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ABSTRACT

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The dynamics of *Heterodera glycines* spatial patterns were studied under different tillage systems in two naturally infested soybean fields in Iowa from 1994 to 1997. At each location, there were four different tillage treatments (conventional tillage, reduced tillage, ridge tillage, and no tillage). Soil samples were taken from 98 contiguous quadrats (5.2 m^2) per plot in the fall of 1994, before any tillage was performed, and in the spring of the following 3 years shortly after planting. Cysts were extracted from soil samples by elutriation and counted, and eggs were extracted from cysts and enumerated. Spatial patterns of *H. glycines* populations were characterized by geostatistical analysis and variance-to-mean (VM) ratios. Semivariance values were calculated for cyst and egg densities and semivariograms were constructed. In general, there was greater spatial dependence among cyst populations than egg populations. In one field with a strongly aggregated initial *H. glycines* population, tillage practices resulted in changes in spatial patterns of *H. glycines* populations, characterized by spherical-model semivariogram parameters (sill, nugget effect, and range of spatial dependence). These parameters indicated increasing aggregation over time in no tillage and ridge tillage treatments, but decreasing aggregation in reduced and conventional tillage treatments. There was an increase of 350% in sill values (maximum semivariance) for cyst populations after 3 years of no tillage, but in the conventional tillage treatment, sill values remained unchanged or decreased over time as tillage was implemented. Semivariograms for cyst and egg population densities revealed strong anisotropy (directional spatial dependence) along soybean rows, coincident with the direction of tillage practices. VM ratios for cyst counts increased each year in the no tillage and ridge tillage treatments, but decreased for 2 years in reduced tillage and conventional tillage treatments. Final VM ratios for cyst and egg counts were highest in the no tillage treatment. In a second field, with low initial aggregation of *H. glycines* populations, there was little measurable change in semivariogram parameters after 3 years of no tillage, but in the conventional tillage treatment, populations became less aggregated, as the range, sill, and the proportion of the sill explained by spatial dependence decreased for cyst population densities. Our results indicated that in soybean fields with initially aggregated populations of *H. glycines*, no tillage and ridge tillage systems promoted aggregation of the nematode population, whereas conventional and reduced tillage systems resulted in a less aggregated spatial pattern.

Additional keywords: *Glycine max*, soybean cyst nematode.

Heterodera glycines Ichinohe, the soybean cyst nematode, is the most damaging pathogen of soybeans (*Glycine max* L., Merr.) not only in the United States but also in most other areas of the world where this nematode is found and soybeans are cropped (8,32). Plant-parasitic nematodes have a limited ability to move on their own power (33), therefore movement of infested soil plays an important role in the dissemination of the nematode within and between fields. Cysts of *H. glycines* have been recovered from soil peds contained in seed stocks (11), from the digestive tract and excrement of birds (12), and from soil on farm machinery, land grading equipment, vehicles, tools, and shoes (9).

Tillage, the mechanical manipulation of the soil for cropping purposes, is another activity that has a major impact in soil movement. Extensive research has been conducted on the impact of tillage on *H. glycines* population densities, indicating that *H. glycines* population densities generally are lower in no tillage systems compared with conventional tillage (10,18,21,23,38,39,42).

The spatial pattern of nematodes often is described as aggregated, but there are few reports quantifying or describing the aggregation (13,17,41). Francl (13), using two-term local variance analysis, reported cyst cluster sizes of *H. glycines* of 1 to 3 m and found that cultivation reduced aggregation of cyst populations. Alston and Schmitt (1), studying spatial patterns of *H. glycines* in relation to soybean phenology, found greater population densities closer to the plant rows than between rows. However, these studies did not investigate the effects of different tillage practices on *H. glycines* spatial patterns on a multi-year basis. Understanding the interseasonal dynamics of spatial patterns is important for predicting the effects of crop production practices on *H. glycines* and for the formulation of management strategies (3).

Geostatistical analysis is one method by which spatial patterns can be characterized and compared by quantitative parameters. Geostatistics have gained increased attention from plant pathologists as a means to characterize spatial patterns of several plant diseases and pathogens, including cyst nematodes (6,7,22,24,25, 28,35,40,41,43,44). Geostatistics encompass a set of statistical methods for characterizing spatial patterns (34,37) and can be used to detect changes in spatial pattern over time (25). The objective of this research was to evaluate the effects of different tillage practices on the spatial patterns of *H. glycines* using geostatistical analysis. Preliminary results of this research have been reported (14–16).

MATERIALS AND METHODS

Experiments were conducted from 1994 to 1997 in fields naturally infested with *H. glycines* on the Iowa State University Bruner Research Farm (Boone County, IA) and the Iowa State University Northern Research and Demonstration Farm (Hancock County, IA). In the Bruner Farm, the soil was a Canisteo silty clay

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loam (fine loamy, mixed [calcareous] mesic Typic Haplaquols) (17.5% sand, 75% silt, and 7.5% clay). At the Northern Research and Demonstration Farm, hereafter designated as the Kanawha Farm, the soil was a Canisteo silty clay loam (22.5% sand, 70% silt, and 7.5% clay). Soybeans were grown in both fields in 1994, and no tillage was performed in the fall of 1994.

Plots were 15 × 30 m with 20 plant rows spaced 0.76 m apart. Plots were planted between mid-May and mid-June of each year with *H. glycines*-susceptible soybean cv. Archer (Phytophthora root rot resistant, brown stem rot resistant, and iron chlorosis tolerant). Row orientation was North-South at the Bruner Farm and East-West at the Kanawha Farm.

Four tillage treatments were implemented beginning in the spring of 1995 in continuous soybean monoculture. Conventional tillage consisted of fall chisel plowing (0.20 m deep) followed by spring disking (0.10 m deep) and field cultivation (0.05 m deep) prior to planting. Reduced tillage consisted of spring disking followed by field cultivation before planting. In ridge tillage plots, there was no soil disturbance except for ridge formation. Ridge tillage is a crop residue management system for corn and soybean, consisting of ridges built during cultivation or in the fall. Planting is done on the ridge top, in the same row, every year. Ridges were built in the spring of 1995 and 1996, prior to planting, and were 0.10 m high. The fourth treatment was no tillage. Each tillage operation consisted of only one pass over the plots following the plant row orientation. In each location, a single plot received each treatment. In 1995, plots receiving conventional tillage were chisel plowed in the spring and then disked. Pre-emergence application of a mixture of dicamba (0.58 liter ha^{-1}) and 2,4-D-amine (4.7 liter ha^{-1}) controlled weeds. All plots were treated with herbicides and, except for no tillage, all plots were cultivated one time for supplemental weed control 30 days after planting. Plots under no tillage were weeded manually.

In 1996, approximately 6 weeks after planting, plants in the Bruner Farm developed a foliar interveinal yellowing that was identified as symptoms of iron deficiency chlorosis. To minimize this problem, chelated iron (Sequestrene 138, Becker Underwood, Ames, IA) was applied to foliage as a liquid suspension at 0.7 kg ha^{-1} on 6 July.

Soil samples were collected systematically on a grid (2.3 × 2.3 m) within each plot (7 by 14 gridlines, 98 samples per plot). Each sample consisted of three 2.5-cm-diameter, 20-cm-deep soil cores, collected from the intersections of the gridlines, then combined and mixed to form a single sample. Flags were posted at each sampling point to facilitate accurate location of the grid for repeated sampling. Samples were collected in the fall of 1994 and in the spring of 1995, 1996, and 1997 within 1 week after planting. Results obtained from the first sampling date represent the initial

TABLE 1. Semivariogram parameters, estimated by the spherical model, and variance-to-mean (VM) ratios for *Heterodera glycines* cyst and egg population densities in plots under different tillage systems at the Kanawha Farm experiment in 1994, 1995, 1996, and 1997

Nematode stage	Tillage system	Sampling time[a]	C_o (×10^3)[b]	$C_o + C$ (×10^3)[c]	$C/(C_o + C)$[d]	A_o (m)[e]	R^2[f]	VM
Cysts	No	F 94	0.3	17.6	0.99	>22	0.99	53
		S 95	0.5	19.3	0.98	>22	0.96	56
		S 96	2.1	20.0	0.89	>22	0.98	70
		S 97	0.1	61.2	1.00	>22	0.97	162
	Ridge	F 94	0.4	0.7	0.44	>22	0.53	17
		S 95	2.0	7.2	0.71	>22	0.94	43
		S 96	3.4	44.5	0.92	>22	0.92	72
		S 97	0.1	41.2	1.00	>22	0.91	98
	Reduced	F 94	0.9	32.0	0.97	>22	0.92	116
		S 95	0.0	20.7	1.00	>22	0.88	58
		S 96	0.2	21.3	0.99	>22	0.94	50
		S 97	1.2	32.3	0.96	>22	0.90	117
	Conventional	F 94	3.0	22.1	0.86	>12[g] >22[h]	0.81	86
		S 95	0.0	13.4	1.00	0.0 >22	0.68	83
		S 96	0.0	9.0	1.00	0.0 >22	0.66	72
		S 97	0.3	18.9	0.98	0.0 >22	0.71	102
Eggs	No	F 94	0.0	61.3	1.00	>12 >22	0.98	5,220
		S 95	1.7	5.8	0.71	>22	0.98	1,548
		S 96	3.8	14.2	0.73	>22	0.89	2,277
		S 97	8.3	59.4	0.88	>22	0.98	6,097
	Ridge	F 94	23.2	64.8	0.64	>12 >22	0.61	4,850
		S 95	5.0	9.9	0.50	20.8	0.95	2,417
		S 96	11.9	53.0	0.78	>22	0.95	3,962
		S 97	8.2	39.3	0.79	>22	0.90	4,368
	Reduced	F 94	16.2	48.0	0.66	>12 >22	0.65	4,051
		S 95	1.6	14.3	0.89	>22	0.83	2,100
		S 96	3.2	5.2	0.38	>22	0.75	1,519
		S 97	2.8	8.9	0.69	>22	0.80	1,692
	Conventional	F 94	22.6	67.2	0.66	>12 >22	0.56	6,059
		S 95	1.9	17.3	0.89	>12 >22	0.60	3,274
		S 96	2.6	17.9	0.86	>12 >22	0.90	2,500
		S 97	3.3	9.8	0.66	0.0 >22	0.64	2,288

[a] F = fall, and S = spring.
[b] C_o = nugget variance, the value of the semivariogram near the origin, representing microdistributional and measurement error.
[c] $C_o + C$ = sill, the limiting value of the semivariogram for large distances or the semivariance value beyond range of spatial dependence.
[d] $C/(C_o + C)$ = proportion of sill explained by spatially structured variance.
[e] A_o = range of spatial dependence, the distance at which the sill is reached or the lag distance at which the semivariance approaches a constant value and the distance at which samples are no longer spatially related.
[f] R^2 = coefficient of determination for spherical model.
[g] The range parameter across plant rows, when anisotropy was present.
[h] The range parameter along plant rows, when anisotropy was present.

spatial pattern for all treatments, whereas results from the spring of 1995 and subsequent years are a result of changes in the spatial pattern due to tillage and the persistence of cysts and eggs over the winter. Soil was stored at 4°C until cysts and eggs were enumerated. Cysts were recovered from a 100-cm^3 aliquant of soil by elutriation (2). Each 100-cm^3 aliquant of soil was soaked for 30 min in a solution (15.75 g/liter) of Electrasol automatic dishwasher detergent (Benckiser Consumer Products Inc., Dunbury, CT) to promote dispersion of soil particles and release *H. glycines* cysts. Sediments were removed from the elutriated samples using a modification of a sucrose flotation method described by Jenkins (20). Because results of preliminary experiments indicated that a higher sucrose concentration increased cyst recovery efficiency, we used a sucrose concentration of 1.37 kg liter^{-1} of water instead of 0.45 kg liter^{-1} as originally described. Floating cysts were recovered after centrifugation. Cysts were counted, and eggs were extracted from cysts with a motorized pestle, stained with acid fuchsin (29), and counted. Eggs were enumerated with a nematode counting slide (Olympic Equine, Issaqua, WA) and a dissecting microscope at ×24 magnification. The numbers of cysts and eggs per 100 cm^3 of soil were calculated for each sample. For 1994, samples taken from the Bruner Farm were not processed through sucrose centrifugation and, therefore, only egg data are available for that date. Soil samples from the ridge tillage treatment collected in 1994 in Kanawha were processed by a sucrose solution of 0.45 kg liter^{-1}, and a second set of samples from the same treatment were processed without the sucrose centrifugation step.

Soybeans were harvested mechanically in the fall with a plot combine. Each entire main plot was harvested in subplots consisting of two soybean rows 6.1 m long (40 subplots per plot). Seed moisture was determined with a grain moisture tester (Dole 400; Eaton Corp., Carol Stream, IL). The seed weight was adjusted to 13% moisture. Linear correlation coefficients were calculated for the associations between soybean yield and mean *H. glycines* egg density for the soil sampling points within the subplot area.

Geostatistical analysis (GS$^+$ version 2.3b; Gamma Design Software, Plainwell, MI) was used to quantify the effects of tillage on the spatial patterns of *H. glycines*. General geostatistical methods and terminology are described by Isaaks and Srivastava (19) and Liebhold et al. (26). Semivariance values (one-half the mean squared difference in *H. glycines* population density between spatially separated samples) were calculated for lag distances (distance between samples) of 2.3 to 22.0 m for both cyst densities and egg densities. The relationship between semivariance and distance between samples was plotted (as semivariograms). The presence of anisotropy (directional effect on semivariance) was assessed by examining semivariograms for 0, 45, 90, and 135°, where 90° is the direction along the soybean rows and 0° is the direction perpendicular with the soybean rows. Linear and nonlinear models were fitted to the semivariance values by weighted least squares regression to estimate semivariogram parameters: the nugget effect, sill, and range. The nugget effect is an apparent discontinuity in the semivariogram near the origin (35). The nugget effect is due to microscale variation or measurement error and is not related to spatial dependence. In general, as the distance between sample points increases, semivariance tends toward a maximum value (the sill). The distance between samples at which semivariance reaches the sill is called the range. The range represents the maximum distance over which there is spatial dependence of *H. glycines* densities. Population densities in samples separated by a distance greater than the range are not correlated.

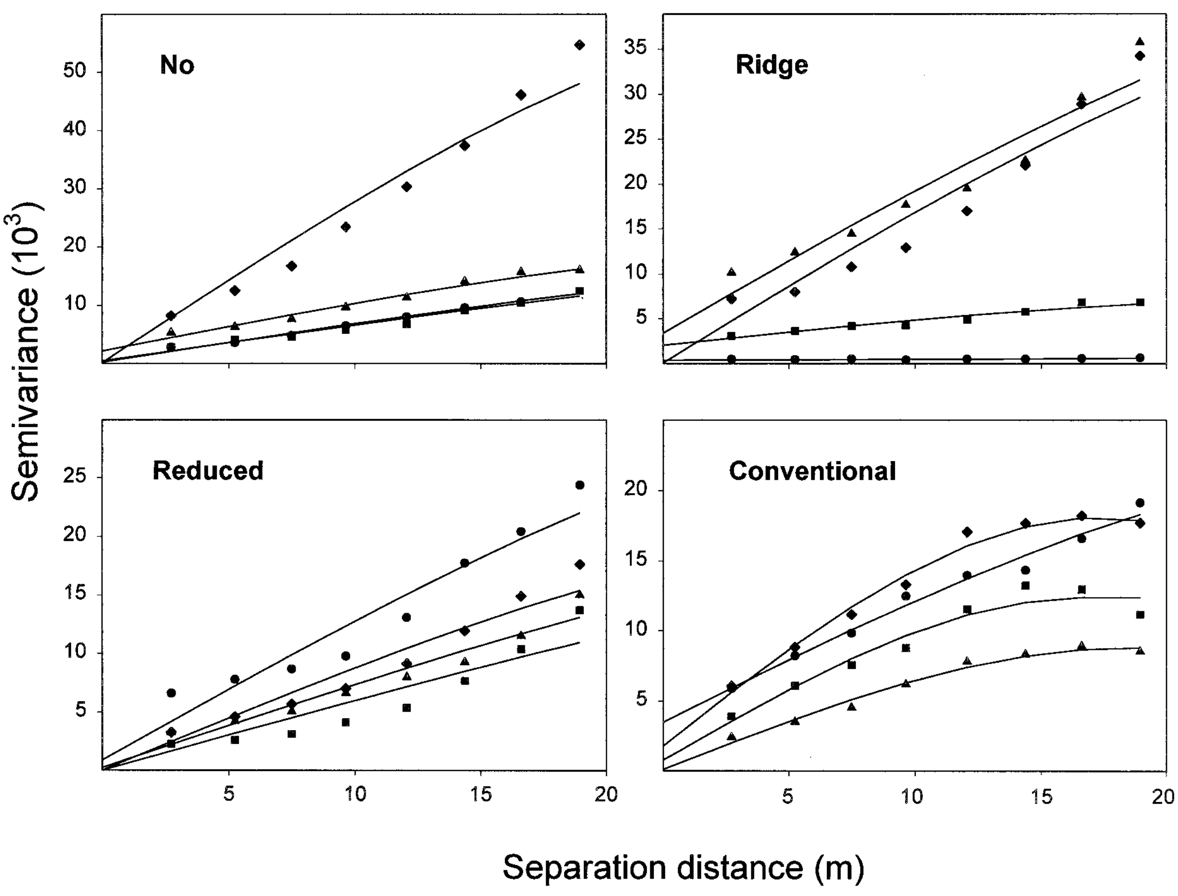

Fig. 1. Isotropic semivariograms of *Heterodera glycines* cyst populations in plots under different tillage systems in 1994 (●), 1995 (■), 1996 (▲), and 1997 (♦) for the experiment at the Kanawha Farm in Hancock County, Iowa. No = no tillage, ridge = no tillage other than ridge formation in 1995 and 1996, reduced = annual spring disking and field cultivation, and conventional = annual fall chisel plowing, spring disking, and field cultivation.

The best-fit model (spherical model) then was used to estimate population densities through kriging, a method of interpolation. Kriged estimates of cyst and egg population densities were generated for a grid of 0.3 × 0.3 m, and maps of these population densities were generated with the kriged estimates.

The variance-to-mean (VM) ratio was calculated for cyst and egg populations in each plot in each year for Kanawha Farm as an alternative method to assess aggregation (4,30) of *H. glycines* populations. For Bruner Farm, VM ratios were calculated only for cyst populations.

RESULTS

Spatial analysis, Kanawha Farm experiment. Semivariograms were described equally well by the spherical and Gaussian models, but results are presented only for the spherical models. Semivariogram parameters for cyst and egg population densities, estimated by the spherical model, are presented in Table 1. Initially, all plots at the Kanawha Farm experiment had aggregated *H. glycines* populations (Figs. 1 to 4) with semivariance values increasing as the distance between pairs of samples increased. In most cases, the predicted range of spatial dependence was beyond the dimensions of the plots.

H. glycines cyst populations became more spatially dependent over time in plots under the no tillage and ridge tillage systems than in the conventional and reduced tillage systems. Increases in sill values and an increase in the proportion of the sill explained by spatial dependence [(sill – nugget)/sill] indicated increases in spatial dependence over time. After 3 years of no tillage, there was an increase of 350% in the sill value, but over the same period of time, nugget variance values fluctuated and ultimately decreased by more than 60% (Table 1). The range of spatial dependence remained >22 m throughout the study. A similar trend was detected in the ridge tillage treatment, with the proportion of the sill explained by spatial dependence increasing from 0.44 to 1.00. In contrast, in the conventional tillage treatment, after soil was disturbed by tillage in the spring of 1995, the range of spatial dependence was reduced to zero across plant rows (Table 1). Isotropic semivariograms (Fig. 1) of the conventional tillage treatment also showed a decreasing sill during the first 2 years of tillage, although the sill increased again in 1997. A decreasing range was evident for the conventional tillage treatment as well (Fig. 1), with the range decreasing to near 22 m for 1995 to 1997. In the reduced tillage treatment, the sill also decreased in 1995 and 1996, but in 1997 returned to a value similar to 1994. There were no major changes in range for the reduced tillage treatment over the period of this study.

Anisotropy in spatial patterns of cysts was detected in several of the treatments during the course of the study (Fig. 2). In general, spatial dependence was more pronounced along the direction of the rows (the direction of tillage operations, 90° orientation in figures) than across the rows (0° orientation), and anisotropy was more evident after tillage had been performed for one or more years (e.g., ridge tillage and conventional tillage treatments).

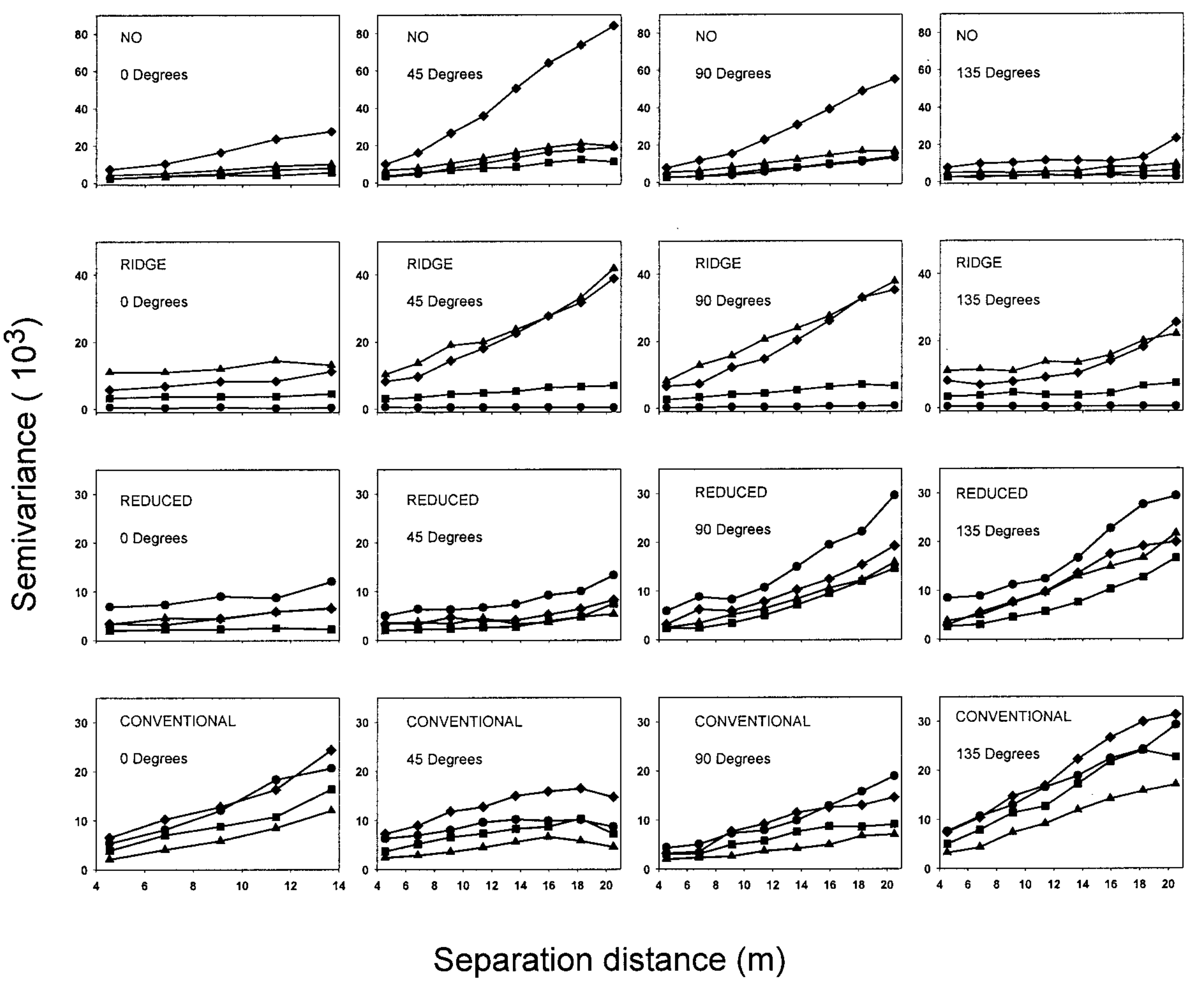

Fig. 2. Anisotropic semivariograms of *Heterodera glycines* cyst populations in plots under different tillage systems in 1994 (•), 1995 (■), 1996 (▲), and 1997 (♦) for the experiment at the Kanawha Farm (Hancock County, Iowa) in different directions in degrees azimuth (0 = across soybean rows). No = no tillage, ridge = no tillage other than ridge formation in 1995 and 1996, reduced = annual spring disking and field cultivation, and conventional = annual fall chisel plowing, spring disking, and field cultivation.

Spatial dependence along the 45 and 135° orientations did not follow a consistent pattern in relation to tillage treatment or time.

H. glycines egg populations also became more uniformly distributed after 3 years of conventional and reduced tillage. Conventional tillage resulted in 85% reduction in sill and nugget variance values, whereas the range of spatial dependence disappeared along the soybean rows (Table 1; Fig. 3). In the reduced tillage treatment, nugget and sill values also decreased by more than 80% over time, but the range of spatial dependence never decreased to <22 m. Spatial dependence initially decreased in the no tillage and ridge tillage treatments, but then increased, indicated by changes in the sill and proportion (sill – nugget)/sill (Table 1; Fig. 3).

Anisotropy in spatial patterns of egg populations was detected in at least 1 year in all treatments (Table 1; Fig. 4). Similar to cyst populations, egg populations generally demonstrated greater spatial dependence along soybean rows than across rows. Semivariograms generally indicated higher ranges and sills for the 45° orientation than the 135° orientation (Fig. 4).

Kriged maps of cyst and egg population densities (Figs. 5 and 6) demonstrated that initially there was a greater population of *H. glycines* in the west portion of most plots than the east. However, populations became less concentrated in this area as conventional tillage was implemented. Conversely, a more pronounced area of higher *H. glycines* population densities developed over the 3 years of the experiment on the west side of the plots under no tillage and ridge tillage.

The VM ratio for the number of cysts and eggs was greater than 1.0 in all plots at all sampling times (Table 1), indicating aggregation of the *H. glycines* population (4). Cyst VM ratios increased from 1994 to 1996 in the no tillage and ridge tillage treatments, whereas they decreased in the reduced and conventional tillage treatments. In 1997, cyst VM ratios increased in all plots, and final ratios were highest in the no tillage treatment. Egg VM ratios were 1 to 2 orders of magnitude higher than those for cysts. Egg VM ratios fluctuated annually in the no tillage and ridge tillage treatments, but generally decreased in the reduced and conventional tillage treatments. Final VM ratios for eggs were more than twice as high in the no tillage and ridge tillage treatments as they were in the reduced and conventional tillage treatments.

Spatial analysis, Bruner Farm experiment. The initial spatial pattern of cyst populations for the Bruner Farm is not presented because cysts were not enumerated from the samples collected in the fall of 1994. Cyst populations measured after 1994 at the Bruner Farm experiment were aggregated (Table 2; Fig. 7), but spatial dependence was not as strong as it was in the plots located at the Kanawha Farm. Sill values generally were less than half those in the Kanawha experiment, and the proportion of the sill explained by spatial dependence ranged from 0.27 to 0.69 compared with 0.44 to 1.00 at Kanawha.

In the no tillage treatment, the semivariance values calculated for 1997 could not be described adequately by any model. Consequently, semivariance results are presented only for 1995 and 1996 data. No major changes in the semivariogram parameters occurred in 2 years in the no tillage treatment. In the conventional tillage treatment, spatial dependence decreased over time. The range of spatial dependence decreased from >22 to 13.2 m, and the proportion of the sill explained by spatial dependence decreased from 0.69 to 0.27. In the reduced tillage treatment, nugget variance and sill increased, but the proportion of the sill explained by spatial dependence did not change. In the ridge tillage treatment, the proportion of the sill explained by spatial dependence did not change over time, but the sill and range increased, suggesting a more aggregated population.

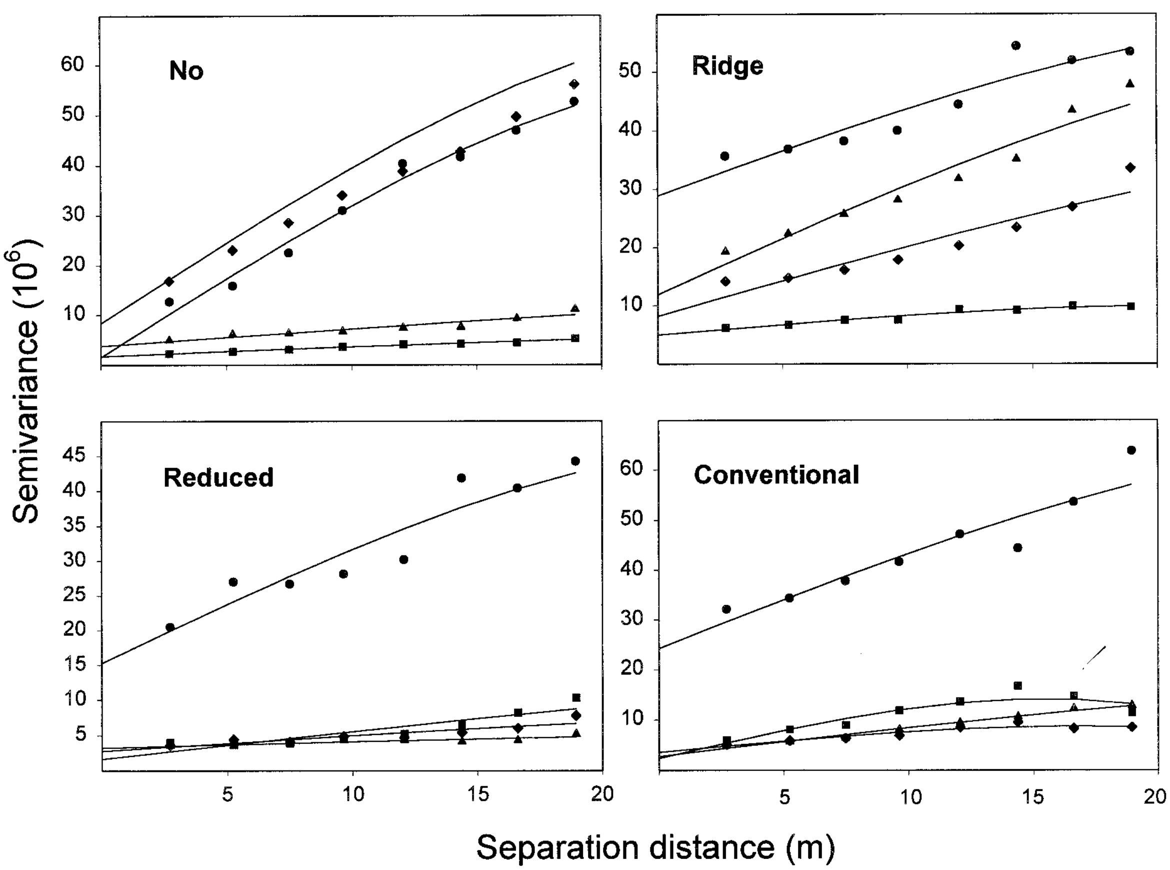

Fig. 3. Isotropic semivariograms of *Heterodera glycines* egg populations in plots under different tillage systems in 1994 (●), 1995 (■), 1996 (▲), and 1997 (♦) for the experiment at the Kanawha Farm in Hancock County, Iowa. No = no tillage, ridge = no tillage other than ridge formation in 1995 and 1996, reduced = annual spring disking and field cultivation, and conventional = annual fall chisel plowing, spring disking, and field cultivation.

Kriged maps of spatial patterns of cysts of *H. glycines* at Bruner Farm (data not shown) showed a trend similar to that demonstrated at the Kanawha Farm for the ridge tillage plot (the area with greater cyst population densities increased over time), but there was not a clear trend in the other tillage treatment plots. Kriging could not be performed on semivariance values for the 1997 no tillage plot, because a model could not be fit to those data.

For *H. glycines* egg populations at Bruner Farm, semivariograms calculated for the conventional tillage treatment were linear with a slope near zero, indicating *H. glycines* egg populations in the plot were not spatially dependent at the 2.3-m sampling interval (data not shown). The absence of spatial dependence for some sampling times and the inconsistency of the semivariogram parameters made it impossible to compare changes in spatial patterns of egg populations.

VM ratios for cysts were >1.0 for all plots and sampling times. VM ratios were smaller than those at Kanawha Farm, and they increased slightly over time in all four treatments.

***H. glycines* population dynamics.** Cyst population densities fluctuated annually in all plots at the Kanawha Farm (Table 3), and trends differed among treatments. In the conventional tillage plot, population density decreased from 1994 to 1995 and stabilized. Initial egg population densities were similar, but final population densities were greater in the no tillage and ridge tillage treatments than in conventional and reduced tillage treatments. There was a general decrease in egg population densities from the fall of 1994 to the spring of 1995; egg population densities then increased in the no tillage and ridge tillage plots and, after 1995, stabilized in the conventional and reduced tillage plots. After 4 years of no tillage, population densities increased in the west portion of the plot and decreased in the east, whereas there was no clear trend in the other tillage treatments.

At the Bruner Farm, cyst population densities generally increased over time, ranging from 137 to 253 cysts per 100 cm^3 in 1995 and from 265 to 570 cysts per 100 cm^3 in 1997. Cyst population densities increased in all plots from the spring of 1995 to the spring of 1996 (Table 3), but there were no trends, in terms of specific areas of the plots, where reproduction was promoted or suppressed. There was a consistent increase in egg population densities from 1994 to 1995. After 1995, egg population densities fluctuated between 3,036 to 5,841 eggs per 100 cm^3 without a consistent trend. Similarly, changes in egg population densities were neither consistent nor restricted to specific areas of the field.

Soybean yield. Soybean yields ranged from 2.2 to 2.3 t/ha at Kanawha in 1994 and decreased over time in all plots, with yields ranging from 1.5 to 2.0 t/ha in 1998. At the Bruner Farm, yields ranged from 1.6 to 2.0 t/ha and did not change over time. Linear correlation coefficients between nematode population densities and soybean yields were significant and negative (Table 4). Consistently lower linear correlation coefficients were obtained for the conventional tillage treatment compared with the no tillage treatment. At the Kanawha Farm, plants in the west portion of the plots, an area coinciding with high *H. glycines* population densities, consistently exhibited symptoms of early maturity by the end of August and beginning of September. Yield was reduced in

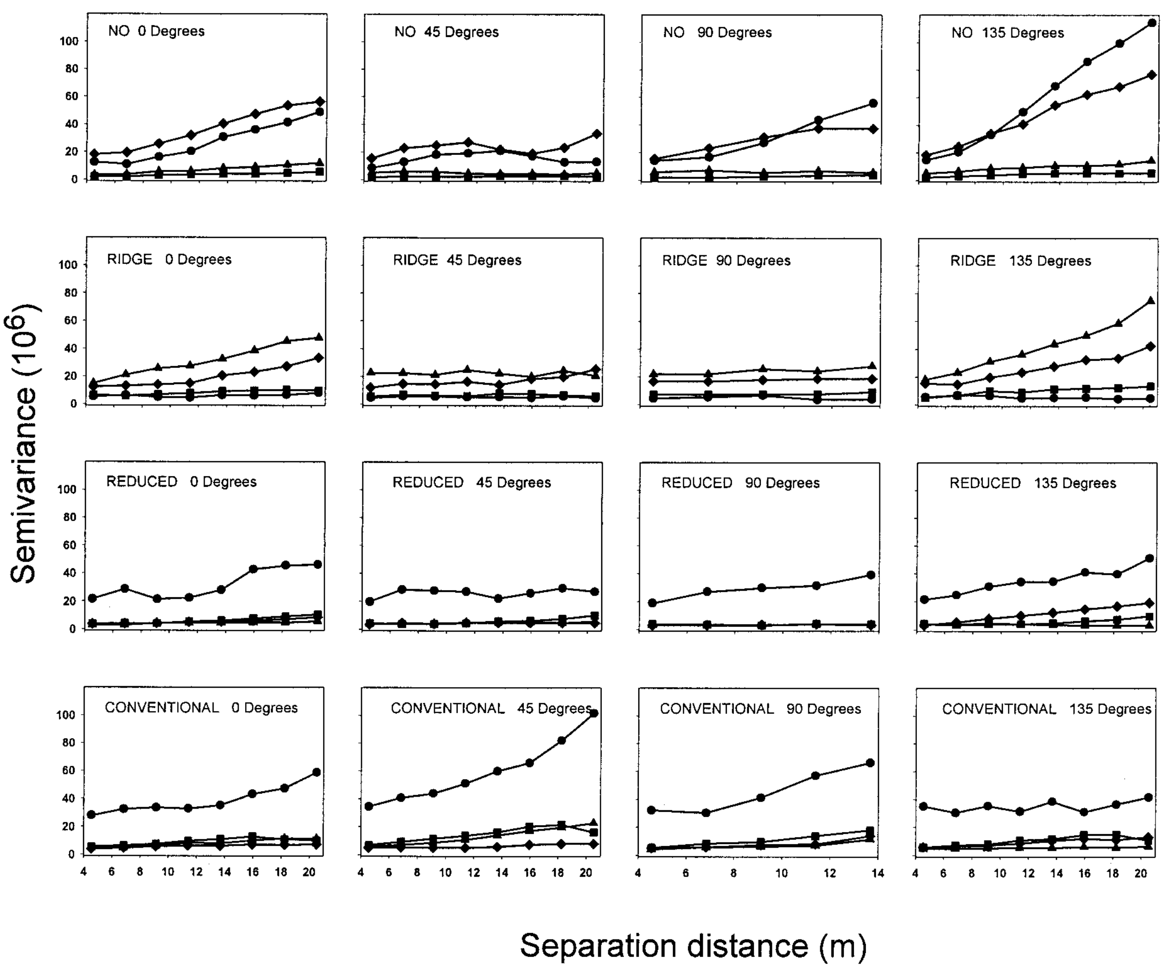

Fig. 4. Anisotropic semivariograms of *Heterodera glycines* egg populations in plots under different tillage systems in 1994 (•), 1995 (■), 1996 (▲), and 1997 (♦) for the experiment at the Kanawha Farm (Hancock County, Iowa) in different directions in degrees azimuth (0 = across soybean rows). No = no tillage, ridge = no tillage other than ridge formation in 1995 and 1996, reduced = annual spring disking and field cultivation, and conventional = annual fall chisel plowing, spring disking, and field cultivation.

this portion of the field. There was no clear association between soybean yield and nematode population densities in the Bruner Farm experiment (Table 4).

DISCUSSION

Geostatistical analysis was used to quantify the effects of tillage on the spatial patterns of *H. glycines*. To our knowledge, this is the first report where geostatistics were used to elucidate the multi-year dynamics of spatial patterns of a soilborne pathogen in plots under different tillage systems. In a field with a well-established and strongly aggregated *H. glycines* population (Kanawha Farm), no tillage and ridge tillage practices promoted aggregation of the nematode population, whereas conventional and reduced tillage disrupted aggregation, resulting in more uniformly distributed populations (reduced semivariance and sill values). These effects are evident from the geostatistical results (Table 1; Figs. 1 and 3), the VM ratios (Table 1), and the population density maps (Figs. 5 and 6). Considering that *H. glycines* is a sedentary endoparasite, it is reasonable to speculate that secondary infections are more likely to occur in roots and plants adjacent to the primary infection site. Then, in the absence of soil disturbance (no tillage treatment), aggregation of nematodes would tend to increase from season to season as nematodes reproduce. A similar effect would be expected in the ridge tillage treatment, which involved raising the seedbed level above the surrounding soil and maintaining plant rows in the same location year after year. Our results also indicated that in a field with less aggregated populations (Bruner Farm), tillage practices had a similar but smaller effect on the spatial pattern of *H. glycines*.

Anisotropy or directional variability in the conventional tillage and ridge tillage treatments at Kanawha was likely a result of the tillage operations. Conventional tillage tended to eliminate spatial dependence across rows (perpendicular to the direction of tillage operations). Similarly, in the ridge tillage treatment, greater spatial dependence along rows was likely a result of ridge-building operations. Anisotropy, with regard to the 45 and 135° orientations, is more difficult to explain in relation to tillage. In fact, these patterns may not have been related to tillage and did not change progressively over time, as would be expected if tillage operations were driving their development.

At the Bruner Farm, nugget effect was high compared with sill and increased over time in the conventional tillage treatment. The different effects of conventional tillage in the two experimental sites can be explained by the fact that cyst populations at the Bruner Farm were initially not as strongly aggregated as those at the Kanawha Farm. Spatial dependence on a scale smaller than 2.3 m could have contributed to high nugget effects at the Bruner Farm.

At the Kanawha Farm, from 1994 to 1996, sill values estimated from the cyst population were reduced as nematode spatial patterns were disrupted by conventional tillage. In 1997, there was an increase in sill values for most treatments, which we cannot explain. At the Bruner Farm experiment, sill values fluctuated without a clear trend after tillage was implemented. We believe that the less aggregated spatial pattern in the Bruner conventional tillage plot (compared with the pattern at the Kanawha Farm) played a role in the variability of sill values. Although a decrease in the sill was not detected, the proportion of the sill explained by spatial dependence decreased markedly in the conventional tillage

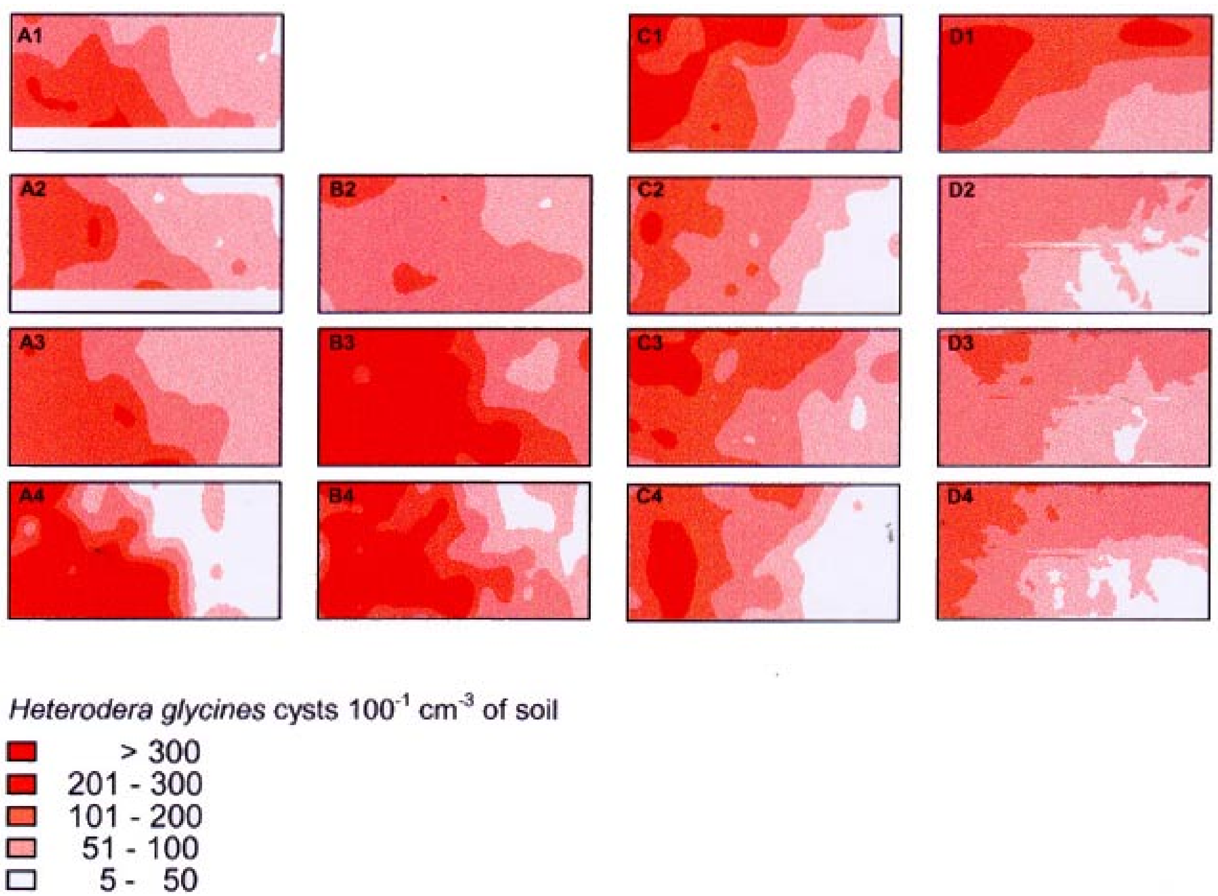

Fig. 5. A, Spatial patterns of *Heterodera glycines* cyst populations in plots under no tillage; **B,** ridge tillage; **C,** reduced tillage; and **D,** conventional tillage in the naturally infested experiment conducted at the Kanawha Farm (Hancock County, Iowa). Numbers following letters represent sampling time: 1 = fall 1994 prior to tillage treatments, 2 = spring 1995, 3 = spring 1996, and 4 = spring 1997. Maps generated by interpolation (kriging) of soil sampling data from a 2.3-m grid. **B,** Ridge-tillage data for the fall of 1994 (1) were not available. Plots were 15 × 30 m. Each map is oriented with North at top.

plot from 1995 to 1997, representing a reduction in spatial dependence. Decreases in semivariance due to tillage were more evident in the conventional tillage treatment at the Kanawha Farm than at the Bruner Farm when the spherical model was fitted to semivariance values from egg data. The decrease in semivariance most likely was caused by a redistribution of the *H. glycines* population, resulting in a more uniform distribution of cysts and, consequently, eggs. Some researchers have reported decreases in spatial variability of soilborne pathogens due to soil tillage. Francl (13), investigating the spatial patterns of *H. glycines* in field plots, observed reduction in variance after the plot was disked and bedded. Olanya and Campbell (31), studying the effects of tillage on the spatial patterns of microsclerotia of *Macrophomina phaseolina*, found that variance, VM ratio, and Morisita's index decreased as tillage was implemented. Similarly, spatial patterns of *Sclerotinia minor* sclerotia became more uniform, as measured by Lloyd's index of patchiness, after the soil was deep plowed (36).

In most plots, there was a strong spatial dependence of the nematode population, indicated by the high proportion of the sill explained by spatially structured variance (sometimes equal to 1.0). In the ridge tillage treatment in 1994, this proportion was very low (0.44). This may have been caused, in part, by poor efficiency of cyst extraction; soil samples from this plot in 1994 were processed with a lower sucrose concentration (20) than the other treatments/sampling times. Another possibility is the presence of spatial dependence at a distance smaller than the 2.3-m grid size used in our experiments. We found that the proportion of the sill explained by spatially structured variance was greater for cyst than for egg population densities, and this may be a result of less error associated with the enumeration of cysts than eggs. Additionally, the presence of nonspatial variance associated with numbers of eggs per cyst may have increased the nugget effect for egg semivariograms.

The range of spatial dependence, estimated by the spherical model, initially was greater than the plot dimensions, indicating that the spatial structure of the *H. glycines* population was beyond the plot limits. There was a definite reduction of range for cyst population densities in the conventional tillage plots at both experimental sites, indicating a reduction in aggregation of the nematode populations. Previous research of spatial patterns of other cyst nematodes have detected ranges of 60 and 29 m for *H. avenae*, 107 m for *Globodera rostochiensis* (41), and 40 m for *H. trifolii* (40). Ranges calculated in this study were based on a scale similar to the above-mentioned studies. A larger plot size in our study would have enabled us to identify the range values more clearly. Our plot size and sampling intensity were designed to capture spatial variability on a smaller scale, as reported by Francl (13), who indicated cluster sizes of approximately 3 m for *H. glycines*. Because this (13) was the only previous study reporting the scale of spatial dependence for *H. glycines*, it was appropriate to design our study accordingly. With a larger plot size, we would not have been able to sample intensively enough to capture small-scale spatial dependence. Furthermore, the range parameter is not species-specific, and it probably will differ among fields according to physical and biological soil characteristics, crop history, and cultural practices.

Analysis of cyst data, in addition to egg data, helped clarify the dynamics of spatial patterns of *H. glycines* because the results of analyses of egg data were not conclusive in some cases. At Bruner

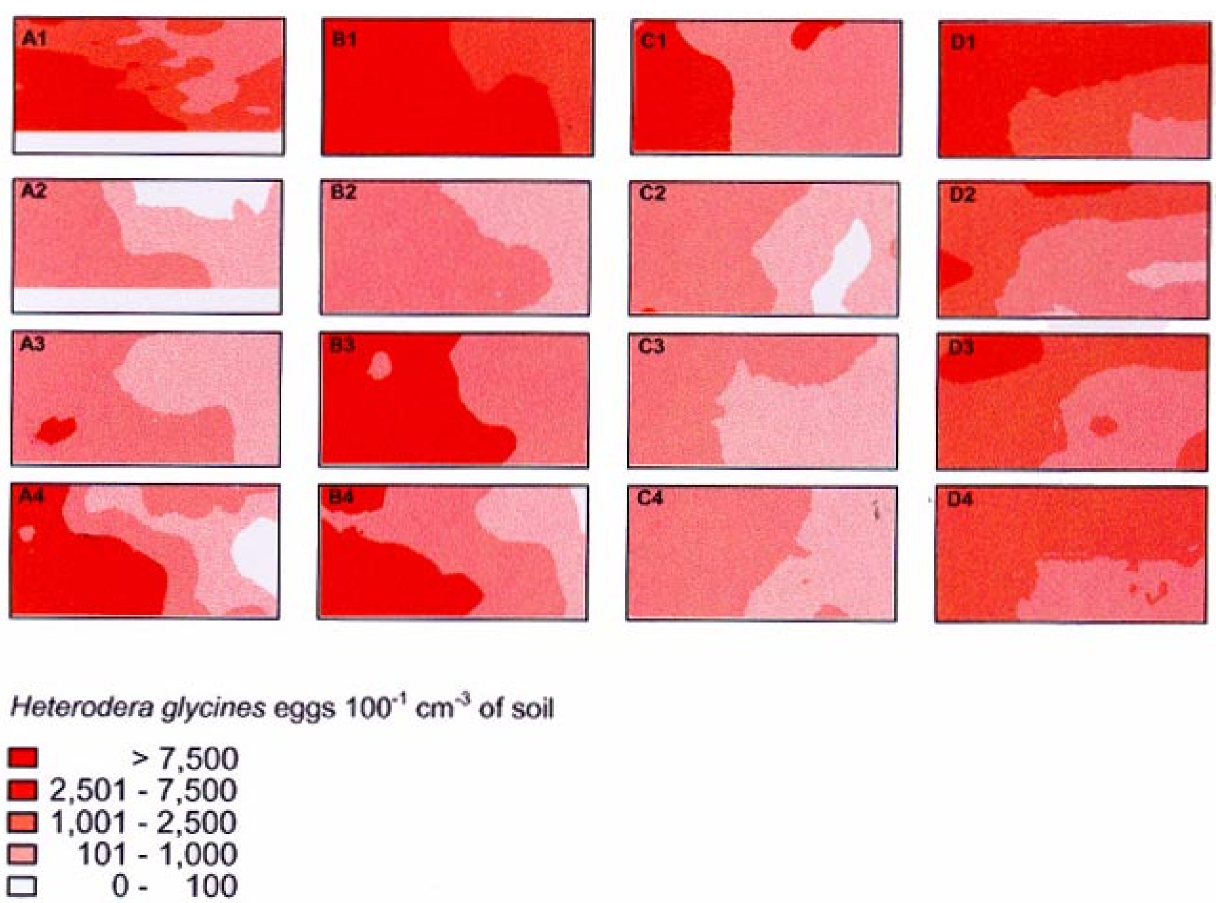

Fig. 6. A, Spatial patterns of *Heterodera glycines* egg populations in plots under no tillage; **B,** ridge tillage; **C,** reduced tillage; and **D,** conventional tillage in the naturally infested experiment conducted at the Kanawha Farm (Hancock County, Iowa). Numbers following letters represent sampling time: 1 = fall 1994 prior to tillage treatments, 2 = spring 1995, 3 = spring 1996, and 4 = spring 1997. Maps generated by interpolation (kriging) of soil sampling data from a 2.3-m grid. Plots were 15 × 30 m. Each map is oriented with North at top.

Farm, spatial dependence was evident from analysis of cyst data, but not egg data. Forces determining *H. glycines* spatial pattern typically are exerted on cysts rather than individual eggs. The variable number of eggs per cyst adds a nonspatial source of variance that may mask spatially structured variance if only egg data are used. This effect was noticeable in both geostatistical analysis and VM ratios. In general, our results suggest that spatial pattern analyses for cyst nematodes are more informative when cyst counts are used instead of egg counts.

Trends in VM ratios generally supported the conclusions drawn from geostatistical analyses. Ratios >1.0 indicate a departure from the expected VM ratio for a Poisson distribution, the expected

TABLE 2. Semivariogram parameters, estimated by the spherical model, and variance-to-mean (VM) ratios for *Heterodera glycines* cyst population densities in plots under different tillage systems at the Bruner Farm experiment in 1995, 1996, and 1997

Tillage system	Sampling time[a]	C_o ($\times 10^3$)[b]	$C_o + C$ ($\times 10^3$)[c]	$C/(C_o + C)$[d]	A_o (m)[e]	R^{2}[f]	VM
No	S 95	3.4	7.5	0.55	>22	0.88	23
	S 96	5.4	8.8	0.38	>22	0.48	22
	S 97	…[g]	…	…	…	…	28
Ridge	S 95	2.5	5.6	0.54	14.2	0.92	21
	S 96	4.1	10.0	0.58	10.4	0.84	27
	S 97	5.8	13.7	0.58	15.8	0.77	31
Reduced	S 95	4.7	6.7	0.30	>22	0.84	31
	S 96	7.8	18.1	0.59	>22	0.62	36
	S 97	10.4	15.4	0.35	>22	0.61	44
Conventional	S 95	2.7	8.5	0.69	>22	0.98	33
	S 96	8.5	14.0	0.40	17.8	0.90	35
	S 97	7.3	10.0	0.27	13.2	0.70	35

[a] S = spring.
[b] C_o = nugget variance, the value of the semivariogram near the origin, representing microdistributional and measurement error.
[c] $C_o + C$ = sill, the limiting value of the semivariogram for large distances or the semivariance value beyond range of spatial dependence.
[d] $C/(C_o + C)$ = proportion of the sill explained by spatially structured variance.
[e] A_o = range of spatial dependence, the distance at which the sill is reached or the lag distance at which the semivariance approaches a constant value and the distance at which samples are no longer spatially related.
[f] R^2 = coefficient of determination for spherical model.
[g] Semivariance values could not be described by any model.

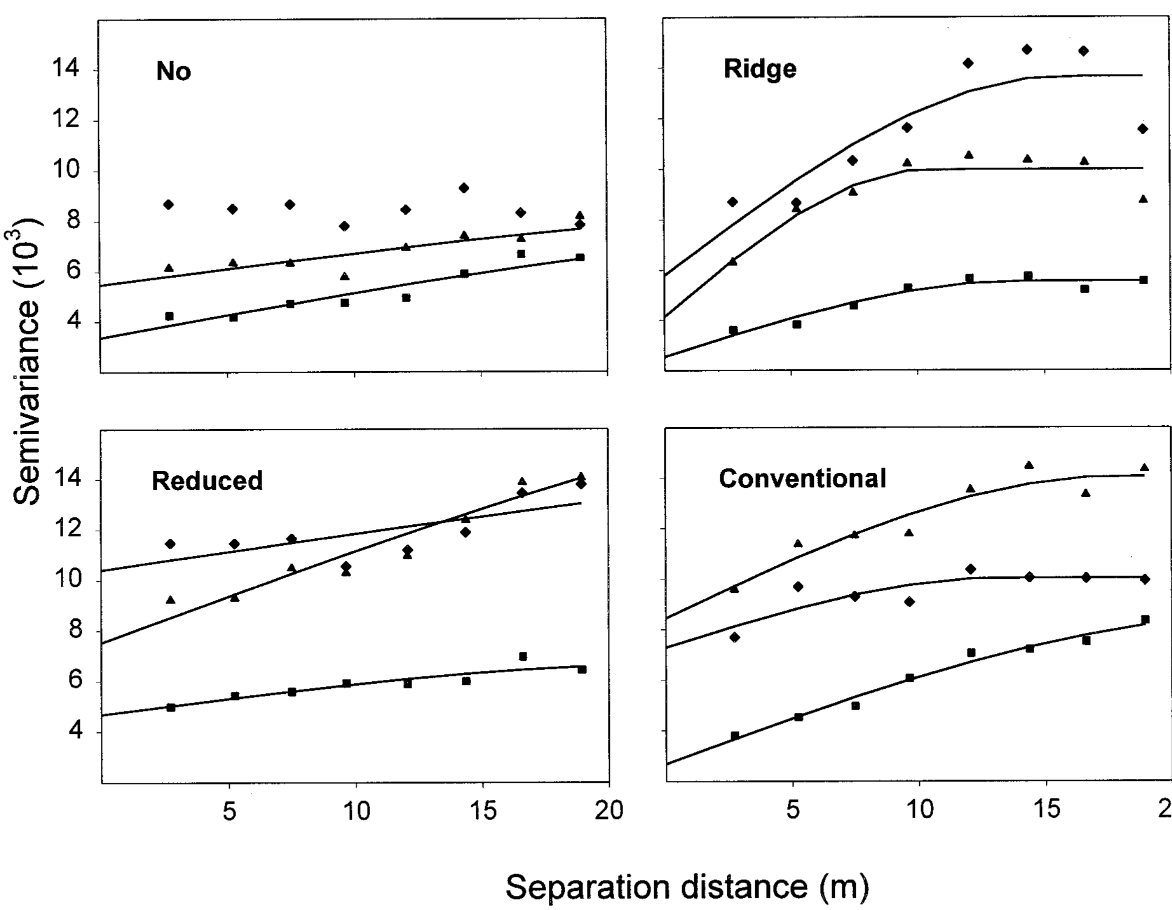

Fig. 7. Isotropic semivariograms of *Heterodera glycines* cyst populations in plots under different tillage systems in 1995 (■), 1996 (▲), and 1997 (♦), for the experiment at the Bruner Farm in Story County, Iowa. No = no tillage, ridge = no tillage other than ridge formation in 1995 and 1996, reduced = annual spring disking and field cultivation, and conventional = annual fall chisel plowing, spring disking, and field cultivation.

distribution for a variable with a random spatial pattern (30). Increases in VM ratio indicate a greater degree of aggregation, whereas decreases indicate a lesser degree (45). VM ratios indicated aggregation for all plots and sampling times and an increase in the degree of aggregation of cysts each year in the no tillage and reduced tillage treatments at Kanawha. Conversely, VM ratios indicated decreases in the degree of aggregation in the reduced and conventional tillage treatments for 2 years (Table 1). VM ratios indicated an increase in aggregation in all plots in 1997. Higher VM ratios for egg counts compared with those for cyst counts were likely a reflection of the variable number of eggs per cyst, with some cysts containing no eggs and others with several hundred eggs. This nonspatial variability probably contributed to the annual fluctuation of VM ratios, and may detract from the value of egg counts for interpretation of VM ratios. Researchers have used VM ratios and other dispersion indices, such as Lloyd's index of patchiness (27), to identify changes in spatial pattern of soilborne pathogens (5,31,36,44). Limitations of VM ratios and other dispersion indices include undesirable effects of sample size and mean (4) and a lack of consideration of the spatial position of samples. Consequently, indices of dispersion do not reflect the spatial structure of soilborne plant pathogen populations (30).

The trend toward higher *H. glycines* populations in the no tillage treatment at Kanawha Farm is in contrast to several other studies (10,21,38,39,42), in which *H. glycines* populations were lower under no tillage systems. Our results may not be directly comparable to these other studies due to differences in methodology. In addition, we do not have statistical evidence to determine whether the populations in our study were significantly different among treatments.

In fields managed with crop rotation, the effects of tillage on the spatial patterns of *H. glycines* probably would take longer to develop than in the present study, considering that soybeans were grown every year in our experiments. Although we had continuous soybean monoculture in our plots, tillage was performed similar to a conventional corn-soybean rotation. Our yields decreased over time, probably a result of the soybean monoculture, which promotes the development of fungal pathogens of soybean.

Adding the sucrose centrifugation step to the *H. glycines* cyst extraction procedures may improve spatial analysis in fields with a low aggregation of the population. For the Bruner Farm, semivariograms calculated from egg data obtained without centrifugation usually revealed low spatial dependence or even a pure nugget effect. In contrast, results of geostatistical analyses from egg data obtained through centrifugation of elutriated samples revealed the presence of spatial dependence that was not detected when samples were processed without the centrifugation. Samples processed through sucrose centrifugation were free of soil particles and eggs were well stained and easily visualized. Preliminary data showed slightly greater egg recovery values for centrifuged samples than samples that were ground after elutriation. We believe that adding the sucrose centrifugation to the extraction procedures for recovery of cysts also reduces error in egg enumeration.

The high population densities of *H. glycines* detected in the west portion of the plots at Kanawha were near the field entrance, indicating the possibility that the nematode might initially have been introduced in that area.

TABLE 4. Linear correlation coefficients of cyst and egg population densities with yield of soybean cv. Archer in plots naturally infested with *Heterodera glycines* and managed with different tillage systems in 1995, 1996, and 1997

Location	Tillage treatment	Nematode stage	Year[a] 1995	1996	1997
Bruner Farm	No	Cysts	–0.15	–0.10	–0.20
		Eggs	–0.27	0.10	–0.02
	Ridge	Cysts	0.02	–0.20	0.03
		Eggs	0.50**	0.05	–0.06
	Reduced	Cysts	–0.44*	–0.08	–0.11
		Eggs	–0.32	–0.19	–0.04
	Conventional	Cysts	0.16	0.24	0.09
		Eggs	0.03	–0.03	–0.49*
Kanawha Farm	No	Cysts	–0.82**	–0.72**	–0.80**
		Eggs	–0.71**	–0.64*	–0.68**
	Ridge	Cysts	–0.69**	–0.47*	–0.69**
		Eggs	–0.81**	–0.60**	–0.73**
	Reduced	Cysts	–0.83**	–0.79**	–0.66**
		Eggs	–0.75**	–0.42*	–0.72**
	Conventional	Cysts	–0.53**	–0.60**	–0.53**
		Eggs	–0.41**	–0.50**	–0.56*

[a] * and ** indicate correlation significant at $P \leq 0.05$ and $P \leq 0.01$, respectively.

TABLE 3. Range and mean *Heterodera glycines* population densities per 100 cm^3 of soil in plots managed with different tillage systems at two locations

Location/ tillage system	Nematode stage	Fall 1994 Range	Fall 1994 Mean	Spring 1995 Range	Spring 1995 Mean	Spring 1996 Range	Spring 1996 Mean	Spring 1997 Range	Spring 1997 Mean
Bruner									
No	Cysts	…[a]	…	81–460	253	154–570	322	122–570	570
	Eggs	150–12,400	3,850	1,050–13,050	5,278	1,000–10,350	3,723	600–17,150	5,838
Ridge	Cysts	…	…	19–345	137	59–607	335	115–699	362
	Eggs	50–10,700	2,389	475–16,600	4,970	550–16,550	4,652	700–19,700	5,841
Reduced	Cysts	…	…	70–406	194	78–682	330	51–598	277
	Eggs	0–11,700	3,020	800–11,400	4,637	900–11,700	4,016	300–13,600	3,823
Conventional	Cysts	…	…	65–438	201	124–622	346	82–562	265
	Eggs	0–14,000	2,752	550–17,900	3,661	550–9,150	3,036	550–28,000	5,445
Kanawha									
No	Cysts	30–372	150	25–371	138	30–455	168	8–639	208
	Eggs	550–28,800	6,795	100–7,700	2,547	350–13,300	3,704	350–13,300	6,680
Ridge	Cysts	5–122	33	19–345	137	53–623	221	18–502	219
	Eggs	1,600–50,789[b]	9,806	75–14,400	3,492	1,400–2,620	8,340	200–22,900	5,839
Reduced	Cysts	11–546	201	8–446	131	28–453	191	14–743	153
	Eggs	250–31,800	7,408	100–13,350	3,245	250–12,700	2,951	250–13,200	3,357
Conventional	Cysts	39–609	214	11–488	117	16–378	133	10–462	150
	Eggs	600–34,700	8,545	150–21,500	3,654	50–14,100	3,933	0–18,300	3,493

[a] Cysts were not enumerated for the 1994 soil samples collected at the Bruner Farm experiment.
[b] Egg data from samples collected in the fall of 1994 were obtained without the sucrose centrifugation step.

Strong aggregation generally was associated with strong correlations between nematode population densities (measured as cysts or eggs) and soybean yields. The reduction in spatial dependence in the conventional-tilled plots was accompanied by a reduction in the linear correlation coefficients between nematode population densities and soybean yield. In addition, at the Bruner Farm where nematode aggregation was weak (and the mean *H. glycines* population densities were lower), there was a weak relationship between nematode population densities and soybean yield regardless of tillage treatment. In the aggregated populations at Kanawha, some sampling units had very high nematode densities and, therefore, yield was greatly suppressed in these sampling units relative to the others. With the more uniform populations at Bruner or in the conventional tillage treatment at Kanawha, individual sampling units did not tend to have populations much higher than the mean; therefore, the yield variability among sampling units was lower. This mechanism could explain the stronger correlation between *H. glycines* population and yield in the plots with greater aggregation of the nematode population. Research is needed to elucidate the relationship between spatial patterns of *H. glycines* and yield losses in soybeans.

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LITERATURE CITED

1. Alston, D. G., and Schmitt, D. P. 1987. Population density and spatial pattern of *Heterodera glycines* in relation to soybean phenology. J. Nematol. 19:336-345.
2. Byrd, D. W., Jr., Barker, K. R., Ferris, H., Nusbaum, W. E., Griffin, W. E., Small, R. H., and Stone, C. 1976. Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. J. Nematol. 8: 206-212.
3. Campbell, C. L., and Benson, D. M. 1994. Spatial aspects of the development of root disease epidemics. Pages 195-243 in: Epidemiology and Management of Root Diseases. C. L. Campbell and D. M. Benson, eds. Springer-Verlag, Berlin.
4. Campbell, C. L., and Madden, L. V. 1989. Spatial aspects of plant disease epidemics II: Analysis of spatial pattern. Pages 289-328 in: Introduction to Plant Disease Epidemiology. John Wiley, New York.
5. Campbell, C. L., and van der Gaag, D. J. 1993. Temporal and spatial dynamics of microsclerotia of *Macrophomina phaseolina* in three fields in North Carolina over four to five years. Phytopathology 83: 1434-1440.
6. Chellemi, D. O., Rohrbach, K. G., Yost, R. S., and Sonoda, R. M. 1988. Analysis of the spatial pattern of plant pathogens and diseased plants using geostatistics. Phytopathology 78:221-226.
7. Donald, P., Donald, W., Keaster, A., Kendig, A., and Sims, B. 1994. Geostatistical analysis of soybean cyst nematode distribution. (Abstr.) J. Nematol. 26:98.
8. Doupnik, B., Jr. 1993. Soybean production and disease loss for north central United States from 1989 to 1991. Plant Dis. 77:1170-1171.
9. Edwards, D. I. 1988. The soybean cyst nematode. Pages 81-86 in: Soybean Diseases of the North Central Region. T. D. Wyllie and D. H. Scott, eds. The American Phytopathological Society, St. Paul, MN.
10. Edwards, J. H., Thurlow, D. L., and Eason, J. T. 1988. Influence of tillage and crop rotation on yields of corn, soybean, and wheat. Agron. J. 80:76-80.
11. Epps, J. M. 1969. Survival of the soybean cyst nematode in seed stocks. Plant Dis. Rep. 53:403-405.
12. Epps, J. M. 1971. Recovery of soybean cyst nematodes (*Heterodera glycines*) from the digestive tracts of blackbirds. J. Nematol. 3:417-419.
13. Francl, L. J. 1986. Spatial analysis of *Heterodera glycines* populations in field plots. J. Nematol. 18:183-189.
14. Gavassoni, W. L., Munkvold, G. P., and Tylka, G. L. 1996. Spatial dependence of soybean cyst nematode cyst and egg populations. (Abstr.) Phytopathology 86(suppl.):S86.
15. Gavassoni, W. L., Munkvold, G. P., and Tylka, G. L. 1998. Tillage alters spatial dependence of *Heterodera glycines*. (Abstr.) J. Nematol. 30:497.
16. Gavassoni, W. L., Munkvold, G. P., and Tylka, G. L. 1999. Spatial patterns of soybean cyst nematode: Relationships with tillage and soybean yield. Page 32 in: Proc. Natl. Soybean Cyst Nematode Conf.
17. Goodel, P., and Ferris, H. 1980. Plant-parasitic nematode distributions in an alfalfa field. J. Nematol. 12:136-141.
18. Hershman, D. E., and Bachi, P. R. 1992. Effect of wheat residue and tillage on *Heterodera glycines* cyst development in doublecrop soybeans in Kentucky. (Abstr.) J. Nematol. 24:597.
19. Isaaks, E. H., and Srivastava, R. M. 1989. Applied Geostatistics. Oxford University Press, New York.
20. Jenkins, W. R. 1964. A rapid centrifugal flotation technique for separating nematodes from soil. Plant Dis. Rep. 48:692.
21. Koenning, S. R., Schmitt, D. P., and Barker, K. R. 1995. Impact of crop rotation and tillage system on *Heterodera glycines* population density and soybean yield. Plant Dis. 79:282-286.
22. Larkin, R. P., Gumpertz, M. L., and Ristaino, J. B. 1995. Geostatistical analysis of *Phytophthora* epidemic development in commercial bell pepper fields. Phytopathology 85:191-203.
23. Lawrence, G. W., Johnson, B. B., and McLean, K. S. 1990. Influence of tillage systems on nematode population development and soybean yield responses. (Abstr.) Phytopathology 80(suppl.):S436.
24. Lecoustre, R., and de Reffye, P. 1986. The regionalized variable theory: Possible applications to agronomical research in particular to oil palm and coconut, with respect to epidemiology. Oléagineux 41:541-548.
25. Lecoustre, R., Fargette, D., Fauquet, C., and de Reffye, P. 1989. Analysis and mapping of spatial spread of African cassava mosaic virus using geostatistics and the kriging technique. Phytopathology 79:913-920.
26. Liebhold, A. M., Rossi, R. E., and Kemp, W. P. 1993. Geostatistics and geographic information systems in applied insect ecology. Annu. Rev. Entomol. 38:303-327.
27. Lloyd, M. 1967. Mean crowding. J. Anim. Ecol. 36:1-30.
28. Nelson, M. R., Felix-Gastelum, R., Orum, T. V., Stowell, L. J., and Myers, D. E. 1994. Geographic information systems and geostatistics in the design and validation of regional plant virus management programs. Phytopathology 84:898-905.
29. Niblack, T. L., Heinz, R. D., Smith, G. S., and Donald, P. A. 1993. Distribution, density, and diversity of *Heterodera glycines* in Missouri. J. Nematol. 25:880-886.
30. Nicot, P. C., Rouse, D. I., and Yandell, B. S. 1984. Comparison of statistical methods for studying spatial patterns of soilborne plant pathogens in the field. Phytopathology 74:1399-1402.
31. Olanya, O. M., and Campbell, C. L. 1988. Effects of tillage on the spatial patterns of microsclerotia of *Macrophomina phaseolina*. Phytopathology 78:217-221.
32. Pratt, P. W., and Wrather, J. A. 1998. Soybean disease loss estimates for the southern United States, 1994 to 1996. Plant Dis. 82:114-116.
33. Prot, J. C., and Netscher, C. 1979. Influence of movement of juveniles on detection of fields infested with *Meloidogyne*. Pages 193-203 in: Root-knot Nematodes (*Meloidogyne* species) Systematics, Biology and Control. F. Lamberti and C. E. Taylor, eds. Academic Press, London.
34. Rossi, R. E., Mulla, D. J., Journel, A. G., and Franz, E. H. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62:277-314.
35. Stein, A., Kocks, C. G., Zadocks, J. C., Frinking, H. D., Ruissen, M. A., and Myers, D. E. 1994. A geostatistical analysis of the spatio-temporal development of downy mildew epidemics in cabbage. Phytopathology 84:1227-1239.
36. Subbarao, K. V., Koike, S. T., and Hubbard, J. C. 1996. Effects of deep plowing on the distribution and density of *Sclerotinia minor* sclerotia and lettuce drop incidence. Plant Dis. 80:28-33.
37. Trangmar, B. B., Yost, R. S., and Uehara, G. 1985. Applications of geostatistics to spatial studies of soil properties. Adv. Agron. 38:45-94.
38. Tyler, D. D., Chambers, A. Y., and Young, L. D. 1987. No-tillage effects on population dynamics of soybean cyst nematode. Agron. J. 79: 799-802.
39. Tyler, D. D., Overton, J. R., and Chambers, A. Y. 1983. Tillage effects on soil properties, diseases, cyst nematodes, and soybean yields. J. Soil Water Conserv. 38:374-376.
40. Wallace, M. K., and Hawkins, D. M. 1994. Applications of geostatistics in plant nematology. J. Nematol. 26:626-634.
41. Webster, R., and Boag, B. 1992. Geostatistical analysis of cyst nematodes in soil. J. Soil Sci. 43:583-595.
42. Workneh, F., Tylka, G. L., Yang, X. B., Faghihi, J., and Ferris, J. M. 1999. Regional assessment of soybean brown stem rot, *Phytophthora*

sojae, and *Heterodera glycines* using area-frame sampling: Prevalence and effects of tillage. Phytopathology 89:204-211.
43. Wu, B. M., van Bruggen, A. H. C., Subbarao, K. V., and Pennings, G. G. H. 2001. Spatial analysis of lettuce downy mildew using geostatistics and geographic information systems. Phytopathology 91:134-142.
44. Xiao, C. L., Hao, J. J., and Subbarao, K. V. 1997. Spatial patterns of microsclerotia of *Verticillium dahliae* in soil and Verticillium wilt of cauliflower. Phytopathology 87:325-331.
45. Yang, X. B. 1995. Analysis of variance-to-mean ratios of plant diseases. J. Phytopathol. 143:513-518.