

Relationship of Soybean Aphid (Hemiptera: Aphididae) to Soybean Plant Nutrients, Landscape Structure, and Natural Enemies

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ABSTRACT In the north central United States, populations of the exotic soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), are highly variable across space, complicating effective aphid management. In this study we examined relationships of plant nutrients, landscape structure, and natural enemies with soybean aphid abundance across Iowa, Michigan, Minnesota, and Wisconsin, representing the range of conditions where soybean aphid outbreaks have occurred since its introduction. We sampled soybean aphid and its natural enemies, quantified vegetation land cover and measured soybean nutrients (potassium [K] and nitrogen [N]) in 26 soybean sites in 2005 and 2006. Multiple regression models found that aphid abundance was negatively associated with leaf K content in 2005, whereas it was negatively associated with habitat diversity (Simpson's index) and positively associated with leaf N content in 2006. These variables accounted for 25 and 27% of aphid variability in 2005 and 2006, respectively, suggesting that other sources of variability are also important. In addition, K content of soybean plants decreased with increasing prevalence of corn-soybean cropland in 2005, suggesting that landscapes that have a high intensification of agriculture (as indexed by increasing corn and soybean) are more likely to have higher aphid numbers. Soybean aphid natural enemies, 26 species of predators and parasitoids, was positively related to aphid abundance; however, enemy-to-aphid abundance ratios were inversely related to aphid density, suggesting that soybean aphids are able to escape control by resident natural enemies. Overall, soybean aphid abundance was most associated with soybean leaf chemistry and landscape heterogeneity. Agronomic options that can ameliorate K deficiency and maintaining heterogeneity in the landscape may reduce aphid risk.

KEY WORDS *Aphis glycines*, biological control, landscape ecology, plant chemistry, potassium

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is an exotic pest of soybean that has established and become widespread in the soybean-producing regions of the United States and Canada (Ragsdale et al. 2004). With its ability to disperse through a winged morph, soybean aphid rapidly colonizes soybeans, and aphid outbreaks (i.e., aphid density exceeding the economic threshold of ≈ 250 aphids per plant) have been common across the north central United States since the discovery of the aphid

in 2000 (Hodgson et al. 2005, Ragsdale et al. 2007). Soybean aphid populations, however, vary widely across time and space (USDA 2008), which may be driven by various ecological components associated with the aphids.

Soybean aphid populations interact with their resources (host plants) and higher trophic levels (natural enemies). The growth and reproduction of aphids are affected by availability of essential nutrients in the phloem sap of host plants (Dixon 1998). Availability of limiting nutrients in plant tissues such as nitrogen is related to variability in aphid population growth (Nevo and Coll 2001, Awmack and Leather 2002, Borer et al. 2009). For soybean aphid, lower concentrations of potassium in soybean leaves and soil have been shown to increase soybean aphid fecundity and population growth (Myers et al. 2005, Myers and Gratton 2006, Walter and DiFonzo 2007). Thus, spatial variability in soil and therefore leaf concentrations of potassium and nitrogen may influence variability in soybean aphid abundance across the landscape.

Natural enemies are also important factors influencing aphid populations. Nearly 30 species of foliar-

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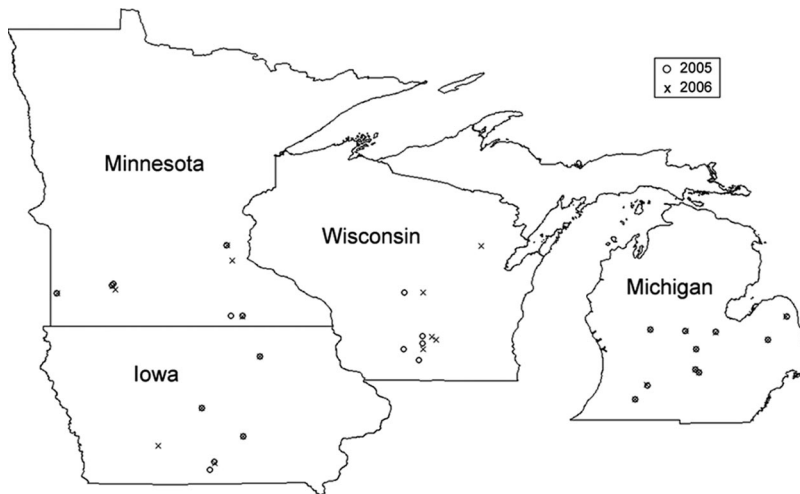


Fig. 1. Locations of soybean sites sampled across four U.S. north central states in 2005 ($n = 26$) and 2006 ($n = 26$).

foraging insect predators and parasitoids have been documented attacking *A. glycines* on soybeans in Michigan alone (Rutledge et al. 2004, Kaiser et al. 2007, Pike et al. 2007, Noma and Brewer 2008). Minute pirate bugs (*Orius* spp.) (Hemiptera: Anthracoridae) and multicolored Asian lady beetle, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), are the most abundant predators associated with high densities of soybean aphid in the north central United States and other locations (Rutledge et al. 2004, Nielsen and Hajek 2005, Brosius et al. 2007, Ragsdale et al. 2007, Chacón et al. 2008, Schmidt et al. 2008). Exclusion cage studies have shown that generalist predators greatly reduced soybean aphid populations (Fox et al. 2004, Costamagna and Landis 2006, Donaldson et al. 2008, Gardiner et al. 2009a). Aphid parasitism has been much less influential during the aphid outbreaks (Lin and Ives 2003, Rutledge et al. 2004, Brosius et al. 2007, Noma and Brewer 2008).

Trophic interactions taking place in soybean fields may also be influenced by the structure and composition of the surrounding landscape. For example, Gardiner et al. (2009a) showed through exclusion cage studies that natural enemies greatly reduced soybean aphid populations and that predation intensity increased with increasing landscape diversity. Other studies also suggest that landscape structure influences the potential for natural enemies to control aphids (Colunga-Garcia et al. 1997, Elliott et al. 1998, Roschewitz et al. 2005, Thies et al. 2005, Rand and Tschardtke 2007, Brewer et al. 2008). In a study conducted in the U.S. Great Plains, higher densities of Russian wheat aphid, *Diuraphis noxia* (Mordvilko) (Hemiptera: Aphididae), were associated with more contiguous wheat production and less habitat diversity on-farm and in the surrounding areas (Brewer et al. 2008). Thies et al. (2005) and Roschewitz et al. (2005) also found varying cereal aphid populations in relation to proportions of arable land and noncrop habitats in the surrounding area. Thus, in addition to

examining factors within fields which may influence aphid populations, such as plant quality and natural enemies, we may also benefit from examining the context of the surrounding landscape.

The goal of this study was to explore the relationship among soybean aphid abundance, host plant quality, landscape structure, and its natural enemy populations. By sampling soybean aphids across a four state region in the upper north central United States, we aimed to capture a wide environmental gradient across which soybean aphid abundance could be examined. We used a regression approach to model aphid population abundance as a function of plant nutrients and variables that describe landscape structure. We evaluated the sensitivity of aphid predators and parasitoids to varying soybean aphid abundance. This study complements the study of Gardiner et al. (2009a), which described the relationship between soybean aphid predation and landscape structure using exclusion cage methodology, by exploring the effect of plant nutrients on aphid populations and examining the relationship of aphids and natural enemies using extant unmanipulated insect populations and agricultural fields.

Materials and Methods

Sampling Sites. This study was conducted in Iowa, Michigan, Minnesota, and Wisconsin, representing the range of conditions where soybean aphid outbreaks have occurred since its introduction (Ragsdale et al. 2007). Twenty-six soybean fields (5–10 fields per state) were sampled in 2005 and 2006 for aphids and soybean leaf nutrients (except leaf nutrients were unavailable from 5 Iowa sites in 2005; Fig. 1). Sampling fields in each state were chosen to represent a wide range of landscape settings in which soybean is cultivated, from areas of relatively high concentration of soybean to soybean highly mixed with other land use. Most fields (79%) were >16 km from other sampled

fields, and the remaining fields were 4–16 km away from the nearest field each year to minimize potential bias caused by spatial autocorrelation (Hargrove and Pickering 1992). Soybean fields consisted of both commercial and research farms and were free of insecticide applications.

Insect Sampling. Soybean aphid and its natural enemies were sampled during the growing season of each year, spanning four periods of aphid activity: (1) during early vegetative growth of soybean when aphids were establishing colonies in soybean (19 June to 5 July), (2) during flowering when aphids were multiplying on soybean (7–26 July), (3) during soybean pod fill when aphids were reaching peak numbers (3–19 August), and (4) when plants were beginning to senesce (30 August to 16 September).

Soybean aphid and aphid natural enemies were sampled in each soybean field at four random locations that were at least 10 m away from field edges. At each location, 10 soybean plants were visually inspected for soybean aphid. Actual number of aphids was counted up to 200 individuals per plant. When the aphid count exceeded 200, it was estimated using a series of count ranges: 201–500, 501–1,000, 1,001–5,000, and 5,001–10,000. To sample aphid natural enemies at the same locations, soybean plants were clipped at the base of the stem and placed in a paper bag (30 by 18 by 42.5 cm). The number of plants collected per location varied as plants grew, from 20 (early season) to 3 (late season). Before bagging, lady beetle larvae and adults were counted and removed from plant cuttings to prevent them from feeding on other aphid enemies (Meyhöfer and Klug 2002). Sample bags with plant material were kept cool while transported to the laboratory. Plant material was placed into emergence canisters: pressed cardboard canisters attached to a funnel (20 cm diameter by 60 cm high) with a clear plastic collection vial (5 cm diameter by 8.5 cm high) that contained 70% ethanol (Prokrym et al. 1998). The canisters were maintained in a horizontal orientation at 20–24°C for 2 wk to allow natural enemies to develop (i.e., time sufficient to allow parasitoid emergence from mummified aphids) and move into the collection vial. Contents of vials and canisters were examined under a microscope ($\times 10$ – 40) to identify and count predators and parasitoids. Insect specimens were identified to species when possible, and the following five groups of natural enemies were considered in our analysis: lacewings (Neuroptera: Chrysopidae and Hemerobiidae), lady beetles (Coleoptera: Coccinellidae), primary aphid parasitoids (Hymenoptera: Aphelinidae and Braconidae), predatory bugs (Hemiptera: Anthocoridae, Lygaeidae, and Nabidae), and predatory flies (Diptera: Cecidomyiidae and Syrphidae).

Soybean Plant Nutrient Sampling. Nutrient contents of soybean leaves were quantified at the onset of flowering stage each year (Peters 2007). The single uppermost, fully expanded trifoliates from 10 plants were collected at each of the same four within-field locations and pooled into one composite sample. Leaf samples were kept in paper bags at room temperatures

allowing leaves to desiccate, further dried at 50°C for 48 h, and pulverized before analysis. Nutrient contents of leaf samples were quantified and expressed as a percent of total dry mass at Agvise Laboratories (Northwood, ND). We focused on potassium (K) and nitrogen (N) as plant nutrients most relevant to soybean aphid populations (Nevo and Coll 2001, Awmack and Leather 2002, Myers et al. 2005, Myers and Gratton 2006, Walter and DiFonzo 2007).

Landscape Measurements. We characterized the structure and composition of the landscape surrounding each soybean field where insects were sampled. The location of each field site was recorded using handheld Global Positioning System (GPS) units (Appendix). Sites were placed in a GIS system (ArcMap 9.0; ESRI, Redlands, CA), and circular areas of 2-km radius around each soybean site were evaluated. We chose the spatial scale of 2 km because it has been shown to be a sensitive scale influencing cereal aphid abundance (Thies et al. 2005). Land cover around each site was identified using the 2007 Cropland Data Layer (CDL; USDA–NASS–RDD 2007). The CDL is a digitized geo-referenced mapping product derived from satellite imagery (ResourceSat-1 loaded with AWiFS sensor) at a spatial resolution of 56 m (USDA–NASS–RDD 2007). Landscape composition was characterized by the percent land cover by crop habitat (corn and soybean combined) and noncrop habitat (forest, grassland, shrub, and wetland combined) as a measurement of relatively undisturbed habitats. We considered these land cover categories because of their relevance to aphid populations (Roschewitz et al. 2005, Thies et al. 2005, Brewer et al. 2008, Gardiner et al. 2009a). We combined corn and soybean, two dominant crops comprising an average of 42% of our landscape measurements (Appendix), as a single variable for the following reasons: (1) although corn is not a host of the soybean aphid, corn plantings identified on the 2007 CDL were likely to be rotated with soybean plantings during our 2005–2006 study period and (2) percent corn and percent soybean were highly correlated to each other in the landscape ($r = 0.64$) (see also Gardiner et al. 2009b), resulting in the same outcome when placed in the regression models separately or as a combined variable. In addition to these crops, and noncrop variables, we also computed habitat diversity using Simpson's diversity index (McGarigal et al. 2002), in which all crop and noncrop vegetation categories discerned on the CDL (a total of 21 habitat categories) were taken into account in terms of their area (ha) within a 2-km radius. The index value ranged between 0 and 1, with a higher number indicating more diverse landscape structure.

CDL information was only available for Iowa and Wisconsin for 2005 and 2006 (the period of the study) and was made available for the entire study region (Iowa, Wisconsin, Minnesota, Michigan) in 2007. To test whether 2007 CDL was an appropriate representation of the entire region for measurement of landscape composition compared with 2005 and 2006 CDL, we examined the correlation between the land cover categories (percent area within 2-km radius) around

each of our study sites in Iowa and Wisconsin ($n = 10$ sites) measured in each year of the CDL data (2005, 2006, and 2007). Inter-year land cover values were highly correlated (2005 versus 2007 and 2006 versus 2007: percent corn and soybean, $r = 0.98$ and 0.95 , respectively; percent noncrop, $r = 0.78$ and 0.85 , respectively), suggesting that using the 2007 land cover data were a reasonable approximation for describing the generally consistent agricultural landscapes in these areas during this time period.

Analysis

Comparison of Soybean Aphid Abundance in Four States of North Central United States. Soybean aphid counts were averaged across the four within-field sampling locations to obtain mean aphid counts per plant on each sampling date. When a count range was used, the mid value of the range was applied in the aphid mean calculation. Aphid abundance across the season was calculated for each sampling site by summing the mean aphid counts per plant across the four sampling dates each year. Season-summed aphid abundance was compared among the four states in an analysis of variance (ANOVA; PROC GLM, SAS Institute 2004). In the model, aphid abundance was described in terms of state (Iowa, Michigan, Minnesota, and Wisconsin) and year (2005 and 2006) and the interaction between state and year. Aphid abundance data (aphids per plant, N) were $\log_{10}(100N + 1/6)$ transformed to normalize the residuals (Mosteller and Tukey 1977). Post hoc, multiple comparisons were performed using Tukey-Kramer's adjustment.

Relationship of Soybean Aphid Abundance to Landscape Structure and Plant Nutrients. The relationships between soybean aphid abundance and both landscape structure and soybean plant nutrients were assessed using information theoretic model selection based on Akaike's information criterion (AIC) (Burnham and Anderson 2002). The analyses were performed separately each year because some landscapes sampled overlapped between years, but not within each year (Fig. 1). In multiple regression modeling, aphid abundance was regressed against all possible combinations (31) of three landscape (corn and soybean combined, noncrop habitat, and habitat diversity) and two plant nutrient (leaf K and N) variables (PROC REG, SAS Institute 2004). Through the model selection procedure, the best-fit model (with the lowest AIC value) and competing models (having an AIC value no more than two units greater than that of the best-fit model) were selected. Finally, the model selection was checked for presence of spatial autocorrelation using semivariance plots and Moran's I (Fortin 2005). There was no evidence of spatial autocorrelation in the models in either year. To check for presence of association between plant nutrient and landscape variables (plant nutrient contents may be influenced by land use patterns quantified by our landscape measurements), pairwise correlation tests were conducted (PROC CORR, SAS Institute 2004).

Relationship of Natural Enemy Abundance to Soybean Aphid Abundance. Abundance of aphid natural enemies was calculated for each of five enemy groups in the same manner soybean aphid abundance was calculated above. Counts of natural enemies were averaged across four within-field sampling locations to obtain mean enemy counts per plant on each sampling date. A season-summed abundance of natural enemies was calculated for each sampling site by summing the mean enemy counts per plant across the four sampling dates each year. The relationship between natural enemy abundance and soybean aphid abundance was determined across 2 yr using an analysis of covariance (ANCOVA; PROC GLM, SAS Institute 2004). In this model, natural enemy abundance (\log_{10} -transformed using the same formula above) was described in terms of natural enemy groups (five categories), soybean aphid abundance as a covariate, and the interaction between the enemy group and aphid abundance. The interaction term (the slope representing the rate of change in natural enemy abundance in relation to change in aphid abundance) was compared among the enemy groups using contrast tests. Finally, the enemy-to-aphid abundance ratio was regressed against soybean aphid abundance (PROC REG, SAS Institute 2004).

Results

Aphid Abundance. Soybean aphid density typically peaked during the pod-filling stage (Fig. 2). The season-summed soybean aphid abundance varied significantly among the states in both years (state by year interaction: $F = 9.52$; $df = 3,44$; $P < 0.0001$). In 2005, aphids were significantly more abundant in Minnesota (964 ± 331 SEM aphids per plant) than Iowa (125 ± 47 SEM aphids per plant; $P = 0.05$), with Michigan and Wisconsin intermediate in aphid abundance (Fig. 2). In 2006, aphids were significantly more abundant in Minnesota (470 ± 103 SEM aphids per plant) than Michigan (16 ± 5 SEM aphids per plant; $P < 0.0001$), with Wisconsin and Iowa intermediate in aphid abundance (Fig. 2).

Relationship of Soybean Aphid Abundance to Landscape Structure and Plant Nutrients. Landscape and leaf nutrient variables ranged widely across the sites and years providing a large gradient of environmental variation for soybean aphids (Table 1). In 2005, the best-fit regression model found that soybean aphid abundance was inversely related to soybean leaf K content ($F = 6.37$; $df = 1,19$; $P = 0.02$; $R^2 = 0.25$; Fig. 3a, Table 2). Consistent aphid-leaf K relationships were also described in two of the three competing models identified in 2005 (Table 2). The competing models in 2005 also captured other, less prominent patterns (indicated by lower partial R^2), including trends for aphid abundance to increase with increasing leaf N content, increasing corn and soybean acreage in the landscape, and decreasing noncrop habitats in the landscape (Table 2). In 2006 the best-fit model found that soybean aphid abundance was inversely associated with habitat diversity (Fig. 3b) and posi-

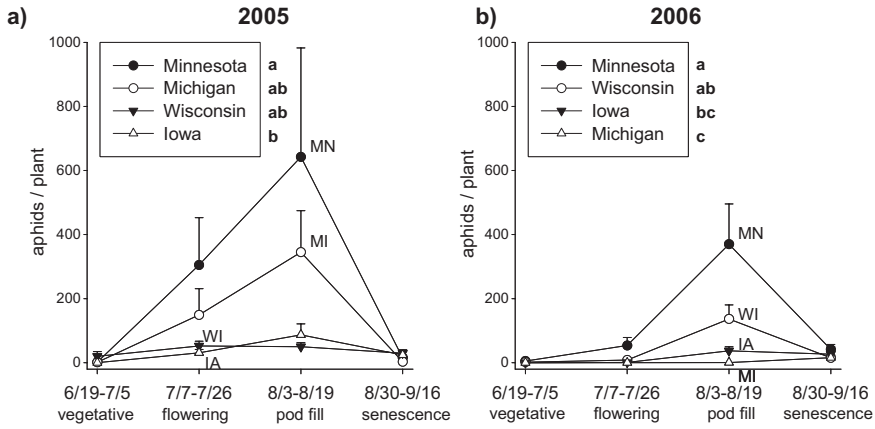


Fig. 2. Comparison of soybean aphid density among four U.S. north central states in relation to sampling dates and soybean growth. (a) 2005. (b) 2006. Vertical bars are SEMs. Different letters next to the legend indicate a significant difference in season-summed aphid abundance ($\alpha = 0.05$).

tively associated with soybean leaf N content (Fig. 3c; $F = 4.15$; $df = 1,24$; $P = 0.03$; $R^2 = 0.27$). The competing model also showed that aphid abundance tended to increase with decreasing habitat diversity in the landscape (Table 2). In addition, there was a negative association between leaf K content and the percent of corn and soybean area surrounding soybean fields, which was significant in 2005 but not in 2006 (2005: $r = -0.59$, $n = 21$, $P = 0.005$; 2006: $r = -0.25$, $n = 26$, $P = 0.21$; Fig. 4).

Relationship of Natural Enemy Abundance to Soybean Aphid Abundance. Twenty-six species of aphid predators and parasitoids were collected from soybeans (Table 3). The proportion of the natural enemy assemblage collected varied as a function of soybean phenology with 3% of all individuals collected during the soybean vegetative stage, 21% during flowering, 58% during pod fill, and 18% during senescence. Thus, most natural enemies occurred during pod fill when soybean aphid populations were also at their peak (Fig. 2). Predatory bugs, predominantly *Orius* spp., were the most abundant natural enemies and parasitoids were the least abundant (Table 3). There was a significant interaction between natural enemy groups and aphid abundance ($F = 6.25$; $df = 4,120$; $P = 0.0001$). Lady beetles, consisting predominantly of

Harmonia axyridis, were most responsive to aphid abundance [slope (\log_{10}) = 0.57], and parasitoids were least sensitive to aphid abundance [slope (\log_{10}) = 0.27; Fig. 5]. The range in total natural enemy abundance found in soybean sites (0.2–10 enemies per plant across the season) was much narrower than that of aphid abundance (2–2,435 aphids per plant across the season). As such, the ratio of enemy to aphid abundance per site decreased exponentially with higher aphid infestation across the season ($r = -0.89$, $n = 52$, $P < 0.0001$; Fig. 6).

Discussion

Nutrient and Landscape Effects on Soybean Aphid Abundance. By surveying extant soybean aphid and natural enemy populations over a 2-yr period, we found that plant nutrients (K and N) and, to a lesser extent, landscape structure affect soybean aphid abundance across four states representing the range of conditions where soybean aphid outbreaks have occurred since its introduction. These findings are consistent with smaller-scale studies that showed that aphid populations tended to be higher when plants and soils were deficient in K (Myers et al. 2005, Myers and Gratton 2006, Walter and DiFonzo 2007) and

Table 1. Variability of landscape and leaf nutrient measurements from the soybean sites (n) sampled across four states in north central United States in 2005 and 2006

Variable	Mean (range)				
	Iowa ($n = 10$)	Michigan ($n = 20$)	Minnesota ($n = 12$)	Wisconsin ($n = 10$)	Overall ($n = 52$)
Landscape^a					
Percent corn and soybean	51.0 (18.8–75.9)	38.4 (13.0–61.5)	51.3 (0.10–87.0)	26.5 (0.50–65.1)	41.5 (0.1–87.0)
Percent noncrop habitat	38.9 (13.4–75.6)	28.8 (13.0–55.4)	22.7 (3.3–47.7)	43.0 (10.4–91.0)	32.1 (3.3–91.0)
Habitat diversity ^b	0.63 (0.53–0.74)	0.79 (0.72–0.83)	0.59 (0.13–0.76)	0.69 (0.45–0.88)	0.69 (0.13–0.88)
Soybean leaf nutrient					
Percent K	2.46 (2.20–2.73)	2.29 (1.93–2.80)	2.15 (1.60–2.68)	2.50 (2.28–2.90)	2.31 (1.60–2.90)
Percent N	4.91 (4.55–5.53)	4.90 (3.70–5.70)	5.38 (4.90–5.95)	4.96 (4.30–5.73)	5.03 (3.70–5.95)

^a Landscapes were quantified within a 2-km radius from each soybean site.

^b Simpson's diversity index ranges between 0 and 1, with a higher no. indicating more diverse landscape structure.

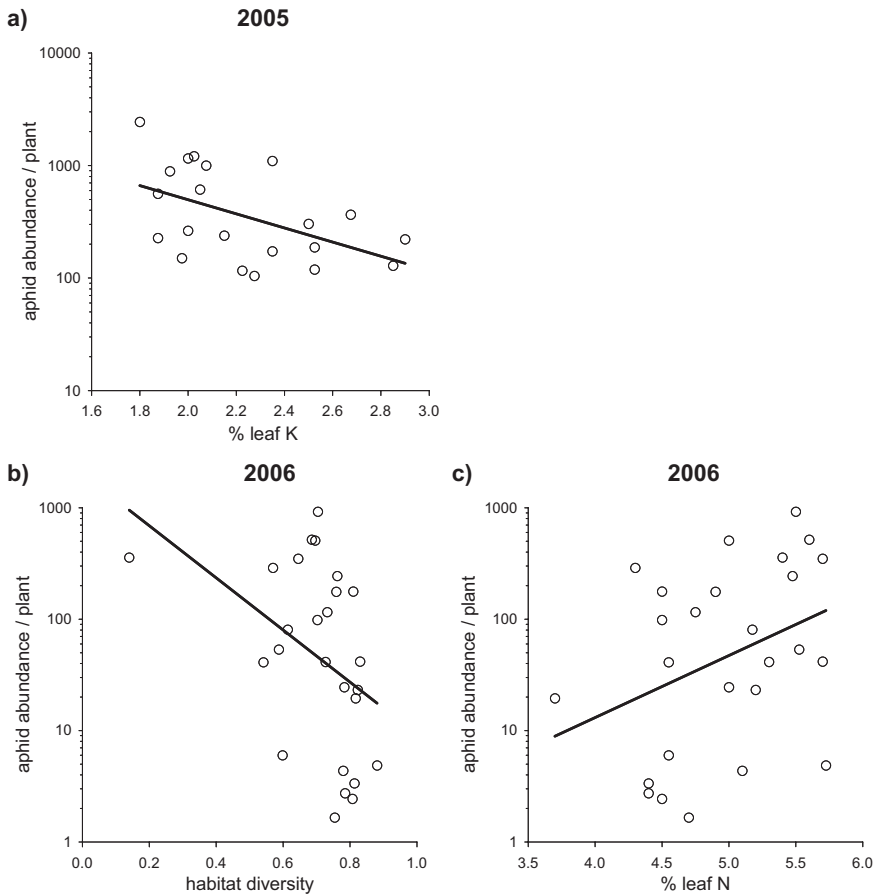


Fig. 3. Relationship of soybean aphid abundance to key leaf nutrient and landscape variables identified by the best-fit regression models. (a) 2005 (aphid abundance = $5.95 - 0.63$ [leaf K]). (b and c) 2006 (aphid abundance = $2.75 - 2.11$ [habitat diversity] + 0.48 [leaf N]). Two regressors in the 2006 model (habitat diversity and leaf N) were not correlated to each other ($R^2 = 0.02$); therefore, their relationships to aphid abundance were plotted separately without factoring out the effect of the other regressor. Aphid abundance was summed across the season and \log_{10} -transformed.

when plant N content increases (Nevo and Coll 2001, Awmack and Leather 2002). These nutrients are thought to be related to the availability of dietary N (free amino acids) in the phloem, a limiting factor for aphid growth and reproduction (Dixon 1998). For instance, K is involved in protein synthesis, and when a plant is K-stressed, protein synthesis can be disrupted, resulting in an accumulation of free amino acids in the phloem (Myers and Gratton 2006, Walter and DiFonzo 2007).

Our results also indicated that landscapes consisting of a more diverse assortment of land cover types were associated with lower aphid populations. This finding is consistent with Brewer et al. (2008), who found that plant diversification on-farm and in neighboring landscape was also associated with lower densities of Russian wheat aphid in wheat fields. In contrast, Thies et al. (2005) and Roschewitz et al. (2005) showed greater cereal aphid colonization in more diverse landscapes containing greater areas of noncrop habitats such as forest and grassland. This difference may be because of the fact that the cereal aphid complex documented

in these two studies (*Metopolophium dirhodum*, *Rhopalosiphum padi*, and *Sitobion avenae*) has a broad host range, including numerous grass species and overwintering hosts of rose family plants (Blackman and Eastop 2000), which may be more common in diverse landscapes dominated by noncrop lands. In comparison, soybean aphid feeds exclusively on soybean in the summer (and *Rhannus* spp. as the overwintering primary host; Voegtlin et al. 2004) and Russian wheat aphid feeds on wheat, barley, and several wheatgrasses (Donahue et al. 2000).

Soil nutrients available for plant uptake are influenced by long-term cropping history and intensity (Tisdale et al. 1993). This suggests that nutrient effects on aphids may interact with landscape structure reflecting agricultural intensity and prevalence. In our study area, farmlands are typically dominated by corn and soybean in a crop rotation. The significant relationship in which soybean K content decreased with increasing prevalence of corn-soybean cropland suggests that, at a broad spatial scale, landscapes that have a high intensification of agriculture (as indexed by

Table 2. The best-fit and competing regression models describing soybean aphid abundance (Y) across four U.S. north central states in terms of landscape and soybean leaf nutrient variables measured in 2005 and 2006

Year	Relative model fit ^a	Model equation ^b	Adjusted R ^{2c}	AIC	Likelihood weight ^d
2005 (n = 21)	Best-fit	Y = 5.95 - 0.62 (%leaf K) 0.25	0.21	-38.78	0.38
	Competing	Y = 4.27 + 0.007 (%corn and soybean) 0.19	0.15	-38.20	0.17
	Competing	Y = 5.86 - 0.53 (%leaf K) - 0.004 (%noncrop) 0.25 0.05	0.22	-38.08	0.16
	Competing	Y = 4.62 - 0.59 (%leaf K) + 0.24 (%leaf N) 0.25 0.05	0.22	-37.16	0.15
2006 (n = 26)	Best-fit	Y = 2.75 - 2.11 (habitat diversity) + 0.48 (%leaf N) 0.17 0.10	0.20	-10.72	0.45
	Competing	Y = 5.31 - 2.34 (habitat diversity) 0.17	0.14	-9.56	0.38

The model selections resulted from information theoretic analysis based on the AIC statistic.

^a Best-fit model had the lowest AIC value among the 31 models analyzed. Competing models had AIC values no more than two units greater than that of the best-fit model, indicating that these models are similarly consistent with the data as the best-fit model.

^b Model predictors considered were three landscape variables (% area of corn and soybean combined, % area of non-crop habitats, and habitat diversity) and two soybean nutrient variables (%leaf K and %leaf N). Italic numbers below the variables are partial R², indicating relative effects of the variables in the model.

^c R² was adjusted for the no. of predictors in the model and sample size for fair comparisons among different models.

^d The probability of the model being the best-fit among all models analyzed.

increasing corn and soybean) are more likely to have higher aphid numbers. The observation that corn-soybean and leaf K variables did not co-appear in the same best-fit or competing models may show the collinearity between these variables. Among crop plants, corn is known to remove particularly high quantities of soil K available to plant uptake (Tisdale et al. 1993). Long-standing corn and soybean rotations in the upper north central United States may be contributing to nutrient deficiencies in soybean plants that encourage aphid population growth (Myers et al. 2005, Walter and DiFonzo 2007). Although spatial gradients of key plant nutrient and landscape variables were associated with patterns of aphid abundance, a larger portion of variability (~75%) in aphid abundance remains unexplained in our regression models. Considering the broad spatial scale covered in this study, many other

sources of aphid variability were likely present. For example, Elliott et al. (1998), used multiple regression to assess the relationship of aphid predator abundance to landscape variables and found that temporal and weather factors generally accounted for nearly as much predator abundance variation as landscape variables (19–48% by temporal and weather variables compared with 27–49% by landscape variables). An-

Table 3. Diversity and percent composition of aphid predators and parasitoids collected at soybean sites across four U.S. north central states in 2005 and 2006

Natural enemy group (no. collected)	Identification	Percent ^a	
Lacewings (174)	Chrysopidae	72	
	Hemerobiidae	28	
Lady beetles (387)	<i>Harmonia axyridis</i>	94	
	<i>Hippodamia convergens</i>	2	
	<i>Coleomegilla maculata</i>	1.6	
	<i>Hippodamia variegata</i>	1	
	<i>Coccinella septempunctata</i>	0.8	
	<i>Cycloneda munda</i>	0.3	
Parasitoids (79)	<i>Hippodamia tredecimpunctata</i>	0.3	
	<i>Aphelinus</i> sp.	58	
	<i>Aphelinus asychis</i>	20	
	<i>Lysiphlebus testaceipes</i>	14	
	<i>Aphidius ervi</i> ^b	4	
	<i>Aphidius colemani</i>	1	
	<i>Diaeretiella rapae</i>	1	
	<i>Ephedrus</i> sp.	1	
	Predatory bugs (1,831)	<i>Orius</i> spp.	98.5
		<i>Nabis</i> sp.	1.2
<i>Geocoris</i> sp.		0.3	
Predatory flies (266)	<i>Aphidoletes aphidimyza</i>	79	
	<i>Allograpta obliqua</i>	9	
	<i>Toxomerus marginatus</i>	5	
	<i>Sphaerophoria contigua</i>	3	
	<i>Eupeodes americanus</i>	2	
	<i>Eupeodes volucris</i>	0.8	
	<i>Toxomerus geminatus</i>	0.4	

^a Percent composition within each natural enemy group.

^b A new record of this parasitoid recovered from *Aphis glycines*.

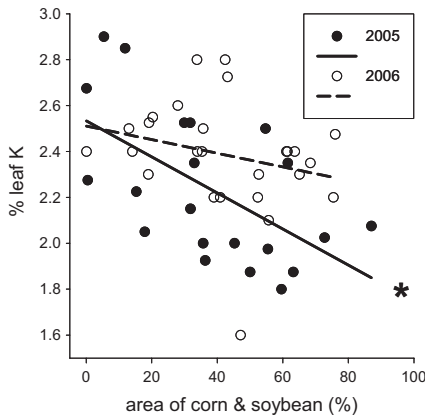


Fig. 4. Relationship between K content in soybean leaves and an extent of corn and soybean production in a 2-km radius around soybean sites sampled in 2005 and 2006. An asterisk indicates a significant correlation ($\alpha = 0.05$).

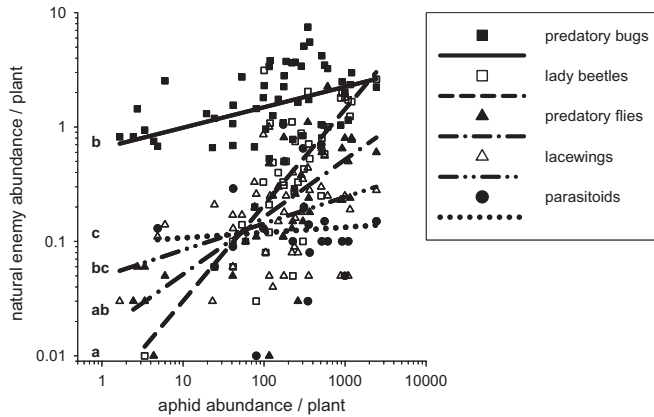


Fig. 5. Relationships of aphid natural enemies (five groups of predators and parasitoids) to soybean aphid sampled in 2005 and 2006. Season-summed aphid and enemy abundances were \log_{10} -transformed. Different letters next to regression lines indicate a significantly different slope ($\alpha = 0.05$).

other potential source of variability involves unavoidable autocorrelation among variables associated with geographical location. In our regional comparison, highest aphid abundance was found in Minnesota, which was also the region associated with the lowest leaf K level, the highest leaf N level, and the highest corn-soybean dominance in the landscape (Table 1). Thus, the sampling design of this study cannot exclude the possibility that geographical location may explain a large amount of the observed spatial pattern of soybean aphid abundance.

Relationship Between Natural Enemies and Soybean Aphids. Diversity and abundance of aphid natural enemies were similar to those documented previously under similar high-density aphid conditions (Fox et al. 2004, Rutledge et al. 2004, Costamagna and Landis 2006, Brosius et al. 2007, Kaiser et al. 2007, Chacón et al. 2008, Noma and Brewer 2008, Gardiner

et al. 2009b), although Nielsen and Hajek (2005) found substantially higher levels of parasitism of soybean aphids in New York state. The strong positive association between the natural enemy complex and soybean aphid abundance indicated that these natural enemies may aggregate to soybean aphid populations. Lady beetles (mostly *H. axyridis*) are particularly sensitive to aphid abundance change in space (see also Costamagna and Landis 2007, Donaldson et al. 2008). In contrast, Gardiner et al. (2009b) found differently that lady beetle (mostly *H. axyridis*) abundance was not associated with soybean aphid density in the soybean fields but was associated with the surrounding landscape composition.

Despite the significant aggregation of natural enemies to soybean aphid depicted in this and other nonmanipulative studies and exclusion cage experiments (Fox et al. 2004; Costamagna and Landis 2006, 2007; Donaldson et al. 2008; Gardiner et al. 2009a), the overall pattern of natural enemy presence was inversely density dependent. This suggests that soybean aphids are able to escape control by resident natural enemies. Other laboratory and field studies have found that, although natural enemies may be able to keep soybean aphids from reaching outbreak levels under some circumstances, outbreaks can nevertheless occur, and there may be aphid densities above which the resident natural enemy pool is less effective at high aphid densities (Rutledge and O'Neil 2005, Noma and Brewer 2008, Gardiner et al. 2009a, Heimpel et al. 2010, Yoo and O'Neil 2009). This is in contrast to Donaldson et al. (2008), who showed that aggregating predators can suppress high densities of soybean aphid. However, these experiments were performed at relatively small spatial scales (2 by 2-m plots). In addition, the continued low incidence of parasitism of soybean aphid in the north central United States suggests that native generalist parasitoids like *Lysiphlebus testaceipes* (Cresson) (Hymenoptera: Braconidae) are not moving onto soybean aphids in large numbers. Parasitoids form an important part of the natural en-

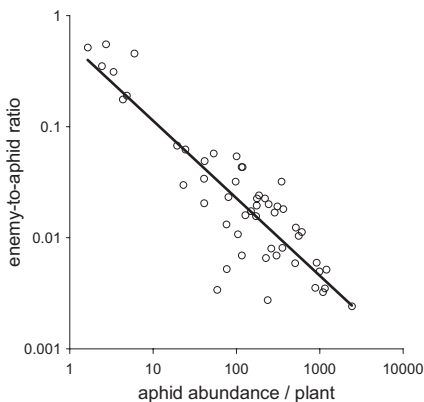


Fig. 6. Relationship of enemy-to-aphid abundance ratio to aphid abundance found in the soybean fields (enemy-to-aphid ratio = $0.70 [\text{aphid}] + 0.85$; $r = -0.89$, $n = 52$, $P < 0.0001$). Natural enemies consisted of aphid predators and parasitoids. Both aphid and the ratio variables were \log_{10} -transformed. Aphid and enemy abundances were summed across four sampling dates each year.

emy complex of soybean aphid in China (Liu et al. 2004, Wu et al. 2004, Miao et al. 2007), and our results support the hypothesis that classical biological control using parasitoids may be effective in filling an important natural enemy gap in North America (Heimpel et al. 2004, Wyckhuys et al. 2007).

In summary, soybean aphid abundance was most associated with soybean leaf chemistry and landscape heterogeneity. The widely adopted corn-soybean crop rotation scheme may be linked to lower K content of soybean leaves, which in turn may contribute to a higher likelihood of higher aphid populations. Agronomic options that can ameliorate K deficiency (e.g., soil testing and potash amendments) may be ways to counteract this effect. In addition, maintaining heterogeneity in the landscape also may reduce aphid risk. Other factors such as climatic conditions and geographical location are also undoubtedly contributing to variation in aphid abundance. Further research will be needed to refine this model to include other variables that may affect aphid populations.

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Appendix. Geographical coordinates and landscape profiles of soybean sampling sites in 2005 and 2006

Year	State	Site no. ^a	Latitude	Longitude	Corn ^b	Soybean ^b	Noncrop habitats ^{b,c}	Habitat diversity ^d	
2005	IA	1	41.985	-93.640	35	18	24	0.68	
		2	40.836	-93.499	37	36	19	0.65	
		3	40.980	-93.420	13	5	76	0.53	
		4	41.456	-92.876	28	18	49	0.74	
		5	42.935	-92.572	52	23	14	0.59	
	MI	1	42.142	-85.607	26	6	53	0.78	
		2	42.403	-85.379	11	4	50	0.77	
		3	43.431	-85.331	28	5	47	0.78	
		4	43.401	-84.678	20	16	24	0.81	
		5	42.690	-84.496	14	4	16	0.82	
		6	43.067	-84.482	42	14	18	0.72	
		7	42.635	-84.432	31	24	14	0.77	
		8	43.387	-84.112	21	16	36	0.81	
		9	43.242	-83.147	34	28	13	0.75	
		10	43.675	-82.804	29	16	24	0.82	
	MN	1	44.111	-96.327	34	29	22	0.70	
		2	44.249	-95.313	38	22	32	0.71	
		3	44.284	-95.286	54	33	7	0.54	
		4	44.990	-93.184	0	0	4	0.13	
		5	43.688	-93.103	41	32	17	0.65	
		6	43.688	-92.886	21	29	38	0.68	
	WI	1	43.064	-89.898	3	2	77	0.53	
		2	44.113	-89.891	0	0	91	0.45	
		3	42.863	-89.615	10	2	66	0.71	
		4	43.317	-89.558	26	4	42	0.77	
		5	43.173	-89.547	29	3	23	0.76	
	2006	IA	1	41.278	-94.452	26	13	52	0.61
			2	41.980	-93.648	48	20	17	0.60
3			40.962	-93.401	13	6	75	0.54	
4			41.455	-92.878	27	16	51	0.73	
5			42.936	-92.572	52	24	13	0.59	
MI		1	42.144	-85.607	23	5	55	0.78	
		2	42.406	-85.394	13	0	35	0.82	
		3	43.431	-85.328	29	5	46	0.78	
		4	43.402	-84.675	20	16	22	0.81	
		5	42.691	-84.494	15	4	17	0.82	
		6	43.068	-84.482	42	14	19	0.73	
		7	42.635	-84.427	29	23	15	0.79	
		8	43.377	-84.114	24	17	37	0.81	
		9	43.244	-83.146	34	28	13	0.75	
		10	43.671	-82.809	26	16	24	0.83	
MN		1	44.112	-96.322	32	31	22	0.70	
		2	44.242	-95.292	38	23	26	0.70	
		3	44.172	-95.243	46	30	18	0.65	
		4	44.990	-93.174	0	0	3	0.14	
		5	44.707	-93.072	27	9	48	0.76	
		6	43.680	-92.886	21	26	37	0.69	
WI		1	43.068	-89.544	20	14	16	0.81	
		2	44.119	-89.543	13	7	28	0.88	
		3	43.296	-89.383	58	7	13	0.57	
		4	43.241	-89.295	43	10	10	0.70	
		5	44.976	-88.463	13	1	64	0.76	

^a Sites are listed in order from west to east in each state and year (Fig. 1).

^b Percent land cover within 2-km radius around the soybean site.

^c Forest, grassland, shrub, and wetland combined.

^d Simpson's diversity index calculated using all crop and noncrop vegetation types identified in a 2-km radius.