RESEARCH/INVESTIGACIÓN

RELATIONSHIP BETWEEN SOYBEAN CYST NEMATODE, *HETERODERA GLYCINES*, AND SOIL NEMATODE COMMUNITIES UNDER LONG-TERM TILLAGE AND CROP ROTATION SYSTEMS

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ABSTRACT

Cheng, Z., H. Melakeberhan, S. Mennan, and P. S. Grewal. 2018. Relationship between soybean cyst nematode, *Heterodera glycines*, and soil nematode communities under long-term tillage and crop rotation systems. Nematropica 48:101-115.

Despite a substantial knowledge of the biology of the soybean cyst nematode (SCN), little is known about its establishment in soil relative to the overall nematode community as affected by tillage and cropping systems. The objective of this study was to determine the relationship between SCN and the soil nematode community under tillage (chisel plow and no-till) and monocropping of either maize (C), SCN-resistant (R), SCN-susceptible (S) soybean, or cropping regimes that alternated resistant or susceptible soybeans with maize on an annual basis (RCRC or SCSC rotations). The SCN was introduced into a Sisson sandy loam (Fine, loamy, mixed, semiactive, mesic Type, Hapludalfs) field in East Lansing, MI, USA, which had never been planted to soybean, and where a native SCN population had not been detected. Six and seven years (2008 and 2009) after SCN introduction, the field was sampled and nematodes were enumerated as plant-parasitic, bacterial-feeding, fungal-feeding, predatory and omnivorous trophic groups. The overall abundance of SCN was lower than initially introduced but tended to positively correlate with total nematodes, plant-parasitic, free-living, and bacteria-feeding nematodes in both years. Generally, the abundance of all free-living and bacteria-feeding nematodes was higher in tilled than in no-till treatments and under SCN-infested than non-infested treatments. In 2009, monocropping of R and S soybeans generally resulted in higher total free-living and bacteria-feeding nematode population densities than where either type of soybean was rotated with maize. Our results suggested that tillage-driven conditions, which favor bacteria-feeding nematodes, also favored SCN establishment. This is the first report that clearly documented SCN establishment and management in a new location relative to tillage and crop rotation and the biological communities that drive the nutrient cycling processes.

Key words: corn, free-living nematode, *Glycine max*, maize, management strategy, resistant, susceptible cultivars

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RESUMEN

Cheng, Z., H. Melakeberhan, S. Mennan y P. S. Grewal. 2018. Relación entre el nematodo del quiste de la soja, *Heterodera glycines*, y las comunidades de nematodos del suelo bajo labranza a largo plazo y sistemas de rotación de cultivos. Nematropica 48:101-115.

A pesar de un conocimiento sustancial de la biología del nematodo del quiste de la soja (SCN), se sabe poco acerca de su establecimiento en el suelo en relación con la comunidad global de nematodos afectados por los sistemas de labranza y cultivo. El objetivo de este estudio fue determinar la relación entre SCN y la comunidad de nematodos del suelo en laboreo (cincel y siembra directa) y monocultivo de maíz (C), soya resistente a SCN (R), soya sensible a SCN (S), o regímenes de cultivo que alternan soja resistente o susceptible con maíz en una base anual (rotaciones RCRC o SCSC). El SCN se introdujo en un campo franco arenoso Sisson (fino, arcilloso, mixto, semiactivo, tipo mésico, Hapludalfs) en East Lansing, MI, EE. UU. Que nunca se había plantado en soja y donde no se había detectado una población SCN nativa. Seis y siete años (2008 y 2009) después de la introducción de SCN, el campo se muestreó y los nematodos se enumeraron como parásitos de plantas, alimentación bacteriana, alimentación fúngica, depredadores y grupos tróficos omnívoros. La abundancia total de SCN fue menor que la introducida inicialmente, pero tendió a correlacionarse positivamente con nematodos totales, parásitos de plantas, vida libre y nematodos que se alimentan de bacterias en ambos años. En general, la abundancia de todos los nematodos de vida libre y alimentación de bacterias fue mayor en los tratamientos con labranza labrada que en los tratamientos sin labranza y bajo infestaciones de SCN que con los no infestados. En 2009, el monocultivo de soja R y S en general dio como resultado densidades de población de nematodos totales de vida libre y de alimentación de bacterias más elevadas que en los casos en que cualquiera de los dos tipos de soja se rotó con maíz. Nuestros resultados sugieren que las condiciones impulsadas por la labranza que favorecen a los nematodos que se alimentan de bacterias también favorecen el establecimiento de SCN. Este es el primer informe que documenta claramente el establecimiento y la gestión de SCN en una nueva ubicación en relación con la labranza y la rotación de cultivos, y las comunidades biológicas que impulsan los procesos de ciclo de nutrientes.

Palabras claves: cultivares resistentes, cultivares susceptibles, estrategia de manejo, *Glycine max*, maíz, nematodo de vida libre

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INTRODUCTION

The soybean cyst nematode (SCN), *Heterodera glycines* Ichinohe, is a serious pest of soybeans (*Glycine max* L., Merr) worldwide, causing an estimated $1.4 billion of crop loss annually in the USA alone (Wrather *et al*., 2001). Despite the availability of over 800 SCN-resistant cultivars, this menacing root pest continues to spread in the U.S. (Riggs, 2004; Donald *et al*., 2006; Anonymous, 2013). This ability to spread is a clear indication that SCN can adapt to a wide range of environmental and heterogeneous soil conditions, making control difficult. An understanding of how SCN establishes and reproduces in a newly established farm site and how these are affected by agronomic practices is lacking.

In the US Midwest, conservation tillage has becoming a prevailing farming practice for soybean production since the 1990s (CTIC, 2000; Horowitz *et al*., 2010), and crop rotation between soybean and maize (*Zea mays* L.) is widely adopted for managing SCN and several other pests and diseases (Riggs, 2004; Donald *et al*., 2009; Gavassoni and Tylka, 2007; Anonymous, 2013). Conservation tillage could play a major role in mitigation of global climate change by increasing carbon sequestration (Lal, 2003, 2004; Lal *et al*., 2003). Little is known, however, about the adaptation of SCN to heterogeneous soil conditions, tillage, and cropping systems. Previous studies on the effects of conservation tillage on established SCN appear to be inconsistent, sometimes short-term but sometimes slightly longer-term, and region dependent to some extent (Tyler *et al*., 1987; Herschman and Bachi, 1995; Noel and Edwards, 1996; Noel and Wax, 2003; Gavassoni and Tylka, 2007; Donald *et al*., 2009). These variable responses of SCN could hinder recommendation of using conservation tillage practice as a tool for managing SCN while sequestering soil carbon.

Tillage and crop rotation may have both direct and indirect effects on the soil food web

(Ferris *et al*., 2001). Some soils may harbor biological antagonists (Chen and Liu, 2005) that may affect SCN population densities. Studies on the effect of long-term conservation tillage and crop rotation on newly established SCN population in relation to soil biological changes are limited. In order to develop integrated and sustainable SCN management strategies in diverse cropping systems, it is important to determine the effects of tillage and crop rotation on the soil ecosystems in which SCN establishes and reproduces. Understanding biological changes in the soil, for which nematodes are an excellent bioindicator (Bongers and Ferris, 1999), is critical for developing soil health management strategies (Melakeberhan, 2010).

Nematode is the most abundant metazoan on the planet that occupies all terrestrial ecosystems. Therefore, nematodes have been used as bioindicators for soil health (Neher, 2001). Nematodes are also central to the soil food web and nutrient cycling processes (Bongers and Bongers, 1998; Neher, 2001; Briar *et al*., 2007). When soil-dwelling nematodes are categorized into trophic groups (plant-parasites, bacterial feeders, fungal feeders, predatory and omnivorous) and colonizer-persister strategies (c-p 1 to 5 where 1 = short lived and high fecundity; 5 = long life span and low fecundity) according to Bongers (1990), they provide useful biological and ecological information. These include succession of soil decomposition pathways, nutrient enrichment, stressful conditions, and levels of soil disturbance (Bongers and Ferris, 1999; Ekschmitt and Korthals, 2006).

A newly established agroecosystem with different agronomic practices at Michigan State University has been investigated on how SCN established and reproduced to cause crop yield losses. Six years after introduction of SCN at damaging threshold to soybean, SCN was barely detectable. SCN densities were lower in no-till than in tilled plots (Melakeberhan *et al*., 2015). Among other things, this suggested a relatively slow rate of introduced SCN establishment in the field. The objective of this study was to determine the relationship between the population density of SCN and the rest of the nematode soil food web under various SCN management regimes including tillage and crop rotation.

MATERIALS AND METHODS

Experimental design and field location

The nematode community analysis data presented herein were generated from the same experiment from where SCN population density relative to agronomic practices was reported (Melakeberhan *et al*., 2015). A factorial designed field experiment was conducted at the same site at Michigan State University where SCN was first introduced 6 yr prior to this experiment as described in Melakeberhan *et al*. (2015). Prior to the introduction of SCN, neither SCN nor soybeans were present at this site. The experiment consisted of 2 tillage practices (main-plot) × 5 crop rotations (sub-plot) × 2 SCN infestation levels (sub-sub-plot) factorial design. Tillage factor consisted of no tillage (no-till) or chisel plowed; crop rotation factors included 1) monocropping of glyphosate-tolerant maize (C) (Armstrong and Sprague, 2010), 2) SCN-resistant (R), or 3) SCN-susceptible (S) soybean, or crop rotations of 4) RCRC and 5) SCSC; whereas infestation levels included SCN-infested and non-infested plots. Each treatment had 4 replications. Thus, a total of 80 field plots of 3.04-m wide and 6.08-m long were established. Once the study was initiated, the area was quarantined and all vehicles and farm machinery that moved in and out of the site were pressure-washed to prevent dispersal of nematodes.

The study was conducted in a Sisson sandy loam (Fine, loamy, mixed, semiactive, mesic Type, Hapludalfs, Anonymous, 2014) with an average soil texture of 64% sand, 22% silt and 14% clay. The center of the field is located at 42°41’ 47.5” N and 84°29’ 37.0 W at the Michigan State University Campus, East Lansing, USA. The field was used for pasture grazing, alfalfa and maize production, and received repeated application of manure until this study was initiated. Consequently, the concentrations of N, P and K were above recommended levels for both of the experimental crops (Vitosh *et al*., 1994). The site was chosen because soybeans had not been grown there and pre-experiment soil samples indicated that no SCN was present.

On July 31, 2001, soil infested with SCN race 3 (HG type 0 in recent classification) was spread on the surface and mechanically raked into individual plots (Melakeberhan *et al*., 2015). The SCN-infested soil was collected during 1999 and 2000 as part of another study and was kept in a cold room (Avendaño *et al*., 2003). After inoculation, four to five random core samples were taken from individual plots, composited, and eggs and cysts extracted (Avendaño *et al*., 2003). Across the crop rotation treatments, the initial population density of SCN ranged from 205 to 896 eggs/100 cm^3 of soil. This inoculum was augmented on May 30, 2002, using the same procedure, which resulted in 3,800 to 8,800 eggs/100 cm^3 of soil across field plots. Because the no-till plots in non-SCN infested treatments were accidentally cultivated in 2003, the first year for the initiation of the crop rotation cycle was 2003 (Melakeberhan *et al*., 2015).

Sampling and processing

SCN population dynamics, stages embedded in roots, and plant growth response up to 2008 have been reported elsewhere (Melakeberhan *et al*., 2015). The relationship between SCN juveniles and other soil-dwelling nematodes in 2008 and 2009 is reported here. In 2008 and 2009, soil collected pre-plant from four to five random cores, and rhizosphere soil and roots from three to four random soybean or maize plants were collected three times (June through August in 2008, and July through September in 2009). In 2008, nematodes were extracted using a semi-automatic elutriator (Avendaño *et al*., 2003). In 2009, the Baermann funnel method was used (Flegg and Hooper, 1970; Briar *et al*., 2007). The reason for the difference in extraction method was change in personnel location. Suspensions were placed in gridded petri dishes, and nematodes enumerated and identified to genus level under inverted microscopes using morphological characteristics (Goodey, 1963; Mai and Lyon, 1975). Each nematode genus was classified into plant-parasitic, bacterial feeder, fungal feeder, predatory or omnivorous trophic groups (Yeates, 1994). Each nematode genus identified was assigned to colonizer-persister (c-p) continuum of 1 to 5, and nematode community indices maturity index (MI), plant-parasitic index (PPI), and combined MI (∑MI) were quantified according to Bongers (1990), Ekschmitt and Korthals (2006) and Yeates (1994), and enrichment (EI) and structure (SI) indices were computed according to Ferris *et al*. (2001).

Statistical analysis

Nematode abundance data were natural log-transformed (ln (x+1)) to normalize the data prior to analysis of variance (ANOVA). Two sets of correlations were performed. The first was to determine the relationships between SCN and total nematode abundance, total nematode abundance (excluding SCN), total free-living (all non-plant-parasites), plant-parasites, plant-parasites (excluding SCN), and bacterial- and fungal-feeding nematodes. The second correlation analysis was to determine SCN abundance relative to nematode community indices as a measure of changes in ecosystem disturbance and soil food web structure. 3-way ANOVA (2 tillage practices × 5 crop rotations × 2 SCN infestation levels) was used to separate the effects of these factors on nematode abundance and soil food web conditions. Differences were considered significant at $P \leq 0.05$, and all data were analyzed using Minitab Release 15 (Minitab Inc., State College, PA).

RESULTS

Correlations between SCN and other nematodes abundance and soil ecosystem disturbance

A total of 39 soil nematode genera were identified. These include 12 plant-parasites, 16 bacterial-feeders, three fungal-feeders, three predators and five omnivores (Table 1). In both years, SCN population density was less than five vermiforms per 100 cm^3 soil across treatments. In 2008, SCN abundance was positively correlated with total nematode abundance, total non-SCN nematode abundance, free-living nematode abundance, plant-parasitic nematode abundance, and bacteria-feeding nematode abundance ($P \leq 0.01$, Table 2). In 2009, SCN abundance was positively correlated with total nematode abundance, total non-SCN nematode abundance, free-living nematode abundance, and bacteria-feeding nematode abundance ($P \leq 0.01$, Table 2). However, abundance of SCN

Table 1. Genera of plant-parasitic, bacterivore, fungivore, predatory, and omnivore nematodes and their colonizer-persister (c-p) values observed in the study in 2008 and 2009.

Nematode	c-p^{y}	Nematode	c-p	Nematode	c-p
Plant-parasites^{z}		**Bacterivores**		**Fungivores**	
Paratylenchus	2	*Diplogaster*	1	*Aphelechoides*	2
Psilenchus	2	*Diploscapter*	1	*Aphelenchus*	2
Tylenchus	2	*Panagrolaimus*	1	*Filenchus*	2
Criconemoides	3	*Pelodera*	1		
Hoplolaimus	3	*Rhabditis*	1	**Predators**	
Helicotylenchus	3	*Turbatrix*	1	*Mononchus*	4
Heterodera	3	*Acrobeles*	2	*Mylonchulus*	4
Pratylenchus	3	*Acrobeloides*	2	*Nygolaimus*	5
Rotylenchus	3	*Cephalobus*	2		
Tylencholaimellus	3	*Eucephalobus*	2	**Omnivores**	
Tylenchorhynchus	3	*Leptolaimus*	2	*Dorylaimus*	4
Longidorus	5	*Monhystera*	2	*Eudorylaimus*	4
		Plectus	2	*Pungentus*	4
		Wilsonema	2	*Aporcelaimus*	5
		Prismatolaimus	3	*Discolaimus*	5
		Alaimus	4		

[y] Colonizer-persister (c-p) in a scale of 1 (colonizer) to 5 (persister) as described by Bongers, 1998.

[z] Nematodes were classified according to Yeates (1994) and Okada and Kadota (2003).

Table 2. Pearson correlations between soybean cyst nematode (SCN) and abundance of all nematodes, all nematode except SCN, all free-living, plant-parasitic, bacteria-feeding and fungal feeding nematodes, as well as nematode community indices (maturity index, MI and ∑MI, enrichment index, EI, and structure index, SI) in 2008 and 2009.

Parameter	r^{y}	*P* value	r	*P* value
Abundance/100 cm^{3} of soil	---------2008-------		-------2009-------	
All nematodes	0.295	< 0.001	0.259	< 0.001
Nematode (except SCN)	0.176	0.002	0.248	< 0.001
Free-living nematode	0.185	0.001	0.262	< 0.001
Plant-parasites	0.371	< 0.001	0.098	0.083
Plant-parasites (except SCN)	0.100	0.076	0.020	0.728
Bacterial-feeders	0.192	0.001	0.26	< 0.001
Fungal-feeders	-0.072	0.200	0.096	0.089
Indices^{z}				
Maturity Index (MI)	0.007	0.900	-0.158	0.005
∑ MI	0.107	0.055	-0.127	0.024
Structure Index	-0.009	0.868	0.062	0.274
Enrichment Index	-0.023	0.688	0.087	0.119

[y] r = Pearson correlation coefficient

[z] MI and ∑MI were calculated according to Bongers (1990), Ekschmitt and Korthal (2006), and Yeates (1994). Enrichment (EI) and structure (SI) indices were calculated according to Ferris *et al.* (2001).

was not correlated with SI in either year, but was negatively correlated with MI ($P \leq 0.01$) and ∑MI ($P \leq 0.01$) in 2009 (Table 2).

Effect of tillage on nematode abundance and soil health indices

Among all 3-way ANOVA performed (total 80 consisted of 10 parameters measured in 4 sampling times in each of the 2 years), only six 3-way ANOVA had significant interactions between main factors, a very small portion of the entire dataset. Therefore, in this section and the next two sections of the Results, we report significant main factor effects where interactions among main factors were not significant.

In 2008, abundance of total free-living nematodes and bacteria feeding nematodes were higher in tilled than in no-till treatments at 76 ($P \leq 0.01$) and 100 days ($P \leq 0.05$) after planting (Fig. 1). There was no difference in fungal-feeding nematode abundance between tilled and no-till treatments (Fig. 1).Similarly, in 2009, abundance of free-living and bacteria-feeding nematodes was significantly higher in tilled than in no-till treatments at the beginning and at 87 days after planting (all $P \leq 0.05$) (Fig. 1). Plant-parasitic nematode abundance in 2009 was significantly lower in tilled than in no-till treatments at 157 days ($P \leq 0.05$) after planting (Fig. 1). Predatory and omnivorous nematodes were barely detectable in both years (data not shown).

The effect of tillage on MI, PPI, ∑MI, EI, and SI were inconsistent over time (Fig. 2). The ∑MI was lower in tilled than in no-till treatments in 2008 at 76 days ($P \leq 0.05$) and in 2009 at 87 days ($P \leq 0.05$) after planting. SI was lower in tilled than in no-till treatments in 2008 at 76 days after planting ($P \leq 0.01$). The reverse was true for PPI at 100 days after planting in 2008 ($P \leq 0.01$) (Fig. 2).

Effect of SCN introduction on nematode abundance and soil health indices

In 2008, free-living and bacterial-feeding nematode abundance was higher under SCN-infested than non-infested treatments at 49 and 76 days after planting ($P \leq 0.05$), but the reverse, although not different, was generally true at planting (Fig. 3). Abundance of fungal-feeding nematodes was lower in SCN-infested than in the non-infested treatment at 100 days after planting ($P \leq 0.01$, Fig. 3). In 2009, abundance of plant-parasitic nematodes was lower in SCN-infested than in non-infested treatments at the beginning ($P \leq 0.05$) and at 87 days after planting ($P \leq 0.05$, Fig. 3).

In 2008, MI at days 49 and 76 days, ∑MI at 49 and 100 days, PPI at 100 days, and SI at 0 and 49 days after planting were lower in SCN-infested than in the non-infested treatments ($P \leq 0.05$, Fig. 4). In 2009, MI and ∑MI at 0 days, PPI at 120 days were significantly lower in SCN-infested than in non-infested treatments ($P \leq 0.05$, Fig. 4).

Effects of cultivar and crop rotation on nematode community abundance

In 2008, there was no difference in total, free-living, plant-parasitic, bacteria-feeding, and fungi-feeding nematode population densities among rotated and non-rotated cropping systems (Fig. 5). In 2009, monocropping of R and S soybean had initially higher total ($P = 0.009$), free-living ($P = 0.014$), and bacteria-feeding ($P = 0.003$) nematode populations compared with RCRC and SCSC rotations and the maize monocrop, but these differences were not significant in the later sampling dates (Fig. 5).

DISCUSSION

The results of this study revealed complex relationships among tillage, crop rotation practices, and infestation of SCN and their effects and infestation of SCN and their effects on nematode community over time. Under the tillage and crop rotation treatments in this study, the low numbers of SCN after seven years of continuous cropping was consistent with earlier conclusions made by Melakeberhan *et al*. (2015) that there was prolonged lag phase in SCN establishment when introduced into a new location. The positive correlation between SCN-abundance with the abundance of total nematodes, total plant-parasitic, total free-living, and bacteria-feeding nematodes suggests that the population density of SCN would increase under conditions that also favor reproduction of majority of other free-living nematodes, in particular the bacterial-feeding nematodes. This result further suggested that soil

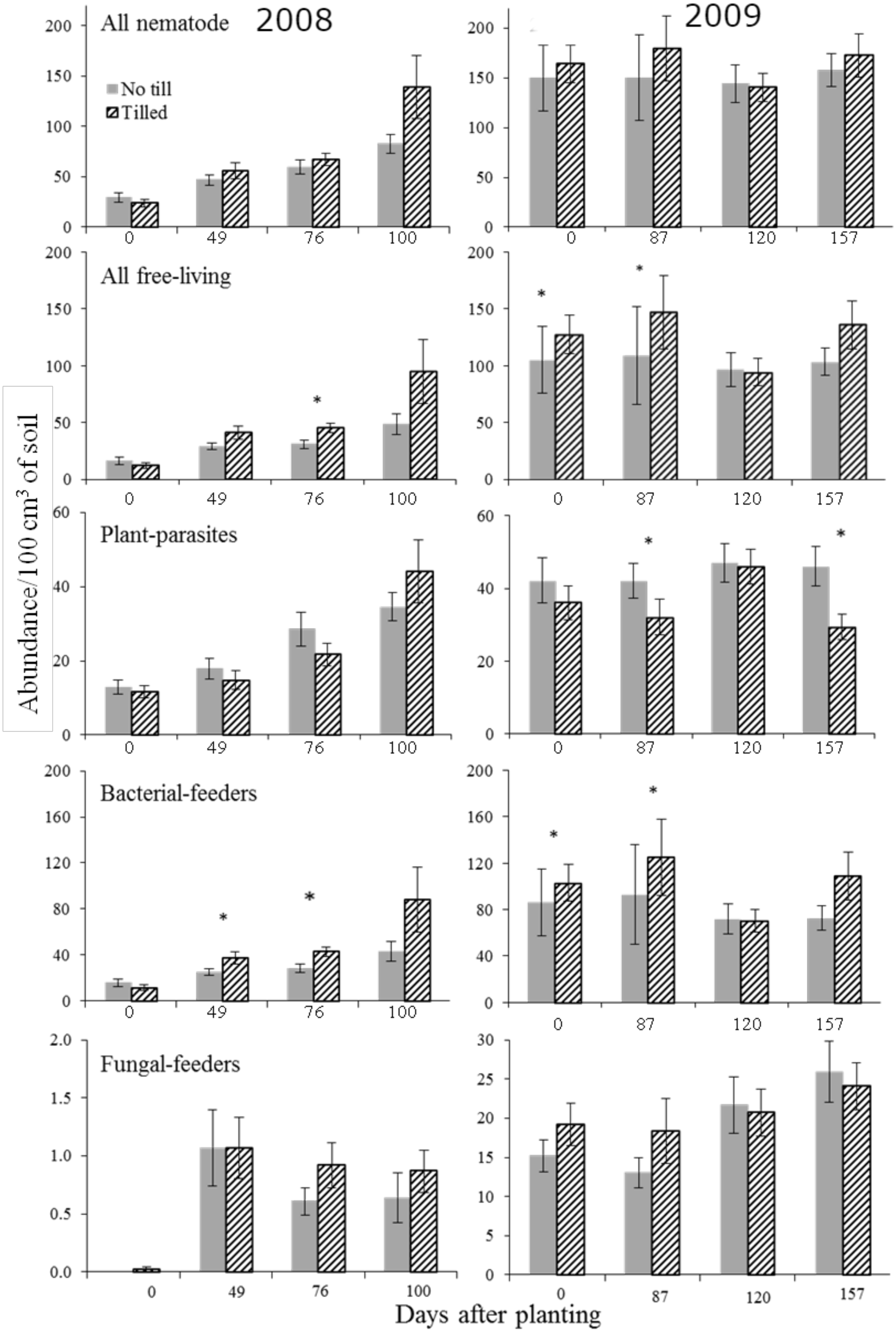

Fig. 1. Effects of tillage on abundance of all nematodes, all free-living, plant-parasites, bacterial feeders and fungal-feeders during the 2008 and 2009 growing seasons. * indicates significant difference ($P \leq 0.05$) within a sampling time. Bar on each column is the standard error of the means.

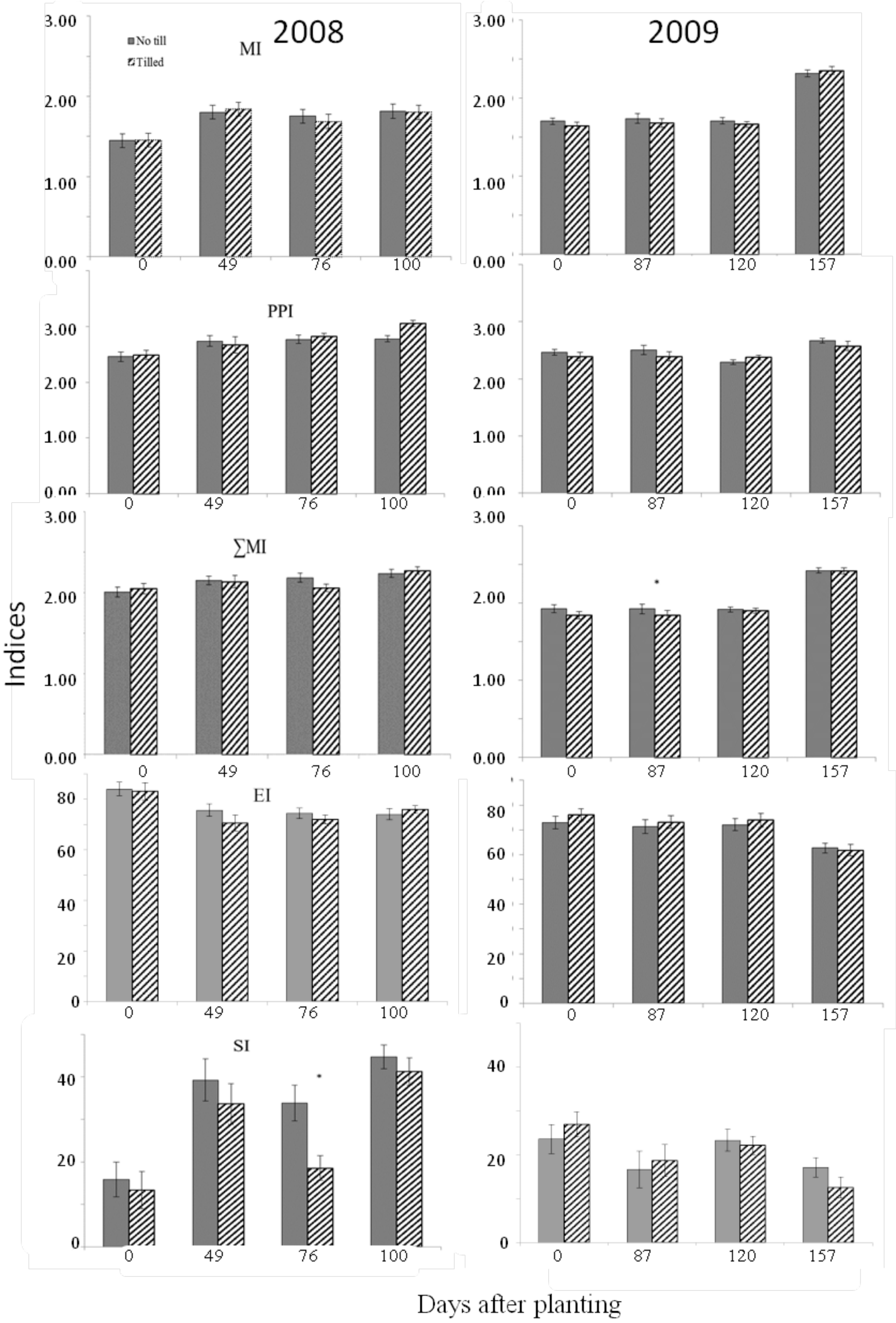

Fig. 2. Effects of tillage on Maturity (MI), Plant-parasitic (PPI), Combined Maturity (ΣMI), Enrichment (EI) and Structure (SI) Indices during the 2008 and 2009 growing seasons. * indicates significant difference ($P \leq 0.05$) within a sampling time. Bar on each column is the standard error of the means.

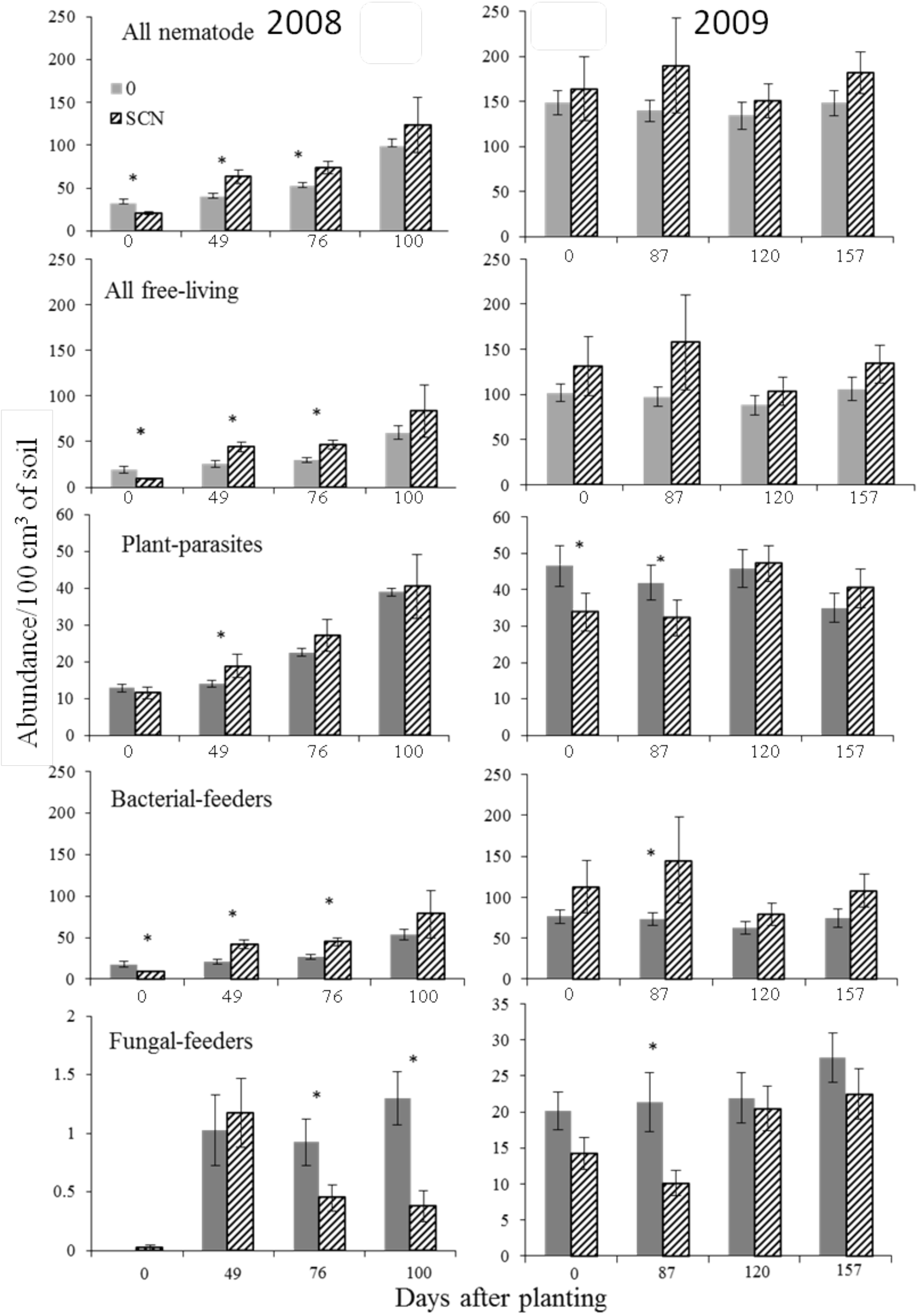

Fig. 3. Effects of soybean cyst nematode (SCN) inoculation on abundance of all nematodes, all free-living, plant-parasites, bacterial feeders and fungal-feeders during the 2008 and 2009 growing seasons. 0 indicates treatment without SCN inoculation, * indicates significant difference ($P \leq 0.05$) within a sampling time. Bar on each column is the standard error of the means.

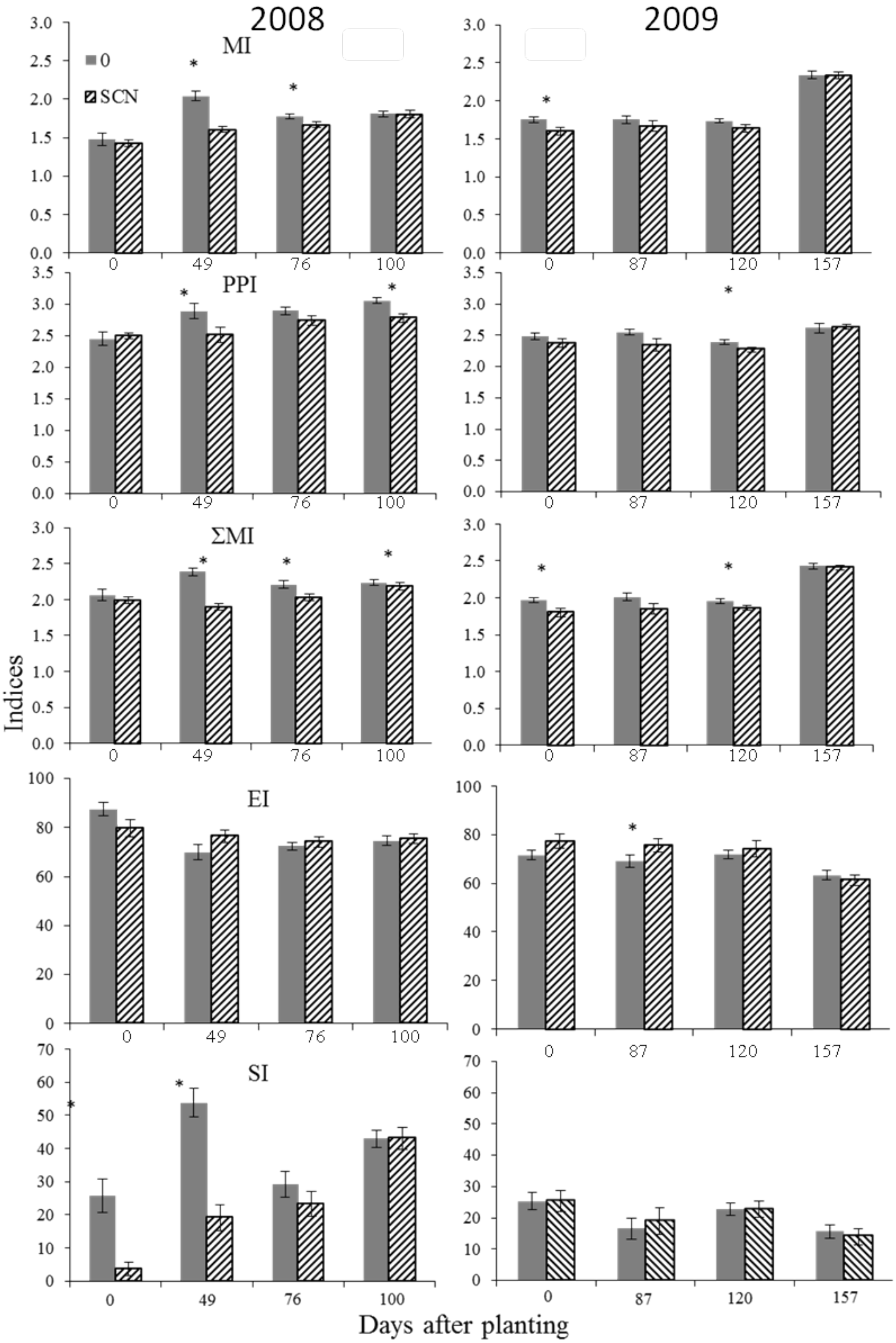

Fig. 4. Effects of soybean cyst nematode (SCN) inoculation on Maturity (MI), Plant-parasitic (PPI), Combined Maturity (ΣMI), Enrichment (EI) and Structure (SI) Indices during the 2008 and 2009 growing seasons. 0 indicates treatment without SCN inoculation, * indicates significant difference ($P \leq 0.05$) within a sampling time. Bar on each column is the standard error of the means.

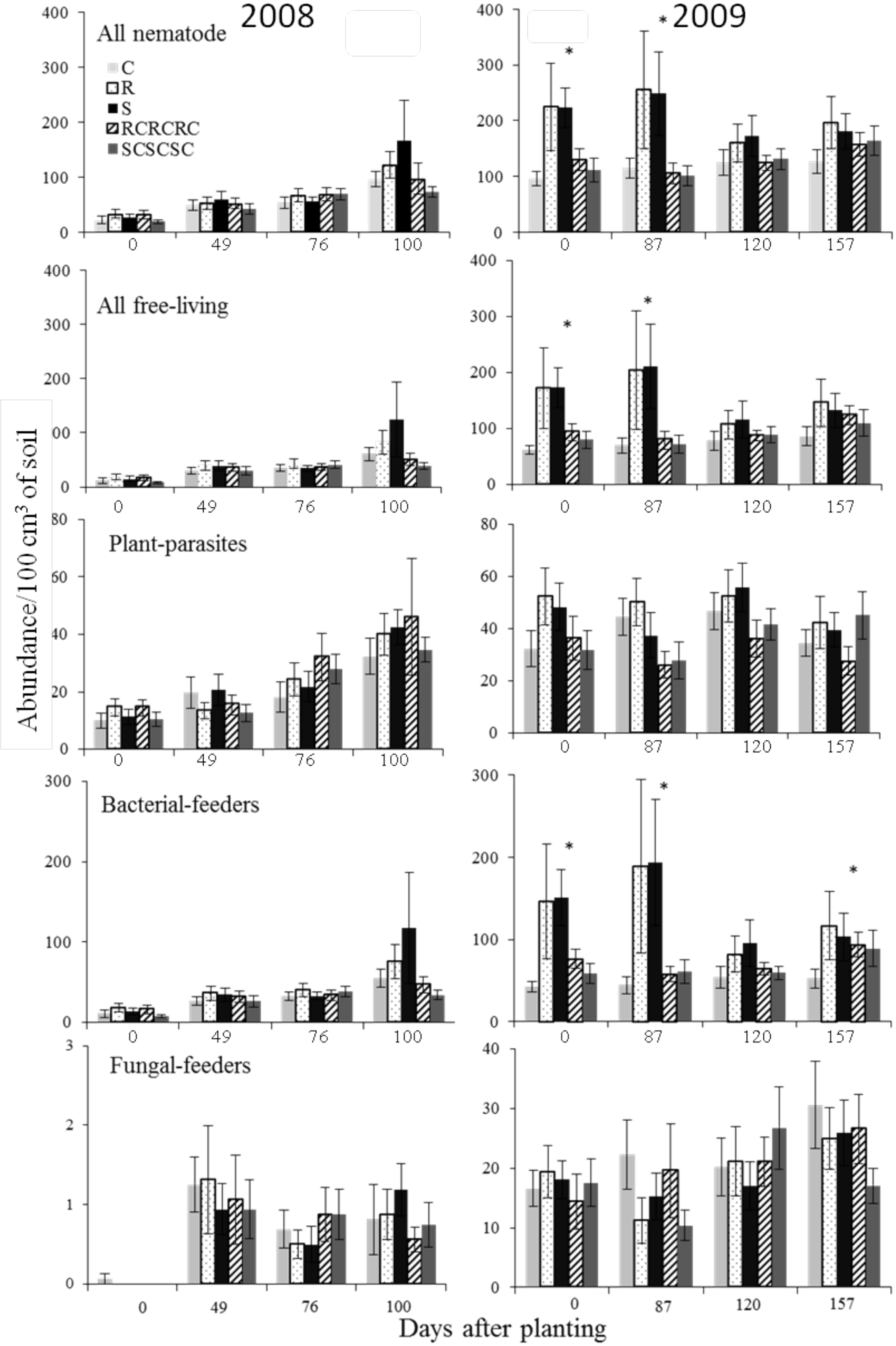

Fig. 5. Effects of monoculture of maize (C), soybean cyst nematode-susceptible (S), and -resistant (R) cultivars, and their rotations: RCRCRC and SCSCSC on abundance of all nematodes, all free-living, plant-parasitic, bacterial feeding and fungal feeding nematodes during the 2008 and 2009 growing seasons. * indicates significant difference ($P \leq 0.05$) within a sampling time. Bar on each column is the standard error of the means.

conditions with high nutrient availability in tilled fields were often associated with higher SCN establishment compared to nutrient-limited conditions that prevail under conservation tillage. Due to low abundance of SCN and total plant-parasitic nematodes in the experimental site, crop rotation with resistant or susceptible soybean cultivars had no effect on overall nematode population densities in fields with no histories of SCN infestation.

This multi-factorial analysis illustrated that high abundance of bacterial- and plant-parasitic nematodes are characteristic of agroecosystems as opposed to the undisturbed forest and grassland ecosystems (Wasilewska, 1979). The current study provided numerical positive relationship on multiple sampling times between abundance of SCN with abundance of other nematode fauna under different soil tillage, SCN infestation, and crop rotation regimes. This result is in contrast with a previous report on the negative correlation between abundance of root-lesion nematode (*P. penetrans*), a different plant-parasitic nematode, and free-living nematodes (Nahar *et al*., 2006). To the best of our knowledge, this is the first report on correlation between abundance of SCN with abundance of free-living nematodes and nematode community indices. Although SCN was negatively correlated with abundance of *P. penetrans* under controlled environments in previous reports (Melakeberhan and Dey, 2003), no such relationship was observed between abundance of SCN and *P. penetrans* or all plant-parasitic nematodes in this study. It seems logical to assume that there may be a threshold beyond which the population density among nematode trophic groups would show a clear relationship. While varying by year and time of sampling, the low nematode abundance across treatments in this study may be due to overall low abundance of nematodes. However, there is a trend that number of nematodes was increased from 2008 to 2009. Continuous observation beyond this experimental period might reveal different results.

Seasonal nematode population dynamics are related to the life cycle of the nematodes, age of the host, and the soil environment (Melakeberhan, 2007) altered by tillage and crop rotation. During the time SCN takes to invade the root system, it will be subjected to the same tillage and rotation driven changes in the soil environment that would affect ecto-parasitic nematodes. Since SCN is a sedentary, obligate endoparasitic nematode, once SCN penetrates the root, it will be exposed to the changes in soil environment for the rest of its life cycle in one position. The increase and/or decrease in some nematode trophic groups relative to SCN is an interesting finding that points to yet unknown factors influencing nematode abundance.

Tilled treatment resulted in higher free-living, especially bacteria-feeding, nematode population density than in no-till treatments at several sampling times. This is expected because bacteria-feeding nematodes usually have low c-p values (short life cycle and opportunistic feeders), and they are resilient to disturbance and respond to nutrient availability rather quickly (Ferris *et al*., 2001). Therefore, the relatively faster turnover due to conventional tillage could have contributed to increased population density of bacteria-feeding nematodes (Ferris *et al*., 2001).

When abundance of opportunistic nematodes decreases, it reflects the overall decrease of biological productivity in the system (Ferris *et al*., 2001), which could affect SCN abundance. For example, a decrease of SCN population density in no-till observed in a previous study (Melakeberhan *et al*., 2015), but a positive correlation between SCN and free-living nematode abundance observed in this study suggests both a direct and an indirect impact of tillage on nematodes. This may explain some of the inconsistencies among many previous studies (Tyler *et al*., 1987; Herschman and Bachi, 1995; Noel and Edwards, 1996; Noel and Wax, 2003; Gavassoni *et al*., 2007; Donald *et al*., 2009). This illustrates the fact that the sources of variability relative to the agronomic practices and biological changes that drive the soil environment need further investigation.

Although the main ecosystem disturbance (MI, PPI, and $\sum$MI) and soil food web (EI and SI) indices did not show consistent trends across treatments or time, some of the $\sum$MI and SI results are noteworthy. For examples, $\sum$MI once in 2008 and in 2009 and SI once in 2008 were higher in no-till than in tilled treatments. In addition, $\sum$MI in 2009 and SI in 2008 were generally higher in the non-infested than in SCN-infested soils. A high $\sum$MI and SI indicate a more diverse and stable soil food web (Ferris *et al*., 2001), which, in turn, may impose higher suppressive pressure on plant-parasitic nematodes (Macfadyen, *et al*., 2009). Whether or not high ∑MI and SI are correlated with SCN suppressiveness is yet to be investigated.

While varying by year, crop rotation influenced nematode community at different sampling time. The higher total, free-living, and bacteria-feeding nematode population density in monocropping of R and S soybean cultivars over RCRCRC and SCSCSC rotations suggested that free-living nematodes may favor soybean monocropping over crop rotation. It is also possible that free-living nematodes needed to adjust to the new environment mediated by new plant roots. Similarly, their food sources may have been disturbed as crop rotation is known to alter microbial communities (Kennedy and Smith, 1995) on which nematodes feed. However, the little impact of crop rotation on plant-parasitic nematode abundance across crops probably suggests broad host range of the nematodes present in the field. From the perspective of soil nematode community, the results indicate that maize-soybean (resistant or susceptible) rotations will likely have a negative impact on SCN population density through overall lowering soil nematode abundance.

In summary, this study documented the effects of seven years of tillage and crop rotation treatments on the relationships between SCN and nematode community in a typical soybean agroecosystem of US Midwest sandy loam soil where SCN was introduced and soybeans had not been grown before. Despite lower SCN population density detected than when it was introduced, SCN population tended to positively correlate with abundance of total nematodes, total non-SCN nematode, free-living nematode, plant-parasitic nematode, and bacteria-feeding nematode. While varying by time, abundance of free-living and bacteria-feeding nematodes was generally higher in tilled than in no-till, and in SCN-infested than in non-infested treatments. Monocropping of R and S soybean cultivars tended to have higher total, free-living, and bacteria-feeding nematode populations compared to C, RCRC, and SCSC rotations. These results suggest that there are direct and indirect effects of tillage and crop rotation on the abundance of SCN and free-living nematodes. The tillage-driven conditions that are in favor of the proliferation of bacteria-feeding nematodes would also increase SCN population densities. This is the first report that clearly documented soil tillage and crop rotation though enhancing soil nutrient cycling processes but are often associated with higher infestation of SCN.

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