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REGULAR ARTICLE

Response of soil nematodes to elevated temperature in conventional and no-tillage cropland systems

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Abstract
Aims Nematodes are sensitive to environmental changes and are strongly affected by tillage practices. However, it remains unclear whether an increase in soil temperature in conventional tillage (CT) and no-tillage (NT) cropland systems would have a significant effect on nematode communities. The response of soil nematodes to increases in temperature will provide valuable information about probable changes in soil ecology under global warming.
Methods A field experiment using infrared heaters to simulate climate warming was performed in North China. The impacts of predicted warming on the nematode community in CT and NT systems were measured during the growing season of maize.
Results The results showed that the diversity of nematodes responded positively to warming in both tillage systems early in the maize growing season, though the diversity in NT declined due to warming late in the growing season. However, no significant warming effects were found on the total nematode density, individual feeding group density or functional indices. Compared to CT, NT presented a rather different nematode community that was characterized by a large nematode diversity, low fungal feeder density due to a strong decrease in *Aphelenchoides*, and high maturity indices.
Conclusions Tillage is an important factor that influences the soil properties and nematode community. It is proposed that future global warming with soil temperature increasing approximately 1 °C will have only small effects on soil nematodes in the two tillage systems.

Keywords Climate change · Diversity · Nematode community · Soil properties · Functional indices

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Introduction

It has been documented that the global temperature has increased by approximately 0.74 °C over the last century, and the temperature is predicted to increase in the future with the continuing increase in greenhouse gases in the atmosphere (Susan 2007). The soil temperature in surface layer is significantly affected by seasonal changes in the air temperature, and has been shown to increase correspondingly with air temperature (Jacobs et al. 2011). Such observations raise questions of whether global warming will affect belowground animals. Soil animals play keys roles in biogeochemical process and physical conditions, and their responses to global change are likely important at the ecosystem level (Blankinship et al. 2011). Blankinship et al. (2011) used a meta-analysis to synthesize results from manipulative experiments to test the response of soil biota to global change, and found that the local climate and ecosystem type best explained the observed responses to warming; although the effect of warming did not depend on the taxon or body size, reduced abundances were more likely to occur at colder and drier sites.

Agricultural activity causes the emission of greenhouse gases, contributing to global warming. No-tillage (NT) management has been promoted as a practice to increase soil organic carbon storage in cropland and reduce CO_2 emissions (Cole et al. 1997), and long-term NT management is thought to partly offset the global warming potential (Six et al. 2004). Furthermore, NT results in distinct soil properties compared to conventional tillage (CT) (Sainju et al. 2006; Ussiri et al. 2009) by improving soil characteristics, helping to conserve soil biota and stimulating their activities (Miura et al. 2008).

Little is known about how global warming affects NT and CT cropland systems, or how the soil fauna in these two systems respond to global warming. Yet, soil nematodes play an important role in soil nutrient processes (Freckman and Caswell 1985); furthermore, nematodes are sensitive to environmental changes, and are suitable indicators of environmental stress (Bongers and Ferris 1999). Therefore, alterations in the nematode community structure induced by global warming may have a considerable influence on ecosystem functioning (Bakonyi et al. 2007). Although the responses of nematodes to global warming have been well studied in Antarctica (Barrett et al. 2008; Convey and Wynn-Williams 2002; Simmons et al. 2009), the effects of warming on soil nematodes in cropland systems have been inadequately studied in temperate regions. The soil environment and food-web development can be assessed by calculating functional indices of nematode community. Indeed, numerous reports have documented the uniqueness of responses of soil nematode communities to alterations in temperature (Bakonyi and Nagy 2000; Bakonyi et al. 2007; Todd et al. 1999). For example, temperature appears to be an important factor determining nematode abundance and diversity in colder areas, such as polar (Simmons et al. 2009) and subarctic regions (Ruess et al. 1999a; Ruess et al. 1999b). In contrast, nematodes in desert soil system are relatively more tolerant to increases in ambient temperature (Darby et al. 2011). Most studies regarding warming effects are conducted in natural or semi-natural systems, and studies in temperate cropland systems are much needed.

In the present work, we used infrared heaters to simulate climate warming, and analyzed the effect of warming on the soil properties and nematodes in CT and NT systems. Previous studies showed that tillage could affect nematode trophic structure and total abundance. Densities of bacterial feeders, fungal feeders and total nematodes were greater in CT than in NT (Parmelee and Alston 1986). Soil properties have a close relationship with nematode community composition (Porazinska et al. 1998; Wang et al. 2004), both of them are quite different between the NT and CT systems (Okada and Harada 2007). As warming may affect nutrient cycling through soil biota, we expected that soil properties will be altered by warming in the two systems. Because warming could induce a greater reproduction rate and result in a higher population density as observed in the experimental study by Ruess et al. (1999b), we expected that the abundance and diversity of nematodes in the two systems will be increased by warming. Finally, we hypothesized that, since the nematode communities between the NT and CT systems are quite distinct from each other, their response to warming may differ between these two tillage systems.

Materials and methods

Study site

The field experiment was conducted between July and September 2011 at the Yucheng Experimental Station of the Chinese Academy of Sciences, Shandong Province, China (116°36′ E, 36°57′ N). The site is in a temperate, seasonal, semi-humid monsoon climate, where the mean annual temperature is 13.1 °C, the mean annual precipitation is 582 mm, concentrated in the summer months. The soil is classified as a Calcaric fluvisols according to the FAO-Uneson system; surface soil texture is silt loam (sand, 12 %; silt, 66 %; clay, 22 %), according to the USDA classification system. The annual temperature in North China where our site is located increased by 1.5 °C between 1951 and 2009 (Zhang et al. 2011). Winter wheat, maize and cotton are the primary crops at this location.

Experimental design and treatments

We used a split-plot design with tillage system (i.e., no-tillage or conventional tillage) in the main plots and warming (i.e., with or without warming treatment) in the subplots. There were six randomly arranged wheat fields, comprising three conventional tillage and three no-tillage fields (7 m×20 m). In each field, one plot (2 m×2 m) was arranged randomly to be warmed continuously from February 2010, and the other plot was maintained at the natural temperature. The warming treatment was achieved by suspending a 165 cm×15 cm MSR-2420 infrared radiator (Kalglo Electronics, Bethlehem, PA, USA) 3 m above each plot, consistently heating both during the day and at night. There was a distance of at least 10 m between the plots. For the plots at the natural temperature, 'dummy' heaters of the same shape, size, and installation were used to mimic the shading effect artificially introduced into the experiment by the warming equipment. The experiment was based on a long-term (since 2003) conservation tillage experiment field. For further details regarding the management of the conservation tillage experiment, see Hou et al. (2012).

The soil temperature at a 5 cm depth was monitored by thermocouples. Pairs of thermocouples were arranged in the soil of each plot under the heater/mimic heater and were separated by a distance of 1 m in each plot. The temperature in each plot was averaged based on the measurements. To assess the soil physicochemical properties, we collected soil samples (2 samples per plot) on the same day of nematode sampling. The samples were submitted to the Yucheng Experimental Station of the Chinese Academy of Sciences to determine the soil moisture and the total nitrogen and organic matter contents. Soil moisture content was determined gravimetrically. Samples were air-dried and passed through a 2-mm sieve for chemical analysis. Total nitrogen was quantified using a Kjeldahl digestion, followed by near infrared spectro-photometry. Organic matter content was determined by oxidation method with $K_2Cr_2O_7$–H_2SO_4 (Lu 1999).

Nematode sampling and processing

Nematode sampling was performed during the maize growing season of 2011 (seedling, 1 July; elongate-booting, 10 August; and milking-ripening, 2 September). For each sampling campaign, 3 soil cores (approx. 35 cm^3 each) were collected per plot under the heater/mimic heater, the top 5 cm of soil was sampled. The soil samples in each plot were pooled and stored at 5 °C for <1 week. The nematodes were extracted from 100 g fresh weight subsamples of the soil samples using the minor modified cotton-wool filter method (Liang et al. 2009; Townshend 1963). After 48 h of extraction through a double layer of filter paper, the nematodes were preserved in 4 % formaldehyde. The number of extracted nematodes in each sample was counted, and 10 % of the individuals (but not less than 100 individuals if available) were identified to the genus level (Bongers 1988; Yin 1998). Nematode density was expressed as the number of nematodes per 100 g of dry soil. Nematodes were assigned to trophic groups—bacterial feeders, fungal feeders, plant feeders, omnivores and predators—according to Yeates (2003) and Bongers and Bongers (1998).

Statistical analyses

The following eight indices were computed for the nematode community in each soil sample. 1) The taxon richness of the total nematodes. 2) The maturity index (MI), for free-living nematodes was used, $MI=\sum[v(i)\times f(i)]$, where v(i) is the colonizer-persister (*c-p*) value of taxon i and f(i) is the frequency of taxon i in a sample (Bongers 1990). The c-p group pools nematode taxa with similar responses to changes in their environment. The c-p value ranges from a colonizer (*c-p*=1) to a persister (*c-p*=5), with the index values representing life-history characteristics associated with r- and K-selection, respectively (Bongers and Bongers 1998). MI is to assess changes in the functioning of the soil ecosystem as a result of disturbances and subsequent recovery. A low MI suggests that nematode community succession is in the early stage and soil is highly disturbed. A high MI suggests that nematode community succession is in the late stage and soil is little disturbed. 3) MI25, the MI value of nematodes excluding the c-p 1 enrichment opportunists, is to assess the general long-term disturbance. 4) The plant parasite index (PPI) is the maturity index exclusively based on plant-parasitic nematodes. PPI has close relation with primary production, and is to assess fertilization (Bongers 1990). 5) PPIMI, the ratio of PPI to MI. In some condition, MI and PPI are inversely related, so the ratio between PPI and MI is proposed as a sensitive parameter for measuring effects of nutrient enrichment (Bongers et al. 1997). 6)

The enrichment index (EI) and structure index (SI) are calculated based on functional guilds. EI is to assess the response of food web to available resources. SI reflects the changes in food-web structure during disturbance and recovery. They are considered together to assess soil enrichment and food web development. For example, if both EI and SI >50, it means that disturbance is minor, and food web is stable and structured (Ferris et al. 2001; Wang and McSorley 2004). 7) The Wasilewska index (WI), WI = (fungal feeders + bacterial feeders)/plant feeders, it reflects the community structure and soil health. The value of WI in the healthy soil is generally above 1. WI = 1 means benefit and harmful nematodes have the equal numbers (Wasilewska 1994). 8) The nematode channel ratio (NCR), NCR = bacterial feeders/(bacterial feeders + fungal feeders), describes the decompostion pathway in detritus food webs (Yeates 2003). These indices are indicators of the soil food web structure and condition (indicating functional diversity) (De Deyn et al. 2004; Ferris and Matute 2003).

The data were analyzed using a split-plot ANOVA with a General Linear Model in SPSS 18.0. Warming, tillage system and different dates were used as fixed factors and block was considered as random factor. The effects of warming, tillage system, and different dates on the soil physicochemical properties (moisture, total nitrogen, and organic matter content), nematode density (total, bacterial feeders, fungal feeders, plant feeders, predators and omnivores) and functional indices of the nematode community (e.g., MI) were tested. Data regarding the nematode density were log-transformed prior to the analysis. Nematode diversity was compared using a diversity profile analysis (Patil and Taillie 1979), a method that overcomes the disadvantage of other diversity measures (e.g., Shannon-Wiener diversity index), which are sensitive in different ways to density changes in rare or common species (Tóthmérész 1995). We used Rényi's diversity index family for diversity ordering which is based on diversity profiles. The result of the diversity ordering is a curve rather than a single number. The left portion of the curve reflects the rare species diversity, whereas the right portion shows the diversity of common species. Community A is considered to be more diverse than B when the curve of the diversity profile of A is above that of B over the entire range of a scale parameter. The DivOrd 1.70 statistical program package was used for the diversity profile analysis (Tóthmérész 1995). Diversity profiles between scale parameters 0–15 of all plots were calculated for each sampling occasion. Scale parameter is related to the relative abundance structure of the community. The scale parameter of 0–15 means whole scale parameters. Usually, in figures 0–4 was good enough to show the results. Significance tests were performed between the treatments, which indicates a higher or lower diversity between the diversity profiles along the range (0–15) of scale parameters.

The initial ordination of the nematode community data revealed a strongly unimodal response. Therefore, the nematode communities were analyzed in relation to environmental variables through a canonical correspondence analysis (CCA) using the CANOCO program, version 4.5 (ter Braak and Smilauer 2002). The influence of the treatments (warming and tillage system) were examined by assigning samples to nominal environmental variables (0 or 1); these variables are represented as centroid points for each class on an ordination diagram. Ordination diagrams are presented in this paper with a focus on inter-species distances. The significance of the relationships between the response data and environmental variables was tested using Monte Carlo permutation tests (ter Braak and Smilauer 2002).

Results

Microclimate effects and soil physicochemical properties

The microclimate data from July to September 2011 revealed increases in the daily soil temperature of 1.20 and 0.62 °C in the warmed conventional tillage (CT) and no-tillage (NT) plots, respectively. However, the increases of temperature differed significantly between CT and NT ($F_{1,162}$=29.907, P<0.001). Although no significant effect of warming or the tillage system on soil moisture was detected, the soil moisture declined with the sampling date (Table 1, average±S.D.: 23.38±1.60 %, 21.95±2.70 % and 18.79±5.38 % for July, August and September, respectively). The total nitrogen and organic matter content did not vary significantly with the sampling date (Table 1). Warming and the tillage system both had significant effects on the amount of total nitrogen, though their interaction effect was not significant (Table 1). Warming significantly increased the total nitrogen content (1.15±0.15 g/kg

Table 1 *F*-value of split-plot ANOVA (GLMs) for the effect of warming (W), tillage system (T) and different date (Date) on soil properties (moisture, total nitrogen and organic matter), nematode density (total, individual feeding groups and key genera) and the functional indices of nematode communities

	W	T	W × T	Date	Date × W	Date × T	Date × W × T
Soil properties							
Moisture	2.593	1.788	1.979	8.331**	1.779	1.799	0.896
Total nitrogen	5.469*	24.387**	1.282	2.895	0.251	0.408	1.170
Organic matter	11.173**	71.821**	9.897**	1.536	2.606	0.321	0.515
Nematode density							
Total nematodes	1.375	9.995*	0.082	11.046**	0.530	0.801	0.654
Bacterial feeders	2.207	2.814	0.002	10.176**	0.605	0.815	0.333
Fungal feeders	0.003	39.154**	2.210	17.320**	2.388	0.559	1.196
Plant feeders	0.042	2.838	0.397	2.204	0.189	2.918	2.087
Predators & omnivores	0.400	1.594	2.926	1.929	5.260*	2.146	2.141
Acrobeloides	0.779	6.590	0.526	11.613**	0.697	0.760	0.142
Aphelenchoides	0.401	17.101*	2.241	13.209**	2.446	0.164	0.966
Functional indices							
Taxa richness	0.152	3.623	1.079	13.697**	0.038	0.510	0.207
MI	0.192	0.077	0.003	3.971*	2.643	3.101	3.293
PPI	0.527	0.032	0.366	7.511**	1.897	0.535	0.244
MI25	1.948	56.620**	0.795	6.787**	4.556*	1.818	2.437
PPIMI	0.940	0.015	0.042	0.671	0.792	1.979	1.204
WI	0.378	7.989*	0.582	1.478	0.404	1.235	0.202
NCR	0.689	1.235	2.095	3.190	1.402	0.380	0.189
EI	0.075	0.081	0.396	2.101	0.618	0.072	0.564
SI	1.169	73.567**	0.214	7.479**	3.433	1.348	1.698

MI maturity index, *PPI* plant parasite index, *MI25* maturity index of cp2-5 nematodes, *PPIMI* the ratio of PPI to MI, *WI* Wasilewska index, *NCR* nematode channel ratio, *EI* enrichment index, *SI* structure index

**P*≤0.05, ***P*≤0.01

and 1.07±0.11 g/kg for warmed and control plots, respectively), with NT showing a significantly higher total nitrogen content than CT (1.19±0.12 g/kg and 1.02±0.09 g/kg for NT and CT, respectively). Warming and tillage also had a significant interaction effect on organic matter content (Table 1): warming significantly increased the amount of organic matter content in NT (20.07±1.94 g/kg and 16.64±3.30 g/kg for warmed and control plots, respectively), whereas no increase was observed in CT (14.67±1.26 g/kg and 14.50±2.79 g/kg for warmed and control plots, respectively).

Nematode density

The total nematode density was significantly affected by the tillage system and sampling date but not by warming (Table 1). NT had a lower density of total nematodes than CT, and the overall density of total nematodes declined from July to September. The density of the individual feeding groups was not significantly affected by warming. In contrast, the tillage system had a significant effect on fungal feeders, with densities of that were significantly lower in NT than CT, though the other nematode feeding groups did not respond significantly to the tillage system. The density of bacterial and fungal feeders, which were significantly affected by the sampling date, declined sharply from July to August (Table 1, Fig. 1). The nematode genera and their densities in each treatment are listed in Table 2. Bacterial-feeding *Acrobeloides* was the most abundant nematode genus followed by fungal-feeding *Aphelenchoides* both being not affected by warming. However, the tillage system significantly affected the density of *Aphelenchoides*, a taxon that was significantly lower in NT than CT (Table 1).

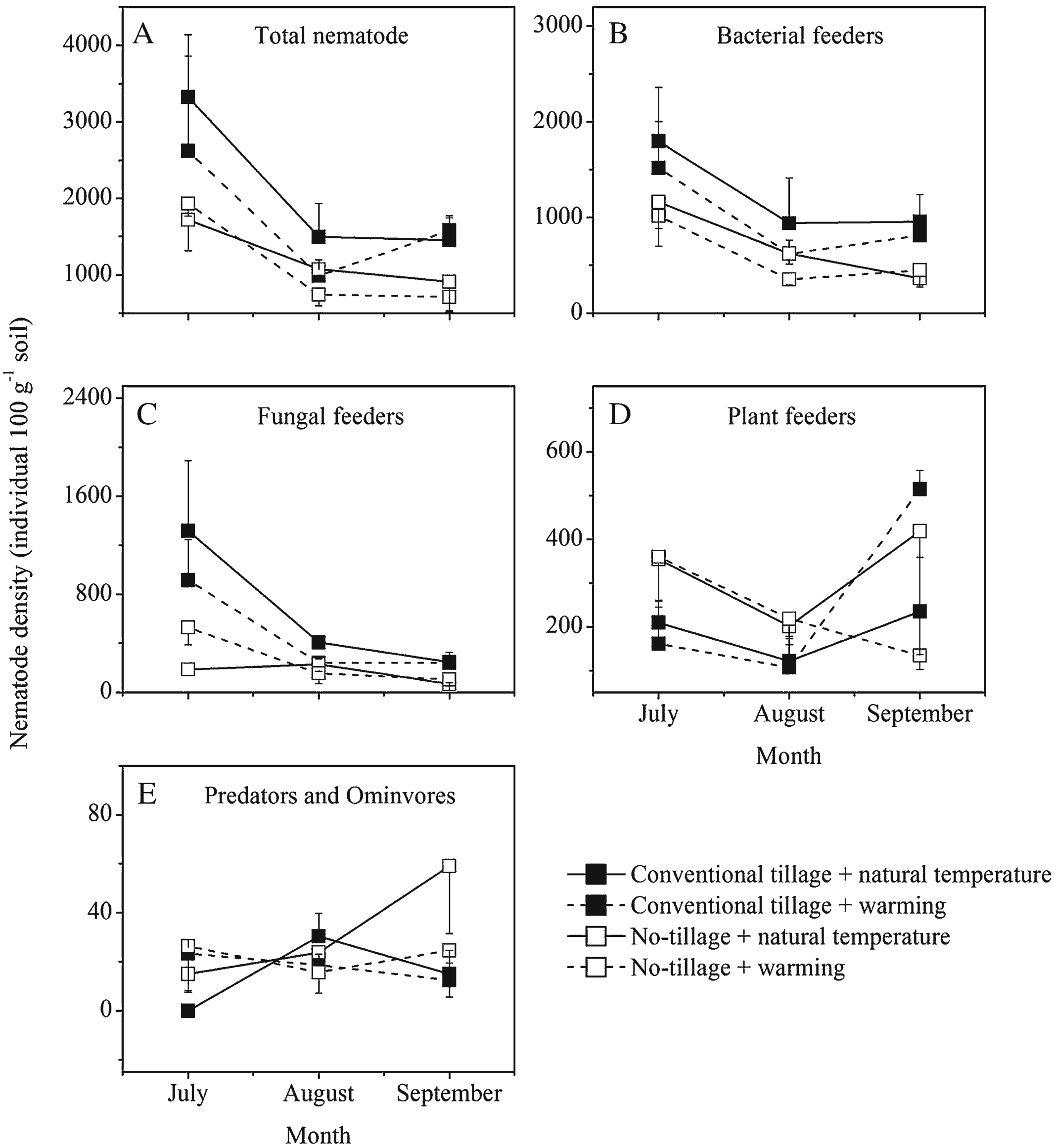

Fig. 1 Seasonal changes in total density and each individual feeding group density of nematodes (Mean ± SE)

Nematode diversity and functional indices

Thirty-six genera of nematodes were found in the plots. Warming or the tillage system did not significantly affect the nematode richness (Table 1), but increased with the sampling date. The diversity of the nematode community changed with the sampling date. In July, warming increased the diversity of the community in both NT and CT (warming: $P<0.001$), and the community in NT was more diverse than that in CT (Fig. 2a). In August, warming decreased the diversity in NT but increased it in CT (warming × tillage system: $P<0.001$, Fig. 2b). In September, the diversity of the treatments reached a similar level, with the exception that the diversity of NT with the warming treatment was the lowest (warming: $P<0.001$, warming×tillage system: $P<0.001$, Fig. 2c). No differences were found in the diversity trends in CT with the warming treatment in comparison with CT with the natural temperature treatment; both increased with the sampling date. However, the diversity in NT with the natural temperature treatment did not increase in September but remained at the

Table 2 The genus and density (average ± S.D.) of nematodes (individual 100 g^{-1} soil) sampled from the different treatments from July to September

Nematode genus	Feeding group [a]	Treatment [b]			
		CT0	CT1	NT0	NT1
Acrobeloides	BF	2698.7±639.0	1886.2±1092.3	956.7±25.6	1065.1±519.1
Acrobelus	BF	2.8±4.8	8.2±7.1	9.7±16.8	5.2±5.9
Alaimus	BF	24.9±31.9	4.1±7.1	2.9±5.1	3.2±2.9
Cephalobus	BF	240.9±149.8	402.4±197.0	49.8±25.3	56.8±45.4
Cervidellus	BF	7.0±12.1	0	2.4±4.2	1.2±2.1
Chiloplacus	BF	59.3±102.8	44.0±50.5	15.1±26.2	9.7±16.7
Diploscapter	BF	139.7±175.1	99.0±156.8	124.2±88.1	27.3±20.5
Ethmolaimus	BF	0	1.6±2.9	1.5±2.6	4.2±7.3
Eucephalobus	BF	278.9±190.9	305.6±306.4	483.0±530.9	268.3±237.9
Mesorhabditis	BF	67.3±110.7	84.7±141.3	114.3±31.8	112.7±78.9
Metatercephalobus	BF	4.6±8.0	8.2±14.1	3.0±2.6	7.8±4.7
Panagrolaimus	BF	44.1±44.9	55.0±60.7	20.7±29.3	10.7±18.4
Plectus	BF	52.4±22.3	12.3±21.2	30.6±29.6	16.8±5.3
Prismatolaimus	BF	60.3±11.9	31.1±7.5	86.2±5.9	86.1±22.8
Protorhabditis	BF	8.9±8.2	5.7±9.9	10.2±11.9	8.8±15.2
Rhabditis	BF	0	0	241.7±412.5	122.9±113.8
Wilsonema	BF	0	4.1±7.1	0	0
Aphelenchoides	FF	1543. 8±1070.8	1042.4±338.6	329.9±20.7	579.1±45.1
Aphelenchus	FF	177.5±117.6	153.3±118.5	52.0±23.3	48.2±25.8
Nothotylenchus	FF	252.4±168.4	198.6±182.4	72.7±32.7	144.9±99.8
Tylencholaimus	FF	0	4.1±7.1	27.4±19.1	15.0±13.0
Boleodorus	PP	32.6±17.6	2.4±4.2	2.4±4.2	0
Filenchus	PP	48.6±15.8	136.5±126.2	271.0±350.4	122.9±69.1
Helicotylenchus	PP	67.0±39.9	58.2±50.8	113.4±149.1	38.6±34.2
Paratylenchus	PP	7.0±12.1	0	0	0
Pratylenchus	PP	2.6±4.5	6.1±1.1	26.1±45.2	44.8±53.3
Psilenchus	PP	0	62.6±62.3	14.7±25.5	3.6±3.6
Rotylenchus	PP	274.8±185.6	287.3±239.5	312.2±255.1	217.8±143.5
Tylenchorhynchus	PP	26.7±25.5	120.7±80.2	185.2±128.9	101.4±59.0
Tylenchus	PP	106.0±143.2	107.8±151.0	48.6±43.6	175.8±189.3
Aporcelaimus	OP	19.3±10.8	24.4±23.2	44.8±13.7	16.8±14.5
Eudorylaimus	OP	0	0	16.6±28.8	0
Isolaimium	OP	2.6±4.5	0	0	0
Mononchus	OP	2.3±4.0	0	0	0
Thornia	OP	18.8±32.6	30.0±14.5	18.1±16.4	21.1±36.5
Tripyla	OP	2.3±4.0	0	17.9±8.8	28.9±43.9

[a] *BF* bacterial feeders, *FF* fungal feeders, *PP* plant feeders, *OP* omnivores and predators

[b] *CT0* conventional tillage system with natural temperature, *CT1* conventional tillage system with warming, *NT0* no-tillage system with natural temperature, *NT1* no-tillage system with warming

August level; the diversity in NT with the warming treatment decreased in September.

No significant effects were found for any of the functional indices due to warming in general. However,

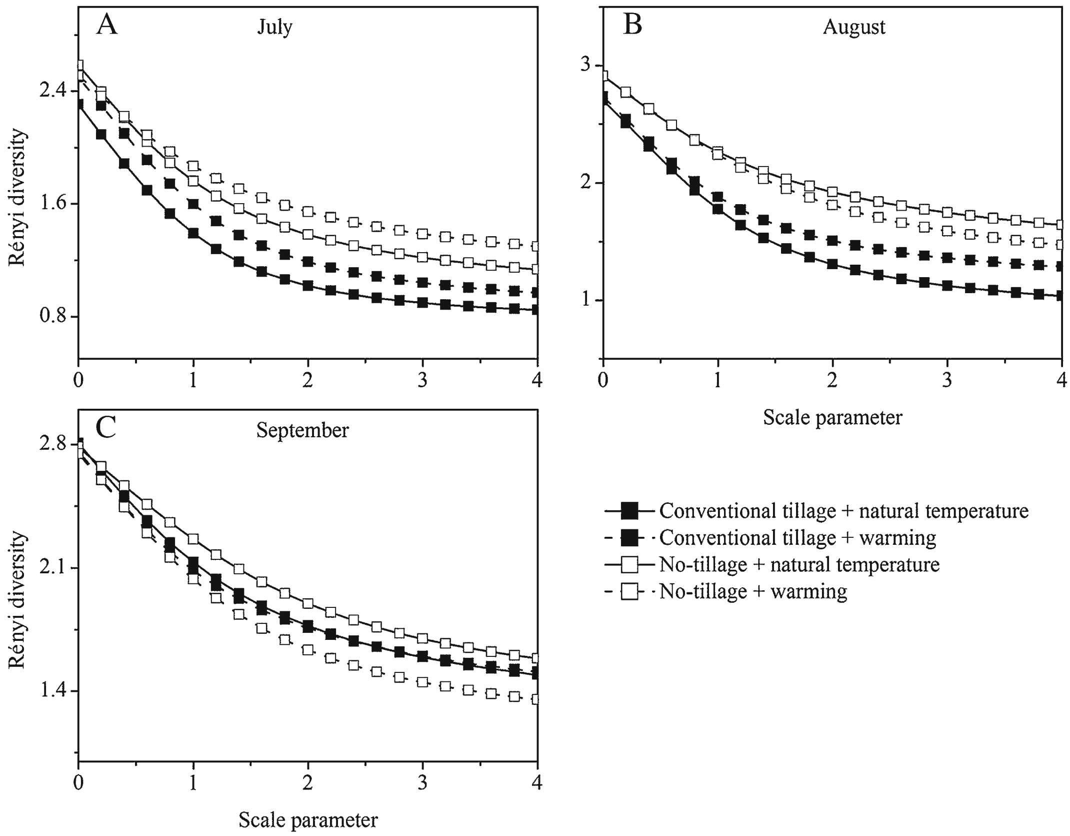

Fig. 2 Diversity ordering of the nematode communities using Rényi's diversity index family in the different treatments in July (**a**), August (**b**), and September (**c**) (mean of three replicates)

the interaction effect of warming and date on MI25 was significant (Table 1). In September, warming significantly reduced MI25. The tillage system significantly increased MI25 and SI, but reduced WI in NT (Table 1, Table 3). Despite monthly fluctuations in some of the indices, MI25 and SI increased, whereas WI decreased with the sampling date.

The CCA diagram indicated that the species-environment correlations were 0.873 for axis 1 (eigenvalue = 0.104) and 0.830 for axis 2 (eigenvalue = 0.062), which together explained 22.9 % of the total variance in the species data (Monte Carlo permutation tests: P=0.002). The total nitrogen and organic matter content were both quite closely associated with axis 1 and warming with axis 2. The directions of total nitrogen and organic matter content indicate the preferences of some nematode genera, e.g., *Prismatolaimus* and *Pratylenchus,* with regard to these variables. Such genera as *Tylenchus* and *Thornia* were associated with high soil moisture, and such genera as *Ethmolaimus* and *Filenchus* were relatively more abundant in the warmed plots than in the control plots. Tillage was the most important variable explaining the variations in nematode community composition between the two systems. *Tripyla* was relatively more abundant in NT, whereas *Nothotylenchus* was more abundant in CT (Fig. 3).

Discussion

Experimental effects on soil properties

Previous studies have reported higher soil temperature and lower soil moisture in CT than NT due to differences in residue retention on the soil surface being higher in NT (Dendooven et al. 2012; Shinners et al. 1994). Dendooven et al. (2012) studied a long-term (since 1991) tillage experiment and found that soil temperature was 1.8 °C higher for CT without residue cover than NT which had residue cover. Indeed, crop

Table 3 Functional indices (average ± S.D.) of nematodes communities in the different treatments from July to September

	CT0	CT1	NT0	NT1
MI	2±0.12	2.02±0.05	2.02±0.29	2.04±0.18
PPI	2.66±0.29	2.55±0.3	2.63±0.29	2.62±0.28
MI25	2.07±0.06	2.05±0.04	2.21±0.2	2.14±0.11
PPIMI	1.33±0.18	1.26±0.14	1.33±0.3	1.28±0.14
WI	16.72±20.85	11.17±9.62	3.71±2.2	4.31±3.24
NCR	0.66±0.18	0.69±0.12	0.81±0.08	0.71±0.18
EI	27.73±9.27	24.88±6.65	24.8±11.09	25.92±9.83
SI	9.4±7.87	7.42±4.65	23.41±17.52	18.48±13.02

CT0 conventional tillage system with natural temperature, *CT1* conventional tillage system with warming, *NT0* no-tillage system with natural temperature, *NT1* no-tillage system with warming

MI maturity index, *PPI* plant parasite index, *MI25* maturity index of cp2-5 nematodes, *PPIMI* the ratio of PPI to MI, *WI* Wasilewska index, *NCR* nematode channel ratio, *EI* enrichment index, *SI* structure index

residue left on the soil surface isolates the soil from increased atmospheric temperature and reflects solar radiation (Shinners et al. 1994). When subjected to equal radiation from infrared heaters, the soil temperature did not increase equally between these two tillage systems in the present study. The increase in NT was smaller than in CT, possibly because of the mulch covering the soil surface in NT. The results suggest that, in the future of global warming scenario, NT has the potential to balance the effects of global warming on soil temperature.

Soil moisture is an important factor relevant to the nematode community (Todd et al. 1999). In the present study, soil moisture was not found to change significantly due to warming or tillage and only declined with the sampling date. This consequence may be related to the frequent rainfall in the summer months, which leads to a high soil-water availability. Warming was

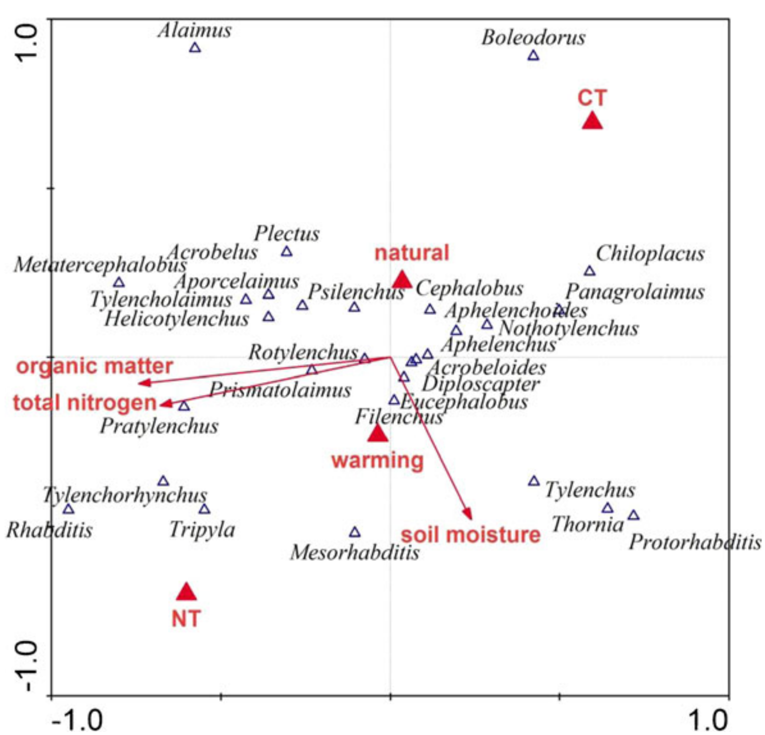

Fig. 3 Treatment-species biplot based on the results of canonical correspondence analysis (CCA). CCA for nematode communities in relation to soil physiochemical properties: soil moisture (%), total nitrogen (g/kg) and organic matter content (g/kg); and treatments: warming and natural temperature ('natural'), conventional tillage ('CT') and no-tillage ('NT') (species weight >5 %). The species-environment correlations were 0.873 for axis 1 (eigenvalue = 0.104) and 0.830 for axis 2 (eigenvalue = 0.062), which together explained 22.9 % of the total variance in the species data

found to increase the total nitrogen content, regardless of the tillage system. One reason may be that increased temperature directly promotes nutrient cycling by increasing the soil and litter decomposition rates, net N mineralization and N cycling through the litter (Ruess et al. 1999b). We found that NT had higher amount of total nitrogen and organic matter content than CT, consistent with other studies regarding the effects of NT on soil properties (Cline and Hendershot 2006; Holland 2004). In NT, warming significantly increased the amount of organic matter content, though no significant effect was found for CT. The effects of warming on the soil organic matter content appeared to be more pronounced in NT than CT.

Warming effects on nematodes

Several studies have demonstrated that warming could alter the soil nematode abundance or diversity. For example, Simmons et al. (2009) found that warming in Antarctic dry valleys could significantly reduce soil nematode populations, and these authors suggested that warming effects were both direct and indirect through alterations in the species-specific habitat suitability for the soil biota. In the present study, the abundance of nematodes in NT and CT had no apparent response to warming, which may relate to the extent of temperature elevation. Many studies have been conducted in grassland ecosystems or relatively unmanaged ecosystems, whereas our experiment was conducted in a temperate cropland ecosystem. There are several studies showing that the nematode communities in managed ecosystems and unmanaged ecosystems are likely to be different due to the application of fertilizer and irrigation and the tillage pattern in managed ecosystems. Therefore, the response of nematodes to warming should be considered on a case by case basis. Farming practices are likely to be more important factors influencing nematode abundance than warming in cropland.

Indices derived through nematode faunal analysis provide indicators of the disturbance of the soil environment and the condition of the soil food web (Ferris et al. 2001). No significant responses of nematode density or community parameters to warming were found in our experiment, indicating that warming had no apparent effect on the nematode community structure. A diversity profile analysis showed that warming increased the diversity of the nematode communities in both of the tillage systems early in the maize growing season. Studies conducted in other ecosystems have reported positive effects of warming on nematode diversity (Bakonyi et al. 2007). Soil temperature could act as a driving force for nematode community organization in summer months (Bakonyi et al. 2007). Differences occur among the thermal preferences of different nematode genera. Increases in diversity may be a result of the adaption of nematodes to warming condition. The diversity in all treatments increased with the date. The diversity in NT responded to warming differently from that in CT. Specifically, the diversity in NT declined due to warming in September. Moreover, warming reduced the MI25 in NT in September. The decreasing MI25 in NT showed that the decreasing diversity appeared to be due to an increase in opportunist nematodes (Bongers 1990). We deduced that the accumulation of organic matter in NT promoted opportunist nematodes, increase in number more rapidly than persister species in response to the increased microbial activity caused by the addition of organic matter (Bongers and Ferris 1999). Consequently the proportion of persister nematodes decreased. As a result, the diversity in NT with the warming treatment ultimately declined.

Tillage effects on nematodes

Tillage practices can alter soil properties and the nematode community. For example, the total C and N were higher in NT than in CT; nematode densities were greater or lower after tillage in some studies (Rahman et al. 2007; Sanchez-Moreno et al. 2006). Our results showed that the total nematode density decreased under a long-term no-tillage system, with the fungal feeder density decreasing. Indeed, the dominant genus, *Aphelenchoides* (fungal feeders), was negatively affected by NT. However, another study found that the density of fungal feeders increased in NT (Okada and Harada 2007), an observation that was contrary to our observations. In other studies, bacterial feeders and fungal feeders were stimulated by tillage and reduced by intermittent fallow (Sanchez-Moreno et al. 2006). The discrepancy may relate to many factors, such as soil type and geographic region. General patterns may be discerned if we focus on the response of specific taxa or functional guild.

It has been reported that nematode communities show higher diversity in NT than CT (Freckman and Ettema 1993; Zhang et al. 2012), and our results confirm this trend. The diversified communities in NT systems may be related to an increase in omnivores and predators. Several K-strategy nematodes, namely, *Eudorylaimus*, *Tylencholaimus,* and *Tripyla*, were relatively more abundant in NT than CT. Furthermore, the microhabitat, organic matter accumulation and slight disturbance of the soil conditions in the NT plots were most likely responsible for the increase in diversity because these factors may favor the presence of diverse nematodes. Tillage practices can strongly influence nematode assemblages and the soil food web (Sanchez-Moreno et al. 2006). In our experiment, tillage had an effect on functional indices, e.g., MI25, WI, and SI, which characterize nematode communities in relation to the soil ecosystem status and function. MI25 and SI were greater in NT than in CT, consistent with other studies (Lenz and Eisenbeis 2000; Okada and Harada 2007). These results support that an NT system develops an undisturbed soil system and a structured food-web. The lower WI in NT than CT can be interpreted by the decreased microbe feeder density in NT. It suggested that CT had a higher level of soil health than NT.

Conclusions

The present study indicated that increased temperature enhanced the nematode diversity in both the CT and NT systems during the early growing season of maize; in contrast, the diversity in NT was reduced due to warming in the late growing season. However, warming caused no apparent effects on the nematode density or all functional indices. Tillage is an important factor influencing both soil properties and nematode communities. Compared to the CT system, the NT system results in distinct soil ecological characteristics, such as high total nitrogen and organic matter content, a large nematode community diversity, and a low density of fungal feeders. The results of this study suggest that future global warming with soil temperature increases of up to approximately 1 °C will have only small effects on the soil nematodes in NT and CT systems.

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