

Toward management guidelines for soybean aphid, *Aphis glycines*, in Quebec. II. Spatial distribution of aphid populations in commercial soybean fields

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Abstract—The study was conducted to document the spatial distribution of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), in commercial fields of soybean, *Glycine max* (L.) Merr. The abundance of aphids was assessed weekly at 12 sites in 2005 and 2006 on more than 135 georeferenced plants per site. Variograms and principal coordinates of neighbour matrices (PCNM) were used to detect significant spatial structures. Variograms indicated a spatially random distribution of aphid populations in a majority (84%) of fields-weeks. For the variograms with a defined structure, the variance between pairs of observations generally increased rapidly with the distance between plants up to a distance where it stabilized, a pattern adequately fitted by spherical models. Structured spatial distributions were more prevalent in 2005 than in 2006, especially at the end of the season. In 2006, PCNM analysis was more sensitive in detecting spatial trends than were variograms. PCNM analysis revealed significant patterns across a broad range of scales, with dominant periods averaging 22.6 and 47.1 m for the short and long transects, respectively. Sampling plants along a 100 m long transect at about 7.5 m intervals in soybean fields would allow detection of the spatial structures identified in this study.

Résumé—Cette étude a été entreprise afin de documenter la distribution spatiale du puceron du soya, *Aphis glycines* Matsumura (Hemiptera : Aphididae), dans des champs commerciaux de soya, *Glycine max* (L.) Merr., de la province de Québec. Le nombre de pucerons a été évalué sur une base hebdomadaire dans 12 sites en 2005 et 2006, en échantillonnant pour chaque site plus de 135 plants géoréférencés. Des variogrammes ainsi que des analyses des coordonnées principales de matrices de voisinage (CPMV) ont été utilisés pour détecter l'existence de patrons spatiaux significatifs. Les variogrammes ont indiqué un patron de distribution spatialement aléatoire des populations de pucerons pour une majorité (84 %) des sites-semaines. En ce qui concerne les variogrammes présentant une structure spatiale définie, la variance entre les paires d'échantillons augmentait généralement rapidement avec la distance entre les échantillons jusqu'à une certaine distance après laquelle la variance se stabilisait; ce patron de distribution spatiale était adéquatement décrit par un modèle de type sphérique. Des distributions spatiales structurées étaient plus fréquemment observées en 2005 qu'en 2006, surtout en fin de saison. En 2006, les analyses basées sur les CPMV furent plus sensibles que les variogrammes pour détecter les tendances spatiales. Les CPMV ont révélé des patrons significatifs pour une vaste gamme d'échelle spatiale, avec des périodes dominantes de 22.6 et 47.1 m en moyenne pour les transects courts et longs. L'échantillonnage des plants de soya le long d'un transect de 100 m avec un pas d'environ 7.5 m permettrait de détecter les patrons de distribution spatiale identifiés par la présente étude.

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Introduction

The recent introduction of the soybean aphid, *Aphis glycines* Matsumura (Hemiptera: Aphididae), to North America poses a serious threat to the production of soybean, *Glycine max* (L.) Merr. (Fabaceae) (Venette and Ragsdale 2004). The aphid has the potential to severely reduce soybean yields, either directly through its feeding activity (Macedo *et al.* 2003; Rhainds *et al.* 2007) or indirectly through the transmission of viral diseases (Wang *et al.* 2006). Under some circumstances, the application of insecticides may be justified (Myers *et al.* 2005; Ragsdale *et al.* 2007). The development of a sound sampling methodology is critical to assessing the abundance of aphids in order to make management decisions. Previous studies have evaluated among-plant variation in density of soybean aphids (Wu *et al.* 2004), which has yielded estimates of the number of plants required for sampling assessments (Onstad *et al.* 2005) and led to the development of a sequential sampling plan (Hodgson *et al.* 2004). Despite the potential importance of the spatial structure of insect populations in influencing sampling assessments (Dungan *et al.* 2002; Legendre *et al.* 2002), limited information on the spatial distribution of soybean aphids is available, other than a comparison between plants near the edge and those in the interior of soybean fields (Hodgson *et al.* 2005).

In the present study, the spatial distribution of soybean aphids was modelled by recording their location and abundance on a large number of plants throughout the soybean growing season. The objective was to document the nature and range of spatial dependence of aphid populations at different scales, to assess the minimum distance between plants that allows spatially independent sampling. Two complementary approaches were used to characterize the spatial distribution of aphids: variograms (Matheron 1965) and principal coordinates of neighbour matrices (PCNM; Borcard and Legendre 2002; Borcard *et al.* 2004).

Materials and methods

Sampling procedure

The study was conducted in 2005 and 2006 in 12 commercial soybean fields located in the province of Quebec (Table 1). One experimental plot was established in each field in mid-June using a grid of flags placed alongside rows

of soybeans that were at the vegetative stage and carried undetectable levels of *A. glycines*. Each experimental plot consisted of fifteen or sixteen 15 m × 15 m subplots spaced 15 m apart along the *x* and *y* axes, depending upon the dimensions of each field (Fig. 1). Each subplot consisted of a grid of nine equidistant flags 7.5 m apart. Subplots were arranged in either a 4 × 4 design (type A grid; 105 m × 105 m) or a 5 × 3 design (type B grid; 75 m × 135 m) corresponding to experimental areas of 1.1 and 1.0 ha, respectively (Fig. 1). Whenever possible, a type A grid was preferentially established in a given field; type B grids were established in narrow or irregularly shaped fields. The rationale behind the arrangement of subplots was that the abundance of aphids on several plants (>135) could be assessed over a large area (1 ha) while maintaining a relatively short distance between plants (7.5 m) in order to detect structures at a fine spatial scale.

Sampling of *A. glycines* populations was initiated in early July of 2005 and 2006 and conducted weekly for a total of 8–9 weeks unless otherwise specified (Table 1). For each sampling period, one plant located in the vicinity of a flag was destructively sampled to record the number of aphids (all life stages combined), corresponding to a sample size of 144 (grid A) or 135 (grid B) plants per field and time period. Plants selected for sampling were uprooted and visually inspected for up to 2 min per plant to count the aphids on above-ground plant structures (stem, leaves, pods). Occasionally patches of plants with fungal diseases were not sampled in specific locations, to avoid spreading the disease. Sampling was terminated earlier in the season in some fields because of hail damage or foliage senescence.

The distribution of aphids at a fine spatial scale was further investigated in 2006 by sampling plants 3.75 m apart along one transect established within the experimental plots for nine fields (105 and 135 m long transects for grids A and B, respectively; Table 1), using flags to identify and locate plants. Plants were sampled along the transect for 3 consecutive weeks, beginning when more than 15% of plants were infested with *A. glycines*.

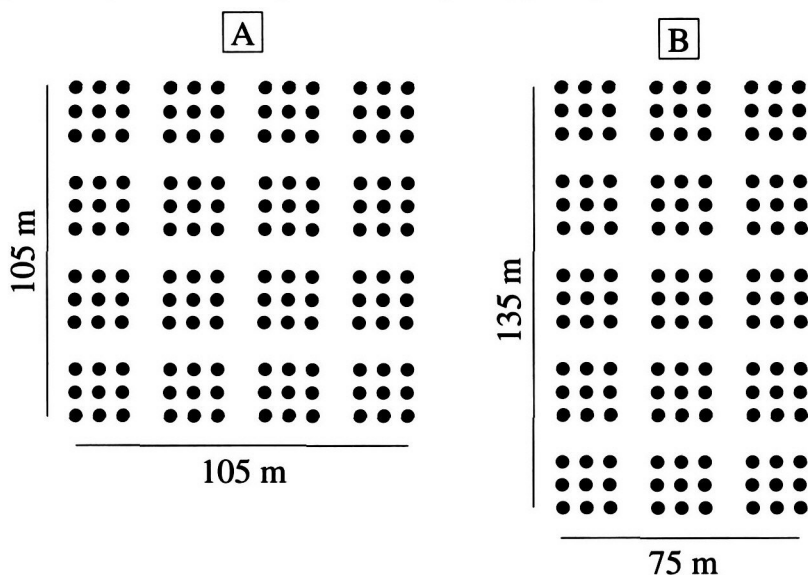
Two distinct approaches were used to determine the spatial distribution of *A. glycines* over distances extending beyond the experimental plots. In 2005, a total of three or four experimental plots 75–105 m apart were established as described above in three fields, and the abundance

Table 1. Characteristics of soybean, *Glycine max*, sampled repeatedly over time to measure the abundance of soybean aphid, *Aphis glycines*.

Year and site	Latitude (°N)	Longitude (°W)	Grid*	No. of grids†	Transect?‡	No. of sampling periods	Surface area (ha)	Distance between rows (cm)	Peak density of aphids (no./plant), mean ± SE
2005									
Saint-Henri de Lévis	46.69	71.07	A	1	No	8	6.9	30.5	326.5±14.8
Saint-Augustin	46.74	71.42	A	1	No	8	35.6	30.5	236.0±10.4
Pont-Rouge	46.74	71.68	B	1	No	7	3.0	17.8	550.1±20.3
Forterville	46.49	72.03	B	1	No	8	6.2	19.1	449.7±16.8
Sainte-Anne de la Pérade	46.57	72.20	A	1	No	7	8.1	76.2	348.4±13.9
Saint-Wenceslas	46.17	72.33	A	1	No	8	8.0	19.1	164.2±13.2
Nicolet	46.23	72.61	A	4	No	8	35.0	30.5	520.7±22.3
Yamachiche	46.28	72.83	A	1	No	8	21.1	53.3	378.0±18.8
Saint-Robert	45.98	73.00	A	3	No	8	8.5	17.8	872.3±29.0
Saint-Cuthbert	46.18	73.23	B	1	No	8	5.0	30.5	184.1±10.8
Sainte-Julie	45.49	73.34	A	1	No	8	21.0	17.8	417.0±18.0
Verchères	45.77	73.35	A	4	No	8	45.6	76.2	847.7±36.9
2006									
Issoudun	46.58	71.68	A	1	Yes	6	11.0	17.8	11.7±1.0
Saint-Barnabé	45.75	72.95	B	1	Yes	9	5.7	76.2	66.9±2.5
La Présentation	45.67	73.06	A	1	Yes	9	36.0	38.1	131.8±6.8
Sainte-Madeleine	45.58	73.10	B	1	Yes	9	7.6	76.2	153.0±8.6
Saint-Alexis	46.47	73.14	A	1	No	7	25.0	38.1	12.1±0.7
Saint-Denis sur Richelieu	45.78	73.15	B	1	Yes	5	3.3	38.1	3.1±0.3 [§]
Berthierville	46.08	73.19	A	1	Yes	9	17.1	30.5	183.1±10.9
Saint-Thomas	46.02	73.34	A	1	No	9	3.4	19.1	41.2±2.3
Sainte-Elizabeth	46.09	73.35	B	1	Yes	9	4.0	15.2	26.0±1.8
Verchères	45.77	73.35	A	1	Yes	9	45.6	76.2	360.6±25.2
Varennes	45.68	73.42	A	1	No	9	2.2	76.2	116.6±8.2
L'Assomption	45.83	73.42	B	1	Yes	9	5.7	35.6	94.2±7.3

*Plants were sampled using the designs shown in Figure 1.
†A total of three or four experimental plots spaced 75–105 m apart were established, and the abundance of aphids was recorded on 432–576 plants per field during 3 consecutive weeks beginning on 11 July 2005.
‡Plants were sampled along one transect for 3 consecutive weeks, beginning after more than 15% of plants were infested with *A. glycines*. Short transects were 105–135 m long, with an interpoint distance of 3.75 m. Long transects were 337.5–390 m long, with an interpoint distance of 7.5 m.
§Sampling was terminated earlier in the season at some sites because of hail damage or foliage senescence.

Fig. 1. Experimental grids used for sampling soybean aphids (*Aphis glycines*) in soybean (*Glycine max*) fields repeatedly over the season in 2005 and 2006; each point represents a wire flag. For each field and time period, one plant located in the vicinity of each flag was destructively sampled to record the number of aphids, corresponding to a sample size of 144 (grid A) or 135 (grid B) plants per field for each time period.



of aphids was recorded on 432–576 plants per field during 3 consecutive weeks beginning on July 11 (Table 1). In 2006 a transect extending outside the experimental plots was established in nine fields along the same rows of soybeans where plants had been sampled at a fine (3.75 m) spatial scale (grid A: 36 additional flags 7.5 m apart for a line extending 270 m beyond the grid; grid B: 32 additional flags 7.5 m apart for a line extending 240 m beyond the grid), and aphids were sampled on one plant in the vicinity of each flag for 3 consecutive weeks (see above).

Data analysis

Geostatistical analysis

Geostatistical analysis aims to detect spatial structure in response variables, in this case the number of soybean aphids per plant. Spatial structures can arise from two processes (Legendre and Legendre 1998): the first is spatial dependence of the response on forcing (*e.g.*, environmental) variables that are themselves spatially structured, and the second is spatial autocorrelation, which results from processes occurring in the response variable itself. Positive autocorrelation, in particular, is found when a process is at work that causes neighbouring units to have values of the response variable that are more similar than those of units that are farther

apart. Variograms quantify the relationship between the spatial locations and the variability of the sampling units using the equation $\gamma(h) = 1/2N_h \sum [z(x_i) \times z(x_i + h)]$, where $\gamma(h)$ is the semivariance for distance lag h , N_h is the number of paired comparisons for distance lag h , $z(x_i)$ is the density estimate at point (x_i), and $z(x_i + h)$ is the density estimate at point ($x_i + h$) located at distance h from point (x_i) (Matheron 1965).

Variogram analyses were conducted using the R statistical language (R Development Core Team 2007) to model the counts of aphids on each plant in relation to its position within the field, using omnidirectional nonergodic (detrended) variograms. In most fields and sampling periods, $\gamma(h)$ values were calculated for distance lags multiples of 7.5 m using a maximum interpoint distance of 52.5 m. In the three fields where two or three plots were sampled during 3 consecutive weeks in 2005, the maximum interpoint distance was set at 120 m. Preliminary results not reported here indicated similar patterns of spatial distribution within and along soybean rows, thus justifying the use of omnidirectional variograms. Analyses were not conducted for fields and time periods where fewer than 5% of plants were infested with aphids. Variograms were standardized for the different fields and weeks by dividing the $\gamma(h)$ values by the sample covariance, thus producing Geary's c coefficient, which has a sill that approximates 1

irrespective of the sample variation. The variofit function of the "geoR" library of the R statistical language (R Development Core Team 2007) was used to characterize the variation of $\gamma(h)$ values as a function of distance lags, fitting spherical models to the empirical observations with an iterative approach minimizing least squares. The iterations for evaluating the parameter estimates of spherical models were programmed for most fields using an extent of variation of 0.2–1.0 for the sill, 7.5–25 m for the range of spatial dependence, and 0.2–1.0 for the nugget, using 25 even lengths for each parameter. The variation for the range was set at 7.5–60 m in the three fields and weeks where more than one plot was sampled.

Spatial analysis based on PCNM

The presence and shape of spatial structure in the transects were modelled using PCNM analysis (Borcard and Legendre 2002; Borcard *et al.* 2004). When the sampling design is regular and unidimensional, PCNM variables appear as a set of orthogonal, sine-shaped functions that can be used as explanatory variables in multiple regressions (as in this research) or canonical ordination (in the multivariate case). A regular transect of n sampling points yields $2n/3$ PCNM variables with decreasing periods (where n is the number of sampling points). The first PCNM variable has the largest period: one complete sine wave covers the entire length of the transect. It therefore models an equally broad feature of the data. The period of the last PCNM variable is roughly equal to 3 times the distance between two sampling points. A combination of PCNM variables of various periods is used to model the spatial structure of the data, decomposing it into sine waves. This technique is therefore akin to Fourier analysis. The PCNM variables are constructed by (i) generating a matrix of intersite Euclidean distances, (ii) truncating the matrix to retain only the closest neighbours, (iii) replacing the other values by an arbitrary large value, and (iv) computing the principal coordinates of the resulting matrix. These principal coordinates are the PCNM variables.

In the present study, the number of aphids per plant on a given transect at a given time was the response variable, and the full set of PCNM variables were the explanatory variables in a multiple regression. In each analysis, only the PCNM variables whose partial regression coefficients were significant at a preselected α level of 0.05 were retained to build the regression

model. This model therefore represents the significant spatial structure of the aphid densities along the transect. Examining the periods of the significant PCNM variables allows one to model the spatial structure of the data at all the scales perceived by a sampling design. The overall significance of the regression model can be tested using a permutation procedure.

The proportion of the response variable's variance explained by the PCNM base functions is expressed using the adjusted coefficient of determination of the regression (Peres-Neto *et al.* 2006; hereinafter R^2_{adj}). If desired, the spatial model can be decomposed into additive submodels corresponding to different spatial scales, which can be used *a posteriori* to explain the origins of the various structures. These submodels are constructed using a selection of the significant PCNM variables weighted by their regression coefficients. Adding the submodels together restores the spatial model. PCNM variables were generated using the SpaceMaker2 program (Borcard and Legendre 2004). PCNM analysis of the transects, *i.e.*, multiple regressions with forward selection of PCNM variables and permutation tests, was carried out using the "Voisin 10" program (D. Borcard, unpublished data).

Other analyses

Other statistical analyses were conducted with the SAS statistical package, version 9.1 (SAS Institute Inc. 2002). In both 2005 and 2006, fluctuations in abundance of soybean aphids over time in different fields (mean number of aphids per plant, proportion of plants infested with aphids) were evaluated using factorial analysis of variance (ANOVA), treating fields (12 levels each year) and time periods (8 levels in 2005 and 9 levels in 2006) as random factors. In the three fields where multiple experimental plots were sampled repeatedly over time in 2005, the relative variation in aphid abundance in relationship with time, fields, and plots within fields was determined by the VARCOMP procedure, which computes estimates of the variance components in a general linear model; the design consisted of a three-way treatment structure, field (3 levels), time period (3 levels), and plot (3 levels in Saint-Robert, 4 levels in Nicolet and Verchères) nested within field, with all factors considered random. For variograms and PCNM analyses, *a posteriori* comparisons of fields with or without a defined spatial structure in relationship to

different variables (year, week of sampling, number of plots sampled per field, length of transects) were conducted using contingency table analysis (χ^2 tests).

Results

Variation in aphid abundance in 2005 and 2006

The density of aphids varied as a function of time and field in both 2005 and 2006 ($P < 0.0001$; Table 1, Fig. 2), but the pattern was different each year. The density of aphids was initially low in early July to mid-July, when soybeans were at the vegetative or flowering stages: 1.8 ± 0.8 (mean \pm SE) and 0.8 ± 0.3 individuals per plant in 2005 and 2006, respectively (Fig. 2A). In 2005 the abundance of aphids increased exponentially from mid-July to mid-August to reach a peak density of more than 400 individuals per plant, and declined by about 50% thereafter (Fig. 2A). In 2006, in contrast, aphids steadily increased in number (though at a relatively low rate) between mid-July and late August to attain a peak density of slightly over 100 individuals per plant (Fig. 2A). The proportion of plants infested with aphids was consistently higher in 2005 than in 2006, except in late August, when the infestation level exceeded 99% each year (Fig. 2B). More than 50% of plants were infested by mid-July in 2005, and about 2 weeks later in 2006 (Fig. 2B).

Spatial distribution of aphids

Within-field variation of population density

In 2005, sampling of aphids in multiple experimental plots for 3 consecutive weeks in three fields (Nicolet, Saint-Robert, Verchères), with the distance between plots exceeding 75 m, allowed exploration of the distribution of aphids within soybean fields on a relatively broad scale. ANOVA components revealed relatively weak differences in abundance of aphids among plots within a field (estimates of variance for plot(field) = 0.00; for week \times plot(field) = 128.89) compared with differences among fields and time periods (estimates of variance: for field = 1152.20; for week = 557.47; for week \times field = 3984.70). Overall, the abundance of aphids in the three fields varied to a considerably greater extent among time periods than among plots within a field (Fig. 3), as indicated by the very low ratio of estimates of variance component of week \times plot(field) divided

Fig. 2. Seasonal abundance (mean \pm SE) of soybean aphids (*Aphis glycines*) in soybean (*Glycine max*) fields in 2005 and 2006, showing the number of aphids per plant (A) and the proportion of plants infested with aphids (B).

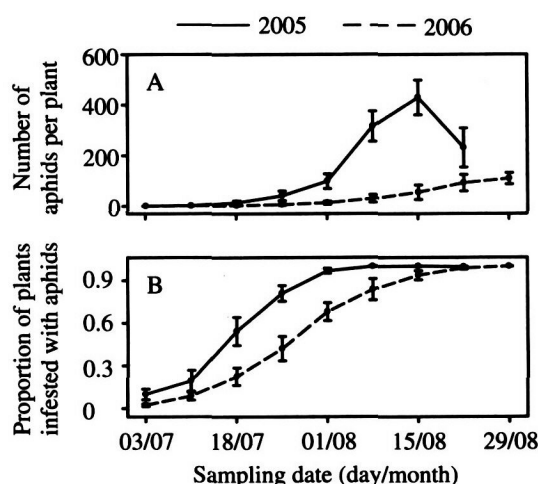
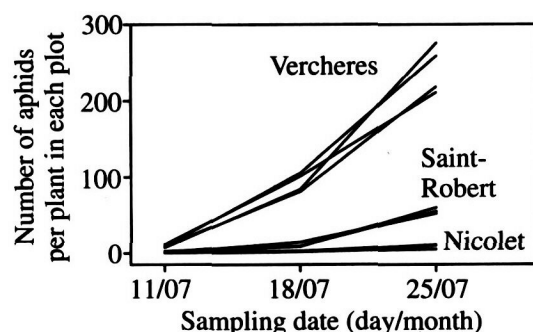


Fig. 3. Abundances of soybean aphids (*Aphis glycines*) over time in experimental plots >75 m apart in three soybean (*Glycine max*) fields.

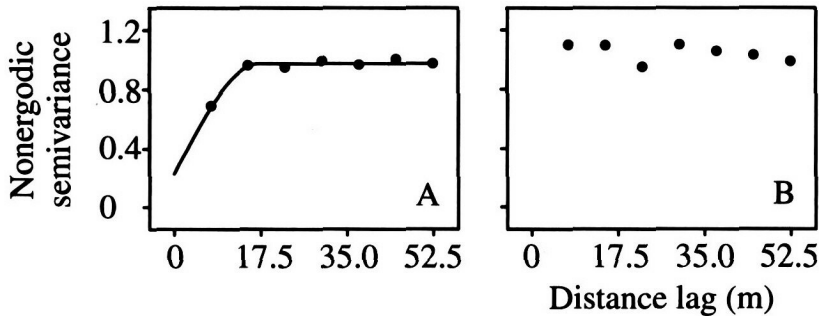


by week \times plot ($128.89 / 3984.70 = 0.032$, or about 3%).

Variogram analyses

Variograms representative of the two types of spatial structure encountered in this study are depicted in Figure 4. The distribution of soybean aphids often appeared spatially random, as indicated by the relatively low (16 %) proportion of the fields-weeks that exhibited a defined spatial structure (26 of 161) (Table 2). For variograms with a defined structure, the variance between pairs of observations increased rapidly with the distance between plants up to a distance where it stabilized, a pattern adequately fitted by

Fig. 4. Nonergodic variograms representative of the different types of spatial structures of populations of soybean aphid (*Aphis glycines*) in soybean (*Glycine max*) fields. (A) Spherical model in fields with an interpoint distance of 7.5 m between plants (Saint-Wenceslas, 15 August 2005). (B) No defined spatial structure (Saint-Robert, 8 August 2005). A summary of the different patterns of spatial structure encountered during this study is provided in Table 2.



spherical models (Fig. 4, Table 2). Structured spatial distributions were more prevalent in 2005 (17 of 82 fields-weeks, or 20.7%) than in 2006 (9 of 79 fields-weeks, or 11.4%), although the difference was not statistically significant ($\chi^2 = 2.59$, $P > 0.10$). Spatial dependence was more commonly observed in the last 2 weeks of 2005 than early in the season (9 of 22 vs. 8 of 60 fields-weeks; $\chi^2 = 7.45$, $P < 0.01$). In 2006, few fields exhibited significant spatial structure at any time during the season (Table 2). Although significant variograms were more commonly observed for the fields where multiple plots were sampled (3 of 9 fields-weeks in Nicolet, Verchères, and Saint-Robert during the period 11–25 July 2005) than for the other fields during the same time interval (2 of 27 fields-weeks) (Table 2), the difference was not statistically significant ($\chi^2 = 3.79$, $P > 0.05$). The range of values observed in Saint-Robert and Verchères on 25 July (78.8 and 103.5 m, respectively) suggests spatial dependence among plants separated by a long distance, although the effect was weak overall, as indicated by the strong nugget effect in both fields (intercept > 0.789) (Table 2).

PCNM analyses

The results of PCNM analyses in 2006 are summarized in Tables 3 and 4, where the numbers of the significant PCNM variables are given to show the significant spatial scales. Spatial structure (revealed by significant regression models) was more commonly observed for the long transects (337.5–390 m, with interpoint distance of 7.5 m) than for the short transects (105–135 m, with interpoint distance of 3.7 m) (20 of 27 vs. 12 of 27 fields-weeks; $\chi^2 = 4.91$,

$P < 0.05$) (Tables 3, 4). The predominance of spatial structure over broad scales suggests that sampling large portions of soybean fields is most appropriate for detecting spatial patterns of *A. glycines* populations and the associated range of variation of population density. A detailed summary of PCNM analyses is provided below, with the objective of reconciling constraints related to the necessity of obtaining accurate estimates of population density (which involves sampling areas as large as possible) and the practical need for a cost-effective monitoring tool (which involves sampling restricted areas).

The decomposition of the significant PCNM models in two fields illustrates the shape of spatial patterns at different scales (Fig. 5). In these examples, significant patterns were observed across a broad range of scales, although intermediate-scale submodels (interpoint distances of 19–60 m) had the most explanatory power (Fig. 5).

Analyses of the short transects with an interpoint distance of 3.75 m revealed that early in the season, only three fields exhibited significant spatial structure, and the R^2_{adj} value of these relationships was low overall (0.150–0.310) (Table 3). The number of fields exhibiting significant spatial structure (5) and the R^2_{adj} values of these relationships (0.342–0.706) increased over the second week of sampling and declined slightly thereafter (Table 3). Significant structures were present at all spatial scales. Interestingly, the fields with the strongest relationships (e.g., Saint-Barnabé and La Présentation during week 2) exhibited strong spatial structures across all scales (down to the finest PCNM, at a resolution of about 12 m) (Table 3).

Table 2. Summary of geostatistical analyses conducted to evaluate the spatial distribution of soybean aphids (*Aphis glycines*) sampled in soybean (*Glycine max*) fields in 2005 and 2006 at repeated intervals.

Year and week (day/month)	Location of the field	Nugget	Sill	Range
2005				
11/07	Nicolet*	0.028	1.035	15.0
18/07	Saint-Wenceslas	0	1.128	16.5
	Saint-Cuthbert	0	1.191	15.1
25/07	Saint-Robert*	0.937	0.123	103.5
	Verchères*	0.789	0.329	78.8
01/08	Sainte-Anne	0.159	1.024	14.1
08/08	Saint-Wenceslas	0.758	0.297	35.2
	Nicolet	0.541	0.559	36.5
15/08	Saint-Henri	0.594	0.469	33.1
	Pont-Rouge	0.673	0.387	18.4
	Fortierville	0.824	0.178	31.1
	Sainte-Anne	0.822	0.401	57.6
22/08	Saint-Wenceslas	0.225	0.748	17.2
	Saint-Augustin	0	1.040	15.4
	Saint-Cuthbert	0.768	0.318	33.7
	Sainte-Julie	0.735	0.419	56.1
	Verchères	0.635	0.426	30.4
2006				
18/07	Issoudun	0	1.445	18.8
	Saint-Denis	0.353	0.730	13.5
01/08	Sainte-Madeleine	0.233	0.890	19.9
08/08	Verchères	0.391	0.697	17.2
	L'Assomption	0	1.211	15.3
22/08	Sainte-Madeleine	0.503	0.595	18.0
	Varennes	0.271	0.612	18.3
29/08	Verchères	0.581	0.473	36.6
	Varennes	0.675	0.463	41.1

Note: The aphids were sampled along grids of plants depicted in Figure 1. For variograms with a defined structure, the variance between pairs of observations increased rapidly with the distance between plants up to a distance where it stabilized, a pattern adequately fitted by spherical models (Fig. 4A). The relationships are not shown for fields that did not exhibit a structured spatial distribution (Fig. 4B). An asterisk denotes a field in which more than one plot was sampled on a given date, which allowed testing for spatial dependence over a broader range.

Analyses of the transects with an interpoint distance of 7.5 m revealed significant spatial structures for at least one sampling period for eight of nine fields, the exception being La Présentation (Table 4). Significant models were observed through the season, and the R_{adj}^2 values of these models were similar for different sampling periods (first sampling period: six significant models with R_{adj}^2 values between 0.175 and 0.535; second sampling period: seven significant models with R_{adj}^2 values between 0.255 and 0.427; third sampling period: seven significant models with R_{adj}^2 values between 0.213 and 0.523) (Table 4). Significant spatial scales encompass the whole range available, from PCNM 1 (around 375 m) to PCNM 34

(around 22 m). The fields with the strongest relationships (e.g., Berthierville and Issoudun in week 1, Sainte-Madeleine in week 3) exhibited significant spatial structures across all scales (down to the finest PCNM, at a resolution of about 22 m) (Table 4).

The significant spatial models detected by the PCNM analyses in different fields and weeks are represented in Figure 6 (105–135 m long transects, with interpoint distance of 3.75 m) and Figure 7 (337.5–375 m long transects, with an interpoint distance of 7.5 m). The significant models with high (>0.400) R_{adj}^2 values provided a good fit with the data overall, in terms of both cyclicity of spatial patterns and relative magnitude of aphid

Table 3. Results of the principal coordinates of neighbour matrices (PCNM) analyses (Borcard and Legendre 2002) for the transects with an interpoint distance of 3.75 m.

Sampling period and location of field	<i>n</i>	R^2_{adj}	PCNM (m)	DP (m)
First sampling period				
Saint-Barnabé	37	0.150	14, 143	24.5
Sainte-Madeleine	37	0.295	14, 16, 19, 23	28.3
L'Assomption	37	0.310	11, 12, 98, 143	16.9
Second sampling period				
Saint-Alexis	29	0.235	24, 45, 113	48.8
Issoudun	29	0.342	17, 18, 113	17.1
Sainte-Madeleine	37	0.357	12, 15, 22, 23	16.4
Saint-Barnabé	37	0.623	12, 14, 19, 23, 31, 35, 40, 143	21.3
La Présentation	29	0.706	11, 12, 14, 15, 20, 23, 38, 113	16.2
Third sampling period				
Sainte-Madeleine	37	0.170	13, 56, 143	20.8
Saint-Denis	37	0.353	13, 15, 35	15.9
La Présentation	29	0.408	12, 14, 15	13.1
Issoudun	29	0.459	23, 31, 55	31.5

Note: *n* is the number of points in the transect and R^2_{adj} is the adjusted R^2 value of the regression model. The relationships are not depicted for the fields where no significant PCNM were detected; given the number of tests involved, *P* values >0.001 have been considered nonsignificant. PCNM is the period of the significant PCNM variables (see the text). DP is the dominant period of the models. The nine fields were sampled during 3 consecutive weeks, commencing after the proportion of plants infested with soybean aphid exceeded 15%. The initial sampling dates (day/month) were as follows: 18/07 in Saint-Alexis, Saint-Denis, and Sainte-Madeleine, 25/07 in Saint-Barnabé and La Présentation, and 01/08 in L'Assomption and Issoudun.

abundances (Figs. 6, 7). The models with low R^2_{adj} values, in contrast, were effective at detecting cycles in data but systematically underestimated peaks of aphid density (Figs. 6, 7).

To allow an assessment of spatial structures in the transects, each significant PCNM submodel (Tables 3, 4) has been characterized by its dominant period. This period is based on the number of times that the (centred) model crosses the abscissa of a graph. For instance, a function crossing the abscissa only once, starting and ending at roughly the same level, would have a period equivalent to the total length of the transect. A function crossing the abscissa 10 times has a period corresponding to about one-fifth of the length of the transect. With regard to the development of cost-effective, reliable sampling procedures, the dominant period provides a useful guideline for estimating the area that needs to be sampled in order to uncover underlying spatial patterns. Assuming a dominant period of 50 m, for example, it would not be adequate to recommend sampling plants along a 10 m long transect because this procedure would not reflect the whole range of variation of population density observed in soybean fields; conversely, sampling plants along a

200 m long transect would be time-consuming while not improving the accuracy of sampling assessments compared with a 50 m long transect. The dominant periods of the significant PCNM models are listed in Table 4. If one averages these dominant periods over two categories of transect (long and short), the average dominant structures show a period of 22.6 m in the short transects with 3.75 m resolution (range 13.1–48.8 m) and 47.1 m in the long transects with 7.5 m resolution (range 29.4–94.3 m) (Table 4). The average dominant period was shorter than 100 m in all fields-weeks, which implies that in a majority of soybean fields, sampling plants along a 100 m long transect would be sufficient to unravel the spatial trends detected in this study.

Discussion

The relationship between the mean and variance of the abundance of *A. glycines* in soybean fields, modelled using either Taylor's power law (Taylor 1961) or mean crowding index (Iwao 1968), suggests that aphid populations are spatially aggregated (Huang et al. 1992; Shi et al. 1994; Hodgson et al. 2004; Onstad et al. 2005).

Table 4. Results of the principal coordinates of neighbour matrices (PCNM) analyses (Borcard and Legendre 2002) for the transects with an interpoint distance of 7.5 m.

Sampling period and location of field	<i>n</i>	R_{adj}^2	PCNM (m)	DP (m)
First sampling period				
Sainte-Madeleine	51	0.175	30, 51, 60	40.0
Verchères	51	0.178	26, 37, 158	31.3
Saint-Alexis	51	0.205	23, 37, 51	33.4
Saint-Barnabé	51	0.250	24, 33, 39, 51, 390	41.7
Berthierville	51	0.530	23, 29, 31, 32, 35, 41, 48, 60, 77, 110, 158, 195, 390	34.3
Issoudun	46	0.535	27, 30, 37, 44, 54, 59, 88, 100, 117	48.5
Second sampling period				
Issoudun	46	0.255	29, 88, 240, 345	94.3
Saint-Barnabé	51	0.273	43, 158, 195	65.5
L'Assomption	51	0.312	22, 29, 33, 86	34.1
Verchères	51	0.331	23, 35, 39, 48, 55	29.4
Saint-Denis	47	0.336	45, 95, 111, 165, 330	69.0
Berthierville	51	0.418	22, 32, 37, 60, 77, 390	68.2
Saint-Alexis	51	0.427	25, 32, 39, 86, 129, 390	56.5
Third sampling period				
Saint-Denis	51	0.213	25, 64, 86	31.3
L'Assomption	51	0.220	46, 48, 51, 55	52.5
Saint-Alexis	51	0.351	26, 37, 39, 77, 86, 195	50.0
Saint-Barnabé	51	0.427	43, 46, 48, 51, 55, 195, 390	43.6
Berthierville	51	0.429	22, 28, 30, 55, 60, 77, 96, 110, 270	43.2
Issoudun	44	0.450	23, 26, 28, 33, 35, 37, 84, 330	32.3
Sainte-Madeleine	51	0.523	23, 31, 39, 46, 51, 60, 86, 195, 390	43.1

Note: *n* is the number of points in the transect and R_{adj}^2 is the adjusted R^2 value of the regression model. The relationships are not depicted for the fields where no significant PCNM were detected; given the number of tests involved, *P* values >0.001 have been considered nonsignificant. PCNM is the period of the significant PCNM variables (see the text). DP is the dominant period of the models. The nine fields were sampled during 3 consecutive weeks, commencing after the proportion of plants infested with soybean aphid exceeded 15%. The initial sampling dates (day/month) were as follows: 11/07 in Berthierville and Verchères, 18/07 in Saint-Alexis, Saint-Denis, and Sainte-Madeleine, 25/07 in Saint-Barnabé and La Présentation, and 01/08 in L'Assomption and Issoudun.

This conclusion ought to be interpreted carefully because the analyses do not take into account the explicit locations of sampling points (Jumars *et al.* 1977), and may therefore be inadequate to measure departure from randomness (Hurlbert 1990).

The intensive, spatially explicit sampling scheme reported in the present study (>135 plants sampled per field each week for several fields and time periods in both 2005 and 2006, a total of 32 412 plants) allows quantification of the spatial distribution of *A. glycines* populations. The two complementary approaches used to characterize spatial dependence (variograms and PCNM analysis) differed in their sensitivity for detecting spatial patterns, although both revealed the occurrence of discernible structures

in some but not all locations and time periods (Tables 2–4). Within the context of surveying soybean aphid populations for the purpose of making pest-management decisions, sampling plants along 100 m long transects in soybean fields would take into account the spatial patterns identified in the present study.

Differential sensitivity of variograms and PCNM analyses

The length of the short transects sampled in 2006 was identical with that of the experimental grids (105–135 m; grids A and B in Figure 1), which allowed comparison of the results of variograms with those of PCNM analyses. Overall, PCNM analysis was more sensitive at detecting significant spatial patterns (44.4% (12 of 27)

Fig. 5. Decomposition of principal coordinates of neighbour matrices (PCNM) models. Spatial model A represents Sainte-Madeleine; a long transect with an interpoint distance of 7.5 m, sampled 01/08; broad scale 86–390 m, medium scale 39–60 m, and fine scale 23–31 m. Corresponds to plot C in Figure 7. Spatial model B represents Saint-Barnabé; a short transect with an interpoint distance of 3.75 m, sampled 01/08; broad scale 143 m, medium scale 19–40 m, and fine scale 12–14 m. Corresponds to Plot B in Figure 6.

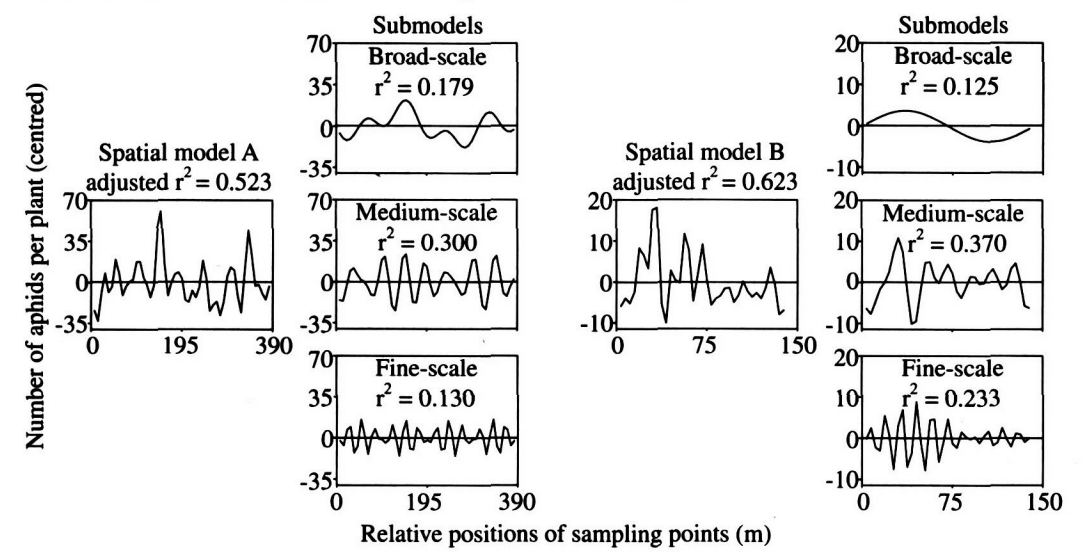


Fig. 6. Abundance of soybean aphids (*Aphis glycines*) per soybean (*Glycine max*) plant along a transect with an interpoint distance of 3.75 m. The upper plots show the data obtained in the various fields and time periods. The lower plots show the data modelled with the principal coordinates of neighbour matrices (PCNM) analyses (summarized in Table 3). For the different fields and time periods ($t = 1-3$; Table 3), the same y scale was used for the upper and lower plots, allowing a visual comparison of the amplitude of variation in abundance of aphids from the raw data with the predictions based on PCNM analyses. The plots are sorted from left to right in the different columns in decreasing R^2 values of the PCNM analyses; the values in the lower plots are the adjusted R^2 values. (A) La Présentation, $t = 2$, $y = 40$. (B) Saint-Barnabé, $t = 2$, $y = 40$. (C) Issoudun, $t = 3$, $y = 50$. (D) La Présentation, $t = 3$, $y = 30$. (E) Sainte-Madeleine, $t = 2$, $y = 70$. (F) Saint-Denis, $t = 3$, $y = 16$. (G) Issoudun, $t = 2$, $y = 16$. (H) L'Assomption, $t = 1$, $y = 6$. (I) Sainte-Madeleine, $t = 1$, $y = 36$. (J) Sainte-Madeleine, $t = 3$, $y = 100$.

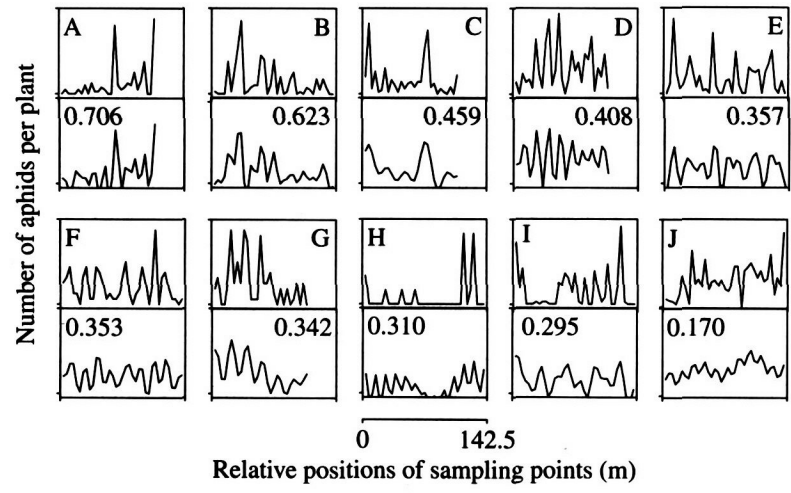
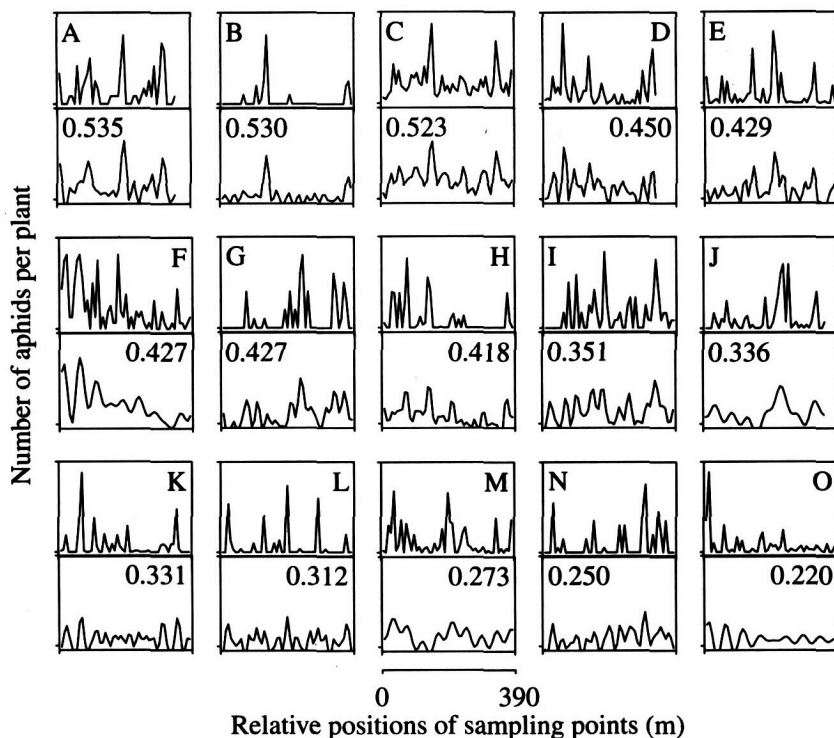


Fig. 7. Abundance of soybean aphids (*Aphis glycines*) per soybean (*Glycine max*) plant along a transect with an interpoint distance of 7.5 m. The upper plots show the data obtained in the various fields and time periods. The lower plots show the data modelled with the principal coordinates of neighbour matrices (PCNM) analyses (summarized in Table 4). For the different fields and time periods ($t = 1-3$; Table 4), the same y scale was used for the upper and lower plots, allowing a visual comparison of the amplitude of variation in abundance of aphids from the raw data with the predictions based on PCNM analyses. The plots are sorted from left to right in the different columns in decreasing R^2 values of the PCNM analyses; the values in the lower plots are the adjusted R^2 values. (A) Issoudun, $t = 1$, $y = 12$. (B) Berthierville, $t = 1$, $y = 20$. (C) Sainte-Madeleine, $t = 3$, $y = 150$. (D) Issoudun, $t = 3$, $y = 50$. (E) Berthierville, $t = 3$, $y = 120$. (F) Saint-Barnabé, $t = 3$, $y = 16$. (G) Saint-Alexis, $t = 2$, $y = 10$. (H) Berthierville, $t = 2$, $y = 100$. (I) Saint-Alexis, $t = 3$, $y = 12$. (J) Saint-Denis, $t = 2$, $y = 30$. (K) Verchères, $t = 2$, $y = 80$. (L) L'Assomption, $t = 2$, $y = 30$. (M) Saint-Barnabé, $t = 2$, $y = 50$. (N) Saint-Barnabé, $t = 1$, $y = 20$. (O) L'Assomption, $t = 3$, $y = 120$.



of short transects; Table 3) than variograms (11.4% (9 of 79) of fields-weeks; Table 2). The differential sensitivity of variograms and PCNM analyses may have several causes.

Variograms and PCNM analyses are based on different methodologies. PCNM analyses model the spatial structures at various scales by fitting a combination of functions of different periods to the data, in much the same way as spectral analysis does. This approach is effective at detecting spatial patterns across a broad range of spatial scales (Borcard *et al.* 2004). In contrast, variograms quantify the variability in abundance of soybean aphids as a function of the distance between plants (Liebhold *et al.* 1993), a relationship that is often characterized by a

rapidly increasing variance up to a distance corresponding to the range of spatial dependence (down to minimum of about 1.5 interpoint distance); the variance for distances beyond the range is constant and spatially independent (Table 2, Fig. 4A; see also Ellsberry *et al.* 1998; Schotzko and Quisenberry 1999).

The rectangular or square grids used in the present study (Fig. 1) may have been suboptimal for geostatistical analysis; for example, it is possible that hexagonal grids would have been more effective at detecting spatial dependence.

PCNM analyses are based on unidimensional transects along soybean rows, whereas the variograms were computed using omnidirectional comparison of population density

across two dimensions. The directionality of spatial dependence may therefore explain the differential sensitivity of PCNM and variograms. However, unidirectional variograms did not reveal a higher level of spatial structure within or across soybean rows.

Soybean plants are most susceptible to feeding damage by *A. glycines* before the initiation of seedpod formation (Rhainds *et al.* 2007). Variograms and PCNM analyses conducted early in the season, when soybean plants were at the vegetative stage, were characterized by a low density of *A. glycines*. The high incidence of zero values (plants not infested with *A. glycines*) may have reduced the sensitivity of variograms.

In short, a variety of factors may explain the differential sensitivity of variograms and PCNM, and it seems likely that the difference in sensitivity resulted at least in part from their distinct methodologies. Variograms and PCNM analyses appear more effective at detecting short-range spatial dependence and broad-scale patterns, respectively. This shows that the two methods are complementary when a detailed assessment of spatial structures is needed.

Variation in spatial dependence over time

Variograms characterizing the spatial distribution of *A. glycines* exhibited either a structured (spherical models; Fig. 4A) or a random distribution ("pure nugget effect"; Fig. 4B). A structured distribution in the different fields and time periods was more prevalent in 2005 than in 2006 (Table 2). The frequent occurrence of structured distribution during the last 2 weeks in 2005 coincided with the peak population of soybean aphids and the late-season decline in density (Fig. 2). In contrast, the spatial distribution of soybean aphids lacked a discernible pattern in a majority of the fields in 2006 (Table 2), a year during which the density of aphids remained relatively low throughout the season (Fig. 2). These results suggest that spatially dependent ecological processes related to the regulation of dense aphid populations (top-down or bottom-up effects) may be responsible for the structured distributions observed during the last 2 weeks of 2005, a hypothesis worth exploring. (i) The quality of soybean as a food source for *A. glycines* declines with plant age (van den Berg *et al.* 1997; but see Rutledge and O'Neil 2006); spatial gradients that affect plant attributes late in the season (e.g., water stress; Irmak *et al.* 2002) may have a particularly detrimental effect on the performance of aphids on

crowded plants. (ii) The aggregation of generalist predators to dense colonies of soybean aphids results in suppression of aphid populations late in the season (Rutledge *et al.* 2004; Desneux *et al.* 2006; Costamagna and Landis 2007; Rhainds *et al.* 2007); the impact of predators on the local abundance of soybean aphids may be complex because patterns of distribution of predators and their prey often do not coincide spatially (Park and Obrycki 2004; Pearce and Zalucki 2006).

Edge effects have been documented in some species of aphids, with plants near the edge of fields supporting a higher population density than plants in the interior of fields (Schotzko and Quisenberry 1999; Winder *et al.* 1999; Jones 2005), although in some cases the effect is relatively small and inconsistent from year to year (Kabaluk *et al.* 2006). For *A. glycines*, however, migrant adults do not seem to preferentially colonize plants near the edge of soybean fields (Hodgson *et al.* 2005), and population density on a given plant seems to be independent of the distance between the plant and the edge of the field (Onstad *et al.* 2005). These results strongly suggest a lack of edge effect for populations of *A. glycines* in soybean fields.

PCNM analyses of the short transects (105–135 m, with an interpoint distance of 3.75 m) indicated fewer significant spatial structures (each with a low R_{adj}^2 value) during the first week of sampling than later in the season (Table 3). The weak level of spatial structure early in the season may be attributed to the "random" pattern of oviposition of winged females that deposit a few nymphs on a given plant, then disperse some distance away to another plant to reproduce further (Ragsdale *et al.* 2004). The highest occurrence and intensity (measured as the R_{adj}^2 value) of significant spatial patterns during the following 2 weeks, when the proportion of infested plants increased steadily, may be attributed to the dispersal of apterous aphids to plants surrounding the ones on which their mother larviposited.

Patterns of spatial distribution and development of sampling designs

Understanding patterns of spatial distribution of arthropod pests has practical implications for implementing reliable sampling procedures. With regard to variograms, for example, maintaining a distance between sampling points greater than the range of spatial dependence is

often recommended, in order to obtain spatially independent samples (Midgarden *et al.* 1993; Park and Tollefson 2005; Bacca *et al.* 2006). Intensive sampling of several fields of soybean repeatedly over time in 2005 and 2006 allowed us to explore the consequences of spatial distribution of *A. glycines* in terms of sampling methodology. Despite the intensive sampling effort in the present study, the largest scale tested was approximately 400 m in the fields with long transects or with multiple experimental plots. It is therefore important to emphasize that our results cannot be extrapolated to fields exceeding approximately 16 ha (400 m \times 400 m) if strong spatial trends exist beyond the scales evaluated in the present study. Because of the practical constraints related to intensive sampling of very large fields in their entirety, it may be difficult (if not impossible) to detect such broad trends.

Variograms did not reveal discernible spatial patterns for a majority of fields-weeks (135 of 161 fields-weeks, or 84%; Table 2, Fig. 4B). A random distribution of soybean aphids would imply that spatially independent estimates of aphid density can be obtained irrespective of the location of sampling points. Because the minimal distance between plants was set at 7.5 m in this study (Fig. 1), inferences cannot be made for smaller distances, and recommendations can only be made on the basis of sampling points that are at least 7.5 m apart.

PCNM analysis provided a useful tool for determining the area of a soybean field that needs to be sampled in order to detect spatial patterns of *A. glycines* populations and the associated range of variation of population density. PCNM analysis of the long transects revealed significant patterns for a majority of the fields-weeks (20 of 27, or 74.1%), and spatial dependence was observed across a wide range of scales from 20 m to several hundred metres (Table 4, Fig. 5), which implies that large portions of the soybean fields should be sampled. The dominant periods of the long transects in different fields-weeks were consistently below 100 m (Table 4), however, which suggests that sampling plants along 100 m long transects at about 7.5 m intervals would be sufficient to detect the spatial patterns identified in the present study.

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