

Modeling Distribution and Abundance of Soybean Aphid in Soybean Fields Using Measurements From the Surrounding Landscape

C. A. BAHLAI,¹ S. SIKKEMA,² R. H. HALLETT,^{1,3} J. NEWMAN,¹ AND A. W. SCHAAFSMA²

Environ. Entomol. 39(1): 50–56 (2010); DOI: 10.1603/EN09127

ABSTRACT Soybean aphid (*Aphis glycines* Matsumura) is a severe pest of soybean in central North America. Outbreaks of the aphid in Ontario are often spotty in distribution, with some geographical areas affected severely and others with few or no aphid populations occurring in soybean for the duration of the season. *A. glycines* spend summers on soybean and overwinter on buckthorn, a shrub that is widespread in southern Ontario and is commonly found in agricultural hedgerows and at the margins of woodlots. *A. glycines* likely use both short distance migratory flights from buckthorn and longer distance dispersal flights in the search for acceptable summer hosts. This study aims to model colonization of soybean fields by *A. glycines* engaged in early-season migration from overwintering hosts. Akaike's information criterion (AIC) was used to rank numerous competing linear and probit models using field parameters to predict aphid presence, colonization, and density. The variable that best modeled aphid density in soybean fields in the early season was the ratio of buckthorn density to field area, although dramatic differences in relationships between the parameters were observed between study years. This study has important applications in predicting areas that are at elevated risk of developing economically damaging populations of soybean aphid and which may act as sources for further infestation.

KEY WORDS *Aphis glycines*, *Rhamnus cathartica*, hedgerow, model selection

Soybean aphid (*Aphis glycines* Matsumura) is an invasive pest of cultivated soybean (*Glycine max* L. Merr.) in North America (Ragsdale et al. 2004). Originally occurring in soybean growing regions throughout Asia (Wu et al. 2004), *Aphis glycines* was first documented in North America in 2000 (Alleman et al. 2002). Since its initial colonization, the aphid frequently reaches economically damaging levels in soybean fields in the midwest and Great Lakes regions of the continent (Hunt et al. 2003, Ragsdale et al. 2004, Venette and Ragsdale 2004). Population dynamics of *A. glycines* in a given soybean field have been difficult to predict. Ragsdale et al. (2004) first remarked on an apparent 2-yr cycle in outbreak populations of *A. glycines*: widespread economic outbreaks were observed in 2001 and 2003 but in 2002 very few North American soybean fields were colonized by *A. glycines*, and in those that were, aphid populations did not reach high densities. In southwestern Ontario, where our study was performed, this general trend has continued to date (Bahlai 2007, Welsman 2007). However, agricultural extension personnel have remarked on exceptions to this "odd year" rule: localized aphid outbreaks are often observed in small geographical areas during 'even' (low) years, with even-year "hot-spots" some-

times only affecting a few soybean fields (T. Baute, personal communication).

Aphis glycines is a heteroecious aphid which overwinters on woody hosts, most typically on buckthorn shrubs of the genus *Rhamnus* and several other closely related shrubs (Voegtlin et al. 2004, 2005). *R. cathartica* L., common buckthorn, is considered the most important overwintering host of *A. glycines* in North America because of its wide distribution and its high density in many soybean growing regions (Voegtlin et al. 2005). *R. cathartica* thrives in habitats that are frequently disturbed and offer intermediate light levels (Kurylo et al. 2007) and is often observed in margins of woodlots and in agricultural hedgerows (Bahlai et al. 2007, Welsman et al. 2007).

Egg hatch of *A. glycines* is temperature dependant and usually occurs between the middle and end of April in southwestern Ontario (Bahlai et al. 2007). After hatching, *A. glycines* undergo several parthenogenetic generations on *R. cathartica* before a generation of winged (alate) aphids are produced (Liu et al. 2004). Apterous *A. glycines* can be found on buckthorn until the first week of June, at which time alates occur and numbers sharply decline on the overwintering host (Welsman et al. 2007). In odd (high) years, this sharp decline corresponds with the initial detection of small numbers of *A. glycines* in soybean fields by the second and third weeks of June (Bahlai 2007, Welsman et al. 2007). In even (low) years, *A. glycines* is seldom detected in soybean fields before the middle of July.

¹ School of Environmental Sciences, University of Guelph, Guelph, Ontario, Canada.

² Department of Plant Agriculture, Ridgetown Campus, University of Guelph, Ridgetown, Ontario, Canada.

³ Corresponding author, e-mail: rhallett@uoguelph.ca.

Aphis glycines likely uses both short distance migratory flights from buckthorn and longer distance dispersal flights aided by weather patterns in the search for acceptable summer hosts (Zhang et al. 2008). Observed colonization patterns within soybean fields are very patchy and not apparently correlated with hedgerows in early summer: winged adults likely move within the field, feeding, and depositing nymphs at multiple locations (Ragsdale et al. 2004). If fields are colonized later in the summer, however, higher populations of *A. glycines* are usually observed near windbreaks (Ragsdale et al. 2004). Given that they act as both windbreaks and overwintering host habitats, agricultural hedgerows, and associated landscape parameters likely play an important role in the colonization of soybean fields by *A. glycines*. However, the ecological mechanisms of this association have not been directly elucidated. Many variables affect population dynamics of *A. glycines*. The effects of natural enemies, weather, plant health, and migratory populations from other locales can be difficult to quantify, especially when aphid populations are low; nonetheless, these factors impact the number of *A. glycines* individuals observed in a given soybean field. Without directly quantifying these variables, detecting patterns in aphid colonization associated with other parameters (such as landscape variables) can be challenging. Analyses relying on null-hypothesis significance tests may not yield a statistically significant result in such variable datasets, and thus, existing scientifically significant patterns may be ignored (Taper and Lele 2004). In systems like these, it is desirable instead to approach the analysis of data using likelihood statistics to rank models relative to each other rather than relative to an arbitrary significance level (Taper 2004). Akaike's information criterion (AIC) is a statistical tool that uses the likelihood function and allows the performance of large sets of competing models to be compared relative to each other simultaneously (Akaike 1974). This study develops and compares models showing associations between colonization and density of midsummer aphid populations in soybean fields and various landscape parameters. This information will be used to identify fields that are most likely to be colonized by *A. glycines* in low (even) years and fields that may act as sources for further infestation in high (odd) years.

Materials and Methods

Study Site and Landscape Parameters. Twenty-five soybean fields in an area spanning ≈ 125 km (east-west) by 70 km (north-south) in the southwestern Ontario soybean growing region were selected in 2005 (Table 1). The study site included fields with very low and very high buckthorn densities in the vicinity and a variety of field shapes and areas (ranges of all measured parameters are provided in Table 2). At each site, the following landscape parameters were measured: buckthorn density B, field area A, field perimeter P, length of field perimeter with facing hedgerow H_F , and facing hedgerow within a 4-km radius of the

Table 1. Location of sites used in survey of soybean aphid populations and landscape parameters

Site no.	°N	°W	2005 sampling	2006 sampling
1	43.107	81.325	Yes	—
2	43.082	81.294	Yes	Yes
3	43.112	81.270	Yes	Yes
4	43.080	81.248	Yes	—
5	43.066	81.268	Yes	Yes
6	43.106	81.297	Yes	Yes
7	43.089	81.287	Yes	—
8	43.039	81.347	Yes	—
9	42.929	81.498	Yes	Yes
10	43.283	80.863	Yes	Yes
11	43.324	80.911	Yes	—
12	43.358	80.798	Yes	—
13	43.340	80.794	Yes	Yes
14	43.345	80.911	Yes	Yes
15	42.844	81.886	Yes	Yes
16	42.868	81.876	Yes	Yes
17	42.865	81.839	Yes	Yes
18	42.868	81.856	Yes	—
19	42.977	81.974	Yes	Yes
20	42.762	81.902	Yes	—
21	43.274	80.791	Yes	Yes
22	43.281	80.624	Yes	—
23	43.131	80.837	Yes	Yes
24	43.151	80.658	Yes	—
25	42.868	81.847	Yes	Yes

Soybean fields were located in southwestern Ontario, Canada.

sampling site in the field H_4 . Buckthorn density was determined by counting the number of shrubs immediately adjacent to the sampling site in a span of 80 m of hedgerow. P, H_F , and H_4 were measured by walking the spans and using a handheld GPS unit to measure distance traveled. Field area was calculated using field perimeter measurements.

Aphid Monitoring. During the week of 15 July 2005, all 25 sites were scouted for aphid populations. Single plants were sampled at sites 5, 25, 45, 65, and 85 m into the field along four transects spaced 20 m from each other and originating at a field edge adjacent to a hedgerow, for a total of 20 plants per field. Each plant was destructively sampled, and all *A. glycines* on sampled plants were counted. In 2006, 15 of the fields were either replanted to soybean or had a field immediately adjacent to the 2005 sites planted to soybean, and these fields were sampled during the week of 15 July. Sampling procedures were similar to that used in 2005 except at each sampling point, three plants were destructively sampled for a total of 60 plants per field.

Models. Data were analyzed separately by year. Parameters used in the models are described in Table 2. Models tested are listed in Table 3. Probit and linear models were used to describe aphid presence, colonization, and density using landscape parameters. Aphid presence was defined as at least one aphid observed during sampling of a field. Aphid colonization was defined as any number of aphids observed on at least two of the sampled plants in a field. All collected data were used to test aphid presence and colonization models. Data were filtered to include only fields where aphid colonization had occurred to test models for aphid density (15 fields in 2005, 8 fields in 2006). In addition to landscape parameters, a ran-

Table 2. Parameters used in analysis for predicting aphid populations using landscape parameters

Variable	Abbreviation	Measurement	Possible values	Observed range (mean \pm SD)
Aphid presence	A _p	At least one aphid observed in field	0, 1	0–1 (0.80 \pm 0.41)
Aphid colonization	A _c	<i>A. glycines</i> observed on at least two plants in field	0, 1	0–1 (0.58 \pm 0.50)
Aphid density	A _d	Total no. of <i>A. glycines</i> observed in a field divided by total no. of plants sampled	Any value \geq 0	0–26.5/plant (4 \pm 8/plant)
Buckthorn presence	B _p	At least one buckthorn shrub observed adjacent to field	0, 1	0–1 (0.65 \pm 0.48)
Buckthorn density	B _d	Total no. of buckthorn shrubs observed in 80 m of hedgerow, divided by 80	Any value \geq 0	0–0.33 plants/m (0.07 \pm 0.10/m)
Field perimeter	P	Total length of perimeter around field	Any value $>$ 0	796–2,815 m (1,777 \pm 545 m)
Field area	A	Total field area	Any value $>$ 0	28,338–293,995 m ² (14.1 \pm 7.7 ha)
Facing hedgerow	H _f	Total length of field perimeter composed of hedgerow or woodlot	Any value \geq 0	105–1,435 m (489 \pm 374 m)
Hedgerow within 4 km	H ₄	Total length of hedgerow within 4km of sampling site	Any value \geq 0	2,968–8,126 m (5,077 \pm 1,536 m)
Estimated no. of buckthorn shrubs facing field	B _d \times H _f	—	Any value \geq 0	0–280 (40 \pm 71)
Estimated no. of buckthorn shrubs within 4 km	B _d \times H ₄	—	Any value \geq 0	0–2,438 (373 \pm 545)
Perimeter to area ratio	P/A	—	Any value \geq 0	0.0078–0.0280/m (0.015 \pm 0.005/m)
Facing hedgerow to area ratio	H _f /A	—	Any value \geq 0	0.0008–0.0095/m (0.004 \pm 0.002/m)
Hedgerow within 4 km to area ratio	H ₄ /A	—	Any value \geq 0	0.0191–0.1206/m (0.05 \pm 0.03/m)
Estimated no. of buckthorn shrubs facing field to area ratio	(B _d \times H _f)/A	—	Any value \geq 0	0–0.0019/m ² (0.0004 \pm 0.0006/m ²)
Estimated no. of buckthorn shrubs within 4 km to area ratio	(B _d \times H ₄)/A	—	Any value \geq 0	0–0.0199/m ² (0.004 \pm 0.006/m ²)

Aphid presence, colonization, and density were treated as dependant variables and the remaining landscape parameters were used as independent variables in all models. Means reported are combined averages for the 2 study yr.

dom number generator (range, 0–100) was used to create 50 dummy independent variable datasets to model aphid presence, colonization, and density, so these models could be used as a point of comparison.

Probit models are best used for bivariate responses (i.e., presence/absence), so this function was used to model aphid presence and colonization. Probit analyses were performed in SAS v. 9.1 (SAS Institute, Cary, NC) using the probit link of PROC LOGISTIC. Linear functions were used to model aphid density. These analyses were performed in SAS using PROC MIXED.

In SAS, AIC is calculated by default and provided in the output of both PROC LOGISTIC and PROC MIXED. Models with the best performance were identified using the minimum AIC estimation method (MAICE) (Akaike 1974). Models with no more than two units difference between their calculated AICs are considered to be equivalent in performance (Burnham and Anderson 2002). Single-parameter models were ranked by their respective AICs, and for each year and each aphid population measure, the single-parameter models with the three lowest AICs were selected for further analyses, provided these models also outperformed the random number generator (i.e., had an AIC more than two units less than the average AIC of the random data models). The selected parameters were squared and were combined

by adding them together to generate new, more complex models, and the performance of these models were evaluated as above and ranked using the AICs generated.

Results

Aphid Presence and Colonization. Aphid presence (at least one aphid observed in the field) was observed in 80% of fields surveyed in both 2005 and 2006 (20/25 and 12/15, respectively). Aphid colonization (aphids observed on at least two sampled plants) was observed in 60% of fields surveys in 2005 (15/25 fields) and 53% of the fields sampled in 2006 (8/15 fields). Average aphid density in fields where aphid colonization was observed was 11.6 \pm 9.6 aphids per plant in 2005 and 0.41 \pm 0.38 aphids per plant in 2006. Average area of fields sampled was similar in both sample years (14.5 \pm 7.8 ha in 2005, 13.6 \pm 7.6 ha in 2006), as was field perimeter (1,783 \pm 554 m in 2005, 1,766 \pm 549 m in 2006).

Many of the models tested provided improvements over random for explaining aphid colonization, that is, generated an AIC more than two units less than the random number models (Table 3). None of the models could explain aphid presence better than a random number generator; thus, the remainder of this section

Table 3. Competing models to explain aphid population measures (presence, A_p ; colonization, A_c ; density, A_d) using landscape parameters and the respective AIC for models tested

Model	AIC					
	A_p		A_c		A_d	
	2005	2006	2005	2006	2005	2006
Average AIC (50 random no. models)	<u>27.9</u>	<u>17.8</u>	<u>36.5</u>	<u>23.9</u>	<u>95.3</u>	<u>10.3</u>
Landscape parameters						
B_p	28.7	18.0	37.6	<u>21.9</u>	—	—
B_d	28.7	19.0	<u>32.8</u>	23.4	91.5	7.5
P	29.0	19.0	37.6	22.3	109.0	23.8
A	28.9	18.9	37.6	22.7	118.3	34.9
H_f	28.9	19.0	37.6	23.5	110.1	24.0
H_d	27.0	18.7	35.0	22.8	113.3	26.1
$B_d \times H_f$	27.5	19.0	<u>31.9</u>	23.8	103.7	15.9
$B_d \times H_d$	28.8	19.0	<u>31.6</u>	23.1	107.8	22.3
P/A	28.8	19.0	37.3	24.6	<u>85.2</u>	<u>2.5</u>
H_f/A	28.9	19.0	37.5	24.3	<u>85.8</u>	<u>1.3</u>
H_d/A	29.0	18.7	37.6	24.5	87.0	5.4
$B_d \times H_f/A$	28.7	18.8	35.2	24.6	<u>82.5</u>	<u>-1.4</u>
$B_d \times H_d/A$	28.9	18.7	34.9	24.3	86.4	2.9
Additive linear models						
$B_p + (B_d \times H_f)$	26.6	19.9	29.2	23.6	—	—
$B_p + (B_d \times H_d)$	29.5	20.0	22.3	23.3	—	—
$(B_d \times H_f) + (B_d \times H_d)$	27.7	20.9	33.4	25.1	—	—
$(P/A) + (H_f/A)$	—	—	—	—	69.7	-8.7
$(P/A) + (B_d \times H_f/A)$	—	—	—	—	66.5	-12.5
$(H_f/A) + (B_d \times H_f/A)$	—	—	—	—	66.4	-12.8
$(H_f/A) + (B_d \times H_f/A) + (P/A)$	—	—	—	—	50.7	-23.6
Higher-order polynomial models						
B_p^2	28.7	18.0	37.6	21.9	—	—
$(B_d \times H_f)^2$	28.6	19.4	32.9	25.3	—	—
$(B_d \times H_d)^2$	28.1	21.0	22.3	21.4	—	—
$(P/A)^2$	—	—	—	—	78.8	-4.2
$(H_f/A)^2$	—	—	—	—	76.4	-7.6
$(B_d \times H_f/A)^2$	—	—	—	—	68.5	-13.8

A random no. generator (0–100) was used to provide a “baseline” AIC for each aphid population measure and sampling year and average AIC generated by 50 random models are outlined in dashed boxes. AICs for the three best ranked single-parameter models for each dataset are outlined by bold boxes. If the best-ranked model for a given dataset was no more than two units below the average AIC for the “random” models, the models were not used for further analysis. Abbreviations used are described in Table 2.

will focus on results pertaining to aphid colonization. Models favored by our data varied between years of study. In 2005, the high aphid year in our period of study, the best single parameter to explain aphid colonization was estimated buckthorn within 4 km ($B_d \times H_d$).

In 2006, the low aphid year in our study, colonization by *A. glycines* in soybean fields was best explained by the simple presence or absence of buckthorn (B_p), followed by field perimeter (P) and field area (A). A marginal improvement over the buckthorn presence model was observed by using a higher-order polynomial model taking into account the length of hedgerow within 4 km of the study site and estimated number of buckthorn within 4 km.

Aphid Density. Models for aphid density were ranked similarly and consistently by datasets from both years. Generally, models incorporating field area as a normalization factor had improved performance over models that did not. The best single parameter for

Table 4. Regression coefficients for linear models for aphid density A_d as a function of field perimeter to area ratio P/A, facing hedgerow to area ratio H_f/A , or estimated no. of buckthorn to field area ratio $B_d \times H_f/A$, respectively

Parameter	Year	Slope	Intercept
P/A	2005	-608 ± 298	20 ± 4
	2006	-18 ± 25	0.6 ± 0.4
H_f/A	2005	-923 ± 814	14 ± 4
	2006	29 ± 51	0.2 ± 0.2
$B_d \times H_f/A$	2005	-4668 ± 4284	11 ± 2
	2006	64 ± 231	0.3 ± 0.2

predicting aphid density was the estimated number of buckthorn shrubs facing the field per unit area of field ($B_d \times H_f/A$), but the field perimeter to area ratio (P/A) and hedgerow length to area ratio (H_f/A) were also high-ranked parameters. The best linear model tested was the additive model including all three of these factors. Models comprised of the square of each of these terms also outranked the linear models. Models involving higher order polynomials (to x^7) were tested but are not reported here because, although these models offered improvements in fit according to their respective AICs, these observed improvements were likely a result of overfitting. Although the three models that best predicted aphid density were consistently ranked between the 2 study yr (Table 3), the relationship (i.e., the sign of the observed regression coefficients) changed between the 2 study yr for the two top-ranked parameters $B_d \times H_f/A$ and H_f/A (Table 4). In 2005, a negative correlation was observed between aphid density and both $B_d \times H_f/A$ and H_f/A , whereas in 2006, a positive correlation was observed between aphid density and these parameters.

Discussion

Statistical Methods. Although consistent improvement in model AICs was observed by increasing the complexity of aphid density models, this result is likely of little biological relevance. First, it has been argued that AIC has a tendency to favor models that overfit data, despite its inclusion of a penalty term for overly complex models (Taper 2004). Second, this study was designed to determine how landscape parameters affect aphid distribution and not to elucidate the exact models of interaction. Populations of *A. glycines* are affected by numerous additional parameters, many of which also likely interact with landscape; thus, it is probable that greater improvements in models would be observed by directly accounting for these factors rather than landscape parameter-only models of increasing complexity. Finally, because the parameters used in many of the multiple-parameter models are auto-correlated, model parsimony may be affected (Zuur et al. 2007).

Factors Affecting Aphid Distribution. Aphid presence and colonization measures can be used to gain insight into which soybean fields are most likely to develop economically damaging aphid infestations later in the season. These two parameters were de-

fined differently and modeled separately to determine which could be more reliably modeled. AIC values for aphid presence models did not vary more than two units from the average of the random models, whereas aphid colonization models produced AICs that indicated larger differences between models and more significant improvements over the random models. Aphid colonization is likely a more reliable measure than aphid presence with which to predict subsequent aphid infestation.

The best predictor of A_{c} , colonization by *A. glycines* in a given field, in a low aphid year is the presence or absence of overwintering hosts. In high aphid years, this relationship is not observed, possibly because of increased dispersal flights in response to high aphid densities early in the season or interactions with natural enemies. Even still, an association between aphid colonization and the estimated number of buckthorn within 4 km of study site was observed in high years. Interestingly, aphid density A_d was shown to be negatively correlated with increasing density of buckthorn or increasing hedgerow face per unit field area in our high aphid year. This effect may be because of interactions between our measured landscape parameters and natural enemy populations and patterns of aphid dispersal.

Aphis glycines relies on buckthorn in hedgerow habitats for overwintering, but these same habitats may favor colonization and population growth of aphid natural enemies. In general, habitats with greater diversity such as agricultural landscapes with abundant hedgerows favor natural enemy populations because they provide alternate food sources, shelter, and varied microclimates (Landis et al. 2000). Aphids occurring in wheat fields adjacent to hedgerows are more effectively controlled by *Coccinella septempunctata* (Bianchi and van der Werf 2003). Similarly, important soybean aphid predators, particularly *Harmonia axyridis*, are more abundant in habitats with more forest and hedgerow habitat (Gardiner et al. 2009a, b). Thus, if abundances of both natural enemies and *A. glycines* are associated with similar landscapes, the dynamics between these species in hedgerows have the potential to dominate over landscape effects in determining aphid density. The degree of natural enemy impact on aphid population density varies from year to year, further confounding the patterns emerging between aphid density and landscape. Landis et al. (2008) quantified the biocontrol service rendered by natural enemies in soybean fields in 2005 and 2006 in a study area geographically adjacent to our study site and found there was a 12-fold decrease in natural enemy impact on soybean aphid in 2006 compared with 2005. If larger numbers of *A. glycines* were present on buckthorn in the hedgerows in the spring of 2005 in our study region, these populations could support greater abundances of natural enemies in the hedgerows. Even if fewer natural enemies were present at the beginning of the year, they would have an opportunity to proliferate while feeding on relatively abundant aphids in hedgerows, potentially causing localized depletions of aphids. Colonization success of *A. glycines*

would be improved for individuals dispersing farther from overwintering sites with high densities of natural enemies rather than those which colonize adjacent soybean. This may help to explain the negative correlations observed in 2005 between aphid densities and increasing density of buckthorn or increasing hedgerow face per unit field area; natural enemies likely exhibited numerical responses to higher densities of overwintering aphid populations in hedgerow habitats in the spring. In 2006, when overwintering aphid populations were less abundant (Welsman et al. 2007), it is likely that natural enemies did not have the same opportunity to aggregate in the hedgerows in spring. Aphids colonizing soybean fields directly adjacent to overwintering sites would be less impacted by predation and thus a positive correlation between aphid density and the two parameters is observed.

This variable and confounding effect of natural enemies on aphid density has likely contributed to the lack of clear association between hedgerows, overwintering hosts, and aphid density remarked on in previous studies (Ragsdale et al. 2004). However, it is possible that natural enemies do not account for this switch between positive and negative correlations observed between the 2 study yr. When population densities are high on overwintering hosts, even in the absence of higher densities of natural enemies, migrating alates of *A. glycines* might be triggered by population cues to fly greater distances from the overwintering site when searching for summer hosts to colonize.

Ragsdale et al. (2004) suggested that the July colonization of Ontario soybean fields is caused by the movement of *A. glycines* from other soybean fields, likely from some distance away, rather than direct movement from overwintering hosts. If this was always the case, we would expect to find either that early summer aphid colonization was not related to presence of buckthorn or that aphid colonization was strongly related to the presence of hedgerows alone, because of windbreak effects. Although these two measures are not mutually exclusive (hedgerows act as habitats for buckthorn, thus an area with more hedgerow has the potential to have more buckthorn), our study found that aphid density was better modeled by buckthorn density than hedgerow-length. This result suggests several possibilities: (1) in their northern range, small populations of *A. glycines* may remain undetected on overwintering hosts longer into the summer than in southerly regions; (2) small populations of *A. glycines* occur undetected in soybean near to overwintering hosts, until they reach detection limits in mid-July; or (3) *A. glycines* arriving in dispersal flights from other geographic areas are more likely to select fields with suitable overwintering habitat nearby for colonization.

Although the first two possibilities seem the most likely, the latter possibility warrants further study. Soybean aphid oviparae occurring on buckthorn in autumn produce a sex pheromone to attract males to their location (Zhu et al. 2006). Alate soybean aphids respond to soybean-produced volatiles (Zhu and Park

2005), and thus it is likely that buckthorn-produced volatiles could influence their behavior as well. Preferential selection of soybean fields with overwintering hosts nearby could be a result of semiochemical cues associated with buckthorn or as a result of signaling from conspecifics already colonizing these fields. Several other species of aphid are known to use aggregation pheromones to help maintain populations at moderate densities; it is thought that these aggregations help aphid populations to dilute individual risk of predation or parasitism (Wertheim et al. 2005).

Using landscape parameters to identify fields at greatest risk of becoming colonized by *A. glycines* and developing high aphid densities is a promising method to improve scouting efficiency within a given geographic area. Landscape parameters would not change dramatically from year to year, and thus could be used to identify fields where scouting efforts should be focused. Fields identified as high risk may also be ideal candidates for prophylactic use of neonicotinoid-treated soybean seed. Although these seed treatments usually do not provide protection into late summer when aphid populations tend to reach economically damaging levels (Johnson et al. 2008), seed treatments could suppress early season aphid population growth and prevent these first-colonized fields from acting as source habitats for movement of aphids into surrounding areas.

The most important landscape factor in determining whether a field is likely to be colonized by *A. glycines* in a low aphid year is the simple presence of buckthorn, the overwintering host. Thus, the ongoing attempts to eradicate common buckthorn from agricultural hedgerows and woodlots (Pergams and Norton 2006, Delanoy and Archibold 2007) can be supported on the basis of their expected beneficial impact on soybean aphid populations. *R. cathartica* is a widely distributed invasive species in North America (Kurylo et al. 2007). Numerous ecosystem and agroecosystem impacts are associated with the invasion of this shrub (Delanoy and Archibold 2007, Knight et al. 2007). If buckthorn was locally eradicated, a field previously at "high risk" for soybean aphid colonization would become lower risk, and the need for insecticide applications targeted against soybean aphid may be reduced or eliminated.

Acknowledgments

We thank A. Welsman for assistance, D. Landis for helpful comments on a presentation of this work, and M. Sears and A. Gradish for comments on this manuscript. We also acknowledge the financial support of the University of Guelph-Ontario Ministry of Agriculture Food and Rural Affairs Sustainable Production Program, the Ontario Soybean Growers, Agriculture and Agri-Food Canada, the Natural Science and Engineering Research Council of Canada, and the Keefer Family Trust.

References Cited

Akaike, H. 1974. A new look at the statistical model identification. *IEEE Trans. Automatic Control* 19: 716–723.

- Alleman, R. J., C. R. Grau, and D. B. Hogg. 2002. Soybean aphid host range and virus transmission efficiency. In *Proceedings of the Wisconsin Fertilizer Agline Pest Management Conference, 15–17 January 2002*, Madison, WI. (<http://www.soils.wisc.edu/extension/wcmc/2002proceedings/Alleman-Conf-2002.pdf>).
- Bahlai, C. A. 2007. Ecological interactions of *Harmonia axyridis* and *Aphis glycines* in Ontario agroecosystems. MSc thesis, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada.
- Bahlai, C. A., J. A. Welsman, A. W. Schaafsma, and M. K. Sears. 2007. Development of soybean aphid (Homoptera: Aphididae) on its primary overwintering host, *Rhamnus cathartica*. *Environ. Entomol.* 36: 998–1006.
- Bianchi, F.J.J.A., and W. van der Werf. 2003. The effect of the area and configuration of hibernation sites on the control of aphids by *Coccinella septempunctata* (Coleoptera: Coccinellidae) in agricultural landscapes: a simulation study. *Environ. Entomol.* 32: 1290–1304.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodal inference: a practical information-theoretic approach. Springer Science + Business Media, New York.
- Delanoy, L., and O. Archibold. 2007. Efficacy of control measures for European buckthorn (*Rhamnus cathartica* L.) in Saskatchewan. *Environ. Manage.* 40: 709–718.
- Gardiner, M. M., D. A. Landis, C. Gratton, N. Schmidt, M. O. Neal, E. Mueller, J. Chacon, G. E. Heimpel, and C. D. DiFonzo. 2009a. Landscape composition influences patterns of native and exotic lady beetle abundance. *Divers. Distrib.* 15: 554–564.
- Gardiner, M. M., D. A. Landis, C. Gratton, C. D. DiFonzo, M. O'Neal, J. M. Chacon, M. T. Wayo, N. P. Schmidt, E. E. Mueller, and G. E. Heimpel. 2009b. Landscape diversity enhances the biological control of an introduced crop pest in the north-central USA. *Ecol. Appl.* 19: 143–154.
- Hunt, D., R. Footitt, D. Gagnier, and T. Baute. 2003. First Canadian records of *Aphis glycines* (Homoptera: Aphididae). *Can. Entomol.* 135: 879–881.
- Johnson, K. D., M. E. Neal, J. D. Bradshaw, and M. E. Rice. 2008. Is preventative, concurrent management of the soybean aphid (Homoptera: Aphididae) and bean leaf beetle (Coleoptera: Chrysomelidae) possible? *J. Econ. Entomol.* 101: 801–809.
- Knight, K., J. Kurylo, A. Endress, J. Stewart, and P. 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 Botanical 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. Natl. Acad. Sci.* 105: 20552–20557.
- Liu, J., K. Wu, K. R. Hopper, and K. 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.
- Pergams, O.R.W., and J. E. Norton. 2006. Treating a single stem can kill the whole shrub: a scientific assessment of buckthorn control methods. *Nat. Areas J.* 26: 300–309.

- 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.
- Taper, M. L. 2004. Model identification from many candidates, pp. 488–524. *In* M. L. Taper and S. R. Lele (eds.), *The nature of scientific evidence: statistical, philosophical, and empirical considerations*. University of Chicago Press, Chicago, IL.
- Taper, M. L., and S. R. Lele (eds.). 2004. *The nature of scientific evidence: statistical, philosophical and empirical considerations*. University of Chicago Press, Chicago, IL.
- 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. Neil, and W. R. Graves. 2004. Tests of suitability of overwintering hosts of *Aphis glycines*: identification of a new host association with *Rhamnus alnifolia* L'Heritier. *Ann. Entomol. Soc. Am.* 97: 233–234.
- 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.
- Welsman, J. A. 2007. Ecology and control of the soybean aphid, *Aphis glycines* Matsumura (Homoptera: Aphididae). PhD dissertation, Department of Environmental Biology, University of Guelph, Guelph, Ontario, Canada.
- Welsman, J. A., C. A. Bahlai, M. K. Sears, and A. W. Schaafsma. 2007. Decline of soybean aphid (Homoptera: Aphididae) egg populations from autumn to spring on the primary host, *Rhamnus cathartica*. *Environ. Entomol.* 36: 541–548.
- Wertheim, B., E.-J. A. van Baalen, M. Dicke, and L.E.M. Vet. 2005. Pheromone-mediated aggregation in nonsocial arthropods: an evolutionary ecological perspective. *Annu. Rev. Entomol.* 50: 321–346.
- Wu, Z., D. Schenk-Hamlin, W. 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.G. 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.
- Zhu, J., and K.-C. Park. 2005. Methyl salicylate, a soybean aphid-induced plant volatile attractive to the predator *Coccinella septempunctata*. *J. Chem. Ecol.* 31: 1733–1746.
- Zhu, J., A. Zhang, K. C. Park, T. Baker, B. Lang, R. Jurenka, J. J. Obrycki, W. R. Graves, J. A. Pickett, D. Smiley, et al. 2006. Sex pheromone of the soybean aphid, *Aphis glycines* Matsumura, and its potential use in semiochemical-based control. *Environ. Entomol.* 35: 249–257.
- Zuur, A. F., E. N. Ieno, and G. M. Smith. 2007. *Analysing ecological data*. Springer, New York.

Received 24 April 2009; accepted 18 August 2009.