

Available online at www.sciencedirect.com



Biological Control 31 (2004) 210-217

Biological Control

www.elsevier.com/locate/ybcon

Spatio-temporal distribution of corn leaf Aphids (Homoptera: Aphididae) and lady beetles (Coleoptera: Coccinellidae) in Iowa cornfields

Yong-Lak Park *, John J. Obrycki

Department of Entomology, Iowa State University, Ames, IA 50011, USA Received 6 January 2004; accepted 18 June 2004

Abstract

Prey-predator interactions are spatially and temporally dynamic and influenced by environmental factors. Field studies were conducted to investigate the dynamics of spatio-temporal interactions among corn leaf aphids, lady beetles, and environmental factors in cornfields by mapping and comparing their distributions. Lady beetle species in this study included *Harmonia axyridis* Pallas, *Coleomegilla maculata* (DeGeer), and *Coccinella septempunctata* L. A global positioning system, geostatistics, and a geographic information system (GIS) were used to locate sample points, characterize distribution patterns, and map the distributions of corn leaf aphids, lady beetles, and environmental factors. Geostatistical analysis showed that both corn leaf aphid and lady beetle populations were aggregated during the peak population period and randomly distributed early and late in the season. Map-correlation analysis, however, showed that the distribution of lady beetles did not always coincide with that of corn leaf aphids. The results also showed that none of the environmental factors we sampled were significantly correlated with corn leaf aphid and lady beetle distributions. This study documents the dynamic relationships in time and space between lady beetles and corn leaf aphids.

Keywords: Harmonia axyridis; Coleomegilla maculata; Coccinella septempunctata; Rhopalosiphum maidis; Prey-predator interaction; Global positioning system; Geostatistics; Geographic information system

1. Introduction

The corn leaf aphid, *Rhopalosiphum maidis* (Fitch), is an occasional pest of field corn; typically its population remains at low levels except during infrequent population outbreaks (Foott, 1977; Wagner and Ruesink, 1982). Corn leaf aphids commonly feed in the whorls of corn plants and move down the plant feeding on leaves, the stalk, and ear after tassel emergence (Foott, 1977). Lady beetle species commonly found in cornfields are *Coleomegilla maculata* (DeGeer), *Hippodamia convergens* Guerin-Meneville, Hippodamia tredecimpunctata (Say), and Coccinella septempunctata L. (Coderre, 1988; Ewert and Chiang, 1966; Foott, 1973; Wagner and Ruesink, 1982). Recently, Harmonia axyridis Pallas was introduced into the Corn Belt (Wheeler and Stoops, 1996) and is now commonly found in Iowa. Although aphids are the main food sources of lady beetles, alternative food sources are frequently available in cornfields. For example, H. tredecimpunctata, C. septempunctata, and C. maculata are known to feed on pollen (Hodek and Honek, 1996). C. maculata can complete development on corn pollen without aphids (Smith, 1960, 1961) and feeds on eggs of corn earworm and European corn borers (Coll and Botrell, 1991). H. axyridis also can feed European corn borer eggs but larvae do not complete development on this prey (Musser and Shelton, 2003).

^{*} Corresponding author. Present address: Department of Entomology, University of California, Riverside, CA 92521, USA. Fax: 1-951-787-3086.

E-mail address: yonglak@ucr.edu (Y.-L. Park).

^{1049-9644/\$ -} see front matter @ 2004 Elsevier Inc. All rights reserved. doi:10.1016/j.biocontrol.2004.06.008

Aphid-lady beetle interactions are not static but spatially and temporally dynamic. Although many studies on the population dynamics of aphids and lady beetles have explained field interactions (Dreistadt and Flint, 1996; Grez and Prado, 2000; Wells and McPherson, 1999; Wright and Laing, 1980) most studies have focused solely on temporal synchrony of aphids and lady beetles, assuming they were spatially coincident. Foott (1973) and Coderre (1988), however, asserted that lady beetles might not be capable of controlling corn leaf aphid populations effectively due to a lack of temporal synchrony. Wagner and Ruesink (1982) found that lady beetles might be temporally coincident with corn leaf aphids but spatially not coincident on the plant; corn leaf aphids and H. convergens were located primarily on the upper part of plant and C. maculata distribution was almost exclusively limited to the lower part of plant. Field cage studies (Hoogendoorn and Heimpel, 2004; Schellhorn and Andow, 1999) also showed that C. maculata larvae were mainly present on the lower or middle parts of the plants, while corn leaf aphids and larvae of Adalia bipunctata and H. axyridis were present on the upper parts of the plants. These studies suggest that lady beetles can effectively reduce corn leaf aphid populations only when they coincide spatially and temporally.

One way to investigate the spatio-temporal synchrony of predator and prey distributions is to generate and compare distribution maps in temporal sequences. Mapping the distribution of prey and predator populations on a within-field basis has not been applied in biological control until recently, due to the lack of appropriate technology. Currently available technology, such as global positioning systems, geostatistics, and geographic information systems, allow one to characterize, analyze, and map insect distributions. Mapping predator-prey distributions provides the basis to compare distributions and to investigate the influence of environmental factors.

This study was conducted to investigate the dynamics of spatio-temporal interactions among corn leaf aphids,

lady beetles, and environmental factors in cornfields by mapping and comparing their distribution maps. The objectives of this study were (1) to determine and characterize the distribution patterns of corn leaf aphids and lady beetles, (2) to investigate the spatio-temporal synchrony of corn leaf aphids and lady beetles, and (3) to investigate the influence of selected environmental factors on the spatial interactions between corn leaf aphids and lady beetles.

2. Materials and methods

Experiments were conducted in two fields of corn planted after corn (continuous cornfields) in central Iowa. Because distribution patterns are often dependent upon the spatial scale, experiments were conducted at two spatial scales. A grid-sampling plan was used to characterize distributions and to generate distribution maps.

2.1. Grid layout

A large-scale experiment was conducted in an 8-ha cornfield in Ankeny (Polk County), Iowa in 2002. A hexagonal-grid-sampling plan was used as it provides the best assessment of spatial structure (Schotzko and O'Keeffe, 1990). The distance between any two adjacent sample points was 25m and 97 sample points were assigned in the cornfield (Fig. 1A). The grid was laid out in the field using the differentially corrected global positioning system (DGPS; Trimble, Sunnyvale, CA). At each sample point, 10 subsample points (i.e., 10 consecutive plants) were assigned. A small-scale experiment was conducted in a $50 \text{ m} \times 50 \text{ m}$ cornfield in Ames (Story County), Iowa in 2002. Inside the $50 \text{ m} \times 50 \text{ m}$ area, 49 sample points were laid out in the field using a DGPS, four subsample points (i.e., four consecutive plants) were added at each grid point (Fig. 1B). A total of 970 and 196 subsample points were assigned for the largeand small-scale studies, respectively.



Fig. 1. Grid layout for large- (A) and small-scale (B) studies. Grids were laid out in the fields with the global positioning system. Ten and four subsample points were assigned at each sample point in large- and small-scale studies, respectively.

2.2. Sampling lady beetles and corn leaf aphids

At each subsample point (i.e., one plant), lady beetle larvae and adults on each plant were counted; subsample values were averaged to estimate the sample value at each sample point. For aphid sampling, a binomial sampling plan (e.g., checking the presence or absence of aphids) was used because the total number of aphids on a plant cannot be accurately counted without destructive sampling, especially when aphids feed in the whorl of corn plants early in the season. Destructive sampling was not applicable to this study because each plant was examined for aphids at each subsample point every week to monitor the changes in aphid densities at each sample point. The presence or absence of aphids on tassels and leaves were checked at each subsample point. Aphid density at each sample point was expressed as the percentage of plants infested with aphids from subsample points. Lady beetle and corn leaf aphid samplings were done weekly from early June to late August.

2.3. Sampling environmental factors

At each subsample point, corn growth stage was determined and plant height was measured weekly. Soil moisture was measured weekly with a HydroSense (Decagon, Pullman, WA) by averaging the values from probing 10 locations within an area of a 1.5-m-radius circle at each sample points. The area within a 1.5-m-radius circle was equivalent to the horizontal resolution of the DGPS we used. Elevation was measured using the DGPS, and the slope and aspect at each sample point were calculated from elevation data with the geographic information system (ArcGIS 8.1, Environmental System Research Institute, San Diego, CA).

2.4. Characterizing and mapping the distributions

Geostatistics was used to characterize and map the distributions of corn leaf aphids, lady beetles, and environmental factors. Geostatistics is a set of procedures that analyzes spatial dependence by using the spatial variation in direction and distance between samples (i.e., variogram modeling) and predicts spatial phenomena at unsampled locations (i.e., kriging). Spatial dependence or spatial correlation means that two sample values that are close to one another tend to be more similar than two values farther apart (Issaks and Srivastava, 1989; Williams et al., 1992). Such spatial dependence can be quantified with semivariograms that also can characterize and determine distribution patterns such as uniformity, randomness, aggregation, and spatial drift or spatial trend. A semivariogram is a graph of the spatial dependence and plots 1/2 the squared difference of a sample pair (i.e., semivariance) against the distance between two points (Davis, 1994). functions Semivariogram can be defined as $\gamma(h) = \frac{1}{2n(h)} \sum [Z(x_i) - Z(x_{i+h})]^2$, where $\gamma(h)$ is one half of the variance of two sampled values at the sample distance h, $Z(x_i)$ is the measured sample value at sample point x_i , $Z(x_{i+h})$ is the sample value at x_{i+h} , and n(h) is the total number of sample pairs for any separation distance (h). The parameters of the semivariogram include the range, sill, and nugget. The range is the distance at which the semivariogram reaches a maximum; range is the lag distance beyond which samples are spatially independent. The sill is the value of the semivariance at any distance greater than or equal to the range. The nugget is the value of the semivariogram when lag distance equals zero. The nugget is composed of experimental errors (i.e., sampling variation) and microscale variation (Cressie, 1993). For uniform and random data the average variance between values does not change with distance, and thus the semivariogram appears nearly horizontal and shows no spatial dependence (i.e., "nugget" model). The aggregated pattern produces a semivariogram that is parabolic in shape because aggregated distributions exhibit spatial dependence (Schotzko and O'Keeffe, 1989; Williams et al., 1992). Spatial trend or drift can be viewed as a pattern of which aggregation size is larger than the sampling space, and thus the semivariogram appears linear but non-horizontal. Overviews of geostatistics are well presented in Issaks and Srivastava (1989), Rossi et al. (1992), and Liebhold et al. (1993).

Semivariograms were generated using GS+ 5.3 (Gammadesign, Plainwell, MI) to characterize distribution patterns. If the number of sample pairs at a certain lag distance was less than 30, the semivariogram value for that lag distance was excluded in semivariogram modeling (Journel and Huijbregts, 1978). Distribution maps were generated with ordinary kriging by using semivariogram parameters and then, cross-validation was conducted to check the performance of semivariogram models in kriging. In a cross-validation process, values were predicted at each sampled location, assuming that a particular sample was missing (Cressie, 1993) and then, the predicted values and the true values were compared. The least squared difference between these two values, i.e., crossvalidated residuals, was used to choose the best surface maps. GS+ 5.3 was used for kriging and cross-validation.

2.5. Map-correlation analysis

The similarity between maps was checked with mapcorrelation analysis. Map-correlation coefficients were calculated based on sample-to-sample correlations by using Pearson's correlation equation (SAS Institute, 1999). High positive correlation between two distribution maps, i.e., correlation coefficients approach 1, assures the distribution maps are more likely to be similar. High negative correlations, i.e., correlation coefficients approach -1, indicate the map-surface patterns on two distribution maps are inversely related.

3. Results

Three species of lady beetles, *C. septempunctata*, *C. maculata*, and *H. axyridis*, were found in the cornfields in this study. Ratios of *C. septempunctata* to *C. maculata* to *H. axyridis* were approximately 1:1:8 in the large-scale study and 1:2:6 in the small-scale study. We pooled all lady beetle data across stages and species because no spatial structures in the beetle distributions were detected due to very low beetle densities when we separately analyzed stage-specific and species-specific data.

3.1. Characterization of distribution patterns

In the large-scale study, semivariograms showed that the spherical, Gaussian, or exponential models provided the best fit for corn leaf aphid and lady beetle distributions during peak population periods and the nugget model provided the best fit early and late in the season (Table 1). This indicates both aphids and lady beetle populations were aggregated during the peak population period and random early and late in the season. In the small-scale study, the spherical, exponential, or Gaussian models fit corn leaf aphid and lady beetle distributions the best during peak population periods, indicating they were aggregated at the peak populations (Table 2).

3.2. Spatio-temporal synchrony of corn leaf aphids and lady beetles

In the large-scale study, both corn leaf aphid and lady beetle populations peaked in late July and their population dynamics seemed to be synchronized throughout the season (Fig. 2). Their distribution maps, however, showed that lady beetles and corn leaf aphids did not always coincide well in space (Fig. 3). Correlations between corn leaf aphids and lady beetles were significant (n = 97; P < 0.05) but their spatial coincidence was dynamic (r = 0.55 on July 8th, r = 0.18on July 15th, r = 0.16 on July 23rd, and r = 0.22 on July 29th). In the small-scale study, corn leaf aphid and lady beetle populations peaked in mid July but both populations fluctuated throughout the season (Fig. 4). Distribution maps also showed the dynamic relationships in lady beetles and corn leaf aphid distributions (Fig. 5). Correlations between corn leaf aphids and lady beetles were r = 0.80 on July 7th, r = 0.60 on July 14th, r = 0.49 on July 21st, and r = 0.18 on July 28th, also indicating the dynamics of the spatio-temporal coincidence.

3.3. Effects of environmental factors on corn leaf aphid and lady beetle distributions

Correlation analysis showed that corn leaf aphid and lady beetle distributions were not significantly correlated (n = 97 and 49 for the large- and small-scale study, respectively; P > 0.05) with any environmental factors, including elevation, slope, aspect, soil moisture, plant height, or plant growth stage.

4. Discussion

Although lady beetles are major aphid predators in cornfields (Coderre, 1988) previous studies (Coderre, 1988; Ewert and Chiang, 1966; Foott, 1973; Wagner and Ruesink, 1982) speculated that lady beetles might

Table 1

Best-fit semivariogram models and parameters (nugget, C_0 ; sill, C_s ; range, a) for spatial distributions of corn leaf aphids and lady beetles at each sample date in the large-scale study

Insect	Parameter	Date											
		6/14	6/20	6/26	7/2	7/8	7/15	7/23	7/29	8/5	8/13	8/19	
Corn leaf aphid	Model	a	_			Nugget ^b	Spher. ^c	Gauss. ^d	Nugget	Nugget		_	
	C_0	_	_			22.9	0.1	220.7	24.1	24.1			
	$C_{\rm S}$	_	_	_		22.9	33.6	118.3	24.1	24.1	_	_	
	<i>a</i> (m)	_	_	_			19.3	18.5			_	_	
	r^2	—		—	—	0.08	0.64	0.47	0.60	0.60		—	
Lady beetles	Model	Nugget	Nugget		_	Nugget	Expon. ^e	Spher.	Nugget			Nugget	
	C_0	0.056	0.012	_		0.005	0.001	0.001	0.003	_	_	0.006	
	$C_{\rm S}$	0.056	0.012	_		0.005	0.008	0.024	0.003	_	_	0.006	
	<i>a</i> (m)						18.1	57.7		_			
	r^2	0.60	0.69		_	0.58	0.93	0.94	0.05	_		0.06	

^a No insects were found at all sample points.

^b Nugget model, $\gamma(h) = C_0 = C_S$.

^c Spherical model, $\gamma(h) = C_0 + (C_S - C_0) \times [1.5 \times (h/a) - 0.5 \times (h/a)^3].$

^d Gaussian model, $\gamma(h) = C_0 + (C_S - C_0) \times [1 - \exp(-h^2/a^2)].$

^e Exponential model, $\gamma(h) = C_0 + (C_S - C_0) \times [1 - \exp(-h/a)].$

Table 2

Best-fit semivariogram models and parameters (nugget, C_0 ; sill, C_s ; range, a) for spatial distributions of corn leaf aphids and lady beetles at each sample date in the small-scale study

Insect	Parameters	Date											
		6/12	6/18	6/24	7/1	7/7	7/14	7/21	7/28	8/4	8/12	8/18	
Corn leaf aphid	Model	a	_	Nugget ^b	Linear ^c	Expon. ^d	Spher. ^e	Gauss. ^f	Linear	_	_	_	
	C_0			22.0	32.2	0.6	0.1	137.0	145.0			_	
	$C_{\rm S}$			22.0		41.7	67.8	584.9				_	
	<i>a</i> (m)					8.9	11.8	48.4					
	r^2		—	< 0.01	0.64	0.82	0.79	0.89	< 0.01		—	—	
Lady beetles	Model	Nugget	Spher.	_		Spher.	Spher.	Linear	Nugget	Nugget		Nugget	
	C_0	0.015	< 0.001		_	0.001	0.010	0.010	0.012	0.012		0.004	
	$C_{\rm S}$	0.015	0.013		_	0.022	0.020	0.013	0.012	0.012		0.004	
	<i>a</i> (m)		15.6		_	11.5	13.1					_	
	r^2	0.08	0.78	_		0.64	0.35	0.38	0.07	0.13	_	0.39	

^a No insects were found at all sample points.

^b Nugget model, $\gamma(h) = C_0 = C_s$.

^c Linear model, $\gamma(h) = C_0 + h \times [(C_S - C_0)/a]$.

^d Exponential model, $\gamma(h) = C_0 + (C_S - C_0) \times [1 - \exp(-h/a)].$

^e Spherical model, $\gamma(h) = C_0 + (C_S - C_0) \times [1.5 \times (h/a) - 0.5 \times (h/a)^3]$.

^f Gaussian model, $\gamma(h) = C_0 + (C_S - C_0) \times [1 - \exp(-h^2/a^2)].$



Fig. 2. Population dynamics of corn leaf aphids and lady beetles in the large-scale study. Arrow indicates week of peak corn anthesis.

not successfully reduce corn leaf aphid densities in cornfields. Foott (1973) and Coderre (1988) pointed out the lack of temporal synchrony of lady beetles and aphids and Wagner and Ruesink (1982) reported that lady beetle populations did not lag behind corn leaf aphid populations throughout the season. Our results showed that temporal synchrony between lady beetles and aphids existed on a large scale (Fig. 2) but this synchrony was not obvious at a small scale (Fig. 4). Our study also showed that distribution patterns of lady beetles and corn leaf aphids might be similar throughout the season (Table 2), but their spatial coincidence was dynamic throughout the growing season (Figs. 3 and 5).

Lady beetles can effectively reduce corn leaf aphids only when lady beetles and corn leaf aphids are coincident spatially and temporally. However, inaccessibility of corn leaf aphids to lady beetles reduces the probability of spatio-temporal synchrony between corn leaf aphids and lady beetles. Corn leaf aphids commonly feed in the whorls of corn plants (Foott, 1977) and this behavior prevents lady beetles from finding corn leaf aphids early in the season. Coderre and Tourneur (1986) asserted that 80% of the aphid population was inaccessible to predators because aphids were hidden and protected under the spathes of the corn ears. Vertical distribution of aphids also reduces accessibility of lady beetles to corn leaf aphids. Wagner and Ruesink (1982) found that corn leaf aphids are located mostly on the upper parts of the plants while C. maculata, a major lady beetle species found in cornfields, is located mainly on the lower parts of corn plants. Field cage studies (Hoogendoorn and Heimpel, 2004; Schellhorn and Andow, 1999) also showed that C. maculata larvae were mainly present on the lower or middle parts of the plants, while corn leaf aphids and larvae of A. bipunctata and H. axyridis were present on the upper parts of the plants. Such a within-plant segregation of lady beetles is possibly due to their ovipositional behavior (Schellhorn and Andow, 1999) or competitive interactions between lady beetles (Hoogendoorn and Heimpel, 2004).

Availability of alternative food sources in the cornfields also reduces the probability of spatial synchrony of lady beetles and corn leaf aphids. For example, *C. maculata* feeds on corn pollen and eggs of European corn borers and corn earworms (Smith, 1960, 1961). Predator–prey relationships may also be dependent upon environmental factors such as agronomic, edaphic, and geographic factors. These factors have the potential to cause imperfect spatio-temporal synchrony of corn leaf aphids and lady beetles. Our correlation analysis,



Fig. 3. Distribution maps of corn leaf aphids and lady beetles during the peak population periods in the large-scale study. *Y* Axis for corn leaf aphids indicates the percent of plants infested with aphids and *Y* axis for lady beetles indicates the number of lady beetles per plants.



Fig. 4. Population dynamics of corn leaf aphids and lady beetles in the small-scale study. Arrow indicates week of peak corn anthesis.

however, showed that none of the environmental factors we measured significantly (P > 0.05) correlated with corn leaf aphids and lady beetles.

This study implies that temporal synchrony of pests and natural enemies may not assure that spatial overlap occurs in the field throughout the growing season. The spatio-temporal synchrony of predators and prey is important for biological control. The success of biological control is more likely with the spatio-temporal overlap of prey and predators; therefore distributions of pests and natural enemies need to be considered in biological control. The knowledge of the spatio-temporal dynamics of prey and predator distributions can potentially provide valuable information on when and where to release or conserve natural enemies.



Fig. 5. Distribution maps of corn leaf aphids and lady beetles during the peak population periods in the small-scale study. *Y* Axis for corn leaf aphids indicates the percent of plants infested with aphids and *Y* axis for lady beetles indicates the number of lady beetles per plants.

Acknowledgments

We thank Wayne King and Kent Berns for managing cornfields and Dr. Jon Tollefson at Iowa State University for providing the global positioning system. Special thanks to the editor, two anonymous reviewers, and Dr. Rayda Krell at University of California, Riverside for their helpful suggestions and comments on the manuscript.

References

Coderre, D., 1988. Effectiveness of aphidophagous insects in maize. In: Hiemczyk, E., Dixon, A.F.G. (Eds.), Ecology and Effectiveness of Aphidophaga. SPB Academic Publishing, The Hague, The Netherlands, pp. 211–214.

- Coderre, D., Tourneur, J.C., 1986. Vertical distribution of aphids and aphidophagous insects on maize. In: Hodek, I. (Ed.), Ecology Aphidophaga II. Academia, Prague, pp. 291–296.
- Coll, M., Botrell, D., 1991. Microhabitat and resource selection of the European corn borer (Lepidoptera: Pyralidae) and its natural enemies in Maryland field corn. Environ. Entomol. 20, 526–533.
- Cressie, N.A.C., 1993. Statistics for Spatial Data, Revised Edition. Wiley, New York.
- Davis, P.M., 1994. Statistics for describing populations. In: Pedigo, L.P., Buntin, G.D. (Eds.), Handbook of Sampling Methods for Arthropods in Agriculture. CRC Press, Boca Raton, FL, pp. 33– 54.
- Dreistadt, S.H., Flint, M.L., 1996. Melon aphid (Homoptera: Aphididae) control by inundative convergent lady beetle (Coleoptera: Coccinellidae) release on chrysanthemum. Environ. Entomol. 25, 688–697.

- Ewert, M.A., Chiang, H.C., 1966. Effects of some environmental factors on the distribution of three Coccinellidae in their microhabitat. In: Hodek, I. (Ed.), Ecology of Aphidophagous Insects. Academia Prague, Liblice, Czech Republic, pp. 195–219.
- Foott, W.H., 1973. Observations on Coccinellidae in corn fields in Essex County. Ontario. Proc. Entomol. Soc. Ont. 104, 16–21.
- Foott, W.H., 1977. Biology of the corn leaf aphid, *Rhopalosiphum maidis* (Homoptera: Aphididae), in southwestern Ontario. Can. Entomol. 109, 1129–1135.
- Grez, A.A., Prado, E., 2000. Effect of plant patch shape and surrounding vegetation on the dynamics of predatory coccinellids and their prey *Brevicoryne brassicae* (Hemiptera: Aphididae). Environ. Entomol. 29, 1244–1250.
- Hodek, I., Honek, A., 1996. Ecology of Coccinellidae. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Hoogendoorn, M., Heimpel, G.E., 2004. Competitive interactions between an exotic and a native lady beetle: a field cage study. Entomol. Exp. Appl. 111, 19–28.
- Issaks, E.H., Srivastava, R.M., 1989. An Introduction to Applied Geostatistics. Oxford University Press, New York, NY.
- Journel, A.G., Huijbregts, C.J., 1978. Mining Geostatistics. Academic Press, New York, NY.
- Musser, F.R., Shelton, A.M., 2003. Predation of Ostrinia nubilalis (Lepidoptera: Crambidae) eggs in sweet corn by generalist predators and the impact of alternative foods. Environ. Entomol. 32, 1131–1138.
- Liebhold, A.M., Rossi, R.E., Kemp, W.P., 1993. Geostatistics and geographic information systems in applied insect ecology. Annu. Rev. Entomol. 38, 303–327.
- Rossi, R.E., Mulla, D.J., Journel, A.G., Franz, E.H., 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62, 277–314.
- SAS Institute, 1999. SAS OnlineDoc, Version 8, SAS Institute Inc., Cary, NC.

- Schellhorn, N.A., Andow, D.A., 1999. Mortality of coccinellid (Coleoptera: Coccinellidae) larvae and pupae when prey become scarce. Environ. Entomol. 28, 1092–1100.
- Schotzko, D.J., O'Keeffe, L.E., 1989. Geostatistical description of the spatial distribution of *Lygus hesperus* (Heteroptera: Miridae) in Lentiles. J. Econ. Entomol. 82, 1277–1288.
- Schotzko, D.J., O'Keeffe, L.E., 1990. Effect of sample placement on the geostatistical analysis of the spatial distribution of *Lygus hesperus* (Heteroptera: Miridae) in lentils. J. Econ. Entomol. 83, 1888–1900.
- Smith, B.C., 1960. A technique for rearing coccinellid beetles on dry foods and influence of various pollens on the development of *Coleomegilla maculata lengi* Timberlake (Coleoptera: Coccinellidae). Can. J. Zool. 38, 1047–1049.
- Smith, B.C., 1961. Results of rearing some coccinellid (Coleoptera: Coccinellidae) larvae on various pollens. Proc. Entomol. Soc. Ont. 91, 270–271.
- Wagner, S.W., Ruesink, W.G., 1982. The distribution of natural enemies of the corn leaf aphid (Homoptera: Aphididae) on field corn. Great Lakes Entomol. 15, 153–157.
- Wells, M.L., McPherson, R.M., 1999. Population dynamics of three coccinellids in flue-cured tobacco and functional response of *Hippodamia convergens* (Coleoptera: Coccinellidae) feeding on tobacco aphids (Homoptera: Aphididae). Environ. Entomol. 28, 768–773.
- Wheeler, A.G., Stoops, C.A., 1996. Status and spread of Palearctic lady beetles *Hippodamia variegata* and *Propylea quatuordecimpunctata* (Coleoptera: Coccinellidae) in PA, 1993–1995. Entomol. News 107, 291–298.
- Williams, L., Schotzko, D.J., MaCaffrey, J.P., 1992. Geostatistical description of the spatial distribution of *Limonius californicus* (Coleoptera: Elateridae) wireworms in the Northwestern United States, with comments on sampling. Environ. Entomol. 21, 983– 995.
- Wright, E.J., Laing, J.E., 1980. Numerical responses of coccinellids to aphids in corn in southern Ontario. Can. Entomol. 112, 977–988.