Determining the Role of Plant-Parasitic Nematodes in the Corn–Soybean Crop Rotation Yield Effect Using Nematicide Application: II. Soybean

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ABSTRACT

Corn (*Zea mays* L.)–soybean [*Glycine max* (L.) Merr.] crop rotation is well-known to increase yields of both crops and is called the rotation effect. This study was conducted to determine the role of plant-parasitic nematodes—particularly soybean cyst nematode (SCN, *Heterodera glycines*),—in the rotation effect for soybean. Research was conducted at a site in Waseca, MN, that was established in 1982 to study corn–soybean rotation. Included in the study were treatments in 1 to 5 yr of SCN-susceptible soybean monoculture following 5 yr of corn, continuous SCN-susceptible soybean monoculture, and continuous soybean with SCN-resistant cultivars since 2010. Granular nematicides have been applied to half of each plot since 2010 to minimize nematode populations across crop sequences as a way to determine the role of nematodes in the rotation effect. Because nematicide was similarly effective in each crop sequence, it was not effective for determining if SCN damage varied by crop sequence. Soybean cyst nematode populations increased ($P \leq 0.05$) in soybean monoculture and were negatively correlated with soybean yield ($P \leq 0.05$). *Pratylenchus* (lesion nematode) populations decreased significantly in soybean monoculture particularly when comparing first and second year in soybean ($P \leq 0.05$). Helicotylenchus (spiral nematode) and *Xiphinema* (dagger nematode) populations were significantly decreased in continuous soybean compared to most sequences in 5 or fewer years of monoculture ($P \leq 0.05$). Trends in nematode populations suggest SCN may have had a role in the rotation effect for soybean yield, but that *Pratylenchus*, *Helicotylenchus*, and *Xiphinema* did not.

Core Ideas

- Growing soybean in monoculture decreases yield.
- Growing soybean in monoculture increases soybean cyst nematode populations.
- There was some evidence that soybean cyst nematode can be involved in monoculture yield decline for soybean.

Soybean and corn production is an integral part of agriculture in the United States and together represents a majority of agricultural production. In 2014, 37 and 34.3 million ha of corn and soybean respectively were planted in the United States, and together this constituted 53.5% of total area planted to principal crops (NASS-USDA, 2014). Corn–soybean rotation has long been known to increase yield of both crops compared to monoculture, a phenomena known as the rotation effect. Conversely, yield decrease when crops are grown in monoculture is known as monoculture yield decline. The mechanisms by which crop rotation increases crop yield are of great interest and have been a focus of much research.

The most widely recognized benefit of corn–soybean rotation is maintance of soil nutrients, particularly N for corn production due to N_2 fixation by soybean (Peterson and Varvel, 1989; Meese et al., 1991; Omay et al., 1998). However, soybean benefits from crop rotation despite fixing its own N (Crookston et al., 1991; Meese et al., 1991; Porter et al., 1997; Wilhelm and Wortmann, 2004; Salvagiotti et al., 2008). Additionally, a number of studies, including ones at the site of the present study, have established that the rotation effect occurs even when sufficient nutrients are supplied by fertilizers (Crookston et al., 1991; Meese et al., 1991; Porter et al., 1997; Howard et al., 1998; Wilhelm and Wortmann, 2004).

There is evidence that other agronomic factors including soil moisture (Copeland et al., 1993; Pedersen and Lauer, 2004), soil structure (Griffith et al., 1988; Nickel et al., 1995), and crop residue volume or chemical properties (Yakle and Cruse, 1984; Crookston et al., 1988; Crookston and Kurle, 1989; Nickel et al., 1995) contribute to the rotation effect and that rotation influences crop physiology (Copeland and Crookston, 1992; Nickel et al., 1995; Pikul et al., 2012). Vesicular-arbuscular mycorrhizae (Johnson et al., 1991) and nutrient mineralization by microbes (Green and Blackmer, 1995; Gentry et al., 2001) may also contribute to the corn–soybean rotation effect. Additionally, corn–soybean rotation helps manage various pathogens and pests that reside or overwinter in plant residue and soil which can contribute to yield benefits of rotation (Gracia-Garza et al., 2002; Rousseau et al., 2007; Pedersen and Grau, 2010; Jirak-Peterson and Esker, 2011; Chu et al., 2013).

Alleviating crop damage by plant-parasitic nematodes may also be an important part of the yield benefits of crop rotation for soybean—a concept that is the focus of this study. Soybean

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Abbreviations: DAP, days after planting; SCN, soybean cyst nematode.

cyst nematode is the most damaging pathogen of soybean in the Midwest causing an estimated 25% of yield loss from disease (Koenning and Wrather, 2010; Wrather and Koenning, 2009). Only soybean and a few other leguminous crops are SCN hosts while most other field crops, including corn, are not hosts (Warnke et al., 2008). Consequently, rotation with corn is used to manage this nematode, and SCN is likely to play a role in the rotation effect in the Midwest (Noel and Edwards, 1996; Chen et al., 2001b; Porter et al., 2001; Conley et al., 2011).

This study utilized a unique, long-term research site in Waseca, MN, involving various corn–soybean crop sequences. This site is a well-established platform for investigating the corn–soybean rotation effect when soil nutrients are supplied in abundance by fertilizers (Crookston et al., 1991; Johnson et al., 1991; Meese et al., 1991; Copeland and Crookston, 1992; Copeland et al., 1993; Nickel et al., 1995; Porter et al., 1997, 2001) including documenting SCN populations trends (Porter et al., 2001). The influence of crop rotation and nematicide on soil ecology based on the nematode community—which includes plant-parasitic and free-living nematodes—has also been documented at this site (Grabau and Chen, 2016). This study focuses on soybean while corn is discussed in an accompanying study.

While previous studies have documented SCN population densities and soybean yield in various corn–soybean crop sequences (Noel and Edwards, 1996; Chen et al., 2001b; Porter et al., 2001; Conley et al., 2011), in the present study, nematicide was applied systematically at the research site to determine damage to soybean—in various crop sequences—by plant-parasitic nematodes through comparison to soybean without nematicide application.

Population densities of all plant-parasitic nematodes at the site are also reported, providing valuable, but not frequently reported information on nematodes other than SCN in soybean production. The objectives of this study were to: (i) investigate the role of crop damage by plant-parasitic nematodes in the rotation yield effect for soybean using nematicide application; (ii) determine the impact of corn–soybean crop sequences and nematicide application on plant-parasitic nematode populations during soybean phases of these crop sequences; and (iii) further document the impact of crop rotation on soybean yield (the rotation effect).

MATERIALS AND METHODS

Experimental Design

The study was conducted at the Southern Research and Outreach Center in Waseca, MN, (44°04′ N, 93°33′ W) on a Nicollet clay loam (fine-loamy, mixed, mesic Aquic Hapludoll). At this field site, plots of various corn–soybean crop sequence treatments have been maintained continuously since 1982. Only the soybean phases at the site are included in this study while the corn phases are included in a separate study. The three sequence types, examined in this study (Table 1) were: (i) 5 yr of soybean following 5 yr of corn with each phase grown each year and treatments of 1, 2, 3, 4, and 5 yr of soybean monoculture included in this study; (ii) continuous soybean monoculture since 1982; (iii) annual rotation between two cultivars, but soybean monoculture. Since 1995, sequence type (iii) has been single-cultivar soybean monoculture. Beginning in 2010, soybean phases in sequence types (i) and (ii) were SCN-susceptible soybean cultivars while sequence type (iii) was SCN-resistant soybean cultivars with PI88788 resistance source. Since each phase of each sequence type was present each year, seven crop sequence treatments were examined in this study: first, second, third, fourth, and fifth-year soybean (following 5 yr of corn); continuous SCN-susceptible soybean cultivars monoculture (since 1982); and continuous soybean monoculture (since 1982) with SCN-resistant soybean since 2010.

From 2010 onward, half of each plot was treated with in-furrow, granular nematicide to create a split-plot experiment arrangement with crop sequence as the main plot factor and nematicide application as the subplot factor. The same experimental design for nematicide application was retained from year to year, so nematicide was applied to the same subplots each year. Subplots were 4.57 m wide by 7.62 m long with six crop rows. In 2010 and 2011, S-[[(1,1-dimethylethyl)thio]methyl] O,O-diethyl phosphorodithioate (terbufos) nematicide (Counter 20G, AMVAC

Table 1. Corn (C) and soybean (S) cropping sequence treatments† in Waseca, MN.

	Crop sequence by year									
Treatments	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014
					10-yr rotation					
1.	C4	C5	S1	S2	S3	S4	S5	C1	C2	C3
2.	C3	C4	C5	S1	S2	S3	S4	S5	C1	C2
3.	C2	C3	C4	C5	S1	S2	S3	S4	S5	C1
4.	C1	C2	C3	C4	C5	S1	S2	S3	S4	S5
5.	S5	C1	C2	C3	C4	C5	S1	S2	S3	S4
6.	S4	S5	C1	C2	C3	C4	C5	S1	S2	S3
7.	S3	S4	S5	C1	C2	C3	C4	C5	S1	S2
8.	S2	S3	S4	S5	C1	C2	C3	C4	C5	S1
9.	S1	S2	S3	S4	S5	C1	C2	C3	C4	C5
10.	C5	S1	S2	S3	S4	S5	C1	C2	C3	C4
					Continuous monoculture					
11.	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss	Ss
					Continuous; SCN-resistance soybean post-2010, alternating cultivars pre-1995					
12.	Ss	Ss	Ss	Ss	Ss	Sr	Sr	Sr	Sr	Sr

† C1 through C5 are first- to fifth-year corn after 5 yr of soybean; S1 through S5 are first- to fifth-year soybean following 5 yr of corn; Ss and Sr are continuous soybean with soybean cyst nematode (SCN)-susceptible and resistant cultivars since 2010, respectively. All soybean, except Sr, were susceptible to SCN.

Chemical Corporation, Los Angeles, CA) at 2.44 kg a.i. ha^{-1} was applied in-furrow at planting. In 2012 to 2014, aldicarb [2-methyl-2-(methylthio) proprionaldehyde O-(methylcarbamoyl) oxime] nematicide (Bolster 15G, AMVAC Chemical Corporation) at 2.94 kg a.i. ha^{-1} was applied in-furrow at planting. Both crop sequence and nematicide factors were randomized complete block designs with four replicates within the split-plot arrangement. Because terbufos had limited effects on nematode populations, but aldicarb effectively suppressed nematode populations, this study only includes data from 2012 to 2014 when aldicarb was applied.

Site Management

Corn and soybean were planted, with concurrent nematicide application to appropriate subplots, on 1 June 2012; 3 June 2013; and 21 May 2014. The SCN-susceptible soybean planted was cultivar Pioneer 92Y22. The SCN-resistant soybean planted was cultivar Pioneer 92Y12. Plots were managed with conventional tillage with the site chisel plowed each fall and field cultivated each spring before planting. Glyphosate [N-(phosphonomethyl) glycine] was applied at rates from 0.96 to 1.42 L a.i. ha^{-1} for post-emergence weed management with two applications in 2012, but single applications in 2013 and 2014. Insecticide was applied as needed with Lambda-cyhalthrin {[1a(S*),3a(Z)]-cyano(3-phenoxyphenyl)methyl-3-(2-chloro-3,3,3-trifluoro-1-propenyl)-2,2-dimethylcyclopropanecarboxylate}foliar insecticide at 0.028 kg ha^{-1} applied to soybeans 19 August 2014 for soybean aphid (*Aphis glycines* [Matsumura]) control. Crops were fertilized such that soil nutrients should not have been a limiting factor. Nitrogen fertilizer was surface-broadcast without incorporation at 224 kg N ha^{-1} (2012-2014) in the form of urea with agrotain to corn plots within 2 wk after planting. In fall 2012 before plowing and spring 2014, after plowing, all plots received P in the form of triple super phosphate at 84 and 78 kg ha^{-1}, respectively and K in the form of potash at 224 and 39 kg ha^{-1}, respectively.

Nematode Population and Corn Yield Assessment

Soil samples for analysis of nematode populations were collected from 2012 to 2014 at three time points during each year: spring (within 1 wk before planting), midseason (47–64 d after planting), and fall (at harvest). Soil samples were taken from all subplots on 30 May, 24 July (54 DAP), and 8 October (130 DAP) 2012; on 3 June, 6 August (64 DAP), and 8 October (127 DAP) 2013; and 19 May, 7 July (47 DAP), and 9 October (139 DAP) 2014. From each subplot, 20 soil cores were taken in the two central rows (within 4 cm of plant rows) to a depth of 20 cm. Soil samples were homogenized by passing soil through a metal screen with 4 mm apertures before further processing.

Vermiform (worm-shaped, all nematodes except SCN females and eggs in this case) plant-parasitic nematode population densities were determined for all soil samples collected in spring, midseason, and fall from 2012 to 2014. Vermiform nematodes from each subplot were extracted from a 100 cm^3 homogenized soil subsample using a modified sucrose floatation and centrifugation method (Jenkins, 1964). From this extraction, a subsample of nematodes from each subplot was identified morphologically to genus and soil population densities were calculated for vermiform stages of SCN, *Pratylenchus* (lesion nematode), *Helicotylenchus* (spiral nematode), and *Xiphinema* (dagger nematode). These genera represent the four major plant-parasitic nematodes consistently present at the site. Vermiform stages of SCN included both males and juveniles.

Additionally, SCN egg population densities were determined for all soil samples collected at spring, midseason, and fall. For SCN egg extraction, a 100-cm^3 soil subsample was taken from each homogenized subplot soil sample following storage at 4°C. Soil was soaked in a 1.76% powder dishwasher detergent solution for at least 15 min then SCN females and cysts were extracted from the soil using a semiautomatic elutriator (Byrd et al., 1976), collected on nested 250-µm-aperture and 850-µm-aperture sieves, and centrifuged in 63% sucrose solution for 5 min at 1100 *g*. Cysts were emaciated with a mechanical crusher to release eggs (Faghihi and Ferris, 2000), which were collected in water and stored at 4°C until population density was determined from counts of a subsample of eggs using a microscope.

Soybean yields were determined based on the two central rows of each plot, and were standardized to 13% moisture. Soybean plants were harvested 2 Oct. 2012, 10 Oct. 2013, and 8 Oct. 2014.

Statistical Analysis

Within each season, each variable was combined by crop sequence treatment across years and the combined data were analyzed using two-way, split-plot ANOVA (McIntosh, 1983). Years and replicates were included in the ANOVA model, but were considered random effects and not tested for significance. Replicate by crop sequence interaction was used as the error term for crop sequence and crop sequence × year interaction while residual error was used as the error term for all other sources of variation (McIntosh, 1983). The ANOVA models were evaluated for homogeneity of variance using Levene's test and for normality of residuals graphically and response variables were transformed as necessary to meet these assumptions (Levene, 1960; Cook and Weisburg, 1999). Soybean cyst nematode eggs in spring and midseason, and vermiform SCN in midseason were transformed by $x^{1/3}$. *Helicotylenchus* population density in midseason was transformed by $x^{1/2}$. Soybean yield and *Xiphinema* population density in spring were not transformed. *Helicotylenchus* in spring and fall, vermiform SCN in spring and fall, *Pratylenchus* in all seasons, *Xiphinema* in midseason and fall, and SCN eggs in fall were transformed by $\ln(x+1)$. For variables with significant crop sequence effects ($P \leq 0.05$), crop sequence treatment means were separated using Fischers protected LSD ($\alpha = 0.05$).

Regression analyses of individual plot soybean yields on SCN egg population densities as well as individual plot soybean yields on vermiform SCN population densities were performed to examine relationships between yield and SCN population densities across crop sequences in this study. Because regression analyses were conducted across different crop sequences, these equations cannot be used to establish generic relationships between soybean yield and nematode densities outside of this study. Only sequences planted to the SCN-susceptible cultivar were included because yield responses would be different for the SCN-resistant cultivar. Midseason nematode populations were used because this produced linear regression models with greater R^2 values than models using spring nematode populations (data not shown). Separate regression models were made for each year because trends differed by year (data not shown). Polynomial, untransformed linear, and transformed linear models as well as inclusion of a term for nematicide application were considered and the best models were chosen based on adjusted R^2 values.

Table 2. Plant-parasitic nematode populations and crop yields for 2012 to 2014 combined as influenced by crop sequence and nematicide application.

ANOVA (*F* values)	Degrees of freedom Numerator, Denominator	Soybean yield	Soybean cyst nematode eggs Pi†	 Pm	 Pf
Crop sequence (C)	6, 54	9.34*	64.90*	47.31*	26.13*
Year (Y) × C	12, 54	0.45	1.66	1.22	1.26
Nematicide (N)	1, 63	47.09*	1.17	5.63	56.26*
N × Y	2, 63	11.67*	0.35	0.45	1.95
C × N	6, 63	0.82	1.33	0.36	2.01
Y × C × N	12, 63	1.42	0.76	0.37	1.25

	Vermiform SCN Pi	 Pm	 Pf	*Pratylenchus* (lesion nematode) Pi	 Pm	 Pf
ANOVA (*F* values)						
Crop sequence (C)	62.44*	59.29*	67.60*	52.06*	51.06*	24.67*
Year (Y) × C	3.22*	1.20	1.75	1.90	1.53	1.12
Nematicide (N)	5.24*	0.50	30.93*	1.52	14.58*	30.95*
N × Y	3.06*	0.12	2.25	1.71	2.45	0.36
C × N	1.40	0.33	0.52	1.20	0.73	2.19
Y × C × N	1.18	0.48	0.81	0.40	0.76	0.55

	Helicotylenchus (spiral nematode) Pi	 Pm	 Pf	*Xiphinema* (dagger nematode) Pi	 Pm	 Pf
ANOVA (*F* values)						
Crop sequence (C)	8.14	6.75*	4.36*	3.07*	4.36*	2.32*
Year (Y) × C	0.60	1.75	1.01	0.63	1.68	1.28
Nematicide (N)	0.42	28.03*	95.42*	0.34	18.47*	33.10*
N × Y	3.40*	0.72	2.44	1.82	1.51	8.79*
C × N	1.09	1.34	1.44	1.06	1.00	1.34
Y × C × N	0.91	0.81	1.54	0.98	1.08	0.87

* Significant effects at $P \leq 0.05$ and $P \leq 0.01$, respectively.

† Pi, Pm, Pf are mean population densities before planting, at midseason (47–64 d after planting), and at harvest, respectively.

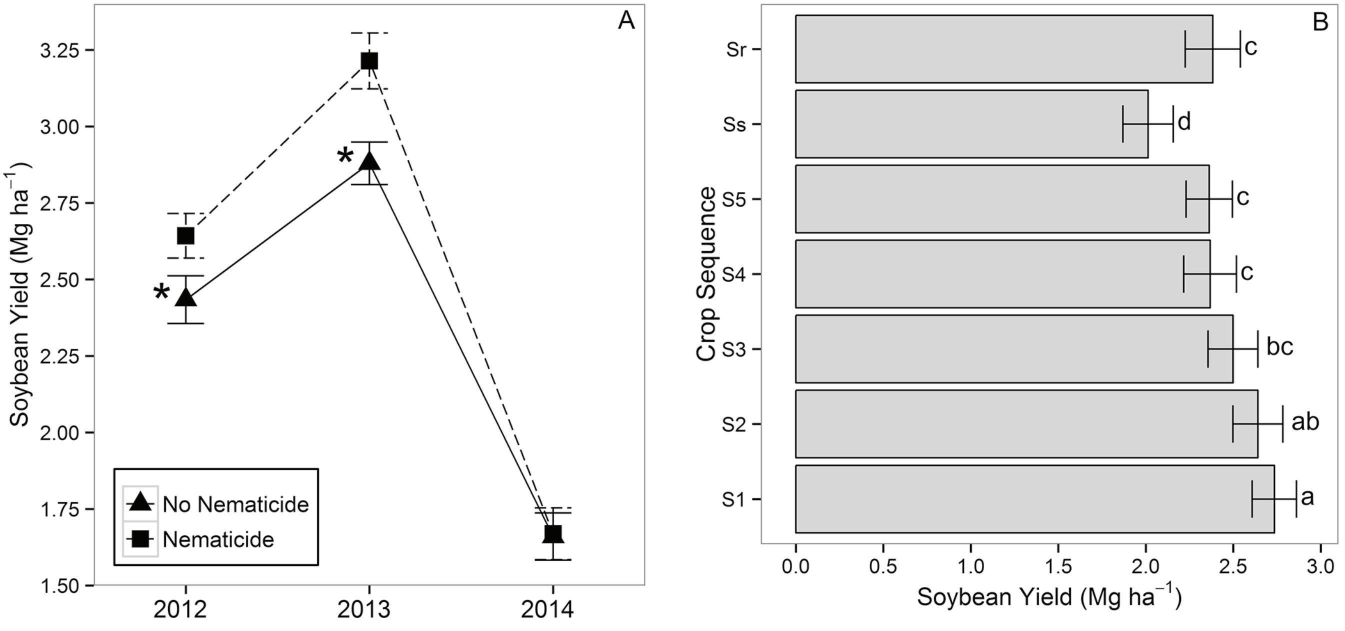

Fig. 1. (A) Soybean yields as influenced by nematicide in individual years combined across crop sequences; and (B) as influenced by crop sequences for 2012 to 2014 combined and combined across nematicide treatments. In subfigure A, * indicates significantly ($P \leq 0.05$) different values between nematicide and no nematicide treatments for the given season according to ANOVA. In subfigure B, different letters indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. S1 through S5 are first- to fifth-year soybean cyst nematode (SCN)-susceptible soybean following 5 yr of corn. Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars, respectively.

All analyses were performed using R version 3.0 (The R Foundation for Statistical Computing, Vienna, Austria).

RESULTS

Soybean Yields

Soybean yields were significantly influenced by nematicide, but this influence varied by year (Table 2). In 2012 and 2013, soybean yields, averaged across crop sequences, were significantly increased by nematicide application compared to no nematicide application, but in 2014, nematicide did not significantly influence soybean yield (Fig. 1A). Averaged across years and crop sequences, soybean yield was significantly (Table 2) greater with than without nematicide with values of 2.52 and 2.33 Mg ha^{-1}, respectively. Soybean yields, combined across years and nematicide treatments, were also significantly affected by crop sequence (Table 2) with yield decreasing in soybean monoculture (Fig. 1B). In particular, soybean yield was greater in first-year soybean than in 3 or more years of SCN-susceptible soybean, greater in second-year soybean than 4 or more years of SCN-susceptible soybean, and smallest in continuous SCN-susceptible soybean—including continuous soybean recently with SCN-resistant cultivar.

Soybean Cyst Nematode Egg Populations

Soybean cyst nematode egg populations, averaged across crop sequences and years, were significantly decreased by nematicide application in midseason and fall (Table 2, Fig. 2A). In all three seasons when soil was sampled, SCN egg populations, averaged across nematicide treatments and years, were significantly affected by crop sequence with populations increasing in soybean monoculture (Table 2, Fig. 2B and 2C). Before planting and at midseason, SCN egg populations were similar between first- and second-year soybean, increased significantly as years in soybean increased from second- to fifth-year soybean, but were similar between fifth year and continuous SCN-susceptible soybean (Fig. 2B and 2C). Before planting and at midseason, population in continuous soybean with SCN-resistant cultivar was significantly smaller than in 3 or more years of SCN-suceptible soybean. In fall, populations increased significantly as years in soybean increased up to 3 yr in soybean, but were similar among sequences in 3 or more years of SCN-susceptible soybean (Fig. 2D). In fall, population in continuous soybean with SCN-resistant cultivar was significantly smaller than in 2 or more years of SCN-suceptible soybean.

Vermiform Soybean Cyst Nematode Populations

Vermiform SCN population, including both males and juveniles, was significantly affected by nematicide in fall (Table 2) with population decreased by nematicide application compared to no nematicide application with 57 and 130 vermiform SCN 100 cm^{-3} soil, respectively. Before planting, there was significant year × nematicide interaction (Table 2) with significant nematicide effects only in 2013 ($P \leq 0.05$, ANOVA). In 2013, vermiform SCN population was significantly decreased by nematicide application compared to no nematicide application with 110 and 186 vermiform SCN 100 cm^{-3} soil, respectively.

Before planting, there was significant year × crop sequence interaction (Table 2) with significant crop sequence effects in all 3 yr (Fig. 3A, 3B, and 3C). In all 3 yr, populations increased in soybean monoculture, with most increases occurring in the first

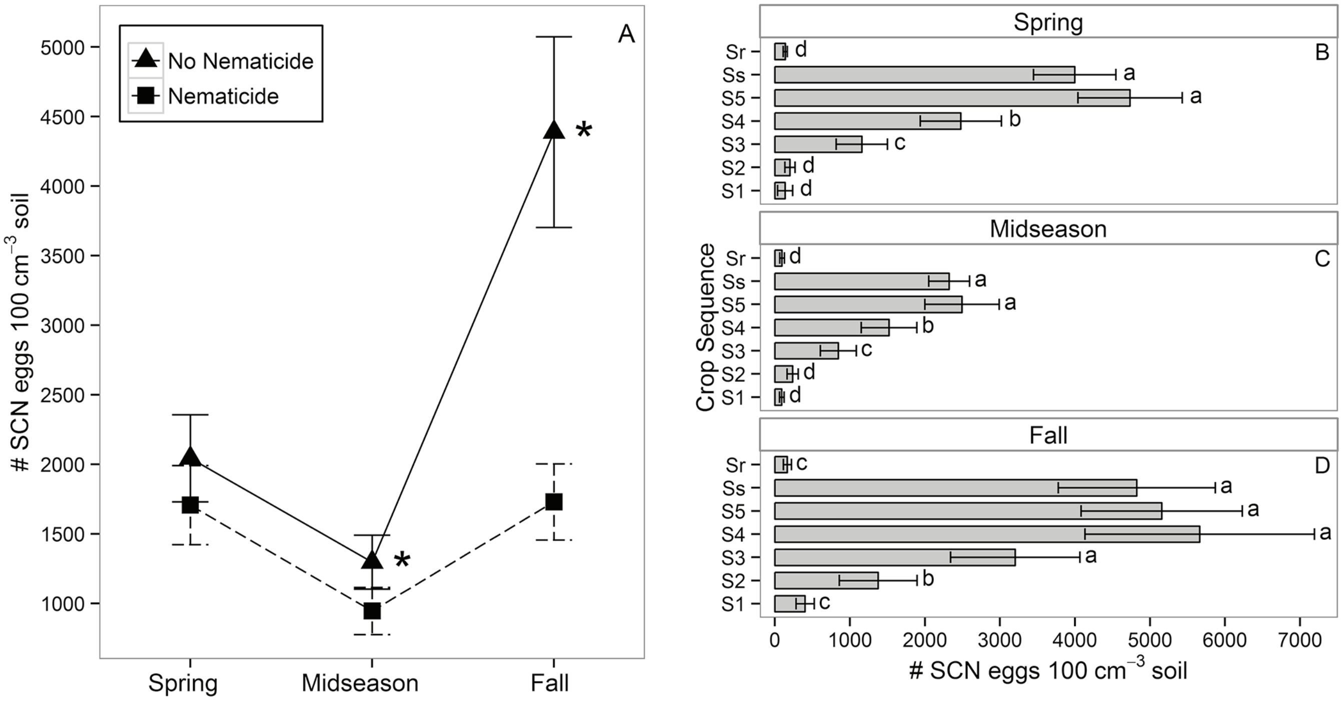

Fig. 2. (A) Soybean cyst nematode (SCN) egg populations as influenced by nematicide application by season for 2012 to 2014 combined and combined across crop sequences. Soybean cyst nematode egg populations as influenced by crop sequences (B) before planting, (C) at midseason, and (D) fall for 2012 to 2014 combined and combined across nematicide treatments. Spring, midseason, and fall are before planting, 47 to 64 d after planting, and at harvest, respectively. In subfigure A, * indicates significantly ($P \leq 0.05$) different values between nematicide and no nematicide treatments for the given season according to ANOVA. For subfigures B, C, and D, different letters within a subfigure indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. S1 through S5 are first- to fifth-year SCN-susceptible soybean following 5 yr of corn. Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars, respectively.

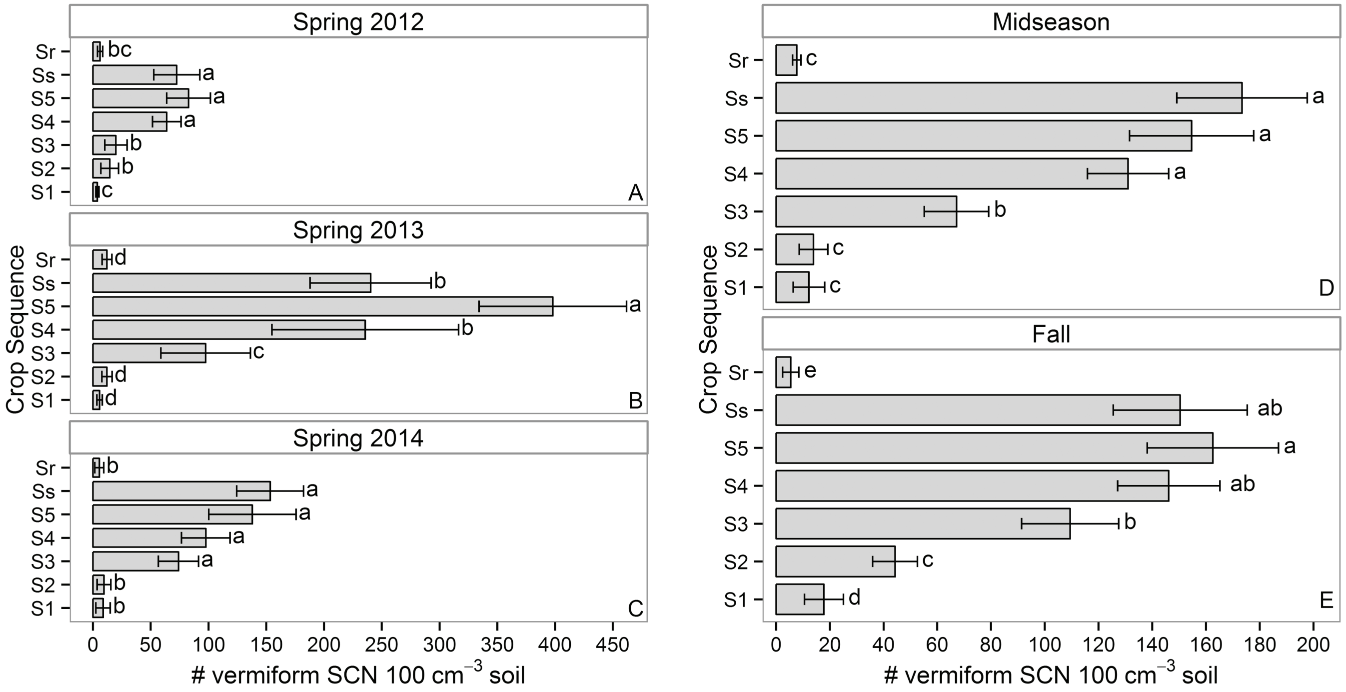

Fig. 3. Vermiform soybean cyst nematode (SCN) populations before planting as influenced by crop sequences in (A) 2012, (B) 2013, and (C) 2014; and as influenced by crop sequences in (D) midseason and (E) fall for 2012 to 2014 combined. All values are combined across nematicide treatments. Spring, midseason, and fall are before planting, 47 to 64 d after planting, and at harvest, respectively. Within a subfigure, different letters indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. S1 through S5 are first- to fifth-year SCN-susceptible soybean following 5 yr of corn. Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars, respectively.

4 yr in monoculture. In 2013, population densities before planting increased as years in soybean increased from second- through fifth-year soybean and population was smaller in continuous than fifth-year SCN-susceptible soybean (Fig. 3B). In 2012 and 2014, there were fewer differences among sequences with populations greater in 3 (2014) or 4 (2012) yr or more of susceptible soybean than other sequences (Fig. 3A and 3C). In all 3 yr, populations before planting were smaller in continuous soybean with SCN-resistant cultivar than any sequence in susceptible soybean for 3 (2012) or 4 (2013 and 2014) yr or more.

Combined across years and nematicide treatments, there were significant crop sequence effects in midseason and fall (Table 2) with populations increasing in SCN-susceptible soybean monoculture (Fig. 3D and 3E). In midseason, populations were significantly greater in 4 or more years in SCN-susceptible soybean than any other sequence, and greater in third-year soybean than first-year, second-year, or resistant soybean (Fig. 3D). In fall, populations were smallest in continuous soybean recently with resistant cultivar, and increased significantly as years in susceptible soybean increased for first to third year in soybean (Fig. 3E). In fall, populations were also significantly greater in fifth- than third-year soybean but similar among third-year, fourth-year, and continuous SCN-susceptible soybean.

Pratylenchus (Lesion Nematode) Populations

Pratylenchus populations, combined across years and crop sequences, were significantly decreased by nematicide application compared to no nematicide application in midseason and fall (Table 2, Fig. 4A). *Pratylenchus* populations, combined across years and nematicide treatments, were significantly affected by crop sequence in all three seasons (Table 2) with populations decreasing in soybean monoculture, particularly from first- to second-year soybean (Fig. 4B, 4C, and 4D). Before planting and at midseason, *Pratylenchus* populations decreased significantly as years in SCN-susceptible soybean increased except from third to fourth year in spring and fourth to fifth year at midseason (Fig. 4B and 4C). In fall, *Pratylenchus* populations were significantly greater in first-year soybean than any other sequence, greater in second- to fourth-year soybean than sequences in soybean 5 or more years, and greater in fifth-year than continuous soybean (Fig. 4D). In continuous soybean, populations were not significantly different between SCN-susceptible and resistant cultivars.

Helicotylenchus (Spiral Nematode) Populations

Helicotylenchus populations, averaged across years and crop sequences, were significantly reduced by nematicide application compared to no nematicide application in midseason and fall (Table 2, Fig. 5A). Before planting, there was significant nematicide × year interaction (Table 2) with nematicide application significantly ($P \leq 0.05$, ANOVA) reducing populations in 2012 compared to no nematicide application with 73 and 143 nematodes 100 cm^{-3} soil respectively, but in 2013 and 2014 there were no significant nematicide effects ($P > 0.05$, ANOVA).

Combined across nematicide treatments and years, there were significant crop sequence effects in all three seasons (Table 2) with populations generally smaller in sequences in soybean monoculture for an extended period (Fig. 5B, 5C, and 5D). Before planting, populations were significantly smaller in continuous resistant or susceptible soybean monoculture than any other soybean sequence (Fig. 5B). At midseason, populations were significantly smaller in 5 or more years of soybean than 4 or fewer years of soybean (Fig. 5C). In fall, populations were significantly smaller in continuous

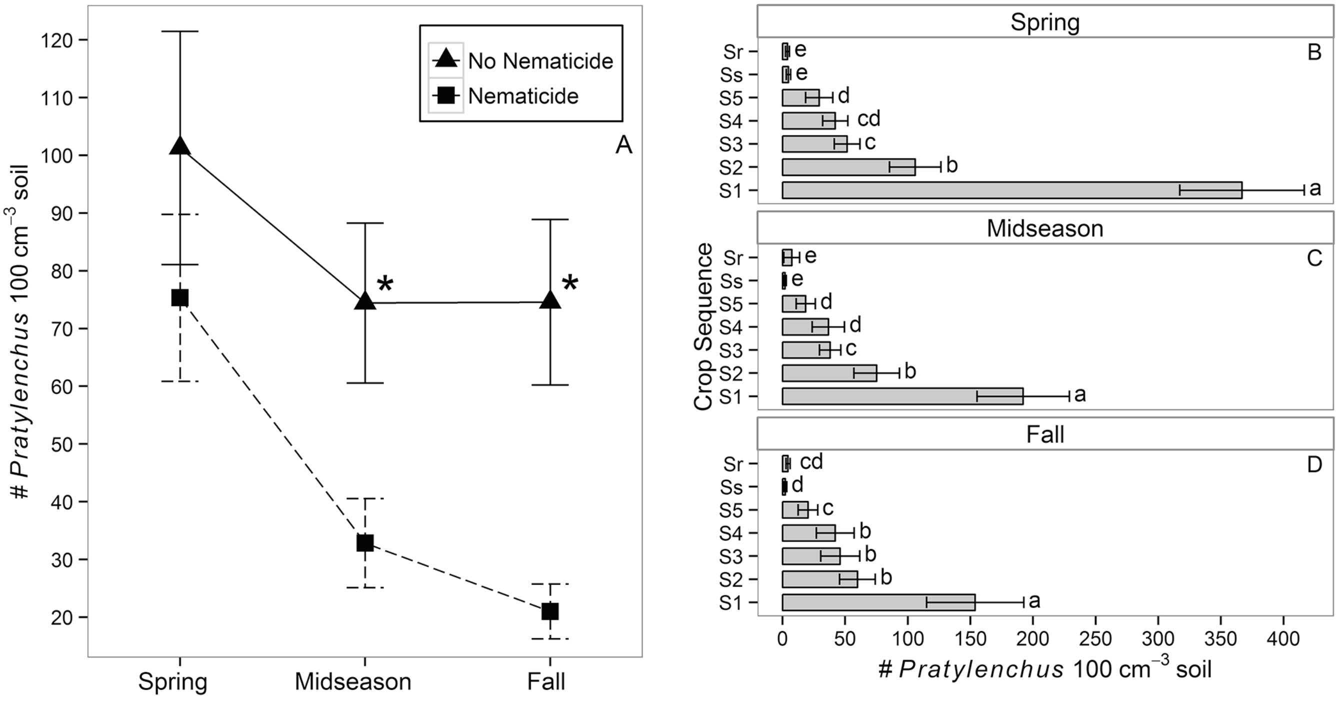

Fig. 4. (A) *Pratylenchus* (lesion nematode) populations as influenced by nematicide application by season for 2012 to 2014 combined and combined across crop sequences. *Pratylenchus* populations as influenced by crop sequences (B) before planting, (C) at midseason, and (D) fall for 2012 to 2014 combined and combined across nematicide treatments. Spring, midseason, and fall are before planting, 47 to 64 d after planting, and at harvest, respectively. In subfigure A, * indicates significantly ($P \leq 0.05$) different values between nematicide and no nematicide treatments for the given season according to ANOVA. For subfigures B, C, and D, different letters within a subfigure indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. S1 through S5 are first- to fifth-year soybean cyst nematode (SCN)-susceptible soybean following 5 yr of corn. Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars, respectively.

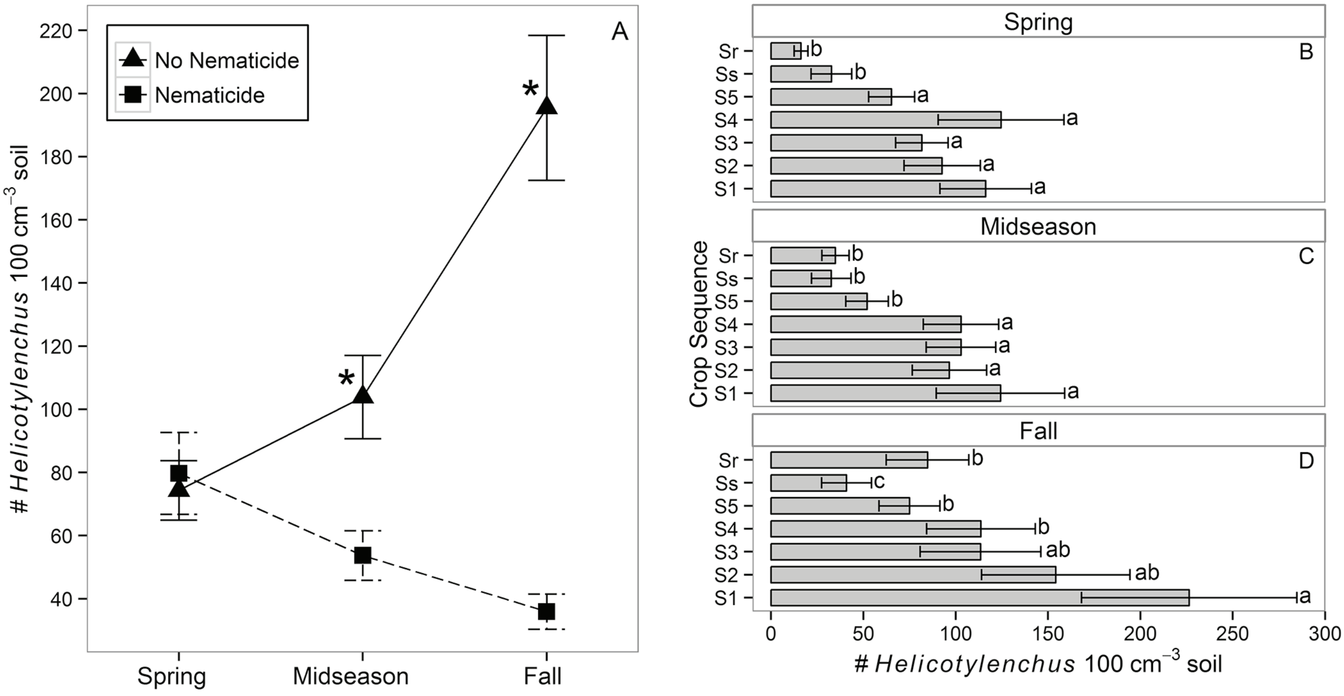

Fig. 5. (A) *Helicotylenchus* (spiral nematode) populations as influenced by nematicide by individual season for 2012 to 2014 combined and combined across crop sequences. *Helicotylenchus* populations as influenced by crop sequences (B) before planting, (C) at midseason, and (D) fall for 2012 to 2014 combined and combined across nematicide treatments. Spring, midseason, and fall are before planting, 47 to 64 d after planting, and at harvest, respectively. In subfigure A, * indicates significantly ($P \leq 0.05$) different values between nematicide and no nematicide treatments for the given season according to ANOVA. For subfigures B, C, and D, different letters within a subfigure indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. S1 through S5 are first- to fifth-year soybean cyst nematode (SCN)-susceptible soybean following 5 yr of corn. Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars, respectively.

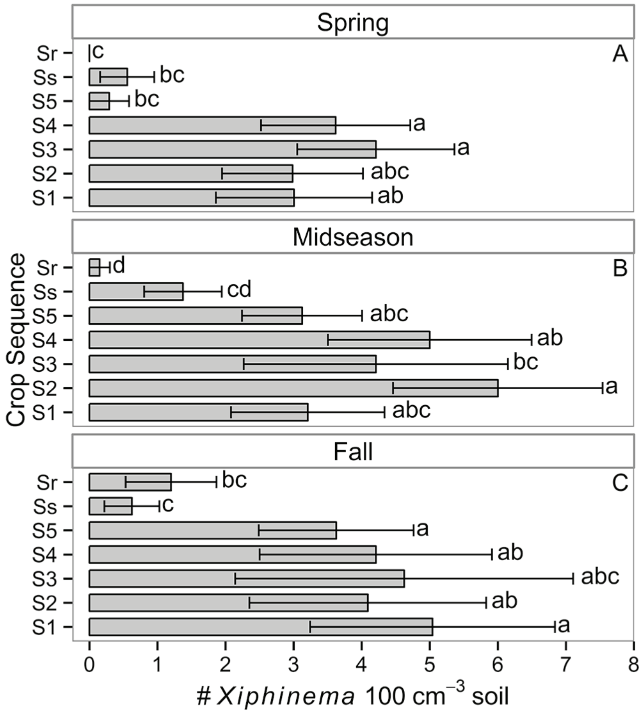

Fig. 6. *Xiphinema* (dagger nematode) populations as influenced by crop sequences (A) before planting, (B) at midseason, and (C) fall for 2012 to 2014 combined. Values are combined across nematicide treatments. Spring, midseason, and fall are before planting, 47 to 64 d after planting, and at harvest, respectively. Within a subfigure, different letters indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. S1 through S5 are first- to fifth-year soybean cyst nematode (SCN)-susceptible soybean following 5 yr of corn. Ss and Sr are continuous soybean recently with SCN-susceptible and resistant cultivars, respectively.

SCN-susceptible soybean monoculture than any other sequence and larger in first-year soybean than sequences in 4 or more years of soybean (Fig. 5D).

Xiphinema (Dagger Nematode) Populations

Xiphinema population, averaged across years and crop sequences, was significantly reduced by nematicide compared to no nematicide treatment in midseason (Table 2) with populations of 2 and 5 nematodes 100 cm^{-3} soil, respectively. In fall, there was significant year by nematicide interaction (Table 2) with significant nematicide effects ($P \leq 0.05$, ANOVA) in 2012 and 2013, but not 2014. In 2012, *Xiphinema* populations were reduced in nematicide (2 nematodes 100 cm^{-3} soil) compared to no nematicide treatments (11 nematodes 100 cm^{-3} soil). In 2013, *Xiphinema* populations were reduced in nematicide (0 nematodes 100 cm^{-3} soil) compared to no nematicide treatment (4 nematodes 100 cm^{-3} soil).

Xiphinema populations, averaged across years and nematicide treatments, were significantly affected by crop sequence in all three seasons (Table 2). *Xiphinema* populations were small across sequences as average populations were below 10 nematodes 100 cm^{-3} soil for all sequences and seasons (Fig. 6A, 6B, and 6C). Population densities were generally not significantly different among sequences in 4 or fewer years of soybean in any season, but populations were significantly smaller in continuous (all seasons) or fifth-year soybean (spring) than in many other sequences (Fig. 6A, 6B, and 6C).

Linear Regression of Soybean Yields on Soybean Cyst Nematode Populations

In all three seasons, linear regressions between soybean yields and SCN egg populations or soybean yields and vermiform SCN populations produced significant models ($P \leq 0.0001$). There were negative correlations between soybean yields and nematode population densities (Fig. 7) with significant ($P \leq 0.001$) slope coefficients in each case (data not shown). There were negative logarithmic relationships between soybean yield and nematode populations except between SCN eggs and yield in 2012 when there was a negative linear relationship. There were separate slopes and intercepts with nematicide and without nematicide for vermiform SCN in 2012 and SCN eggs in 2013 while there was a separate intercept for vermiform SCN in 2013. Based on adjusted R^2 values, the regression models explained 25 to 48% of the variability in soybean yield. In 2013 and 2014, SCN egg and vermiform models had similar explanatory value, but in 2012, the egg model was better than the vermiform model.

Because regression analyses were conducted across different crop sequences, these equations cannot be used to establish generic relationships between soybean yield and nematode densities outside of this study. Rather, these analyses are limited to describing the relationship between soybean yield—across crop sequences—and nematode populations in this study.

DISCUSSION

Nematicide applications were effective for increasing soybean yields in 2012 and 2013 while in 2014 a September hail storm decreased soybean yield and may have obscured any nematicide effects. Nematicide applications reduced SCN egg populations after planting suggesting SCN control contributed to yield increase with nematicide. For vermiform SCN, nematicide mainly affected populations in fall and reductions were not substantial. Aldicarb has successfully reduced SCN populations in studies in the Midwest (Noel, 1987; Smith et al., 1991; Niblack et al., 1992) although it was ineffective in one study (Rotundo et al., 2010) and efficacy was inconsistent to varying degrees in every study.

While there was evidence SCN control contributed to yield benefits of nematicide application, spring and midseason SCN populations averaged across crop sequences were less than 2000 eggs 100 cm^{-3} soil, which is considered to represent a moderate damage threat in the region (Schmitt et al., 1987; Niblack et al., 1992; MacGuidwin et al., 1995; Chen et al., 2001a). This suggests that reduction in SCN egg population may not have been the only factor that contributed to the observed yield increase with nematicide application. Aldicarb also affects insects (Todd and Canerday, 1972; Herbert et al., 1987), and is known to increase soybean growth in the absence of disease pressure under certain environmental conditions (Barker et al., 1988), so these benefits may have also contributed to yield increase with nematicide application. Nematicide consistently reduced *Pratylenchus*, *Helicotylenchus*, and *Xiphinema* populations across crop sequences after planting, but these nematodes did not reproduce well on soybean based on small population sizes, and decreasing populations in soybean monoculture, suggesting these nematodes did not have a major influence on soybean yield. Additionally, the potential for these nematodes to damage soybean is not well defined (Ferris and Bernard, 1971; Zirakparvar, 1980; McGawley and Chapman, 1983; Niblack, 1992), and damage by SCN is a much greater concern (Schmitt et

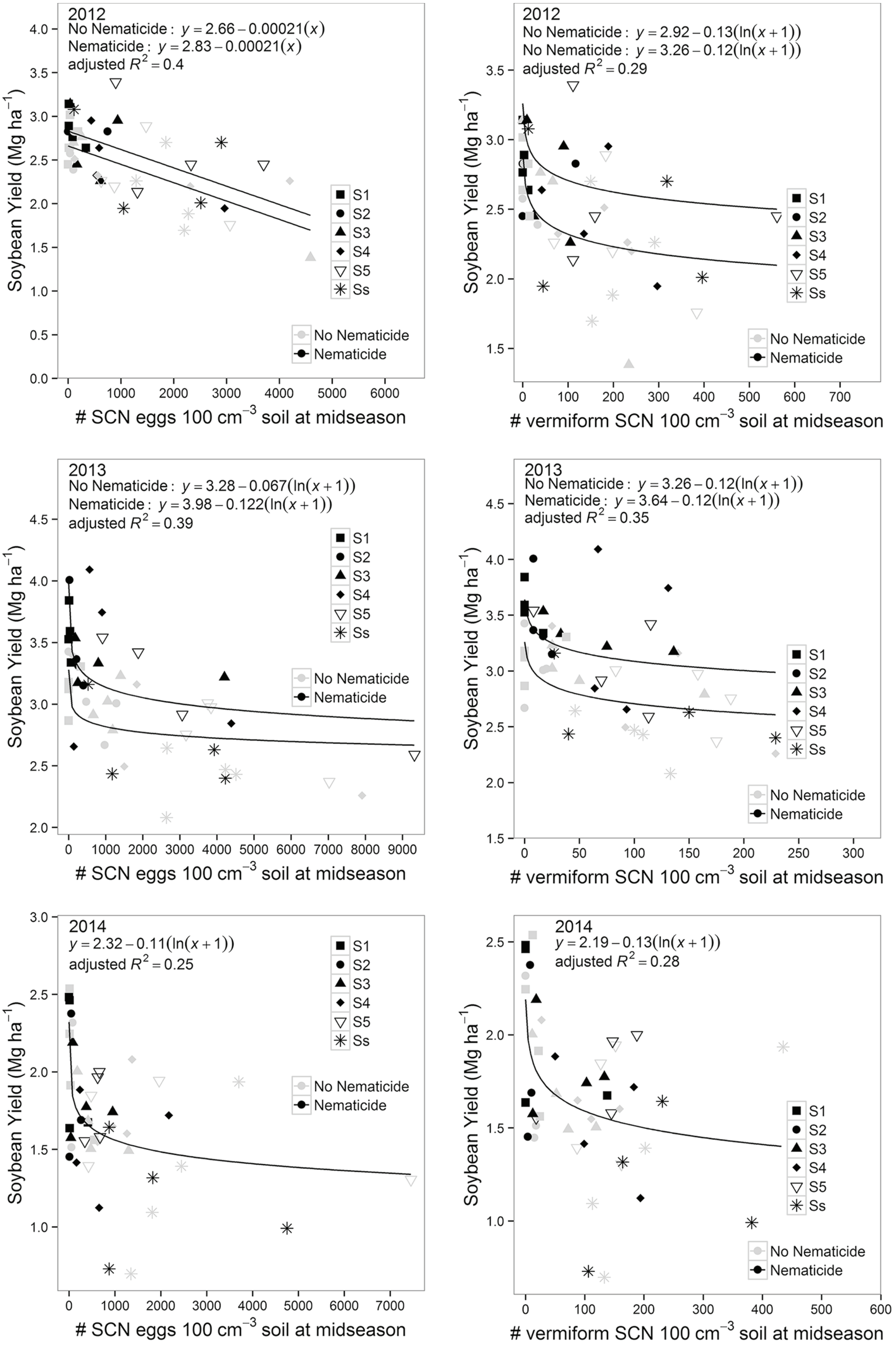

Fig. 7. Linear regression of soybean yield on soybean cyst nematode (SCN) egg and vermiform populations at midseason in 2012, 2013, and 2014 (54, 64, and 47 d after planting, respectively). Regression lines display equations from regression analysis, which are specified in each subfigure. Ss is continuous SCN-susceptible soybean. S1 through S5 are first- to fifth-year SCN-susceptible soybean after 5 yr of corn.

al., 1987; Niblack, 1992; Niblack et al., 1992; Chen et al., 2001a). Efficacy of aldicarb against these nematodes has been demonstrated elsewhere as aldicarb reduced *Pratylenchus* and *Xiphinema* populations 70 to 90%, and *Helicotylenchus* population 50% in an Iowa study across various sites (Norton et al., 1978).

Crop sequences clearly impacted nematode populations. In particular, increasing SCN populations in soybean monoculture reinforced the problems soybean monoculture creates for managing SCN population densities (Koenning et al., 1995; Noel and Edwards, 1996; Chen et al., 2001b; Porter et al., 2001). Differences in SCN population densities were particularly large when comparing sequences in the first 3 yr of soybean monoculture demonstrating that SCN population can increase rapidly when SCN-susceptible soybean is grown as observed elsewhere (Chen et al., 2001a, 2001b). This suggests even 2 or 3 yr of SCN-susceptible soybean monoculture can cause long-term SCN management problems. Previous research at the Waseca site where the present study was conducted and a partner site in Lamberton, MN, showed similar increases in SCN egg populations in soybean monoculture, although maximum populations were greater at Lamberton (Porter et al., 2001). In previous research at the site of the present study, SCN second stage juvenile population increase under soybean monoculture was similar to results for vermiform SCN in the present study (Chen and Reese, 1999). In the present study, SCN populations also plateaued after 4 or 5 yr in soybean suggesting SCN populations reached carrying capacities in that field for the given season.

Soybean cyst nematode suppression has been documented at a site in long-term continuous soybean monoculture near the site of the present study (Chen, 2007a; Bao et al., 2011, 2013). At that site, SCN suppression is attributed in part to fungal antagonists of SCN (Chen, 2007a; Bao et al., 2011, 2013), and in previous research at the site of the present study, the fungus *Hirsutella rhossiliensis* parasitized 20 to 30% of SCN juveniles in most soybean monoculture sequences during the growing season (Chen and Reese, 1999). In the present study, vermiform SCN population was decreased in continuous soybean monoculture compared to fifth-year soybean. Soybean cyst nematode populations were also moderate for soybean monoculture sequences at the site, considering SCN field population densities may reach 10,000 SCN eggs 100 cm^{-3} soil or greater in the area after a single season of SCN-susceptible soybean following corn (Chen et al., 2001b, 2001c) or SCN-resistant soybean (Chen, 2007b). In a previous study, populations were smaller at the site of the present study than at the identically managed site in Lamberton, MN (Porter et al., 2001). In the present study use of nematicide decreased overall SCN population densities, but it is possible that biotic factors such as fungal antagonists or unknown abiotic factors also limit SCN populations at the site.

Decreased SCN populations under SCN-resistant compared to SCN-susceptible continuous soybean monoculture show SCN-resistant soybean was effective for managing SCN populations, even after 5 yr of monoculture. Other studies have also demonstrated that SCN-resistant cultivars are effective, including after 3 or 4 yr (Chen et al., 2001b; Chen, 2007b) of SCN-resistant soybean monoculture. Development of resistance-breaking SCN populations is a concern when cultivars with the same source of SCN resistance are grown repeatedly (Zheng et al., 2006; Niblack et al., 2008; Kim et al., 2011), but this has not occurred at the site of this study yet, based on continuing efficacy of resistant cultivars in managing SCN.

Rotation with soybean helped manage *Pratylenchus* populations based on rapid population decline of this nematode in soybean monoculture. This is not consistent with the reported host range for *Pratylenchus*, which includes both corn and soybean for most species in this region (Zirakparvar, 1980; Belair et al., 2002; Chen and Tsay, 2006). Additionally, previous research suggests *Pratylenchus* populations developed just as well in corn–soybean rotation (Todd, 1991), and soybean monoculture (Johnson et al., 1975) as corn monoculture in short-term studies. However, since host range may vary by nematode population (Zirakparvar, 1980; Belair et al., 2002; Chen and Tsay, 2006), soybean could be a poor host of the particular *Pratylenchus* population at this site, resulting in reduced *Pratylenchus* population under soybean monoculture.

Alternatively, competition between SCN and *Pratylenchus* on soybean may have contributed to *Pratylenchus* population declines under soybean monoculture. Previous greenhouse experiments suggest *Pratylenchus penetrans* outcompetes SCN on soybean when their initial population densities are similar or favor *P. penetrans*, but SCN may outcompete *P. penetrans* if the initial ratio is greatly (3:1) in favor of SCN (Melakeberhan and Dey, 2003). However, this competition model (Melakeberhan and Dey, 2003) does not explain *Pratylenchus* population decreases in soybean phases of 10-yr rotation as before entering the soybean period, the ratio of *Pratylenchus* to SCN was very great since it followed 5 yr of corn monoculture. It is possible that the outcome of competition between the specific SCN and *Pratylenchus* populations at the site or outcomes in field settings over longer periods of time differs from the outcomes in the short-term greenhouse study (Melakeberhan and Dey, 2003). Further research is needed to determine the outcome of SCN-*Pratylenchus* interaction and the cause of *Pratylenchus* population decreases under soybean monoculture in this study.

Similar to *Pratylenchus*, *Helicotylenchus* has a wide host range that includes both corn and soybean for the populations tested in the few available reports (Ferris and Bernard, 1971; McGawley and Chapman, 1983). However, in the present study, *Helicotylenchus* populations were not large in soybean sequences and decreased in long-term soybean monoculture which suggests soybean may be a poor host of this *Helicotylenchus* population. Competition with SCN may have also contributed to these declines in *Helicotylenchus* population density, but more research would be needed to determine this. *Xiphinema* populations were very small across sequences although somewhat smaller in extended soybean monoculture. This suggests soybean was not a good host for this *Xiphinema* populations, but also that site conditions–such as soil type, tillage practices, or other nematodes present–were not favorable for establishing large *Xiphinema* population densities.

Soybean yield was also influenced by crop sequences as soybean yield declined gradually but continued over extended time periods. In past studies at the Waseca and Lamberton long-term rotation sites (Crookston et al., 1991), the Arlington, WI, site (Meese et al., 1991), and another at the Lamberton site (Porter et al., 2001), soybean yields generally declined as length of soybean monoculture increased although less gradually than in the present study. This varied somewhat by location and environment variation though as in other studies at the Minnesota and Wisconsin long-term rotation sites (Porter et al., 1997, 2001), soybean yield declined in the initial 2 or 3 yr of monoculture and leveled off with further increases in years in soybean. Additionally, in the present study, using SCN-resistant cultivars instead of susceptible cultivars in continuous soybean monoculture improved soybean yield. This is consistent with the concurrent decrease in SCN population and with previous research on the efficacy of SCN-resistant cultivars in the region (MacGuidwin et al., 1995; Chen et al., 2001a).

In this study, determining the role of nematodes in the rotation yield effect by minimizing nematode populations using nematicide was a major objective. However, there were not significant crop sequence × nematicide interactions for soybean yield or SCN populations. This shows that both soybean yield increase and SCN population decrease due to nematicide application was similar in each crop sequence.

Because SCN control by nematicide was similar in each cropping sequence, it was unclear, based solely on effects of nematicide application, if crop damage by SCN differed by cropping sequence. However, there is other evidence from the present study that SCN damage varied by crop sequence and that SCN had a role in the rotation yield effect. In the present study and other studies (Chen et al., 2001b; Porter et al., 2001) SCN populations increased as time in soybean monoculture increased. The negative impact of SCN on soybean yield is well-documented (Schmitt et al., 1987; Chen et al., 2001a, 2001b; Chen, 2007b; De Bruin and Pedersen, 2008), and in the present study, the negative relationship between soybean yield and SCN population density, across crop sequences, was described using regression analysis. These results from the present study as well as previous studies suggest yield loss from SCN increases as the length of time in soybean monoculture increases and management of SCN populations may have a role in the rotation effect for soybean yield. *Pratylenchus*, *Helicotylenchus*, and *Xiphinema* populations decreased and, to varying extent, had small populations in soybean monoculture. This suggests these nematodes were unlikely to have affected soybean yield and thus unlikely to have had a role in the rotation effect for soybean.

In summary, this study documented the distinct way different corn–soybean crop sequences influence SCN, *Pratylenchus*, *Helicotylenchus*, and *Xiphinema* populations. Additionally, the benefits of crop rotation for crop yield and the presence of the rotation yield effect for soybean were documented in this study. Increasing SCN populations and decreasing yield in soybean monoculture suggested alleviating damage by SCN contributed to the benefits of crop rotation for soybean yield.

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REFERENCES

Bao, Y., S. Chen, J. Vetsch, and G. Randall. 2013. Soybean yield and *Heterodera glycines* responses to liquid swine manure in nematode suppressive soil and conducive soil. J. Nematol. 45:21–29.

Bao, Y., D.A. Neher, and S. Chen. 2011. Effect of soil disturbance and biocides on nematode communities and extracellular enzyme activity in soybean cyst nematode suppressive soil. Nematology 13:687–699. doi:10.1163/138855410X541230

Barker, K.R., S.R. Koenning, A.L. Bostian, and A.R. Ayers. 1988. Growth and yield responses of soybean to aldicarb. J. Nematol. 20:421–431.

Belair, G., Y. Fournier, N. Dauphinais, and O. Dangi. 2002. Reproduction of *Pratylenchus penetrans* on various rotation crops in Quebec. Phytoprotection 83:111–114. doi:10.7202/706233ar

Byrd, D.W., K.R. Barker, H. Ferris, C.J. Nusbaum, W.E. Griffin, R.J. Small, and C.A. Stone. 1976. Two semiautomatic elutriators for extracting nematodes and certain fungi from soil. J. Nematol. 8:206–212.

Chen, S. 2007a. Suppression of *Heterodera glycines* in soils from fields with long-term soybean monoculture. Biocontrol Sci. Technol. 17:125–134. doi:10.1080/09583150600937121

Chen, S. 2007b. Tillage and crop sequence effects on *Heterodera glycines* and soybean yields. Agron. J. 99:797–807. doi:10.2134/agronj2006.0150

Chen, S., P. Porter, J. Orf, C. Reese, W. Stienstra, N. Young et al. 2001a. Soybean cyst nematode population development and associated soybean yields of resistant and susceptible cultivars in Minnesota. Plant Dis. 85:760–766. doi:10.1094/PDIS.2001.85.7.760

Chen, S., P. Porter, C. Reese, and W. Stienstra. 2001b. Crop sequence effects on soybean cyst nematode and soybean and corn yields. Crop Sci. 41:1843–1849. doi:10.2135/cropsci2001.1843

Chen, S., and C. Reese. 1999. Parasitism of the nematode *Heterodera glycines* by the fungus *Hirsutella rhossiliensis* as influenced by crop sequence. J. Nematol. 31:437–444.

Chen, P., and T.T. Tsay. 2006. Effect of crop rotation on *Meloidogyne* spp. and *Pratylenchus* spp. populations in strawberry fields in Taiwan. J. Nematol. 38:339–344.

Chen, S.Y., W.C. Stienstra, W.E. Lueschen, and T.R. Hoverstad. 2001c. Response of *Heterodera glycines* and soybean cultivar to tillage and row spacing. Plant Dis. 85:311–316. doi:10.1094/PDIS.2001.85.3.311

Chu, C., J.L. Spencer, M.J. Curzi, J.A. Zavala, and M.J. Seufferheld. 2013. Gut bacteria facilitate adaptation to crop rotation in the western corn rootworm. Proc. Natl. Acad. Sci. USA 110:11917–11922. doi:10.1073/pnas.1301886110

Conley, S.P., J.M. Gaska, P. Pedersen, and P. Esker. 2011. Soybean yield and *Heterodera glycines* response to rotation, tillage, and genetic resistance. Agron. J. 103:1604–1609. doi:10.2134/agronj2011.0043

Cook, R.D., and S. Weisburg. 1999. Response transformations In: Applied regression including computing and graphics. Wiley-Interscience, New York. p. 316–333.

Copeland, P., R. Allmaras, R. Crookston, and W. Nelson. 1993. Corn soybean rotation effects on soil-water depletion. Agron. J. 85:203–210. doi:10.2134/agronj1993.00021962008500020008x

Copeland, P., and R. Crookston. 1992. Crop sequence affects nutrient composition of corn and soybean grown under high fertility. Agron. J. 84:503–509. doi:10.2134/agronj1992.00021962008400030028x

Crookston, R., and J. Kurle. 1989. Corn residue effect on the yield of corn and soybean grown in rotation. Agron. J. 81:229–232. doi:10.2134/agronj1989.00021962008100020018x

Crookston, R., J. Kurle, P. Copeland, J. Ford, and W. Lueschen. 1991. Rotational cropping sequence affects yield of corn and soybean. Agron. J. 83:108–113. doi:10.2134/agronj1991.00021962008300010026x

Crookston, R., J. Kurle, and W. Lueschen. 1988. Relative ability of soybean, fallow, and triacontanol to alleviate yield reductions associated with growing corn continuously. Crop Sci. 28:145–147. doi:10.2135/cropsci1988.0011183X002800010031x

De Bruin, J.L., and P. Pedersen. 2008. Soybean cultivar and planting date response to soil fumigation. Agron. J. 100:965–970. doi:10.2134/agronj2007.0116

Faghihi, J., and J.M. Ferris. 2000. An efficient new device to release eggs from *Heterodera glycines*. J. Nematol. 32:411–413.

Ferris, V.R., and R.L. Bernard. 1971. Effect of soil type on population densities of nematodes in soybean rotation fields. J. Nematol. 3:123–128.

Gentry, L., F. Below, M. David, and J. Bergerou. 2001. Source of the soybean N credit in maize production. Plant Soil 236:175–184. doi:10.1023/A:1012707617126

Grabau, Z.J., and S. Chen. 2016. Influence of long-term corn-soybean crop sequences on soil ecology as indicated by the nematode community. Appl. Soil Ecol. 100:172–185. doi:10.1016/j.apsoil.2015.12.016

Gracia-Garza, J., S. Neumann, T. Vyn, and G. Boland. 2002. Influence of crop rotation and tillage on production of apothecia by *Sclerotinia sclerotiorum*. Can. J. Plant Pathol. 24:137–143. doi:10.1080/07060660309506988

Green, C., and A. Blackmer. 1995. Residue decomposition effects on nitrogen availability to corn following corn or soybean. Soil Sci. Soc. Am. J. 59:1065–1070. doi:10.2136/sssaj1995.03615995005900040016x

Griffith, D., E. Kladivko, J. Mannering, T. West, and S. Parsons. 1988. Long-term tillage and rotation effects on corn growth and yield on high and low organic matter, poorly drained soils. Agron. J. 80:599–605. doi:10.2134/agronj1988.00021962008000040011x

Herbert, D.A., R. Rodriguez-Kabana, P.A. Backman, and T.P. Mack. 1987. Effects of aldicarb on nematodes, early season insect pests, and yield of soybean. Ann. Appl. Nematol. 1:78–83.

Howard, D., A. Chambers, and G. Lessman. 1998. Rotation and fertilization effects on corn and soybean yields and soybean cyst nematode populations in a no-tillage system. Agron. J. 90:518–522. doi:10.2134/agronj1998.00021962009000040013x

Jenkins, W.R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 48:692.

Jirak-Peterson, J.C., and P.D. Esker. 2011. Tillage, crop rotation, and hybrid effects on residue and corn anthracnose occurrence in Wisconsin. Plant Dis. 95:601–610. doi:10.1094/PDIS-11-10-0837

Johnson, A.W., C.C. Dowler, and E.W. Hauser. 1975. Crop rotation and herbicide effects on population densities of plant-parasitic nematodes. J. Nematol. 7:158–167.

Johnson, N., F. Pfleger, R. Crookston, S. Simmons, and P. Copeland. 1991. Vesicular arbuscular mycorrhizas respond to corn and soybean cropping history. New Phytol. 117:657–663. doi:10.1111/j.1469-8137.1991.tb00970.x

Kim, M., D.L. Hyten, T.L. Niblack, and B.W. Diers. 2011. Stacking resistance alleles from wild and domestic soybean sources improves soybean cyst nematode resistance. Crop Sci. 51:934–943. doi:10.2135/cropsci2010.08.0459

Koenning, S.R., D.P. Schmitt, K.R. Barker, and M.L. Gumpertz. 1995. Impact of crop rotation and tillage system on *Heterodera glycines* population density and soybean yield. Plant Dis. 79:282–286. doi:10.1094/PD-79-0282

Koenning, S.R., and J.A. Wrather. 2010. Suppression of soybean yield potential in the continental United States by plant diseases from 2006 to 2009. Plant Health Prog. doi:10.1094/PHP- 2010-1122-01-RS.

Levene, H. 1960. Robust tests for equality of variances. In: I. Olkin, editor, Contributions to probability and statistics. Stanford Univ. Press, Palo Alto, CA. p. 278–292.

MacGuidwin, A.E., C.R. Grau, and E.S. Oplinger. 1995. Impact of planting bell, a soybean cultivar resistant to *Heterodera glycines*, in Wisconsin. J. Nematol. 27:78–85.

McGawley, E.C., and R.A. Chapman. 1983. Reproduction of *Criconemoides simile, Helicotylenchus pseudorobustus*, and *Paratylenchus projectus* on soybean. J. Nematol. 15:87–91.

McIntosh, M.S. 1983. Analysis of combined experiments. Agron. J. 75:153–155. doi:10.2134/agronj1983.00021962007500010041x

Meese, B., P. Carter, E. Oplinger, and J. Pendleton. 1991. Corn soybean rotation effect as influenced by tillage, nitrogen, and hybrid cultivar. J. Prod. Agric. 4:74–80. doi:10.2134/jpa1991.0074

Melakeberhan, H., and J. Dey. 2003. Competition between *Heterodera glycines* and *Meloidogyne incognita* or *Pratylenchus penetrans*: Independent infection rate measurements. J. Nematol. 35:1–6.

NASS-USDA. 2014. Acreage (June 2014). Natl. Agric. Statistics Serv.-USDA, Washington, DC.

Niblack, T.L. 1992. *Pratylenchus, Paratylenchus, Helicotylenchus,* and other nematodes on soybean in Missouri. J. Nematol. 24:738–744.

Niblack, T.L., N.K. Baker, and D.C. Norton. 1992. Soybean yield losses due to *Heterodera glycines* in Iowa. Plant Dis. 76:943–948. doi:10.1094/PD-76-0943

Niblack, T.L., A.L. Colgrove, K. Colgrove, and J.P. Bond. 2008. Shift in virulence of soybean cyst nematode is associated with use of resistance from PI 88788. Plant Health Prog. doi:10.1094/PHP-2008-0118-01-RS.

Nickel, S., R. Crookston, and M. Russelle. 1995. Root-growth and distribution are affected by corn-soybean cropping sequence. Agron. J. 87:895–902. doi:10.2134/agronj1995.00021962008700050020x

Noel, G.R. 1987. Comparison of Fayette soybean, aldicarb, and experimental nematicides for management of *Heterodera glycines* on soybean. Ann. Appl. Nematol. 1:84–88.

Noel, G.R., and D.I. Edwards. 1996. Population development of *Heterodera glycines* and soybean yield in soybean-maize rotations following introduction into a noninfested field. J. Nematol. 28:335–342.

Norton, D.C., J. Tollefson, P. Hinz, and S.H. Thomas. 1978. Corn yield increases relative to nonfumigant chemical control of nematodes. J. Nematol. 10:160–166.

Omay, A., C. Rice, L. Maddux, and W. Gordon. 1998. Corn yield and nitrogen uptake in monoculture and in rotation with soybean. Soil Sci. Soc. Am. J. 62:1596–1603. doi:10.2136/sssaj1998.03615995006200060017x

Pedersen, P., and C.R. Grau. 2010. Effect of agronomic practices and soybean growth stage on the colonization of basal stems and taproots by *Diaporthe phaseolorum* var. *sojae*. Crop Sci. 50:718–722. doi:10.2135/cropsci2009.06.0289

Pedersen, P., and J. Lauer. 2004. Soybean growth and development response to rotation sequence and tillage system. Agron. J. 96:1005–1012. doi:10.2134/agronj2004.1005

Peterson, T., and G. Varvel. 1989. Crop yield as affected by rotation and nitrogen rate. 3. corn. Agron. J. 81:735–738. doi:10.2134/agronj1989.00021962008100050007x

Pikul, J.L., Jr., S.L. Osborne, and W.E. Riedell. 2012. Corn yield and nitrogen- and water-use under no-tillage rotations. Commun. Soil Sci. Plant Anal. 43:2722–2734. doi:10.1080/00103624.2012.719980

Porter, P., S. Chen, C. Reese, and L. Klossner. 2001. Population response of soybean cyst nematode to long term corn-soybean cropping sequences in Minnesota. Agron. J. 93:619–626. doi:10.2134/agronj2001.933619x

Porter, P., J. Lauer, W. Lueschen, J. Ford, T. Hoverstad, E. Oplinger, and R. Crookston. 1997. Environment affects the corn and soybean rotation effect. Agron. J. 89:442–448. doi:10.2134/agronj1997.00021962008900030012x

Rotundo, J.L., G.L. Tylka, and P. Pedersen. 2010. Source of resistance affect soybean yield, yield components, and biomass accumulation in *Heterodera glycines*-infested fields. Crop Sci. 50:2565–2574. doi:10.2135/cropsci2009.12.0724

Rousseau, G., S. Rioux, and D. Dostaler. 2007. Effect of crop rotation and soil amendments on *Sclerotinia* stem rot on soybean in two soils. Can. J. Plant Sci. 87:605–614. doi:10.4141/P05-137

Salvagiotti, F., K.G. Cassman, J.E. Specht, D.T. Walters, A. Weiss, and A. Dobermann. 2008. Nitrogen uptake, fixation and response to fertilizer N in soybeans: A review. Field Crops Res. 108:1–13. doi:10.1016/j.fcr.2008.03.001

Schmitt, D., H. Ferris, and K. Barker. 1987. Response of soybean to *Heterodera glycines* race 1 and race 2 in different soil types. J. Nematol. 19:240–250.

Smith, G.S., T.L. Niblack, and H.C. Minor. 1991. Response of soybean cultivars to aldicarb in *Heterodera glycines*-infested soils in Missouri. J. Nematol. 23:693–698.

Todd, T. 1991. Effect of cropping regime on populations of *Belonolaimus* sp. and *Pratylenchus scribneri* in sandy soil. J. Nematol. 23:646–651.

Todd, J.W., and T.D. Canerday. 1972. Control of soybean insect pests with certain systemic insecticides. J. Econ. Entomol. 65:501–504. doi:10.1093/jee/65.2.501

Warnke, S.A., S. Chen, D.L. Wyse, G.A. Johnson, and P.M. Porter. 2008. Effect of rotation crops on hatch, viability and development of Heterodera glycines. Nematology 10:869–882. doi:10.1163/156854108786161391

Wilhelm, W., and C. Wortmann. 2004. Tillage and rotation interactions for corn and soybean grain yield as affected by precipitation and air temperature. Agron. J. 96:425–432. doi:10.2134/agronj2004.0425

Wrather, J. A., and S.R. Koenning. 2009. Effects of diseases on soybean yields in the United States 1996 to 2007. Plant Health Progress doi:10.1094/PHP-2009-0401-01-RS

Yakle, G., and R. Cruse. 1984. Effects of fresh and decomposing corn plant residue extracts on corn seedling development. Soil Sci. Soc. Am. J. 48:1143–1146. doi:10.2136/sssaj1984.03615995004800050038x

Zheng, J., Y. Li, and S. Chen. 2006. Characterization of the virulence phenotypes of *Heterodera glycines* in Minnesota. J. Nematol. 38:383–390.

Zirakparvar, M.E. 1980. Host range of *Pratylenchus hexincisus* and its pathogenicity on corn, soybean, and tomato. Phytopathology 70:749–753. doi:10.1094/Phyto-70-749