

Spatial Distribution of *Aphis glycines* (Hemiptera: Aphididae): A Summary of the Suction Trap Network

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ABSTRACT The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), is an economically important pest of soybean, *Glycine max* (L.) Merrill, in the United States. Phenological information of *A. glycines* is limited; specifically, little is known about factors guiding migrating aphids and potential impacts of long distance flights on local population dynamics. Increasing our understanding of *A. glycines* population dynamics may improve predictions of *A. glycines* outbreaks and improve management efforts. In 2005 a suction trap network was established in seven Midwest states to monitor the occurrence of alates. By 2006, this network 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 spring, movement among soybean fields during summer, and emigration from soybean to *Rhamnus* in 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, alates were not commonly collected in suction traps until June. The most alates were collected during a 3-wk period in the summer (late July to mid-August), followed by the fall, with a peak capture period during the last 2 wk of September. Alate captures were positively correlated with latitude, a pattern consistent with the distribution of *Rhamnus* in the United States, suggesting that more southern regions are infested by immigrants from the north.

KEY WORDS forecasting, migration, dispersal

The soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae) is an economically important

pest of soybean, *Glycine max* (L.) Merrill, in the United States. *A. glycines* has a 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). When conditions are favorable, *A. glycines* is capable of doubling its population in as few as 1.5 d on soybean, 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 U.S. soybean growing region at risk for *A. glycines* infestation, including areas where buckthorn is absent. Later in the growing season, a combination of fac-

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tors including reduced photoperiod and lower temperatures trigger the production of winged females (gynoparae) and males, which migrate in search of buckthorn, (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 United States 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 a capacity for long-distance movement. In general, the development of alate aphids 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). 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 nonoutbreak year), summer flights were first observed at initial flowering stage of soybeans, whereas in 2003 (an outbreak year), alates were observed approximately 2 wk earlier when soybeans were in vegetative stages (Hodgson et al. 2005). Alate production peaked in both years when plants reached the R5 stage (beginning of seed set; Fehr et al. 1971). In a flight mill study using alate *A. glycines* reared on soybean, 12–24 h after 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 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). *S. 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*, are capable of traveling great distances when aided by meteorological phenomena (Wikteliu 1984).

Currently, the best predictive sampling tool for *A. glycines* is in situ field scouting, which is labor intensive and costly to growers. Forecasting the timing of *A. glycines* movement 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 United States 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 ≈ 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 may allow researchers to identify spatial distributions of insects on a regional basis (Rhainds et al. 2010a, Isard and Gage 2001). Because migration is necessary to colonize both the summer and overwintering host plants, a regional suction trap network may provide 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 to 2008, and to determine if there were directional and spatial trends among the suction traps. We used regression and 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 because of a greater abundance of buckthorn, and that trap catches at one location will not be spatially dependent on its neighboring locations.

Materials and Methods

Aphid Data. The STN was first 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; Fig. 1) that account for $\approx 68.7\%$ of the total U.S. soybean acreage harvested in 2009 (USDA-NASS 2009). By 2008, the dimensions of the area covered by the STN were >1,100 km (east to west) and >1,200 km (north to south), encompassing $\approx 844,800$ km² (Fig. 1). The average distance between any two traps was ≈ 100 km and varied from 9 to 1,456 km (Fig. 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 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 jar filled with propylene glycol. The fan operated only during daylight hours. 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). All sites in the STN collected alates during years 2005–2008. Response variables for each year were summarized as: “absolute first” the date at which the absolute first alate was collected in a single trap location “average first” the average date at which the absolute first alate was collected for all trap locations, “summer peak” the date when alate captures peaked for all trap locations between June and August, and “fall peak” the date when alate captures peaked for all trap locations between September and November.

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

Trap number ^a and name ^b	Decimal degrees			
	Latitude	Longitude	County	Nearest City
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	Butler
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	Aug.
(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
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.

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).

Maps of the STN were plotted using ArcMap 9.3 (ESRI 2008) for 2005–2008 data, and using proportional symbols to indicate alate counts for each trap

(i.e., traps with a larger symbol collected more alates than those with a smaller symbol). Alate data were divided into individual sample dates (7-d intervals) for all years.

Data Analysis. A linear regression analysis was used to determine the relationship between *A. glycines* and azimuth (direction) or XY coordinates of each trap using JMP eight (SAS Institute 2009). In addition, we used a linear regression model to determine the relationship between dependent variables, alate counts

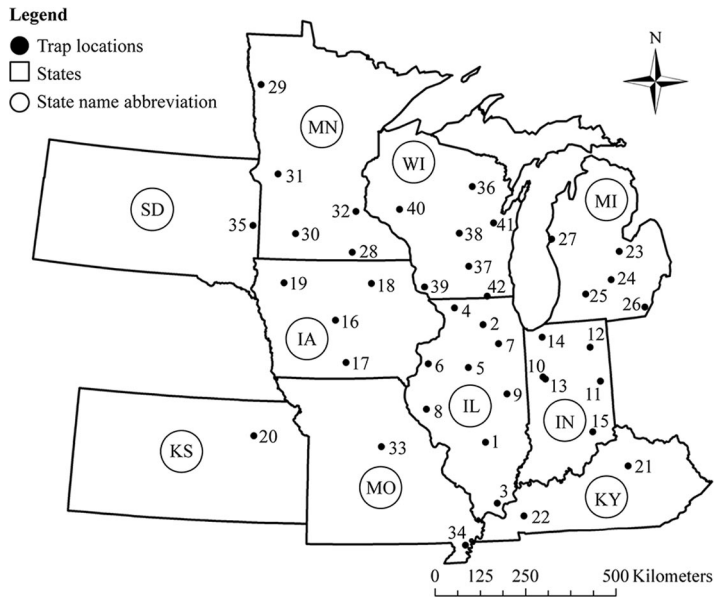


Fig. 1. Map of trap locations (labeled with numbers from Table 1) for the 42 suction traps in the Midwest United States.

pooled across season (summer: June through August, and fall: September through November), and independent variables, XY coordinates of each trap.

As described previously, one motivation behind analyzing data from the STN was to explore the spatial distribution of alate counts within 10 states. Given the suspected movement patterns for alates, we expected 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 more similar than expected by chance alone (Legendre and Fortin 1989). The presence and strength of the spatial autocorrelation (or dependence) can be quantified using geostatistics. One such tool is the variogram (a function of the degree of spatial dependence for a spatial random field). The estimated variogram using data collected over space is called the empirical variogram and is often used to detect the range of dependence over the domain of interest, the strength, and directional patterns in the field. However, we have a limited number of samples (only 42 locations) for our data set making the estimation of the variogram meaningless.

Another popular method for testing global spatial autocorrelation is Moran's I (Moran 1950). This test is constructed on the simple concept that when there is no spatial dependence, observations taken at nearby sites are not more similar than observations taken at sites situated far apart. Moran's I is often used as a screening detection tool of spatial dependence, in part because of its intuitive interpretation (a value of 0 indicates no spatial dependence, while a value of one 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 were

collected at a very large number of locations). For our data we only have at best 42 locations available, which results in inconclusive preliminary calculations of Moran's I.

In an effort to understand spatial dependence in our data, we developed a randomization test for spatial autocorrelation, which we call a "nearest neighbor model." This model tests for spatial dependence by constructing a similarity measure between sites, and compares this measure for sites located "nearby" and "far" away. If the two measures are comparable for both near and far, then one can conclude that there is no evidence of spatial autocorrelation. In other words, there is no difference in alate count data between the nearby and far location. The nearest neighbor model was performed using the default R statistical package (R Development Core Team 2008).

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) defines a similarity measure between sites. To proceed, we defined "sites nearby" as a neighborhood.

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

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
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 because of that suction trap not yet operational in places later constructed.

Although the size of neighborhoods was arbitrary selected, we considered neighbors as being co-located within a "sphere of influence" defined as sites within a certain radius from a given site (Noreen 1989). 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 the corresponding neighbors (NS_j), we quantified the similarity among observations within a neighborhood by taking the average of the absolute differences between observa-

tions at a given location and its neighbors (denoted by D_j close). Using absolute differences rather than simple differences ensures that averages were not deceptively small simply because of the direction in which the difference was calculated. Another 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 because of a lack of neighbors). Much the same, a measure of similarity between a given site and all other nonneighboring

Table 3. Linear relationship of first alate catch with X or Y coordinates

Year	X coordinates ^a				Y coordinates ^b		
	df	Slope	Intercept	Adj. R ^{2c}	Slope	Intercept	Adj. R ^{2c}
2005	1, 30	-5.3	262.9	0.02	-100.7	1739.2	0.13*
2006	1, 34	15.1	17.5	0.01	-281.9	4541.7	0.42*
2007	1, 38	9.6	68.3	0.03	-89.2	1562.8	0.04
2008	1, 40	3.2	206.7	0.03	-293.1	4769.4	0.67*

^a X coordinates are analogous to longitude or Easting.

^b Y coordinates are analogous to latitude or Northing.

^c Adjusted R² with significant treatment differences represented by (*P < 0.05).

sites was calculated as the average of the absolute values of differences (D_j far). We repeated the construction of the two measures for each trap location. Finally, we constructed our test statistic as the ratio between the average of all the D_j close and the average of all the D_j far, and it is hereafter referred to as the "nearest neighbor statistic." The nearest neighbor statistic is based on the ratio between averages and is well suited here because 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 zero neighbors for a given site, in which case eliminating the site from the calculation could lead to biases.

We then adapted the Noreen (1989) method for generating null reference distributions. We did so by redistributing observed data over the trap locations, and recalculating the sample statistic as described previously. In other words, collection data were randomly assigned to the fixed (observed) spatial locations. Randomization and recalculation was repeated 5,000 times to generate the reference distribution (Noreen 1989). 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., leading to a *P* value < 0.05) indicates that any null hypothesis of spatial independence can be rejected.

One benefit of using Noreen's (1989) method was that we could identify the extent of the spatial autocorrelation by repeating the test for various neighborhood sizes. Selecting the incorrect neighborhood size can lead to a type 1 error, or rejecting the null hypothesis when it is actually true. Considerations when selecting the neighborhood size were that they were not too small (many sites with no neighbors) or too large (nearly all sites are neighbors of each other). We tested distances every 25 km 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 one-fourth

the largest existing distance ($\approx 1,400$ km) (Cressie 1993).

Results

Over 4 yr, a total of 141,106 *A. glycines* gynoparae and 1,121 males were collected in the STN. The earliest absolute first alate capture was in 2007, followed by 2005, 2006, and 2008, with corresponding dates 25 May, 22 June, 30 June, and 13 August. Average first alate capture produced the same trend as absolute first alate capture, with corresponding dates 13 July, 13 July, 2 August, and 7 September. The summer peak of alates was earliest in 2007, followed by 2006, 2005, and 2008, with corresponding dates 3 August, 4 August, 12 August, and 22 September. In contrast, the fall peak was earliest in 2005, followed by 2007, 2006, and 2008, with corresponding dates 16 September, 28 September, 29 September, and 28 October. Regression analyses of first record of an alate collected in all traps suggests that X coordinates (East to West) explain little of the variation in any of the years. However, Y coordinates (North to South) explained significantly more of the variation in the occurrence of the first captured alate (Table 3).

The amount of alates captured per week were greatest in 2005 followed by 2007 > 2008 > 2006, and typically followed a bimodal distribution, peaking in August and again in late September (Fig. 2). 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 (Figs. 2–6). The peak in average alates captured for all traps was 685 aphids per trap between 5–12 August 2005 (Fig. 3). The greatest number of alates captured in a single location on any given date was 5,970 collected during 26 September, 2008 at Lamberton, MN (Fig. 6). The second highest catches of alates were reported in the fall of 2006 and summer of 2007. Peak alate catch during the summer was 4,440 alates collected on 12 August 2005 in East Lansing, MI (Figs. 2 and 3). Overall, a greater amount of variation in total alate counts was accounted for by the Y coordinates than the X coordinate of each trap (Table 4). In any given year the coordinates of a trap accounted for the most variability in total alate counts during the summer > all combined > fall (Table 4).

Our nearest neighbor analysis indicates when traps at set distances capture similar abundances of alates



Fig. 4. Weekly alate *A. glycines* data by week from the suction trap network in 2006. Symbols are proportional to the total collected for each trap over a seven-day period. Only weeks where alate *A. glycines* collected are shown.

tion trap locations are not appropriate for many of the collection dates (Table 5).

Discussion

As noted by Hiempel et al. (2010), the ability for soybean aphids to establish within North America was facilitated by the previous establishment of its primary and secondary hosts, buckthorn and soybeans, respectively. The amount and timing of alates captured within the STN provides insight into how *A. glycines* is moving between these two hosts, which can occupy very different habitats within the United States. One observation from our analysis of the STN is that few if any alates were collected during the spring when *A. glycines* migrate from buckthorn to soybeans. The low density of *A. glycines* on buckthorn during the spring (Welsman et al. 2007) likely contributes to the low numbers of alates captured during this period. In general, the number of aphids moving from buckthorn in the spring is typically less than aphids dispersing during the summer or fall months. In addition, the timing of the first captures of *A. glycines* may give some insight into what part of its phenology is accounted for by the STN. *A. glycines* have been reported in soybean fields as early as 24 May 2007 in WI, 28 May 2007 in Minnesota, and 31 May 2006 in Iowa (Rice and O'Neal 2006, 2007). In contrast, the first records of an alate *A. glycines* collected in the corresponding states from the STN was 24 June 2005 (Fig. 3), 30 June 2006 (Fig. 4), 25 May 2007 (Fig. 5), and 11 July 2008 (Fig. 6). This suggests that 2007 may be the only year when alates were collected traveling directly from buckthorn to

soybean, limited to two traps in Michigan (Kellogg and Monroe County), which collected a total of four alates (Fig. 5). Therefore, either the STN may not effectively detect early spring flights of *A. glycines* alates moving from buckthorn to soybean or sampling needs to be initiated earlier in the season.

Several studies have 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 among traps. Spring flight of *A. glycines* from buckthorn to soybean may extend only as far as adjacent soybean fields; therefore, initial flights may be limited to short-dispersal events. If this is true, then the amount of buckthorn around a trap will greatly influence the amount of alates captured in the spring. Currently all suction traps are located in states where buckthorn is present (Kurylo et al. 2007), though the amount of buckthorn present around each trap is not known. Bahlai et al. (2010) determined that the ratio of buckthorn density to the area of a soybean field was a best predictor of aphid density when considering features of the landscape surrounding a soybean field. Additional improvements to our understanding of regional abundance of soybean aphids may require more precise estimates of buckthorn abundance within the landscape beyond presence and absences.

An alternative explanation for why so few alates were collected during the spring is that migration by

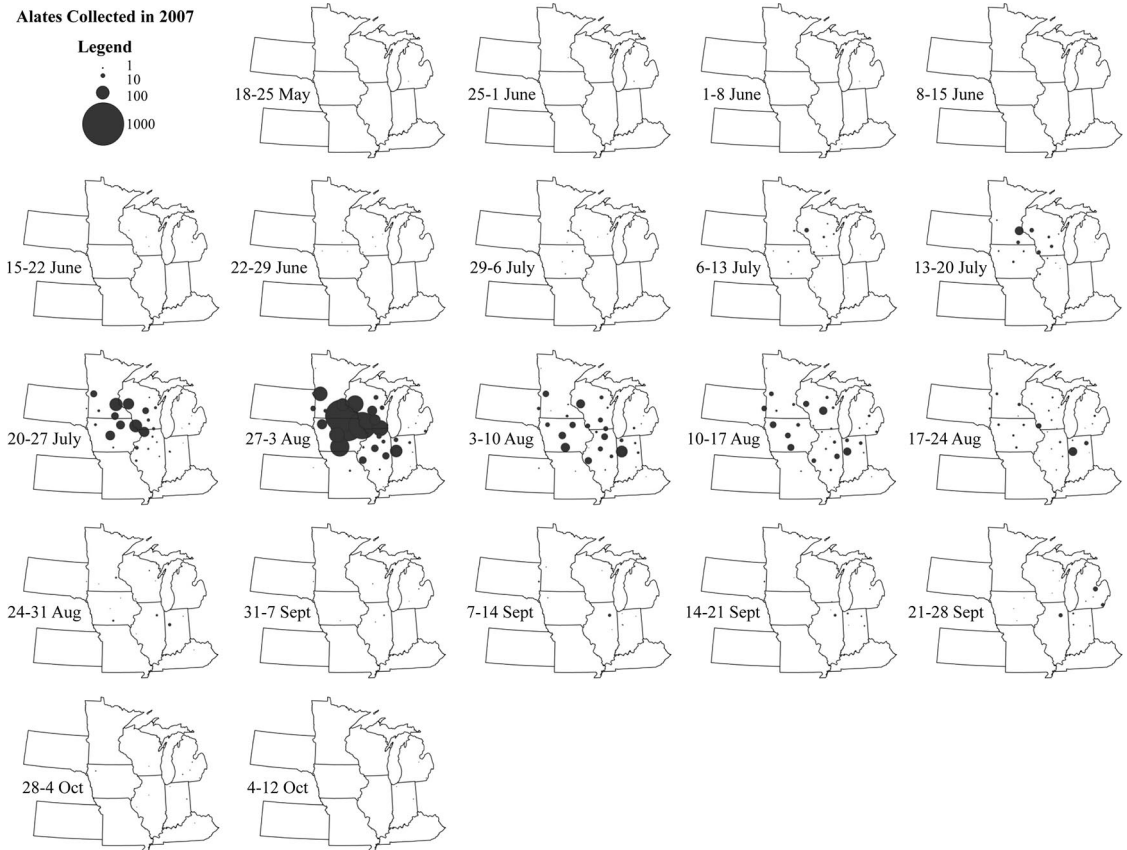


Fig. 5. Weekly alate *A. glycines* data by week from the suction trap network in 2007. Symbols are proportional to the total collected for each trap over a seven-day period. Only weeks where alate *A. glycines* collected are shown.

A. glycines from buckthorn to soybeans occurs at altitudes too low for collection in the suction traps. Kennedy and Booth (1963) described the migratory behavior of aphids based on observations of the black bean aphid, *Aphis fabae* Scopoli, which exhibits positive phototaxis before and after takeoff 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). Because of the aphids’ small size, air currents are able to carry them above the surface boundary layer (Loxdale and Lushai 1999, Isard and Gage 2001), promoting the long range dispersal of migrants. *A. glycines* migration from buckthorn to soybeans may not involve vertical flight limiting the capacity of a suction trap to capture alates.

In our analyses, the abundance of *A. glycines* captured in the STN were positively correlated with Y coordinates (latitude) (Tables 3 and 4). Our analyses showed that data from trap locations were not always independent of one another, making conclusions based on the regression analysis, which assumes in-

dependence, unsuitable. 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. Odd numbered years (2005 and 2007) were preceded by low aphid infestations in much of the Midwest and alates were collected earlier in the year (Table 3). In contrast, even numbered years (2006 and 2008) were preceded by high aphid infestations and alates were collected later (Table 3). This oscillation has been reported within Indiana, a state encompassed by the STN (Rhainds et al. 2010b). The factors that are responsible for this oscillation are not clear. Welsman et al. (2007) observed a decline in *A. glycines* egg abundance by $\approx 70\%$ on *R. cathartica*; however, the source of mortality was not identified but they suggest predation and cold temperatures may play a role. If weather does play a role in the occurrence of alates from year to year, it is possibly related to whether temperatures reach the supercooling point of *A. glycines*, which for eggs is -34°C (McCornack et al. 2005). Additional sources of egg mortality could be the duration of

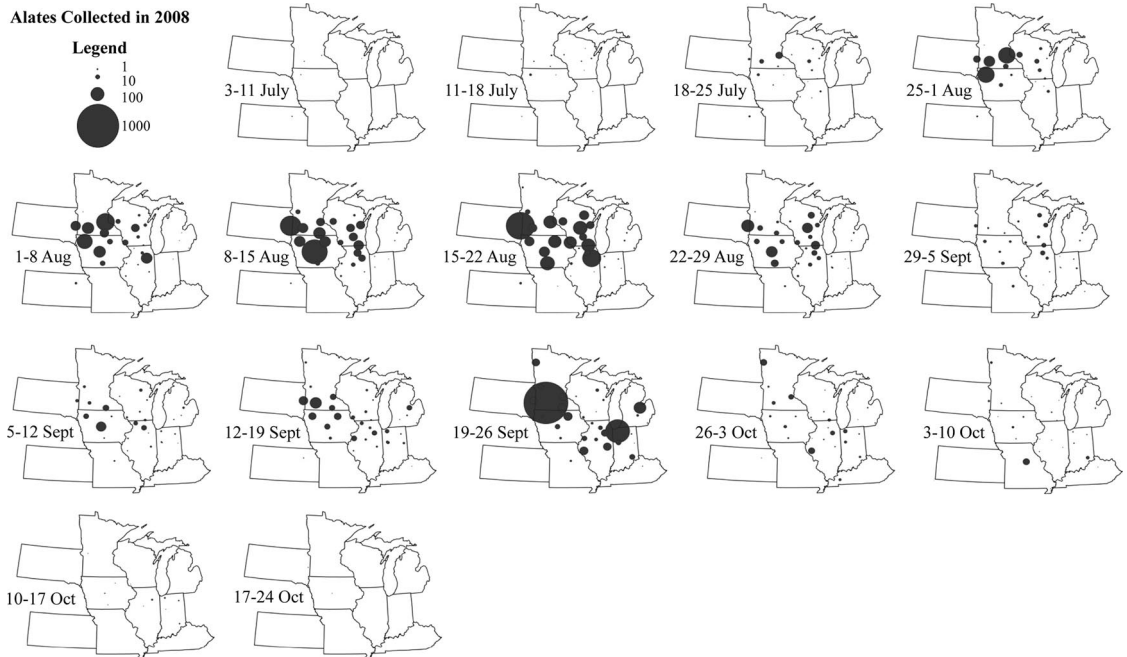


Fig. 6. Weekly alate *A. glycines* data by week from the suction trap network in 2008. Symbols are proportional to the total collected for each trap over a seven-day period. Only weeks where alate *A. glycines* collected are shown.

winter or extended cold periods (Leather 1981, 1992; Welsman et al. 2007), rain dislodging eggs (Dunn and Wright 1955), and humidity (Peterson 1920). Other factors may include mortality by natural enemies (Leather 1981, 1992; Welsman 2007; Nielsen and Hajek 2005). Although several natural enemies exist within North America that contribute to *A. glycines* mortality, absent from this community are parasitoids that play a significant role in regulating *A. glycines* population in soybean fields within Asia. We are not

aware of studies estimating the extent that parasitoids contribute to *A. glycines* mortality in buckthorn within Asia.

In 2005, 2006, and 2008 we observed a greater abundance of alates captured in traps in the northern region of the STN. This is likely because of greater overwintered *A. glycines* populations, which reside on *R. cathartica*. *R. cathartica* is distributed throughout the Midwest, but is more abundant at northern latitudes (Kurylo et al. 2007). Soybean is also distributed

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

Season	df	X coordinates ^a			Y coordinates ^b		
		Slope	Intercept	Adj. R ^{2c}	Slope	Intercept	Adj. R ^{2c}
2005							
Summer	1,287	1.5	-16.6	0.04*	20.2	306.8	0.15*
Fall	1,210	-0.5	7.9	0.01	5.3	-80.0	0.02*
All dates ^d	1,499	0.6	-5.9	0.01*	13.6	-206.4	0.08*
2006							
Summer	1,328	-0.8	11.5	0.04*	11.5	-175.5	0.20*
Fall	1,321	0.0	1.3	0.00	-2.4	38.1	0.00
All dates	1,651	-0.4	5.9	0.01*	4.2	-63.5	0.02*
2007							
Summer	1,586	-0.3	4.5	0.00	6.4	-96.6	0.04*
Fall	1,234	-0.1	1.5	0.00	2.6	-40.2	0.04*
All dates	1,822	-0.2	3.8	0.01*	5.5	-83.5	0.04*
2008							
Summer	1,309	-1.1	16.3	0.03*	17.3	-263.2	0.21*
Fall	1,280	-0.3	6.3	0.00	10.5	-158.1	0.10*
All dates	1,591	-0.7	11.6	0.02*	13.9	-212.3	0.17*

^a X coordinates are analogous to longitude or Easting.

^b Y coordinates are analogous to latitude or Northing.

^c Adjusted R² with significant treatment differences represented by (*P < 0.05).

^d 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	**	—	—	—	—	—	—	—	—
30	**	**	*	*	—	—	—	—	—
Oct. 7	—	—	—	—	—	—	—	—	—
2006									
July 21	*	*	*	**	**	*	*	—	—
28	**	**	**	**	**	**	**	**	**
Aug. 4	**	**	**	**	**	**	**	**	**
11	**	**	**	*	*	—	—	—	—
18	*	*	**	**	**	*	*	*	*
25	—	—	—	—	—	—	—	—	—
Sept. 1	—	—	**	*	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—
15	—	—	—	—	—	—	—	—	—
22	—	—	—	—	—	—	—	—	—
29	—	—	—	—	—	—	—	—	—
Oct. 6	**	**	*	**	—	—	—	—	—
13	*	—	—	—	—	—	—	—	—
20	—	—	—	—	—	—	—	—	—
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 nonsignificance (trap catches are different).

*significant at $P < 0.1$ (trap catches are the similar).

** significant at $P < 0.05$ (trap catches are the similar).

west. 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 source populations earlier in the season.

The nearest neighbor analysis reveals the presence of 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-h 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, or even regional insecticide use. 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/

throughout the Midwest, but is more evenly dispersed; therefore, *A. glycines* movements within and between habitats are likely taking place at relatively large scales throughout the summer and early fall across the Mid-

sink estimates and to facilitate identification of weather and plant stage factors affecting aphid movement. Over the 4 yr, >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.

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