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Soil Nematode Responses to Crop Management and Conversion to Native Grasses

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Abstract: Soil nematode community response to treatments of three, four-year crop rotations (spring wheat-pea-spring wheat-flax, spring wheat-green manure-spring wheat-flax, and spring wheat-alfalfa-alfalfa-flax) under conventional and organic management, and native tall grass restoration (restored prairie) were assessed in June 2003, and July and August 2004. The research site was the Glenlea Long-term Rotation and Crop Management Study, in the Red River Valley, Manitoba, established in 1992. The nematode community varied more with sample occasion than management and rotation. The restored prairie favored high colonizer-persister (c-p) value omnivores and carnivores, and fungivores but less bacterivores. The restored prairie soil food web was highly structured, mature and low-to-moderately enriched as indicated by structure (SI), maturity (MI) and enrichment (EI) index values, respectively. Higher abundance of fungivores and channel index (CI) values suggested fungal-dominated decomposition. Nematode diversity was low even after more than a decade of restoration. A longer time may be required to attain higher diversity for this restored fragmented prairie site distant from native prairies. No consistent differences were found between organic and conventional management for nematode trophic abundance, with the exception of enrichment opportunists of the c-p 1 group which were favored by conventional management. Although EI was lower and SI was higher for organic than conventional their absolute values suggested decomposition channels to be primarily bacterial, and fewer trophic links with both management scenarios. A high abundance of fungivores in the rotation including the green manure indicates greater fungal decomposition.
Key words: nematode diversity, organic management, prairie restoration, soil food web.

Nematodes represent many trophic components of the food web (Yeates et al., 1993) and play essential roles in ecosystem functioning (Ingham et al., 1985; Ferris and Bongers, 2006). Nematode communities are sensitive to change in environmental conditions due to natural or anthropogenic causes and are therefore considered useful bioindicators for soil health assessment (Neher and Olson, 1999; Yeates and Bongers, 1999). Colonizer-persister (c-p) values of nematode taxa ordinated on a 1-5 scale based on r-k life-history characteristics are useful in interpreting the trophic status of the soil food web in different habitats (Bongers, 1990). Maturity index calculations based on these taxa rankings have been widely used to describe the effects of different crop management practices on the soil food webs (Bongers and Ferris, 1999; Porazinska et al., 1999). Further, nematode faunal analysis based on the relative weighted abundance of c-p classes provides a quantitative measure of the nematode community structure and the probable condition of the soil food web (Ferris et al., 2001). The analysis includes calculation of indices of food web enrichment (EI), structure (SI) and channel index (CI) which provides information about belowground processes. The EI indicates the response of primary decomposers (bacteria and fungi) to available resources, SI indicates prevalence of trophic linkages in the soil food web, and CI provides prevalent decomposition channels in the soil food web.

Synthetic fertilizers, pesticides, and herbicides are important inputs in conventional agricultural systems which can impact nematode community composition in different ways. For example, fertilizer application in cultivated soils decreased omnivore and fungal-feeding nematodes (Sohlenius and Wasilewska, 1984; Sohlenius and Boström, 1986) but increased both plant-parasitic and bacterial feeding nematodes (Sohlenius and Boström, 1986). Yardim and Edwards (1998) found adverse effects of insecticide applications on the abundances of bacterivores and fungivores while plant-parasites were favoured compared to an untreated control. Tenuta and Ferris (2004) demonstrated in solution studies that high c-p (3-5) but not low c-p value (1-2) nematodes were killed from low concentrations of ammonium fertilizer.

Organic farming practices do not rely on the application of synthetic inputs and soil fertility is managed through suitable crop rotation and cover crops, supplemented with animal and crop wastes or green manures (Clark et al., 1999). Organically managed soils posses greater microbial activity and bacterial feeding nematodes than those managed with conventional practices (Bulluck et al., 2002; Briar et al., 2007). Abundance of fungal- and bacterial-feeding nematodes tend to increase in organic management systems (Freckman, 1988; Griffiths et al., 1994), presumably because prey, fungi and bacterial numbers increase after application of organic amendments (Bongers and Ferris, 1999; McSorley and Frederick, 1999). In addition, other soil management practices such as tillage, irrigation and crop rotation, common to both organic and conventional management, may affect the soil ecosystem by changing the microbial and nematode trophic structure (Parmelee and Alston, 1986; McSorley and Gallaher, 1994; López-Fando and Bello, 1995; Yeates et al., 1999; Bouwman and Arts,

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2000; Fu et al., 2000; Berkelmans et al., 2003; Wang et al., 2004). Berkelmans et al. (2003) observed that the increase in high c-p value nematodes from 12 years of organic management was destroyed by intensive tillage. Organic systems containing annual crops rely on frequent tillage events to reduce weeds. It is unclear if this frequent tillage negates the promotion of nematode and food web biodiversity with organic management.

Post soil disturbance (tillage, synthetic inputs), nematode communities are dominated by fast-growing, r-strategist bacterivores that, over time, transform to a more diverse community including slower-growing higher c-p (2 and 3) value bacterivores and fungivores and, ultimately, even higher c-p (4 and 5) omnivore and carnivore nematodes, once the level of disturbance is minimized or eliminated (Yeates et al., 1999; Fu et al., 2000). In previous studies, application of nematode community and faunal analysis comparing organic and conventional farming systems was done for commercial fields with different crop management histories (Neher, 1999; Neher and Olson, 1999).

Nematode community and faunal analysis has been used to assess soil food web responses to agroecosystem management in temperate, cool winter, and warm summer climate areas (Ekschmitt et al., 2001; Viketoft, 2007; Háněl, 2008). At present, nematode faunal analysis has not been applied to determining the responses to agroecosystem management in a temperate continental climate with short, very warm summers and long, very cold winters such as the Red River Valley of central North America at the eastern edge of the Canadian Prairies. The Red River Valley is a 11,500,000 ha region drained by the Red River (a.k.a. the Red River of the North) in North Dakota and Minnesota to Manitoba with clay soil.

Prairies are rich in nematode diversity (Todd et al., 2006) and posses the ability to provide ecosystem services such as pest regulation, prevention of nutrient losses and green house gas emissions compared to agricultural systems (Buyanovsky et al., 1987; Culman et al., 2010; Glover et al., 2010). Studies done in the past lacked an undisturbed control, such as tall grass prairie, established in close proximity as part of the same experimental setup for comparisons with crop managements systems. Moreover, there has been a lack of characterization of nematode communities following the reversion of cropland to restored prairie, especially in a northern, cold continental climate. It is uncertain if upon conversion of cultivated land to undisturbed grasslands, it can regain richness. The main objectives of this study were to determine soil nematode community responses to long-term crop management and prairie restoration using a replicated field plot design.

Materials and Methods

Study site description and treatments: This research was conducted at the Glenlea Long-Term Crop Rotation and Management Study site established in 1992, it is Canada's oldest organic-conventional management comparison study. The site is located at the University of Manitoba, Glenlea Research Station, 20 km south of Winnipeg, MB (N 49, 39, 0/W 97, 7, 0). The soil is a Typic Hapludert of Red River or Scantenbury series (Michalyna, 1970). The texture of the soil is clay (9% sand, 26% silt, and 66% clay) with a pH of 7.4 and an organic matter concentration of 77g/kg. The climate for the site is temperate humid continental, having cold winters and warm summers. According to the climate normal database for the weather station at the Glenlea Research Station (Environment Canada 2011), January is the month averaging the lowest mean temperature (-18.5 °C) and July the warmest month (19.3 °C). Total sunshine in July averages 304 hours. Total precipitation averages 532 cm with 432 occurring as rain, and 100 as snow. The frost free period averages 122 days, beginning the last week of May and ending last week of September.

The experimental design of the study was a randomized complete block in a split plot arrangement with three replicates for crop rotation and management treatments. A treatment of restored native prairie (Restored Prairie) was also included in each replicate block. The main plot effect was the three crop rotation treatments as well as the restored prairie treatment. Crop rotations were spring wheat (*Triticum aestivum* L.)-pea (*Pisum sativum* L.)-spring wheat-flax (*Linum usitatissimum* L.) (WPWF), spring wheat-green manure (Fababean (*Vicia faba* L.))-spring wheat-flax (WGmWF) and spring wheat-alfalfa (*Medicago sativa* L.)-alfalfa-flax (WAAF). The split plot effect was crop management (conventional or organic). Under organic management, no fertilizers or pesticides were applied. Under conventional management, NPK fertilizers were applied to soil test recommendations (Manitoba Soil Fertility Guide) based on laboratory analysis of composite soil samples for each treatment and herbicides were applied at label rates based on economic thresholds. The size of each subplot was 4 by 25m and that for restored prairie being 25 by 25m. Flax and wheat were grown in 2003 and 2004, respectively.

The restored prairie was planted in 1992 to the native grasses *Andropogon gerardii* Vitman var. gerardii, *Sorghastrum nutans* L., *Panicum virgatum* L., *Agropyron smithii* Rydb., *Elymus lanceolatus* Scribn., and Smith Gould., and *Elymus trachycaulus* Link Gould ex Shinners, with the plots having been undisturbed and unharvested except for controlled burns in 1998 and 2002 to rejuvenate the vegetation.

Soil sampling: Soil samples from each plot were collected on three occasions, June 2003, and July and August, 2004. Fifteen soil samples were taken in a "W" pattern across each plot to a depth of 15 cm using a tube sampler (2.5 cm-diameter), with samples taken between the rows of plants and within the row of plants for the crop rotation treatments. The soil collected for a plot was mixed together to provide one sample for analysis. All samples were placed in sealed polyethylene bags, and placed in an ice chest immediately upon sampling. The soil samples were transported to the laboratory and stored at 4°C until processing. Nematodes were extracted and identified within a week of soil sample collection.

Nematode analysis: Nematode extraction, identification and enumeration were done as described by Forge and Tenuta (2008). Briefly, nematodes were extracted from 100 g soil using the Cobb sieving sugar/flotation method (Ingham, 1994) and numbers reported here per 100 g dry soil weight. The total number of nematodes in each sample was determined using a stereo microscope at 50-x magnification and the first 100 individuals were identified to genus/family level using a compound microscope at 100-400 x magnification using the taxonomic keys provided by Bongers (1994).

Soil food web analysis: All identified nematode taxa were assigned to a trophic group: bacterial- and fungal-feeder, omnivore, carnivore, root-associates and obligate plant-parasites (Yeates et al., 1993). Nematode genera were also assigned a colonizer-persister value (c-p value) (Bongers, 1990; Bongers and Bongers, 1998) and a functional guild (Ferris et al., 2001). Maturity index (MI) for free-living nematodes (all nematodes except plant-parasitic nematodes) was calculated from c-p values and abundance of the nematode taxa in each sample using the formula MI = $\Sigma \nu_i x f_i$, where ν_i is the c-p value of taxon i, f_i is the frequency of taxon i in a sample (Bongers, 1990; 1999). Enrichment (EI) and structure (SI) indices were calculated according to Ferris et al. (2001). The two indices allow quantitative measure of the nematode community structure and the probable condition of the soil food web. Basal components (b) of the food web (bacterial- and fungal-feeders in the c-p 2 guild) calculated as $b = \sum k_b n_b$ where k_b is the weighted constant for the guild (Ferris et al., 2001), and n is the number of nematodes in that guild. Enrichment (e) and structure (s) components were similarly calculated, using nematode guilds indicative of enrichment (bacterial-feeders of c-p 1, and fungal-feeders of c-p 2), and guilds supporting structure (bacterial-feeders of c-p 3-5, fungal-feeders of c-p3-5, omnivores of c-p 3-5, and carnivores of c-p 3-5). The EI was calculated as $100 \mathrm{x} e/(e+b)$, and the SI as $100 \mathrm{x}\ s/(s+b)$. Channel Index (CI), which provides an index of nature of decomposition, was calculated as 100 x (0.8 fungivores c-p 2 / (3.2 bacterivores c-p 1 + 0.8 fungivores c-p 2) where the coefficients are the ke enrichment weightings for the respective guilds (Ferris et al., 2001). Shannon diversity (H'), was calculated for nematode diversity, using the following formulae: *Shannon-Weiner Index* $H' = \sum Pi\ (ln\ Pi)$, where Pi is the proportion of genera ni in the nematode community n (Pielou, 1977).

Statistical analysis: Repeated measures analysis of variance (PROC GLM SAS Ver. 9.00, SAS Institute, Cary, NC) was performed on nematode taxa, trophic group abundance and food web indices using a split plot experimental design with rotation as the main, management as the split effect and sample occasion as source of the repeated measures. Mean comparison tests were performed to compare rotations and sample occasions only if the ANOVA results were significant at $P \leq 0.1$. Repeated measure ANOVA was also performed for comparing organic management across all rotations to the restored prairie treatment. To meet the requirements of normality (Ryan-Joiner test) and homogeneity of variance (Levene's test) nematode taxa and trophic group abundance was transformed as ln (x+1) prior to analysis.

Results

Response to crop management and rotation: A total of 35 nematode taxa as 33 genera and 2 families were identified from the soil samples over the study (Table 1). The most abundant taxa in the cropped treatments across sample days (6% or greater of average abundance of all taxa) were *Filenchus* (13%), *Eucephalobus* (11%), *Aphelenchus* and *Tylenchus* (10%), Rhabditidae, *Aphelenchoides*, and *Plectus* sp. 1 (8%), *Cephalobus* and *Pangrolaimus* (6%). Abundance of Rhabditidae and *Prismatolaimus* was higher ($P < 0.10$) in the conventional while *Tylencholaimus*, Dorylaimidae and *Xiphinema* were lower than in the organic management treatment (Table 1). *Aphelenchus* was favored the most ($P < 0.10$) by wheat-green manure-wheat-flax, *Psilenchus* and *Eudorylaimus* by the wheat-pea-wheat-flax and *Chiloplacus* by the wheat-alfalfa-alfalfa-flax rotation (data not presented).

Across cropped treatments and sample days, the relative abundance of trophic groups in decreasing order was bacterivores (40%), root associates (30%), fungivores (20%), and omnivores plus carnivores (5%). The relative abundance of obligate plant-feeders was 1% with organic management while absent in conventional management.

The abundance of trophic groups varied most with sample day than management and rotation (Table 2). Abundance of four of the six trophic groups varied significantly with sample day ($P < 0.05$). However, there was no apparent trend in the abundance on sample days for the four trophic groups. Bacterivores in c-p 1 class were marginally favored ($P = 0.06$) with conventional management (Table 2). Likewise, there was a weak ($P = 0.07$) difference in abundance of fungivores with the wheat-green manure-wheat-flax being higher than the wheat-pea-wheat-flax rotation (Table 2).

The soil food web indices including EI and SI varied most with sample day ($P = 0.001$) but also with management ($P = 0.01$) (Table 3). CI varied only with sample

TABLE 1. Mean abundance[a] (±1SE) of nematode individuals (per 100 g dry soil) for three sample occasions for the crop managements and restored prairie treatment. Values for conventional and organic managements are for across the three crop rotations. See text for guild descriptions.

Nematode		Treatment		
Family	Genera (guild)	Conventional (n=27)	Organic (n=27)	Restored Prairie (n=9)
Tylenchidae	*Filenchus* (Ra-2)	152 ± 12	155 ± 18 B	425 ± 68 A
Cephalobidae	*Eucephalobus* (Ba-2)	147 ± 28	126 ± 15 A	16 ± 5 B
Tylenchidae	*Tylenchus* (Ra-2)	122 ± 19	112 ± 16	199 ± 102
Aphelenchoididae	*Aphelenchoides* (Fu-2)	95 ± 19	102 ± 19 A	24 ± 10 B
Rhabditidae	unknown (Ba-1)	106 ± 21 a	94 ± 26 bA	23 ± 11 B
Aphelenchidae	*Aphelenchus* (Fu-2)	139 ± 21	97 ± 14 A	38 ± 11 B
Plectidae	*Plectus* sp. 1 (Ba-2)	81 ± 11	96 ± 15 A	44 ± 23 B
Cephalobidae	*Cephalobus* (Ba-2)	71 ± 10	76 ± 12 A	21 ± 6 B
Panagrolaimidae	*Panagrolaimus* (Ba-1)	80 ± 25	56 ± 17 A	6 ± 3 B
Tylenchidae	*Psilenchus* (Ra-2)	37 ± 11	52 ± 14	27 ± 14
Tylenchidae	*Malenchus* (Ra-2)	33 ± 7	46 ± 10	32 ± 10
Leptonchidae	*Tylencholaimus* (Fu-4)	6 ± 2 b	28 ± 7 aB	638 ± 256 A
Qudsianematidae	*Eudorylaimus* (O-4)	15 ± 4	27 ± 6	40 ± 15
Prismatolaimidae	*Prismatolaimus* (Ba-3)	38 ± 9 a	21 ± 10 b	30 ± 11
Plectidae	*Plectus* sp. 2 (Ba-2)	12 ± 4	17 ± 6	7 ± 5
Dorylaimidae	Unknown (O-4)	7 ± 3 b	14 ± 4 a	6 ± 5
Cephalobidae	*Acrobeles* (Ba-2)	2 ± 1	11 ± 4	5 ± 3
Cephalobidae	*Cervidellus* (Ba-2)	6 ± 2	10 ± 4 A	0 ± 0 B
Hoplolaimidae	*Helicotylenchus* (Pp-3)	1 ± 1	9 ± 4	50 ± 35
Cephalobidae	*Chiloplacus* (Ba-2)	13 ± 5	7 ± 3 A	0 ± 0 B
Aporcelaimidae	*Aporcelaimus* (O-5)	1 ± 1	7 ± 3	11 ± 6
Aphelenchidae	*Paraphelenchus* (Fu-2)	8 ± 4	6 ± 3	1 ± 1
Longidoridae	*Xiphinema* (Pp-5)	0 ± 0 b	4 ± 2 aA	0 ± 0 B
Leptonchidae	*Dorylaimoides* (O-4)	1 ± 1	4 ± 2	7 ± 5
Thornenematidae	*Ecumenicus* (O-5)	9 ± 4	4 ± 2	12 ± 6
Thornenematidae	*Mesodorylaimus* (O-5)	3 ± 3	2 ± 1 B	10 ± 7 A
Actinolamidae	*Discolaimus* (Ca-4)	<1 ± <1	2 ± 1	0 ± 0
Dorylaimidae	*Dorylaimus* (O-5)	1 ± 1	2 ± 1	5 ± 5
Mononchidae	*Clarkus* (Ca-5)	3 ± 1	1 ± 1	23 ± 9 A
Cephalobidae	*Acrobeloides* (Ba-2)	0 ± 0	<1 ± <1	0 ± 0
Mononchidae	*Mononchus* (Ca-4)	0 ± 0	<1 ± <1	0 ± 0
Dolichodoridae	*Tylenchorhynchus* (Pp-3)	0 ± 0	<1 ± <1	0 ± 0
Paratylenchidae	*Paratylenchus* (Pp-2)	0 ± 0	<1 ± <1	0 ± 0
Hoplolaimidae	*Hemicycliophora* (Pp-3)	0 ± 0	0 ± 0 B	9 ± 7 A
Panagrolaimidae	*Panagrobelus* (Ba-1)	4 ± 3	0 ± 0	0 ± 0
Alaimidae	*Alaimus* (Ba-4)	6 ± 3	0 ± 0	0 ± 0

[a] Lower case letters indicate significant differences between the two crop managements (conventional vs. organic) while capital letters indicate significant differences between restored prairie and organic management treatment at $P < 0.1$.

days but not with management ($P > 0.1$). No differences were observed for nematode diversity among the management scenarios. The EI was highest on June 2003 which corresponded to the lowest MI of the sample days. The SI was highest on July 2004 and lowest on Aug 2004. CI was highest in August 2004 and lowest in June 2003. The MI and SI were significantly higher in the organic while EI was lower than the conventional management. Plotting EI versus SI revealed conventional management exhibiting majority of data points in the range of enriched-highly enriched but low structured, whereas majority of the data points for the organic management scored low enriched-moderately enriched and low structured-structured soil food web.

Response to prairie restoration: Fewer taxa were obtained in the soil samples collected from restored prairie with a total of 26, of which 23 were genera and 2 were families over the study (Table 1). Bacterivore genera including *Panagrobelus*, *Acrobeloides*, *Cervidellus* and *Chiloplacus* and *Alaimus* were not observed in the restored prairie treatment. *Mononchus*, *Paratylenchus* and *Xiphinema* of low abundance with organic management were also not present in the restored prairie. Further, the restored prairie was dominated by fewer taxa. The highest relative abundance of taxa across sample days was *Tylencholaimus* (37%), *Filenchus* (25%), and *Tylenchus* (12%). The other taxa had relative abundance no greater than 3%. Rhabditidae, *Panagrolaimus*, *Cephalobus*, *Eucephalobus*, *Plectus* sp. 1, *Aphelenchoides* and *Aphelenchus* were lower ($P < 0.10$) in the restored prairie while *Tylencholaimus*, *Mesodorylaimus* and *Filenchus* were higher in restored prairie than with organic management. *Hemicycliophora* was observed in the restored prairie and not in organic management (Table 1).

Across sample occasions, the relative abundance of trophic groups in decreasing order was root-associates (44%), fungivores (34%), bacterivores (11%), omnivores

TABLE 2. Nematode trophic group abundance (± SE) for conventional and organic management and three crop rotations, and the restored prairie treatment. See text for rotation description.

		Nematode trophic group abundance per 100 g dry soil weight					
Rotation	Management	Bact. c-p1	Other Bact.	Fungivores	Omn. + Carn.	Obligate root-feeders	Root associates
WAAF	Conventional	234[a]	433	260	53	2	347
WAAF	Organic	190	524	247	93	12	341
WGmWF	Conventional	220	387	328	63	<1	340
WGmWF	Organic	167	303	305	55	2	356
WPWF	Conventional	119	323	155	50	0	351
WPWF	Organic	96	294	145	79	29	408
- - - -	Rest. Prairie	29	147	700	24	0	688
Averages							
Management	Conventional	191	381	248	55	<1	346
	Organic	151	374	233	76	15	368
Rotation	WAAF	212	478	254 AB	73	7	344
	WGmWF	193	345	317 A	59	2	348
	WPWF	107	309	150 B	64	15	379
Sampling	June 03	393 a	332	294 a	86 a	4	298 b
	July 04	71 b	434	186 b	91 a	8	332 ab
	Aug 04	49 b	366	240 ab	20 b	12	442 a
ANOVA							
Management & Rotation[b]	*df*						
Management (M)	1	0.06	NS	NS	NS	NS	NS
Rotation (R)	2	NS	NS	0.07	NS	NS	NS
Sampling (S)	2	0.001	NS	0.03	0.001	NS	0.05
R x M	2	NS	NS	NS	NS	NS	NS
S x M	4	NS	NS	NS	NS	NS	NS
Restored Prairie & Organic management[c]							
Treatments (T)	1	0.007	0.006	0.01	0.03	NS	0.04
Sampling (S)	2	0.006	0.01	0.002	NS	NS	NS
T x S	2	NS	NS	0.01	NS	NS	NS

[a] Values shown are the average of three replicates and three sampling times.
[b] Includes three rotations and two management treatments (conventional and organic).
[c] Includes restored prairie and organic management only. Capital letters to the right of mean values in columns indicate significant differences between the crop rotations while lower case letters indicate significant differences between sample occasions. NS= not significant $P > 0.1$.

plus carnivores (8%), and obligate plant-feeders (4%) of the total nematode abundance.

Sample occasion effect was significant ($P < 0.05$) for bacterivores and fungivores but not for other trophic groups (Table 2). Abundance of bacterivores in c-p 1 class ($P = 0.007$) and other bacterivores c-p2-4 was lower ($P < 0.006$) in the restored prairie while fungivores ($P = 0.01$), carnivore plus omnivore ($P = 0.03$) and root associates ($P = 0.04$) were higher than in the organic management treatment (Table 2). No differences ($P > 0.1$) were observed for the obligate plant-feeders.

The restored prairie had higher MI ($P = 0.001$) and SI ($P = 0.001$), while EI was marginally lower ($P = 0.09$) and *H'* was significantly lower ($P = 0.001$) than the organic management (Table 3). Sample occasion x management interaction was weakly significant ($P = 0.07$) for MI but not EI, SI, CI and *H'*. Plotting of EI versus SI revealed low-moderately enriched but highly structured soil food web (Figure 1).

Discussion

The nematode community in the restored prairie treatment had fewer genera than the adjacent cropping system. This contrasts with other studies where high nematode diversity has been reported from prairie landscapes (Todd, 1996; DuPont et al., 2010; Cullman et al., 2010). General trend of nematode community in terms of diversity and trophic group abundance in the cropping systems at the study site were similar to those of other agricultural systems and regions (Freckman and Ettema, 1993; Neher and Campbell, 1994; Neher, 1999)). Nematode abundance varied over the sampling time across the management and rotation treatments. However, no apparent trend of nematode community over the sample occasions precludes establishing any cause and effect relationship for sample time.

Prairie restoration: The nematode assemblages of native prairie lands are characterized by low abundance of bacterivores and correlate with low nutrient enrichment (Todd, 1996; Todd et al., 1999; Todd et al., 2006). Our study results showed an agreement with this pattern. Both total abundance and the relative abundance of bacterivores in the restored prairie treatment were lower compared to cropping management treatment. The relative abundance of bacterivores was only 11% as opposed to 40% in the cropping management. In particular c-p1 enrichment opportunists contributed little

TABLE 3. Nematode community indices (MI: maturity; EI: enrichment; SI: structure; CI: channel and *H'*: Shannon diversity index) for conventional and organic management and, three crop rotations and a restored prairie. See text for rotation description.

Rotation	Management	Nematode indices				
		MI	EI	SI	CI	*H'*
WAAF	Conventional	2.06[a]	59	40	28	2.39
WAAF	Organic	2.14	52	45	33	2.45
WGmWF	Conventional	2.03	54	34	37	2.39
WGmWF	Organic	2.11	51	37	54	2.41
WPWF	Conventional	2.13	52	43	36	2.38
WPWF	Organic	2.31	51	56	30	2.41
- - - -	Restored Prairie	3.40	46	92	50	1.74
Averages						
Management	Conventional	2.08	55	39	34	2.39
	Organic	2.20	50	47	39	2.42
Rotation	WAAF	2.10	56	42	30 B	2.42
	WGmWF	2.07	52	35	46 A	2.41
	WPWF	2.22	52	49	33 B	2.39
Sampling	June 03	1.89 c	72 a	40 b	18 c	2.33
	July 04	2.36 a	45 b	57 a	38 b	2.45
	Aug 04	2.14 b	43 b	30 c	53 a	2.43
ANOVA						
Management & Rotation[b]	*df*					
Management (M)	1	0.01	0.01	0.01	NS	NS
Rotation (R)	2	NS	NS	NS	0.09	NS
Sampling (S)	2	0.001	0.001	0.001	0.001	NS
R x M	2	NS	NS	NS	NS	NS
S x M	4	NS	NS	NS	NS	NS
Restored Prairie &Organic management[c]						
Treatments (T)	1	0.001	0.09	0.001	NS	0.001
Sampling (S)	2	0.002	0.001	NS	0.001	NS
T x S	2	0.07	NS	NS	NS	NS

[a] Values shown are the average of three replicates and three sampling times.
[b] Includes three rotations and two management treatments (conventional and organic).
[c] Includes restored prairie and organic management only. Lower case letters to the right of mean values in columns indicate significant differences between sample occasions. NS= not significant $P > 0.1$.

to the total abundance of bacterivores in the restored prairie treatment. Correspondingly nitrogen concentration assessed in the restored prairie soil samples was also lower than the cropping management treatments (Welsh et al., 2009). This may be an indication of the system recovery after restoration of an agricultural land to native prairie tall grasses.

Restored prairie treatment favored root associates (Tylenchidae) the most and these constituted a greater proportion of the total than all other trophic groups. Although root associated nematodes are common with prairie grasses (Todd, 1996; Todd et al., 1999), their feeding habits probably vary; as an aggregate they are considered either root hair or fungal feeders (Yeates et al., 1993; Okada et al., 2002). Perennial prairie grasses have deeper roots with more extensive root hairs than the crop plants (Glover et al., 2010), which may have supported higher numbers of root associates by providing more feeding sites. Likewise fungivore/s in this group may have responded to the availability of greater food resources as evident from the higher percent of arbuscular mycorrhizae fungi observed on the prairie grass root system at the same study site (Welsh, 2007). We speculate that the combination of factors favored these nematodes in the restored prairie. Root hair feeder/s belonging to this group are not expected to cause measurable damage to the plants, rather have

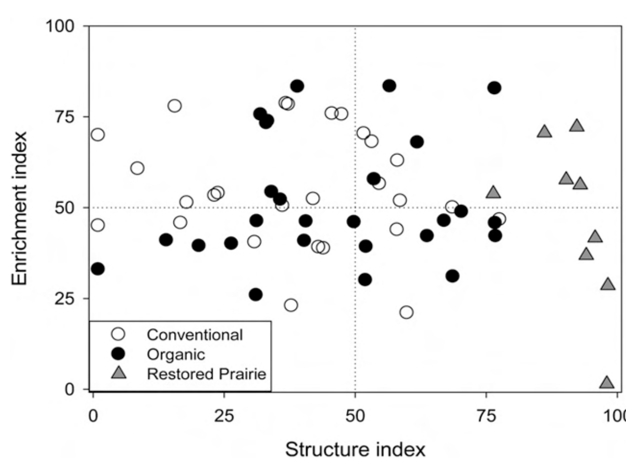

FIG.1. Comparison of nematode food web enrichment and structure conditions in conventional and organic managements, and restored prairie treatment. Data points represent enrichment and structure index scores for all three sampling times.

been reported to increase C and N mineralization, microbial activity and plant growth (Bardgett et al., 1999). As a fungal feeder/s it would result in lending more weight to the inference of slow fungal-dominated decomposition channels. Either way, high occurrence of root associates suggests them as an ecologically significant nematode group in regulating the restored prairie soil food web in this cold continental climatic condition.

Greater c-p value nematodes are generally associated with low stress and undisturbed environments (Bongers, 1999; Ferris et al., 2001). Higher buildup of greater c-p (3-5) value nematodes in the restored prairie treatment resulted in higher SI and MI values suggesting more structured food webs than those supported by the cropping system. Both lack of synthetic applications and physical disturbances in the restored prairie treatment likely attributed to the greater buildup of higher c-p value nematodes.

The EI is a measure of the abundance of enrichment opportunists relative to the abundance of basal taxa. It quantifies the level of resource enrichment and serves as an indicator of soil productivity (Ferris et al., 2001). A typical undisturbed natural system like prairie grasslands would have a soil food web exhibiting low EI while agricultural systems possess high EI values (Ferris et al., 2001). Range of EI values indicated low-moderately enriched soil food web in the Restored Prairie treatment (Figure 1). Higher EI values than expected in some samples only resulted due to correspondingly low abundance of basal taxa, though the c-p 1 bacterivores (enrichment indicators) were low in numbers. In addition, higher abundance of fungivores observed in the restored prairie soil sample implies fungal decomposition and less bacterial decomposition pathways. Considered together, the restored prairie treatment exhibited a soil food web with low enriched conditions and greater contribution of fungal-decomposition pathways. Slow decomposition posses potential benefits of nutrient conservation by preventing excessive N leaching and losses to denitrification (Glover et. al., 2010). Nematode community assessment however, provides only putative evidence of the benefits of converting crop land to tall grasses, further work will be required for quantification of nutrient losses from the site.

Prairie landscapes are considered not only rich in nematode diversity but also comprised of unique nematode genera rarely observed in agricultural systems (Todd et al., 2006; Culman et al., 2010). No distinct genera (except for *Hemicycliophora*) were observed, but rather a rapid decline in the diversity was noted with a major influence on several bacterivores and obligate plant-feeders. Secondly, there was a rapid shift in the relative abundance of several taxa. For example Rhabditidae, *Panagrolaimus*, *Cephalobus*, *Eucephalobus*, *Plectus* sp. 1, *Aphelenchoides* and *Aphelenchus* were in low abundance, while *Tylencholaimus*, *Mesodorylaimus* and *Filenchus* were very high in abundance. Even though there was no external application of mineral fertilizers, shifts in major soil nutrients were observed in the restored prairie (Welsh et al., 2009). Soil phosphorus levels were unusually higher while N was lower than the adjacent cropping system. It appears that a switch in above ground vegetation from crop plants to tall grasses and/or changes in nutrient dynamics influenced the below ground nematode community. Responses of below ground communities to shifts in land use related to plant cover and soil properties has been discussed in other studies (Yeates 1991; Yeates and Bongers, 1999; Cadet et al., 2003). Further, it was likely that in our climatic condition the time lapse since restoration was not enough to attain higher diversity, possibly due to low migration of taxa from other native prairie locations to this restored fragmented prairie site, surrounded mainly by croplands (Yeates, 1991). Low nematode diversity, even after more than a decade of converting agricultural land to native prairie grassland, highlights the importance of native prairies especially when such landscapes have significantly shrunk in North America due to anthropogenic activities (Wolters et al., 2000; Todd et al., 2006).

Crop management effects: Abundance of c-p 1 bacterivores was marginally higher in the conventional than the organic management while no differences were seen for the abundance of other trophic groups. C-p 1 bacterivore nematodes are more opportunistic in response than other bacterivores to resource enrichment (Ferris et al., 2004). Higher number of c-p 1 bacterivores also translated to marginally higher EI values suggesting a soil food web to be slightly more bacterial dominated than the organic management. Application of external organic matter inputs such as manures and crop residues increases energy availability and leads to increase of c-p 1 bacterivores abundance in particular (Alon and Steinberger, 1999; Bulluck and Ristaino, 2002; Ferris et al., 2004). In the present study, crop managements did not differ in terms of application of external inputs of organic matter. Therefore, increase in opportunistic nematode taxa in the organic management was not expected. In contrast, synthetic fertilizer and herbicide applications in conventional management plots appeared to have enhanced the decomposition process and resulted in marginally higher abundance of c-p 1 bacterivores under this cold continental climate system.

Total abundance of omnivores plus carnivores did not differ among the managements, probably due to soil disturbances in both systems (Freckman and Ettema, 1993; Fiscus and Neher, 2002). However, higher numbers of c-p 4 fungivore (*Tylencholaimus*) and correspondingly lower abundance of basal taxa (c-p 2 value) translated to significantly higher SI and MI values in the organic than the conventional management. Structured systems as inferred from higher MI and SI values are expected to demonstrate top-down regulation and reduction in plant-parasitic nematode pressure (Sánchez-Moreno and Ferris, 2007). Lack of differences for omnivores plus carnivores and very low build up of obligate plant-feeders in both managements revealed no synchrony among predators and prey in our study results.

Although nematode classifications into trophic groups masked the differences, individual nematode genus/family comparisons revealed some differences among the managements. Conventional plots underwent both chemical (synthetic inputs) and mechanical disturbance (mainly tillage) while organic management had only mechanical disturbance. Some nematode genera are sensitive to chemical inputs but tolerant to mechanical disturbances while others could be sensitive or tolerant to both (Fiscus and Neher, 2002). Differences in disturbances among the managements would explain why selective nematode genera were favored by one management over the other in the present study.

Crop rotations did not affect nematode community except for fungivores and CI values being marginally higher in the rotation wheat-green manure-wheat-flax, than the other two rotations. Although contribution of bacterivores to nutrient mineralization is estimated to be higher than the fungivores (Ferris et al., 1996; Chen and Ferris, 1999; Okada and Ferris, 2001), simultaneously higher abundance of fungivores indicate slow decomposition with protection from nutrient leaching and availability for the next crop in rotation (Ferris et al., 2004). Similar benefit can be expected from having faba beans as a green manure crop in the rotation.

Of the factors examined, sample occasion resulted in the greatest variation in nematode community composition. Determination of the drivers of the variation caused by sample occasion was not possible with the undertaken three samplings. Future studies of management effects on nematode community composition should contain more sample occasions. Despite just three sample occasions, several responses in nematode community composition were observed with prairie restoration, crop management and rotation. The restored prairie soil food web was highly structured, mature and low-to-moderately enriched as indicated by structure (SI), maturity (MI) and enrichment (EI) index values, respectively. Both, high population of fungivores and low numbers of enrichment opportunist bacterivores suggested slow fungal-dominated decomposition channels at the restored prairie site with potential benefits of preventing nutrients losses. Despite being restored with tall grasses for about ten years, the restored prairie treatment lacks undisturbed prairie characteristics of even greater nematode diversity and species richness. A longer time span may be required to attain higher levels of nematode diversity for this restored fragmented prairie site surrounded by croplands. No consistent differences were observed between organic and conventional for the abundance of nematode trophic groups except for enrichment opportunist c-p 1 bacterivores marginally favored by the conventional management. Although EI was lower and SI was higher for organic than conventional management, their absolute values suggested decomposition channels to be primarily bacterial and relatively fewer trophic links with both management regimes. A high abundance of fungivores in the rotation including the green manure crop indicates greater fungal decomposition than the other two rotations.

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