1999

Relationships among tillage, spatial patterns of Heterodera glycines, and soybean yield

Walber Luiz Gavassoni

Iowa State University

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Relationships among tillage, spatial patterns of *Heterodera glycines*, and soybean yield

by

Walber Luiz Gavassoni

A dissertation submitted to the graduate faculty
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Major: Plant Pathology

Major Professors: Gary P. Munkvold and Gregory L. Tylka

Iowa State University

Ames, Iowa

1999
Graduate College
Iowa State University

This is to certify that the Doctoral dissertation of

Walber Luiz Gavassoni

has met the dissertation requirement of Iowa State University

Signature was redacted for privacy.

Co-major Professor
Signature was redacted for privacy.

Co-major Professor
Signature was redacted for privacy.

For the Major Program
Signature was redacted for privacy.

For the Graduate College
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ACKNOWLEDGEMENTS
To Angela and Matheus,

For your love, support, and encouragement.
CHAPTER 1

GENERAL INTRODUCTION

Introduction

_Heterodera glycines_ Ichinohe, the soybean cyst nematode, is the most important pathogen of soybean (_Glycine max_ (L.) Merr., with estimated world yield losses of three million metric tons in 1994 (Wrather et al., 1997). In the United States, _H. glycines_ was first reported in North Carolina in 1954 (Winstead et al., 1955). Since then, the nematode has been detected in several other soybean-producing states, including Iowa. In a recent survey where soybean fields were randomly selected using an area-frame sampling design, Workneh et al. (1999) found _H. glycines_ present in 74% of the fields in Iowa.

_Heterodera glycines_ Dissemination

_Heterodera glycines_, like other plant-parasitic nematodes, has very limited active dissemination, moving on its own power only a few centimeters. Instead, movement of propagules in soil by passive dissemination agents such as animal traffic, plant shipments, cultivation equipment, and other human activities may result in both short- and long-range dispersal (Campbell and Benson, 1994). Cysts of _H. glycines_ have been recovered from seed-size soil peds contained in seed stocks (Epps, 1969), from the digestive tract and excrement of birds (Epps, 1971), and from infested soil adhered to farm machinery, land grading equipment, vehicles, tools, and shoes (Edwards, 1988). It is possible that _H. glycines_ was involuntarily
introduced into the United States when soil was imported from China and Japan to introduce *Bradyrhizobium japonicum* and increase soybean yield (Noel, 1992).

**Spatial Analysis**

Gilligan (1982) defined spatial pattern of a pathogen as the arrangement of inoculum propagules relative to each other. Spatial patterns of pathogens are a result of species-specific characteristics, interspecific associations, and physical, biological, and environmental factors (Campbell and Noe, 1985). The study of spatial patterns of plant-parasitic nematodes provides quantitative information on pathogen population dynamics, and it is important for modeling and simulation activities and design of experiments and sampling strategies (Campbell and Madden, 1990). Spatial patterns have been recognized as aggregated, random, and regular. Generally, plant-parasitic nematodes have an aggregated spatial pattern under field conditions, but this characteristic is scale dependent (Ferris and Wilson, 1987).

The study of spatial patterns of soilborne pathogens, including plant-parasitic nematodes, gained attention in the 1980’s (Nicot et al., 1984; Campbell and Noe, 1985; Noe and Campbell, 1985). However, few reports have been published describing the spatial patterns of plant-parasitic nematodes (Campbell and Benson, 1994). Table 1 shows the frequency and type of spatial analysis used in papers published between 1980 and 1994. There are three general categories that encompass the techniques for quantification of spatial patterns based on the type of data collected. The three categories are based on position of healthy or diseased plants within a row or series of rows, quadrat or plot count data,
Table 1. Frequency and type of analysis used in 13² papers published between 1980-1994 on the analysis of spatial patterns of soilborne plant-parasitic nematodes.

<table>
<thead>
<tr>
<th>Type of Analysis</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maps</td>
<td>5</td>
</tr>
<tr>
<td>Frequency distribution</td>
<td>5</td>
</tr>
<tr>
<td>Indices of aggregation</td>
<td></td>
</tr>
<tr>
<td>V/M</td>
<td>0</td>
</tr>
<tr>
<td>Lloyd’s index of patchiness</td>
<td>2</td>
</tr>
<tr>
<td>Iₜ (morisita)</td>
<td>1</td>
</tr>
<tr>
<td>Taylor’s b (power law)</td>
<td>4</td>
</tr>
<tr>
<td>Morisita’s index of dispersion</td>
<td>1</td>
</tr>
<tr>
<td>Iwao’s patchiness regression</td>
<td>1</td>
</tr>
<tr>
<td>Quadrat variance</td>
<td>1</td>
</tr>
<tr>
<td>Spatial autocorrelation</td>
<td>1</td>
</tr>
<tr>
<td>Runs</td>
<td>0</td>
</tr>
<tr>
<td>Doublets</td>
<td>0</td>
</tr>
<tr>
<td>Geostatistics</td>
<td>3</td>
</tr>
</tbody>
</table>

²Alby et al. (1983); Alston and Schmitt (1987); Boag and Topham (1984); Ferris et al. (1990); Francl (1986); Goodell and Ferris (1980); McSorley and Dickson (1991); McSorley and Parrado (1982); Noe and Campbell (1988); Pennaccio et al., (1985); Todd and Tisserat (1990), Wallace and Hawkins (1994); Webster and Boag (1992).

The sum of the numbers exceed 13 because more than one type of analysis was reported in a paper.

Modified from Campbell and Benson, 1994.
and on distance measurements. A summary of the types of spatial analysis available in plant nematology is presented in Table 2.

**Doublet and Runs Analysis**

Doublet and run analysis has been used to detect whether diseased plants in a homogeneous field have a random or nonrandom occurrence within plant rows (Campbell and Madden, 1990). There are no reports of this technique being used to quantify the spatial patterns of plants parasitized by nematodes (Campbell and Benson, 1994).

**Discrete Distributions**

Early studies of nematode spatial patterns had the objective of fitting a discrete probability distribution to quadrat count frequency data to indicate whether a spatial pattern was random or nonrandom (Noe and Campbell, 1985). The negative binomial most often is the probability distribution used for plant pathosystems (Campbell and Madden, 1990). The negative binomial distribution can be represented as:

\[ P(x) = \left( \frac{k + x - 1}{k - 1} \right) p^k (1-p)^x, \]

where \( P(x) \) is the probability of a quadrat containing \( x \) individuals \( (x = 0, 1, 2, \ldots) \), and \( k \) and \( p \) are parameters, \( k \) can be interpreted as an index of dispersion (Campbell and Madden, 1990).

Goodel and Ferris (1980) systematically sampled an alfalfa field in a 6 m x 6 m grid (1,936 grid intersections over a 7 ha area). Nematodes were extracted from the soil samples using a semi-automatic elutriator and the sucrose flotation
Table 2. Types of analyses available for quantifying the spatial patterns of soilborne propagules of pathogens and root diseases and the information gained from each analysis.²

<table>
<thead>
<tr>
<th>Type of analysis</th>
<th>Random variable</th>
<th>Type of sample unit</th>
<th>Information gained or application</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mapping</td>
<td>Count</td>
<td>Any</td>
<td>Visual display of pattern</td>
</tr>
<tr>
<td>Fitting probability</td>
<td>Count</td>
<td>Quadrat or other discrete area</td>
<td>Random/nonrandom indication; mechanism underlying distribution if sample size and number of data sets are sufficient</td>
</tr>
<tr>
<td>distribution</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Indices of dispersion</td>
<td>Count</td>
<td>Quadrat</td>
<td>Degree of aggregation</td>
</tr>
<tr>
<td>Blocked quadrat variance</td>
<td>Count</td>
<td>Quadrat</td>
<td>Mean size of clusters</td>
</tr>
<tr>
<td>Spatial autocorrelation</td>
<td>Count</td>
<td>Quadrat or sample points at specific locations</td>
<td>Occurrence, size, and shape of clusters, suggestion of type of dispersal</td>
</tr>
<tr>
<td>Geostatistics</td>
<td>Count</td>
<td>Quadrat or sample points at specific locations</td>
<td>Occurrence, size, and shape of clusters, suggestion of type of dispersal, estimation of variable at unsampled locations</td>
</tr>
</tbody>
</table>

²Modified from Campbell and Benson, 1994.
technique. Goodness-of-fit tests on the distributions showed that three of the five species of plant-parasitic nematodes (Helicotylenchus digonicus, Meloidogyne arenaria, and Melinius brevidens) consistently present in the field were described by a negative binomial distribution. The spatial patterns of plant-parasitic nematodes in three fallow vegetable fields located in south Florida also were found to be nonrandom, as their distribution frequencies were best fitted to a negative binomial distribution (McSorley and Parrado, 1982).

Indices of Dispersion

Indices of dispersion or aggregation also have been used by several authors to study spatial patterns of plant-parasitic nematodes. They include variance-to-mean ratio, Lloyd's index of patchiness, Morisita's index of dispersion, Taylor's b (power law), Morisita's index of clumping, and Iwao's patchiness regression (Campbell and Benson, 1994).

The variance-to-mean ratio (VM) is an easy index to calculate and it is the basis for many other indices. It is obtained by computing the mean and variance from all cells or quadrats:

$$VM = \frac{s^2}{\bar{x}},$$

where $s^2$ is the sample variance and $\bar{x}$ is the sample mean. The VM ratio is expected to be less than one for a regular spatial pattern, equal to one for a random pattern, and greater than one for an aggregated pattern. The VM index is dependent on the size of the sampling quadrat, the population density (number of individuals in one sample), and the mean. Spatial pattern of $H.\ glycines$ cyst population densities
were examined before and after spring cultivation (Francl, 1986). The VM ratio of *H. glycines* cysts decreased after plots were cultivated in the spring.

Taylor’s power law establishes that the variance of a population is proportional to a fractional power of the mean (Ferris et al., 1990):

\[ S^2 = a \times^b \]

Where \( S^2 \) and \( x \) are estimates of \( \sigma^2 \) and \( \mu \), respectively, and \( a \) and \( b \) are parameters. Taylor’s \( b \) is considered a dispersion index. It was initially proposed to be species-specific, but the current thought is that \( b \) is not fixed for any one species (Campbell and Madden, 1990). Boag and Topham (1984) used Taylor’s power law to determine aggregation of several nematode species. They found that aggregation of *Longidorus elongatus* and other plant-parasitic nematodes varied according to the sampling scale; samples taken at distance of 3 to 5.7 cm apart revealed no aggregation whereas samples taken at distances greater than 5.7 cm indicated presence of spatial aggregation.

Another index is Lloyd’s index of patchiness (LIP), developed by Lloyd (1967). It is calculated as:

\[
LIP = \frac{\bar{x} + (s^2 / \bar{x}) - 1}{\bar{x}}
\]

\( s^2 \) and \( \bar{x} \) are estimates of \( \sigma^2 \) and \( \mu \), respectively.

Lloyd’s index of patchiness was used to characterize the spatial pattern of *Paratylenchus dianthus* in a commercial crop of carnations grown in greenhouse (Pennacchio et al., 1985). Soil samples were collected systematically, and LIP was greater than one, indicating that the population was aggregated. As the nematode
population density increased, the aggregation decreased but the spatial pattern did not evolve to a random spatial pattern. Ferris et al. (1990) suggested that ectoparasitic nematodes, like *Paratylenchus dianthus*, spend part of their life moving and selecting feeding sites and eggs are deposited individually as they move through the soil, resulting in a less aggregated spatial pattern compared to sedentary parasites.

The Morisita index of dispersion is calculated as:

$$I_d = \frac{n}{\left(\sum x\right)^2} \left[\sum \left(x^2\right) - \sum x\right]$$

where $x$ represents the count in each sample. The Morisita index of dispersion and the Lloyd's index of patchiness are very similar and tend to have the same numerical value when counts are very high (Campbell and Madden, 1990).

In an analysis of the spatial pattern of *Pratylenchus scribneri* and *Hoplolaimus galeatus* associated with soybean roots, Alby et al. (1983) used Morisita’s index to quantify changes in the nematode spatial pattern due to tillage and nematicide treatment. Application of carbofuran reduced aggregation of *H. galeatus* and had an opposite effect on *P. scribneri*. Conventional tillage resulted in higher aggregation of *P. scribneri* than no tillage. It was suggested that carbofuran reduced population densities of *P. scribneri* below detectable levels in many plots, whereas residual population densities of *H. galeatus* were present in all plots following the nematicide application.

Dispersion indices based on the mean and variance typically ignore the information on the location of the variate units (Campbell and Benson, 1994). It has
been demonstrated that distinct spatial patterns may have identical variance and mean (Nicot et al. 1984). Important spatial information may be lost if dispersion indices are used as the only indication of spatial processes.

The quadrat variance spatial analysis provides more information on the average size of clusters of propagules than frequency distributions or indices of dispersion (Campbell and Madden, 1990). Spatial patterns of Meloidogyne incognita, Tylenchorhynchus claytoni, Helicotylenchus dihystera, and Criconemella ornata were analyzed using two term local quadrat variance (Noe and Campbell, 1985). Data were collected from tobacco fields in a systematic manner, and it was found that clusters were ellipsoidal with long axes oriented along plant rows. Franci (1986), studying the spatial pattern of H. glycines, found that clusters were 1-3 m long before cultivation and 5-6 m after cultivation.

Spatial patterns of plant-parasitic nematodes also have been studied through autocorrelation analysis. Spatial autocorrelation detects aggregation by comparing the degree of similarity in nematode populations among adjacent quadrats (Campbell and Benson, 1994). Noe and Campbell (1985) examined spatial patterns of Meloidogyne incognita, Tylenchorhynchus claytoni, Helicotylenchus dihystera, and Criconemella ornata in seven tobacco fields. They found that spatial autocorrelation was greater in the fall than in the spring and was greater among 1 x 1 m quadrats than among 3 x 3 m quadrats.

Geostatistics has been used increasingly by plant pathologists to characterize spatial patterns of pathogens and plant diseases at plot, field, and regional scales (Nelson et al., 1999). A geostatistical analysis typically consists of three steps:
description of the spatial structure allowing quantification of spatial dependency; modeling; and kriging, which is prediction at unsampled locations (Maravelia, 1996). Spatial patterns of *Globodera rostochiensis* and *Heterodera avenae* were found to be aggregated with the range of spatial dependence of approximately 60 m (Webster and Boag, 1992). Geostatistics also were used to characterize the spatial pattern of plant-parasitic nematodes in a reed canary-grass field in Minnesota (Wallace and Hawkins, 1994). Except for *Tylenchus maius*, all other consistently present nematodes were present in varying degrees of spatial aggregation.

Previous research has not elucidated the effects of tillage on *H. glycines* spatial pattern, dissemination, and population densities. The spatial pattern of *H. glycines* and other nematodes within conventionally tilled fields has been investigated (Alston and Schmitt, 1987; Francl, 1986), and these studies have provided some basis of our knowledge of the effect of spatial pattern on yield loss. There has been some research on the effects of cultural practices, including tillage, on overall *H. glycines* population density (Koenning et al., 1993; Niblack et al., 1994; Schmitt, 1991), but these studies have not detected consistent effects and the full range of tillage types has not been studied. None of these studies has investigated the effects of tillage on *H. glycines* dissemination and subsequent effects on yield loss to the nematode. The objectives of this research were:

1. Quantify changes in the spatial pattern and population density of *H. glycines* in plots naturally infested and subjected to different tillage systems.

2. Determine the impact of tillage practices on *H. glycines* dissemination, reproduction, and yield impact on soybeans.
3. Determine the relationship among soil properties and *H. glycines* population densities.

**Dissertation Organization**

This dissertation consists of five chapters, organized as a general introduction, three chapters presented as separate journal manuscripts, a general summary, and an appendix. The three separate papers will be submitted for publication to Phytopathology, Plant Disease, and Journal of Nematology. Tables and figures follow the literature cited section within each paper. The appendix contains supplemental data from the first paper.

**Literature Cited**


CHAPTER 2

RELATIONSHIPS BETWEEN TILLAGE WITH SPATIAL PATTERNS OF

HETERODERA GLYCINES

A paper to be submitted to Phytopathology

Walber L. Gavassoni, Gary P. Munkvold, and Gregory L. Tylka

First author: Departamento de Ciências Agrárias, Universidade Federal de Mato Grosso do Sul, Caixa Postal 533, 79804-970 Dourados, MS, Brazil.

Second and third authors: Department of Plant Pathology, Iowa State University, Ames 50011-1020.

Accepted for publication

Corresponding author: G. P. Munkvold; E-mail address: munkvold@iastate.edu

Abstract

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) applied to 15 x 30 m plots. Soil samples were taken from 98 5.2-m² contiguous quadrats in the fall of 1994, before any tillage was performed, and in the spring of the following three years shortly after planting. Cysts were extracted from soil samples by elutriation and counted, then eggs were extracted from cysts and enumerated. Semivariance values were calculated for cyst and egg densities and semivaro grams were constructed. Tillage practices resulted in changes in semivariogram parameters (sill, nugget effect, and
range of spatial dependence) estimated by the spherical model. In one field, which had an aggregated initial *H. glycines* population, there was an increase of 350% in the sill values for cyst populations after three years of no tillage, but the range of spatial dependence did not change, with values remaining close to the initial (38.4 m). In the conventional-tillage treatment, the range of spatial dependence for cyst and egg populations and the sill for egg populations decreased over time as tillage was implemented. Semivariograms for cyst and egg population densities revealed strong anisotropy along the soybean rows, coincident with the direction of tillage practices. In a second field, with low initial aggregation of *H. glycines* population densities, there was little measurable change in the spatial pattern after three years; in the conventional-tillage treatment sill and the proportion of the sill explained by spatial dependence decreased for the cyst population densities. Our results indicated that in fields with initial aggregated population densities, no tillage and ridge tillage promoted aggregation of the nematode population, but conventional and reduced tillage resulted in a more uniform spatial pattern.

**Introduction**

*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 in most areas of the world where this nematode is found and soybeans are cropped (Doupnik, 1993; Pratt and Wrather, 1998). Plant-parasitic nematodes have a limited ability to move on their own power (Prot and Netscher, 1979), so movement of infested soil plays an important role in the dissemination of the
nematode within and between fields. Cysts of *Heterodera glycines* have been recovered from soil peds contained in seed stocks (Epps, 1969), from the digestive tract and excrements of birds (Epps, 1971), and from soil on farm machinery, land grading equipment, vehicles, tools, and shoes (Edwards, 1988).

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 *Heterodera glycines* population densities generally are lower in no-tillage systems compared to conventional tillage (Tyler et al., 1983; Tyler et al., 1987; Lawrence et al., 1990; Edwards et al., 1988; Hershman and Bachi, 1992; Koenning et al., 1995; Workneh et al., 1999).

The spatial pattern of nematodes often is described as aggregated, but there are few reports quantifying or describing the aggregation (Goodel and Ferris, 1980; Franci, 1986; Webster and Boag, 1992). Franci (1986), using two-term local variance analysis, measured cyst cluster sizes of *H. glycines* of 1 to 3 m and found that cultivation reduced aggregation of the cyst population. Alston and Schmitt (1987), studying spatial pattern of *H. glycines* in relation to soybean phenology, found greater population densities closer to the plant rows than in between rows. However, these studies did not investigate the effects of different tillage practices on *H. glycines* spatial pattern on a multi-year basis. The study of the interseasonal dynamics of spatial patterns may be important for the understanding of epidemic processes and formulation of management strategies (Campbell and Benson, 1994).
Geostatistics have gained increased attention from plant pathologists for characterizing spatial patterns of plant diseases and pathogens, including cyst nematodes (Lecoustre and de Reffye, 1986; Chellemi et al., 1988; Webster and Boag, 1992; Donald et al., 1994; Lecoustre et al., 1989; Nelson et al., 1994; Stein et al., 1994; Wallace and Hawkins, 1994; Larkin et al., 1995; Xiao, 1997). Geostatistics encompass a set of statistical methods for characterizing spatial patterns (Rossi et al. 1992) and can be used to detect changes in spatial pattern over time (Lecoustre et al., 1989). The objective of this research was to evaluate the effects of tillage on the spatial patterns of *H. glycines* using geostatistical analysis. Preliminary results of this research were reported earlier (Gavassoni et al. 1996, Gavassoni et al. 1998, and Gavassoni et al. 1999).

**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 Northern Research and Demonstration Farm (Hancock County, IA). In the Bruner Farm, the soil was a Canisteo silty clay loam (17.5% sand, 75% silt, 7.5% clay). At the Northern Research and Demonstration Farm, hereafter designated as Kanawha Farm, the soil was a Canisteo silty clay loam, fine loamy, mixed (calcareous) Typic Haplaquolls (22.5% sand, 70% silt, 7.5% clay). Both areas were cropped to soybeans in 1994, and no tillage was performed in the fall of 1994.

Plots were 15 x 30 m with 20 plant rows spaced 0.76 m apart. Plots were planted between mid May and mid June of each year with the *H. glycines* -
susceptible soybean cv. Archer (Phytophthora root rot resistant, brown stem rot resistant and iron chlorosis tolerant). Row orientation was north-south in the Bruner Farm and east-west in 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 the 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 in the plant row orientation, in alternating directions in successive years. In each location, a single plot received each treatment. In 1995, plots receiving conventional tillage were chisel plowed in the spring and then were disked. Pre-emergence application of a mixture of dicamba (0.58 l ha$^{-1}$) and 2,4-D amine (4.7 l ha$^{-1}$) controlled weeds. All plots were treated with herbicides and, except for no tillage, all plots were cultivated for supplemental weed control 30 days after planting. Plots under no tillage were manually weeded.

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

Soil samples were collected from a 2.3-m, square grid superimposed on the plant rows (98 5.2-m\(^2\) contiguous quadrats). Flags were posted in each plot to facilitate accurate location of the grid for repeated sampling. Samples were collected in the fall of 1994 and then in the spring of 1995, 1996, and 1997 within a week of planting. Results obtained from the first sampling date represent the initial spatial pattern for all treatments whereas results from the spring of 1995 are a result of changes in the spatial pattern are due to tillage and over winter survival. Sampling in the subsequent years always was done in the spring after tillage and planting. Soil cores were collected systematically from each plot; three 2.5-cm-diameter, 20-cm-deep soil cores were collected from each intersection of the grid. The soil cores from each intersection were combined and mixed to form a single sample and were stored at 4\(^\circ\)C. Cysts were recovered from an 100-cm\(^3\) aliquant of soil by elutriation (Byrd et al., 1976). Each 100 cm\(^3\) aliquant of soil was soaked for 30 min in a 15.75 g/L solution 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 (1964). The sucrose concentration used was 1.37 kg L\(^{-1}\) water instead of 0.45 kg L\(^{-1}\) as originally described, and floating cysts were recovered after the centrifugation in water. Results of preliminary experiments indicated that greater sucrose concentration increased cyst recovery efficiency. For 1994, samples taken in 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 using a sucrose solution of 0.45 kg L\(^{-1}\), and a second set of samples from the same treatment were processed without the sucrose centrifugation step. Cysts were counted, then eggs were extracted from cysts using a motorized pestle and were stained in acid fuchsin (Niblack et al., 1993), then counted. Eggs were enumerated using a nematode counting slide (Olympic Equine, Issaquah, WA) and a dissecting microscope at 24x magnification. The numbers of cysts and eggs 100\(^{-1}\) cm\(^3\) of soil were calculated for each sample.

Soybeans were harvested mechanically in the fall with a plot combine in subplots consisting of two soybean rows 6.1 m long (40 subplots per plot). Seed moisture was determined by a Dole 400 Grain Moisture Tester (Eaton Corp., Carol Stream, IL). The seed weight was adjusted to a 13% moisture level. Linear correlation coefficients were calculated for the relationship between soybean yield and mean \(H. \text{glycines}\) egg density within the subsample area.

Geostatistical analysis was used to quantify the effects of tillage on the spatial patterns of \(H. \text{glycines}\). Geostatistics is a set of statistical tools for detection, modeling, and prediction of spatial patterns (Rossi et al., 1992). A geostatistical analysis typically consists of three steps: description of the spatial structure allowing quantification of spatial dependency, modeling, and kriging, which is prediction of values at unsampled locations (Maravelia et al., 1996). The semivariogram is the function most frequently used to characterize spatial dependency, and it is a plot of the semivariance (half of the squared difference between values separated by a
distance h) on the y axis versus distance between pairs of samples on the x axis (Oliver and Webster, 1991, Oliver, 1987). If values are spatially dependent, semivariance values increase as the distance between pairs of samples increase and then semivariance values level off. The constant semivariogram value is called the sill, and it is related to the overall variance of the samples. The two components of the sill are the spatially structured variance and the nugget effect. The ratio of the spatially structured variance to the sill indicates the proportion of the sill explained by spatial dependence. The distance at which the sill is reached is called the range of spatial dependence and represents the maximum distance between pairs of samples that are spatially related. In theory the semivariogram value for distance zero is zero, but the y-intercept usually has some positive value called the nugget effect. Nugget effect is caused by measurement error and by spatial dependence at distances smaller than the smallest sampling distance. When semivariance values immediately take their maximum values, resulting in a flat semivariogram, the phenomenon is known as pure nugget effect and represents a random spatial pattern (Lecoustre et al., 1989).

Spatial dependency was analyzed using a geostatistical program, GS$^+$ version 2.3b (Gamma Design Software, Plainwell, MI). Semivariance values for cyst and egg densities were calculated using an active lag of 22.0 m (maximum 31.5 m) and the minimum active step of 2.3 m. Semivariograms may depend not only on distance between pairs of samples but also on the direction (anisotropy). The presence or absence of anisotropy was tested by examining semivariograms for 0, 45, 90, and 135°, where 0° is the direction along the soybean rows and 90° is the
direction perpendicular with the soybean rows. Linear and non-linear models were fitted to the semivariogram values by weighted least squares regression to estimate the nugget effect, sill, and range. The best-fit model then was used to estimate population densities through kriging on a grid of 0.3 x 0.3 m. Maps of cyst and egg population densities were generated with the kriged estimates from isotropic models. Lloyd’s index of patchiness (LIP), an aggregation index developed by Lloyd (1967), was calculated for cyst and egg data for each tillage system and sampling date.

Results

Geostatistical Analyses

Kanawha Farm Experiment

Semivariograms were best described by the spherical and Gaussian models. Semivariogram parameters for cyst and egg population densities, estimated by the spherical model, are presented in Tables 1 and 2. Initially, all plots at the Kanawha Farm experiment had aggregated *H. glycines* populations (Figs. 1-4) with semivariance values increasing as the distance between pairs of samples increased. Eventually the semivariance values became a constant value.

Cyst Populations

*Heterodera glycines* cyst populations became more spatially dependent over time in plots under no tillage and ridge tillage than in conventional and reduced tillage. Increases in range and sill values, an increase in the proportion of the sill explained by spatial dependence, and a decrease in the size of the nugget effect indicated increases in spatial dependence. After three years of no tillage, there was
an increase of 350% in the sill value but over the same time period, the nugget variance values decreased by more than 60%. The range of spatial dependence oscillated between 31.6 and 45.3 m but maintained values close to the initial (38.4 m). 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.

Anisotropy was detected in the conventional tillage treatment in the fall of 1994, before any tillage had been implemented (Table 1). After soil was disturbed by conventional tillage in the spring of 1995, the range of spatial dependence was reduced to zero across the plant rows and by 35% along the plant rows (37.2 m to 24.3 m). After 1994, the nugget variance was negligible and the sill decreased for two years, but then increased in 1997. In the reduced-tillage treatment, the sill also decreased, but returned to a value similar to 1994 in 1997. There were no major changes in the range for the reduced-tillage treatment over the time period of this study.

Kriged maps of cyst population densities are presented in Fig. 5. Initially there was a greater population in the west portion of most plots compared to the east side. However, this area became less prominent as conventional tillage was implemented. Conversely, an area of greater cyst population densities developed over the 3 years of the experiment in the plots under no tillage and ridge tillage.

*Egg Populations*

Anisotropy was detected in at least one year in all treatments (Table 2). In the no-tillage, ridge-tillage, and reduced-tillage treatments, anisotropy disappeared between the fall of 1994 and the spring of 1995, while in the conventional-tillage
treatment, it was still present by the spring of 1998. Spatial dependence initially decreased in the no-tillage and ridge-tillage treatments (indicated by a reduction in the sill), but then it began to increase. *Heterodera glycines* egg populations became more uniformly distributed after three years of conventional and reduced tillage being implemented in the plots. Conventional tillage resulted in 85% reduction in the sill and nugget variance values, while the range of spatial dependence disappeared along the soybean rows and was reduced from 36.1 m to 29.7 m across the rows. The nugget and sill variance also decreased in the reduced-tillage treatment, but the range of spatial dependence remained similar from 1994 to 1997.

Kriged maps of egg densities are presented in Fig. 6. As with cyst population densities, initially there were greater egg population densities in the west portion of all plots than in the east portion. In the conventional-tillage and reduced-tillage plots, this area of greater population densities became less concentrated as tillage was implemented in the plots.

**Bruner Farm Experiment**

*Cyst Populations*

The initial spatial pattern of cyst populations 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, but spatial dependence was not as strong as in the plots located at the Kanawha Farm (Table 3, Figs. 7 and 8). Sill values generally were less than half those occurring in the Kanawha experiment, and the proportion of the sill explained by spatial dependence...
ranged from 0.27 to 0.69 compared to 0.44 to 1.00 at Kanawha. Anisotropy was
detected in the no-tillage and reduced-tillage plots.

In the no-tillage treatment, the semivariance values calculated for 1997 could
not be described by any model. Consequently, only 1995 and 1996 data are
compared. No major changes in the semivariogram parameters occurred in two
years in the no-tillage treatment. In the conventional-tillage treatment, spatial
dependence decreased over time. The range of spatial dependence decreased from
24.1 m 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, sill,
and range 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 the range increased.

Kriged maps of spatial patterns of cysts of *H. glycines* are shown in Fig. 9. No
model could describe the semivariance values for the 1997 no-tillage plot and,
consequently, kriging could not be performed. The area with greater cyst population
densities increased over time in the ridge tillage plot, but there was not a clear trend
in the other tillage treatment plots.

*Egg Populations*

Semivariograms calculated for the conventional-tillage treatment were linear
with a slope near zero, indicating *H. glycines* egg populations in that plot were not
spatially dependent at the 2.3 m sampling interval (Table A1, Fig. A1). The absence
of spatial dependence for some sampling times and the inconsistency of the
semivariogram parameters made impossible any attempt to compare changes in
spatial patterns. Anisotropic semivariograms are presented in Fig. A2. Because no model could be fitted adequately to the egg semivariograms, only the densities measured at the sampling points are presented in Fig. A3.

*Heterodera glycines* population dynamics

**Kanawha Farm Experiment**

Cyst population densities fluctuated annually in all plots (Table 4), without a consistent trend across treatments. In the conventional-tillage plot, the population density decreased from 1994 to 1995 and then stabilized. Initial egg population densities were similar, but final population densities were greater in the no-tillage and ridge-tillage treatments compared to conventional- and reduced-tillage treatments. There was a general decrease in the 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.

Maps of change in the cyst and egg populations are illustrated in Figs A4 and A5. After four years of no tillage, the population densities increased in the west portion of the plot and decreased in the east portion, while there was no clear trend in the other tillage treatments. The average population changes are presented in Table A3.

**Bruner Farm Experiment**

Cyst population densities generally increased overtime, ranging from 137 to 253 cysts in 1995 and from 265 to 570 cysts $100^{-1}$ cm$^{-3}$ in 1997. Cyst population densities increased in all plots from the spring of 1995 to the spring of 1996 (Table
4), but maps of the population change (Fig. A6) do not reveal any trend in terms of specific areas of the plots where reproduction was promoted or suppressed. The average population density changes are presented in Table A3. There was a consistent increase in the egg population densities from 1994 to 1995. After 1995, egg population densities fluctuated between 3,036 to 5,841 eggs 100\(^{-1}\) cm\(^{-3}\) without a consistent trend. Similarly, changes in egg population densities were not consistent nor restricted to specific areas of the field (Fig. A7).

**Lloyd’s Index of Patchiness**

Lloyd’s index of patchiness for the number of cysts and eggs was greater than 1.0 in all plots at both locations, indicating aggregation of the *H. glycines* population (Tables 1, 2, 3 and A1). But LIP did not indicate changes in the spatial pattern of *H. glycines* populations as geostatistical analyses did. Lloyd’s index of patchiness values generally were greater for egg populations than cyst populations and greater at the Kanawha location than the Bruner location.

**Soybean Yield**

Yields of soybean at both locations are presented in Table 5. Soybean yields decreased over time in all plots at the Kanawha Farm Experiment, and linear correlation coefficients between nematode population densities and soybean yields were significant and negative (Table 6). Consistently lower linear correlation coefficients were obtained for the conventional-tillage treatment compared with the no-tillage treatment. In general, soybean yields at the Bruner Farm experiment were
lower than at the Kanawha plots. Soybean planted in the no-tillage and reduced-tillage plots yielded less than in the conventional- and ridge-tillage plots. Yield decreased over time in the ridge- and conventional-tillage plots and was relatively constant in the no-tillage and reduced-tillage plots. There was no clear relationship between soybean yield and nematode population densities in the Bruner Farm Experiment (Table 6). At the Kanawha Farm, plants in the west portion of the plots, an area coincident with high *H. glycines* population densities, would consistently exhibit symptoms of early maturity by the end of August and beginning of September. Yield was reduced in this portion of the field.

**Discussion**

Geostatistical analysis was used to quantify the effects of tillage on the spatial patterns of *H. glycines*. This is the first report where geostatistics is used to elucidate the 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. Considering that *H. glycines* is a sedentary endoparasite, it is reasonable to speculate that secondary infections are more likely to happen adjacent to the primary infection site. Then, in the absence of soil disturbance by tillage, aggregation would tend to increase over the years. A similar effect would be expected in the ridge-tillage treatment, which involved raising the seedbed level above the
surrounding soil and then having the plant rows in the same location year after year. Our results also indicated that in a field with less aggregated populations (Bruner Farm), different tillage practices may result in little or no measurable change in the spatial pattern of *H. glycines*.

Most of the oriented semivariograms for cyst populations from the Kanawha Farm experiment revealed no anisotropy, indicating that semivariance values were dependent only on the distance between pairs of samples and not on the orientation. Anisotropy or directional variability was detected only in the conventional tillage treatment, and spatial dependence was eliminated across the soybean rows and reduced along the plant rows. Conventional tillage always was performed along the major axis of the plot and, consequently, it may have strengthened anisotropy.

Conventional tillage tended to reduce the range of spatial dependence at the Kanawha Farm, but it did not reduce the range to distances smaller than the sampling interval (2.3 m) and, consequently, the nugget effect did not increase. At the Bruner Farm, nugget effect was high compared to the sill and it 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 not as strongly aggregated as at the Kanawha Farm.

At the Kanawha Farm, from 1994 to 1996 the sill values estimated from the cyst population were reduced as the nematode spatial patterns were disrupted by conventional tillage. In 1997, there was an increase in the sill values for most treatments, which we can not explain. At the Bruner Farm experiment, sill values fluctuated without a clear trend as tillage was implemented. We believe that the
more random spatial pattern in the Bruner conventional-tillage plot 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 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 the semivariance values from egg data. The decrease in variability most likely was caused by a redistribution of the *H. glycines* population, resulting in a more uniform distribution of cysts and, consequently, eggs. Other researchers have reported decrease in the spatial variability of soilborne pathogens due to soil tillage. Francl (1986), investigating the spatial patterns of *H. glycines* in field plots, also observed reduction in variance after the plot was disked and bedded. Olanya and Campbell (1988), studying the effects of tillage on the spatial patterns of microsclerotia of *Macrophomina phaseolina*, found that variance, variance-to-mean ratio, and Morisita’s index decreased as tillage was implemented. Spatial patterns of *Sclerotinia minor* sclerotia became more uniform, as measured by LIP, after the soil was deep plowed (Subbarao et al., 1996).

In most plots, there was a strong spatial dependence of the nematode population as indicated by the high proportion of the sill explained by spatially structured variance (sometimes equal to 100%). In the ridge-tillage treatment in 1994, the nugget variance was high in relation to the sill value, resulting in only 44% of the sill being explained by spatial dependence. This relatively low proportion of sill to nugget variance could be caused, in part, by the poor efficiency of the cyst
extraction since soil samples were processed using only 1/3 of the sucrose concentration used for the other treatments/sampling times. Another possibility is the presence of spatial dependence at a distance smaller than the 2.3 m used in our experiments. Samples collected from the ridge-tillage plot after 1994 exhibited smaller values of the nugget variance compared to 1994. 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 non-spatial variance associated with numbers of eggs per cyst may have increased the nugget effect for egg semivariograms. The range values were greater for cyst populations than for egg populations in the no-tillage and ridge-tillage plots, while the opposite was true for the conventional- and reduced-tillage treatments. The presence of numerous recently formed cysts, containing more eggs than older cysts, would tend to have a disproportionate, greater effect on egg semivariograms compared to cyst semivariograms. In the no-tillage and ridge-tillage treatments, these new cysts probably remained in close proximity to their original sites, resulting in a shorter range for egg semivariograms. The movement of newly formed cysts (and their high egg numbers) in the tilled treatments resulted in longer ranges for egg semivariograms in these treatments.

The range of spatial dependence, estimated by the spherical model, initially was greater than the plot dimensions, indicating that the spatial structure of *H. glycines* population was beyond the plot limits. There was a definite reduction of the range for cyst population densities in the conventional-tillage plots at both
experimental sites. Previous research of spatial patterns of cyst nematodes have
detected ranges of 60 m and 29 m for *Heterodera avenae*, 107 m for *Globodera
rostochiensis* (Webster and Boag, 1992), and 40 m for *Heterodera trifolii* (Wallace
and Hawkins, 1994). Ranges obtained in this study were on a similar scale to these
studies. The range parameter is not species-specific, and it probably will change
between fields according to physical and biological soil characteristics, crop history,
and cultural practices.

In a field 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 continuously grown in our experiments.
Although we had continuous soybean monoculture in our plots, tillage was
performed as in a conventional corn-soybean rotation.

Adding the sucrose centrifugation step to the *H. glycines* extraction
procedures may improve the 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 when samples
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.

Analysis of cyst data in addition to the egg data helped clarify the dynamics of spatial patterns of *H. glycines* because the results of the analyses of egg data were not conclusive in some cases. Forces determining *H. glycines* spatial pattern typically are exerted on cysts rather than individual eggs. The variable number of eggs per cyst adds a non-spatial source of variance that may mask spatially structured variance if only egg data are used.

High population densities of *H. glycines* were detected at west portion of the plots at Kanawha. That area is where the field entrance is located, indicating the possibility that the nematode might initially have been introduced in that area.

The degree of aggregation, as measured by LIP, varied with treatment, sampling time, and nematode life stage enumerated. Lloyd's index of patchiness obtained from egg counts was greater than when LIP was calculated from the cyst data. It is possible that the variable number of eggs per cyst, with some cysts containing no eggs and others with several hundred eggs, played a major role in this result. Lloyd's index of patchiness is affected by the magnitude of the mean (Campbell and Madden, 1989). At the Bruner Farm, egg counts resulted in semivariograms with slopes near zero, indicating absence of spatial dependence at the sampling intensity of 2.3 m grid, while LIP indexes for the same treatments and sampling time were greater than 1.0, indicating aggregation of the nematode population. It is possible that spatial dependence, if present, occurred on a scale too large or too small to be detected with the plot size and sampling interval we used.
We were not able to detect changes in the LIP index due to tillage. Other researchers have used LIP and other dispersion indexes, such as variance-to-mean ratio and Morisita’s index of dispersion, successfully to identify changes in spatial pattern of soilborne pathogens (Olanya and Campbell, 1988; Campbell and van der Gaag, 1993; Subbarao et al., 1996; Xiao et al., 1997). The limitation of LIP and other dispersion indices is that they do not take into account the position of the samples and, consequently, do not reflect the spatial structure of soilborne plant pathogens (Nicot et al., 1984).

Strong aggregation generally was associated with strong correlations between nematode population densities and soybean yields. The reduction in the spatial dependence in the conventional-tilled plots was accompanied by a reduction in the linear correlation coefficients between nematode population densities and soybean yield. Also, at the Bruner Farm where nematode aggregation was weak, there was a weak relationship between the nematode population densities and soybean yield regardless of tillage treatment. It is likely that nematode damage is greater in localized areas of the field when *H. glycines* populations are aggregated than in areas with a more uniform spatial pattern. Research is needed to elucidate the relationship between spatial patterns of *H. glycines* and yield losses in soybeans.

**Literature Cited**


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.


validation of regional plant virus management programs. Phytopathology 84:898-905.


Table 1. Semivariogram parameters, estimated by the spherical model, and Lloyd's Index of Patchiness (LIP) for *Heterodera glycines* cyst population densities in plots under different tillage systems at the Kanawha Farm experiment in 1994, 1995, 1996, and 1997.

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time</th>
<th>( C_0 ) (x10^3)</th>
<th>( C_0 + C ) (x10^3)</th>
<th>( C/(C_0 + C) )</th>
<th>( A_0 ) (m)</th>
<th>( R^2 )</th>
<th>LIP</th>
</tr>
</thead>
<tbody>
<tr>
<td>No F94</td>
<td>0.3</td>
<td>17.6</td>
<td>0.99</td>
<td>38.4</td>
<td>0.99</td>
<td>1.3</td>
<td></td>
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<tr>
<td>S95</td>
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<td>23.6</td>
<td>0.71</td>
<td>1.7</td>
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</tbody>
</table>

^F=fall, S=spring
\( C_0 \)=Nugget variance, the value of the semivariogram near the origin, representing microdistributional and measurement error.
\( C_0 + C \)=Sill, the limiting value of the semivariogram for large distances or the semivariance value beyond range of spatial dependence.
\( C/(C_0 + C) \)=proportion of the sill explained by spatially structured variance.
\( A_0 \)=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.
^wThe range parameter across the plant rows, when anisotropy was present.
^lThe range parameter along the plant rows, when anisotropy was present.
Table 2. Semivariogram parameters, estimated by the spherical model, and Lloyd’s
Index of Patchiness (LIP) for *Heterodera glycines* egg population densities in plots
under different tillage systems at the Kanawha Farm experiment in 1994, 1995,

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time</th>
<th>( C_0^\gamma ) ( \times10^6 )</th>
<th>( C_0+C^x ) ( \times10^6 )</th>
<th>( C/(C_0+C)^w )</th>
<th>( A_0^\gamma ) (m)</th>
<th>( R^2 )</th>
<th>LIP</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td>F 94</td>
<td>0.0</td>
<td>61.3</td>
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<td>9.9</td>
<td>0.50</td>
<td>20.8</td>
<td>0.95</td>
<td>1.7</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>11.9</td>
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<td>0.78</td>
<td>31.8</td>
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<td>1.5</td>
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<tr>
<td>Reduced</td>
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<td>8.2</td>
<td>39.3</td>
<td>0.79</td>
<td>38.3</td>
<td>0.90</td>
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<tr>
<td></td>
<td>F 94</td>
<td>16.2</td>
<td>48.0</td>
<td>0.66</td>
<td>19.3</td>
<td>38.9</td>
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</tr>
<tr>
<td></td>
<td>S 95</td>
<td>1.6</td>
<td>14.3</td>
<td>0.89</td>
<td>47.8</td>
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<td></td>
<td>S 96</td>
<td>3.2</td>
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</tr>
<tr>
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<td>S 97</td>
<td>2.8</td>
<td>8.9</td>
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<td>41.0</td>
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<tr>
<td>Conventional</td>
<td>F 94</td>
<td>22.6</td>
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<td>22.9</td>
<td>36.1</td>
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<tr>
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<td>36.6</td>
<td>39.1</td>
<td>0.90</td>
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<tr>
<td></td>
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<td>0.66</td>
<td>0.0</td>
<td>29.7</td>
<td>0.64</td>
</tr>
</tbody>
</table>

^2F=fall, S=spring
\(^\gamma C_0=Nugget variance, the value of the semivariogram near the origin, representing microdistributional and measurement error.
\(^x C_0+C=Sill, the limiting value of the semivariogram for large distances or the semivariance value beyond range of spatial dependence.
\(^w C/(C_0+C)=proportion of the sill explained by spatially structured variance.
\(^\gamma A_0=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.

^uThe range parameter along the plant rows, when anisotropy was present.

^lThe range parameter across the plant rows, when anisotropy was present.
Table 3. Semivariogram parameters, estimated by the spherical model, and Lloyd’s Index of Patchiness (LIP) for *Heterodera glycines* cyst population densities in plots under different tillage systems at the Bruner Farm experiment in 1995, 1996, and 1997.

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time</th>
<th>C₀ (^{\text{a}}) (x10^3)</th>
<th>C₀+C (^{\text{a}}) (x10^3)</th>
<th>C/(C₀+C) (^{\text{a}})</th>
<th>A₀ (^{\text{a}}) (m)</th>
<th>R²</th>
<th>LIP</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td>S 95</td>
<td>3.4</td>
<td>7.5</td>
<td>0.55</td>
<td>33.8</td>
<td>0.88</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>5.4</td>
<td>8.8</td>
<td>0.38</td>
<td>34.6</td>
<td>0.48</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>S 97</td>
<td>..</td>
<td>..</td>
<td>..</td>
<td>..</td>
<td>..</td>
<td>1.1</td>
</tr>
<tr>
<td>Ridge</td>
<td>S 95</td>
<td>2.5</td>
<td>5.6</td>
<td>0.54</td>
<td>14.2</td>
<td>0.92</td>
<td>1.1</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>4.1</td>
<td>10.0</td>
<td>0.58</td>
<td>10.4</td>
<td>0.84</td>
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<td></td>
<td>S 97</td>
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<td>0.58</td>
<td>15.8</td>
<td>0.77</td>
<td>1.1</td>
</tr>
<tr>
<td>Reduced</td>
<td>S 95</td>
<td>4.7</td>
<td>6.7</td>
<td>0.30</td>
<td>23.5</td>
<td>0.84</td>
<td>1.2</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>7.8</td>
<td>18.1</td>
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<td>39.8</td>
<td>0.62</td>
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<td>S 97</td>
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<td>63.2</td>
<td>0.61</td>
<td>1.2</td>
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<td>24.1</td>
<td>0.98</td>
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</tr>
<tr>
<td></td>
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<td>17.8</td>
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<td>1.1</td>
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<tr>
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<td>0.27</td>
<td>13.2</td>
<td>0.70</td>
<td>1.1</td>
</tr>
</tbody>
</table>

\(^{\text{a}}\)S=spring  
\(^{\text{b}}\)C₀=Nugget variance, the value of the semivariogram near the origin, representing microdistributional and measurement error.  
\(^{\text{c}}\)C₀+C=Sill, the limiting value of the semivariogram for large distances or the semivariance value beyond range of spatial dependence.  
\(^{\text{d}}\)C/(C₀+C)=proportion of the sill explained by spatially structured variance.  
\(^{\text{e}}\)A₀=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.  
\(^{\text{f}}\)The range parameter along the plant rows, when anisotropy was present.  
\(^{\text{g}}\)The range parameter across the plant rows, when anisotropy was present.  
\(^{\text{h}}\)Semivariance values could not be described by any model.
Table 4. Range and average *Heterodera glycines* population densities 100^1 cm^3^ of soil in plots under different tillage systems at two locations.

<table>
<thead>
<tr>
<th></th>
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<tbody>
<tr>
<td>Bruner</td>
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<td>Range</td>
<td>Average</td>
<td>Range</td>
<td>Average</td>
</tr>
<tr>
<td>No</td>
<td>cysts</td>
<td>..</td>
<td>81 - 460</td>
<td>253</td>
<td>154 - 570</td>
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<tr>
<td></td>
<td>eggs</td>
<td>150 - 12,400</td>
<td>3,850</td>
<td>1,050 - 13,050</td>
<td>5,278</td>
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<tr>
<td>Ridge</td>
<td>cysts</td>
<td>..</td>
<td>19 - 345</td>
<td>137</td>
<td>59 - 607</td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>50 - 10,700</td>
<td>2,389</td>
<td>475 - 16,600</td>
<td>4,970</td>
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<tr>
<td>Reduced</td>
<td>cysts</td>
<td>..</td>
<td>70 - 406</td>
<td>194</td>
<td>78 - 682</td>
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<tr>
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<td>eggs</td>
<td>0 - 11,700</td>
<td>3,020</td>
<td>800 - 11,400</td>
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<td>cysts</td>
<td>..</td>
<td>65 - 438</td>
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<td>124 - 622</td>
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<tr>
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<td>0 - 14,000</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No</td>
<td>cysts</td>
<td>30 - 372</td>
<td>150</td>
<td>25 - 371</td>
<td>138</td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>550 - 28,800</td>
<td>6,795</td>
<td>100 - 7,700</td>
<td>2,547</td>
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<tr>
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<td>cysts</td>
<td>5 - 122</td>
<td>33</td>
<td>19 - 345</td>
<td>137</td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>1,600 - 50,789</td>
<td>9,806</td>
<td>75 - 14,400</td>
<td>3,492</td>
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<td>cysts</td>
<td>11 - 546</td>
<td>201</td>
<td>8 - 446</td>
<td>131</td>
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<tr>
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<td>eggs</td>
<td>600 - 23,400</td>
<td>6,361</td>
<td>100 - 13,350</td>
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<td>cysts</td>
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<td>214</td>
<td>11 - 488</td>
<td>117</td>
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<tr>
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<td>eggs</td>
<td>600 - 34,700</td>
<td>8,545</td>
<td>150 - 21,500</td>
<td>3,654</td>
</tr>
</tbody>
</table>

*Cysts were not enumerated for the 1994 soil samples collected at the Bruner Farm experiment.*

*Egg data from samples collected in the fall of 1994 were obtained without the sucrose centrifugation step.*
Table 5. Yields of soybean in plots under different tillage systems in the Bruner and Kanawha Farms experiments.

<table>
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<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
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</thead>
<tbody>
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<td>1,763</td>
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<tr>
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<td>1,945</td>
<td>1,724</td>
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<tr>
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</tr>
<tr>
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<td>1,656</td>
<td>2,031</td>
</tr>
<tr>
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<td>Ridge</td>
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<td>1,929</td>
<td>1,746</td>
<td>1,574</td>
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<tr>
<td></td>
<td>Reduced</td>
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<td>2,195</td>
<td>1,700</td>
<td>1,701</td>
</tr>
<tr>
<td></td>
<td>Conventional</td>
<td>2,319</td>
<td>2,175</td>
<td>1,845</td>
<td>1,883</td>
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</tbody>
</table>

Kg ha\(^{-1}\)

\(^{y}\)Data from Bruner Farm were not collected in 1998.


<table>
<thead>
<tr>
<th>Location</th>
<th>Tillage treatment</th>
<th>Nematode stage</th>
<th>Year</th>
</tr>
</thead>
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</tr>
<tr>
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<td>eggs</td>
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</tr>
<tr>
<td></td>
<td>Ridge</td>
<td>cysts</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>eggs</td>
<td>0.50**</td>
</tr>
<tr>
<td></td>
<td>Reduced</td>
<td>cysts</td>
<td>-0.44*</td>
</tr>
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<td></td>
<td></td>
<td>eggs</td>
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</tr>
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<td>cysts</td>
<td>0.16</td>
</tr>
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<td>eggs</td>
<td>0.03</td>
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<td>-0.71**</td>
</tr>
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</tr>
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<td></td>
<td>eggs</td>
<td>-0.81**</td>
</tr>
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<td>cysts</td>
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</tr>
<tr>
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<td></td>
<td>eggs</td>
<td>-0.75**</td>
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<td>cysts</td>
<td>-0.53**</td>
</tr>
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<td></td>
<td></td>
<td>eggs</td>
<td>-0.41**</td>
</tr>
</tbody>
</table>

\(^{*}=correlation significant at P≤0.05;**=correlation significant at P≤0.01.\)
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.
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 in different directions in degrees azimuth (0° = across soybean rows).
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.
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 in different directions in degrees azimuth (0° = across soybean rows).
Fig. 5. Spatial patterns of *Heterodera glycines* cyst populations in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the naturally infested experiment at the Kanawha Farm. Numbers following letters represent sampling time: (1) fall 1994, (2) spring 1995, (3) spring 1996, and (4) spring 1997. Maps generated by interpolation of soil sampling (kriging) data from a 2.3 m grid. Ridge-tillage data for the fall of 1994 (B1) were not available. Plots were 15 x 30 m.
Fig. 6. Spatial patterns of *Heterodera glycines* egg populations in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the naturally infested experiment at the Kanawha Farm. Numbers following letters represent sampling time: (1) fall 1994, (2) spring 1995, (3) spring 1996, and (4) spring 1997. Maps generated by interpolation of soil sampling (kriging) data from a 2.3 m grid. Plots were 15 x 30 m.
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.
Fig. 8. Anisotropic 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 different directions in degrees azimuth (0° = along soybean rows).
Heterodera glycines cysts 100⁻¹ cm⁻³ of soil

- >300
- 201 - 300
- 101 - 200
- 51 - 100
- 5 - 50

Fig. 9. Spatial patterns of Heterodera glycines cyst populations in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the naturally infested experiment at the Bruner Farm. Numbers following letters represent sampling time: (1) spring 1995, (2) spring 1996, and (3) spring 1997. Maps generated by interpolation of soil sampling (kriging) data from a 2.3 m grid. Egg population densities could not be estimated by the kriging method for the no-tillage plot because no model could be fitted to the semivariance values. Plots were 15 x 30 m.
CHAPTER 3

RELATIONSHIPS AMONG TILLAGE PRACTICES, DISSEMINATION AND SPATIAL PATTERNS OF *HETERODERA GLYCINES*, AND SOYBEAN YIELD

A paper to be submitted to Plant Disease

Walber L. Gavassoni, Gary P. Munkvold, and Gregory L. Tylka

First author: Departamento de Ciências Agrárias, Universidade Federal de Mato Grosso do Sul, Caixa postal 533, 79804-970 Dourados, MS, Brazil

Second and third authors: Department of Plant Pathology, Iowa State University, Ames 50011-1020.

Accepted for publication

Corresponding author: G. P. Munkvold; Email address: munkvold@iastate.edu

Abstract

A study was conducted from 1995 to 1998 in central Iowa to determine the impact of tillage practices on *Heterodera glycines* dissemination, reproduction, and yield impact on soybeans. In one experiment, treatments were no tillage, non-infested (control); no tillage; ridge tillage; conventional tillage; and reduced tillage (all *H. glycines*-infested except control). Soil samples were collected at the intersections of a 1.15-m grid for determination of *Heterodera glycines* population densities. After 1 year, nematode population densities were lower in the infested, no-tillage treatment compared to infested, conventional- and reduced-tillage treatments (α=0.05). After 2 years, *H. glycines* had been disseminated 6.9 m away from the original infested site in the conventional- and reduced-tillage treatments compared to
0.5 and 1.4 m for the no-tillage and ridge-tillage treatments, respectively. *Heterodera glycines* population densities were greater ($\alpha=0.05$) in the conventional- and reduced-tillage treatments than in no tillage and ridge tillage. Soybean yield decreased in all treatments over time, but the decrease was more pronounced in the conventional-tillage treatment. Lloyd’s index of patchiness values were lower in the conventional- and reduced-tillage treatments compared to no- and ridge-tillage treatments. A second experiment was established in 1996 to evaluate the effect of spatial patterns of *H. glycines* populations on yield of soybeans. There were three treatments: non infested, aggregated infestation, and uniform infestation. The overall nematode population density introduced in each infested plot was the same within each replication. Soil samples were collected at the intersections of a 2.3 m-grid (18 samples) in each plot in the spring and fall of 1996, 1997, and 1998. *Heterodera glycines* population densities were consistently greater ($\alpha=0.05$) in the uniformly infested treatment than the aggregated treatment, except in the spring of 1998. There were no significant differences in soybean yield among the three treatments in 1996, 1997, and 1998. These results indicate that tillage quickly disseminates *H. glycines* in newly infested fields, facilitating more rapid nematode reproduction and subsequent yield loss. Yield reduction in tilled, infested plots may have been due to a combination of greater dispersal of *H. glycines* and other unidentified effects of tillage on the nematode.
Introduction

*Heterodera glycines,* the most important pathogen of soybeans (*Glycine max* (L.) Merr.), was first reported in the U.S.A. in 1954 (Winstead, 1955). In Iowa, the nematode was first found in 1978 (Edwards, 1988) in Winnebago County, and since then, *H. glycines* has been detected in 90 of the 99 counties (G. L. Tylka, personal communication). A recent random survey of soybean fields in Iowa found *H. glycines* in 74% of the fields sampled (Workneh et al., 1999).

From 1989 to 1998, the area of Iowa cropped with no-tillage soybeans increased more than 1,700% (CTIC, 1998). Although no-tillage practices can increase the potential of soybean diseases caused by pathogens able to survive in the infested crop residue (Schmitthenner, 1985; Adee et al., 1997), the impact on *H. glycines* is not fully understood. Because of its survival capabilities, host requirements, and dependence on soil movement for dissemination, *H. glycines* may be affected by tillage in a different way than residue-borne pathogens. Because of the prominence of *H. glycines* as a soybean pest and the increasing use of conservation tillage systems, the effects of different tillage practices on *H. glycines* is an important issue.

Suppression of *H. glycines* population densities by no tillage has been reported by several researchers (Edwards et al., 1988; Koenning et al., 1995; Lawrence et al., 1990; Tyler et al., 1987). Mechanisms for this suppression have been suggested but not fully investigated. Most studies were conducted in fields naturally infested with *H. glycines,* where the nematode likely was present for several years, and did not take into account the nematode spatial pattern.
Generally, plant-parasitic nematodes have an aggregated spatial pattern under field conditions (Ferris and Wilson, 1987). The study of spatial patterns of soilborne pathogens, including nematodes, gained attention in the 1980s (Nicot et al., 1984; Campbell and Noe, 1985; Barker and Noe, 1987). However, few reports quantifying nematode spatial patterns have been published (Campbell and Benson, 1994), and the relationships between nematode spatial patterns and yield are unclear.

In general, pathogen (or disease) spatial patterns are believed to influence yield losses (Hughes, 1988). Aggregation of disease or pest damage often has been associated with greater yield loss compared to uniform or random damage (Bardner and Fletcher, 1974; James, 1974). However, predicted yield losses due to aggregated populations of plant-parasitic nematodes have been found to be overestimates (Noe and Barker, 1985; Perry, 1983; Seinhorst, 1973).

The objectives of this research were: 1) to elucidate the impact of tillage on dissemination and population densities of *H. glycines* and soybean yield in *H. glycines* artificially infested plots; and 2) to study the relationship between different spatial patterns of *H. glycines* and soybean yield.

**Material and Methods**

Two experiments were conducted in an area of a field initially free of *H. glycines* and previously cropped to corn and oats at the Iowa State University (ISU) Crossley Farm (Story County, IA). *Heterodera glycines* was not detected in soil samples collected in April 1995 from the area of the field where the experiments
were established. The soil was a Nicollet fine loamy, mixed, mesic Aquic Hapludolls (35% sand, 52.5% silt, 12.5% clay). The first experiment, established in 1995, was designed to evaluate the effects of different tillage practices on the dissemination, population density, and spatial pattern of a newly established *Heterodera glycines* infestation within the field. The second experiment, initiated in 1996, was established to evaluate the effect of spatial patterns of *Heterodera glycines* on the yield of soybeans.

**Inoculum preparation.** Some treatments in both experiments included infestation of the soil with nematode cysts. *Heterodera glycines* was cultured in a greenhouse on susceptible soybean *Glycine max* (L.) Merr. cv. Corsoy 79 plants. Soybean seeds were planted in 30-cm-diameter clay pots containing *H. glycines*-infested soil obtained from the ISU Plant Pathology Greenhouse. After 8 weeks, plants were clipped at the soil level, the shoots were discarded, and roots were removed. The infested soil was transferred to metal barrels and was kept at room temperature (approximately 20 to 22°C). Infected roots were placed on a 850-μm-pore sieve nested over a 250-μm-pore sieve. Females and cysts of *H. glycines* were removed from the roots by spraying with a stream of tap water and were recovered on the 250-μm-pore sieve. The *H. glycines* cysts and females recovered from the roots were mixed into the infested soil, and then the inoculum was divided in five equal portions (one for each replicate block). Each portion of inoculum was thoroughly mixed using a cement mixer for 30 minutes, then each portion of inoculum was further divided into subportions for the number of treatments of the experiment. Each inoculum subportion then was thoroughly mixed and sampled to quantify the
nematode population density. Inoculum was stored at 4°C until processing. Cysts were extracted from the soil samples by elutriation (Byrd et al., 1976). Each 100 cm³ aliquant of soil was soaked for 30 min in a 15.75 g/L solution of Electrasol automatic dishwasher detergent (Benckiser Consumer Products Inc., Dunbury, CT) to promote dispersion of soil particles and release *H. glycines* cysts. Cysts were crushed using a motorized pestle to release eggs (Niblack et al., 1993). Eggs were stained with acid fuchsin, and enumerated. The average nematode population density of the inoculum was 17,610 eggs 100^-1 cm³.

**Effects of tillage on the dissemination and population densities of *H. glycines*.**

This experiment was conducted from 1995 to 1998. The experimental design was a randomized complete block with five treatments and five replications. The treatments were: no tillage, non-infested (control); no tillage, *H. glycines*-infested; ridge tillage, *H. glycines*-infested; conventional tillage, *H. glycines*-infested; and reduced tillage, *H. glycines*-infested. Conventional tillage consisted of fall chisel plowing (0.20 m deep) and spring disking (0.10 m deep), followed by field cultivation before planting. In the reduced-tillage treatment, plots were disked in the spring and field cultivated before planting. Ridge tillage is a crop residue management system used for corn and soybean production in the Midwest that consists of raising the seed bed level above that of the surrounding soil and planting the crop on the same ridges, in the same rows, every year. In the ridge-tillage treatment, the soil was disturbed only for building and maintaining the ridges. Ridges were built (0.20 m high) before planting in the spring of 1995, spring of 1996, and fall of 1998. The soil in plots under no-tillage was not disturbed except for planting.
Prior to planting, a 1-m$^2$ area of each plot was infested (Fig. 1) with a 1:1 (vol:vol) mixture 1:1 of *H. glycines*-infested soil and sand. The inoculum mixture was incorporated into the delimited area using shovels to a depth of 5 cm. In the control plots, a non-infested mixture of soil and sand was incorporated into a 1-m$^2$ area as done for the other treatments. The overall *H. glycines* population density in the infested area after the incorporation was 1,800 eggs 100$^{-1}$ cm$^{-3}$ of soil. Tillage always was performed in an east-to-west direction. Plots were 6.1 m wide x 12.2 m long with a 1.5-m border between adjacent plots to prevent dispersal of the nematode into non-infested plots. Each plot had eight soybean rows spaced 0.76 m apart, and plots were planted each year with the *H. glycines*-susceptible cv. Archer (Phytophthora root rot-resistant, brown stem rot-resistant, and iron chlorosis-tolerant). Plant rows were oriented east-west. Pre-emergence application of a mixture of dicamba (0.58 l ha$^{-1}$) and 2,4-D amine (4.7 l ha$^{-1}$) controlled weeds. All plots were treated with herbicides and, except for the no-tillage plots, were cultivated for supplemental weed control 30 days after planting. Plots under no tillage were manually weeded.

Within a week of planting each spring, soil samples were collected from each plot on a 1.15-m, square grid (66 samples per plot). Each soil sample consisted of three 2.5-cm-diam., 20-cm-deep soil cores taken at the intersection of the grid; the three soil cores were combined and mixed. Samples were processed for enumeration of *H. glycines* eggs as already described.

In the fall of 1995, 1996, 1997, and 1998, the eight soybean rows in each plot were mechanically harvested using a plot combine, then seed weight and moisture
were recorded. Seed moisture was determined by a Dole 400 Grain Moisture Tester (Eaton Corp., Carol Stream, IL). The plot seed weights were adjusted to a 13% moisture level for statistical analyses.

For each plot, we recorded the maximum distance from the *H. glycines*-infested site at which egg population densities greater than 100 eggs 100^{-1} cm^{-3} of soil were detected. Lloyd's index of patchiness (LIP), a dispersion index developed by Lloyd (1967), was calculated for *H. glycines* data and used as an indicator of the aggregation of the nematode population in the plots. Maps of *H. glycines* distribution in each plot were generated using geostatistical modeling and kriging (GS*^* 3.1, Gamma Design Software, Plainwell, MI). Soybean yield and *H. glycines* egg population density data were subjected to ANOVA, and Fisher's least significance difference (LSD) test was used to separate means (α=0.05) when significant differences (P<0.05) were detected among treatments. Egg population density data were \log_{10}(x+1) transformed to standardize the variance prior to statistical analysis.

**Effects of *H. glycines* spatial pattern on yield.** This experiment was conducted from 1996 to 1998. The experimental design was a randomized complete block consisting of three treatments and five replications. The treatments were: non-infested (control), aggregated infestation, and uniform infestation. Plots were 6.1 m wide \times 12.2 m long, consisting of eight soybeans rows spaced 0.76 m apart. In the spring of 1996, plots were infested with *H. glycines*. Before infestation, all plots were field cultivated (5 cm deep) to facilitate inoculum incorporation. In the aggregated treatment, a 3.0-m-diam., circular area in the center of the plot was infested, and in the uniform treatment, the total area of the plot was infested with *H. glycines*.
inoculum (Fig. 2). An equal number of *H. glycines* eggs was applied to plots in both infested treatments. Inoculum was applied using a lawn fertilizer spreader (Browde et al., 1994). After infestation, inoculum was incorporated in each plot using shovels. The population density in the infested area, after inoculum incorporation, was 810 and 177 eggs 100\(^{-1}\) cm\(^{-3}\) of soil in the aggregated and uniformly infested treatments, respectively. Plots then were planted with soybean cv. Archer. No tillage was performed in this experiment after the plots were infested. Soil samples were collected from plots in a 2.3-m, square grid pattern (18 samples per plot) after planting and again in the fall each year, after the soybeans were harvested. Samples were taken at each intersection of the grid and consisted of three 2.5-cm-diameter, 20-cm-deep soil cores. Soil samples were processed for *H. glycines* egg enumeration as described previously. When necessary, weeds were manually removed. Plots were harvested mechanically with a plot combine, and yield data were adjusted to 13% moisture level. Lloyd’s index of patchiness for *H. glycines* population densities at each sampling time was calculated as an indicator of the nematode spatial pattern. Data were analyzed as described in the previous experiment.

**Results**

**Effects of tillage on the dissemination and population densities of *H. glycines*.**

One year after plots were infested and after one soybean crop season, *H. glycines* population densities were greater in conventional and reduced tillage compared to no tillage and ridge tillage (Fig. 3). This trend was increasingly evident in 1997 and
1998. There were no significant differences in *H. glycines* population densities among the other treatments in the three years of this study. Population densities significantly increased (\( \alpha = 0.05 \)) annually in the conventional- and reduced-tillage plots, but an increase in population densities was detected only in 1998 in the other treatments. Low numbers of *H. glycines* were recovered from soil samples collected in the non-infested treatment plots in all three years of this study.

*Heterodera glycines* was detected in the spring of 1996 at greater distances from the original infestation site in the conventional- and reduced-tillage treatments compared to the no-tillage and ridge-tillage treatments (Fig. 4). In the spring of 1997, after two crop seasons and after spring tillage had been performed, *H. glycines* was detected at the maximum possible distance (6.9 m) from the infestation site in the conventional- and reduced-tillage treatments. Nematode dissemination in the no-tillage and ridge-tillage treatments was relatively small compared to that in treatments that received tillage.

Lloyd's index of patchiness values were greater than 1.0, indicating aggregation of the egg populations in all treatments at all sampling times (Table 1). The lowest LIP values consistently occurred in the reduced-tillage and conventional-tillage treatments. In 1996, LIP values were significantly greater in the ridge-tillage treatment compared to reduced tillage. In 1997 and 1998, conventional and reduced tillage had significantly lower indices compared to the other treatments. Between 1996 and 1998 the LIP values decreased significantly (\( \alpha = 0.05 \)) in the conventional-, ridge-, and reduced-tillage treatments and numerically increased in the other treatments.
Maps of spatial patterns of *H. glycines* egg populations are presented in Fig. 5. *Heterodera glycines* eggs were distributed throughout the conventional- and reduced-tillage plots, whereas the nematode was restricted to an area near the original infestation site in the ridge-tillage and no-tillage plots.

In the first year of this study, 1995, there were no differences in soybean yield among treatments (Fig. 6). Differences in yield among treatments became apparent in 1996, when yield was lower in the ridge-tillage treatment compared to all other treatments except no-tillage, infested. In 1997, the yields of the conventional- and reduced-tillage treatments were significantly lower than yield of the no-tillage, infested treatment. In 1998, yield in the conventional-tillage treatment was significantly lower than yield in the other treatments. In general, yield decreased over time in all treatments.

There were significant (P<0.01) and negative correlations between *H. glycines* population density and soybean yield in 1996 and 1997 (-0.68 and -0.61, respectively) and between LIP and nematode density (-0.60) in 1998. Although not significant, positive correlation was detected between LIP and soybean yield.

Cysts were observed on the root systems of plants located in the infested treatments in 1996, 1997, and 1998. In the summer of 1998, Fusarium root rot was observed in the no-tillage treatments; plants were stunted and roots displayed a reddish brown decay. *Fusarium solani* was isolated from the decayed roots.

**Effects of *H. glycines* spatial pattern on yield.** Yields were lower in the infested treatments than in the non-infested control in all 3 years, but the differences were not significant (Fig. 8). After 1996, yields decreased in all three treatments.
There were differences in egg population densities among the two *H. glycines*-infested treatments at all sampling times except in the spring of 1998 (Fig. 7). As in the previous experiment, low numbers of *H. glycines* eggs were recovered from non-infested plots.

Lloyd's index of patchiness was greater than 1.0 in all treatments and at all sampling dates (Table 2). Differences in LIP values between infested treatments were evident only in the spring and fall of 1997 when LIP was significantly greater in the aggregated treatment. There was no significant change in LIP values among the different sampling times and years except in the non-infested treatment.

Linear correlations among soybean yield, nematode population density, and LIP generally were not significant. The only exception was a significant ($P \leq 0.01$) negative correlation in 1997 between soybean yield and *H. glycines* population density (-0.79).

Discussion

*Heterodera glycines*, like most plant-parasitic nematodes, is dependent on passive mechanisms for dissemination within and between fields (Edwards, 1988). We have studied the effects of tillage on population densities and spread of *H. glycines* in artificially infested plots and also the relationship between different spatial patterns of the nematode and soybean yield. We have found that from the initial infestation site, *H. glycines* was disseminated by conventional and reduced tillage practices an average of nearly 3.5 m per year. Population densities of the nematode increased more in conventional and reduced tillage than in ridge- and no-tillage
treatments probably because greater spread of the nematode in the tilled treatments provided access to more soybean plants and facilitated more rapid reproduction than in no tillage and ridge tillage. In the conventional- and reduced-tillage treatments, 70-100% of the plants were exposed to *H. glycines* inoculum by the end of the third crop season, but in most of the no-tillage treatment plots, only 2-5% of the plants were exposed (Fig. 5A1).

One year after establishment of our study on the effects of tillage, the limiting effects of no tillage and ridge tillage on *H. glycines* populations were apparent. The mechanism of this limited *H. glycines* reproduction probably was restricted dissemination of the nematode and, thus, limited access to a food source. However, other unidentified mechanisms may have been involved. Lower population densities of *H. glycines* in no-tillage compared to conventional-tillage treatments were found by Edwards et al. (1988), Koenning et al. (1995), Hershman and Bacchi (1992), Lawrence et al. (1990), Tyler et al. (1983), and Tyler et al. (1987). Most of these studies were conducted in naturally infested fields, and pre-existing or changing *H. glycines* spatial patterns were not considered. It may take several years for no tillage to affect nematode population densities (Schmitt, 1992). However, there have been reports of short-term effects of tillage on *H. glycines* population densities (Tyler et al., 1983, Young, 1987). In a greenhouse study, with conditions mimicking no tillage and conventional tillage, Young (1987) was able to recover more cysts from disturbed soil cores than undisturbed cores 30 days after planting.

Several mechanisms have been proposed to explain the apparent suppression of *H. glycines* reproduction in no-tillage systems. No tillage results in
changes in edaphic environmental factors compared to conventional tillage, such as lower soil temperatures, additional soil water, increased soil organic matter, increased soil compaction, and increased presence of antagonists (Griffith et al., 1986; Schmitt, 1992) which may individually or interactively have a suppressive effect on the pathogen. In some studies, no-tillage soybeans were planted in chemically killed wheat or in wheat crop residue (Baird and Bernard, 1984; Edwards et. al, 1988; Tyler et al., 1983; Young, 1987). Hershman and Bachi (1995) suggested that lower *H. glycines* population densities in no tillage were due to the presence of wheat residue and not due to no tillage *per se*. However, our results show that no tillage suppressed *H. glycines* populations in the absence of wheat residue and under susceptible soybean monoculture.

Previous studies on tillage and *H. glycines* population dynamics have not considered spatial pattern as a factor influencing differential *H. glycines* reproduction among tillage treatments. The more uniform spatial pattern of *H. glycines* due to conventional tillage in our experiment increased the probability of soybean plants being infected by the nematode compared to the no-tillage treatment, consequently resulting in greater *H. glycines* population densities.

Recovery of *Heterodera glycines* eggs at farther distances in conventional- and reduced-tillage plots than in no tillage and ridge tillage illustrates that tillage can quickly disseminate the nematode within a field. Dispersal of *H. glycines* by tillage has been suggested by several authors (Sasser, 1989; Workneh et al., 1999), but there are very few published studies reporting quantitative effects of cultivation on the dissemination of *H. glycines*. Ueda (1996) investigated the effects of the
application of organic materials on the dispersal of *H. glycines*. Organic materials and cysts of *H. glycines* were incorporated one month before planting, and tillage was performed twice a year. *Heterodera glycines* was recovered 4 m from the infested site in the first year of the study. By the second year, the nematode was recovered 14 m from the original infested site. In our tillage study, after 2 years the nematode was moved 6.9 from the infestation site in the conventional- and reduced-tillage plots. The frequency of tillage activities in our tilled plots was less than that of Ueda (1996), possibly explaining the difference in our results.

Lower Lloyd's index of patchiness values in plots under conventional or reduced tillage compared to no- and ridge-tillage treatments were consistent throughout our experiment. Researchers (Olanya and Campbell, 1988; Subbarao et al., 1996) studying the impact of tillage on pathogen propagules have postulated that decreases in the dispersion index values are the result of redistribution of the pathogen population. We believe that the reduced LIP values in the conventional- and reduced-tillage treatments were a result of the redistribution of eggs within plots.

There were no differences among the different treatments in relation to soybean yield in the first year of the tillage study, possibly because the nematode population densities were low. After 1996, however, soybean yield decreased in the conventional-tillage treatment and population densities of *H. glycines* increased. Low soybean yields associated with high nematode population densities and tillage have been reported earlier (Tyler et al., 1983; Tyler et al., 1987; Lawrence et al., 1990). A similar result was reported for effects of tillage on *Sclerotinia minor* dissemination and lettuce (Subbarao et al., 1996). Yields in the no-tillage infested treatment were
not affected by *H. glycines*, probably due to the consistently low nematode population densities in this treatment.

Soybean yields decreased over the years in all treatments of our experiments. Decreasing soybean yields in monoculture also have been reported previously (Koenning, et al., 1993; Koenning et al. 1995; Noel and Edwards, 1996) and may be due to the cumulative effects of soilborne fungal pathogens. Fusarium root rot symptoms were observed only in the no-tillage treatments in 1998, but reduction in yield compared to the other treatments was not evident.

Although differences in population densities of *H. glycines* and yield among treatments were detected after 1995, no stunting or chlorosis, symptoms sometimes associated with *H. glycines* attack, were observed in the plants in the infested plots during the years of this study. This fact was not unexpected. Even with yield losses of up to 38%, soybeans may not show obvious symptoms of *H. glycines* parasitism (Niblack, 1995).

In the second experiment, *H. glycines* population densities were consistently greater in the uniform infested treatment than in the treatment with an aggregated infestation, however no differences in soybean yield were found. For the first year, we were not expecting detectable differences in yield among treatments because of the relatively low initial nematode population density, even though population densities as low as 10 to 50 eggs 100^-1 cm^-3 soil have been reported as affecting soybean yield (Niblack et al., 1992). In 1997 and 1998, though, no differences among treatments were detected, even with higher initial population densities than in
1996. We may not have been able to detect small differences in yield because of unexplained yield variance among replications.

In our second experiment, there was a linkage between spatial pattern and population density. *Heterodera glycines* population densities were consistently greater in the uniformly infested treatment than in the treatment with the aggregated infestation. Thus, we were not able to separate the effects of spatial pattern from the effects of nematode population density on soybean yield. Because of the relationship between spatial pattern and population density, it is not possible (and possibly not relevant) to speculate on yield losses that might occur with equal *H. glycines* populations but different spatial patterns. One way to address the relationship of spatial pattern and yield would be additional yearly infestations of the aggregated infestation plots to maintain equal population densities between aggregated and uniformly infested treatments.

Yield losses caused by stand-reducing pests may be more severe under an aggregated spatial pattern than a uniform spatial pattern due to better yield compensation in a uniform pest attack (Crawley, 1983). Soybean yield compensation usually is due to increased number of pods, seeds per pod, and seed weight (Stivers and Swearingin, 1980). We believe that in the *H. glycines*-soybean pathosystem, yield compensation is unlikely to occur, regardless of the nematode spatial pattern. Published reports on soybean yield compensation rely on stand-reducing factors. *Heterodera glycines* rarely causes stand reduction (Sinclair and Backman, 1989). It is unlikely that a plant heavily infected by *H. glycines* would occur adjacent to a non-infected plant that could compensate for the yield loss of the
neighboring diseased plant. Because we did not measure yield on a scale smaller than individual plots, we do not know if yields were greatly suppressed in the infested areas of the aggregated treatment. However, these areas had \textit{H. glycines} population densities more than four times greater than the whole plot population mean for the uniformly infested treatment. Losses in these infested areas may have been similar to whole-plot losses in the uniform infestation treatment, resulting in similar yields between treatments.

Our results illustrate the utility of no-tillage practices in the management of \textit{H. glycines} and may provide a key explanation for the association of no tillage with lower population densities of the nematode. Adoption of no tillage in fields where the nematode has not been detected or in recently infested fields should limit dissemination, reproduction, and yield losses caused by \textit{H. glycines}.

\textbf{Literature Cited}


Table 1. Effects of different tillage systems on Lloyds index of patchiness (LIP) in plots artificially infested with *Heterodera glycines*.

<table>
<thead>
<tr>
<th>Treatment</th>
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<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>No-tillage / Infested</td>
<td>13.3 ab A</td>
<td>19.7 a A</td>
<td>12.8 a A</td>
<td></td>
</tr>
<tr>
<td>No-tillage / Non-infested</td>
<td>11.4 ab A</td>
<td>12.3 a A</td>
<td>5.7 b B</td>
<td></td>
</tr>
<tr>
<td>Ridge / Infested</td>
<td>15.7 a A</td>
<td>15.8 a A</td>
<td>6.7 b B</td>
<td></td>
</tr>
<tr>
<td>Conventional / Infested</td>
<td>10.4 ab A</td>
<td>4.6 b A</td>
<td>2.0 b B</td>
<td></td>
</tr>
<tr>
<td>Reduced / Infested</td>
<td>5.8 b A</td>
<td>3.5 b B</td>
<td>2.3 b C</td>
<td></td>
</tr>
</tbody>
</table>

^ Average of five replications. Data were transformed in log(x) for statistical analyses purposes.

^ Values followed by the same lowercase letter in columns or uppercase letter in rows are not significantly different according to Fisher's LSD test (α=0.05).

Table 2. Lloyds index of patchiness (LIP) in plots artificially infested with *Heterodera glycines*.

<table>
<thead>
<tr>
<th>Treatment</th>
<th>LIP</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Spring</td>
<td>Fall</td>
<td>Spring</td>
<td>Fall</td>
</tr>
<tr>
<td>Non-infested</td>
<td>4.9 ab B</td>
<td>9.2 a AB</td>
<td>14.7 a A</td>
<td>6.7 a B</td>
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<tr>
<td>Uniform</td>
<td>3.7 a A</td>
<td>1.9 a A</td>
<td>2.9 c A</td>
<td>1.8 b A</td>
</tr>
<tr>
<td>Aggregated</td>
<td>6.8 a A</td>
<td>7.1 a A</td>
<td>7.3 b A</td>
<td>5.9 a A</td>
</tr>
</tbody>
</table>

^ Average of five replications. Data were transformed in log(x) for statistical analyses purposes.

^ Values followed by the same lowercase letter in columns or uppercase letter in rows are not significantly different according to Fisher's LSD test (α=0.05).

^ Samples are being processed.
Fig. 1. Diagram of plot and *H. glycines* infestation site (■). The arrow within the plot indicates the direction of tillage operations.

Fig. 2. Diagram of plots of the aggregated (A) and uniform (B) *H. glycines* infestation patterns. The shaded area represents the distribution of the nematode inoculum within each plot.
Fig. 3. Population densities of *Heterodera glycines* in artificially infested plots under different tillage treatments. Values presented are means of five replications. Bars within each year with the same letter are not significantly different according to Fisher's LSD test ($\alpha=0.05$). Data were $\log_{10}(x+1)$ transformed for statistical analysis.
Fig. 4. Distance from the original infestation site at which *H. glycines* was detected in plots under different tillage treatments. Values presented are means of five replications. Bars with the same letter within each year are not significantly different according to Fisher's LSD test (α=0.05). The maximum distance from the infestation site to the edge of the plot was 6.9 m.
Heterodera glycines eggs 100^{-1} cm^{-3} soil

- > 1,500
- 501 - 1,500
- 251 - 500
- 101 - 250
- 0 - 100

Fig. 5. Spatial patterns of Heterodera glycines egg populations in plots under no tillage (A), ridge tillage (B), conventional tillage (C), and reduced tillage (D) in artificially infested plots at the Crossley Farm. Numbers following letters represent replications. Maps generated through geostatistical analyses of results obtained from soil samples collected in the spring of 1997. Plot dimensions were 15 x 30 m.
Fig. 6. Soybean yields in plots artificially infested with *Heterodera glycines* and under different tillage systems. Values presented are means of five replications. Bars within each year with the same letter are not significantly different according to Fisher's LSD test ($\alpha=0.05$).
Fig. 7. *Heterodera glycines* population densities in plots at different sampling times and under different infestation patterns at Crossley Farm. Values presented are means of five replications. Bars within each year with the same letter are not significantly different according to Fisher's LSD test ($\alpha=0.05$). Data were transformed by $\log_{10}(x+1)$ for statistical analysis.
Fig. 8. Soybean yields in plots with different spatial patterns of *Heterodera glycines*. Values presented are means of five replications. Bars within each year with the same letter are not significantly different according to Fisher's LSD test ($\alpha=0.05$).
CHAPTER 4

RELATIONSHIPS AMONG SOIL PROPERTIES AND HETERODERA GLYCINES IN NO-TILLAGE PLOTS

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W. L. Gavassoni, G. P. Munkvold, and G. L. Tylka

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2Graduate Research Assistant and Associate Professors, respectively, Department of Plant Pathology, Iowa State University, Ames, IA 50011-1020. Present address of first author: Universidade Federal de Mato Grosso do Sul, Departamento de Ciências Agrárias, Caixa Postal 533, 79804-970, Dourados, MS, Brazil.

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E-mail: munkvold@iastate.edu

RH: H. glycines and soil properties: Gavassoni et al.
Abstract: The relationships among soil properties and *Heterodera glycines* population densities were studied under a no-tillage crop residue management system. Field experiments were conducted at two Iowa locations (Bruner and Kanawha farms) from 1995 to 1997 in fields naturally infested with *H. glycines*. Soil samples were taken on a 7x14 grid (98 5.2-m² contiguous quadrats) in the spring of each year, shortly after planting a cultivar susceptible to *H. glycines*. For each soil sample, pH, organic matter, phosphorus, and potassium were determined, cysts of *H. glycines* were extracted and counted, then eggs from cysts were extracted and counted. Soybean yield was determined in subplots consisting of two soybean rows 6.1 m long (40 subplots per plot). At the Kanawha Farm, there were significant correlations among *H. glycines* population densities, soil pH, and organic matter during all three years. There were positive correlations between *H. glycines* cyst and egg population densities and soil pH (r = 0.26 to 0.47, P< 0.01). In 1996 and 1997, correlation coefficients for cyst densities versus organic matter were -0.37 and -0.34, respectively, and were similar to those calculated for egg population densities in the same time period. Generally, correlations of nematode population densities with K and P were not significant. Additionally, soybean yields were negatively correlated with *H. glycines* densities and soil pH and positively correlated with organic matter and K. At the Bruner Farm experiment, correlations among *H. glycines* population densities, soil properties, and soybean yield were poor and not significant. Overall results indicate that *H. glycines* population densities and yield impact on soybeans are related to soil pH and organic matter; however the nature of these interactions is unknown.
INTRODUCTION

Most plant-parasitic nematodes are soilborne, and spend part of their life cycle in the soil. Consequently, edaphic factors may directly affect their distribution and population dynamics. *Heterodera glycines* Ichinohe, the soybean cyst nematode, has several life stages occurring in the soil, including egg-mass and encysted eggs, second-stage juveniles, and adult males. Additionally, females break through the root tissue as they develop and are exposed to the soil environment on the surface of the root (Tylka, 1995). Nematodes also may be indirectly affected by soil factors through the host plant (Burns, 1971). Recently the relationship of soil properties and *H. glycines* began to receive some attention (Anand et al., 1995; Franci, 1993; Grau et al. 1999; Tylka et al., 1998).

Several researchers have investigated the relationship of soil pH and plant-parasitic nematodes. Burns (1971) reported greater colonization of soybean roots by *Pratylenchus allenii* when plants were grown at pH 6.0 and 8.0 compared to pH 4.0. In a survey conducted in Scotland, *H. avenae* cyst population densities were found to be positively correlated with soil pH. Population densities of *H. glycines* have been found to increase with soil pH within fields in Iowa (Tylka et al., 1998), and among small plots in Wisconsin (Grau et al, 1999). Other edaphic factors, such as soil texture and organic matter, also have been found to affect nematode populations (Norton et al., 1971; Norton and Schmitt, 1974).

Spatial variability of plant-parasitic nematodes may reflect to some extent variability in the soil environment (Noe and Barker, 1985). Precision agriculture technologies have the potential to improve nematode management due to detailed
information on spatial patterns of soil properties, nematode population densities, and crop yield (Barker and Koenning, 1998; Strickland et al., 1998). However, results of research on the relationships of soil properties and plant-parasitic nematodes are sometimes conflicting and may be field-specific. The objective of this research was to investigate the relationships among edaphic properties and *H. glycines* population densities in two naturally infested fields in central and north central Iowa.

**MATERIALS AND METHODS**

Experiments were conducted in fields naturally infested with *H. glycines* from 1995 to 1997 at the Iowa State University Bruner Research Farm (Boone County, IA) and from 1995 to 1996 at the Northern Research and Demonstration Farm (Hancock County, IA), hereafter designated as Bruner Farm and Kanawha Farm, respectively. At both locations the soil was a Canisteo silty clay loam. The texture in the Bruner Farm was 17.5% sand, 75% silt, 7.5% clay and at the Kanawha Farm was 22.5% sand, 70% silt, 7.5% clay. Both fields previously were cropped to soybeans.

Plots were 15 x 30 m with 20 plant rows spaced 0.76 m apart. Plots were planted between mid May and mid June of each year with the *H. glycines*-susceptible soybean cv. Archer (Phytophthora root rot resistant, brown stem rot resistant, and iron chlorosis tolerant). Plant row orientation was north-south in the Bruner Farm and east-west in the Kanawha Farm. Plots were kept under a no-tillage crop residue management system. Preemergence application of a mixture of
dicamba (0.58 l ha\(^{-1}\)) and 2,4-D amine (4.7 l ha\(^{-1}\)) controlled weeds. Plots were manually weeded for supplemental weed control.

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

Soil samples were collected from plots in a 7 x 14 square grid with the long axis parallel to the soybean rows. Samples were collected in the spring of 1995, 1996, and, at Kanawha, 1997 within a week of planting. Soil samples consisted of six 2.5-cm-diameter, 20-cm-deep soil cores collected from each intersection of the grid. The soil cores from each sample were mixed and stored at 4°C. A 100 cm\(^3\) aliquant of soil was used to determine \(H.\) glycines population densities and the remaining soil was used for soil nutrient analyses. To promote dispersal of soil particles to release \(H.\) glycines cysts, each 100 cm\(^3\) aliquant of soil was soaked for 30 min in a 15.75 g/liter solution of Electrasol automatic dishwasher detergent (Benckiser Consumer Products Inc, Dunbury, CT). Then, \(H.\) glycines cysts were extracted from the soil by elutriation (Byrd et al., 1976) followed by a modified sucrose flotation method (Jenkins, 1964). Results of preliminary tests indicated two modifications of the sucrose flotation extraction method greatly increased the extraction efficiency for \(H.\) glycines cysts. The sucrose concentration used was 1.37 kg L\(^{-1}\) water instead of the 0.45 kg L\(^{-1}\) water described when the procedure was initially described. Cysts present in the supernatant from the centrifugation in water
were saved and added to the beaker containing cysts recovered from the sucrose centrifugation. Cysts were counted, then eggs were extracted from cysts using a motorized pestle and were stained in acid fuchsin (Niblack et al., 1993) and counted. Eggs were enumerated using a nematode counting slide (Olympic Equine, Issaquah, WA) and a dissecting microscope at 24x magnification. The remaining soil from each sample was sent to Minnesota Valley Testing Laboratories (Nevada, IA) for analyses of pH, phosphorus (P), potassium (K), and organic matter.

Soybean yield was determined in subplots consisting of two soybean rows 6.1 m long (40 subplots per plot). Seed moisture was determined by a Dole 400 Grain Moisture Tester (Eaton Corp., Carol Stream, IL). The seed weight was adjusted to a 13% moisture level.

Data were analyzed using the correlation analysis procedure of SAS (SAS Institute, Cary, NC) to determine if there were linear relationships among *H. glycines* cyst and egg population densities, yield, and soil properties. For the *H. glycines* and soybean yield correlations, nematode population densities enumerated from samples collected in each subplot (6.1 m long x 1.52 m wide) were averaged. Maps of nematode population densities, soil properties, and soybean yields were generated using the geostatistical software GS* version 3.1* (Gamma Design Software, Plainwell, MI).

**RESULTS**

*Heterodera glycines* population densities ranged from 2,547 to 6,680 eggs 100⁻¹ cm⁻³ soil (Table 1) at the two experiments. In the spring of 1995, *H. glycines*
egg population densities at the Bruner Farm were 107% greater than at the Kanawha Farm. Generally, population densities decreased at the Bruner Farm and increased at the Kanawha Farm during the course of our experimentation.

A summary of the soil properties at both experimental sites at the different sampling times is presented in Table 2. In 1995 and 1996, soil pH, organic matter, and K levels were higher at the Bruner Farm experiment compared to the experiment at the Kanawha Farm. There was a wider range of values for soil pH and organic matter at the Kanawha than at the Bruner Farm.

At the Kanawha Farm, there were significant correlations among *H. glycines* population densities, soil pH, organic matter, and P (Table 3). There were consistent positive correlations (*P*< 0.01) between *H. glycines* population densities and soil pH, with correlation coefficients ranging from 0.26 to 0.47. In 1996 and 1997, correlation coefficients for cyst population densities versus organic matter were -0.37 and -0.43, respectively, and were similar to those calculated for egg population densities in the same time period. Most of the correlations of nematode population densities with K and P were not significant, except for P in 1997. At the Bruner Farm experiment, correlations between cyst and egg population densities and soil properties were poor and not significant, except for the relationship between organic matter and cyst population densities in the spring of 1995 (*r*=0.35, *P*< 0.01).

Correlations among soil properties generally were significant at both experiments in most sampling times. Across the two experiments and sampling times there were significant negative correlations between K and soil pH (-0.43 to -0.65) and positive correlations between K and soil organic matter content (0.36 to
Phosphorus and soil pH were negatively correlated at the Bruner Farm experiment in both sampling times and had no consistent trend at Kanawha. Organic matter and phosphorus were negatively correlated in 1995 at the Kanawha Farm experiment, whereas at the Bruner Farm, these two variables were positively correlated in 1995 and 1996. Phosphorus and K were positively correlated at the Bruner Farm experiment in 1995 and 1996 and at the Kanawha Farm in 1996. Organic matter content and soil pH were negatively correlated (-0.60 to -0.83) in both experimental sites.

Soybean yield had a significant negative correlation with nematode population densities at the Kanawha Farm experiment, but not at the Bruner Farm. Correlation coefficients of soybean yield with nematode population densities were negative, but near zero and not significant at the Bruner Farm. Soybean yield was positively correlated with organic matter content and inversely related to soil pH during the three years of the experiment at the Kanawha Farm. No relationships were observed among soil pH, organic matter, and soybean yield at the Bruner Farm. Overall average soybean yields at the Kanawha Farm experiment were 2,239, 1,757, and 1,656 kg ha$^{-1}$ in 1995, 1996, and 1997, respectively, whereas soybean yields at the Bruner Farm site were 1,632 and 1,858 kg ha$^{-1}$ in 1995 and 1996.

Maps of $H.~glycines$ egg population densities, pH, organic matter, and soybean yields from the Kanawha Farm plots are illustrated in Fig. 1. The areas with greater nematode population densities in each sampling time are coincident with areas with higher pH, lower organic matter content, and low soybean yields. These areas with greater nematode population densities at the Kanawha Farm consistently
occurred in the west portion of the plot. Plants located in that portion of the plot generally began senescing by the end of August of every year, approximately 2 weeks earlier than areas of the field with lower *H. glycines* population densities.

**DISCUSSION**

The relationship of *H. glycines* with soil properties was studied in two naturally infested fields in central and north central Iowa from 1995 to 1997. In one location, we found a significant correlation of *H. glycines* population densities with soil pH and organic matter. There were no consistent relationships among P, K, and nematode population densities at either experimental site.

At the Kanawha Farm experiment, correlations between *H. glycines* cyst and egg population densities and soil pH were consistently positive and significant from 1995 to 1997. Others have reported high soil pH in association with high population densities of *H. glycines* (Anand et al., 1995; Grau et al., 1999; Tylka et al., 1998, and Tylka et al., 1999) and *Heterodera avenae* (Duggan, 1963). Additionally, lower colonization of soybean var. Amsoy roots by *Pratylenchus alleni* was observed in plants grown at pH 4.0 compared to with those of pH 6.0 and 8.0. It was suggested that thickened epidermal cell walls of the root, observed in soil pH of 4.0, played a role in physically or chemically suppressing *Pratylenchus alleni* colonization (Burns, 1971). Such a mechanism also might affect *H. glycines*. It is possible, however, that soil pH directly affects *H. glycines* in other ways or that soil pH triggers some plant-mediated mechanism (Tylka et al., 1998). The nature of the relationship between *H. glycines* and soil pH currently is unknown.
There were significant negative correlations between *H. glycines* cyst population densities and organic matter content at Kanawha in 1996 and 1997 and between egg population densities and organic matter content in 1997. In contrast, a positive and significant correlation between cyst densities and organic matter was detected at Bruner Farm in 1995 but not 1996. Norton et al. (1971) reported an inverse relationship between plant-parasitic nematode population densities and soil organic matter content. In Wisconsin, Grau et al. (1999) reported positive and significant correlations between organic matter and *H. glycines* population densities.

At the Bruner Farm experiment, percent organic matter increased as soil pH increased, whereas at Kanawha Farm there was an inverse relationship between soil pH and organic matter. Fungal predators of *H. glycines* also are affected by organic matter (Gintis et al., 1983) and organic matter certainly affects other natural enemies. In our study, the difference in the relationship of organic matter and *H. glycines* population densities at Bruner and Kanawha may be explained by the distinct soil characteristics of the two locations.

Another possible explanation for the relationships between *H. glycines* population densities and soil pH and organic matter content would be the differential efficiency of nematode extraction due to variable levels of organic matter across the plot. However, we do not believe that the differences in nematode densities detected were greatly influenced by variable efficiency of the extraction method. In our experiments, soil samples were soaked in detergent solution to increase dispersion of soil particles and release cysts of *H. glycines* prior to processing the soil sample. Although this process may have had variable success on samples with differing
levels of organic matter or varying soil texture, it is very unlikely that the variability in extraction efficiency following the detergent soaking step would result in the consistent and significant inverse correlation between *H. glycines* densities and soil organic matter content. Also, soybean yields were consistently low in the areas of the field where high population densities were recovered, indicating that greater nematode parasitism occurred in the areas of the field where greater nematode densities were detected relative to areas of the field with low *H. glycines* population densities.

Liming, the neutralization of soil acidity, can improve soybean production by reducing potentially toxic elements, increasing availability of soil nutrients, and improving nodulation and N₂ fixation (Mengel et al., 1987). We have not studied the effects of liming on *H. glycines*, thus we can not speculate whether raising the level the soil pH with lime would increase nematode population densities. The range of pH in our experimental fields was well above the level that would warrant lime application. Conversely, lowering the soil pH in highly alkaline soils may not reduce *H. glycines* population densities and also may not be technically feasible, economical, and potentially could increase problems with soybean fungal diseases.

In our experiments, soil K levels were not correlated with *H. glycines* population densities. This lack of relationship also has been reported in a commercial soybean field experiment in Wisconsin (Grau et al., 1999). Some reports have related greater nematode population densities or nematode damage with decreased plant K content (Oteifa et al., 1964; Burns, 1971; Luethers et al., 1979), however, Hanson et al. (1988) found little effect of K on cyst population densities.
Although we did not measure plant K content, potassium levels in the soil were at optimum levels for soybean production in both locations at all sampling times. No K deficiency symptoms were observed. Consequently, it is reasonable to assume that plants in our experiments were not K-deficient and, thus, nematode populations may not have been affected by this element.

Cyst and egg population densities were highly aggregated at the Kanawha Farm experiment, but not at the Bruner Farm. The areas with high nematode population densities at Kanawha were coincident with the areas of the plot with high pH and low organic matter. We believe that the aggregation of the *H. glycines* population may be a result of the interaction of the soil properties and also due to the limited active dispersal of the nematode. In the Bruner Farm experiment, populations of the nematode were more uniform than at Kanawha and there was not a consistent relationship between *H. glycines* population densities and soil properties or soybean yield. If soil pH and organic matter content are the main edaphic factors affecting *H. glycines* population densities, then this may explain the greater nematode population densities at the Bruner Farm than at the Kanawha Farm. Additionally, soil pH and organic matter content may be related directly or indirectly to the different nematode spatial patterns at the two locations.

Evidently there was a linkage among nematode population densities, organic matter, and soil pH in our experiments. However, the role of edaphic factors in the *H. glycines* – soybean pathosystem are not fully known. Future research should address the issue of how organic matter and soil pH affect *H. glycines* in controlled experiments.
LITERATURE CITED


TABLE 1. *Heterodera glycines* population densities $100^{-1} \text{ cm}^{-3}$ of soil in plots at two experimental locations.

<table>
<thead>
<tr>
<th>Location</th>
<th>Nematode stage</th>
<th>Spring 1995</th>
<th>Spring 1996</th>
<th>Spring 1997</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>Bruner</td>
<td>cysts</td>
<td>81 - 460</td>
<td>154 - 570</td>
<td>322</td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>1,050 - 13,050</td>
<td>1,000 - 10,350</td>
<td>3,723</td>
</tr>
<tr>
<td>Kanawha</td>
<td>cysts</td>
<td>25 - 371</td>
<td>30 - 455</td>
<td>168</td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>100 - 7,700</td>
<td>350 - 13,300</td>
<td>3,704</td>
</tr>
</tbody>
</table>

*a* Experiment at Bruner Farm was not repeated in 1997.

TABLE 2. Summary of soil properties in plots at two locations.

<table>
<thead>
<tr>
<th>Location</th>
<th>Spring 1995</th>
<th>Spring 1996</th>
<th>Spring 1997</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>Bruner</td>
<td>pH</td>
<td>7.4 - 8.1</td>
<td>7.5 - 8.1</td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td>5.1 - 6.6</td>
<td>5.7 - 7.6</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>13 - 33</td>
<td>1 - 17</td>
</tr>
<tr>
<td></td>
<td>K</td>
<td>90 - 230</td>
<td>100 - 200</td>
</tr>
<tr>
<td>Kanawha</td>
<td>pH</td>
<td>5.7 - 7.8</td>
<td>5.6 - 7.8</td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td>3.8 - 6.0</td>
<td>3.9 - 12.7</td>
</tr>
<tr>
<td></td>
<td>P</td>
<td>28 - 61</td>
<td>31 - 68</td>
</tr>
<tr>
<td></td>
<td>K</td>
<td>60 - 140</td>
<td>70 - 130</td>
</tr>
</tbody>
</table>

*a* Experiment at Bruner Farm was not repeated in 1997.

*b* Organic matter

<table>
<thead>
<tr>
<th>Location / year</th>
<th>Variable</th>
<th>Nematode stage</th>
<th>pH</th>
<th>OM*</th>
<th>K</th>
<th>P</th>
<th>Soybean yield</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bruner 1995</td>
<td><em>H. glycines</em> cysts</td>
<td>-0.14</td>
<td>0.35**</td>
<td>0.12</td>
<td>0.11</td>
<td>-0.15</td>
<td></td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>0.03</td>
<td>0.14</td>
<td>0.02</td>
<td>-0.07</td>
<td>-0.27</td>
<td></td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td></td>
<td>-0.30**</td>
<td>-0.43**</td>
<td>-0.36**</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td></td>
<td>0.36**</td>
<td>0.52**</td>
<td>0.05</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>K</td>
<td></td>
<td></td>
<td>0.76**</td>
<td>-0.19</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kanawha 1995</td>
<td><em>H. glycines</em> cysts</td>
<td>0.32**</td>
<td>-0.17</td>
<td>-0.19</td>
<td>-0.11</td>
<td>-0.82**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>0.26**</td>
<td>-0.17</td>
<td>-0.14</td>
<td>-0.09</td>
<td>-0.71**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td></td>
<td>-0.83**</td>
<td>-0.65**</td>
<td>0.36**</td>
<td>-0.97**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td></td>
<td>0.82**</td>
<td>0.36**</td>
<td>0.90**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>K</td>
<td></td>
<td></td>
<td>0.06</td>
<td>0.84**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.45</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kanawha 1996</td>
<td><em>H. glycines</em> cysts</td>
<td>0.37**</td>
<td>-0.37**</td>
<td>-0.18</td>
<td>-0.10</td>
<td>-0.72**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>0.40**</td>
<td>-0.34</td>
<td>-0.15</td>
<td>-0.03</td>
<td>-0.64**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td></td>
<td>-0.60**</td>
<td>-0.59**</td>
<td>-0.09</td>
<td>-0.85**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td></td>
<td>0.45**</td>
<td>0.12</td>
<td>0.75**</td>
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<tr>
<td></td>
<td>K</td>
<td></td>
<td></td>
<td>0.23*</td>
<td>0.76**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>0.35</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kanawha 1997</td>
<td><em>H. glycines</em> cysts</td>
<td>0.47**</td>
<td>-0.43**</td>
<td>-0.16</td>
<td>-0.41**</td>
<td>-0.80**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>eggs</td>
<td>0.42**</td>
<td>-0.40**</td>
<td>-0.12</td>
<td>-0.36**</td>
<td>-0.88**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>pH</td>
<td></td>
<td>-0.80**</td>
<td>-0.58**</td>
<td>-0.06</td>
<td>-0.83**</td>
<td></td>
</tr>
<tr>
<td></td>
<td>OM</td>
<td></td>
<td>0.58**</td>
<td>0.06</td>
<td>0.85**</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>K</td>
<td></td>
<td></td>
<td>0.08</td>
<td>0.76**</td>
<td></td>
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<tr>
<td></td>
<td>P</td>
<td></td>
<td></td>
<td></td>
<td>-0.02</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* Organic matter

*=correlation significant at P<0.05; **correlation significant at P<0.01.
**Table 1.** Spatial patterns of *Heterodera glycines* egg population (A), soil pH (B), organic matter (C), and soybean yield (D) in the Kanawha Farm experiment. Numbers following letters represent sampling time: (1) spring 1995, (2) spring 1996, and (3) spring 1997. Plot dimensions were 15 x 30 m.

### Heterodera glycines (eggs 100 cm$^{-3}$ soil) vs. Soil pH (pH) vs. Organic matter (%) vs. Soybean yield (kg ha$^{-1}$)

<table>
<thead>
<tr>
<th>Heterodera glycines (eggs 100 cm$^{-3}$ soil)</th>
<th>Soil pH</th>
<th>Organic matter (%)</th>
<th>Soybean yield (kg ha$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>&gt; 7,500</td>
<td>7.3 - 7.8</td>
<td>7.0 - 9.0</td>
<td>2,500 - 3,500</td>
</tr>
<tr>
<td>2,501 - 7,500</td>
<td>7.0 - 7.2</td>
<td>6.0 - 6.9</td>
<td>2,000 - 2,500</td>
</tr>
<tr>
<td>1,001 - 2,500</td>
<td>6.5 - 6.9</td>
<td>5.0 - 5.9</td>
<td>1,500 - 2,000</td>
</tr>
<tr>
<td>101 - 1,000</td>
<td>6.0 - 6.4</td>
<td>4.0 - 4.9</td>
<td>1,000 - 1,500</td>
</tr>
<tr>
<td>0 - 100</td>
<td>5.7 - 5.9</td>
<td>2.9 - 3.9</td>
<td>698 - 1,000</td>
</tr>
</tbody>
</table>

Fig. 1. Spatial patterns of *Heterodera glycines* egg population (A), soil pH (B), organic matter (C), and soybean yield (D) in the Kanawha Farm experiment. Numbers following letters represent sampling time: (1) spring 1995, (2) spring 1996, and (3) spring 1997. Plot dimensions were 15 x 30 m.
CHAPTER 5

GENERAL SUMMARY

The research presented in this dissertation comprised three components. The first component involved study of *Heterodera glycines* spatial patterns in plots naturally infested with *H. glycines*, with each plot subjected to one of four tillage systems. We used geostatistical analyses and modeling to identify changes in spatial patterns of *H. glycines* under different tillage systems in these naturally infested fields. Four tillage systems were implemented beginning in the spring of 1995. Conventional tillage consisted of fall chisel plowing, followed by spring disking and field cultivation prior to planting. Reduced tillage consisted of spring disking followed by field cultivation before planting. In ridge tillage, the seedbed was raised during cultivation or in the fall, and planting was done in the ridge top, in the same row, every year. The initial *H. glycines* spatial patterns were aggregated in one field and more uniform in the second location. After three years and three soybean crop seasons, we detected changes in the *H. glycines* spatial patterns in the plots with an original aggregated spatial pattern. In contrast, results of geostatistical analysis from the plots located in the field with a more uniform initial spatial pattern generally were inconsistent. No tillage and ridge tillage promoted aggregation of *H. glycines* cyst and egg population densities, whereas conventional and reduced tillage disrupted aggregation resulting in more uniformly distributed populations. Results indicate that
changes in the spatial pattern of *H. glycines* due to tillage are dependent at least in part, on the initial nematode population spatial pattern.

In the second component of the research described in this dissertation, the relationships among tillage, dissemination and population density of *H. glycines*, and soybean yield were evaluated in artificially infested fields. In one experiment, treatments consisted of no tillage, non-infested; no tillage, *H. glycines*-infested; ridge tillage, *H. glycines* infested; conventional tillage, *H. glycines* infested; and reduced tillage, *H. glycines*-infested. For infested treatments, a 1-m² area was infested with *H. glycines* in the spring of 1995 prior to planting and tillage. One year after the establishment of the experiment, population densities of *H. glycines* were lower in the infested, no-tillage treatment compared to infested, conventional- and reduced-tillage treatments. After three crop seasons, *H. glycines* population densities were higher in the conventional- and reduced-tillage treatments than in the no- and ridge-tillage treatments. Additionally, conventional and reduced tillage disseminated *H. glycines* 6.9 m away from the original infested site compared to 0.5 and 1.4 m for the no-tillage and ridge-tillage treatments, respectively. Soybean yield decreased in all treatments over time, but the decrease was more pronounced in the conventional-tillage treatment than any other treatment. A second experiment, initiated in 1996 was established to evaluate the effect of spatial patterns of *H. glycines* populations on yields of soybeans. There were three treatments: non infested, aggregated infestation, and uniform infestation. In the aggregated infestation treatment, a 3.0-m-dia. circular area in the center of the plot was infested with *H. glycines* whereas in the uniform treatment, the total area of the plot was infested with the nematode. The
overall nematode population density introduced in each infested plot was the same within each replication. Throughout the three years of the experiment, *Heterodera glycines* population densities consistently were greater in the uniformly infested treatment compared to the aggregated treatment. There were no significant differences in soybean yield among the three treatments in 1996, 1997, and 1998. Results indicated that tillage rapidly disseminates *H. glycines* in fields that are recently, promoting rapid nematode reproduction and increasing yield losses.

In the third component of the described research, the relationships of soil properties and *H. glycines* population densities in no-tillage plots were investigated. Experiments were conducted in fields naturally infested with *H. glycines* from 1995 to 1997. Soil samples consisted of six soil cores and were taken on 2.3 m grid in the spring of each year, shortly after planting a *H. glycines*-susceptible soybean cultivar. At one location, there were consistently positive correlations between *H. glycines* population densities and soil pH and an inverse relationship between organic matter and nematode population densities. Generally correlations of nematode population densities with K and P were not significant. The relationships among *H. glycines* population densities, soil pH, and organic matter appear to be site-specific and the nature of the relationship is not fully known.

In summary, the results of our research indicate the beneficial aspects of no tillage in the management of *H. glycines*. In fields with well-established and strongly aggregated *H. glycines* populations, no-tillage and ridge-tillage practices may promote aggregation of the nematode population, whereas conventional- and reduced-tillage practices will disrupt aggregation, resulting in more uniformly
distributed nematode populations. Our results also indicate that different tillage practices do not result in measurable changes in the spatial pattern of *H. glycines* in fields with less aggregated nematode populations. Tillage quickly disseminates *H. glycines* in newly infested fields, facilitating more rapid nematode reproduction and subsequent yield loss. In contrast, adoption of no tillage in fields where *H. glycines* has been recently introduced may limit nematode reproduction, dissemination, and soybean yield losses. Additionally, soil pH and organic matter are related to *H. glycines* population densities and their impact on soybean yield, at least in some fields. The nature of the relationship, however, is unknown at this time.

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time</th>
<th>Co(^y) (x10(^5))</th>
<th>Co+C(^z) (x10(^3))</th>
<th>C/(Co+C)(^w)</th>
<th>Ao(^\prime) (m)</th>
<th>R(^2)</th>
<th>LiP</th>
</tr>
</thead>
<tbody>
<tr>
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<td>7.6</td>
<td>0.18</td>
<td>50.9</td>
<td>0.31</td>
<td>1.7</td>
<td></td>
</tr>
<tr>
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<td>2.6</td>
<td>4.0</td>
<td>0.33</td>
<td>6.6</td>
<td>0.26</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S 96</td>
<td>8.2</td>
<td>11.0</td>
<td>0.25</td>
<td>0.0(^1)</td>
<td>19.3(^3)</td>
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</tr>
<tr>
<td>S 97</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ridge F 94</td>
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<td>12.3</td>
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<td>91.2</td>
<td>0.30</td>
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<td>9.6</td>
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</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
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<td>0.52</td>
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<td>0.47</td>
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<td>5.6</td>
<td>0.27</td>
<td>6.3</td>
<td>0.30</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S 96</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S 97</td>
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<td>0.89</td>
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<td>Conventional F 94</td>
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<td>15.4</td>
<td>0.41</td>
<td></td>
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</tr>
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<td></td>
<td></td>
<td></td>
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<td>S 96</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S 97</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^2\)F=fall, S=spring
\(^y\)Co=Nugget variance, the value of the semivariogram near the origin, representing microdistributional and measurement error.
\(^z\)Co+C=Sill, the limiting value of the semivariogram for large distances or the semivariance value beyond range of spatial dependence.
\(^w\)C/(Co+C)=proportion of the sill explained by spatially structured variance.
\(^\prime\)Ao=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.
\(^1\)Semivariance values could not be described by any model.
\(^3\)The range parameter along the plant rows, when anisotropy was present.
\(^4\)The range parameter across the plant rows, when anisotropy was present.
Table A2. Change of *Heterodera glycines* population densities in plots naturally infested with *H. glycines* under different tillage systems.

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
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<td></td>
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<td>135.3</td>
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<tr>
<td>Ridge</td>
<td></td>
<td>cysts</td>
<td>482.4</td>
<td>178.0</td>
<td>-22.4</td>
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</tr>
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<td>380.8</td>
<td>-17.5</td>
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<tr>
<td>Reduced</td>
<td></td>
<td>cysts</td>
<td>-28.1</td>
<td>101.4</td>
<td>-24.0</td>
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<tr>
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<td>eggs</td>
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<tr>
<td>Bruner</td>
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<td>-0.6</td>
</tr>
<tr>
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<td>eggs</td>
<td>338.0</td>
<td>9.1</td>
<td>111.7</td>
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<tr>
<td>Ridge</td>
<td></td>
<td>cysts</td>
<td>*</td>
<td>302.1</td>
<td>19.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>eggs</td>
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</tr>
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<td></td>
<td>cysts</td>
<td>*</td>
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<tr>
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</tr>
<tr>
<td>Conventional</td>
<td></td>
<td>cysts</td>
<td>*</td>
<td>98.0</td>
<td>-16.3</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>eggs</td>
<td>134.8</td>
<td>25.5</td>
<td>148.2</td>
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</tbody>
</table>

<sup>2</sup> Change was obtained by \( \frac{(Pf-Pi)}{Pi} \times 100 \)

<sup>x</sup> Cysts were not enumerated in 1994.
**Table A3.** Cross validation parameters of estimated cyst population densities of *Heterodera glycines* by point kriging at the Kanawha Farm experiment.

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time&lt;sup&gt;x&lt;/sup&gt;</th>
<th>Regression coefficient&lt;sup&gt;y&lt;/sup&gt;</th>
<th>Standard error&lt;sup&gt;x&lt;/sup&gt;</th>
<th>$R^2$&lt;sup&gt;y&lt;/sup&gt;</th>
<th>Y-intercept&lt;sup&gt;y&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
<td>F 94</td>
<td>0.71</td>
<td>0.056</td>
<td>0.67</td>
<td>43.8</td>
</tr>
<tr>
<td></td>
<td>S 95</td>
<td>0.68</td>
<td>0.055</td>
<td>0.66</td>
<td>43.3</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>0.56</td>
<td>0.054</td>
<td>0.53</td>
<td>73.4</td>
</tr>
<tr>
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<td>S 97</td>
<td>0.80</td>
<td>0.045</td>
<td>0.78</td>
<td>40.9</td>
</tr>
<tr>
<td>Ridge-tillage</td>
<td>F 94</td>
<td>0.20</td>
<td>0.045</td>
<td>0.17</td>
<td>26.6</td>
</tr>
<tr>
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<td>S 95</td>
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<td>S 96</td>
<td>0.57</td>
<td>0.054</td>
<td>0.53</td>
<td>131.7</td>
</tr>
<tr>
<td></td>
<td>S 97</td>
<td>0.71</td>
<td>0.052</td>
<td>0.66</td>
<td>63.9</td>
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<tr>
<td>Reduced</td>
<td>F 94</td>
<td>0.61</td>
<td>0.057</td>
<td>0.56</td>
<td>78.5</td>
</tr>
<tr>
<td></td>
<td>S 95</td>
<td>0.73</td>
<td>0.053</td>
<td>0.67</td>
<td>35.5</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>0.71</td>
<td>0.049</td>
<td>0.68</td>
<td>55.8</td>
</tr>
<tr>
<td></td>
<td>S 97</td>
<td>0.65</td>
<td>0.052</td>
<td>0.62</td>
<td>53.6</td>
</tr>
<tr>
<td>Conventional</td>
<td>F 94</td>
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<td>0.050</td>
<td>0.65</td>
<td>76.2</td>
</tr>
<tr>
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<td>S 95</td>
<td>0.69</td>
<td>0.064</td>
<td>0.55</td>
<td>37.6</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
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<td>0.063</td>
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<td>40.4</td>
</tr>
<tr>
<td></td>
<td>S 97</td>
<td>0.79</td>
<td>0.054</td>
<td>0.70</td>
<td>33.4</td>
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</table>

<sup>x</sup>F=fall, S=spring
<sup>y</sup>Regression coefficient represents a measure of the goodness of fit for the least-squares model describing the linear regression equation.
<sup>x</sup>Standard error of the regression coefficient.
<sup>y</sup>$R^2$ is the proportion of variation explained by the best fit line.
<sup>y</sup>Y-intercept of the best fit line.
**Table A4.** Cross validation parameters of estimated egg population densities of *Heterodera glycines* by point kriging at the Kanawha Farm experiment.

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time</th>
<th>Regression coefficient</th>
<th>Standard error</th>
<th>$R^2$</th>
<th>$Y$ intercept</th>
</tr>
</thead>
<tbody>
<tr>
<td>No</td>
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<tr>
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</tr>
<tr>
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<td>0.58</td>
<td>0.052</td>
<td>0.56</td>
<td>2,808</td>
</tr>
<tr>
<td>Ridge</td>
<td>F 94</td>
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<td>0.045</td>
<td>0.16</td>
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<td>0.051</td>
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</tbody>
</table>

$^a$F=fall, S=spring  
$^b$Regression coefficient represents a measure of the goodness of fit for the least-squares model describing the linear regression equation.  
$^c$Standard error of the regression coefficient.  
$^d$R² is the proportion of variation explained by the best fit line.  
$^e$Y-intercept of the best fit line.
Table A5. Cross validation parameters of estimated cyst population densities of *Heterodera glycines* by point kriging at the Bruner Farm experiment.

<table>
<thead>
<tr>
<th>Tillage system</th>
<th>Sampling time</th>
<th>Regression coefficient</th>
<th>Standard error</th>
<th>$R^2$</th>
<th>Y-intercept</th>
</tr>
</thead>
<tbody>
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<td>No</td>
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<td>0.047</td>
<td>0.23</td>
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</tr>
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<td>S 96</td>
<td>0.13</td>
<td>0.040</td>
<td>0.10</td>
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</tr>
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<td></td>
<td>S 97</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
<td>&quot;</td>
</tr>
<tr>
<td>Ridge-tillage</td>
<td>S 95</td>
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<td>0.048</td>
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<td></td>
<td>S 96</td>
<td>0.26</td>
<td>0.051</td>
<td>0.21</td>
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<tr>
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<td>0.041</td>
<td>0.13</td>
<td>163</td>
</tr>
<tr>
<td></td>
<td>S 96</td>
<td>0.24</td>
<td>0.048</td>
<td>0.21</td>
<td>249</td>
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<td>0.053</td>
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</table>

*F*=fall, *S*=spring

Regression coefficient represents a measure of the goodness of fit for the least-squares model describing the linear regression equation.

Standard error of the regression coefficient.

$R^2$ is the proportion of variation explained by the best fit line.

Y-intercept of the best fit line.

Semivariance values could not be described by any model.
Fig. A1. Isotropic semivariograms of *Heterodera glycines* egg populations in plots under different tillage systems in 1994 (○), 1995 (■), 1996 (▲) and 1997 (◆), for the experiment at the Bruner Farm.
Fig. A2. Anisotropic semivariograms of *Heterodera glycines* egg populations in plots under different tillage systems in 1994 (●), 1995 (■), 1996 (▲) and 1997 (◆), for the experiment at the Bruner Farm in different directions in degrees azimuth (0° = along soybean rows).
Fig. A3. Spatial patterns of *Heterodera glycines* egg population densities in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the experiment at the Bruner Farm. Numbers following letters represent sampling time: (1) fall 1994, (2) spring 1995, (3) spring 1996, and (4) spring 1997.
Fig. A4. Change (%) in *Heterodera glycines* cyst population densities in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the Kanawha Farm experiment. Numbers following letters represent different sampling times used for calculating the change: (1) 1994/1995, (2) 1995/1996, and (3) 1996/1997.
Fig. A5. Change (%) in *Heterodera glycines* egg population densities in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the Kanawha Farm experiment. Numbers following letters represent different sampling times used for calculating the change: (1) 1994/1995, (2) 1995/1996, and (3) 1996/1997.
Fig. A6. Change (%) in *Heterodera glycines* cyst population densities in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the Bruner Farm experiment. Numbers following letters represent different sampling times used for calculating the change: (1) 1995/1996 and (2) 1996/1997.
Change (%) of *Heterodera glycines* egg population density

-100 to -60
-80 to -60
-60 to -40
-40 to -20
-20 to 0
0
0 to 10
10 to 20
20 to 40
40 to 60
60 to 1688
No Data

Fig. A7. Change (%) in *Heterodera glycines* egg population densities in plots under no tillage (A), ridge tillage (B), reduced tillage (C), and conventional tillage (D) in the Bruner Farm experiment. Numbers following letters represent different sampling times used for calculating the change: (1) 1994/1995, (2) 1995/1996 and (3) 1996/1997.
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