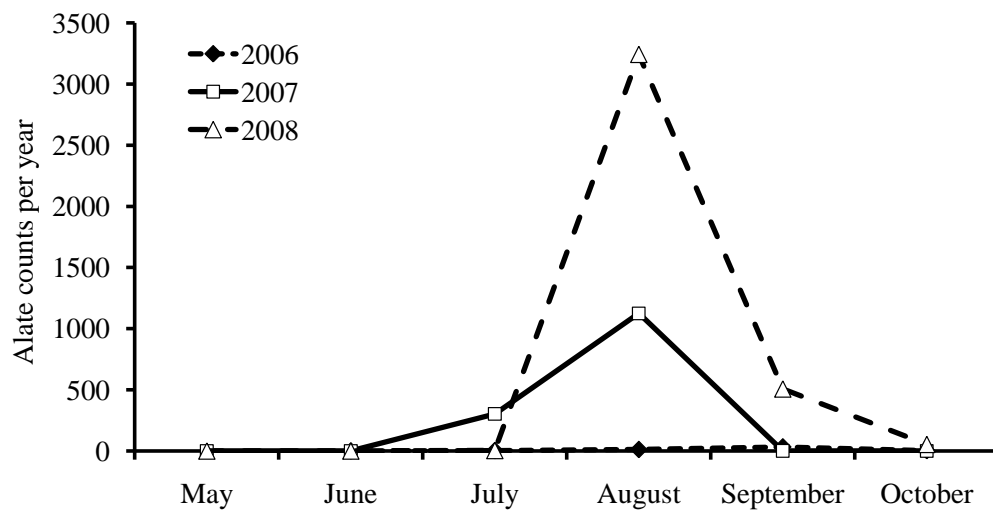


Fig. 7

Chapter 3

How does proximity to prairie affect the abundance of soybean aphids and aphidophagous natural enemies in soybean?

A paper to be submitted to *Environmental Entomology*

Nicholas P. Schmidt and Matthew E. O'Neal

Abstract

Most agroecosystems are highly disturbed environments with limited amounts of natural habitat. The extent to which natural enemies utilize these environments is not fully understood. Our objective was to determine if biological control of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), could be improved through the placement of natural habitats adjacent to soybean, *Glycine max* L. Merr., fields. Specifically, we wanted to determine if remnant and reconstructed prairie harbors an aphidophagous community, and whether soybean adjacent to prairie would have a greater abundance of natural enemies and reduced *A. glycines* population. We hypothesize that prairie increases the abundance and diversity of the aphidophagous community in nearby soybean, and that such an increase reduces *A. glycines* establishment and population growth. This project was conducted in 2006 – 2008 at four sites in central Iowa. We measured *A. glycines* abundance in soybean, and predation using caged and uncaged sentinel plants in soybean and prairie. In addition, we measured natural enemy abundance in soybean and prairie. In 2006, *A. glycines* populations near prairie were significantly lower than those further away, however there was no difference in 2007 and 2008. The soybean aphidophagous community was characterized by a 13.2% greater abundance of natural enemies than prairie, but composition of the two communities was quite similar based on nonmetric multidimensional scaling (NMDS) analyses. Sentinel plant results suggest there was no difference in *A. glycines* predation between soybean and prairie. Analysis of prairie vegetation between sites using NMDS, suggests prairies were composed of non-overlapping plant communities and, thus, are not replicates of one another. Our results suggest that remnant and reconstructed prairies are limited in their ability to harbor all aphidophagous natural enemies. It is recommended that future studies impose a plant selection criterion that specifically addresses their management goals.

KEYWORDS: Conservation, spillover, *Harmonia axyridis*

Introduction

Soybean, *Glycine max* (L.) Merr., grown in the United States had escaped many of the insect pests and diseases associated with it in Asia. As a result, soybean producers in the US had a limited need for pest management interventions for many years (Fernandez-Cornejo and Jans 1999). The introduction of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), has resulted in a serious new economic insect pest of soybean in North America. First discovered in 2000 in Wisconsin, *A. glycines* has been found in 22 US states and parts of Canada (Venette and Ragsdale 2004). It has been estimated that by controlling *A. glycines* over the next 10 years, soybean producers will save between \$949 million to \$1.623 billion (Kim et al. 2008).

The introduction of agroecosystems in Iowa and other states comprising the US Corn Belt has been accompanied by a profound loss of native plant diversity (Smith 1998). Presettlement estimates suggest land in Iowa was approximately 79.5% prairie, 11.7% forest, 6.7% savanna, and 1.4% wetland (Smith 1998). Today, Corn, *Zea mays* L., and soybean dominate Iowa composing approximately 62.8% of the land (USDA 2007), whereas the native prairie occupy < 0.1% of the land (Smith 1998). This decrease in native plant biodiversity may have diminished ecosystem services, including the natural control of insect pests (Kreuss and Tscharntke 1994, Thies and Tscharntke 1999, Elliott et al. 2002, Menalled et al. 2003). Habitat management can help recover some ecosystem services lost by agriculture intensification by conserving natural enemies, resulting in more effective biological control of pests and a sustainable integrated pest management program (Gurr and Wratten 1999, Landis et al. 2000).

The extent to which soybean aphid can be managed in North America by conserving endemic natural enemies is not clear, given its escape from most of its co-evolved natural enemies from its native range in Asia (Rutledge et al. 2004). In Asia, *A. glycines* populations are held below economically damaging levels by the endemic natural enemy community (Liu et al. 2004, Miao et al. 2007). In the US, *A. glycines* is attacked by > 30 predator species, eight parasitoids and several fungal pathogens (Rutledge et al. 2004). *Harmonia axyridis*

(Pallas), *Coccinella septempunctata* L. (Coleoptera: Coccinellidae), and *Orius insidiosus* (Say; Hemiptera: Anthocoridae), have dominated the foliar predator community (Rutledge et al. 2004, Schmidt et al. 2007, Schmidt et al. 2008), and in their absence *A. glycines* populations increase 3-7 fold (Fox et al. 2004, Schmidt et al. 2007, Miao et al. 2007, Gardiner et al. 2009a). Despite evidence for biological control of *A. glycines*, economic losses continue to impact many growers across the north central US, resulting in an increased need for foliar insecticides to maintain acceptable yields (Johnson et al. 2008, Johnson et al. 2009).

Habitat management at the field level via prairie may improve the effectiveness of biological control and lead to a more consistent suppression of *A. glycines* in soybean agroecosystems. Because prairie was once the dominant land cover in Iowa, we anticipate the response of natural enemies in remnant and reconstructed prairie plantings to be improved due to greater availability of alternative foods such as pollen and nectar; greater plant cover that provides shelter from environmental disturbances or a suitable microclimate for overwintering; and greater availability of alternative prey (Landis et al. 2000). Our objective was to determine if the abundance and diversity of the aphidophagous community in soybean is affected by the nearby presence of prairie. Specifically, we hypothesized that the abundance of natural enemies in soybean is greater near prairie, and that the abundance of *A. glycines* is reduced near prairie.

Materials and Methods

Experimental Design. The experiment was conducted over three years (2006 – 2008) at four locations in central Iowa where a single soybean field was planted adjacent to a single established prairie (Figure 1). Characteristics of prairie and soybean fields varied by location (Table 1); but each location was large enough to allow three transects (400 m) from soybean into prairie. The same soybean and prairie fields used in 2006 were used in 2008 at Neal Smith (Table 1). Transects ran perpendicular to the adjoining soybean/prairie field edge and were each 400 m in length (200 m each in soybean and prairie) and 50 m apart (Figure 2). To minimize edge effects, at least 50 m of soybean and prairie remained outside of transects one and three and beyond the ends of all three transects.

Impact of Prairie on *A. glycines* and Natural Enemy Abundance. Using the methods described above, we tested the hypothesis that prairie increases the abundance and diversity of natural enemies and reduces the abundance of *A. glycines* in an adjacent soybean field. Data were collected in both soybean and prairie at 25, 50, 100, 150 and 200 m from the soybean-prairie interface. *Aphis glycines* abundance (all stages) was estimated in soybean, whereas natural enemy abundance (adult, larva or nymph stages) and diversity were estimated from both soybean and prairie. In soybean, *A. glycines* abundance was estimated along each transect using *in situ* field-counts on 20 consecutive plants. The diversity and abundance of aphidophagous natural enemies were measured by sampling with sweep-net (38 cm diameter) and yellow-sticky cards (27 by 45 cm folded in half so it was sticky on both sides; Pherocon AM, Trécé, Inc. Adair, OK). Multiple sampling techniques were used because some natural enemy taxa are more efficiently sampled with sweep-nets and others yellow-sticky cards (Schmidt et al. 2008). A single yellow-sticky card was suspended above the plant canopy on a wooden stake; in addition, 20 pendulum sweep-net samples were conducted perpendicular to transects.

Sampling was conducted over a 7-d period in June, July, and August. On day one, yellow-sticky cards were deployed, *A. glycines* was counted, and sweep-net samples were collected. Seven days later, yellow-sticky cards were removed, and again *A. glycines* was counted, and sweep-net samples were collected. All natural enemies collected from yellow-sticky cards and sweep-net samples were bagged and stored at -20°C until specimens could be sorted. Natural enemies were identified to family except for *O. insidiosus*, *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae), and members of Coccinellidae, which were identified to species. Both adult and immature stages of natural enemies were counted and voucher specimens were deposited in the Iowa State Insect Collection at Iowa State University, Ames, IA.

Data Analysis. We used a mixed model analysis of variance (ANOVA) to determine if distance from prairie affected the abundance of *A. glycines* for each year. The average number of aphids per plant was calculated and transformed ($\ln + 1$) to meet the assumptions

of ANOVA (Sokal and Rohlf 1995). Data collected in the month of June was removed from analyses in all years due to extremely low aphid populations; in addition, data collected in July of 2006 had low aphid populations so it was also removed. Due to the variability in *A. glycines* abundances, years were analyzed separately. To determine whether *A. glycines* abundance was affected by distance from prairie, the model used month, transect, and distance as fixed factors and site as a random factor, with month as a repeated measure (PROC MIXED, SAS Institute 2008). Pairwise comparisons, produced using LSMEANS, were made using the Tukey-Kramer test to control the experimentwise error rate.

Natural enemy data were similar between sites; therefore all sites were combined for analyses. Averages of natural enemy abundance for both sweep-net samples and yellow-sticky cards were calculated for each year, and transformed using $(\ln + 1)$ to reduce heteroscedascity. The abundance of individual aphidophagous taxa collected were also summarized for sweep-nets and yellow-sticky cards in June, July, and August in soybean and prairie. Natural enemy data did not meet the assumptions of ANOVA due to a non-normal distribution; therefore, nonparametric analyses were used. To determine differences between aphidophagous community in soybean and prairie, nonmetric multidimensional scaling (NMDS) was used with the Bray-Curtis distance measure (Bray and Curtis 1957). NMDS summarizes relationships between pairs of species data and represents them in multiple dimensions as distances, so the closer two points were, the more similar they were (Kenkel and Orlóci 1986). In addition, a principal components analysis (PCA) was used to determine which natural enemies explained most of the variability in data from prairie and soybean (Oksanen et al. 2010, R Development Core Team 2009). The covariance matrix was created using monthly count data to determine the variance of species and the degree to which species were correlated. Individual natural enemies that explain most of the variation within the PCA were identified and a nonparametric test (the Spearman rank correlation) was used to determine whether natural enemy abundance was affected by distance from prairie and soybean (Harrell et al. 2009, R Development Core Team 2009). A Bonferroni correction ($P < 0.05$) was used to control the experimentwise error rate.

Sentinel Plant Study. In 2007 and 2008, within the study sites established from the previous experiment, we tested the hypotheses that aphid predation is greater in prairie, and in soybean nearer prairie. Paired sentinel plants were placed at 25 and 200 m in both soybean and prairie (Fig. 2). A sentinel plant was a single V3 (three fully developed trifoliolate leaf nodes; Pederson 2004) soybean plant reared in a growth chamber and infested with 50 *A. glycines* from a colony maintained at the Department of Entomology, Iowa State University. This colony was developed from *A. glycines* collected in a soybean field in Story Co., IA, in August 2006 and maintained on vegetative stage soybean in growth chambers. To determine if aphid densities were the response of natural enemies, one of the two sentinel plants at each distance were caged with fine-mesh "no-seeum" netting (Balson-Hercules, New York, NY). Sentinel plants were established for a 72 h period in June, July, and August of 2007, and July and August of 2008 (delays in planting, due to flooding, did not allow us to conduct the experiment in June). At each site, sentinel plants were placed in two of the three transects, with the rows selected at random. Post 72 h, *A. glycines* was counted and recorded for both the caged and uncaged sentinel plant. In addition, we searched for natural enemies and aphid mummies on uncaged plants, which were then caged and held for 72 h, and inspected a second time for the development of additional aphid mummies.

Data Analysis. We used a mixed model analysis of variance (ANOVA) to determine if a difference in *A. glycines* was observed between sentinel plants (caged and uncaged), in addition to uncaged sentinel plants at 25 and 200 m. We calculated an average number of aphids (all stages were counted) per plant and this average was $(\ln + 1)$ transformed to meet the assumptions of ANOVA (Sokal and Rohlf 1995). Data from 2007 and 2008 were analyzed across all sites. To determine whether there was a cage effect on *A. glycines* abundance, the model used month, transect, crop and cage as fixed factors with site as a random factor. To determine whether there was an effect of distance on uncaged *A. glycines* in soybean, the model used month, transect, crop and distance as fixed factors with site as a random factor (PROC MIXED, SAS Institute 2008). No natural enemies or aphid mummies were observed on uncaged sentinel plants, so no further analyses were conducted.

Prairie Plant Community. In 2007 and 2008, we tested the hypothesis that prairie plant communities were different between sites. At each prairie in late July to early August, data were collected at 15 random locations along 3-100 m transects in a 1-m quadrat. Within each quadrat, percent canopy cover was estimated for each plant species. Because not all plants exhibited enough characteristics to be identified to species, some were identified only to genus.

Data Analysis. To determine differences between plant communities at the four sites, species richness and evenness (Simpson's diversity indices [1-D]) were calculated. In addition, nonmetric multidimensional scaling (NMDS) or ordination was used with the Bray-Curtis distance measure (Bray and Curtis 1957).

Results

Impact of Prairie on *A. glycines* and Natural Enemy Abundance. There was a large amount of variation in *A. glycines* populations between years (Figure 3). In 2006, *A. glycines* populations were extremely low in June and July; and in August the field average peaked at eight aphids per plant at the only site tested (Neal Smith). Despite these low populations, significant differences in *A. glycines* abundance due to distance from prairie were observed ($F_{4,8} = 4.3$; $P = 0.03$). Soybean plants near prairie (25, 50, and 100 m) had lower aphid densities than those far from prairie (200 m; Figure 4). In 2007, average seasonal population densities of *A. glycines* populations were greater (Doolittle – 43, Morris – 138, Grant Ridge – 184 aphids/plant), and in 2008 populations peaked at 629 aphids/plant at the only site tested (Neal Smith). No significant differences in *A. glycines* abundance by distance were observed in either 2007 ($F_{4,32} = 0.07$; $P = 0.99$) or 2008 ($F_{4,8} = 3.41$; $P = 0.07$).

A total of 2,047 natural enemies were collected with sweep-nets (948 in soybean and 1,099 in prairie) and 2,030 with yellow-sticky cards (1,358 in soybean and 672 in prairie; Table 2). We observed a greater diversity of natural enemies collected with sweep-nets in prairie (26) than soybean (23); however, the species richness of natural enemies collected on yellow-sticky cards in prairie and soybean was the same (13; Table 2). *Orius insidiosus* was the most abundant natural enemy collected with sweep-nets and 98% of those were collected

in soybean (Table 2). In contrast, parasitic wasps (Ichneumonidae and Braconidae) were the most abundant natural enemy collected in prairie with sweep-nets and only 26% of the total collected were observed in soybean (Table 2). On yellow-sticky cards, adult syrphids were the most abundant natural enemy collected in soybean and 77% of those collected were in soybean (Table 2). In contrast, parasitic wasps were the most abundant natural enemy collected in prairie on yellow-sticky cards and 43% of the total collected came from soybean (Table 2).

The mean abundance of natural enemies collected with sweep-nets (Figure 5A) and yellow-sticky cards (Figure 5B) were pooled across years and sites. We observed the following trends in the abundance of natural enemies observed from sweep-net data: June natural enemies in soybean < prairie; July, soybean > prairie; and August, soybean > prairie (Figure 5A). We observed the following trends for natural enemies collected on yellow-sticky cards: June, soybean < prairie; July, soybean \approx prairie; August, soybean > prairie (Figures 5B).

We summarized the total abundance of individual aphidophagous taxa, collected in June, July, and August in soybean and prairie by sweep-nets (Figures 6A, 6B) and yellow-sticky cards (Figure 7A, 7B). Soybean sampled in June with sweep-nets collected none or a very low number of natural enemies (Figure 6A); whereas a large number of Araneae and parasitic wasps were collected in prairie (Figure 6B). A moderate number of multiple natural enemies and a large number of Araneae were collected in soybean in July with sweep-nets (Figure 6A), whereas large numbers of syrphids, parasitic wasps, and Araneae were collected in prairie (Figure 6B). Moderate numbers of *Chrysoperla* spp. and *Nabis* spp., and a large number of *O. insidiosus*, were collected in soybean sampled in August with sweep-nets (Figure 6A), whereas a moderate number of Araneae (Figure 6B) was collected in prairie.

The pattern of natural enemy abundance was different when observed with yellow sticky cards. Yellow-sticky cards in June collected a large number of parasitic wasps in both soybean and prairie (Figure 7A, 7B). A large number of syrphids were collected in soybean sampled with yellow-sticky cards in July (Figure 7A); whereas cards in prairie collected a moderate number of syrphids and parasitic wasps (Figure 7B). Yellow-sticky cards collected

a large number of *Chrysoperla* spp. and syrphids in soybean in August (Figure 7A); whereas cards in prairie collected a moderate number of syrphids (Figure 7B).

Because natural enemy abundance in soybean was not normally distributed, we were not able to use ANOVA to determine the effect of distance from prairie on this community. Therefore, we employed Spearman rank correlations on taxa that were the most frequently observed with both sampling methods. We used PCA to determine which natural enemies explained the greatest variability within the larger community (N.P.S. unpublished data). Five aphidophagous taxa (parasitic wasp, syrphids, *O. insidiosus*, *Nabis* spp., and *Chrysoperla* spp.) were selected from yellow-sticky card data, and six (parasitic wasp, Araneae, syrphids, *O. insidiosus*, *Nabis* spp., and *Chrysoperla* spp.) from sweep-net data. Spearman rank correlations ($n=18$) were conducted on each taxon identified above, for both sampling methods and all months. Syrphids in soybean and prairie collected in July with sweep-nets were the only natural enemy whose abundance in soybean was significantly correlated (up to 200 m in soybean; $P < 0.05$) with its abundance in prairie (Table 3).

To determine if there were differences in the aphidophagous community in soybean and prairie, NMDS was used with the Bray-Curtis distance measure (Figure 8). The overlapping hulls suggest that soybean and prairie had a similar aphidophagous community (Figure 8).

Sentinel Plant Study. To determine whether natural enemies in both soybean and prairie were able to provide top down control of *A. glycines*, half of the sentinel plants were caged to exclude natural enemies. We found significantly more *A. glycines* in caged than uncaged plants ($F_{1,150} = 36.90$; $P < 0.0001$), suggesting that natural enemies in both soybean and prairie were capable of suppressing *A. glycines* populations (Figure 9). We also wanted to determine whether uncaged plants in prairie and soybean in closest proximity to prairie (25 m) would have reduced *A. glycines* populations compared to those in soybean furthest away (200 m). We did not observe a significant difference in the abundance of aphids on the uncaged plants at 25 m or 200 m into either habitat ($F_{1,38} = 0.45$; $P = 0.51$; Figure 10).

Prairie Plant Community. Plant surveys suggest that there were differences in the percent

cover of the prairie plant community between sites (Table 4). In 2006 and 2008 the same prairie was used, however, we only sampled the plant community in 2008. Plant species richness was greatest at Morris (52) > Doolittle (46) > Grant Ridge (41) > Neal Smith (19), and evenness, measured by Simpson's diversity index (1-D), was greatest in Doolittle (0.95) > Morris (0.89) > Grant Ridge (0.88) > Neal Smith (0.79; Table 4). To determine differences among sites, NMDS was used with the Bray-Curtis distance measure; the non-overlapping hulls suggest that sites have different plant communities (Figure 11).

Discussion

Our results suggest that remnant and reconstructed prairies in central Iowa were capable of harboring some natural enemies (Table 2). In addition, natural enemies were able to suppress *A. glycines* on sentinel plants (Figure 9); however, suppression of *A. glycines* was not greater in soybean that was near prairie (Figure 10). *Aphis glycines* populations in 2006 were much lower than those in 2007 and 2008, and it was the only year when populations were significantly lower on soybean nearest prairie (Figure 4). An explanation for this may be reduced *A. glycines* populations allowed more time for the natural enemy community to respond. Since sampling was only conducted over one 7-d period each month, it is difficult to pinpoint the mechanism(s) driving this event.

In prairie, both sweep-nets and yellow-sticky cards collected a large abundance of natural enemies in June (Figure 5), which was dominated by parasitic wasps (Figures 6, 7). In soybean, sweep-nets collected no parasitic wasps in June, suggesting they were not landing on soybean (Figure 6); however, parasitic wasps were the most abundant natural enemy collected on yellow-sticky cards, suggesting they were flying through soybean fields (Figure 7). This suggests an endemic parasitic wasp community may be enhanced by nearby remnant and reconstructed prairie. The impact that this guild of natural enemies may have on *A. glycines* is not clear. We did not identify parasitic wasps to a level at which aphid parasitoids could be identified. Only three parasitized aphid mummies were observed in soybean over the three years of this study. The phenological asynchrony between parasitic wasps and *A. glycines*, which typically do not establish until July, may be an explanation as to why very few parasitized *A. glycines* were observed on soybean.

Orius insidiosus and *H. axyridis* are considered important predators for control of *A. glycines* (Costamagna and Landis 2006, Rutledge et al. 2004), and regardless of collection method, 98 – 91.4% were exclusively found in soybean throughout the three years of this study (Table 2). This suggests that remnant and reconstructed prairies may not be suitable habitat for *O. insidiosus* and *H. axyridis* during summer months (Table 2). Soybean sampled in a four state region (Iowa, Michigan, Minnesota, and Wisconsin), found *O. insidiosus* and *H. axyridis* to be the two most abundant predators (Gardiner et al. 2009a, Noma et al. 2010). Saulich and Musolin (2008), found *O. insidiosus* are active on wild flowering herbaceous plants in March and April, however, in June they emigrate to crop plants (soybean, corn, etc.). Furthermore, *O. insidiosus* are especially attracted to flowering corn (Saulich and Musolin 2008), therefore levels of *O. insidiosus* in soybean may be influenced by adjacent corn. Rand and Louda (2006) observed greater pest suppression in agriculturally dominated landscapes because of a spillover of generalist predators from surrounding agroecosystems. In contrast, *Harmonia axyridis* prefers wooded habitats in its native range (Chapin and Brou 1991). Gardiner et al. (2009b) found the abundance of exotic coccinellids in soybean was negatively correlated with the occurrence of grassland-dominated landscapes (Gardiner et al. 2009b). Specifically, *H. axyridis* was positively associated with forested landscapes, and the lowest abundance of *H. axyridis* in soybean was in grassland-dominated landscapes (Gardiner et al. 2009b).

Although this was not our initial hypothesis, our results support Gardiner et al. (2009b), that prairie may “buffer” against the establishment of *O. insidiosus* and *H. axyridis* within soybean. If true, prairie may not harbor natural enemies that are important for the biological control of *A. glycines*. However, *H. axyridis* is invasive within North America and is considered a pest in urban and some fruit production systems (Koch and Galvan 2008). Therefore, the benefit of incorporating prairie into a landscape may vary depending upon the management goals. Our results suggest that it may be possible to limit the abundance of *H. axyridis* in these habitats by increasing the amount of grassland (i.e. prairie) within the landscape.

Despite the limited numbers of *O. insidiosus* and *H. axyridis* observed in prairie, we still observed a large abundance of both in soybean during August (Figures 6, 7). During

August we observed the highest density of *A. glycines*, suggesting that the occurrence of *O. insidiosus* and *H. axyridis* in soybean is potentially influenced by a density-dependent response to increased *A. glycines* populations (Figures 6, 7; Rutledge et al. 2004).

Syrphids were also observed in both soybean and prairie (Table 2), and were the only natural enemy whose abundance in soybean was positively correlated (up to 200 m) with its abundance in prairie (Table 3). In a similar study, Jauker et al. (2009) observed more syrphids at distances greater than 2,000 m from semi-natural habitat, suggesting that syrphids may respond to landscapes at a larger scale than addressed in this study. Larvae of some syrphids are predaceous and since the arrival of *A. glycines* in North America, syrphids have been observed more frequently in soybean (Schmidt et al. 2008). However, it is not clear if larvae of syrphids are a significant source of *A. glycines* mortality.

Comparison of *A. glycines* on caged and uncaged sentinel plants, suggests natural enemies were capable of suppressing *A. glycines* (Figure 9). These data support previous research utilizing cage experiments to determine the top-down suppression natural enemies provide for control of *A. glycines* (Fox et al. 2004, Costamagna and Landis 2006, Schmidt et al. 2007, Gardiner et al. 2009a). However, no differences were observed in the amount of aphid suppression on uncaged sentinel plants between prairie and soybean at 25 and 200 m, refuting our hypothesis that the abundance of *A. glycines* will be reduced near prairie at the spatial scale tested (Figure 10). This lack of difference in aphid suppression between 25 and 200 m may be due to the similarity in the aphidophagous community in soybean and prairie (Figure 8). The majority of these natural enemies were generalists. So, although some predators may respond positively to prairie (i.e. syrphids), the suppression of *A. glycines* may have been dampened due to an increase in the amount of intraguild predation in soybean. Furthermore, the length of transects may have been too short to observe decay over distance in the abundance of individual natural enemies and the suppression of *A. glycines*.

Comparison of the plant communities at the four sites suggests that the remnant and reconstructed prairies were quite different (Figure 11). To what extent this variation contributed to our measurements of natural enemy abundance and diversity, as well as *A. glycines* suppression is not clear. Fiedler et al. (2008) suggested that native plants may best enhance the biodiversity of organisms. Some native plant species found in the prairies of our

study are attractive to beneficial insects (Fiedler and Landis 2009). For example, *Aster laevis*, *Ratibida pinnata*, *Silphium perfoliatum*, and *Zizia aurea* were present in some of the prairies (Table 4), and are considered moderately to highly attractive to natural enemies (Fiedler and Landis 2009). The number of individuals of these species within any one prairie was often limited, as estimated by the percent cover. So even though three of the prairies had a species rich environment (Table 4), the diversity and abundance of plants may not have been optimal for enhanced biological control of *A. glycines*.

In summary, an aphidophagous community does exist in both soybean and prairie; however, biological control of *A. glycines* in soybean did not improve with decreased distance to prairie over the 200-m scale tested. Not knowing the extent to which these generalist natural enemies interact makes it difficult to determine which species is responding to particular prey species. It would be interesting to analyze predator gut contents to determine the level of intraguild predation among the natural enemies. Harwood et al. (2009) identified *O. insidiosus* as a valuable natural enemy because it exerted significant predation on *A. glycines* and had a limited consumption of *H. axyridis*. In contrast, Gardiner and Landis (2007) identified *H. axyridis* as an intraguild predator, yet *H. axyridis* was able to suppress *A. glycines* compared to control treatments. It is also unclear whether soybean functions as a source or sink for natural enemies. As discussed by Landis et al. (2000) and Fiedler et al. (2008), future attempts to measure the impact of mixed species habitats on ecosystem service delivery, should consider limiting the variability of the plant community to those species most likely to improve the targeted service.

Acknowledgments

We thank Cindy Hildebrand for allowing us to perform research in the Grant Ridge prairie, William C. Watson and Anna MacDonald for identifying prairie plants, Adam Pinter for assistance with statistical analyses, and the following summer workers for assisting in data collection: Finn Pillsbury, Dustin Paulson, Daniel Stull, Robert Moore, Monica McGrew, Cory Dunlay, Amy Harvey, Daniel Au, Satish Hanmanthgari, Matthew Raymond, Nathan Johnson, Matthew Maher, and Andrew Thraenert. This journal paper of the Iowa Agriculture and Home economics Experiment Station, Ames, Iowa, Project No. 5032, was supported by Hatch Act and State of Iowa funds.

References

- Bray, J. R., and J. T. Curtis. 1957.** An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27: 325-349.
- Chapin, J. B., and V. A. Brou. 1991.** *Harmonia axyridis* (Pallas), the third species of the genus to be found in the United States (Coleoptera: Coccinellidae). *Proc. Entomol. Soc. Wash.* 93: 630-635.
- Costamagna, A., and D. A. Landis. 2006.** Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecol. Applic.* 16: 1619-1628.
- Elliott, N. C., R. W. Kiekefer, G. J. Michaels, and K. L. Giles. 2002.** Predator abundance in alfalfa fields in relation to aphids, within-field vegetation, and landscape matrix. *Environ. Entomol.* 31: 253-260.
- Fernandez-Cornejo, J., and S. Jans. 1999.** Pest management in U.S. Agriculture. Resource Economics Division, Economic Research Service, U.S. Department of Agriculture. Agriculture Handbook No 717.
- Fiedler, A. K., D. A. Landis, and S. D. Wratten. 2008.** Maximizing ecosystem services from conservation biological control: The role of habitat management. *Biol. Control* 45: 254-271.
- Fiedler, A. K., and D. A. Landis. 2009.** Which plants are best?
<http://nativeplants.msu.edu/results.htm>
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004.** Predators suppress *Aphis glycines* Matsumura population growth in soybean. *Environ. Entomol.* 33: 608-618.
- Gardiner, M. M., and D. A. Landis. 2007.** Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biol. Control* 40: 386-395.
- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. Chacon, M. Wayo, N. P. Schmidt, E. Mueller, and G. E. Heimpel. 2009a.** Landscape diversity enhances the biological control of an introduced crop pest in the north-central USA. *Ecol. Applic.* 19: 143-154.

- Gardiner, M. M., D. A. Landis, C. Gratton, N. P. Schmidt, M. O'Neal, E. Mueller, J. Chacon, G. E. Heimpel, and C. D. DiFonzo. 2009b.** Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity Distrib.* 15: 554-564.
- Gurr, G. M., and S. D. Wratten. 1999.** 'Integrated biological control': A proposal for enhancing success in biological control. *Int. J. Pest Manage.* 45: 81-84.
- Harrell, F. E. Jr and with contributions from many other users. 2009.** Hmisc: Harrell Miscellaneous. R package version 3.7-0. <http://CRAN.R-project.org/package=Hmisc>
- Harwood, J. D., H. J. S. Yoo, M. H. Greenstone, D. L. Rowley, and R. J. O'Neil. 2009.** Differential impact of adults and nymphs of a generalist predator on an exotic invasive pest demonstrated by molecular gut-content analysis. *Biol. Invasions* 11: 895-903.
- Jauker, F., T. Diekötter, F. Schwarzbach, and V. Wolters. 2009.** Pollinator dispersal in an agricultural matrix: Opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecol.* 24: 547-555.
- Johnson, K. D., M. E. O'Neal, J. D. Bradshaw, and M. E. Rice. 2008.** Is preventative, concurrent management of the soybean aphid (Hemiptera: Aphididae) and bean leaf beetle (Coleoptera: Chrysomelidae) possible? *J. Econ. Entomol.* 101: 801-809.
- Johnson, K. D., M. E. O'Neal, D. W. Ragsdale, C. D. Difonzo, S. M. Swinton, P. M. Dixon, B. D. Potter, E. W. Hodgson, and A. C. Costamagna. 2009.** Probability of cost-effective management of soybean aphid (Hemiptera: Aphididae) in North America. *J. Econ. Entomol.* 102: 2101-2108.
- Kenkel, N. C., and L. Orlóci. 1986.** Applying metric and nonmetric multidimensional scaling to ecological studies: Some new results *Ecology* 67: 919-928.
- Kim, C. S. G. Schaible, L. Garret, R. Lubowski, and D. Lee. 2008.** Economic impacts of the U.S. soybean aphid infestations: A multi-regional competitive dynamic analysis. *Agri. Res. Econ. Rev.* 227-242.
- Koch, R. L., and T. L. Galvan. 2008.** Bad side of a good beetle: The North American experience with *Harmonia axyridis*. *BioControl* 53: 23-35.

- Kreuss, A. and T. Tschardtke. 1994.** Habitat fragmentation, species loss, and biological control. *Science* 264: 1581-1584.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000.** Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175-201.
- Liu, J., K. M. Wu, K. R. Hopper, and K. J. Zhao. 2004.** Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and its natural enemies in soybean in northern China. *Ann. Entomol. Soc. Am.* 97: 235-239.
- Menalled, F. D., A. C. Costamagna, P. C. Marino, and D. A. Landis. 2003.** Temporal variation in the response of parasitoids to agricultural landscape structure. *Agric. Ecosyst. Environ.* 96: 29-35.
- Miao, J., K. Wu, K. R. Hopper, and G. Li. 2007.** Population dynamics of *Aphis glycines* (Homoptera: Aphididae) and impact of natural enemies in northern China. *Environ. Entomol.* 36: 840-848.
- Noma, T., C. Gratton, M. Colunga-Garcia, M. J. Brewer, E. E. Mueller, Kris, A. G. Wyckhuys, G. E. Heimpel, and M. E. O'Neal. 2010.** Relationship of soybean aphid (Homoptera: Aphididae) to soybean plant nutrients, landscape structure, and natural enemies. *Environ. Entomol.* 39: 31-41.
- Oksanen, J. F., G. Blanchet, R. Kindt, P. Legendre, R. G. O'Hara, G. L. Simpson, P. M. Solymos, H. H. Stevens, and H. Wagner. 2010.** *Vegan: Community Ecology Package*. R package version 1.17-0. <http://CRAN.R-project.org/package=vegan>
- Packard, S., and C. F. Mutel. 1997.** *The tallgrass restoration handbook for prairies, savannas, and woodlands*. Society for ecological restoration, Ed. Island Press. Washington, DC.
- Pederson, P. 2004.** Soybean growth and development. Iowa State University Extension.
- R Development Core Team. 2009.** *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>
- Rand, T. A., and S. M. Louda. 2006.** Spillover of agriculturally subsidized predators as a potential threat to native insect herbivores in fragments landscapes. *Conserv. Biol.* 20(6): 1720-1729.

- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004.** Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240-248.
- SAS Institute Inc., 2008.** SAS OnlineDoc, Version 9.2 SAS Institute Inc. Cary, NC.
- Saulich, A. Kh., and D. L. Musolin. 2009.** Seasonal development and ecology of anthocorids (Heteroptera: Anthocoridae). *Entomol. Rev.* 89: 501-828.
- Schmidt, N. P., M. E. O'Neal, and P. M. Dixon. 2008.** Aphidophagous predators in Iowa soybean: A community comparison across multiple years and sampling methods. *Ann. Entomol. Soc. Am.* 101: 341-350.
- Schmidt, N. P., M. E. O'Neal, and J. W. Singer. 2007.** Alfalfa living mulch advances biological control of soybean aphid. *Environ. Entomol.* 36: 416-424.
- Sokal, R. R., and F. J. Rohlf. 1995.** Biometry: The Principles and Practice of Statistics in Biological Research. 3rd edition. W. H. Freeman and Co.: New York.
- Thies, C., and T. Tscharntke. 1999.** Landscape structure and biological control in agroecosystems. *Science* 285: 893-895.
- United States Department of Agriculture (USDA). 2007.** National Agricultural Research Service. 2007 census of agriculture report, Vol. 1, U.S. summary and state reports (Table 26). Washington, D.C.
- Venette, R. C., and D. W. Ragsdale. 2004.** Assessing the invasion by soybean aphid (Homoptera: Aphididae): Where will it end? *Ann. Entomol. Soc. Am.* 97: 219-226.

Table 1. Characteristics of the four study sites in central Iowa

Year			Coordinates ^a			
	Site	County Name	Latitude, Longitude	Field	Type	Size (ha)
2006						
	Neal Smith ^b	Jasper	41.5352, -93.2689	Prairie	Reconstructed ^c	27
	-	Jasper	41.5352, -93.2745	Soybean	38 cm row, No-till	28
2007						
	Doolittle ^d	Story	42.1474, -93.5888	Prairie	Remnant ^e	16
	-	Story	42.1536, -93.5888	Soybean	76 cm row, Tilled	27
	Grant Ridge ^f	Story	41.9673, -93.4709	Prairie	Reconstructed	20
	-	Story	41.9673, -93.4754	Soybean	76 cm row, Tilled	30
	Morris ^g	Jasper	41.7710, -92.9627	Prairie	Remnant	8
	-	Jasper	41.7693, -92.9627	Soybean	38 cm row, No-till	14
2008						
	Neal Smith	Jasper	41.5352, -93.2689	Prairie	Reconstructed	27
	-	Jasper	41.5352, -93.2745	Soybean	38 cm row, No-till	28

^a Decimal degrees.

^b Neal Smith National Wildlife Refuge, public land managed by the U.S. Fish and Wildlife Service. The same fields were used in 2006 and 2008. Prairie was located east of soybean field.

^c Prairie planted on plowed ground (Packard and Mutel 1997).

^d Doolittle prairie, public land managed by Story County Conservation. Prairie was located south of soybean field.

^e Prairie with all or a portion of its presettlement characteristics intact (Packard and Mutel 1997).

^f Grant Ridge prairie, private land managed by Cindy Hildebrand. Prairie was located east of soybean field.

^g A. C. & Lela Morris prairie, public land managed by Jasper County Conservation. Prairie was located north of soybean field.

Table 2. Total natural enemies collected in soybean and prairie by sweep-net and yellow-sticky cards, in addition to the total percent observed in soybean

Trapping method	Total		Percent
Taxon collected	Soybean	Prairie	Observed in Soybean
Sweep-net			
<i>Orius insidiosus</i>	303	6	98
<i>Harmonia axyridis</i>	26	1	96
<i>Nabis</i> spp.	159	74	68
<i>Podisus maculiventris</i>	18	10	64
<i>Chrysoperla</i> spp.	108	74	59
<i>Hippodamia convergens</i>	1	1	50
<i>Coleomegilla maculata</i>	3	4	42
<i>Cycloneda munda</i>	6	9	40
Syrphidae	98	156	39
Oxyopidae	18	31	37
Araneae (unidentified)	51	92	36
<i>Coccinella septempunctata</i>	11	27	29
Hemerobiidae	2	5	29
Parasitic wasp	75	218	26
Lycosidae	5	19	21
Tetragnathidae	36	142	20
<i>Hippodamia parenthesis</i>	1	4	20
Agelenidae	2	10	17
Thomisidae	11	78	12
Reduviidae	3	23	12
Opiliones	5	39	11
Salticidae	4	45	8
Linyphiidae	2	23	8
<i>Brachiacantha ursina</i>	0	7	0
<i>Coccinella hieroglyphica</i>	0	1	0
Totals	948	1,099	46
Richness	23	26	-
Yellow-sticky cards			
<i>Orius insidiosus</i>	27	1	96
<i>Harmonia axyridis</i>	70	8	90
Hemerobiidae spp.	16	2	89
<i>Hippodamia convergens</i>	23	3	88
<i>Coleomegilla maculata</i>	5	1	83
Syrphidae	601	183	77
<i>Chrysoperla</i> spp.	301	92	77
<i>Nabis</i> spp.	6	2	75

Table 2. Continued

Trapping method	Totals		Percent
	Soybean	Prairie	Observed in Soybean
<i>Coccinella septempunctata</i>	66	37	64
<i>Cycloneda munda</i>	13	9	59
<i>Hippodamia parenthesis</i>	4	4	50
Parasitic wasp	221	293	43
<i>Brachiacantha ursina</i>	5	37	12
Total	1,358	672	67
Richness	13	13	-

Table 3. Spearman rank correlations of distances in prairie and soybean with syrphid abundance^a (*Significant correlation at $P < 0.05$ with Bonferroni correction)

Variables ^b	P-25	P-50	P-100	P-150	P-200	S-25	S-50	S-100	S-150	S-200
P-25	1									
P-50	0.18	1								
P-100	0.14	0.53*	1							
P-150	0.24	0.20	0.03	1						
P-200	-0.02	0.31	0.27	-0.18	1					
S-25	0.03	0.32	0.16	-0.18	0.02	1				
S-50	0.15	0.47	0.40	-0.18	0.43	0.49	1			
S-100	0.51*	0.08	0.07	0.36	-0.01	0.11	0.29	1		
S-150	0.32	0.23	0.03	-0.14	0.29	0.28	0.42	0.20	1	
S-200	0.02	0.56*	0.49	0.16	0.27	0.19	0.54*	0.18	0.04	1

^a Syrphids collected from sweep-net samples summed across all study sites.

^b Prairie (P) and soybean (S) at distances 25, 50, 100, 150, and 200 m.

Table 4. Plant species, as measured by percent cover by species, observed at the four prairie study sites in central Iowa

Species name	Percent Cover			
	Doolittle	Grant Ridge	Morris	Neal Smith ^a
<i>Achillea millefolium</i>	-	0.1	0.1	-
<i>Agrostis gigantea</i>	0.2	-	0.2	-
<i>Ambrosia artemisiifolia</i>	0.1	0.5	-	-
<i>Ambrosia trifida</i>	-	-	0.3	1.0
<i>Amphicarpaea bracteata</i>	-	-	0.3	-
<i>Andropogon gerardii</i>	5.9	5.5	0.6	31.0
<i>Apocynum sibiricum</i>	0.1	-	0.7	-
<i>Aster ericoides</i>	2.4	1.3	0.6	-
<i>Aster laevis</i>	-	1.3	0.6	-
<i>Aster lanceolatus</i>	6.7	-	1.5	-
<i>Aster oblongifolius</i>	-	-	-	0.3
<i>Aster pilosus</i>	-	1.0	0.1	-
<i>Aster</i> sp.	-	0.1	-	0.8
<i>Bromus inermis</i>	-	1.8	11.9	2.0
<i>Calamagrostis canadensis</i>	3.7	-	-	-
<i>Calystegia sepium</i>	-	-	1.1	-
<i>Carex</i> sp.	3.2	-	1.4	-
<i>Chamaecrista fasciculata</i>	-	-	0.1	1.3
<i>Cirsium arvense</i>	-	0.2	-	-
<i>Cirsium discolor</i>	-	0.5	-	-
<i>Cirsium</i> sp.	-	-	-	0.2
<i>Comandra umbellata</i>	0.9	-	-	-
<i>Cornus foemina</i>	-	-	0.1	-
<i>Cryptotaenia canadensis</i>	-	-	0.5	-
<i>Cuscuta</i> sp.	-	-	0.1	-
<i>Dalea purpurea</i>	0.1	0.7	-	-
<i>Daucus carota</i>	-	-	0.9	-
<i>Dichanthelium</i> sp.	0.1	-	0.1	-
<i>Echinacea pallida</i>	-	-	1.0	-
<i>Eleocharis macrostachya</i>	0.1	-	-	-
<i>Elymus canadensis</i>	0.1	1.5	-	2.5
<i>Elymus virginicus</i>	-	-	1.2	-
<i>Equisetum arvense</i>	-	-	1.1	-
<i>Erigeron annuus</i>	-	0.3	-	-
<i>Erigeron</i> sp.	0.1	-	-	-
<i>Eryngium yuccaefolium</i>	0.3	0.2	-	-
<i>Euphorbia corollata</i>	-	-	0.9	-
<i>Festuca</i> sp.	-	0.1	-	-

Table 4. Continued

Species name	Percent Cover			
	Doolittle	Grant Ridge	Morris	Neal Smith ^a
<i>Fragaria</i> sp.	-	-	0.7	-
<i>Fragaria virginiana</i>	4.0	-	-	-
<i>Galium</i> sp.	2.1	0.1	-	-
<i>Geum</i> sp.	-	-	0.4	-
<i>Hackelia</i> sp.	-	-	0.1	-
<i>Helenium autumnale</i>	-	0.1	-	-
<i>Helianthus grosseserratus</i>	9.5	13.4	8.4	-
<i>Helianthus rigidus</i>	-	2.0	-	-
<i>Helianthus tuberosus</i>	-	-	1.5	-
<i>Heliopsis helianthoides</i>	-	0.1	-	-
<i>Lactuca</i> sp.	-	0.2	-	-
<i>Lespedeza capitata</i>	-	0.2	0.6	-
<i>Liatris pycnostachya</i>	-	0.1	-	-
<i>Lithospermum canescens</i>	0.1	-	-	-
<i>Lobelia spicata</i>	0.1	-	-	-
<i>Lycopus americanus</i>	0.7	-	-	-
<i>Lysimachia ciliata</i>	-	-	4.1	-
<i>Lysimachia quadriflora</i>	0.7	0.1	-	-
<i>Lythrum alatum</i>	0.3	0.1	-	-
<i>Melilotus alba</i>	-	-	0.5	-
<i>Monarda fistulosa</i>	-	1.0	0.3	0.2
<i>Muhlenbergia frondosa</i>	-	-	0.3	-
<i>Panicum virgatum</i>	2.5	-	-	-
<i>Pastinaca sativa</i>	-	-	1.7	-
<i>Phalaris arundinacea</i>	-	-	9.7	-
<i>Phlox pilosa</i>	0.9	-	-	-
<i>Physalis virginiana</i>	0.3	-	-	-
<i>Physocarpus opulifolius</i>	-	-	0.8	-
<i>Plantago rugelii</i>	-	0.3	-	-
<i>Poa pratensis</i>	0.8	0.1	0.3	0.7
<i>Polygonum</i> sp.	-	0.4	-	-
<i>Potentilla arguta</i>	-	2.1	-	-
<i>Potentilla recta</i>	-	-	0.1	-
<i>Potentilla simplex</i>	0.5	-	0.3	-
<i>Prunus americana</i>	-	-	22.1	-
<i>Pycnanthemum virginianum</i>	2.2	0.7	-	-
<i>Ratibida pinnata</i>	2.2	2.9	0.5	4.1
<i>Rosa</i> sp.	5.0	0.3	1.7	0.1
<i>Rubus</i> sp.	-	-	0.1	-

Table 4. Continued

Species name	Percent Cover			
	Doolittle	Grant Ridge	Morris	Neal Smith ^a
<i>Rudbeckia hirta</i>	0.3	-	-	-
<i>Sanicula canadensis</i>	-	-	0.3	-
<i>Sanicula</i> sp.	-	-	0.1	-
<i>Schizachyrium scoparium</i>	1.9	-	-	3.3
<i>Senecio</i> sp.	0.1	-	-	-
<i>Silene</i> sp.	-	-	0.1	-
<i>Silphium laciniatum</i>	6.5	0.5	-	0.3
<i>Silphium perfoliatum</i>	-	-	0.3	1.0
<i>Sisyrinchium campestre</i>	0.2	-	-	-
<i>Solidago canadensis</i>	3.5	6.1	2.8	6.6
<i>Solidago gigantea</i>	-	1.3	-	-
<i>Solidago rigida</i>	3.2	18.5	-	10.2
<i>Sorghastrum nutans</i>	2.5	4.1	-	13.3
<i>Spartina pectinata</i>	4.1	-	0.7	-
<i>Sporobolus heterolepis</i>	3.2	-	-	-
<i>Stachys palustris</i>	0.9	-	-	-
<i>Taraxacum officinale</i>	-	0.5	-	0.1
<i>Thalictrum dasycarpum</i>	-	0.1	-	-
<i>Trifolium</i> sp.	-	-	0.2	-
<i>Urtica dioica</i>	-	-	0.1	-
<i>Vernonia fasciculata</i>	1.1	-	-	-
<i>Viola pedatifida</i>	0.1	-	-	-
<i>Viola sororia</i>	1.8	-	-	-
<i>Viola</i> sp.	-	-	1.9	-
<i>Vitis riparia</i>	-	-	1.7	-
<i>Zizia aurea</i>	2.9	7.1	-	-
Total ^b	88.0	76.9	86.9	79.1
Species Richness	46	41	52	19
Simpson's diversity index (1-D)	0.95	0.88	0.89	0.79

^a The same prairie at Neal Smith was used in 2006 and 2008, and sampling was only conducted in 2008.

^b Remainder of total was bare ground.

Figure Legends

Figure 1. Map of four study sites located in central Iowa, United States.

Figure 2. Schematic diagram of the experimental design used to compare *A. glycines* establishment in soybean and natural enemy populations in both soybean and prairie. At each site, three transects were established that extended 200 m into both soybean and prairie fields.

Figure 3. Mean *A. glycines* populations in soybean for each study site by month and year.

Figure 4. Mean *A. glycines* populations by distance from prairie. In 2006, June and July were not analyzed due to extremely low aphid numbers; however, in August significant differences were observed by distance indicated by letters ($F_{4,8} = 4.3$; $P = 0.03$). In 2007 and 2008, no significant differences were observed by distance.

Figure 5. Mean total natural enemy populations collected from sweep-net samples (A) and yellow-sticky cards (B) pooled across sites.

Figure 6. Total abundance of individual natural enemies collected by sweep-nets, and by month in soybean (A) and prairie (B).

Figure 7. Total abundance of individual natural enemies collected by yellow-sticky cards, and by month in soybean (A) and prairie (B).

Figure 8. A comparison of the aphidophagous community in soybean and prairie across sites, using nonmetric multidimensional scaling with the Bray-Curtis distance measure. The overlapping hulls suggest that the aphidophagous community in soybean and prairie are similar.

Figure 9. Mean *A. glycines* on caged and uncaged sentinel plants in soybean and prairie. There were significantly more *A. glycines* observed on caged sentinel plants. Letters indicate significant treatment differences ($F_{1,150} = 36.9$; $P < 0.0001$).

Figure 10. Mean *A. glycines* on uncaged sentinel plants in soybean and prairie. There were no differences between *A. glycines* in prairie and soybean at 25 or 200 m ($F_{1,38} = 0.45$; $P = 0.51$).

Figure 11. A comparison of prairie plant communities between sites, using nonmetric multidimensional scaling with the Bray-Curtis distance measure. The non-overlapping hulls suggest that sites have different plant communities.

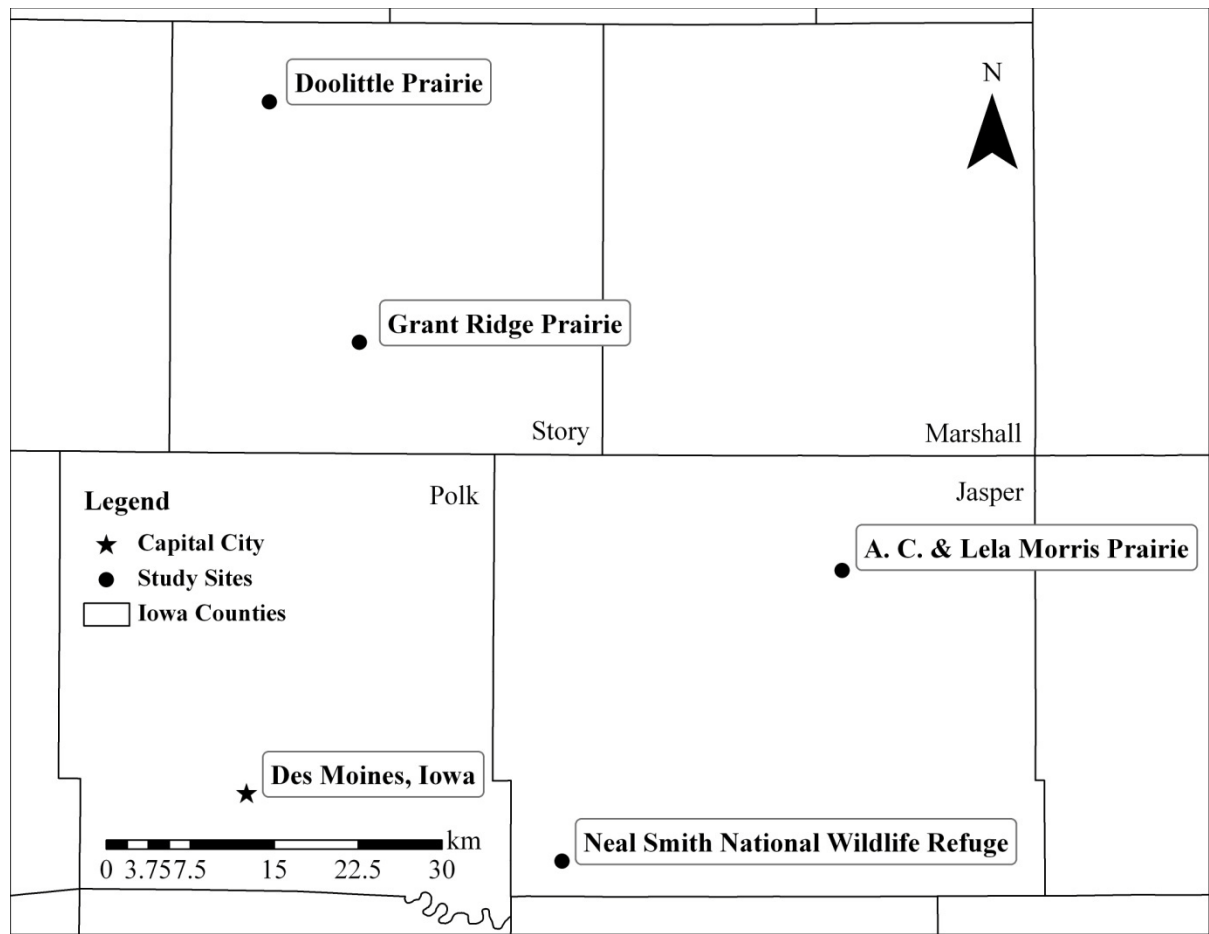


Fig. 1

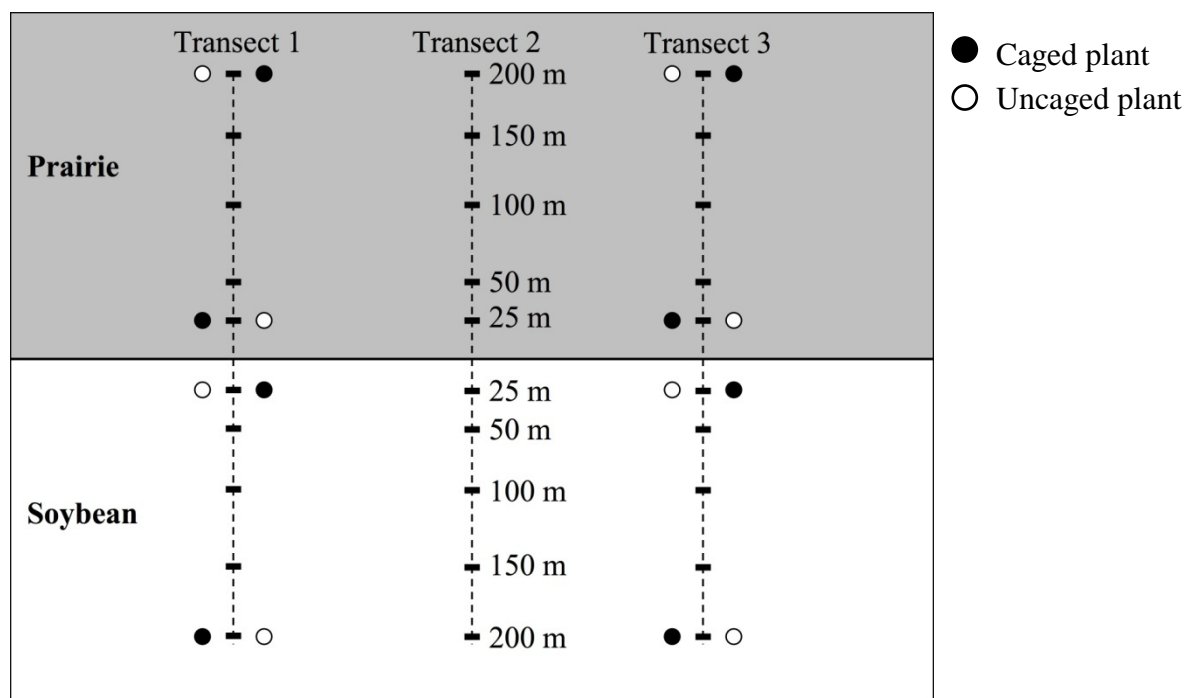


Fig. 2

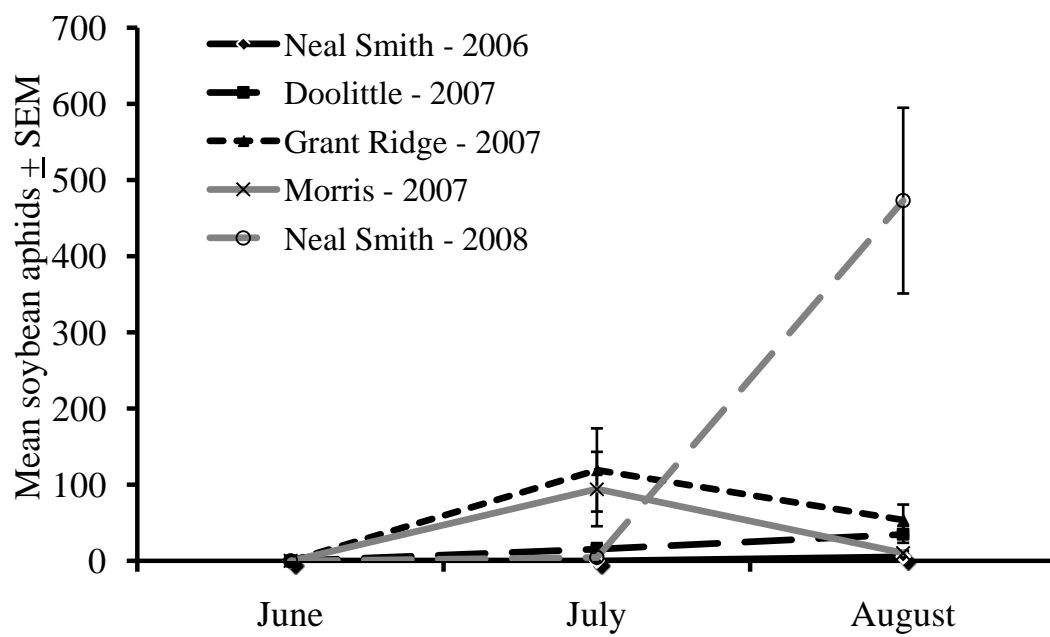


Fig. 3

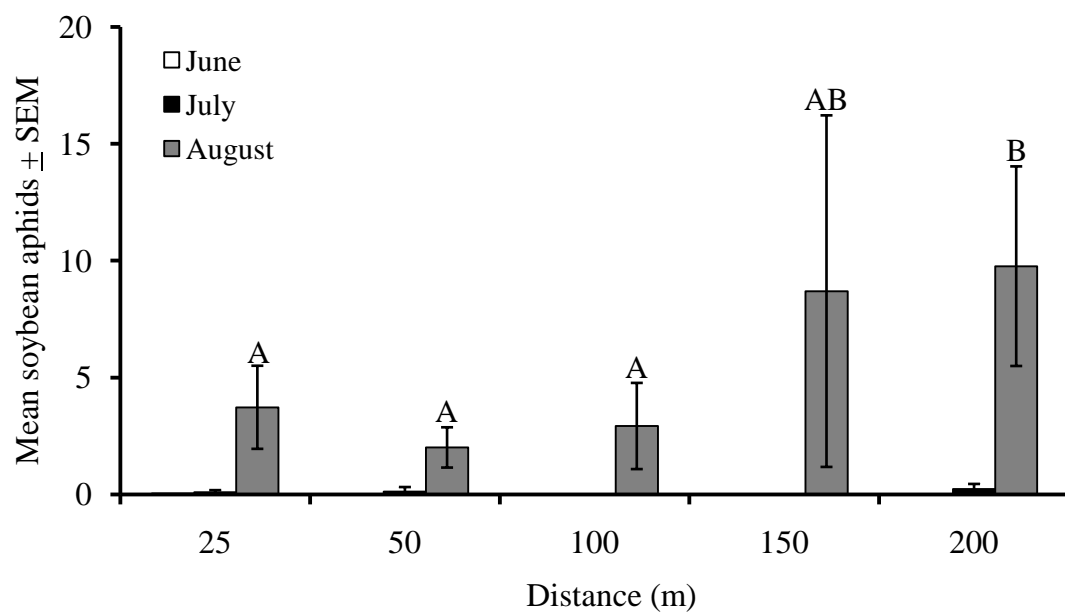


Fig. 4

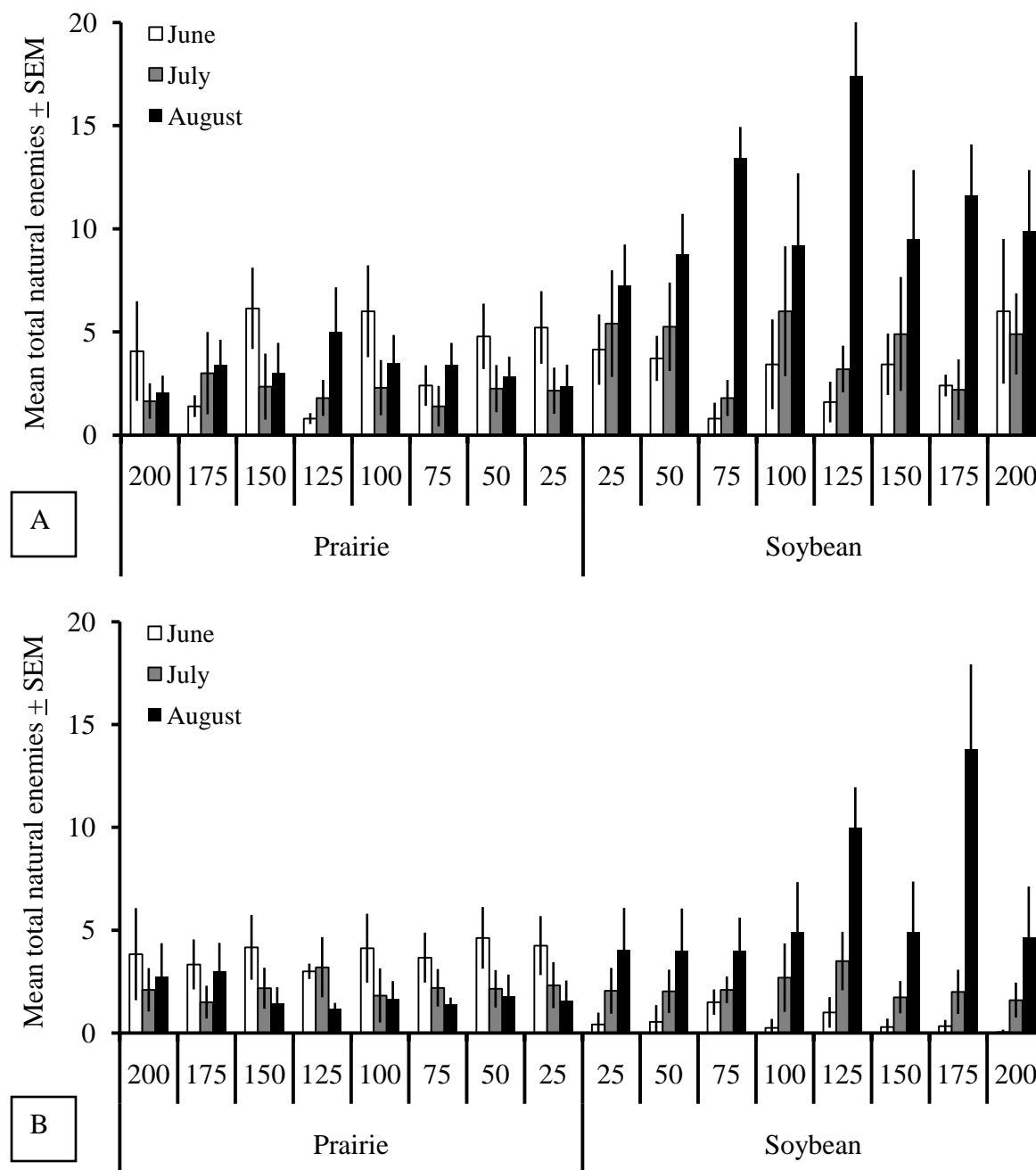


Fig. 5

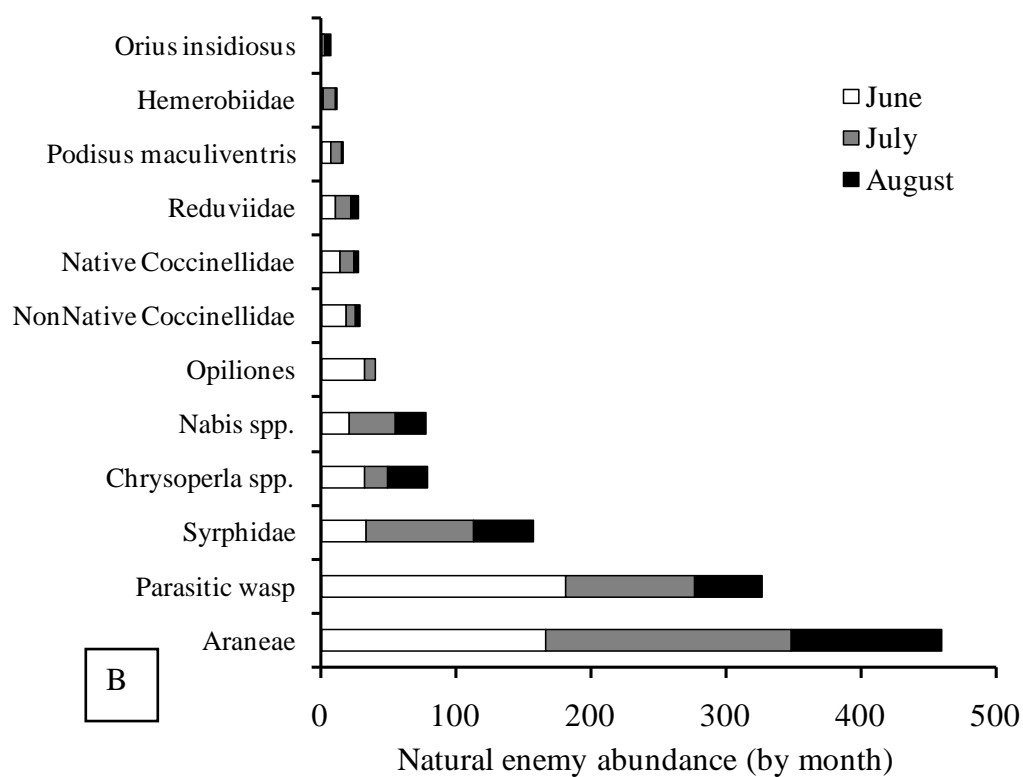
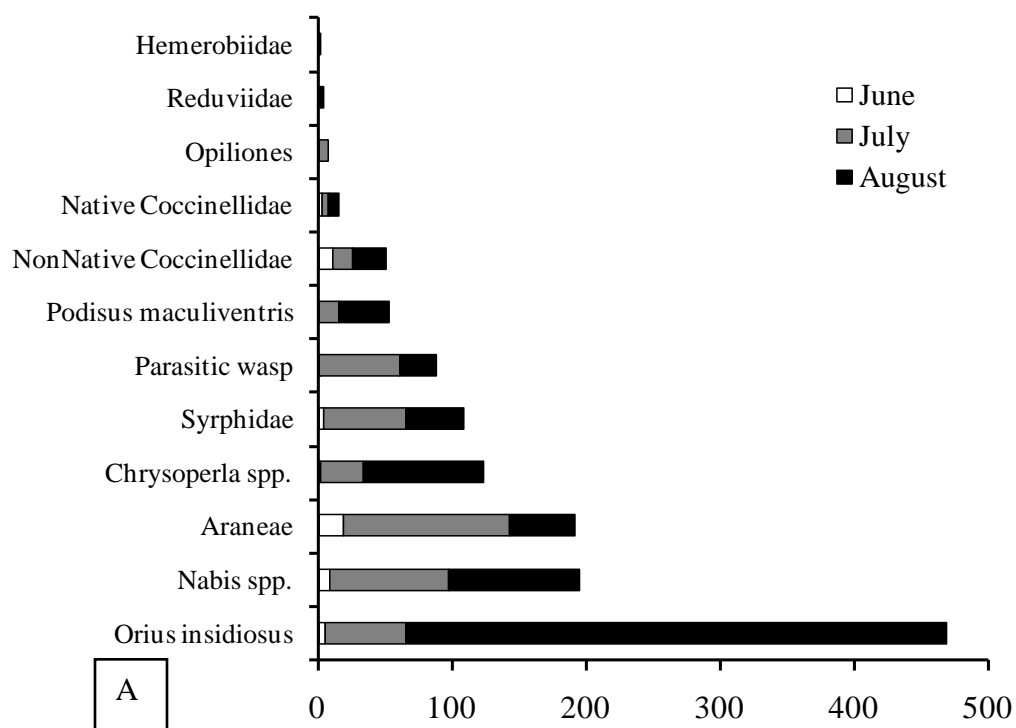


Fig. 6

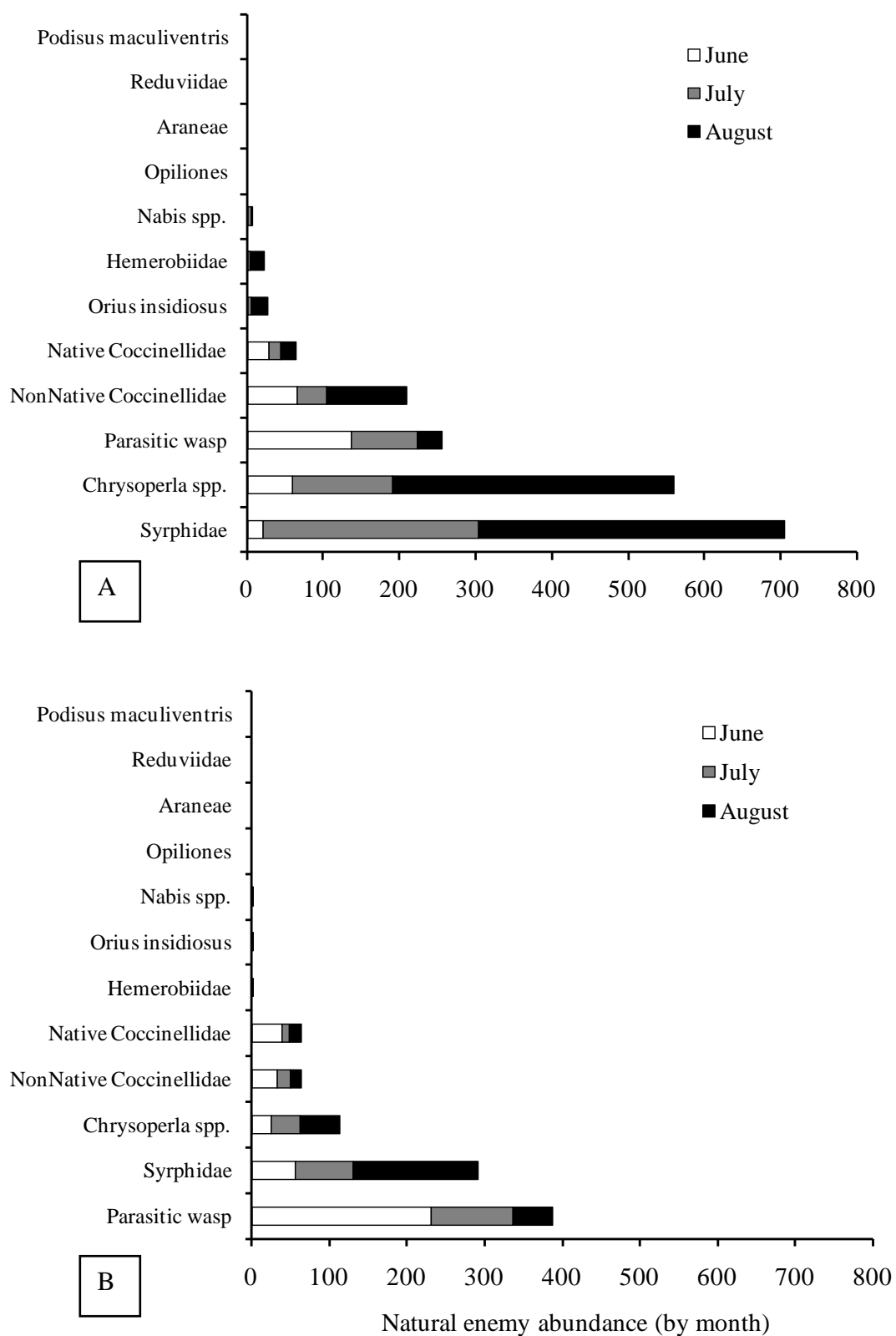


Fig. 7

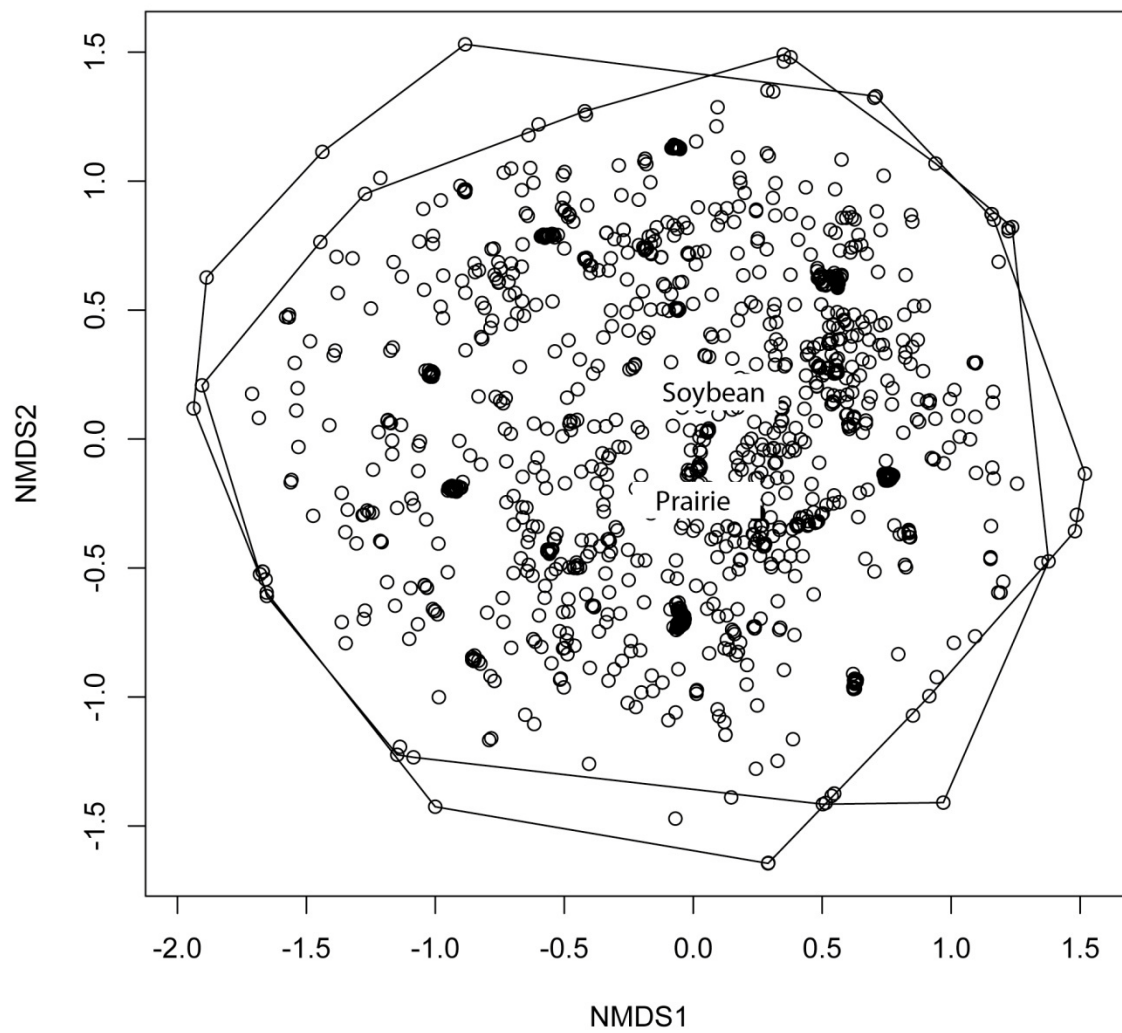


Fig. 8

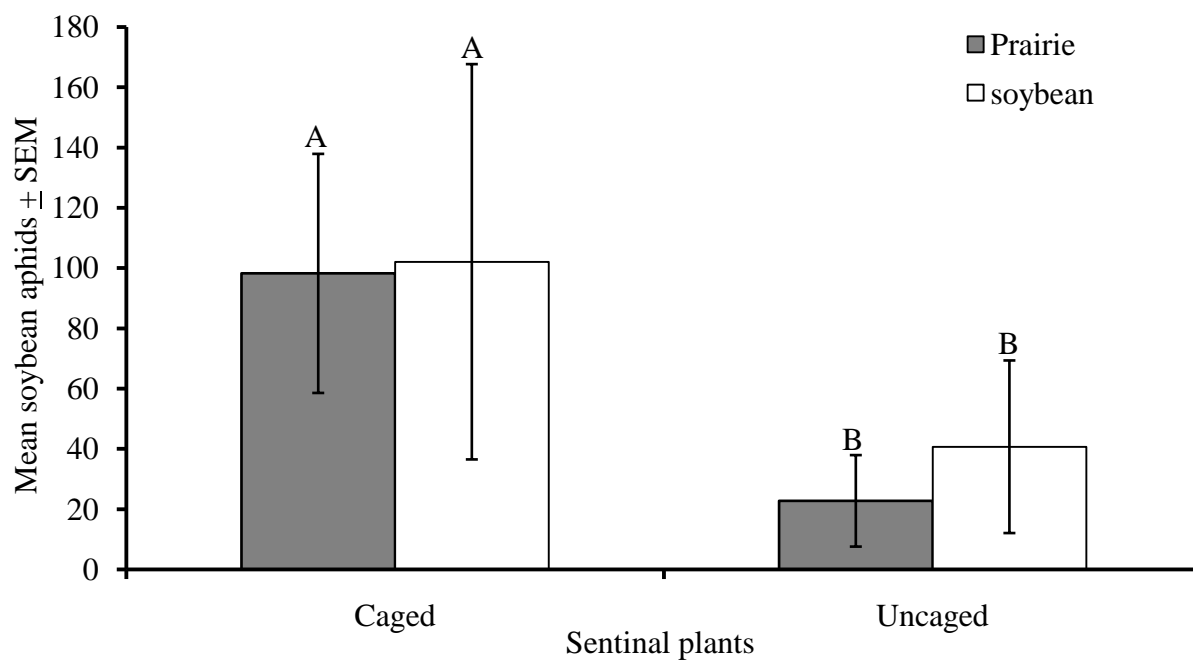


Fig. 9

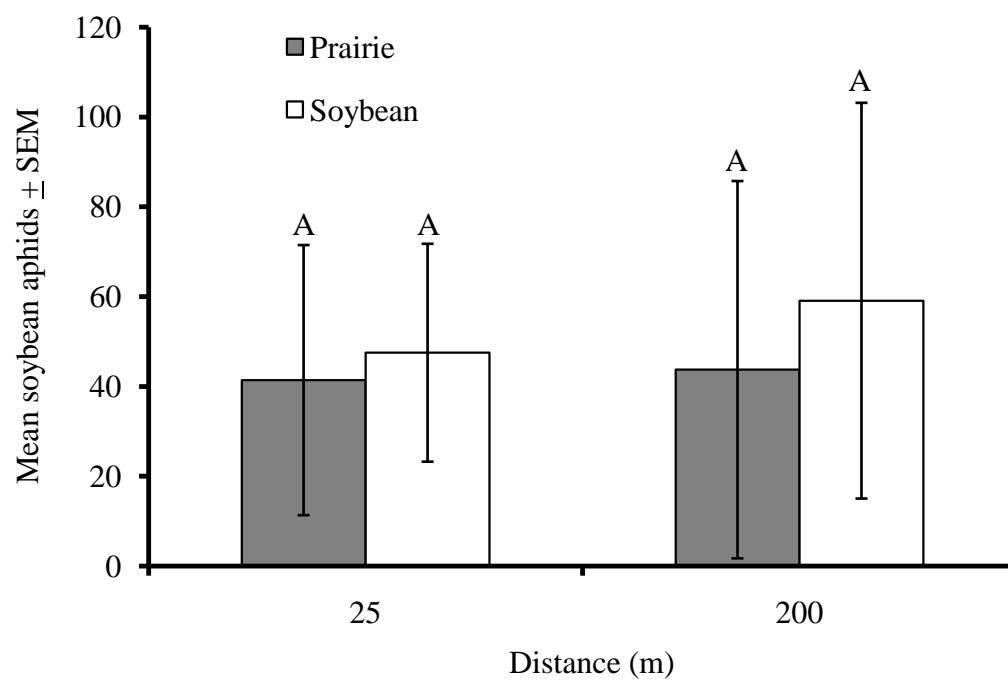


Fig. 10

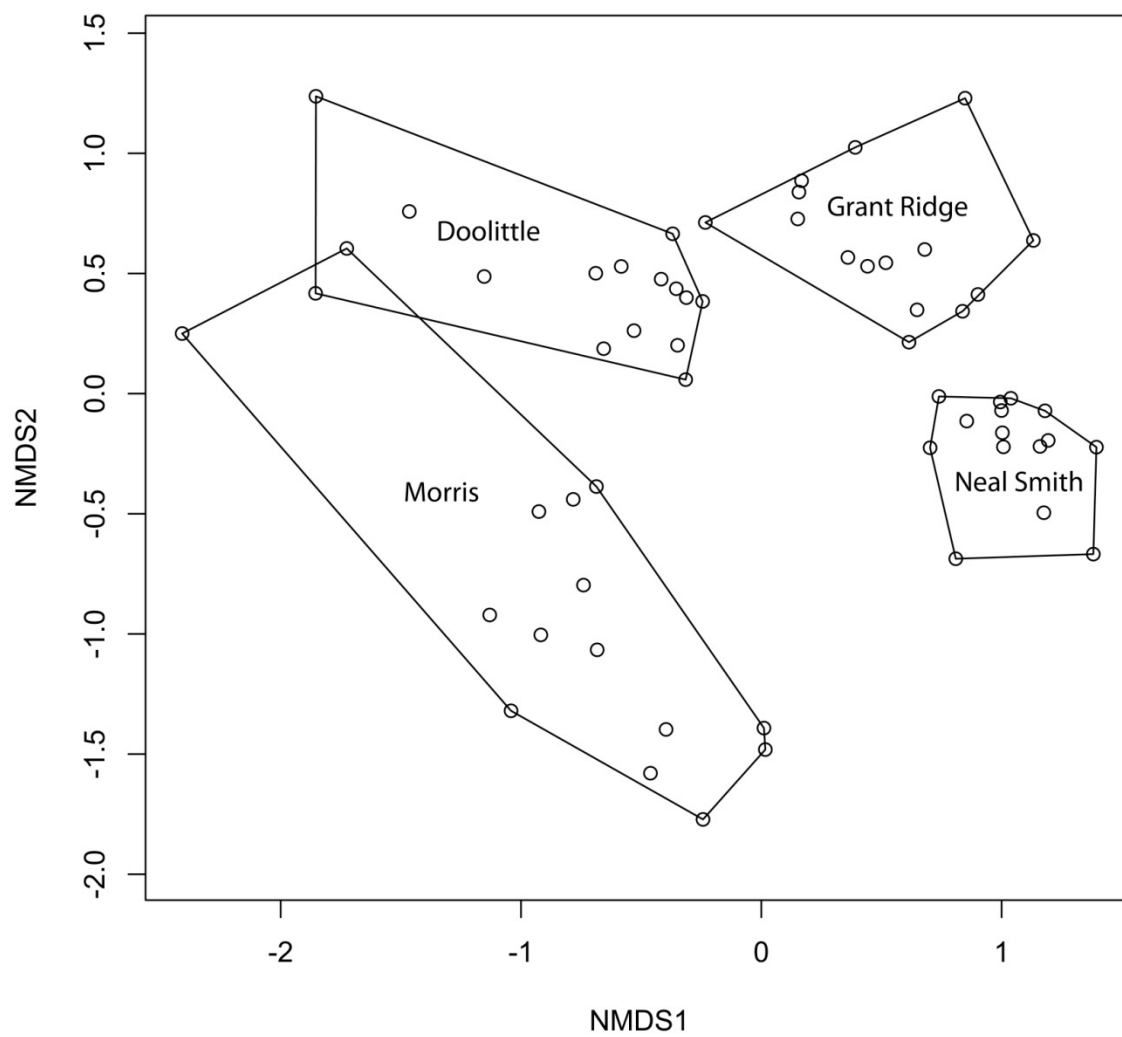


Fig. 11

Chapter 4

Spatial distributions of soybean aphids: A summary of the suction trap network

A paper to be submitted to *Environmental Entomology*

Nicholas P. Schmidt, Matthew E. O'Neal, Paul F. Anderson, Doris Lagos, David Voegtlin, Petrutza Caragea, Wayne Bailey, Eileen Cullen, Christina DiFonzo, Claudio Gratton, Douglas Johnson, Christian H. Krupke, Brian McCornack, Robert O'Neil, David W. Ragsdale, Kelley J. Tilmon, and Jeff Whitworth

Abstract

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is an economically important pest of soybean, *Glycine max* (L.) Merr., in the US. Phenological information of *A. glycines* is limited; for example, little is known about the factors guiding migrating aphids and the potential impacts of long distance flights on local population dynamics. Increasing our understanding of the aphid's population dynamics may improve predictions of *A. glycines* outbreaks and improve integrated pest management efforts. In 2005 a suction trap network (STN) was established in seven Midwest states to monitor the occurrence of winged aphids (alates). By 2006 this network was expanded to 10 states and consisted of 42 traps. The goal of the STN was to monitor movement of *A. glycines* from their overwintering host *Rhamnus* spp. to soybean in the spring, movement among soybean fields during the summer, and emigration from soybean to *Rhamnus* spp. in the fall. The objective of this study was to infer movement patterns of *A. glycines* on a regional scale based on trap captures, and determine the suitability of certain statistical methods for future analyses. Overall, alate *A. glycines* were not commonly collected in suction traps until June, after the spring flight. The greatest alate counts were recorded during summer flights (a three-week period in late July to mid August). This was followed by the fall flight, which peaked during the last two weeks of September. In addition, alate catches were positively correlated with latitude. This pattern is consistent with greater abundance of *Rhamnus* spp. in northern parts of the north-central US, suggesting that more southern regions are infested by immigrants from the north.

KEYWORDS: Forecasting, migration, dispersal

Introduction

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) is an economically important pest of soybean, *Glycine max* (L.) Merr., in the United States. *Aphis glycines* has a typical heteroecious holocyclic life cycle. Eggs hatch on buckthorn, *Rhamnus* spp. in spring, giving rise to wingless fundatrices, followed by asexual reproduction for up to four generations (Ragsdale et al. 2004). Depending on the year, the third or fourth generation consists of winged adults (alates), which emigrate in search of their secondary host, soybean (Ragsdale et al. 2004). Under favorable conditions on soybean, *A. glycines* is capable of doubling its population in as few as 1.5 days, resulting in up to 15-18 overlapping generations of wingless and winged morphs (McCornack et al. 2004, Myers et al. 2006). This high reproductive rate, coupled with an ability to migrate great distances, puts a large percentage of the US soybean growing region at risk for *A. glycines* infestation, including areas where buckthorn is absent. Later in the growing season, a combination of factors including reduced photoperiod and lower temperatures trigger the production of winged females (gynoparae) and males, which migrate in search of buckthorn, *Rhamnus cathartica* L. (Rhamnaceae; Ragsdale et al. 2004). On buckthorn, gynoparae feed and produce nymphs that develop into oviparae. Males emigrate from soybean in search of oviparae and mate (Ragsdale et al. 2004). Mated females oviposit on buckthorn, typically at the base of the bud, and the eggs overwinter (Ragsdale et al. 2004, Wu et al. 2004, McCornack et al. 2005, Voegtlin et al. 2005).

Since its discovery in the US in 2000, *A. glycines* has spread to 22 states and three Canadian provinces (Ragsdale et al. 2007). The rapid spread of *A. glycines* across North America has been aided in part by its capacity for long-distance movement. In general, the development of alates is directed by multiple stimuli, including photoperiod, temperature, over-crowding, and host plant quality (Dingle 1996). Aphid species have been reported moving great distances (> 1,000 km) from their point of origin (Kring 1972). Using a flight chamber, Kennedy and Booth (1963) found that the black bean aphid, *Aphis fabae* Scopoli, exhibits positive phototaxis before and after take off with three flight phases. Initially, alates engage in a brief “erratic or wild” phase with both vertical and horizontal flight, typically

reaching the maximum rate of climb within the first minute. Second, a “cruising” flight lasts many minutes or hours in the horizontal plane. Finally, the aphid terminates flight with erratic descending movements driven by negative phototaxis (Kennedy and Booth 1963). Due to the aphids' small size, air currents are able to carry them above the surface boundary layer (Loxdale and Lushai 1999, Isard and Gage 2001). Moreover, small insects have been observed in large-scale studies moving in random directions, with their final distribution influenced by wind direction (Loxdale and Lushai 1999).

To date, little is known about the factors influencing *A. glycines* migration events and their potential for movement across the landscape. In 2002 (a non-outbreak year), summer flights were first observed at initial flowering stage, whereas in 2003 (an outbreak year), alates were observed approximately two weeks earlier during vegetative stages (Hodgson et al. 2005a). Alate production peaked in both years at the R5 stage (beginning of seed set; Hodgson et al. 2005a). In a similar study, Hodgson et al. (2005b) evaluated pan trap placement within fields for detecting initial summer migrants. This study demonstrated that trap catches were similar in all directions between the interior and edges of fields. In a flight mill study using alate *A. glycines* reared on soybean, individuals at age 12 – 24 h following the adult molt exhibited the strongest flight potential, with average flight times of 3.3 – 4.1 h, corresponding to distances of 4.6 – 5.1 km (Zhang et al. 2008). The optimum flight temperature was 16 – 28°C and optimum relative humidity was 75% (Zhang et al. 2008). The grain aphid, *Sitobion avenae* F., is considered a long distance migrant and demonstrated average flight distances of 2.7 – 4.8 km (Zhang et al. 2008). *Sitobion avenae* has been known to travel 2,000 km from Australia to New Zealand on prevailing westerly winds (Close et al. 1978). This demonstrates that weak flying insects, like *A. glycines*, can nevertheless travel great distances with the help of wind.

Currently, the best predictive sampling tool for *A. glycines* is *in situ* field scouting, which is labor intensive and costly to growers. Region-wide abundance information and forecasting of aphid risk would help growers more efficiently time scouting efforts. Beginning in 2005, a suction trap network (STN) was established across the north-central region of the US to monitor aphid movement. By 2006, this network consisted of 42 traps in 10 states. For *A. glycines*, the objectives of the STN are to monitor movements of alates from

buckthorn to soybean fields in the spring, among soybean fields in the summer, and soybean fields to buckthorn in the fall. At a height of approximately 6 m, suction traps are designed to capture alates on their descent from long distance flights, but capture of alates during their ascent and/or those moving laterally from field to field cannot be excluded. When deployed across a region, suction traps allow researchers to identify spatial distributions of insects on a regional basis (Isard and Gage 2001). Because aphid movement is necessary to colonize both the summer and overwintering host plants, a regional suction trap network provides insight into the spatial-temporal and source-sink dynamics of *A. glycines*. In turn, this may allow for the development of predictive maps to warn growers of impending aphid outbreaks in their region.

The objectives of this study were to summarize regional suction trap data based on trap captures from 2005 – 2008, and to determine if there were directional trends and spatial autocorrelation between suction trap sites. We employed spatial analyses to infer the pattern of *A. glycines* movement within the region outlined by the STN. Specifically, we hypothesized that alate *A. glycines* captures will be greater in the north, presumably due to a greater abundance of buckthorn, and that trap catches are not spatially dependent on neighboring locations.

Materials and Methods

Aphid Data. The STN was established in Illinois in 2005 and expanded in 2006 and 2007 to neighboring states. By 2007, suction traps were deployed in 10 of 32 soybean-growing states (Table 1 and Figure 1), accounting for ~68.7% of the total US soybean acreage harvested in 2009 (USDA NASS 2009). By 2009, the dimensions of the area covered by the STN were > 1,100 km (east to west) and > 1,200 km (north to south), encompassing ~ 844,800 km² (Figure 1). The average distance between any two traps was ~100 km and varied from 9 to 1,456 km (Figure 1). Suction trap locations were selected based on their proximity to a weather station and ease of access for collaborators. Traps were designed according to the protocol outlined by Allison and Pike (1988). Each suction trap (Figure 2) consisted of a ~6-m vertical tube (diameter at top 30.5 cm and bottom 38 cm) with an electric fan drawing 10 m³ of air per minute. Captured alates were drawn into a propylene glycol-filled jar. The fan

operated only during daylight hours. Samples from each trap were assumed to represent a 50-km radius of the surrounding area (Halbert et al. 1992). The jar was replaced weekly and the samples were sent to the Illinois Natural History Survey where the aphids were identified and counted. Sample dates varied for each trap and year. Most suction traps were in operation from May – September; however, a few were in operation for as short a time as June – August (Table 2).

Geographic Data. All STN coordinates were collected in decimal degrees (Latitude and Longitude; Table 1), but were converted to UTM units (universal transverse mercator) measured in meters, to facilitate interpretation of distances. For simplicity, X coordinates are analogous to longitude or Easting and Y coordinates to latitude or Northing.

Descriptive maps of the STN were created using ArcMap 9.3 (ESRI 2008) for 2005 – 2008 data and indicate total alate catch by trap. Alate data were divided into individual sample dates (7-d intervals) for all years.

Data Analysis. All sites in the STN collected alates during years 2005 – 2008. Regression analyses were used to determine the relationship between *A. glycines* and azimuth (direction). Specifically, we used a linear regression model to determine the relationship between Julian date of first alate capture for each site and XY coordinates of the STN using Excel (Microsoft Office 2004). In addition, we used a linear regression model to determine the relationship between alate counts, pooled across season (summer: June through August, and fall: September through November), and XY coordinates of STN.

As described in the introduction, one motivation behind analyzing data from the STN was to explore the spatial distribution of the alate counts within the 10 states. Given the suspected migration patterns for the alates, we expect to observe spatial autocorrelation within the geographical region of interest. Essentially, spatial autocorrelation refers to a situation in which observations collected at nearby sites are likely to be of a size more similar than expected by chance alone (Legendre and Fortin 1989). The strength of the spatial autocorrelation (or dependence) can be quantified using spatial statistics.

Geostatistics, a type of spatial statistics, is one approach used to identify the

magnitude of spatial dependence for a given spatial domain, and it is based on estimating variograms (which are functions of the degree of spatial dependence of a spatial random field) using the data collected over space. In theory, an empirical variogram is a useful measure to detect the range of dependence over the domain of interest, the strength, and directional patterns in the field. Unfortunately, the sample size available for constructing the empirical variogram (42 locations), as well as the range of distance available for calculations make it impractical for our analysis.

Moran's I is another popular method for testing global spatial autocorrelation (Moran 1950). This is a simple measure of the strength of the spatial dependence based on the concept that, should there be no spatial dependence, observations taken at nearby sites are not more similar than observations taken at larger distances. Moran's I is often used as a screening method for detection of spatial dependence, in part due to its intuitive interpretation (a value of 0 indicates no spatial dependence, while a value of 1 indicates strong positive spatial dependence), as well as its simple method of calculation. However, all the theoretical properties of the Moran's I statistic are developed asymptotically (i.e. assuming data was collected at a very large number of locations). This was not the case for our data set (we only have, for the most complete cases, 42 locations available), resulting in inconclusive preliminary calculations of Moran's I.

In an effort to understand spatial dependence in our data to some degree, we developed a randomization test for spatial autocorrelation, which we call a "nearest neighbor model" calculated using R statistical packages (R Development Core Team 2008). The idea is to test for spatial dependence by constructing a similarity measure between sites, and compare this measure for sites located nearby with sites located further away. If the two measures are comparable (for nearby sites and further sites), then we conclude that there is no evidence of spatial autocorrelation.

Randomization tests were formally introduced by Fisher (1935) as methods for sample-based inferences. The main concept for any randomization test is to construct a reference distribution for a given test statistic so that significance can be assessed without making any parametric assumptions. When the number of randomizations is large, at least several thousands, the tests are as powerful as parametric tests (Crowley 1992, Manly 1997).

To conduct a test based on the construction of a reference distribution, we used the methods of Noreen (1989), consisting of the following steps:

The first step is stating the question, or hypothesis. In our case, the null hypothesis is that there was no spatial autocorrelation, with an alternative hypothesis of significant spatial autocorrelation. The second step was to construct a test statistic, which Noreen (1989) defined as a similarity measure between sites. To proceed, we defined “sites nearby” as a neighborhood. Although the size of neighborhoods was arbitrarily selected, a common approach is to consider neighbors as being co-located within a “sphere of influence” defined as sites within a certain radius from a given site. We repeated the test for a number of neighborhood choices to identify the extent of spatial dependence. However, for each run of the test, the neighborhood size was fixed. Given a site (S_j) and its neighbors, we quantified the similarity among observations within a neighborhood by taking the average of the absolute values of differences between a given location and its neighbors (D_{close_j}). The reason for using the absolute values of differences rather than simple differences was to ensure that averages were not deceptively small simply due to the direction in which the difference was calculated. The reason for calculating averages was to account for an unequal number of neighbors, thus preventing sites with fewer neighbors leading to smaller differences (i.e. more similar to its neighbors simply due to a lack of neighbors). Much the same, a measure of similarity between a given site and all other non-neighborhood sites was calculated as the average of the absolute values of differences (D_{far_j}). We repeated the construction of the two measures for each site and, finally, constructed our test statistic as the ratio between the average of all the D_{close_j} and the average of all the D_{far_j} . We refer to this test statistic as the “nearest neighbor statistic”. The construction of the test statistic as the ratio between averages is motivated by the idea that, in the presence of spatial autocorrelation, locations within a neighborhood are, on average, more similar than locations situated far apart. Another motivating factor for taking averages rather than simple summations was that for a given neighborhood size, there may be no neighbors for a given site, in which case eliminating the site from the calculation could lead to biases.

The third step according to Noreen (1989) is to generate the null reference distribution. We did so by redistributing observed data over the locations, and recalculating

the sample statistic as described in the previous step. In other words, collection data were randomly assigned to the fixed spatial locations. Randomization and recalculation was repeated 5,000 times to generate the reference distribution. The final step was to compare the observed statistic to the reference distribution and draw conclusions based on the usual rules for statistical inference. We calculated a P -value, associated with the observed test statistic, as the probability of obtaining a test statistic as large as the one observed for our data under the null hypothesis. An observed test statistic much larger than expected by chance (i.e., $P < 0.05$) indicates the null hypothesis of spatial independence can be rejected.

One benefit of using this test was that we could identify the extent of the spatial autocorrelation by repeating the test for various neighborhood sizes. Considerations when selecting neighborhood size were that they were not too small (many sites with no neighbors) or too large (nearly all sites are neighbors). We tested distances from 150 to 350 km. The former was chosen to ensure that we did not have an excessively large number of no-neighbor sites; the latter was chosen based on principles used in the estimation of the empirical variogram, namely that one should not test distances greater than half largest existing distance (Cressie 1993). Thus, we considered only neighborhoods with a diameter less than half the greatest pair-wise distance between locations.

Results

Over four years, a total of 141,106 *A. glycines* gynoparae and 1,121 males were collected in the STN. The earliest capture date was in 2007, followed by 2005, 2006 and 2008, with corresponding Julian days of 145, 175, 181, and 224 (Table 3). Julian date averaged across all traps produced the same pattern (Table 3). Regression analyses of first record of an alate collected in any trap on X and Y coordinates suggests that X coordinates explain little of the variation in any of the years (2005: $R^2 = 0.02$; 2006: $R^2 = 0.01$; 2007: $R^2 = 0.03$; 2008: $R^2 = 0.03$). However, Y coordinates explain significantly more of the variation (2005: $R^2 = 0.13^*$; 2006: $R^2 = 0.42^*$; 2007: $R^2 = 0.04$; 2008: $R^2 = 0.67^*$; where asterisk indicates $P < 0.05$; Table 3).

Weekly alate captures were greatest in 2005 followed by 2007 > 2008 > 2006, and typically followed a bimodal distribution, peaking in August and again in late September

(Figure 3). The abundance of alates captured in the summer followed the same pattern across years, but fall alate catches were greatest in 2008 followed by 2006 > 2005 > 2007 (Figures 3-7). The peak in average alates captured for all traps was 685 aphids per trap between 5 – 12 August 2005 (Figure 4). Peak alate catch for a single trap was 5,970 collected on 26 September, 2008 at Lamberton, MN (Figure 7). Peak alate catch during the summer was 4,440 alates collected on 12 August 2005 in East Lansing, MI (Figures 3, 4). Regression analyses of total alate counts by season and year on XY coordinates suggest more variability was explained by summer > all dates combined > fall (Table 4). Furthermore, Y coordinates explained significantly more of the variation during the summer in all four years than summer and X coordinates (Table 4).

The nearest neighbor analysis revealed that the distance of alate captures among traps varied by year and within any given year. During 2005 traps were similar to one another within radii from ~125 – ~325 km for much of the summer and 150 – 350 km during the fall (Table 5 and Figure 4). In 2006, all traps were similar within radii from ~150 – 350 km during the summer and differed significantly by date and distance during the fall (Table 5 and Figure 5). In 2007 traps were more similar to one another within radii from 150 – 175 km during the summer (though differing significantly by date and distance) and ~150 – 350 km during the fall (Table 5 and Figure 6). In 2008, traps were similar to one another within radii from ~150 – 350 km during the summer and differed significantly by date and distance during the fall (Table 5 and Figure 7).

The second highest catches of alates were reported in the fall of 2006 and summer of 2007; however, the fall flight of 2006 was of uncharacteristically long duration (Table 5). Alates were collected earlier in the summer of 2007 than any other year on record; however, the only difference observed among traps was that alate catches were more asynchronous than in other years (Table 5). In general, these data suggest that the current placement of the 42 traps in the STN can explain movement of alate *A. glycines* at large distances up to 350 km (Table 5) typically around peak flights (Figure 3) (i.e. alates collected in one location are similar to the alates collected in other traps within 350 km). The nearest neighbor analyses suggest that statistical analyses, which assume independence between suction trap locations, are not appropriate for many of the collection dates (Table 5).

Discussion

Aphis glycines has been reported in soybean fields as early as 24 May 2007 in WI, 28 May 2007 in MN, and 31 May 2006 in IA (Rice and O'Neal 2006, 2007). In contrast, the first records of an alate *A. glycines* collected in the STN was 24 June 2005, 30 June 2006, 25 May 2007, and 11 July 2008 (Table 3). This suggests that 2007 may be the only year when an alate was collected traveling directly from buckthorn to soybean and was limited to two traps in MI (Kellogg and Monroe County), which collected a total of four alates. This indicates that the STN may not effectively detect spring flights of alate *A. glycines* moving from buckthorn to soybean, which are critical for predicting initial infestation of relatively young and vulnerable soybean plants. Explanations for this may include one or more of the following: 1) Spring flight from buckthorn to soybean may extend only as far as the nearest soybean field; therefore, initial flights may be confined to a small area away from traps. 2) The first aphid flight may represent more of a ranging type of movement occurring at an altitude too low for collection in the suction traps. 3) The number of aphids migrating from buckthorn in the spring are typically much smaller than from soybeans during the summer or fall and are thus much more difficult to sample using the STN. Moreover, studies suggested that migrating aphids discriminate between crop and natural habitats, probably using visual cues (Plantegenest and Kindlmann 1999, Favret and Voegtlin 2001). Thus, trap placement may impact the magnitude of alate catch on any given sampling date (Favret and Voegtlin 2001), and whether the trap is near crop or natural habitats may have played a role in the variability observed in alate catches between traps.

To date, the environmental variable that best predicts aphid outbreaks is unknown. Harrington et al. (2007) found correlations of latitude and temperature with the phenology of 29 aphid species. Earlier first flights were associated with warmer winters, perhaps through increased survival and development rates (Harrington et al. 2007). In our analyses, *A. glycines* numbers were positively correlated with increased latitude (Tables 3 and 4). Our analyses showed that data from trap locations were not always independent of one another, making a regression analysis, which assumes independence, inappropriate. First alate catch does not violate this assumption because it occurred before dependence was observed in the

STN (Table 3). However, because a trend was observed between first alate catch and increased latitude, we expanded on this by determining if this northern trend was consistent through the summer and fall flights. In general, two trends occurred with first alate catch. In odd numbered years (2005 and 2007) preceded by low aphid infestations in much of the Midwest, alates were collected earlier in the year (Table 3). In contrast, in years (2006 and 2008) preceded by high aphid infestations, alates were collected later (Table 3). If temperature does play a role in the occurrence of alates from year to year, it is likely related to the supercooling point (SCP) of *A. glycines*, which for eggs is -34°C (McCornack et al. 2005).

We observed a slight directional trend for greater alate captures in northern traps. This is likely due to greater overwintered *A. glycines* populations, which reside on *R. cathartica*. *Rhamnus cathartica* is distributed throughout the Midwest, but is more abundant at northern latitudes (Kurylo et al. 2007; Figure 8). Soybean is also distributed throughout the Midwest, but is more evenly dispersed; therefore, *A. glycines* movements within and between habitats are likely taking place at relatively large scales and throughout the summer and early fall across the Midwest. Because *A. glycines* also can overwinter on *R. alnifolia* (Voegtlin et al. 2005), the overwintering range may extend to Tennessee, West Virginia, Virginia, Maryland and Delaware. Thus, expanding the STN to the east, west, and parts of Canada may be necessary to better understand *A. glycines* movements. Conversely, traps within the STN may be too far apart. In the case of *S. avenae*, Vialatte et al. (2007) found that risk of outbreaks is determined at a local scale by dynamics of genetically similar aphids. Therefore, the authors suggested using small management units for predicting aphid outbreaks. If *A. glycines* has a similar phenology, we may need to increase the number of suction traps and minimize the distance between traps to identify and manage source populations earlier in the season?

The nearest neighbor analysis does suggest spatial association within the STN up to 350 km; therefore, at various times of the year the STN can detect similarities between suction traps in alate *A. glycines* counts (Table 5). In addition, temporal dynamics appear to vary from year to year (Table 5). In general, these data suggest the STN can be used to estimate aerial abundances of *A. glycines* alates during summer and fall flights. It should be

noted that although the STN is likely capturing both emigrating and immigrating aphids, the ability to observe source-sink dynamics might be compromised by the sampling interval. Samples were collected every 7 d, but aphid migration events generally occur within a 24-hour period (Dingle 1996); therefore, a single sample likely represents multiple aphid movement events.

There are a number of issues to consider if the STN is to serve as the basis for predictive models of *A. glycines* outbreaks. Spatial patterns are not always detectable until some “threshold value” is reached, and sampling up to a decade or longer may be necessary to observe certain phenomena (DeMers 2001). In the case of *A. glycines*, our ability to detect these phenomena may vary depending on overwintering success, source population(s) size and location, natural enemy abundance, regional insecticide use, etc. Patterns in *A. glycines* movements undoubtedly exist, but the mechanism determining those patterns may not be apparent (DeMers 2001, O’Neill et al. 1986). The scale at which patterns are sought is important because patterns observed at small scales may not be visible at larger scales and vice versa. Consideration of the concept of hierarchy theory, where events at smaller scales can help explain processes at larger scales (O’Neill et al. 1986), may be crucial when developing future studies dealing with source-sink dynamics of aphid movements.

These data have advanced our understanding of *A. glycines* phenology, however, future research is needed to fully understand the mechanism(s) driving aphid movements. Future research should include determining the relationship between alate catches by suction traps to aphid infestations in surrounding areas, and using genetic markers to determine source populations of overwintering aphids. Future studies would also benefit from reduced intervals between sample collections to increase the precision of source/sink estimates and to facilitate identification of weather and plant stage factors affecting aphid movement. Over the four years, more than 60 species of aphids were collected in the STN and the implications for aphid management and monitoring (including monitoring for novel and/or invasive species) are promising, but not well-defined. Expanding the STN within existing states and/or to adjoining states would not only help soybean researchers, but also potentially help manage other aphid crop pests.

Acknowledgments

We thank Keith Hinrichs, Lyle Paul, Eric Adee, Pete Fandel, Mike Vose, Lindell Deal, Steve Ebelhar, Russ Higgins, Don Biehle, Jon Leuck, Jeff Boyer, Phil Walker, Tim Wood, Peg Reedy, Andy Merry, Kevin Jarek, Scott Chapman, Patrick Branick, Steven Kirk, Kelly Tindall, Dave Haden, Ken Penckiosky, Nick Piekema, Mike Fiscus, Bruce Potter, George Nelson, Ian MacRae, Doug Johnson, Michael McCornack, Ned Birkey, and Mike Lewett who collected field data. This journal paper of the Iowa Agriculture and Home economics Experiment Station, Ames, Iowa, Project No. 5032, was supported by Hatch Act and State of Iowa funds.

References Cited

- Allison, D., and K. S. Pike. 1988.** An inexpensive suction trap and its use in an aphid monitoring network. *J. Agric. Entomol.* 5:103-107.
- Close, R. C., N. T. Moar, A. I. Tomlinson, and A. D. Lowe. 1978.** Aerial dispersal of biological material from Australia to New Zealand. *Int. J. Biometeorology* 22: 1-19.
- DeMers, M. N. 2001.** GIS modelling in raster. John Wiley and Sons, New York.
- Dingle, H. 1996.** Migration: The biology of life on the move. Oxford University Press, Inc., New York, NY.
- Environmental Systems Research Institute (ESRI). 2008.** ArcGIS 9.3. www.esri.com
- Favret, C., and D. J. Voegtlin. 2001.** Migratory aphid (Hemiptera: Aphididae) habitat selection in agricultural and adjacent natural habitats. *Environ. Entomol.* 30: 371-379.
- Halbert, S. E., L. Elbertson, and J. B. Johnson. 1992.** Suction trapping of the Russian wheat aphid: What do the numbers mean? *In*: WP Morrison, editor. Proceedings: Fifth Russian Wheat Aphid Conference, pp. 282-297. Great Plains Agricultural Council, Lubbock, TX.
- Harrington, R., S. J. Clark, S. J. Welham, P. J. Verrier, C. H. Denholm, M. Hulle, D. Maurice, M. D. Rounsevell, and N. Cocu. 2007.** Environmental change and the phenology of European aphids. *Global Change Biol.* 13: 1550-1564.
- Hodgson, E. W., R. C. Venette, M. Abrahamson, and D. W. Ragsdale. 2005a.** Alate production of soybean aphid (Homoptera: Aphididae) in Minnesota. *Environ. Entomol.* 34: 1456-1463.
- Hodgson, E. W., R. L. Koch, and D. W. Ragsdale. 2005b.** Pan trapping for soybean aphid (Homoptera: Aphididae) in Minnesota soybean fields. *J. Entomol. Sci.* 40: 409-419.
- Isard, S. A., and S. H. Gage. 2001.** Flow of life in the atmosphere: An airscape approach to understanding invasive organisms. Michigan State University Press, East Lansing, MI.
- Kennedy, J. S., and C. O. Booth. 1963.** Free flight of aphids in the laboratory. *J. Exp. Biol.* 40: 67-85.
- Kring, J. B. 1972.** Flight behaviour of aphids. *Annu. Rev. Entomol.* 17: 461-492.

- Kurylo, J. S., K. S. Knight, J.R. Stewart, and A. G. Endress. 2007.** *Rhamnus cathartica*: Native and naturalized distribution and habitat preferences. J. Torrey Bot. Soc. 134: 420-430.
- Lima, M., R. Harrington, S. Saldana, and S. Estay. 2008.** Non-linear feedback processes and a latitudinal gradient in the climatic effects determine green spruce aphid outbreaks in the UK. Oikos 117: 951-959.
- Loxdale, H. D., and G. Lushai. 1999.** Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. Philos. Trans. R. Soc. Lond. 354: 1479-1495.
- McCornack, B. P., M. A. Carrillo, R. C. Venette, and D. W. Ragsdale. 2005.** Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). Environ. Entomol. 34: 235-240.
- McCornack, B. P., D. W. Ragsdale, and R. C. Venette. 2004.** Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. J. Econ. Entomol. 97: 854-861.
- Microsoft Office. 2004.** Microsoft Corporation, Version 11.4.
- Myers, S. W., and C. Gratton. 2006.** Influence of potassium fertility on soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), population dynamics at a field and regional scale. Environ. Entomol. 35: 219-227.
- Noreen, E. W. 1989.** Computer intensive methods for testing hypotheses: An introduction. New York. Wiley & Sons.
- O'Neill, R. V., D. L. DeAngelis, J. B. Waide, and T. F. H. Allen. 1986.** A hierarchical concept of ecosystems. Princeton University Press, Princeton, NJ.
- Plantegenest, M., and P. Kindlmann. 1999.** Evolutionarily stable strategies of migration in heterogeneous environments. Evol. Ecol. 13: 229-244.
- R Development Core Team. 2008.** R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. (<http://www.R-project.org>).
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004.** Soybean aphid biology in North America. Ann. Entomol. Soc. Am. 97: 204-208.

- Ragsdale, D. W., B. P. McCornack, R. C. Venette, B. D. Potter, I. V. MacRae, E. W. Hodgson, M. E. O'Neal, K. D. Johnson, R. J. O'Neil, C. D. DiFonzo, T. E. Hunt, P. A. Glogoza, and E. M. Cullen. 2007.** Economic threshold for soybean aphid (Hemiptera: Aphididae). *J Econ. Entomol.* 100: 1258-67.
- Rice, M. E., and M. E. O'Neal. 2007.** Soybean aphids found in Minnesota and Wisconsin. Integrated Crop Management 498, Available online: <http://www.ipm.iastate.edu/ipm/icm/2007/6-4/soybeanaphid.html>
- Rice, M. E., and M. E. O'Neal. 2006.** First soybean aphids found in May. Integrated Crop Management 496(14), Available online: <http://www.ipm.iastate.edu/ipm/icm/2006/6-5/aphids.html>
- Sokal, R. R., and F. J. Rohlf. 1995.** Biometry: The Principles and Practice of Statistics in Biological Research. 3rd edition. WH Freeman and Co., New York.
- USDA-National Agricultural Statistics Service. 2009.** Available at www.nass.usda.gov/QuickStats/PullData_US.jsp. USDA-NASS, Washington, DC, last visited 15 Oct, 2009.
- Vialatte, A., M. Plantegenest, J. C. Simon, and C. A. Dedryver. 2007.** Farm-scale assessment of movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows. *Agric. For. Entomol.* 9: 337-346.
- Voegtlin, D. J., R. J. O'Neil, W. R. Graves, D. Lagos, and H. J. S. Yoo. 2005.** Potential winter hosts of soybean aphid. *Ann. Entomol. Soc. Am.* 98: 690-693.
- Wu, Z. S., D. Schenk-Hamlin, W. Y. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004.** The soybean aphid in China: A historical review. *Ann. Entomol. Soc. Am.* 97: 209-218.
- Zhang, Y., L. Wang, K. Wu, K. A. Wyckhuys, and G. E. Heimpel. 2008.** Flight performance of the soybean aphid, *Aphis glycines* (Hemiptera: Aphididae) under different temperature and humidity regimens. *Environ. Entomol.* 37: 301-6.

Table 1. Suction trap identification numbers, locations, geographic coordinates, county and nearest city, by state

State (Abbreviation)	Decimal Degrees		County	Nearest City
Trap Number ^a & Name ^b	Latitude	Longitude		
Illinois (IL)				
(1) Brownstown	38.95	88.96	Fayette	Brownstown
(2) Dekalb	41.84	88.86	Dekalb	Shabbona
(3) Dixon Springs	37.44	88.67	Pope	Simpson
(4) Freeport	42.28	89.70	Stephenson	Freeport
(5) Metamora	40.80	89.41	Woodford	Eureka
(6) Monmouth	40.93	90.72	Warren	Monmouth
(7) Morris	41.352	88.384	Grundy	Morris
(8) Perry	39.81	90.82	Pike	Perry
(9) Urbana	40.10	88.19	Champaign	Urbana
Indiana (IN)				
(10) ACRE	40.4704	86.9939	Tippecanoe	West
Lafayette				
(11) DPAC	40.2545	85.1503	Randolph	Farmland
(12) NEPAC	41.1051	85.3876	Whitley	Columbia City
(13) PIT	40.4153	86.9185	Tippecanoe	West
Lafayette				
(14) PPAC	41.4442	86.9303	LaPorte	Wanatah
(15) SEPAC	39.0351	85.5292	Jennings	Butlerville
Iowa (IA)				
(16) Ames	42.017	93.778	Boone	Ames
(17) McNay	40.980	93.420	Lucas	Chariton
(18) Nashua	42.935	92.575	Floyd	Nashua
(19) Sutherland	42.925	95.537	O'Brien	Sutherland
Kansas (KS)				
(20) Manhattan	39.208	96.594	Riley	Manhattan
Kentucky (KY)				
(21) Lexington	38.1275	84.5120	Fayette	Lexington
(22) Princeton	37.0964	87.8606	Caldwell	Princeton
Michigan (MI)				
(23) Bean and Beet	42.379	84.112	Saginaw	St. Charles
(24) East Lansing	42.713	84.478	Ingham	East Lansing
(25) Kellogg	42.410	85.373	Kalamazoo	August
(26) Monroe County	41.949	83.459	Monroe	Monroe
Sanilac ^c	43.456	82.833	Sanilac	Sandusky
(27) Oceana ^c	43.836	86.368	Oceana	Hart

Table 1. Continued

State (Abbreviation) Trap Number ^a & Name ^b	Decimal Degrees		County	Nearest City
	Latitude	Longitude		
Minnesota (MN)				
(28) Albert Lea	43.70509	93.22767	Freeborn	Albert Lea
(29) Crookston	47.77	96.61	Polk	Crookston
(30) Lamberton	44.14384	95.18917	Cottonwood	Lamberton
(31) Morris	45.59091	95.86886	Stevens	Morris
(32) Rosemount	44.70679	93.10066	Dakota	Rosemount
Missouri (MI)				
(33) Columbia	38.907	92.281	Boone	Columbia
(34) Portageville	36.43	89.71	New Madrid	Portageville
South Dakota (SD)				
(35) Brookings	44.305	96.671	Brookings	Brookings
Wisconsin (WI)				
(36) Antigo	45.25	89.00	Langlade	Antigo
(37) Arlington	43.30	89.25	Columbia	Arlington
(38) Hancock	44.12	89.53	Waushara	Hancock
(39) Lancaster	42.83	90.78	Grant	Lancaster
(40) Pioneer	44.75	91.58	Eau Claire	Eau Claire
(41) Seymour	44.33	88.32	Outagamie	Appleton
(42) Walworth	42.53	88.68	Walworth	Elkhorn

^a Number is used to identify traps in Figure 1.

^b Trap names correspond with North Central Regional soybean aphid suction trap network (<http://www.ncipmc.org/traps/>).

^c The Oceana trap was shut down after 2008 and replaced by Sanilac, which is in Eastern MI, in 2009.

Table 2. Initial and end sampling dates of suction traps for all years and traps

State	Trap Name ^a	Sampling Dates ^b			
		2005	2006	2007	2008
Illinois					
	Brownstown	3 Jun : 7 Oct	12 May : 27 Oct	18 May : 21 Sep	6 Jun : 12 Sep
	Dekalb	3 Jun : 14 Oct	12 May : 27 Oct	18 May : 12 Oct	23 May : 17 Oct
	Dixon Springs	3 Jun : 14 Oct	12 May : 27 Oct	18 May : 19 Oct	23 May : 26 Sep
	Freeport	3 Jun : 23 Sep	12 May : 27 Oct	15 Jun : 31 Aug	3 Jul : 17 Oct
	Metamora	3 Jun : 7 Oct	12 May : 13 Oct	25 May : 12 Oct	6 Jun : 17 Oct
	Monmouth	3 Jun : 14 Oct	12 May : 20 Oct	11 May : 12 Oct	30 May : 17 Oct
	Morris	3 Jun : 14 Oct	12 May : 13 Oct	8 Jun : 26 Oct	30 May : 17 Oct
	Perry	3 Jun : 14 Oct	12 May : 20 Oct	18 May : 12 Oct	23 May : 17 Oct
	Urbana	3 Jun : 14 Oct	12 May : 27 Oct	18 May : 26 Oct	2 May : 31 Oct
Indiana					
	ACRE	17 Jun : 14 Oct	2 Jun : 3 Nov	18 May : 26 Oct	23 May : 24 Oct
	DPAC	17 Jun : 14 Oct	2 Jun : 3 Nov	25 May : 26 Oct	23 May : 24 Oct
	NEPAC	17 Jun : 14 Oct	9 Jun : 27 Oct	18 May : 26 Oct	23 May : 17 Oct
	PIT	17 Jun : 14 Oct	2 Jun : 3 Nov	18 May : 26 Oct	23 May : 24 Oct
	PPAC	17 Jun : 14 Oct	2 Jun : 3 Nov	25 May : 19 Oct	23 May : 17 Oct
	SEPAC	17 Jun : 14 Oct	9 Jun : 3 Nov	18 May : 19 Oct	23 May : 17 Oct
Iowa					
	Ames	8 Jul : 28 Oct	9 Jun : 20 Oct	18 May : 26 Oct	6 Jun : 7 Nov
	McNay	8 Jul : 7 Oct	9 Jun : 20 Oct	18 May : 19 Oct	9 May : 17 Oct
	Nashua	8 Jul : 14 Oct	9 Jun : 20 Oct	25 May : 19 Oct	23 May : 17 Oct
	Sutherland	8 Jul : 28 Oct	16 Jun : 27 Oct	18 May : 19 Oct	9 May : 17 Oct
Kansas					
	Manhattan	19 Aug : 14 Oct	21 Apr : 13 Oct	15 Jun : 28 Sep	23 May : 24 Oct
Kentucky					
	Lexington	NS	NS	11 May : 28 Sep	4 Jan : 26 Dec
	Princeton	NS	7 Apr : 27 Oct	11 May : 26 Oct	4 Jan : 26 Dec
Michigan					
	Bean and Beet	24 Jun : 14 Oct	9 Jun : 20 Oct	11 May : 26 Oct	23 May : 31 Oct
	East Lansing	24 Jun : 14 Oct	9 Jun : 20 Oct	11 May : 26 Oct	16 May : 31 Oct
	Kellogg	24 Jun : 14 Oct	9 Jun : 20 Oct	25 May : 19 Oct	23 May : 24 Oct
	Monroe County	NS	23 Jun : 20 Oct	25 May : 26 Oct	30 May : 24 Oct
	Oceana	NS	23 Jun : 27 Oct	25 May : 26 Oct	25 July : 10 Oct

Table 2. Continued

State	Sampling Dates ^b			
Trap Name ^a	2005	2006	2007	2008
Minnesota				
Albert Lea	8 Jul : 14 Oct	16 Jun : 6 Oct	8 Jun : 7 Sep	6 Jun : 26 Sep
Crookston	NS	1 Sep : 6 Oct	1 Jun : 24 Aug	23 May : 17 Oct
Lamberton	8 Jul : 21 Oct	26 May : 20 Oct	8 Jun : 12 Oct	23 May : 17 Oct
Morris	8 Jul : 21 Oct	9 Jun : 27 Oct	8 Jun : 12 Oct	23 May : 17 Oct
Rosemount	8 Jul : 28 Oct	9 Jun : 13 Oct	1 Jun : 12 Oct	23 May : 17 Oct
Missouri				
Columbia	NS	7 Jul : 20 Oct	11 May : 26 Oct	28 Mar : 7 Nov
Portageville	NS	NS	11 May : 12 Oct	28 Mar : 26 Dec
South Dakota				
Brookings	NS	1 Sep : 20 Oct	11 May : 26 Oct	9 May : 7 Nov
Wisconsin				
Antigo	NS	23 Jun : 20 Oct	25 May : 26 Oct	6 Jun : 17 Oct
Arlington	24 Jun : 14 Oct	9 Jun : 20 Oct	1 Jun : 12 Oct	16 May : 17 Oct
Hancock	24 Jun : 14 Oct	16 Jun : 27 Oct	1 Jun : 26 Oct	30 May : 29 Aug
Lancaster	24 Jun : 14 Oct	9 Jun : 27 Oct	1 Jun : 26 Oct	30 May : 31 Oct
Pioneer	24 Jun : 14 Oct	9 Jun : 20 Oct	8 Jun : 7 Sep	13 Jun : 10 Oct
Seymour	NS	23 Jun : 27 Oct	15 Jun : 26 Oct	6 Jun : 17 Oct
Walworth	24 Jun : 14 Oct	9 Jun : 20 Oct	1 Jun : 26 Oct	6 Jun : 17 Oct

^a Names correspond with North Central Regional soybean aphid suction trap network (<http://www.ncipmc.org/traps/>).

^b Sampling dates (dates when samples were collected) indicate the initial and end sampling date for each trap and year. NS indicates no sample collected due to that suction trap not yet operational in places later constructed.

Table 3. Julian dates of the absolute first, average first, summer peak, and fall peak of alate *Aphis glycines* collected in the suction trap network (STN); plus regression values of first alate catch with XY coordinates

Year	Julian Date for Alate Collection in STN				Adjusted R ^{2a}	
	Absolute First	Avg First	Summer Peak	Fall Peak	X Coord ^b	Y Coord ^c
2005 ^d	175	194	224	259	0.02	0.13*
2006 ^e	181	214	216	272	0.01	0.42*
2007 ^f	145	194	215	271	0.03	0.04
2008 ^g	224	249	266	301	0.03	0.67*
Mean	181	213	230	275		
Stdev	33	26	24	18		

^a Significant treatment differences are represented by (*, $P < 0.05$).

^b X coordinates are analogous to longitude or Easting.

^c Y coordinates are analogous to latitude or Northing.

^d 2005 df = 1, 30.

^e 2006 df = 1, 34.

^f 2007 df = 1, 38.

^g 2008 df = 1, 40.

Table 4. Regression values of total alate *Aphis glycines* counts and XY coordinates

Season	Adjusted R ^{2a}	
	X Coordinates ^b	Y Coordinates ^c
2005 ^d		
Summer	0.04*	0.15*
Fall	0.01	0.02*
All Dates ^h	0.01*	0.08*
2006 ^e		
Summer	0.04*	0.20*
Fall	0.00	0.00
All Dates	0.01*	0.02*
2007 ^f		
Summer	0.00	0.04*
Fall	0.00	0.04*
All Dates	0.01*	0.04*
2008 ^g		
Summer	0.03*	0.21*
Fall	0.00	0.10*
All Dates	0.02*	0.17*

^a Significant treatment differences are represented by (*, $P < 0.05$).

^b X coordinates are analogous to longitude or Easting.

^c Y coordinates are analogous to latitude or Northing.

^d 2005 summer df = 1, 287; fall df = 1, 210; all df = 1, 499.

^e 2006 summer df = 1, 328; fall df = 1, 321; all df = 1, 651.

^f 2007 summer df = 1, 586; fall df = 1, 234; all df = 1, 822.

^g 2008 summer df = 1, 309; fall df = 1, 280; all df = 1, 591.

^h All dates is a combination of summer and fall dates.

Table 5. Nearest neighborhood analysis designed to test for spatial association (similarity in alate *A. glycines* catches) between sites

Year	Date ^b	Distance (km) ^a								
		150	175	200	225	250	275	300	325	350
2005										
July	8	*	*	*	**	-	-	-	-	-
	15	**	**	**	**	**	**	*	-	-
	22	**	**	*	*	*	-	-	-	-
	29	**	**	**	**	**	**	**	*	-
Aug.	5	**	**	**	**	**	**	**	*	-
	12	**	**	**	**	**	**	**	*	-
	19	-	-	-	*	**	**	**	**	*
	26	-	-	-	-	-	-	-	-	-
Sept.	2	**	**	**	**	**	**	**	**	**
	9	-	-	-	-	-	-	-	-	-
	16	**	**	**	**	**	**	**	**	**
	23	**	-	-	-	-	-	-	-	-
Oct.	30	**	**	*	*	-	-	-	-	-
	7	-	-	-	-	-	-	-	-	-
2006										
July	21	*	*	*	**	**	*	*	-	-
	28	**	**	**	**	**	**	**	**	**
Aug.	4	**	**	**	**	**	**	**	**	**
	11	**	**	**	*	*	-	-	-	-
	18	*	*	**	**	**	*	*	*	*
	25	-	-	-	-	-	-	-	-	-
Sept.	1	-	-	**	*	-	-	-	-	-
	8	-	-	-	-	-	-	-	-	-
	15	-	-	-	-	-	-	-	-	-
	22	-	-	-	-	-	-	-	-	-
Oct.	29	-	-	-	-	-	-	-	-	-
	6	**	**	*	**	-	-	-	-	-
	13	*	-	-	-	-	-	-	-	-
	20	-	-	-	-	-	-	-	-	-

^a Distance is radii in kilometers.

^b Date correlates to the end sampling date.

- indicates non significance.

* significant at $P < 0.1$.

** significant at $P < 0.05$.

Table 5. Continued

Year	Date ^b	Distance (km) ^a								
		150	175	200	225	250	275	300	325	350
2007										
July	13	-	*	-	-	-	-	-	-	-
	20	-	-	-	-	-	-	-	-	-
	27	*	*	*	*	-	-	-	-	-
Aug.	3	**	*	*	-	-	-	-	-	-
	10	**	*	*	-	-	-	-	-	-
	17	**	*	-	-	-	-	-	-	-
	24	-	-	-	-	-	-	-	-	-
	31	**	*	*	-	-	-	-	-	-
Sept.	7	*	**	**	**	**	**	**	**	*
	14	**	**	**	**	**	**	**	**	**
	21	**	-	-	-	-	-	-	-	-
	28	-	-	*	*	*	*	-	-	-
2008										
July	25	*	*	*	*	*	*	*	*	*
Aug.	1	-	-	-	-	-	-	-	-	-
	8	-	*	*	**	**	*	*	*	*
	15	*	-	-	-	*	-	-	-	-
	22	*	*	**	**	**	**	**	**	**
	29	*	*	*	*	*	*	*	*	*
Sept.	5	*	**	**	**	**	**	**	**	**
	12	-	-	-	-	-	-	-	-	-
	19	*	*	*	*	*	*	*	*	**
	26	*	*	*	*	*	*	*	*	**
Oct.	3	-	-	-	-	*	*	*	*	*
	10	*	*	-	-	-	-	-	-	-
	17	-	-	-	-	-	-	-	-	-

^a Radius from suction trap.^b Date corresponds to the end sampling date per sampling interval.

- indicates non significance.

* significant at $P < 0.1$.** significant at $P < 0.05$.

Figure Legends

Figure 1. Map of trap locations (labeled with numbers from Table 1) for the 42 suction traps in the Midwest United States.

Figure 2. There were 42 suction traps distributed throughout 10 Midwest states between 2005 – 2008. Each trap consists of an ~6-meter vertical tube with an electric fan that draws in air and deposits winged aphids into a glycol-filled jar.

Figure 3. Average weekly occurrence of alate *Aphis glycines* collected in suction traps from 2005 – 2008.

Figure 4. Weekly alate *Aphis glycines* data by week for 2005. Symbols are proportional to the total collected for each trap over a seven-day period.

Figure 5. Weekly alate *Aphis glycines* data by week for 2006. Symbols are proportional to the total collected for each trap over a seven-day period.

Figure 6. Weekly alate *Aphis glycines* data by week for 2007. Symbols are proportional to the total collected for each trap over a seven-day period.

Figure 7. Weekly alate *Aphis glycines* data by week for 2008. Symbols are proportional to the total collected for each trap over a seven-day period.

Figure 8. The established range of *Rhamnus cathartica* in the continental United States (courtesy of Kurylo et al. 2007).

Legend

● Trap locations

□ States

○ State name abbreviation

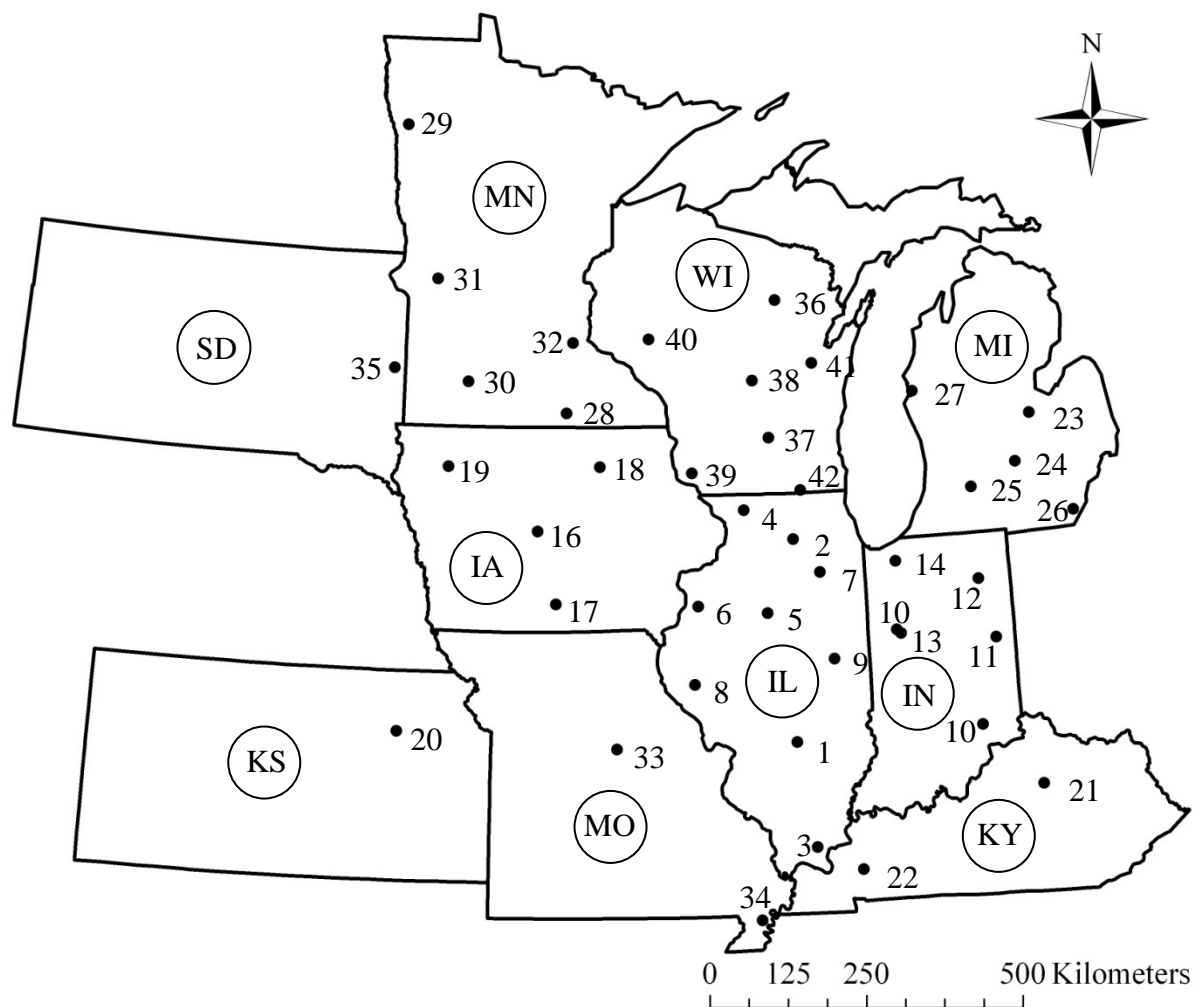


Fig. 1



Fig. 2

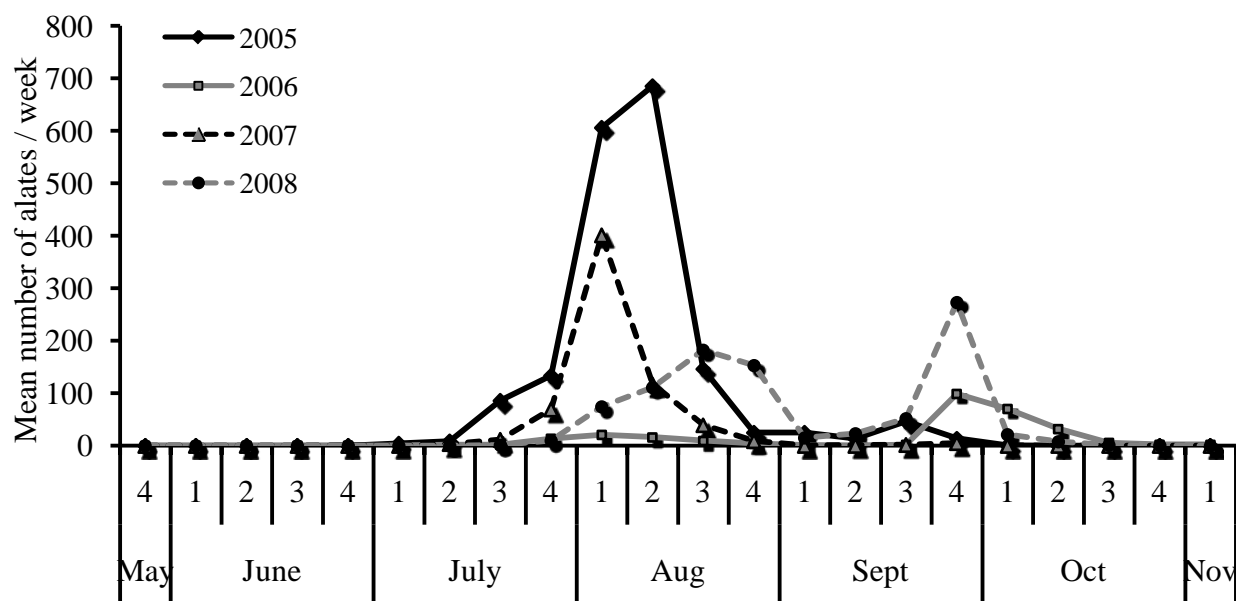


Fig. 3

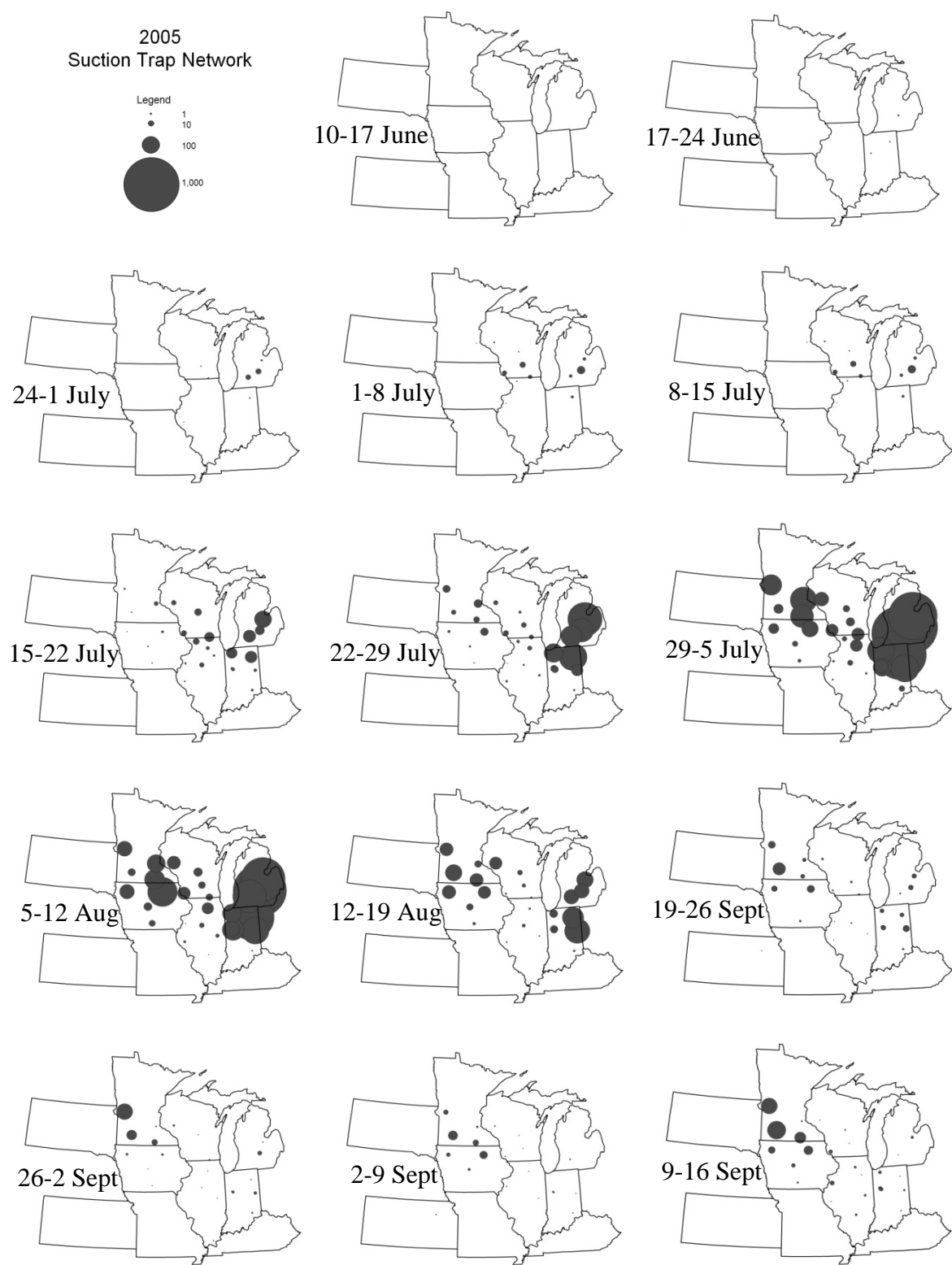


Fig. 4

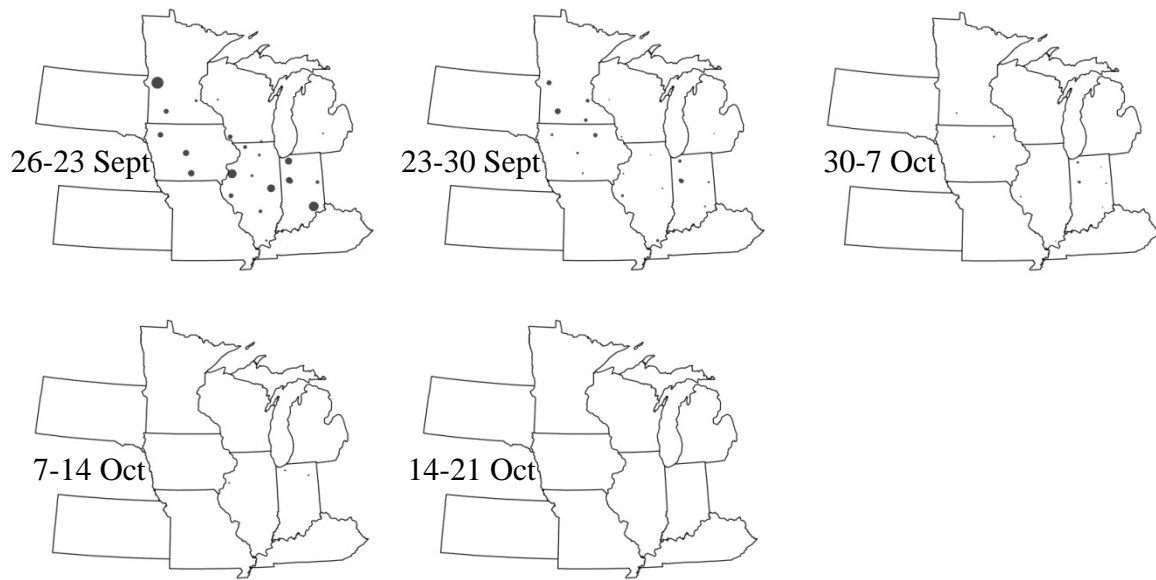


Fig. 4 Continued

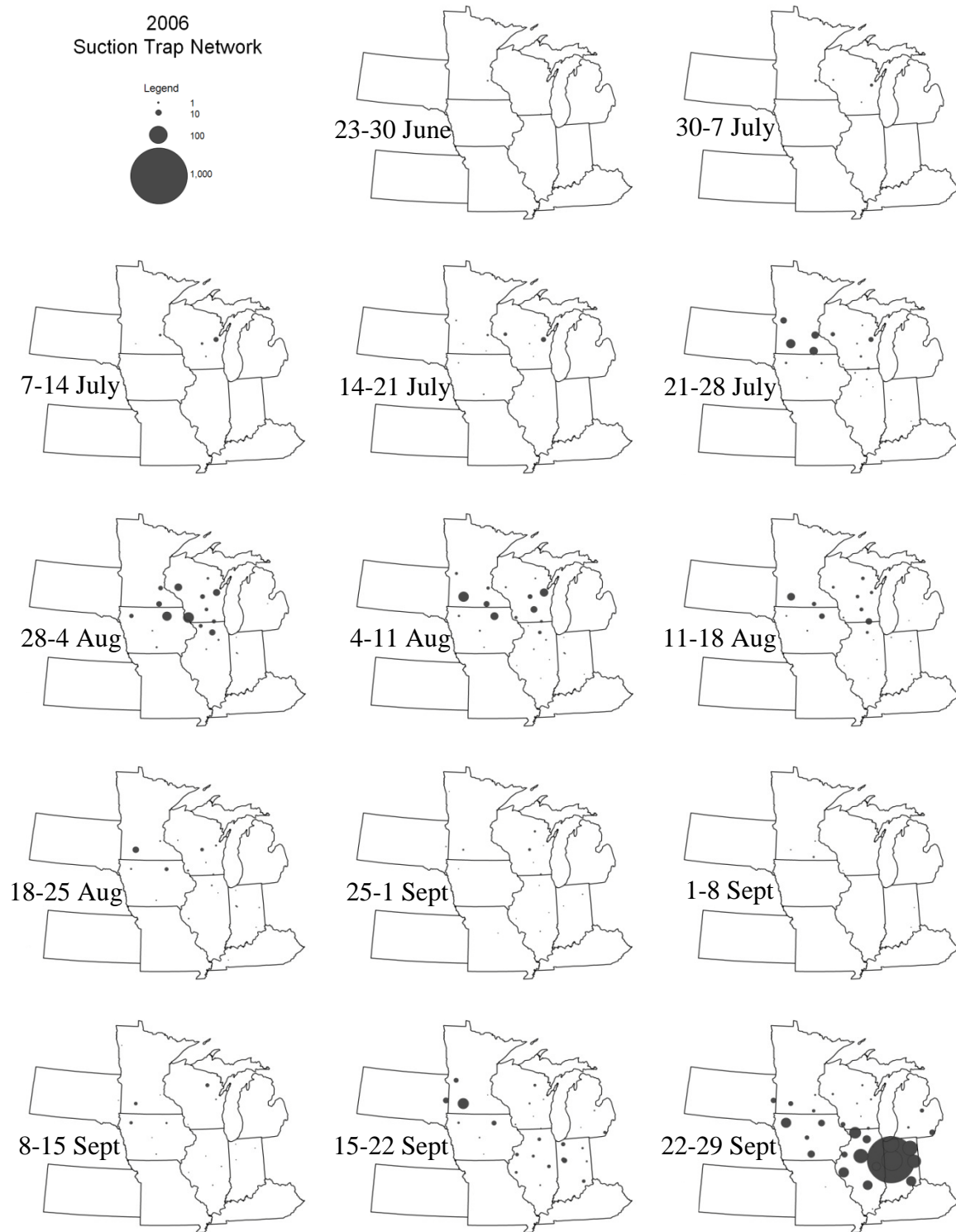


Fig. 5

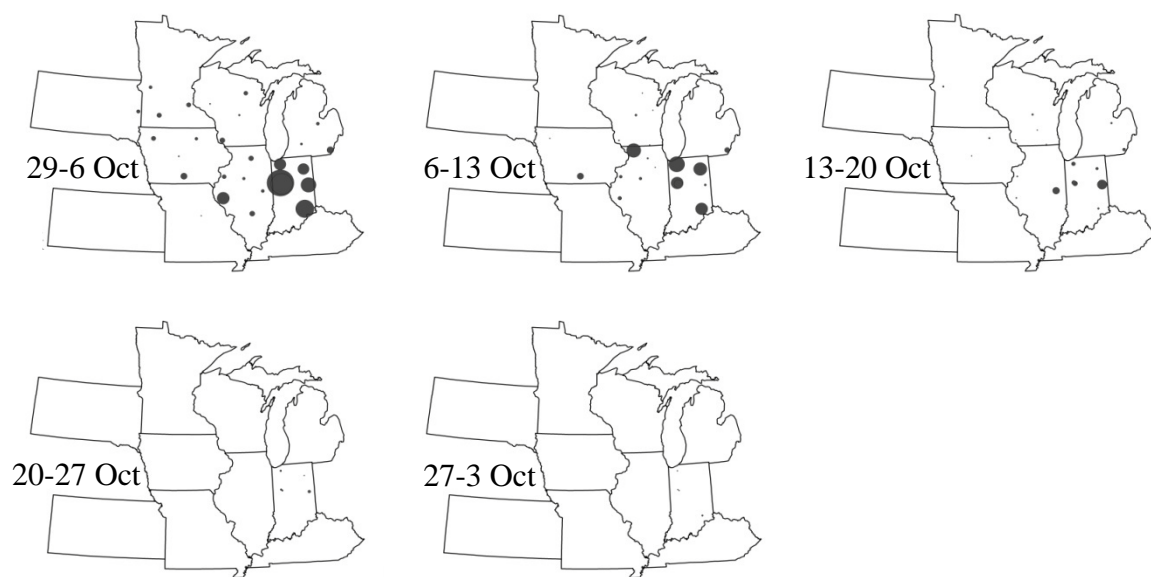


Fig. 5 Continued

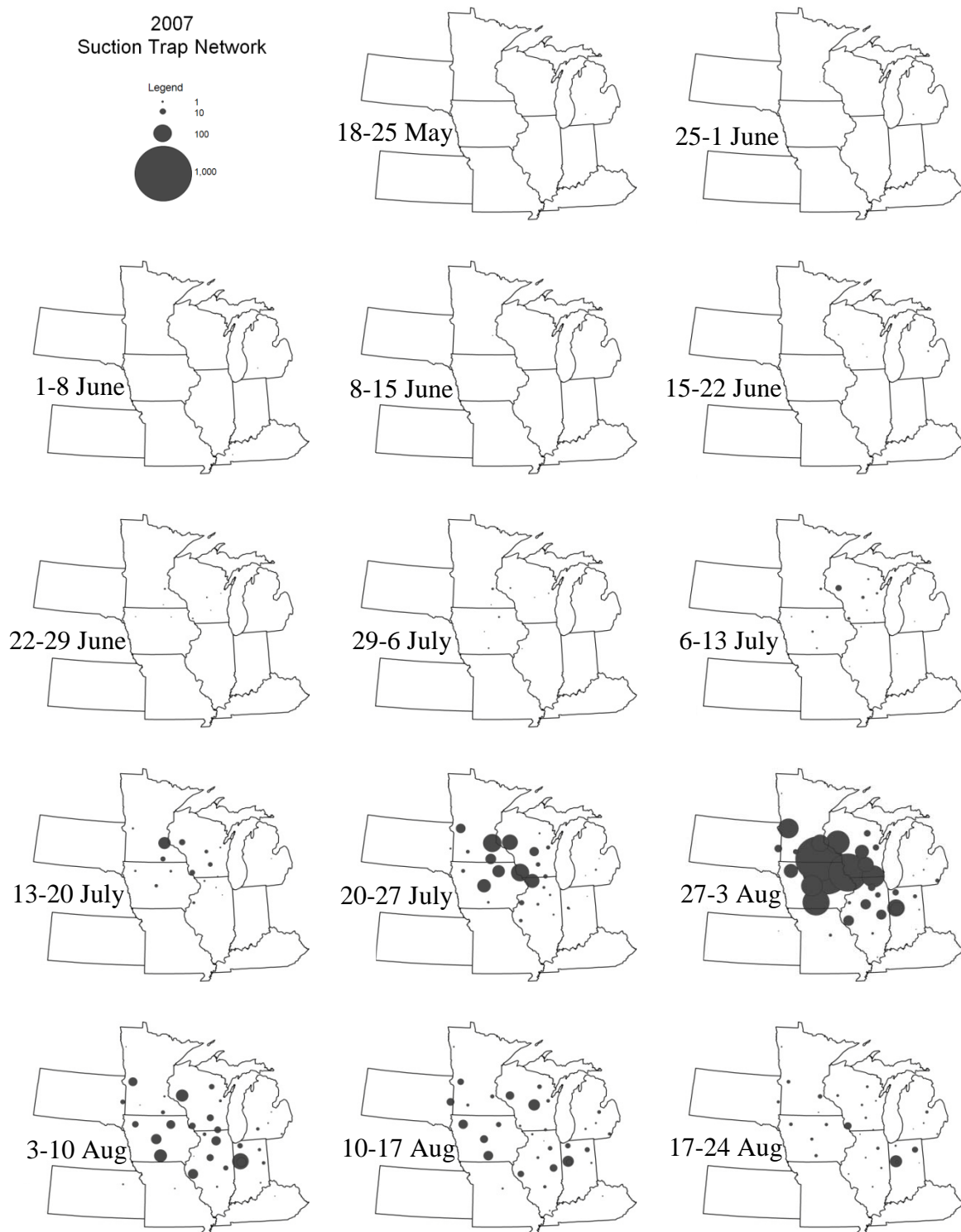


Fig. 6

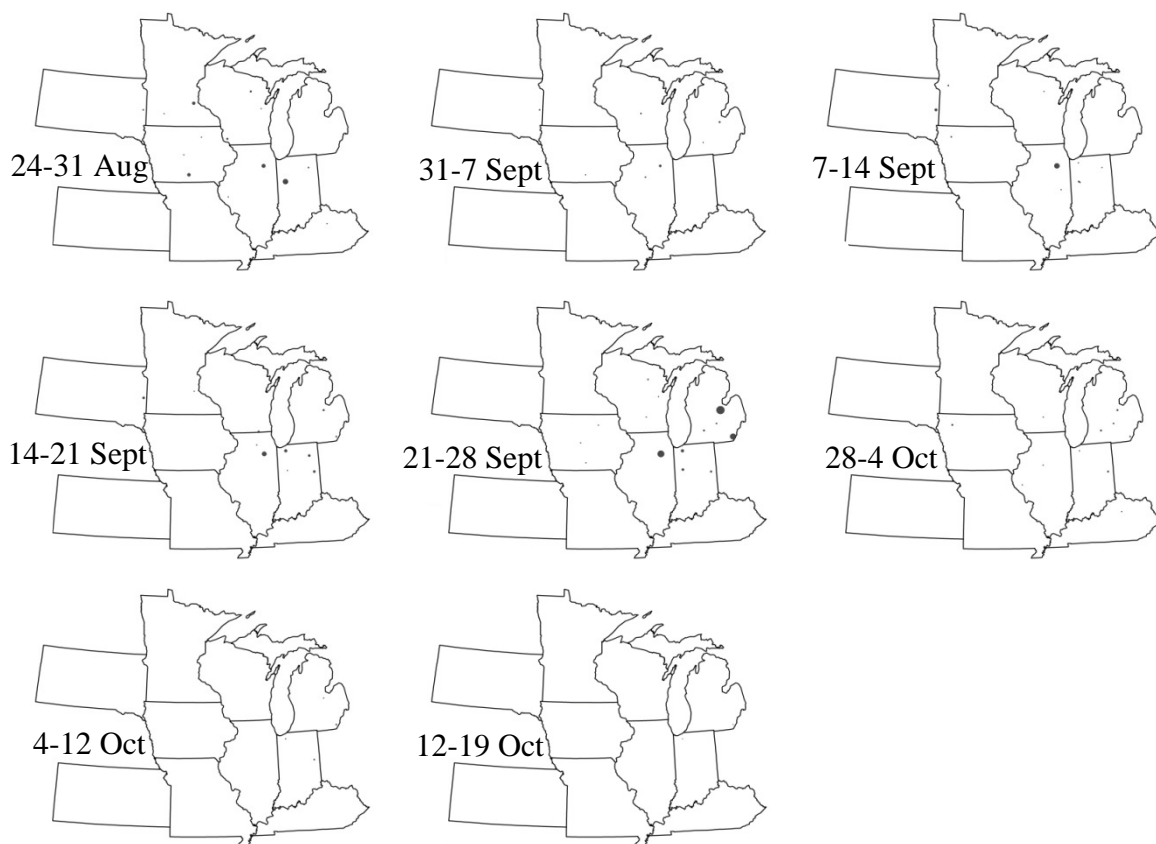


Fig. 6 Continued

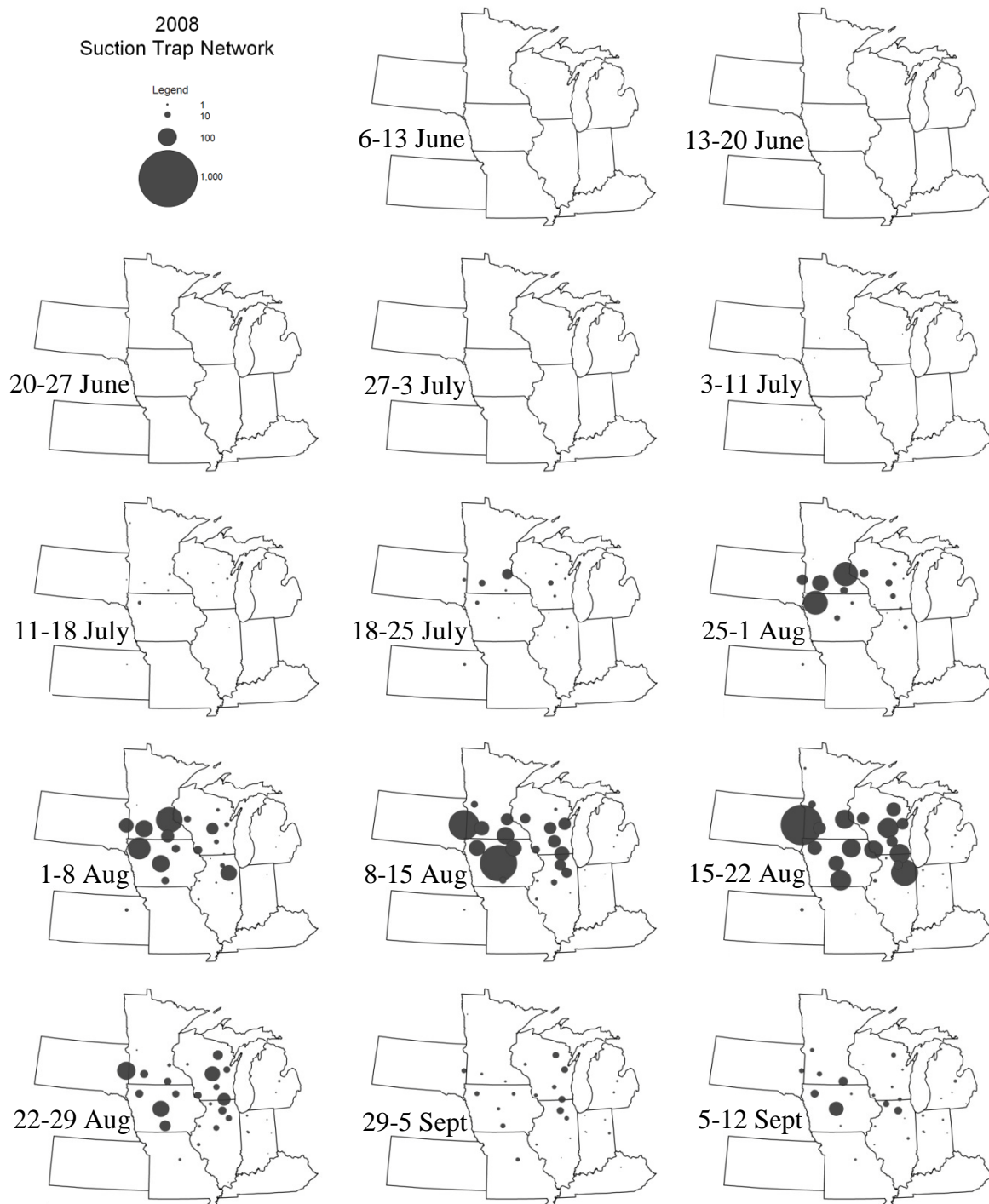


Fig. 7

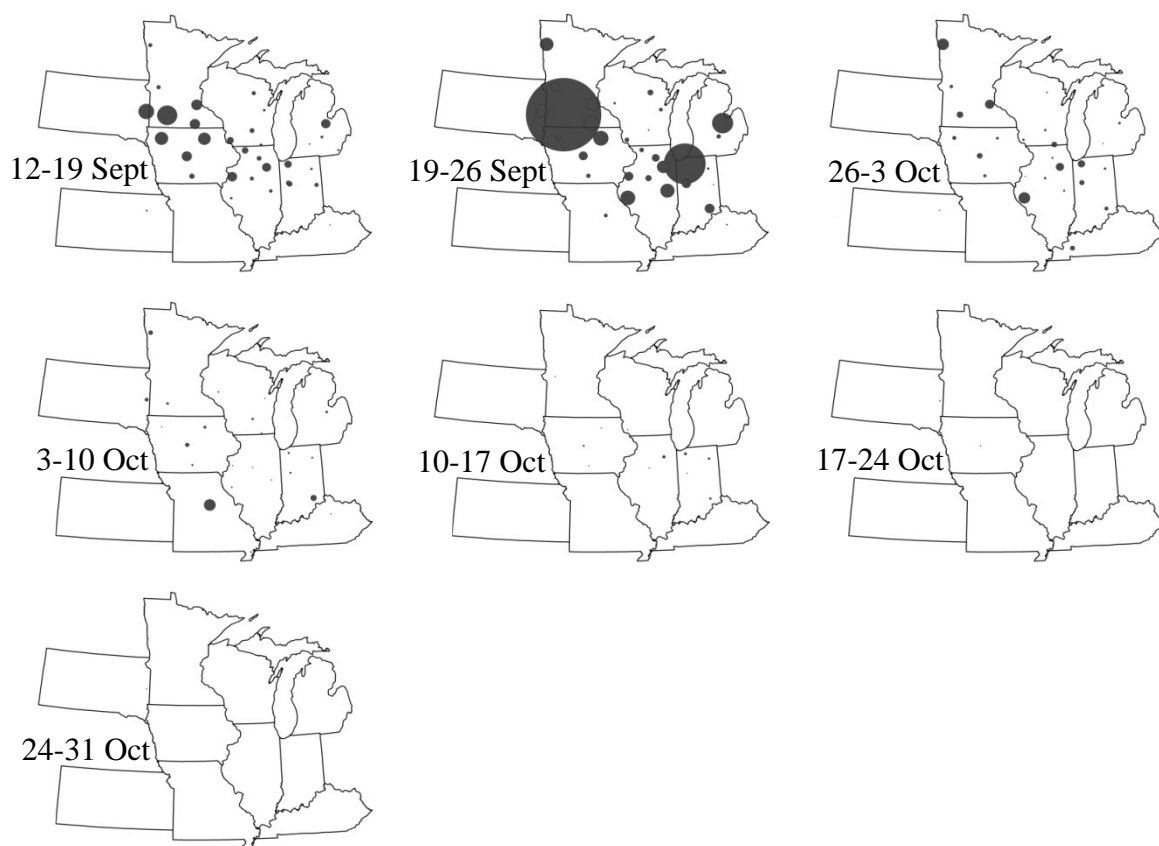


Fig. 7 Continued

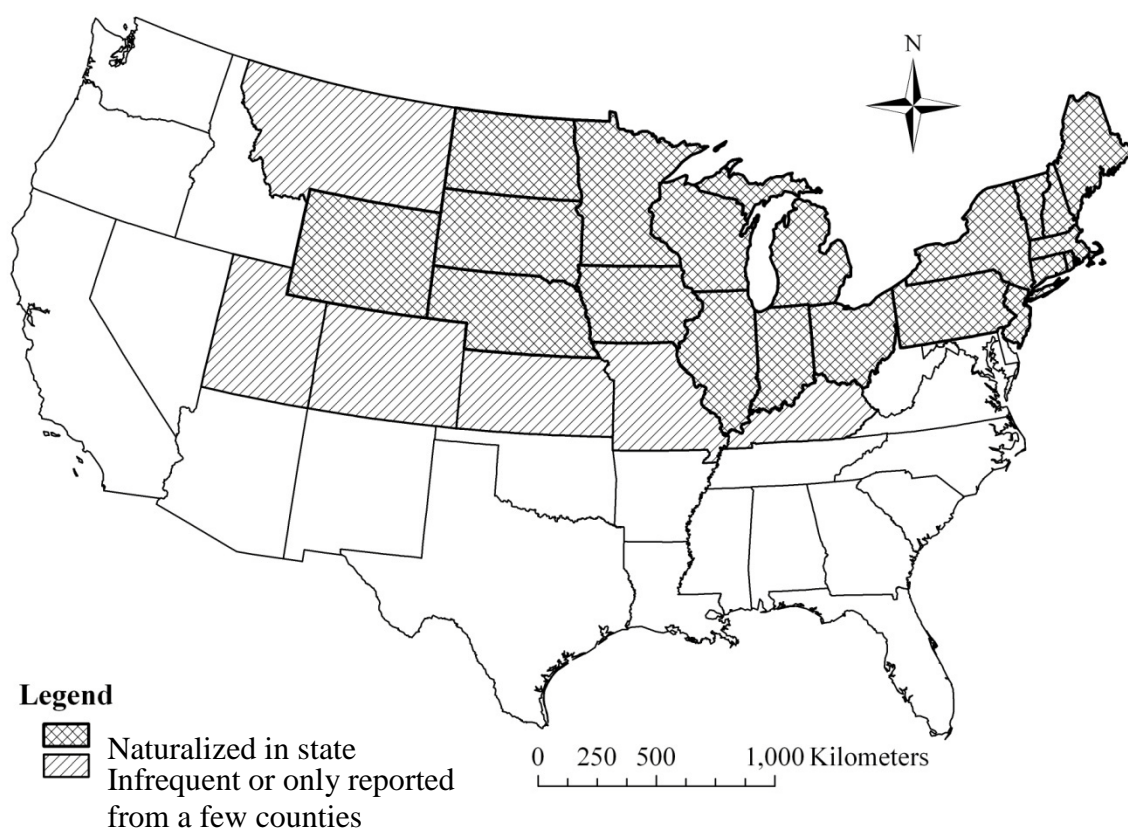


Fig. 8

Chapter 5

Predicting overwintering sites of *Aphis glycines* (Hemiptera: Aphididae) and *Harmonia axyridis* (Coleoptera: Coccinellidae) based on supercooling temperatures

A paper to be submitted to *Environmental Entomology*

Nicholas P. Schmidt, Matthew O'Neal, Kate Elliot, and Paul Anderson

Abstract

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), has been a major pest of soybean *Glycine max.* L. in North America since its introduction in 2000. Outbreaks of *A. glycines* are influenced by abiotic and biotic factors that can be observed at the landscape level. Specifically, natural enemies such as *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) can suppress outbreaks, but biological control is inconsistent. The extent to which variability in overwintering success by *A. glycines* and its natural enemies explain this inconsistent biological control is not clear. Objectives of this study were to create maps of lowest recorded temperatures in the Midwest United States from 2005 – 2009. Specifically, we wanted to determine if and where temperatures in a 10 state area reached or exceeded the supercooling point (SCP) for *A. glycines* (-34°C) and *H. axyridis* (-11.9°C), and if low temperatures can predict first alate catch of *A. glycines* in suction traps. Kriged statistical surfaces suggest that in 2005 and 2009, the *A. glycines* SCP was reached in the northwestern region of the study area, and in 2009 in a central portion of the study area. The SCP of *H. axyridis* was observed in all regions examined, except southern Missouri in 2005 and 2006, and the majority of Michigan in 2006. Regression analyses suggest that the early first captures of alate *A. glycines* in 2006 and 2008 were related to low temperature events, which was the opposite of what we predicted. Other explanations for these data may include the presence of common buckthorn, *Rhamnus cathartica* L., the overwintering host plant of *A. glycines*, in the surrounding landscape. Future research and management decisions are discussed.

KEYWORDS: Cold hardiness, climate, vineyard

Introduction

Soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), has become a persistent economic pest of soybean, *Glycine max* (L.) Merr., in the United States and Canada. *Aphis glycines* has a heteroecious holocyclic life cycle that alternates between common buckthorn, *Rhamnus cathartica* L. (Rhamnaceae), and soybean, and reproduces sexually in the fall (Ragsdale et al. 2004, Wu et al. 2004). Mated females lay and deposit eggs on buckthorn, typically at the base of the leaf bud where they overwinter (Ragsdale et al. 2004, Wu et al. 2004, McCornack et al. 2005, Voegtlin et al. 2005). Buckthorn is a native of Eurasia and was first introduced to North America in the 1800s as an ornamental shrub, and was chosen for its hardiness and ability to thrive in many soil and light conditions (Knight et al. 2007). Since its introduction, it has become established through much of the Midwest, northeastern US, and parts of Canada (Knight et al. 2007, Kurylo et al. 2007). *Aphis glycines* can survive winter temperatures by supercooling, which decreases the freezing point of body fluids. The supercooling point (SCP) of the overwintering egg stage for *A. glycines* is -34°C (McCornack et al. 2005), giving it the capacity to survive in much of buckthorn's range in North America.

During the growing season, alate *A. glycines* migrate from buckthorn to soybeans. Suction traps deployed across a region allow researchers to identify spatial distributions of aphids on a regional scale (Isard and Gage 2001). Vialatte et al. (2007) suggested the occurrence of alates in a suction trap network (STN) may be an indication of when aphids emigrate from local overwintering sites to initially colonize an annual crop. A STN was established across the north-central region of the US in 2005 to monitor aphids. Suction traps are designed to capture dispersing alates during descent (~ 6 m in height), but capture of alates during ascent or when moving laterally from field to field cannot be excluded. Alate *A. glycines* are first collected by the STN usually in mid-to-late June. The abundance of alate *A. glycines* collected increases, often by three orders of magnitude, in July and typically peaks in August (Schmidt et al. Chapter 3, Rhainds et al. 2010). The capture of alate *A. glycines* in the STN was positively related to aphid densities on soybean plants (Rhainds et al. 2010). It is possible that the predictive power of STN data can be improved with additional data related to *A. glycines* overwintering success.

The current arrangement of the STN does not consistently detect the movement of alate *A. glycines* from buckthorn to soybean fields (Schmidt et al. Chapter 3). In 2007, two traps in Michigan collected alate *A. glycines* as early as 24 May, however, in all other years alates were collected almost one month later (Schmidt et al. 2008). This suggests alates collected in the STN, even the first captures, are likely moving among soybean fields. Schmidt et al. (Chapter 3) also suggested alate *A. glycines* population levels are positively correlated with latitude. This relationship may be driven by temperature or by buckthorn, which also has a northern distribution (Kurylo et al. 2007). In a model that did not include temperature, Bahlai et al. (2010) found early season *A. glycines* densities in soybean were positively correlated with nearby buckthorn density.

Once *A. glycines* colonizes soybeans its populations can double in as little as 1.5 days under favorable conditions, resulting in up to 15 – 18 overlapping generations of apterae and alates on soybean (McCornack et al. 2004). On soybeans, natural enemies are a significant source of *A. glycines* mortality (Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2006, Schmidt et al. 2007). *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae) is an abundant predator in soybean agroecosystems across North America (Evans and Gunther 2005, Costamagna et al. 2008, Schmidt et al. 2008) and is considered an important source of mortality of *A. glycines* (Mignault et al. 2006, Gardiner and Landis 2007, Xue et al. 2009). *Harmonia axyridis* also has some degree of cold hardiness (Koch et al. 2004). The overwintering stage of *H. axyridis* is the adult, and its SCP is -11.9°C (Koch et al. 2004). Overwintering strategies for *H. axyridis* often include mass aggregations in or near prominent objects where temperatures may be warmer. Furthermore, survival from low temperatures in North America may be more dependent on the quality of overwintering sites rather than its cold hardiness (Koch et al. 2004). However, Labrie et al. (2008) found *H. axyridis* had a 25 – 53% survival rate inside houses in Quebec, suggesting that even in a sheltered environment low temperatures, during the overwintering period, still affect its survivorship.

Our objective was to predict first alate *A. glycines* capture in suction traps based on overwintering temperatures. We hypothesized that low temperatures will reduce overwintering *A. glycines* populations and that first alate captures will occur later. We

created maps of low temperatures, which include isotherms of the SCP of *A. glycines* (-34°C) and *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae; -11.9°C), in the Midwest US from 2005 – 2009.

Materials and Methods

The STN was established in Illinois in 2005 and expanded to a total of 10 states and 42 locations by 2007 (Figure 1). Each suction trap, designed according to Allison and Pike (1988), consisted of a ~6-m vertical tube, through which air was drawn by an electric fan operated only during daylight hours. Alates collected were deposited into a propylene glycol-filled jar and replaced weekly. Samples were sent to the Illinois Natural History Survey where *A. glycines* were identified and counted. Sample dates varied for each trap and year, but the majority of traps operated from May – September. Data for the STN were obtained from the North Central IPM Center (NC-IPM 2009).

Temperature data from 58 weather stations in years 2005 – 2009 were obtained from two sources. We used data from the automated surface observing systems (ASOS) located at the Iowa Environmental Mesonet (IEM 2010). When ASOS data were unavailable, historical data were obtained from Weather Underground (WU 2010). ASOS weather stations were located at airports, whereas Weather Underground stations varied by location, ranging from radio stations to town centers. Weather stations were selected based on proximity to suction traps (Figure 1). Specifically, the nearest weather station was identified for each suction trap (N = 42), and 16 more were selected around the perimeter of the STN to interpolate more accurate spatial temperature profiles (Figure 1).

The variables used in the analysis included the lowest recorded temperature per year for each suction trap (Table 1) and Julian date of the first alate *A. glycines* captured in the STN for 2005 – 2009 (Table 2). Regression analyses were used to determine how much if explain the variation in date of first alate capture from the STN is explained by low temperatures (Table 2). Statistical analyses were conducted using Excel (Microsoft Office 2004). Data transformations were not necessary to meet the assumptions of ANOVA (Sokal and Rohlf 1995).

Universal kriging was used to interpolate minimum temperatures between suction traps using a spherical model in ArcMap 9.3 (ESRI 2008) for years 2005 – 2009. Kriged statistical surfaces were validated by comparing observed to predicted temperatures. Contour lines or isotherms were created from kriged surfaces to help identify areas where -34°C or -11.9°C was observed using ArcMap 9.3 (ESRI 2008).

Results and Discussion

In general, low temperature surfaces suggest that the northwest portion of the study area (including northern Minnesota and South Dakota) consistently experienced the coldest temperatures (Figures 2-6). In 2005 and 2009, the SCP for *A. glycines* was reached at multiple locations, including southeast Minnesota, southwest Wisconsin, and northeast Iowa in 2009 (Figures 2, 6). For most locations in the STN, the occurrence of low temperatures reaching the SCP of *A. glycines* was rare and spatially limited. These data support McCornack et al. (2005), who concluded from ~ 73 years of historical data from 395 weather stations that reaching the SCP of *A. glycines* is unlikely most years in this region. However, the SCP for *H. axyridis* (-11.9°C) was reached throughout the study area in all years except two regions in 2005 and 2006 (Table 1): southeastern Missouri (Figures 2-3), and most of Michigan (Figure 3).

Using regression analysis we found that variability observed in first alate catch was partially explained by low temperature in 2006 ($R^2 = 0.11$; $F_{1,34} = 4.21$; $P = 0.05$) and 2008 ($R^2 = 0.62$, $F_{1,40} = 67.08$; $P < 0.01$; Table 2). In both 2006 and 2008, early first alate catch corresponded to lower temperatures, which is contrary to our expectations. We explore two explanations for this result. Although we rarely reached the SCP of *A. glycines*, we frequently reached the SCP of *H. axyridis*. To what extent *H. axyridis* population level is affected by overwintering mortality is not clear. Koch et al. (2004) suggested that the SCP for *H. axyridis* is a poor predictor of its range. However, the abundance of *H. axyridis* within its range will likely vary in part due to overwintering success. Considering the relatively warm winter temperatures experienced in 2006, the overwintering success of *H. axyridis* may have been much greater in 2006 than 2005. Confounding this pattern is the impact of landscape on *H. axyridis*, which varies within our study region. In 2005 and 2006,

populations of *H. axyridis* were greatest in Wisconsin > Michigan > Minnesota > Iowa, and the pattern of abundance was positively correlated with forested habitat in the landscape (Gardiner et al. 2009b). Gardiner et al. (2009a) observed that biological control of *A. glycines* in 2005-2006 was greater in landscapes comprised of non-crop habitat, particularly forest. The trends we observed during this period suggest overwintering temperatures may contribute to *H. axyridis* abundance and the biological control they provide for *A. glycines*.

Alternatively, the abundance of buckthorn may also explain the positive correlation of cold temperature with the time of first capture of alates in the STN. The coldest temperatures occurred in northern locations of the STN, where buckthorn is more abundant (Kurylo et al. 2007). Our results may reflect a correlation between the time of first capture of *A. glycines* and abundance of their overwintering host buckthorn, rather than a relationship with low temperature per se.

The STN is limited in its ability to collect *A. glycines* moving from buckthorn to soybean (Schmidt et al. Chapter 3). Therefore, identifying overwintering source populations of *A. glycines* will be crucial in improving predictions. We suggest the next step is to create a distribution map of buckthorn across the north-central US. The parameters needed to create a map to identify buckthorn are complex, but some basic biological information is known (Knight et al. 2007, Kurylo et al. 2007).

Both *A. glycines* and buckthorn are invasive species that reduce soybean yield (Ragsdale et al. 2004; Johnson et al. 2009) and the integrity of forest stands (Knight et al. 2007), respectively. A biological bottleneck is created in the lifecycle of *A. glycines* when sexual morphs are required to find one another on buckthorn to mate (Ragsdale et al. 2004). Currently, soybean producers are limited primarily to therapeutic measures for controlling *A. glycines*, however, future integrated pest management (IPM) programs may include the management of the two invasive species with both preventative and therapeutic control measures. For example, concurrent management of buckthorn may improve preventative management efforts of *A. glycines* by reducing the number of overwintering aphids. Buckthorn is found in the US east of the Rocky Mountains and south of the Canada border to the central states (Figure 7). To initiate a dual IPM program for buckthorn and *A. glycines*, more details on the distribution of buckthorn are required. In this manuscript our objective

was to examine if low temperature maps could be used as a tool to identify *A. glycines* overwintering source populations. However, a management plan targeted at reducing the abundance of buckthorn to reduce the abundance of *A. glycines* would be a bold first step in developing a more long-term cost-effective IPM program.

Acknowledgements

We thank Keith Hinrichs, Lyle Paul, Eric Adee, Pete Fandel, Mike Vose, Lindell Deal, Steve Ebelhar, Russ Higgins, Don Biehle, Jon Leuck, Jeff Boyer, Phil Walker, Christian Krupke, Tim Wood, Peg Reedy, Eileen Cullen, Andy Merry, Kevin Jarek, Dennis Laskowski, Bill Schaumberg, Scott Chapman, Patrick Branick, Steven Kirk, Kelly Tindall, Dave Haden, Ken Penckiosky, Nick Piekema, Mike Fiscus, Bruce Potter, George Nelson, Ian MacRae, Jeff Whitworth, Doug Johnson, Michael McCornack, Kelley Tilmon, Chris DiFonzo, Michael McCornack, Ned Birkey, and Norm Myers who coordinated and collected suction trap data, David Voegtlin and Doris Lagos for identification of alates in STN, and Todd Hanson for assisting with GIS analyses. This journal paper of the Iowa Agriculture and Home economics Experiment Station, Ames, Iowa, Project No. 5032, was supported by Hatch Act and State of Iowa funds.

References Cited

- Allison, D., and K. S. Pike. 1988.** An inexpensive suction trap and its use in an aphid monitoring network. *J. Agric. Entomol.* 5: 103-107.
- Bahlai, C. A., S. Sikkema, R. H. Hallett, J. Newman, and A. W. Schaafsma. 2010.** Modeling distribution and abundance of soybean aphid in soybean fields using measurements from the surrounding landscape. *Environ. Entomol.* 39: 50-56.
- Costamagna, A. C., and D. A. Landis. 2006.** Predators exert top-down control of soybean aphid across a gradient of agricultural management systems. *Ecol. Appl.* 16: 1619-1628.
- Costamagna, A. C., D. A. Landis, and M. J. Brewer. 2008.** The role of natural enemy guilds in *Aphis glycines* suppression. *Biol. Control* 45: 368-379.
- Environmental Systems Research Institute (ESRI). 2008.** ArcGIS 9.3. www.esri.com
- Evans, E. W., and D. I. Gunther. 2005.** The link between food and reproduction in aphidophagous predators: A case study with *Harmonia axyridis* (Coleoptera: Coccinellidae). *Eur. J. Entomol.* 102: 423-430.
- Fox, T. B., D. A. Landis, F. F. Cardoso, and C. D. Difonzo. 2004.** Predators suppress *Aphis glycines* matsumura population growth in soybean. *Environ. Entomol.* 33: 608-618.
- Gardiner, M. M., and D. A. Landis. 2007.** Impact of intraguild predation by adult *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Hemiptera: Aphididae) biological control in cage studies. *Biol. Control* 40: 386-395.
- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. Chacon, M. Wayo, N. P. Schmidt, E. Mueller and G. E. Heimpel. 2009a.** Landscape diversity enhances the biological control of an introduced crop pest in the north-central USA. *Ecol. Applic.* 19: 143-154.
- Gardiner, M. M., D. A. Landis, C. Gratton, N. P. Schmidt, M. O'Neal, E. Mueller, J. Chacon, G. E. Heimpel and C. D. DiFonzo. 2009b.** Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity Distrib.* 15: 554-564.

- Iowa Environmental Mesonet (IEM). 2010.** Iowa State University Department of Agronomy: ASOS data download.
<http://mesonet.agron.iastate.edu/request/download.phtml>, last visited 1, May 2010.
- Isard, S. A., and S. H. Gage. 2001.** Flow of life in the atmosphere: An airscape approach to understanding invasive organisms. Michigan State University Press, East Lansing.
- Johnson, K. D., M. E. O’Neal, J. D. Bradshaw, and M. E. Rice. 2008.** Is preventative, concurrent management of the soybean aphid (Hemiptera: Aphididae) and bean leaf beetle (Coleoptera: Chrysomelidae) possible? *J. Econ. Entomol.* 101: 801-809.
- Johnson, K. D., M. E. O’Neal, D. W. Ragsdale, C. D. Difonzo, S. M. Swinton, P. M. Dixon, B. D. Potter, E. W. Hodgson, and A. C. Costamagna. 2009.** Probability of cost-effective management of soybean aphid (Hemiptera: Aphididae) in North America. *J. Econ. Entomol.* 102: 2101-2108.
- Koch, R. L., M. A. Carrillo, R. C. Venette, C. A. Cannon, and W. D. Hutchison. 2004.** Cold hardiness of the multicolored Asian lady beetle (Coleoptera: Coccinellidae). *Environ. Entomol.* 33: 815-822.
- Knight, K. S., J. S. Kurylo, A. G. Endres, J. R. Stewart, and P. B. Reich. 2007.** Ecology and ecosystem impacts of common buckthorn (*Rhamnus cathartica*): A review. *Biol. Invasions* 9: 925-937.
- Kurylo, J. S., K. S. Knight, J. R. Stewart, and A. G. Endress. 2007.** *Rhamnus cathartica*: Native and naturalized distribution and habitat preferences. *J. Torrey Bot. Soc.* 134: 420-430.
- Labrie, G., D. Coderre, and E. Lucas. 2008.** Overwintering strategy of multicolored Asian lady beetle (Coleoptera: Coccinellidae): Cold-free space as a factor of invasive success. *Ann. Entomol. Soc. Am.* 101: 860-866.
- McCornack, B. P., D. W. Ragsdale, and R. C. Venette. 2004.** Demography of soybean aphid (Homoptera: Aphididae) at summer temperatures. *J. Econ. Entomol.* 97: 854-861.
- McCornack, B. P., M. A. Carrillo, R. C. Venette, and D. W. Ragsdale. 2005.** Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). *Environ. Entomol.* 34: 235-240.

- Microsoft Office. 2004.** Microsoft Corporation, Version 11.4.
- Mignault, M. P., M. Roy, and J. Brodeur. 2006.** Soybean aphid predators in Quebec and the suitability of *Aphis glycines* as prey for three Coccinellidae. *Biocontrol* 51: 89-106.
- North Central IPM Center (NC-IPM). 2009.** Regional soybean aphid suction trap network. <http://www.ncipmc.org/traps/>, last visited 5, April 2010.
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004.** Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97: 204-208.
- Rhainds, M. H. J. S. Yoo, K. L. Steffey, D. J. Voegtlin, C. S. Sadof, S. Yaninek, and R. J. O'Neil. 2010.** Potential of suction traps as a monitoring tool for *Aphis glycines* (Hemiptera: Aphididae) in soybean fields. *J. Econ. Entomol.* 103: 186-189.
- Rutledge, C. E., R. J. O'Neil, T. B. Fox, and D. A. Landis. 2004.** Soybean aphid predators and their use in integrated pest management. *Ann. Entomol. Soc. Am.* 97: 240-248.
- Schmidt, N. P., O. N. M. E., and J. W. Singer. 2007.** Alfalfa living mulch advances biological control of soybean aphid. *Environ. Entomol.* 36: 416-24.
- Schmidt, N. P., M. E. O'Neal, and P. M. Dixon. 2008.** Aphidophagous predators in Iowa soybean: A community comparison across multiple years and sampling methods. *Ann. Entomol. Soc. Am.* 102: 341-350.
- Schmidt, N. P., M. E. O'Neal, P. F. Anderson, D. Voegtlin, D. Lagos, C. Gratton, E. Cullen, D. W. Ragsdale, B. McCornack, J. Whitworth, K. J. Tilmon, C. DiFonzo, D. Johnson, W. Bailey, R. O'Neil, and C. H. Krupke. Chapter 3 of dissertation.** Spatial distributions of Soybean aphid: A summary of the suction trap network. To be submitted to *J. Insect Sci.*
- Sokal, R. R., and F. J. Rohlf. 1995.** *Biometry: The Principles and Practice of Statistics in Biological Research.* 3rd edition. W. H. Freeman and Co.: New York.
- Vialatte, A., M. Plantegenest, J. C. Simon, and C. A. Dedryver. 2007.** Farm-scale assessment of movement patterns and colonization dynamics of the grain aphid in arable crops and hedgerows. *Agric. For. Entomol.* 9: 337-346.
- Voegtlin, D. J., R. J. O'Neil, W. R. Graves, D. Lagos, and H. J. S. Yoo. 2005.** Potential winter hosts of soybean aphid. *Ann. Entomol. Soc. Am.* 98: 690-693.

Weather Underground Inc. (WU). 2010. Weather history.

<http://www.wunderground.com/history/>

Wu, Z. S., D. Schenk-Hamlin, W. Y. Zhan, D. W. Ragsdale, and G. E. Heimpel. 2004.

The soybean aphid in China: A historical review. *Ann. Entomol. Soc. Am.* 97: 209-218.

Xue, Y, C. A. Bahlai, A. Frewin, M. K. Sears, A. W. Schaafsma, and R. H. Hallett. 2009.

Predation by *Coccinella septempunctata* and *Harmonia axyridis* (Coleoptera: Coccinellidae) on *Aphis glycines* (Homoptera: Aphididae). *Biol. Control* 38(3): 708-714.

Table 1. Suction trap and nearest weather station names, in addition to minimum temperatures for the years 2005 – 2009

State (Abbreviation)		Low Temperatures (°C)				
Trap Name ^a	Weather Station ^b	2005	2006	2007	2008	2009
Illinois (IL)						
Brownstown	Effingham	-21	-15	-18	-18	-20
Dekalb	DeKalb	-21	-18	-23	-23	-29
Dixon Springs	Metropolis	-13	-12	-13	-13	-16
Freeport	Freeport	-23	-19	-26	-26	-32
Metamora	Peoria	-21	-19	-22	-22	-28
Monmouth	Galesburg	-23	-22	-23	-24	-30
Morris	Morris	-19	-17	-25	-22	-28
Perry	Pittsfield	-18	-19	-19	-18	-22
Urbana	Urbana	-20	-15	-23	-20	-27
Indiana (IN)						
ACRE	Layfayette	-18	-13	-22	-20	-28
DPAC	Muncie	-20	-13	-21	-18	-26
NEPAC	Warsaw Muni	-21	-14	-22	-20	-28
PIT	Layfayette	-18	-13	-22	-20	-28
PPAC	Valparaiso	-19	-15	-23	-22	-29
SEPAC	Columbus	-19	-13	-18	-17	-24
Iowa (IA)						
Ames	Ames	-28	-26	-25	-28	-34
McNay	Des Moines	-22	-22	-23	-24	-28
Nashua	Waterloo	-28	-28	-27	-25	-36
Sutherland	Spencer	-29	-29	-30	-30	-32
Kansas (KS)						
Manhattan	Manhattan	-24	-15	-19	-22	-18
Kentucky (KY)						
Lexington	Lexington	-14	-16	-17	-16	-19
Princeton	Paducah	-13	-14	-14	-14	-16
Michigan (MI)						
Bean and Beet	Saginaw	-19	-11	-21	-21	-23
East Lansing	Lansing	-23	-9	-22	-21	-23
Kellogg	Kalamazoo	-21	-9	-26	-19	-23
Monroe County	Monroe	-22	-9	-22	-19	-26
Oceana	Bad Axe	-27	-9	-22	-22	-31
Minnesota (MN)						
Albert Lea	Albert Lea	-25	-27	-27	-28	-31
Crookston	Crookston	-36	-23	-32	-34	-37
Lamberton	Tracy	-28	-19	-25	-26	-31
Morris	Morris	-32	-21	-29	-32	-36

Table 1. Continued

State (Abbreviation)		Low Temperatures (°C)				
Trap Name ^a	Weather Station ^b	2005	2006	2007	2008	2009
Minnesota (MN)						
Rosemount	South St. Paul	-24	-16	-26	-24	-30
Missouri (MO)						
Columbia	Columbia	-18	-18	-18	-18	-20
Portageville	Portageville	-9	-11	-13	-13	-13
South Dakota (SD)						
Brookings	Brookings	-30	-24	-28	-31	-34
Wisconsin (WI)						
Antigo	Antigo	-31	-19	-31	-32	-33
Arlington	Dells	-23	-16	-27	-27	-29
Hancock	Wautoma	-26	-29	-27	-33	-29
Lancaster	Boscobel	-27	-28	-29	-31	-36
Pioneer	Eau Claire	-25	-18	-29	-28	-32
Seymour	Green Bay	-23	-16	-26	-26	-29
Walworth	Burlington	-23	-19	-28	-23	-28
Mean Low Temperature (\pm Stdev)		-22(6.6)	-18(6.7)	-23(7.3)	-23(6.0)	-27(6.0)

^a Trap names are from the website (NC-IPM 2009) where suction trap data is reported for each location. Specific locations can be found in Schmidt et al. (Chapter 3).

^b ASOS weather stations are located at airports; those used in this analysis were selected from airports nearest each suction trap (IEM 2010).

Table 2. Summary of regression analyses of Julian dates of first alate *Aphis glycines* capture in a suction trap on low temperatures recorded at the nearest weather stations across the suction trap network in 10 Midwestern states (see Fig. 1).

Year	First Alate Catch			
	Adjusted R ²	F-value	P-value	df
2005	0.01	0.68	0.42	1, 30
2006	0.11	4.21	0.05	1, 34
2007	0.07	3.00	0.09	1, 38
2008	0.62	67.08	<0.01	1, 40
2009	0.07	2.58	0.12	1, 36

Figure Legends

Figure 1. Locations of weather stations and suction traps.

Figure 2. 2005 lows interpolated from observed low temperatures. Dashed line, -12 and -34°C isotherms.

Figure 3. 2006 lows interpolated from observed low temperatures. Dashed line, -12°C isotherm.

Figure 4. 2007 lows interpolated from observed low temperatures. Dashed line, -34°C isotherm.

Figure 5. 2008 lows interpolated from observed low temperatures. Dashed line, -34°C isotherm.

Figure 6. 2009 lows interpolated from observed low temperatures. Dashed line, -34°C isotherm.

Figure 7. Established range of *Rhamnus cathartica* in the United States (courtesy of Kurylo et al. 2007).

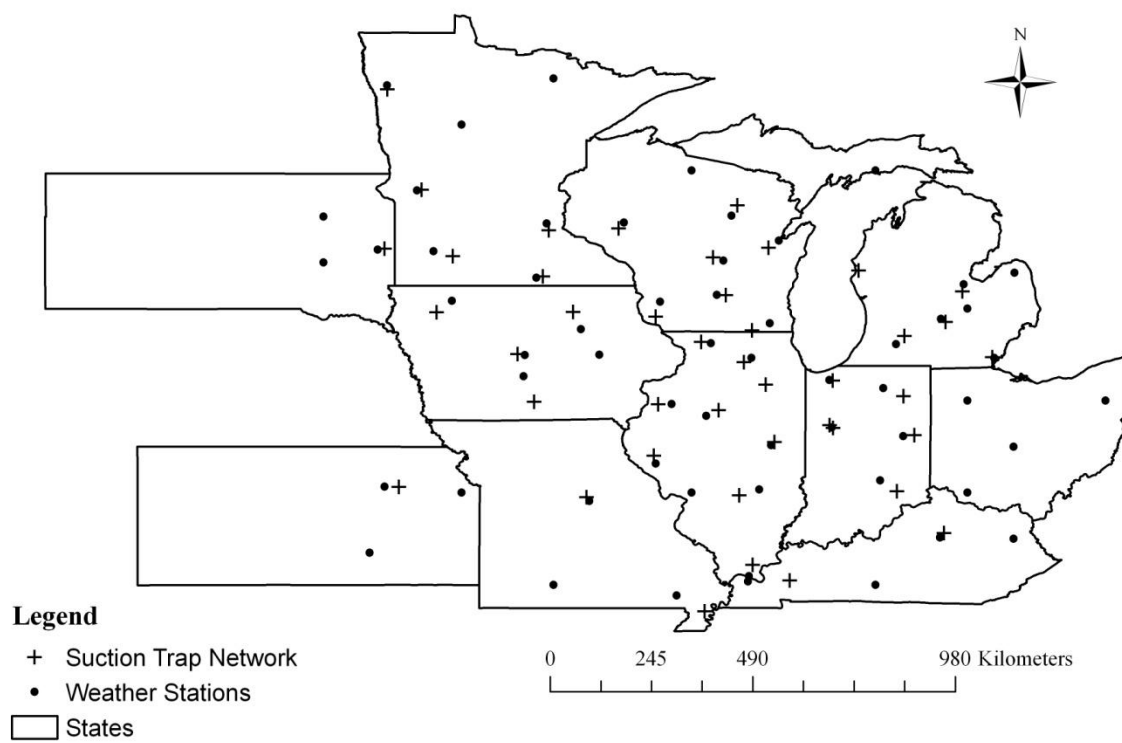


Fig. 1

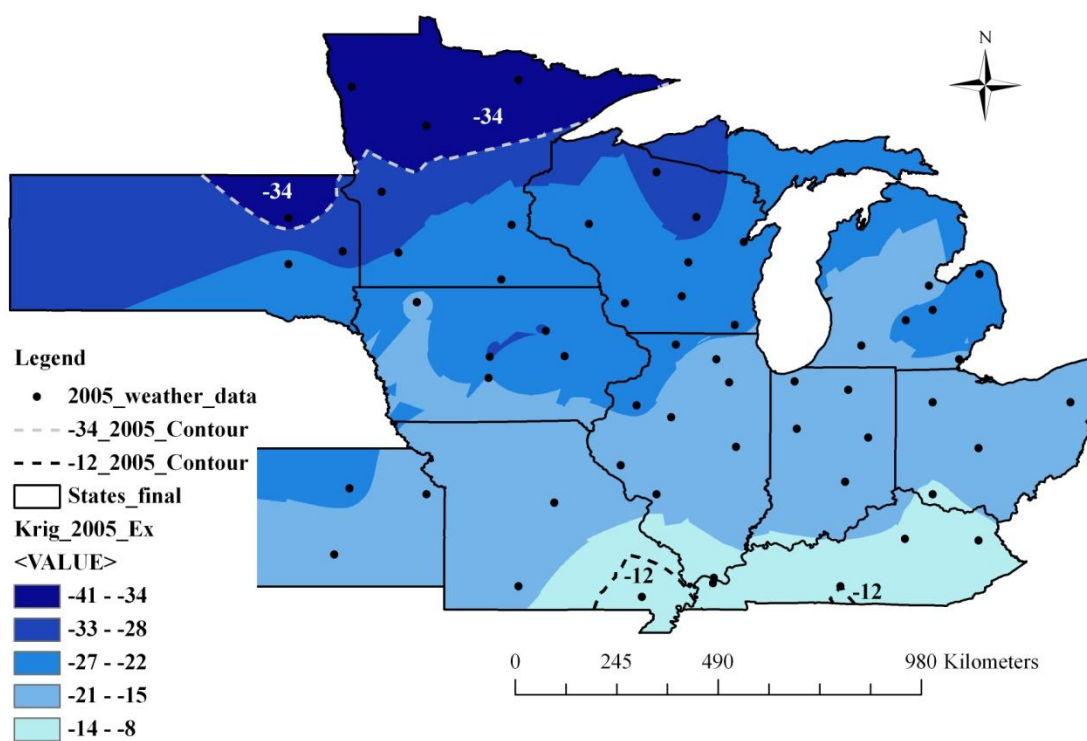


Fig. 2

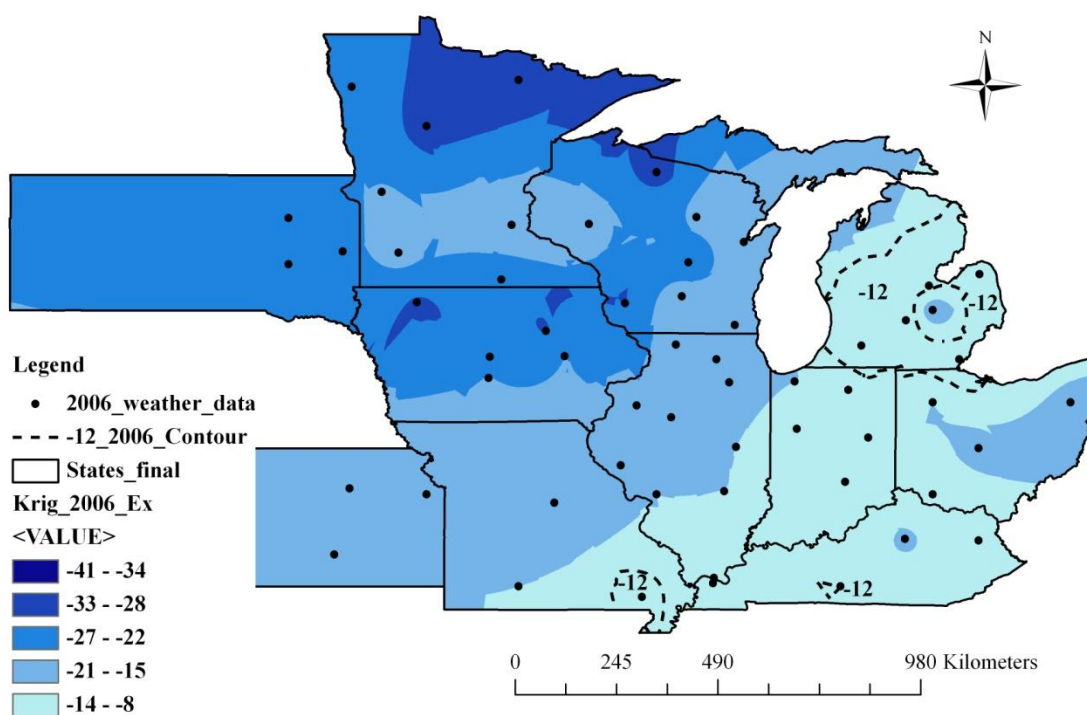


Fig. 3

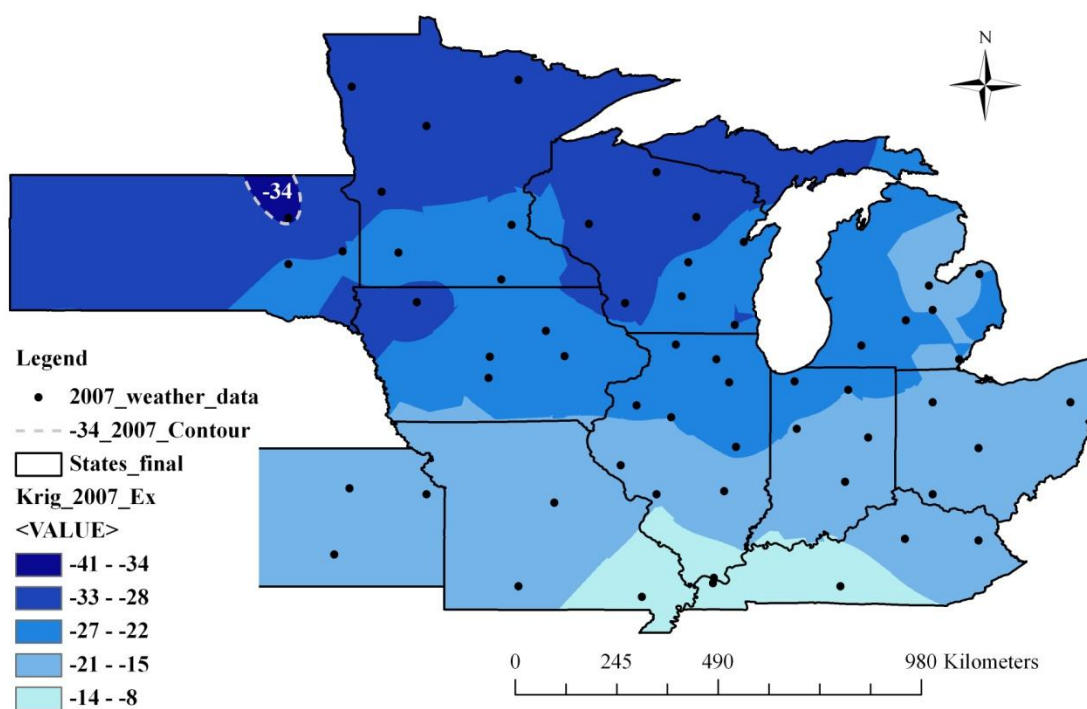


Fig. 4

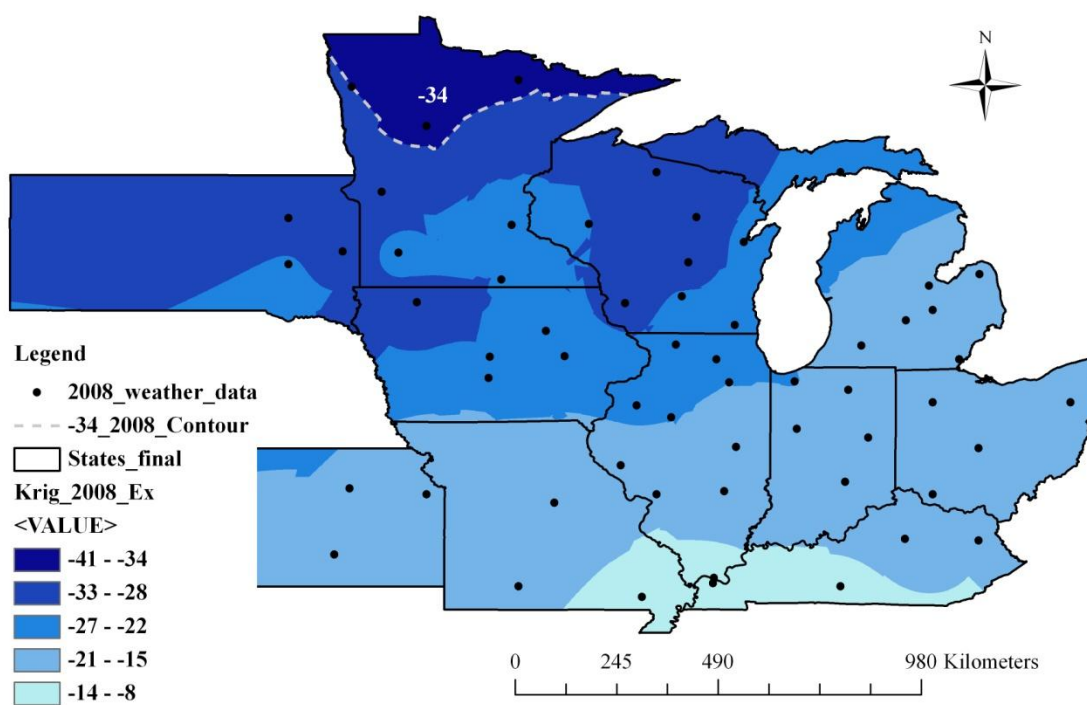


Fig. 5

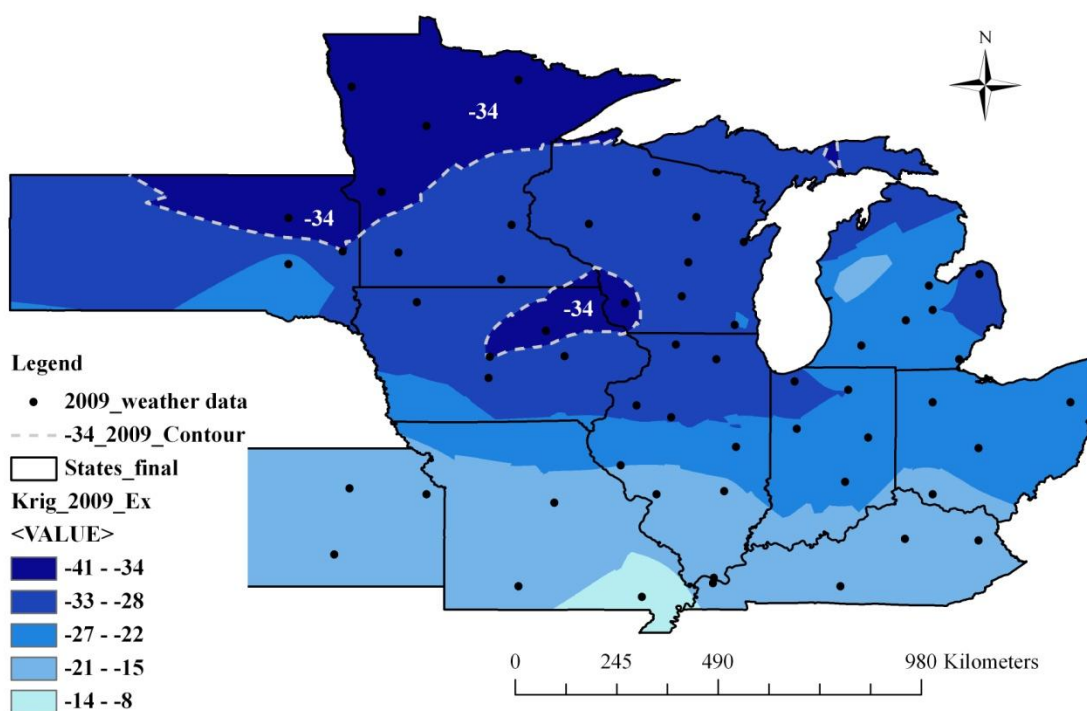


Fig. 6

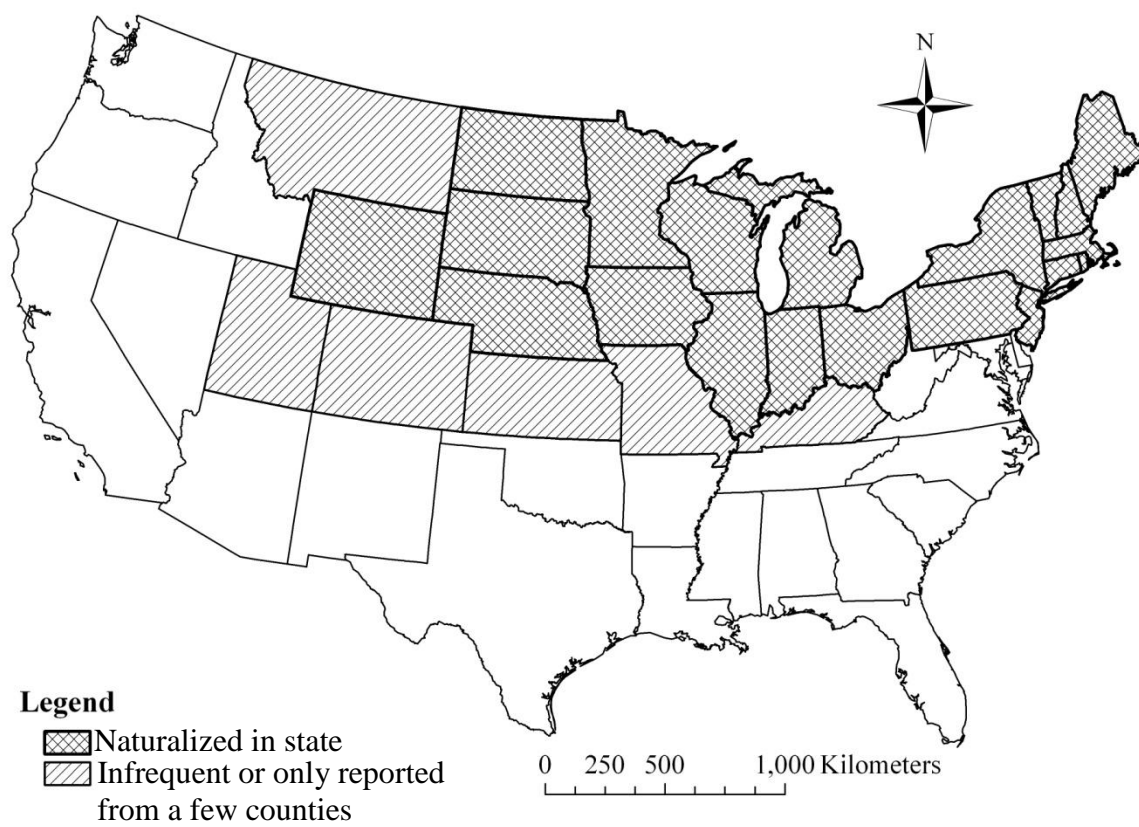


Fig. 7

Chapter 6

General Conclusions

The goal of this research was to advance our knowledge of the mechanisms driving *Aphis glycines* Matsumura (Hemiptera: Aphididae) and aphidophagous natural enemy population dynamics in soybean, *Glycine max* (L.) Merr., agroecosystems in the north-central United States. In 2006 the primary objective was to determine how landscape composition and diversity influence the abundance of *A. glycines* and its associated natural enemies in central Iowa. I learned landscape composition and diversity explained little of the variation in the abundance of *A. glycines* and natural enemies. Instead, "Year" accounted for much of the variation. Possible explanations for this include: 1) the abundance of "keystone" predators, such as *Orius insidiosus* (Say) and *Harmonia axyridis* (Pallas), varied from year to year regardless of landscape, and 2) immigration of *A. glycines* alates varied from year to year to such an extent that it overwhelmed any effects of landscape as measured in our study. In 2007 and 2008 the abundance of half the natural enemy taxa, including *O. insidiosus* and *H. axyridis*, were reduced compared to 2006. In conversations with soybean growers, I discovered that many of them started planting soybean seed treated with an insecticide around this time. Corn tissue from seed treated with a neonicotinoid has a detrimental effect on coccinellids feeding on it (Moser et al. 2008; Moser and Obrycki 2009). Alates collected from a nearby suction trap suggest immigration of *A. glycines* may be a critical component driving aphid outbreaks in central Iowa. A three-fold increase in *A. glycines* immigrants may have been enough to overcome the potential for top-down control by the resident natural enemy community, resulting in an aphid outbreak.

In a field study, I sampled the natural enemy community in both soybean and remnant and reconstructed prairie. In 2006 *A. glycines* populations were much lower than those in 2007 and 2008, and it was the only year when aphid populations were significantly lower on soybean near prairie. Approximately 20% of the natural enemy taxa were most commonly collected in soybean, leaving 80% of the taxa dominant in prairie. Over 96% of *O. insidiosus* and *H. axyridis* collected were exclusively found in soybean fields. With the use of sentinel plants, I observed similar levels of top-down control of *A. glycines* in both soybean and

prairie. These results indicate an aphidophagous community existed in both soybean and prairie, however, soybean experienced little recruitment of natural enemies at the 200 m scale sampled. Syrphidae was the only taxon observed in soybean that was significantly correlated with distance from prairie. Comparison of the plant communities at the four sites suggests remnant and reconstructed prairies were quite different. Three of the prairies had a species rich environment; however, based on evidence from Landis et al. (2000) and Fiedler and Landis (2009), the “right” plant diversity may not have been present to optimize biological control of *A. glycines*. To what extent this variation contributed to our measurements of natural enemy abundance and diversity, as well as *A. glycines* suppression is not clear.

Alate *A. glycines* count data have been recorded from a regional suction trap network since 2005 across the north-central US. Results indicate that this network is not good at detecting movement of spring migrants, alates flying from *Rhamnus cathartica* L. to soybean fields. However, it does successfully detect movement of alates during summer and fall months. During peak flights in summer and fall, alate catches were similar across the network, which suggested suction traps could collect similar alate catches in suction traps up to 350 km from a single location. Implications of this may be important for future analyses, designing experiments, and potentially management decisions. When data are spatially dependent, accounting for the resulting bias is necessary, otherwise results can be skewed. Knowing data are spatially dependent also suggests the current 42 traps could be used to monitor alate *A. glycines* flights, except that spring migrants are not collected. There was a greater abundance of alate *A. glycines* collected in traps located in the north, corresponding to the northern distribution of its overwintering host, *R. cathartica* (Kurylo et al. 2007). Therefore, these findings are likely due to a greater abundance of overwintered *A. glycines*. An alternative explanation to this northern trend may be related to temperature and the *A. glycines* supercooling point (SCP; -34°C), the temperature at which fluids spontaneously freeze (McCornack et al. 2005). Therefore, I tested whether the first date of alate collection in suction traps was associated with low overwintering temperatures. Minimum temperatures varied between years but the SCP was reached in all years and as far south as northern Iowa in 2009. However, from 2005 – 2009 low temperatures only predicted first alate captures in 2008. Because the suction trap network had limited success in collecting spring migrants,

first alate captures may not have accurately portrayed the springtime distribution of *A. glycines*. Therefore, using low temperature data to predict first alate captures may not be practical with the current arrangement of suction traps.

In summary, advances in understanding the phenology of *A. glycines* and its natural enemies were determined in this research, and recommendations are discussed below.

Recommendations

- As discussed by Landis et al. (2000) and Fiedler et al. (2008), future attempts to measure the impact of mixed species habitats for biological control should consider limiting the variability of the plant community to those species most likely to attract predatory insects.
- Consider non-target effects of seed treatments. Soybean seed treated with an insecticide may have a detrimental effect on early season herbivores and natural enemies, altering the food web. A reduction in predators caused by the coincident widespread introduction of soybean seed treatments could explain the large immigration of aphids experienced in 2007 and 2008.
- Undefined interactions among generalist natural enemies makes it difficult to determine which species is responding to what prey species. It could be informative to analyze gut contents of all aphidophagous natural enemies to determine the level of intraguild predation among the group.
- In the suction trap network, use genetic markers to determine source-sink dynamics of alate *A. glycines*.
- Service suction traps daily to increase the precision of source-sink estimates and to facilitate identification of weather and plant stage factors affecting aphid movement.

- Map the range of buckthorn and validate it. There is a weak link in the *A. glycines* lifecycle when sexual morphs are required to find one another on *R. cathartica* to mate (Ragsdale et al. 2004). Disrupting sexual morphs and/or management of *R. cathartica* may improve long-term management goals for *A. glycines*.

References Cited

- Fiedler, A. K., D. A. Landis, and S. D. Wratten. 2008.** Maximizing ecosystem services from conservation biological control: The role of habitat management. *Biol. Control* 45: 254-271.
- Fiedler, A. K., and D. A. Landis. 2009.** Which plants are best?
<http://nativeplants.msu.edu/results.htm>
- Kurylo, J. S., K. S. Knight, J. R. Stewart, and A. G. Endress. 2007.** *Rhamnus cathartica*: Native and naturalized distribution and habitat preferences. *J. Torrey Bot. Soc.* 134: 420-430.
- Landis, D. A., S. D. Wratten, and G. M. Gurr. 2000.** Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annu. Rev. Entomol.* 45: 175-201.
- McCornack, B. P., M. A. Carrillo, R. C. Venette, D. W. Ragsdale. 2005.** Physiological constraints on the overwintering potential of the soybean aphid (Homoptera: Aphididae). *Environ. Entomol.* 34: 235-240.
- Moser, S. E., J. D. Harwood, and J. J. Obrycki. 2008.** Larval feeding on *Bt* hybrid and non-*Bt* corn seedlings by *Harmonia axyridis* (Coleoptera: Coccinellidae) and *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Environ. Entomol.* 37(2): 525-533.
- Moser, S. E., and J. J. Obrycki. 2009.** Non-target effects of neonicotinoid seed treatments; mortality of coccinellid larvae to zoophytophagy. *Biol. Control* 51: 487-492.
- Ragsdale, D. W., D. J. Voegtlin, and R. J. O'Neil. 2004.** Soybean aphid biology in North America. *Ann. Entomol. Soc. Am.* 97: 204-208.

Acknowledgments

I thank the Department of Entomology at Iowa State University for assisting me with both M.S. and Ph.D. degrees. During my time here, I have grown an incredible amount, and was especially fortunate to find the love of my life, Nina. Together we have climbed mountains and glaciers, paddled canoes and kayaks across rivers, lakes and oceans, and drove thousands of miles around various parts of this world in search of new and exciting adventures. It sounds crazy, but I am also appreciative of my pest, Brita and Marlow. Playing with these two after a stressful day at work is much better than any medication you can get from a doctor. I also thank my parents Pat and Joyce, sisters Trich and Beth, and nephew Cody, Andrew and Evelyn for everything they've done for me; without them I wouldn't be where I am today. They have always encouraged me to be the best in everything I do and most importantly to never give up.

I am also greatly indebted to Dr. Matthew O'Neal for believing in me and allowing me to work with him. Matt has always challenged me and helped me become who I am today. In addition, I thank my committee members, Drs. Lisa Schulte-Moore, Marlin Rice, Paul Anderson, and Thomas Sappington for all the critiques, edits, and thought provoking questions.

To all the graduate students, coworkers, and friends I have gotten to know over the years; thank you for the occasional and usually well-needed outing. Especially Kevin Johnson, who has been by my side since the first hour I showed up at ISU. I look forward to future meetings when we can reflect back on all this and continue to resolve the problems of this world.

I also send a special thanks to all the undergraduate research help I have had over the years. Summer research in Iowa is not always enjoyable; especially with the occasional day or week(s) when the heat index exceeds 100° F, with humidity so thick it's difficult to breath. Yet, the following individuals hung in there with me day after day and some year after year: Greg VonNostrand, Finn Pillsbury, Dustin Paulson, Daniel Stull, Robert Moore, Doug Ruby, Monica McGrew, Cory Dunlay, Amy Harvey, Daniel Au, Satish Hanmanthgari, Hasib Jahangir, Matthew Raymond, Nathan Johnson, Matthew Maher, Andrew Thraenert, and Kate Elliot.