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

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ABSTRACT

Corn–soybean [*Zea mays* L.–*Glycine max* (L.) Merr.] crop rotation increases yields of both crops, a phenomenon known as the rotation effect. Plant–parasitic nematodes can decrease corn yield, and this study was conducted to determine their role in the rotation effect for corn. This study was conducted at a long-term research site that included crop sequence treatments in 1 to 5 yr of corn monoculture following 5 yr of soybean, and continuous corn monoculture since 1982. Granular nematicides were applied to half of each plot to minimize nematode populations as a way to determine their role in the rotation effect. Populations of soybean cyst nematode (SCN, *Heterodera glycines*), decreased rapidly in corn monoculture ($P \le 0.05$) and *Xiphinema* (dagger nematode)densities were small—averaging 5 nematodes 100 cm^{-3}. Averaged across crop sequences, nematicide applications increased ($P \le 0.05$) corn yield 3 to 11% and decreased *Pratylenchus* (lesion nematode) and *Helicotylenchus* (spiral nematode) populations. *Pratylenchus* and *Helicotylenchus* increased ($P \le 0.05$) in corn with *Pratylenchus* often increasing incrementally as years in corn increased, but *Helicotylenchus* populations generally greater in continuous corn than most other sequences. Yield decreased ($P \le 0.05$) in monoculture, particularly for first through third year corn. Nematicide was more effective in increasing yield in third and fifth year corn than other sequences. *Pratylenchus* and *Helicotylenchus* populations corresponded negatively with yield in regression models ($P \le 0.05$) explaining 36 to 42% and 10 to 19% of variation in yield, respectively. Results suggest nematodes, particularly *Pratylenchus*, contributed to declining corn yield in monoculture.

Core Ideas

- Growing corn in monoculture decreases yield.
- Growing corn in monoculture increases population densities of nematodes parasitic to corn.
- Plant–parasitic nematodes can contribute to corn yield decline in monoculture.

Corn and soybean production is an integral part of agriculture and together represents a majority of agricultural production in the United States. 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. Corn–soybean rotation helps maintain soil nutrient levels, particularly N due to N_2 fixation by soybean, which can increase corn yield (Peterson and Varvel, 1989; Meese et al., 1991; Omay et al., 1998). However, soil nutrients are not the only cause of the rotation effect as corn benefits from rotation with crops that do not fix N (Robinson, 1966; Barber, 1972; Bolton et al., 1976; Maloney et al., 1999). Additionally the rotation effect can occur 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 be an important part of the yield benefits of crop rotation—a

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

concept that is the focus of this study. There are many damaging plant–parasitic nematodes of corn (Norton and Hinz, 1976; Norton et al., 1978; Malek et al., 1980; Norton, 1984; Todd and Oakley, 1996). While SCN is known to decline when corn is grown (Koenning et al., 1995; Chen et al., 2001; Porter et al., 2001) since corn is a non-host for SCN (Warnke et al., 2008), few studies have examined the influence of corn–soybean crop rotation on plant–parasitic nematodes of corn in the United States (Johnson et al., 1975; Todd, 1991; McSorley and Gallaher, 1993). Therefore, the interaction between corn–soybean crop rotation and plant–parasitic nematodes of corn is not well studied, and the role of these nematodes in declining corn yield in monoculture is not well known.

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 fertlizers (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). 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 corn while soybean is discussed in an accompanying study.

In the present study, nematicide was applied systematically to determine damage to corn—in various crop sequences—by plant–parasitic nematodes through comparison to corn without nematicide application. Specifically, the objectives of this study were to: (i) investigate the role of crop damage by plant–parasitic nematodes in the rotation yield effect for corn using nematicide application; (ii) determine the impact of corn–soybean crop sequences and nematicide application on plant–parasitic nematode populations during corn phases of these crop sequences; and (iii) further document the impact of crop rotation on corn 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 corn phases at the site were analyzed in this study while the soybean phases were analyzed in a separate study. The three sequence types, examined in this study (Table 1) were: (i) 5 yr of corn following 5 yr of SCN-susceptible soybean with each phase grown each year (ii) continuous corn monoculture since 1982; (iii) annual rotation between two cultivars—but corn monoculture. Since 1995, sequence type (iii) has been single-cultivar corn monoculture. Beginning in 2010, corn phases in sequence types (i) and (ii) were cultivars with *Bacillus thuringiensis* Berliner (*Bt*) trait while sequence type (iii) was cultivars without *Bt* trait. 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 corn (following 5 yr of SCN-susceptible soybean); continuous corn monoculture (since 1982) with *Bt* corn since 2010; and continuous corn monoculture (since 1982) with non-*Bt* cultivars 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 containing six crop rows. In 2010 and 2011, S-[[(1,1-dimethylethyl)thio] methyl] O,O-diethyl phosphorodithioate (terbufos) nematicide (Counter 20G, AMVAC Chemical Corporation, Los Angeles, CA) was applied in-furrow at planting at 2.44 kg a.i. ha^{-1}. In 2012 to 2014, aldicarb [2-methyl-2-(methylthio) proprionaldehyde O-(methylcarbamoyl) oxime] nematicide (Bolster 15G, AMVAC Chemical Corporation) was applied in-furrow at planting at 2.94 kg a.i. ha^{-1}. For both nematicides, these rates,

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

Treatments	Crop sequence by year									
	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	Cc	Cc	Cc	Cc	Cc	Cc	Cc	Cc	Cc	Cc
	Continuous monoculture: non-*Bt* corn post-2010, alternating cultivars pre-1995									
12	Cc	Cc	Cc	Cc	Cc	Cn	Cn	Cn	Cn	Cn

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

which were approximately double the label rate, were used to achieve maximum nematode control for completing the research objectives. 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 which is when aldicarb was applied.

Site Management

Crops were planted, with concurrent nematicide application to appropriate subplots, on 1 June 2012; 3 June 2013; and 21 May 2014. *Bt*-trait corn cultivar planted was De Kalb 46-61 in 2012 and De Kalb 50-66 in 2013–2014. *Bt*-free corn hybrid planted was DeKalb 44-92 in 2012, and DeKalb 50-67 in 2013–2014. Plots were managed with conventional tillage with the site chisel plowed each fall and field cultivated each spring before planting. Single applications of glyphosate [N-(phosphonomethyl)glycine] were applied for post-emergence weed management at rates from 0.96 to 1.42 L a.i. ha^{-1} in each year of the study. 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 superphosphate 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 days after planting [DAP]), and fall (at harvest). Soil samples were taken from all subplots on 30 May, 24 July (54 DAP), and 8 Oct. (130 DAP) 2012; 3 June, 6 Aug. (64 DAP), and 8 Oct. (127 DAP) 2013; 19 May, 7 July (47 DAP), and 9 Oct. (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 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 flotation 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*, *Helicotylenchus*, and *Xiphinema* (lesion, spiral, and dagger nematodes, respectively). 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 density was 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 densities were determined from counts of a subsample of eggs using a microscope.

Corn yields were determined each year based on the two central rows of each plot and were standardized to 15.5% moisture. Corn was harvested 5 Oct. 2012, 29 Oct. 2013, and 21 Oct. 2014.

Statistical Analysis

Nematode data were analyzed separately for each season. 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 × 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 evaulated 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). *Helicotylenchus* and vermiform SCN in all seasons, *Pratylenchus* and *Xiphinema* in midseason and fall, and SCN eggs in fall were transformed by $\ln(x+1)$. *Pratylenchus* and *Xiphinema* in spring as well as SCN eggs in spring and midseason were transformed by $x^{1/3}$. Yield was transformed by x^2.

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 corn yields on *Pratylenchus* populations as well as individual plot corn yields on *Helicotylenchus* populations were performed to formally describe relationships between nematode population densities and yield 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 corn yield and nematode densities outside of this study. Only sequences planted to a *Bt* cultivar were included because yield responses may differ by cultivar. Midseason nematode populations were used because this produced linear regression models with greater adjusted 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. All analyses were performed using R version 3.0 (The R Foundation for Statistical Computing, Vienna).

Table 2. Effects of crop sequence and nematicide on plant–parasitic nematode populations and crop yield 2012 to 2014 combined for corn sequences only.

ANOVA (*F* values)	Degrees of freedom Numerator, Denominator		Corn yield	SCN† eggs Pi‡	Pm	Pf
Crop sequences (C)	6, 54		18.20*	43.44*	32.20*	18.53*
Year (Y) × C	12, 54		0.81	1.94*	1.82	0.72
Nematicide (N)	1, 63		42.20*	0.79	0.03	0.04
N × Y	2, 63		4.78*	0.96	0.28	0.72
C × N	6, 63		2.62*	0.23	1.63	0.87
Y × C × N	12, 63		1.84	0.91	1.28	1.75
	Vermiform SCN			*Pratylenchus* (lesion nematode)		
	Pi	Pm	Pf	Pi	Pm	Pf
ANOVA (*F* values)						
Crop sequences (C)	51.21*	20.80*	8.23*	42.23*	23.97*	15.40*
Year (Y) × C	2.89*	2.53*	3.47*	0.99	0.73	0.56
Nematicide (N)	0.40	3.16	3.51	10.82*	151.7*	197.8*
N × Y	2.27	3.31*	13.91*	1.64	0.35	4.19*
C × N	0.37	3.27*	16.35*	1.25	1.44	1.59
Y × C × N	2.21*	2.24*	21.87*	0.96	1.74	0.98
	Helicotylenchus (spiral nematode)			*Xiphinema* (dagger nematode)		
	Pi	Pm	Pf	Pi	Pm	Pf
ANOVA (*F* values)						
Crop sequences (C)	7.68*	5.55*	1.86	1.18	1.68	0.30
Year (Y) × C	2.58*	1.33	0.69	0.72	1.82	0.84
Nematicide (N)	16.68*	63.50*	156.58*	9.86*	88.99*	72.19*
N × Y	3.43*	4.62*	0.32	1.87	10.34*	11.72*
C × N	1.24	3.12*	0.72	0.70	2.02	0.64
Y × C × N	0.63	1.09	0.81	1.32	1.60	0.43

* Significant effects at $P \le 0.05$.

† SCN, soybean cyst nematode.

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

Table 3. Vermiform soybean cyst nematode (SCN) population densities as influenced by crop sequences and nematicide application in 2010 to 2012.

Treatments	2012 Pi†‡	Pm	Pf	2013 Pi	Pm	Pf	2014 Pi	Pm	Pf
Crop sequence§									
C1	60a	30a	14	358a	100a	135a	211a	147a	89a
C2	39a	9bc	6	50b	13b	22b	53b	59a	60a
C3	31ab	11ab	6	25bc	3b	16b	15c	7bc	11bc
C4	14bc	13bc	14	20bc	4b	2c	4d	6bc	3bc
C5	1d	2c	0	14cd	38b	6c	11c	13b	15b
Cc	3cd	2c	0	3d	23b	0c	3d	1c	0c
Cn	1d	9bc	0	7d	22b	0c	2d	2c	0c
Nematicide									
Not applied	24	12	6	56	25	25	33	19B	20
Applied	18	9	5	59	29	20	51	46A	28
ANOVA (*F* values)									
Crop sequence (C)	14.63*	4.64*	1.30	37.0*	2.76*	10.9*	27.7*	10.8*	17.3*
Nematicide (N)	0.58	1.68	0.22	1.07	0.09	0.18	1.57	8.66*	1.88
C × N	1.41	4.28*	1.82	1.86	1.09	2.93*	1.08	1.30	0.82

* Significant effects at $P \le 0.05$.

† Pi, Pm, Pf are mean population densities (nemas 100 cm^{-3} soil) before planting; 54 (2012), 64 (2013), or 47 (2014) d after planting; and at harvest.

‡ Different letters in the same column indicate significant differences (Fischer's LSD, $P \le 0.05$) between transformed mean values within the same factor.

§ Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars, respectively since 2010; C1, C2, C3, C4, and C5 are first, second, third, fourth, and fifth year corn following 5 yr of soybean.

RESULTS

Corn Yields

Nematicide effects were significantly different by year (Table 2), but, combined across crop sequences, corn yield was significantly greater with than without nematicide application in all years with yield increases of 3, 11, and 11% in 2012, 2013, and 2014, respectively (Fig. 1). Crop sequences significantly affected combined corn yield (Table 2, Fig. 2A), but there was also significant crop sequence × nematicide interaction (Table 2). For the treatment without nematicide, corn yield decreased significantly as years in corn increased, through third year corn, but there were minimal differences in 4 or more years of corn (Fig. 2B). Yield also decreased in monoculture when nematicide was applied, but the trend was more gradual than without nematicide (Fig. 2C). Within individual crop sequence treatments, nematicide significantly increased corn yield only in third and fifth year corn (Fig. 2B and 2C).

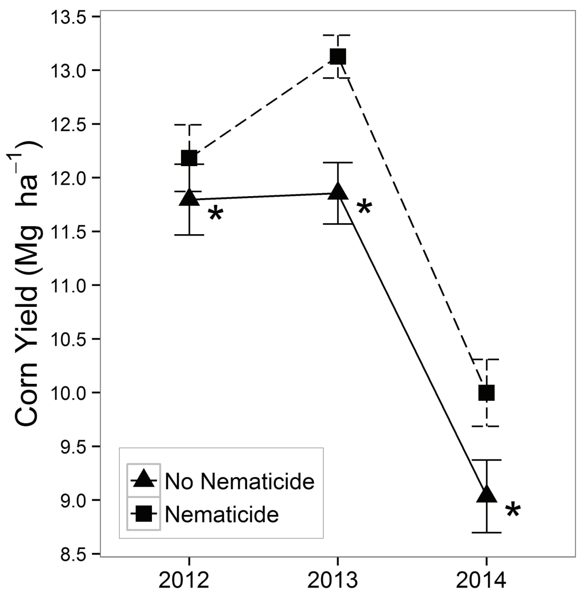

Fig. 1. Corn yields as influenced by nematicide application in 2012, 2013, and 2014. Values are combined across crop sequences. * Significantly different values ($P \leq 0.05$) between nematicide and no nematicide treatments within the given year according to ANOVA.

Soybean Cyst Nematode Egg Populations

Soybean cyst nematode egg populations were not significantly affected by nematicide application, but were affected by crop sequence in every season (Table 2). In spring, there was significant crop sequence × year interaction (Table 2), and in each year, SCN egg populations were greater entering initial years of corn monoculture than extended corn monoculture (Fig. 3A, 3B, and 3C). In 2012, population before planting was greater entering first year corn than all other sequences except second year corn (Fig. 3A). In 2013, population was significantly greater in first year corn, immediately following 5 yr of soybean, than any other sequences (Fig. 3B) while in 2014 populations were greater in first and second year corn than other sequence (Fig. 3C). In all years, entering third year corn, populations were below 500 eggs 100 cm^{-3} soil and near 200 eggs 100 cm^{-3} soil, a level considered to present minimal damage risk to soybean in Minnesota for the season in which this population level is detected (Chen, 2011). In midseason and fall, combined across years and nematicide treatments, SCN egg populations significantly decreased from first to second to third year corn, but there were minimal population changes with further increases in length of corn monoculture (Fig. 3D and 3E). In both midseason and fall, populations were near or below 200 eggs 100 cm^{-3} in sequences in the third or more year

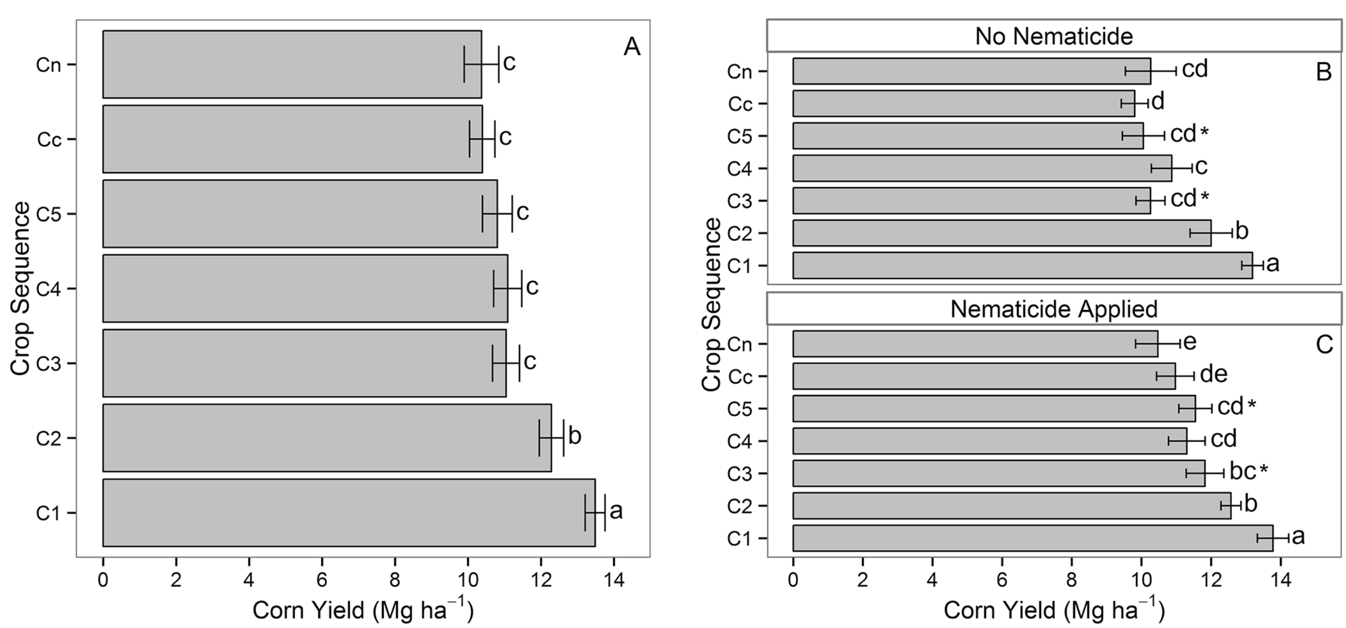

Fig. 2. Corn yields as influenced by (A) crop sequences for 2012 to 2014 combined and combined across nematicide treatments; and as influenced by crop sequences (B) with or (C) without nematicide application for 2012 to 2014 combined. Within subfigures, different letters indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. In subfigures B and C, * indicates significantly different values ($P \leq 0.05$) between nematicide and no nematicide treatments for the given crop sequence according to ANOVA. Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars, respectively since 2010. C1 through C5 are first to fifth year *Bt* corn after 5 yr of SCN-susceptible soybean.

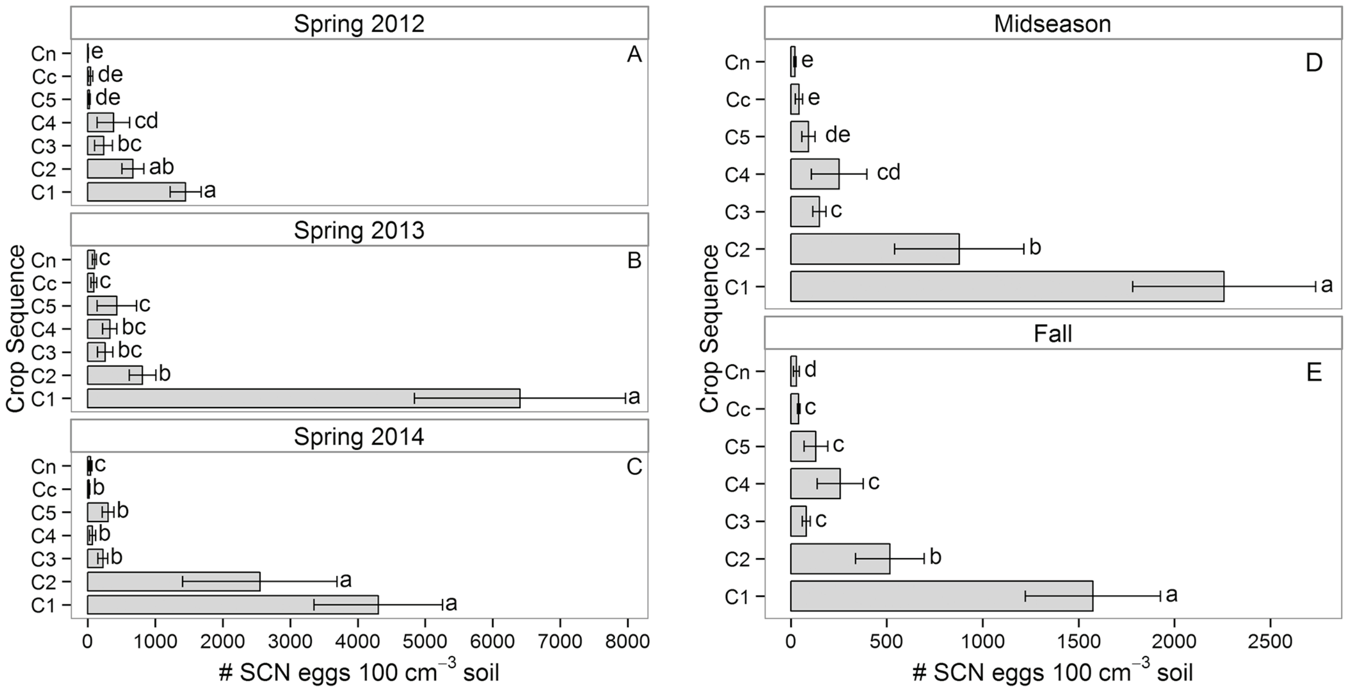

Fig. 3. Soybean cyst nematode (SCN) egg populations as influenced by crop sequences before planting in (A) 2012, (B) 2013, and (C) 2014; (D) in midseason (47–64 d after planting) for 2012 to 2014 combined; and (E) in fall (at harvest) for 2012 to 2014 combined. Values are combined across nematicide treatments. Within subfigures, different letters indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010. C1 through C5 are first to fifth year *Bt* corn after 5 yr of SCN-susceptible soybean.

or corn monoculture. By fall, eggs were near 500 eggs 100 cm^{-3} soil in second year corn.

Vermiform Soybean Cyst Nematode Populations

There were three-way year × nematicide × crop sequence interactions for vermiform SCN populations in every season (Table 2), so data was analyzed separately by year (Table 3). In most seasons, nematicide did not significantly affect vermiform SCN populations, but crop sequence did affect populations (Table 3). In 2012, populations were small across crop sequences, but tended to be significantly smaller in 5 yr or more of corn. In 2013, populations were significantly greater in first year corn, following 5 yr of soybean than any other sequence. In 2014, populations were significantly greater in first and second year corn than in any other sequence. There were significant nematicide × crop sequence interactions in midseason 2012 and fall 2013 (Table 3), but trends under individual nematicide treatments were similar to trend in populations under crop sequences for combined nematicide treatments (data not shown).

Pratylenchus (Lesion Nematode) Populations

Nematicide applications significantly reduced *Pratylenchus* populations, combined across years and crop sequences, every season compared to treatment without nematicide application with reductions of 36, 79, and 87% in spring, midseason, and fall, respectively (Table 2, Fig. 4A). In fall, there was also significant year × nematicide application interaction (Table 2), but nematicide applications significantly ($P \leq 0.01$, ANOVA) reduced populations compared to treatment without nematicide application in every year. Extent of reduction varied with 92, 91, and 78% reductions with nematicde treatments in 2012, 2013, and 2014, respectively from populations of 261, 611, and 390 nematodes 100 cm^{-3} soil without nematicide in 2012, 2013, and 2014, respectively.

Crop sequence significantly affected *Pratylenchus* populations in every season (Table 2). Across seasons, *Pratylenchus* populations increased in corn monoculture, particularly the initial years in corn monoculture (Fig. 4B, 4C, and 4D). Before planting, populations increased significantly from first to second to third year in corn monoculture and were greater in 5 or more years of corn than 4 or fewer (Fig. 4B). In midseason, populations increased significantly from first to second to third year in corn monoculture and were greater in long-term corn monoculture than in 3 or fewer years of corn (Fig. 4C). In fall, populations increased significantly as years in corn monoculture increased, from first to fourth year in corn, but were significantly smaller in continuous corn with *Bt* cultivar than fourth or fifth year corn (Fig. 4D).

Helicotylenchus (Spiral Nematode) Populations

There were significant nematicide × year interactions for *Helicotylenchus* populations in spring and midseason (Table 2), so nematicide effects are presented by individual seasons and not combined across years (Fig. 5). *Helicotylenchus* populations, combined across crop sequences, were significantly reduced by nematicide application compared to treatment without nematicide in every season except spring 2012 (Fig. 5). *Helicotylenchus* populations were reduced 50 to 78% before planting, 56 to 84% at midseason, and 81 to 89% in fall by nematicide applications.

Before planting, there was significant year × crop sequence interaction for *Helicotylenchus* population (Table 2). In 2012 and 2013, before planting, populations were generally greater in continous corn than most other sequences, but similar

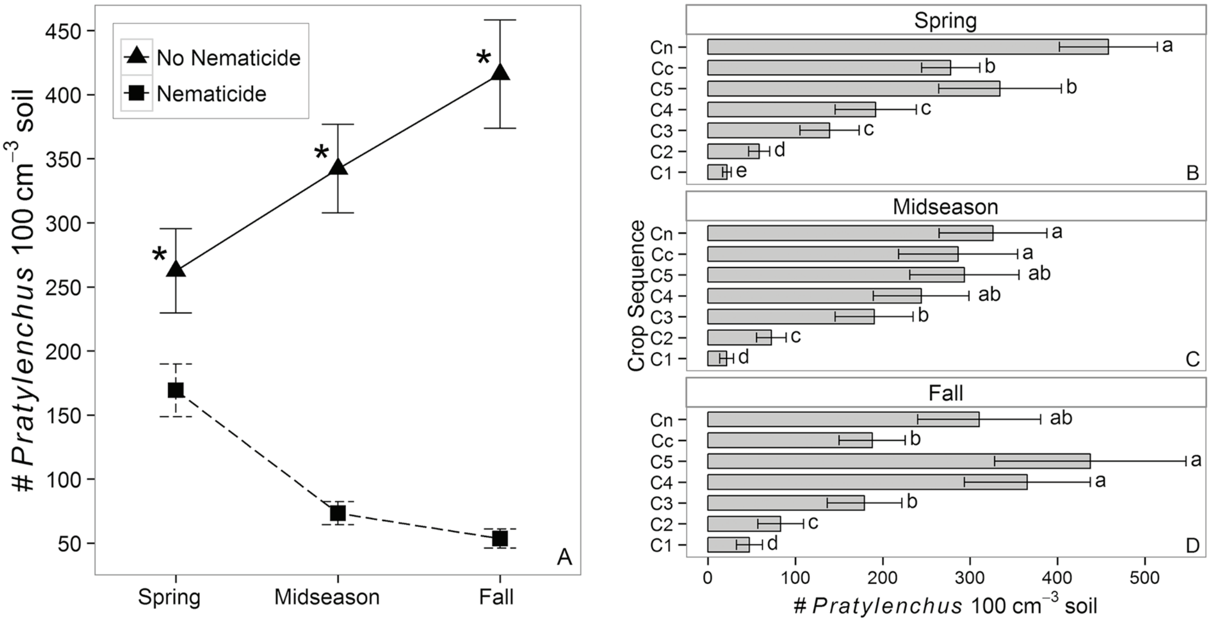

Fig. 4. *Pratylenchus* (lesion nematode) populations as influenced by (A) nematicide for 2012 to 2014 combined and combined across crop sequences in spring (before planting), midseason (47–64 d after planting), and fall (at harvest). *Pratylenchus* populations as influenced by crop sequences in (B) spring, (C) midseason, and (D) fall combined from 2012 to 2014 and 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. For subfigures (B), (C), and (D), within a subfigure different letters indicate significantly ($P \leq 0.05$) different values based on transformed values according to protected Fischer's LSD. Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010. C1 through C5 are first to fifth year *Bt* corn after 5 yr of SCN-susceptible soybean.

among most sequences in 5 or fewer years of corn (Fig. 6A and 6B). In 2014, before planting, there were no significant ($P >$ 0.05, ANOVA) differences among crop sequences (Fig. 6C). In midseason, there was significant crop sequence × nematicide interaction (Table 2). There were no significant crop sequence effects with nematicide ($P > 0.05$, ANOVA), but without nematicide *Helicotylenchus* populations were significantly smaller in first year corn than any other sequence and significantly larger in continuous corn than any sequence but fifth year corn (Fig. 6D). Within individual crop sequence treatments, *Helicotylenchus* populations were significant decreased with than without nematicide in every corn sequence except first year corn (Fig. 6D).

Xiphinema (Dagger Nematode) Populations

Overall, *Xiphinema* soil populations were small in corn sequences at the site, averaging 5 nematodes 100 cm^{-3} soil across plots and seasons. There were significant nematicide × year interactions for *Xiphinema* populations in midseason and fall (Table 2), so nematicide effects are presented by individual season rather than combined across years. In most seasons, populations were significantly reduced by nematicide application compared to the treatment without nematicide application (Fig. 7). Crop sequence did not significantly affect *Xiphinema* populations in any season (Table 2).

Regression of Corn Yields with *Pratylenchus* and *Helicotylenchus* Populations

In all 3 yr, linear regressions between corn yield and midseason *Pratylenchus* population density or corn yield and midseason *Helicotylenchus* population density produced significant ($P \leq 0.05$) models with negative logarithmic relationships

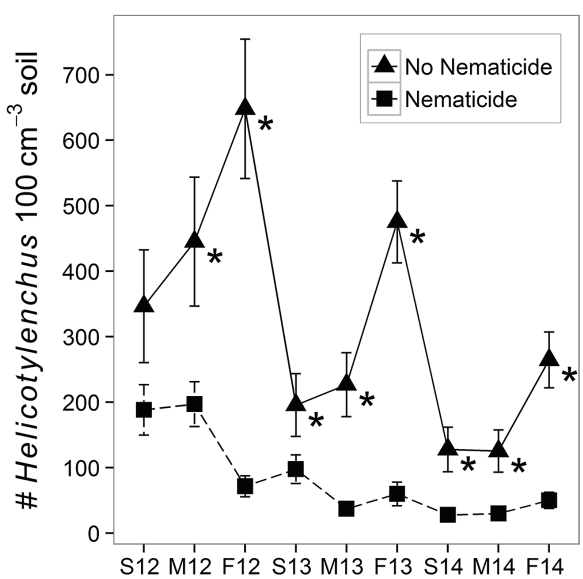

Fig. 5. *Helicotylenchus* (spiral nematode) populations as influenced by nematicide application by individual seasons from 2012 to 2014. Values are combined across crop sequences. * Significantly ($P \leq 0.05$) different values between nematicide and no nematicide treatments for the given season. S12, M12, and F12 are before planting, midseason (54 days after planting [DAP]), and at harvest in 2012. S13, M13, and F13 are before planting, midseason (64 DAP), and at harvest in 2013. S14, M14, and F14 are before planting, midseason (47 DAP), and at harvest in 2014.

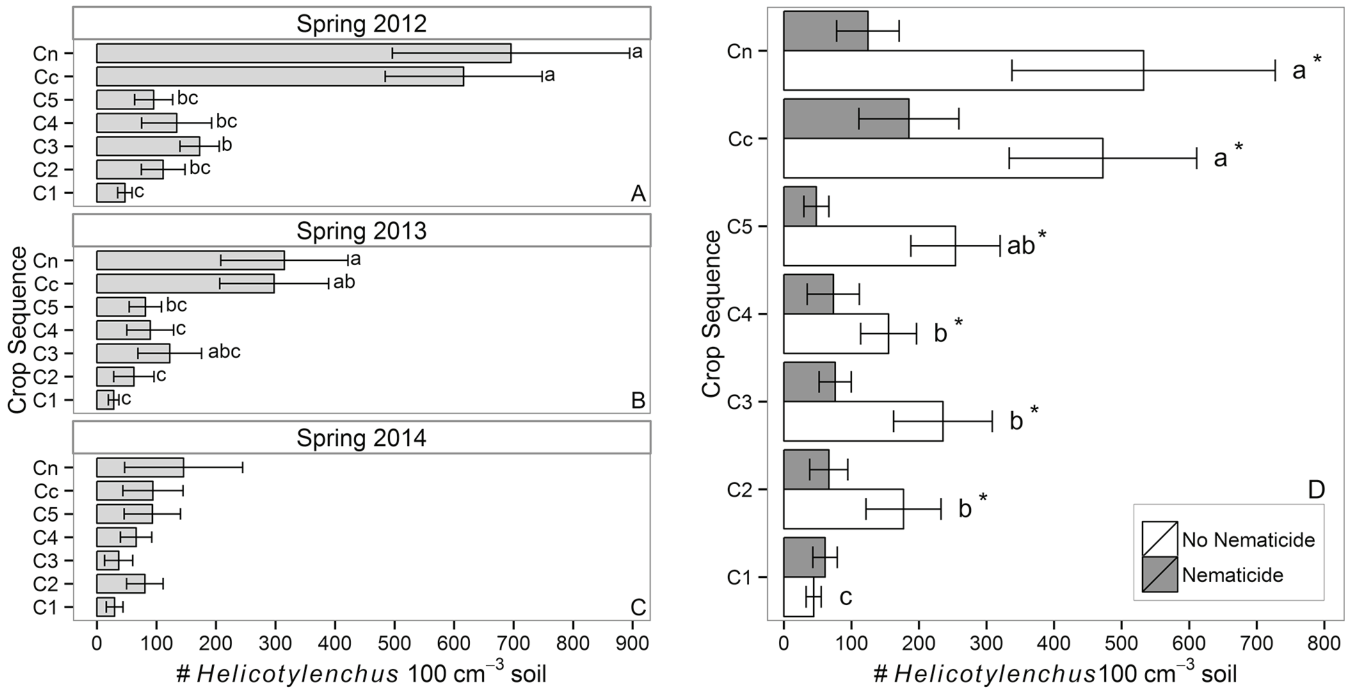

Fig. 6. *Helicotylenchus* (spiral nematode) populations before planting as influenced by crop sequences in (A) 2012, (B) 2013, and (C) 2014 combined across nematicide treatments; and (D) as influenced by crop sequences with or without nematicide application in midseason (47–64 d after planting) for 2012 to 2014 combined. Within a subfigure, different letters indicate significantly ($P \le 0.05$) different values based on transformed values according to protected Fischer's LSD. Cn and Cc are continuous corn with non-*Bt* and *Bt* cultivars respectively since 2010. C1 through C5 are first to fifth year *Bt* corn after 5 yr of SCN-susceptible soybean.

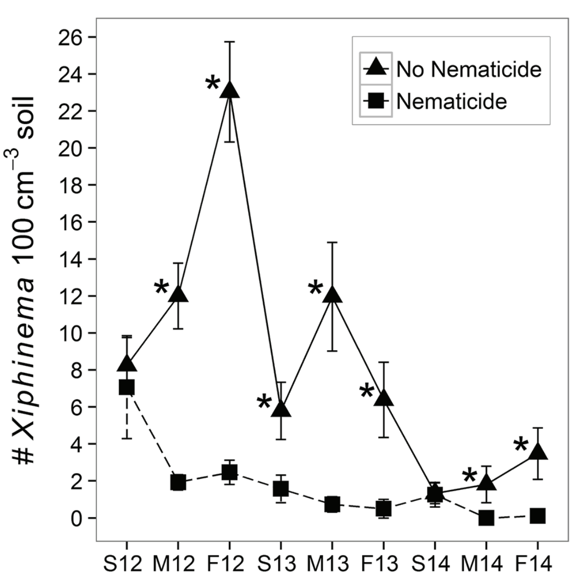

Fig. 7. *Xiphinema* (dagger nematode) populations as influenced by nematicide in individual seasons. Values are combined across crop sequences. * Significantly ($P \le 0.05$) different values between nematicide and no nematicide treatments for the given season. S12, M12, and F12 are before planting, midseason [54 days after planting (DAP)], and at harvest in 2012. S13, M13, and F13 are before planting, midseason (64 DAP), and at harvest in 2013. S14, M14, and F14 are before planting, midseason (47 DAP), and at harvest in 2014.

between corn yield and nematode populations (Fig. 8). All slope coefficients were significant ($P \le 0.05$) except for *Helicotylenchus* population density in 2013. In all 3 yr, R^2 was larger for *Pratylenchus* than *Helicotylenchus* models (Fig. 8), so midseason *Pratylenchus* population densities explained more variation in corn yield than midseason *Helicotylenchus* population densities in this study. Because these regression analyses were conducted across different crop sequences, these equations cannot be used to establish generic relationships between corn yield and nematode densities outside of this study. Rather, these analyses are limited to estimating the relationship between corn yield—across crop sequences—and nematode populations in this study.

DISCUSSION

Nematicide applications reduced *Pratylenchus*, *Helicotylenchus*, and *Xiphinema* populations and increased corn yields consistently across seasons suggesting one or more of these nematodes caused corn yield loss. *Xiphinema* population densities were small at the site regardless of whether or not nematicide was applied, so it is unlikely substantial damage to corn was caused by these nematodes in this study. In linear models, *Pratylenchus* explained more variation in yield than *Helicotylenchus* suggesting *Pratylenchus* contributed more substantially to corn yield loss than *Helicotylenchus*. Previous research suggests *Pratylenchus* has more potential to reduce corn yield than *Helicotylenchus* (Norton and Hinz, 1976; Norton, 1977, 1984; Norton et al., 1978; Niblack, 1992; Todd and Oakley, 1996). Yield increase with aldicarb nematicide cannot be attributed solely to nematode control with certainty because aldicarb has other effects. Aldicarb also affects insects (Todd and Canerday, 1972; Herbert et al., 1987) although *Bt*

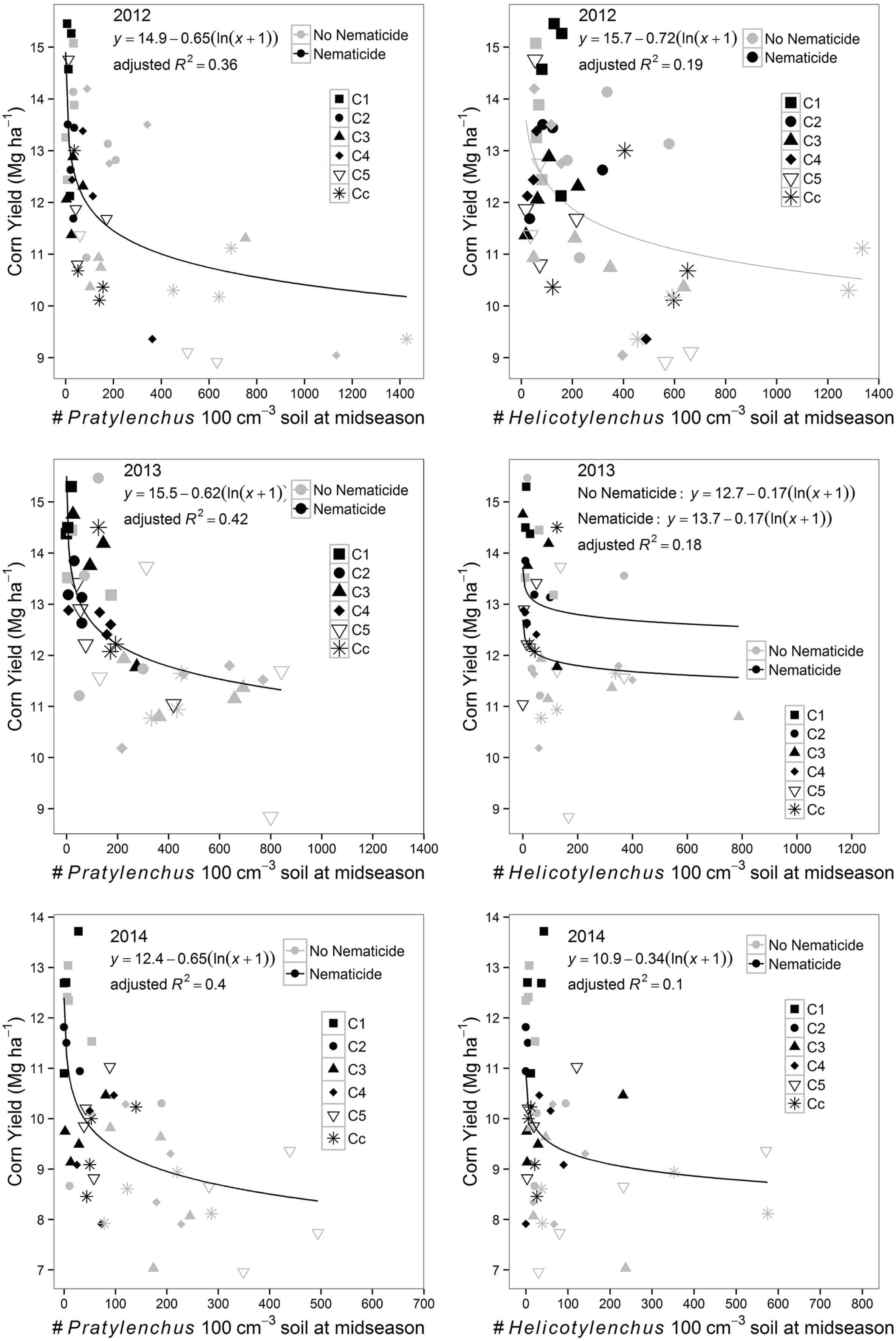

Fig. 8. Regression analysis of corn yield on *Pratylenchus* (lesion nematode) and *Helicotylenchus* (spiral nematode) populations at midseason in 2012, 2013, and 2014 (54, 64, and 47 d after planting respectively). Regression lines display equations from regression analysis, which are specified in each subfigure. Cc is continuous corn with *Bt* cultivars. C1 through C5 are first to fifth year *Bt* corn after 5 yr of SCN-susceptible soybean.

corn was used to minimize the impact of insects on corn yield. Additionally, under certain environmental conditions, aldicarb may increase plant growth even in the absence of disease pressure when applied at certain rates (Barker et al., 1988). Efficacy of aldicarb against *Pratylenchus* and *Helicotylenchus* has been demonstrated elsewhere as aldicarb reduced *Pratylenchus* populations 70 to 90%, and *Helicotylenchus* population 50% in an Iowa study at various sites (Norton et al., 1978). Nematicide applications did not effectively reduce SCN populations in the corn phases in this study, probably because SCN populations were too small, on average across corn sequences, to detect differences, or unhatched SCN eggs in cysts were resistant to nematicide.

Crop sequences clearly impacted SCN, *Pratylenchus*, and *Helicotylenchus* populations. The benefit of rotation with corn, a non-host of SCN (Warnke et al., 2008), for SCN management was clearly demonstrated by the rapid decrease of SCN populations in corn monoculture. In spring, following the second year of corn monoculture, SCN populations were consistently near or below 200 eggs 100 cm^{-3} soil, a level at which risk of damage to soybean is considered minimal for the upcoming season (Chen, 2011). This suggests SCN-susceptible soybean could be grown following 2 yr of corn at this site with minimal yield impact. In a separate study in Minnesota, 4 yr of corn monoculture did not reduce SCN populations below 200 eggs 100 cm^{-3} soil (Chen et al., 2001), suggesting optimum crop rotation for SCN management varies depending on location and conditions, including other management practices employed.

Corn was a good host for the *Pratylenchus* population at this site based on consistently increasing populations in corn monoculture, often incrementally by year in less than 5 yr of corn. This is consistent with the reported host range for *Pratylenchus* (Zirakparvar, 1980; Schmitt and Barker, 1981; Todd, 1991; Belair et al., 2002). This also demonstrates *Pratylenchus* can be a problem in corn monoculture in the clay loam soil in this study in addition to problems demonstrated in coarser soils (Johnson et al., 1975; Zirakparvar et al., 1980; Todd and Oakley, 1996).

Helicotylenchus has a wide host range, and both corn and soybean have been hosts for all *Helicotylenchus* populations that have been tested (Ferris and Bernard, 1971; McGawley and Chapman, 1983; Windham, 1998). In this study, *Helicotylenchus* population increase in corn monoculture was minimal in less than 5 yr of monoculture. Before planting in most years and without nematicide at midseason, *Helicotylenchus* populations had clearly increased in continuous corn monoculture—more than 30 yr in corn—compared to 5 or fewer years in corn. This suggests *Helicotylenchus* population increase in corn monoculture may be relatively gradual in environments similar to this study. The relationship between *Xiphinema* and corn is not well established. Corn monoculture did not affect *Xiphinema* populations and populations were small overall at the site. This suggests site conditions, such as soil type, tillage practices, or nematicide application, were not favorable for *Xiphinema* or that corn was not a good host for this *Xiphinema* population.

Crop sequences also affected corn yield. In this study, nearly all corn yield decline under monoculture occurred during the first 3 yr of monoculture. Previous studies have also documented similar trends at the site of the present study and its partner long-term rotation sites in Lamberton, MN, and Arlington, WI, (Crookston et al., 1991) although decreasing corn yields throughout the length of corn monoculture were observed for one study in Arlington (Meese et al., 1991).

In this study, determining the role of nematodes in the rotation yield effect by minimizing nematode populations using nematicide was a major objective. Nematicide was more effective at increasing corn yield in the third and fifth year of corn monoculture—when nematode populations not treated by nematicide were large—than in other sequences suggesting damage by plant–parasitic nematodes had a role in monoculture yield decline. Supporting this, *Helicotylenchus* populations were minimized by nematicide across crop sequences at midseason and *Pratylenchus* populations were reduced by nematicide overall providing evidence nematode pressure was reduced. Other results from this study also suggest damage by *Pratylenchus* contributed to corn monoculture yield decline. *Pratylenchus* population densities increased while yield decreased in corn monoculture, and it has been demonstrated elsewhere that *Pratylenchus* causes corn yield loss (Norton and Hinz, 1976; Norton et al., 1978; Norton, 1984; Todd and Oakley, 1996).

The negative relationship between corn yield and *Pratylenchus* population density in this study was also demonstrated by regression analysis in which *Pratylenchus* density explained 36 to 42% of variation in corn yield. In contrast, the relationship between *Helicotylenchus* and corn yield was relatively weak in this study suggesting damage by *Helicotylenchus* accounted for a smaller portion of monoculture corn yield decline in this case than damage by *Pratylenchus*. *Helicotylenchus* population densities were mostly similar among treatments in 5 or fewer years of corn while yield declined in corn monoculture. Regression models reinforced this as *Helicotylenchus* population density explained only 10 to 19% of the variation in yield. This is in line with previous research that suggests *Helicotylenchus* is a minor pest and that only large populations are damaging to corn (Norton, 1977; Norton et al., 1978; Niblack, 1992).

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 corn–soybean rotation yield effect were documented in this study. There was evidence that alleviation of damage by plant–parasitic nematodes, particularly *Pratylenchus*, can contribute to corn yield increase when corn is rotated with soybean rather than grown in monoculture in the Midwest.

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