RESEARCH/INVESTIGACIÓN

CHARACTERIZING NEMATODE COMMUNITIES IN CARROT FIELDS AND THEIR BIOINDICATOR ROLE FOR SOIL HEALTH

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ABSTRACT

Habteweld, A., D. Brainard, A. Kravchenko, P. S. Grewal, and H. Melakeberhan. 2020. Characterizing nematode communities in carrot fields and their bioindicator role for soil health. Nematropica 50:200-210.

Plant-parasitic nematodes (PPN) are known to reduce quality and yield of carrot (*Daucus carota* var. *sativus*). Efficient nematode management begins with identifying the predominant PPN present in a given field before taking any management decisions. The management decisions should also consider suppression of PPN and promotion of beneficial nematodes represented by bacterivores, fungivores, omnivores, and predators to improve soil health conditions. We selected four carrot fields suspected to have PPN problems in Mason and Oceana counties in Michigan, USA. The counties are located in the major carrot-producing regions of Michigan. These sites have not been previously sampled for nematode quantification. The objectives were to identify economically important PPN genera and to characterize nematode communities found at the study sites. We hypothesized that: (1) identifying the predominant PPN will help growers to implement appropriate management strategies to reduce economic loss, and (2) understanding the nematode community structure may indicate soil health condition of the study sites. The predominant PPN was root-lesion nematode (*Pratylenchus* spp.) at all the sites, suggesting appropriate management practices are required to reduce nematode densities and damage to carrots. We also found differences in overall soil health conditions among the study sites using nematode community structure as an indicator. The high abundance of root-lesion nematode in these carrot fields deserves the attention of growers, researchers, and extension agents.

Key words: Carrots, food web indices, lesion nematode, Maturity indices, *Pratylenchus*, soil health

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RESUMEN

Habteweld, A., D. Brainard, A. Kravchenko, P. S. Grewal, y H. Melakeberhan. 2020. Caracterización de la comunidad de nematodos en campos de zanahoria y su rol bioindicador de salud del suelo. Nematropica 50:200-210.

Los nematodos parásitos de plantas (PPN) son conocidos por reducir los rendimientos y calidad de la zanahoria (*Daucus carota* var. *sativus*). El manejo eficiente de nematodos inicia con la identificación de los PPN predominantes en un determinado campo antes de tomar alguna decisión de manejo. Las decisiones de manejo deben además considerar la supresión de PPN y la promoción de nematodos beneficiosos representados por bacterióvoros, fungívoros, omnívoros, y depredadores para mejorar las condiciones de salud del suelo. Seleccionamos cuatro campos de zanahoria con sospecha de tener problemas con PPN en los condados de Mason y Oceana en Michigan, USA. Los condados están ubicados en la región más productora de zanahoria en Michigan. Estos sitios no han sido previamente muestreados para cuantificación de nematodos. Los objetivos fueron identificar géneros de PPN económicamente importantes y caracterizar las comunidades de nematodos encontradas en los sitios de estudio. Se realizaron las siguientes hipótesis: (1) la identificación de los PPN predominantes ayudará a los productores a implementar estrategias de manejo apropiadas para reducir pérdidas económicas; (2) la comprensión de la estructura de la comunidad de nematodos puede indicar el estado de salud del suelo en los sitios de estudio. El PPN predominante fue el nematodo lesionador (*Pratylenchus* spp.) en todos los sitios, lo que sugiere la necesidad de prácticas de manejo apropiadas para reducir las densidades de nematodos y el daño en la zanahoria. Además, se encontraron diferencias en las condiciones generales de la salud del suelo entre los sitios de estudio, con el uso de la estructura de la comunidad de nematodos como indicadores. La alta abundancia de nematodos lesionadores en estos campos de zanahorias merece la atención de productores, investigadores y agentes de extensión.

Palabras clave: Zanahoria, índices de la red trófica, nematodo lesionador, índices de madurez, *Pratylenchus*, salud del suelo

INTRODUCTION

Carrot (*Daucus carota* var. *sativus*) production, including fresh market and processing carrots, is a nearly $800 million industry spanning over 35,000 ha in the United States (NASS-USDA, 2016). In 2018, Michigan produced 69 million kg of carrots worth $14.5 million, making Michigan the fourth highest fresh carrot-producing state in the United States (NASS-USDA, 2019). Plant-parasitic nematodes (PPN) are a major cause of carrot disease as they can cause stunting, galling, cracking, or forking of carrot roots, reduce water and nutrient uptake efficiency, and decrease crop growth (Wesemael and Moens, 2008; Grabau *et al*., 2017). PPN may also increase secondary infection of carrot roots by other pathogens such as fungi (LaMondia, 2006). Despite this high potential for economic loss caused by PPN, no nematode-resistant cultivars are commercially available and pesticide options are extremely limited due to Food Quality Protection Act-driven restrictions (Abawi and Widmer, 2000).

Although PPN are common problems in Michigan carrot-producing areas, there are few published works on PPN in carrot production fields. Northern root-knot (*Meloidogyne hapla* Chitwood, 1949), carrot cyst (*Heterodera carotae* Jones, 1950), root-lesion (*Pratylenchus penetrans* Cobb, 1917), pin (*Paratylenchus* spp. Micoletzky 1922) and stunt (*Tylenchorynchus* spp. Cobb, 1913) have been identified from Michigan carrot fields (Hausbeck, 2008; Grabau *et al*., 2017). Among the PPN, northern root-knot and carrot cyst nematodes were considered as the most damaging under Michigan conditions (Hausbeck, 2008).

Growers usually focus on managing PPN because of their negative impact on yield, neglecting beneficial nematodes. Nematodes are the most abundant multicellular organisms on the earth occurring at multiple trophic levels that contribute to the soil food web, and play key roles in other ecosystem services such as nutrient cycling and pest regulation (Bongers and Bongers, 1998; Ferris *et al*., 2001; Habteweld *et al*., 2018). Thus, nematode management should encompass suppression of PPN and enhancement of beneficial nematodes. This kind of nematode management strategy requires documenting and determining the PPN present in a given field. Investigating the association between PPN and nematode community and food web indices with on-farm practices could be useful to develop appropriate management strategies. This further enables growers to understand the impact of management practices on soil health and consequently the sustainability of their farming.

A total of four commercial carrot fields alleged to have PPN problems were selected for nematode identification. One of the fields was in Mason County and the other three were in Oceana County in Michigan. These counties are among the major carrot-producing regions in the State (Hausbeck, 2008). Generating such data should provide insight to growers, researchers, and county agents on potentially damaging PPN in these major carrot-growing areas. The overall goal of the present study was to identify the presence of economically important PPN genera and their abundance at the study sites. We also described the soil health conditions of the sites using nematode community analysis as an indicator.

MATERIAL AND METHODS

Field selection and soil sampling

The survey of the four carrot fields was conducted in September 2014. Field sizes ranged from 8 to 10 ha planted with a processing carrot cultivar 'Cupar'. All the fields were planted with mixed vegetables in the previous growing season. All the fields received 110-120 kg N/ha and 2.3 kg/ha oxamyl (active ingredient in Vydate). Each carrot field was divided into 2-ha sections for sampling. One composite soil sample containing 20 soil cores, 2.5 cm diam., 30 cm deep, was collected from each 2-ha section of the farms using a zig-zag sampling pattern. Each soil core was collected within 10 cm of the carrot root to increase chance of recovering PPN. We collected 5 composite soil samples from sites 1 and 4 that were 10-ha in area and 4 composite soil samples from sites 2 and 3 that were 8-ha in area. We also randomly collected 5 carrot roots from each 2-ha section (five 2-ha sections for sites 1 and 4, and four 2-ha sections for sites 2 and 3) and categorized them as marketable and unmarketable (stunt, fork, crack, or rotten carrots) following carrot grade standards (Anonymous, 1965). The composite soil and carrot root samples were transported to Agricultural Nematology Laboratory, Department of Horticulture, Michigan State University and stored at 5°C.

Nematode extraction, identification and enumeration

Within three days of sample collection, nematodes were extracted from 100 cm^3 of soil using a semi-automatic elutriator as described by Avendaño *et al*. (2003). The nematodes were fixed in triethanolamine-formalin (TAF) solution as described by Hooper (1986). Nematodes were enumerated and identified to the genus level following diagnostic keys by Bongers (1994) and the University of Nebraska-Lincoln nematode identification website (http:nematode.unl.edu/konzlistbutt.htm). Nematodes were assigned to PPN, bacterivore, fungivore, omnivore, or predator trophic groups according to Yeates *et al*. (1993) and Okada and Kadota (2003). A colonizer-persister (c-p) value was assigned according to Bongers and Bongers (1998).

Nematode community and food web analysis

Shannon-Weaver diversity (Shannon and Weaver, 1949) and Hill's diversity (Hill, 1973) were calculated to study nematodes' diversity. Maturity index (MI) of all non-plant parasitic nematodes of c-p 1 to 5 and MI for c-p 2 to 5 of non-plant parasitic nematodes (MI25) were calculated to study nematode community structure (Bongers, 1990). Separate plant-parasitic index (PPI) was calculated by including c-p 2 to c-p 5 PPN genera (Bongers, 1990). Soil food web enrichment index (EI), structure index (SI), basal index (BI), and channel index (CI) were calculated, and the soil food web condition of the sites were graphically described as a function of EI (indicator of nutrient availability) and SI (indicator of food web food web complexity) as described in Ferris *et al*. (2001). Nematode trophic group ratios such as fungivores-to-bacterivores (Freckman and Ettema, 1993) and decomposers-to-PPN (Wasilewska, 1994) were calculated to determine a predominant nutrient mineralization pathway. PPI/MI was also calculated as a measure of changes in the functioning of the soil ecosystem (Bongers *et al*., 1997).

Data analysis

One-way analysis of variance (ANOVA) was performed using the General Linear Model (GLM) in SAS vr. 9.3 (SAS Institute, Cary, NC). Dependent variables included the carrot quality category, abundances of nematode trophic groups, beneficial (non-PPN) and total nematodes, percentage of root-lesion nematode (RLN) in beneficial and total nematodes, nematode community and food web indices, PPI/MI, and trophic ratios. The independent variable was the carrot field site. The means for the dependent variables of each site were established from five and four 2-ha sections for sites 1 and 4 and sites 2 and 3, respectively. Nematode taxa and trophic group abundances were expressed on an absolute basis (number of nematodes in a taxon per 100 cm^3 of soil). Multiple comparisons among means were made with Fisher's protected Least Significant

Difference (LSD) Test. Prior to analysis, nematode population abundance was transformed to ln (x+1) to meet the assumptions of normality and equal variances, but untransformed arithmetic means are presented. The probability level $P < 0.05$ was regarded as significant.

RESULTS

Carrot quality

The randomly selected carrots were categorized based on their quality and whether they were marketable or unmarketable. Marketable carrot was significantly higher at sites 3 and 4 compared with sites 1 and 2, and at site 1 compared with site 2 (Table 1). Visually rotten carrots were also very common at site 2 compared with the rest of the study sites (Fig. 1). Stunted and cracked carrot roots were not detected in any of the sites.

Nematode genera present and their abundances

A total of 38 nematode genera comprised of 9, 16, 6, 6, and 1 PPN, bacterivores, fungivores, omnivores, and predators genera, respectively, were detected (Table 2). Total nematode abundance ranged from 35 to 203 nematodes/100 cm^3 of soil. The average abundance of PPN was 19, 44, 36, and 45 nematodes/100 cm^3 of soil at sites 1, 2, 3, and 4, respectively. Bacterivore abundance was 45, 44, 78, and 110 nematodes/100 cm^3 soil at sites 1, 2, 3, and 4, respectively. The abundance of fungivore was generally low with 6, 11, 9, and 11 nematodes/100 cm^3 of soil at sites 1, 2, 3, and 4, respectively. Abundance of omnivore was 10, 8, 4, and 2 nematodes/100 cm^3 of soil at sites 1, 2, 3, and 4, respectively.

Among the PPN, *Basiria*, *Cephalenchus*, and *Psilenchus* were detected at sites 1, 2, and 3. *Malenchus* was detected at sites 2 and 4. *Tylenchus* was detected at all the sites except site 2. A single *Xiphinema* and *Tylenchorynchus* were detected at sites 2 and 3, respectively. RLN was detected at all the sites. *Basiria*, *Cephalenchus*, *Malenchus*, *Psilenchus*, and *Tylenchus* were found at less than 4 nematodes/100 cm^3 of soil. On average, *Helicotylenchus* was detected at site 4 at an abundance of 4 nematodes/100 cm^3 of soil.

There was a significant difference in PPN among the study sites (Table 3). The abundance of PPN was significantly higher at site 4 compared with the rest of the sites. Similarly, bacterivore abundance was significantly higher at site 4 compared with sites 1 and 2. However, there was no significant difference in the abundances of fungivores, omnivores, and predators among the study sites. Beneficial (non-PPN) and total nematode abundances were significantly higher at site 4 compared with sites 1 and 2 (Table 3). Total nematode abundance was significantly higher at site 3 compared with site 1. The most abundant PPN was RLN representing 98, 99, 92, and 78% of total PPN at sites 1, 2, 3, and 4, respectively (Table 3). This percentage was significantly higher at sites 1, 2, and 3 compared with site 4. RLN was represented by 25, 42, 25, and 21% of the total nematode abundance at sites 1, 2, 3, and 4, respectively (Table 3).

Nematode diversity and maturity indices

There was no significant difference in nematode diversity among the study sites (Table 3). PPI was significantly higher at site 1 and compared with site 4. MI was significantly higher at site 2 compared with sites 3 and 4. MI was also

Table 1. Quality of randomly collected carrots (marketable vs. unmarketable) from the survey sites.

	Survey sites			
Carrot quality	1^x	2^y	3^y	4^x
Marketable	2.8 ± 1.1 b^z	0.0 ± 0.0 c	4.0 ± 1.1 a	4.2 ± 0.4 a
Unmarketable	2.2 ± 1.1 b	5.0 ± 0.0 a	1.0 ± 1.1 c	0.8 ± 0.4 c

^{x}Farm areas for sites 1 and 4 were 10-ha and a total of 25 randomly collected carrots (5 carrots from each 2-ha) were used to determine the quality. Values are means ± standard deviations.
^{y}Farm areas for sites 2 and 3 were 8-ha and a total of 20 randomly collected carrots (5 carrots from each 2-ha) were used to determine the quality. Values are means ± standard deviations.
^{z}Fisher's protected least significant difference ($P \leq 0.05$).

Figure 1. Carrot quality (Marketable vs. unmarketable (forked and rotten)) of randomly collected carrots at site 1 (A), site 2 (B), site 3 (C), and site 4 (D).

significantly higher at site 1 compared with site 4. MI25 was significantly higher at site 1 compared with sites 3 and 4. Similarly, MI25 was significantly higher at site 2 compared with site 4.

Food web indices, trophic ratios, and PPI/MI

None of the soil food web indices except SI were significantly different among the study sites (Table 3). SI was significantly higher at sites 1 and 2 compared with site 4. Overall, CI was low (<50%) at all the sites indicating a predominant bacterial decomposition pathway. The soil food web was diagnosed as maturing at sites 1 and 2 (Quadrant B), but disturbed at sites 3 and 4 (Quadrant B) (Fig. 2). There was no significant difference in fungivore-to-bacterivore ratio, but fungivore+bacterivore-to-PPN ratio was signify-cantly lower at site 2 compared with the rest of the sites (Table 3). PPI/MI was significantly lower at sites 1 and 2 compared with site 4, but significantly lower at site 2 compared with site 3.

DISCUSSION

The overall abundance of PPN, except RLN, was very low in the present survey. RLN was predominant, representing 78-99% of the total PPN abundance. In previous studies, *M. hapla*, *P. penetrans*, *H. carotae*, *Paratylenchus* spp., and *Tylenchorynchus* spp. were reported from Michigan carrot fields (Hausbeck, 2008; Grabau *et al*., 2017). However, Melakeberhan *et al*. (2007) did not report RLN from carrot fields in Michigan. RLN has been shown to cause serious damage on vegetables (LaMondia, 2006; Bao and Neher, 2011). The above-ground symptoms such as wilting and patches of poor growth observed during the survey and the greater carrot damage at site 2 (Table 1) were possibly associated with RLN, which represented 99 and 40% of PPN and total nematode abundances, respectively.

RLN is one of the most prevalent PPN worldwide with a wide host range (Castillo and Volvas, 2007; Bao and Neher, 2011). The damage threshold level for this nematode may vary with changes in weather conditions, crop cultivars, and other environmental factors (Sasser *et al*., 1974; Ferris, 1978). In some states, RLN abundance above 100 individuals/100 cm^3 of preplant soil is considered as a damage threshold level with potential yield reduction (Bao and Neher, 2011). In the present study, RLN abundance was between 7 to 60 individuals/100 cm^3 of soil. Unfortunately, the RLN abundance reported in the present study

Table 2. List of nematode genera from plant-parasitic, bacterivore, fungivore, omnivore, and predator trophic groups detected during the field survey. Numbers within brackets represent c-p values following Bongers and Bongers (1998).

Plant-parasitic	Bacterivores	Fungivores	Omnivores	Predators
Basiria (2)	*Eumonhystera (1)*	*Aphelenchoides (2)*	*Eudorylaimus (4)*	*Prionchulus 4)*
Cephalenchus (2)	*Mesorhabditis (1)*	*Aphelenchus (2)*	*Mesodorylaimus (4)*	
Malenchus (2)	*Panagrolaimus (1)*	*Ditylenchus (2)*	*Microdorylaimus (4)*	
Psilenchus (2)	*Rhabditis (1)*	*Filenchus (2)*	*Thonus (4)*	
Tylenchus (2)	*Acrobeles (2)*	*Diphterophora (3)*	*Aporcelaimellus (5)*	
Helicotylenchus (3)	*Acrobeloides (2)*	*Tylencholaimellus (4)*		
Pratylenchus (3)	*Cephalobus (2)*			
Tylenchorhynchus (3)	*Cervidellus (2)*			
Xiphinema (5)	*Chiloplacus (2)*			
	Eucephalobus (2)			
	Heterocephalobus (2)			
	Plectus (2)			
	Wilsonema (2)			
	Microlaimus (3)			
	Prismatolaimus (3)			
	Alaimus (4)			

cannot be compared with other threshold values because soil sampling was collected during carrot growth when most RLN were inside of the carrots. However, a relatively high RLN population at these sites suggest RLN could reach a threshold level and cause damage to carrots unless appropriate management strategies are implemented.

Previous studies demonstrated that a spring application of oxamyl is effective in suppressing RLN (Walters *et al*., 2009; Zasada and Walters, 2016). In the present study, oxamyl might not persist long enough to impact RLN until soil sampling time in the fall because of high temperatures during summer and fall months (Haydock *et al*., 2012). Because of the restrictions on broad-spectrum nematicides due to the Food Quality Protection Act and lack of nematode-resistant carrot cultivars, crop rotation with non- and/or poor-host, cover cropping, and compost amendments can be implemented as alternative nematode management strategies. Rotation to non-host crops can substantially reduce the PPN population density (Kimpinski and Sanderson, 2004; LaMondia, 2006), though this is difficult because of the wide host range of RLN (Bao and Neher, 2011). Cover crops such as white clover, saia oat, poly marigold, and sudangrass, in rotation or as green manure, reduced the number of RLN (LaMondia, 2006; Bao and Neher, 2011). Use of cover crops with suppressive effects to more than one PPN would have greater impact. Organic amendments such as animal manure and compost can also be effective at controlling diseases and PPN through the release of toxic compounds (Widmer *et al*., 2002), or by providing more suitable habitable environment for antagonists of nematodes (LaMondia *et al*., 1999).

The abundances of beneficial and total nematodes were higher at site 4 compared with sites 1 and 2 due to the high number of bacterivores. Bacterivores were more abundant in disturbed or nutrient enriched soils (Bongers, 1990; Bongers and Bongers, 1998). Disturbance/enrichment enhances microbial activity, and as a result, the abundance of enrichment opportunist bacterivores increases (Ferris *et al*., 2001). There was no difference in fungivores in the present study, but increased abundance of fungivores may occur when complex organic material becomes available in the soil, either through natural or anthropogenic processes, or when fungal activity is enhanced under conditions less favorable for bacterivores (Chen and Ferris, 2000). Overall abundances of omnivores and predators were low in the present study and did not show significant difference among the study sites. However, omnivore abundance was relatively greater at sites 1 and 2. Results of the present study was consistent with previous studies that omnivores and predators were generally less abundant in agroecosystems than in natural areas due to their greater sensitivity to nitrogen fertilizers, tillage, and pesticides (Fiscus and Neher, 2002; Nahar *et al*., 2006).

Lower MI, MI25, and SI values at site 4, suggests relatively disturbed soil health conditions (Bongers, 1990; Ferris *et al*., 2001). Agricultural practices such as incorporating fertilizers into the soil, stimulate microbial activity and provide resources for enrichment opportunist bacteria-feeding nematode species. Consequently, there is a rapid decrease in the MI followed by a gradual increase during subsequent succession. MI indicates the successional maturity of nematode communities and, thus, the biological condition of the soil habitat. It has been shown to be a sensitive instrument for monitoring recovery after disturbances, comparison of agricultural systems and measuring pollution-induced stress (Ettema and Bongers, 1993; Frechman and Ettema, 1993; Korthals *et al*., 1996).

The MI25 offers the possibility to measure pollution induced stress factors in the soil because in a stressed environment with a low soil microbial

Table 3. Nematode abundances (nematodes/100 cm^3), trophic group ratios, and maturity, diversity and soil food web indices of the survey sites. Values are means ± standard deviations.

	Survey sites			
Variable	1[u]	2	3	4
Nematode abundances				
Plant parasites	19.2 ± 12.7 b	43.5 ± 16.2 b	35.75 ± 18.5 b	45.2 ± 4.1 a
Bacterivores	45.4 ± 19.3 b	43.5 ± 22.7 b	78.0 ± 4.6 ab	110.4 ± 18.9 a
Fungivores	6.4 ± 6.5 a	10.8 ± 8.0 a	9.3 ± 4.8 a	11.4 ± 5.0 a
Omnivores	9.8 ± 7.8 a	7.5 ± 5.4 a	3.8 ± 2.0 a	1.6 ± 0.5 a
Total nematodes	81.6 ± 28.0 c	105.8 ± 49.2 bc	126.8 ± 21.3 ab	168.6 ± 20.5 a
Non-plant parasites	62.4 ± 30.7 b	62.3 ± 33.2 b	91.0 ± 8.6 ab	123.4 ± 23.5 a
% of RLN/total[v]	25.4 ± 16.7 a	42.0 ± 5.2 a	25.1 ± 10.3 a	21.2 ± 6.2 a
% of RLN/non-plant parasites[w]	98.2 ± 4.0 a	98.7 ± 1.5 a	92.4 ± 4.5 a	77.8 ± 17.7 b
Trophic group ratios				
FV-to-BV[x]	0.13 ± 0.1 a	0.23 ± 0.1 a	0.12 ± 0.1 a	0.1 ± 0.0 a
(FV+BV)/HV[y]	2.3 ± 1.1 a	1.2 ± 0.2 b	3.0 ± 1.5 a	2.7 ± 0.7 a
Maturity indices				
PPI	3.0 ± 0.04 a	3.0 ± 0.03 a	2.9 ± 0. 05 ab	2.8 ± 0.14 b
MI	2.2 ± 0.3 ab	2.2 ± 0.1 a	1.8 ± 0.2 bc	1.7 ± 0.2 c
MI25	2.6 ± 0.4 a	2.5 ± 0.2 ab	2.2 ± 0.2 bc	2.1 ± 0.1 c
PPI/MI	1.4 ± 0.2 bc	1.3 ± 0.1 c	1.6 ± 0.2 ab	1.7 ± 0.3 a
Diversity indices				
H'[z]	2.4 ± 0.4 a	2.2 ± 0.3 a	2.4 ± 0.3 a	2.4 ± 0.1 a
Hill's N1	11.6 ± 4.2 a	9.7 ± 2.9 a	11.7 ± 3.3 a	11.2 ± 3.3 a
Hill's N0	15.0 ± 3.0 a	16.0 ± 5.2 a	16.5 ± 3.0 a	17.0 ± 4.2 a
Soil food web indices				
BI	21.7 ± 9.3 a	27.4 ± 9.1 a	24.0 ± 8.3 a	28.4 ± 10.2 a
CI	4.9 ± 4.1 a	11.6 ± 2.1 a	6.6 ± 4.0 a	7.2 ± 4.7 a
EI	66.2 ± 10.7 a	56.4 ± 13.5 a	71.5 ± 10.7 a	68.4 ± 13.7 a
SI	57.0 ± 27.6 a	58.1 ± 9.9 a	34.6 ± 16.0 ab	19.3 ± 9.6 b

[u]Different letters in the same row indicate significant differences based on Fisher's protected least significant difference ($P \leq 0.05$).

[v]Percentage of root-lesion nematode in total nematodes.

[w]Percentage of root-lesion nematode in non-plant parasitic nematodes.

[x]Fungivores-to-bacterivores ratio (Freckman and Ettema, 1993).

[y]Fungivores plus bacterivores-to-herbivores ratio (Wasilewska, 1994).

[z]Shannon-Weaver diversity index (Shannon and Weaver, 1949).

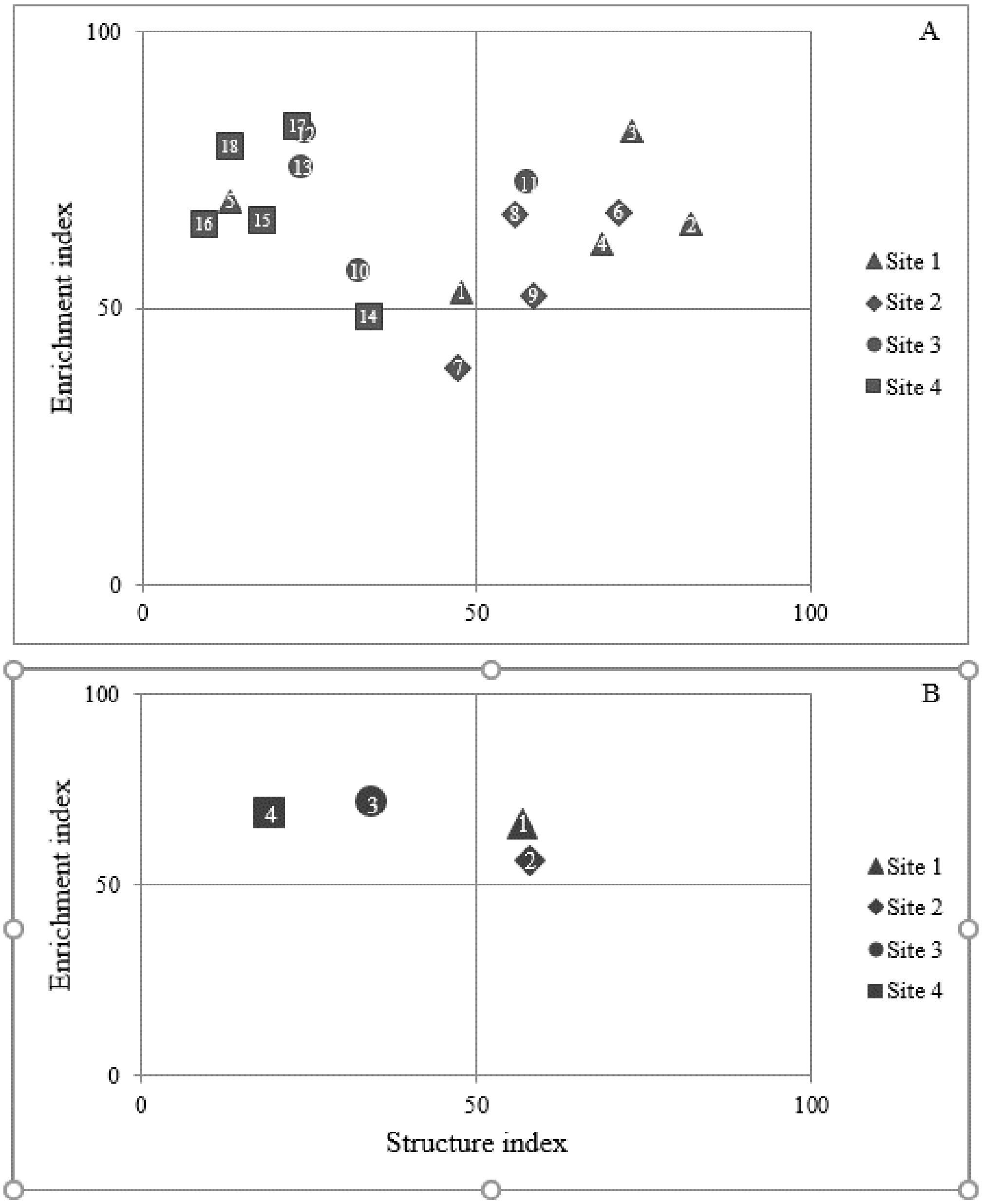

Figure 2. Faunal profiles representing the structure (SI) and enrichment (EI) conditions of the soil food webs in the survey sites from each experimental unit (2 ha) (A) and each site (B).

activity such as in acidic soils, the general opportunist bacteria-feeding nematodes dominate (de Goede and Bongers, 1994). Using MI25 rather than MI, provides relevant information on the impact of pollution/stress factors by excluding enrichment opportunists that respond to both enrichment and pollution/stress factors. The lower PPI at site 4 compared with other sites could be because of lower abundance of RLN (78% of PPN) at site 4.

Lower SI at site 4 could be due to a relatively low abundance of omnivores, which are indicators of soil food web structure (Ferris *et al*., 2001). The SI indicates the lack of, or recovery from, environmental stress and/or resource depletion, which contribute to abundance of predators and omnivores. Sánchez-Moreno *et al*. (2009) found that highest SI in plots treated with compost and cover crops compared with conventionally treated plots. SI values are usually low in agroecosystems because of physical and agrochemical disturbances (Fiscus and Neher, 2002; Briar *et al*., 2011).

The greater abundance of RLN from less disturbed and relatively healthy soils (sites 1 and 2) was unexpected because healthy soils typically reduce the abundance of PPN through microbial/predatory mechanisms and enhanced plant resistance (Khan and Kim, 2007; Schlatter *et al*., 2017; da Silva *et al*., 2018). Microbial composition is one of the major drivers involved in soil suppressiveness against plant pathogens (da Silva *et al*., 2018). Microorganisms promote plant growth through the production of plant hormones or solubilization of nutrients that enhance plant resistance or can induce plant resistance or defend plants from pathogens via antibiosis or competitive exclusion (Schlatter *et al*., 2017). Moreover, healthy soils are less disturbed and conducive to predators and omnivores, which feed on soil microorganisms including PPN and reduce PPN population (Khan and Kim, 2007).

The increase in RLN could be due to enhanced root growth and/or past management practices that favored RLN reproduction. Some winter cover crops such as winter rye, vetch, and oilseed radish are good hosts for RLN (Abawi and Ludwig, 1995; Bao and Neher, 2011; Grabau *et al*., 2017). Although the use of these cover crops in the previous season at the study sites was not confirmed, use of such cover crops would increase RLN pressure on carrots, and potentially reduce yield. Different studies on cover crops mentioned earlier suggested that identifying the type of PPN present and selecting appropriate cover/rotation crops are important steps in PPN management.

The soil food web analysis indicated that the soil food webs were disturbed at sites 3 and 4 (Quadrant A), but maturing at sites 1 and 2 (Quadrant B), suggesting soil food webs with greater trophic links and potential pest suppression ecosystem service at sites 1 and 2 (Ferris *et al*., 2001; Sánchez-Moreno and Ferris, 2007). The lower PPI/MI value at sites 1 (1.39) and 2 (1.34) compared with site 4 (1.66) indicates nutrient enrichment with high microbial activity at sites 1 and 2, but severely nutrient-enriched at site 4 where resource utilization by the carrots was far from optimal (Bongers *et al*., 1997). As we expected, the nematode community analysis revealed differences in soil health conditions among the study sites. Overall, sites 1 and 2 showed greater successional maturity of the nematode community and soil food web structure compared with sites 3 and 4, suggesting soil food webs with greater trophic links and potential pest suppression ecosystem service at sites 1 and 2 (Ferris *et al*., 2001; Sánchez-Moreno and Ferris, 2007). Hence, sites 1 and 2 had better soil health conditions than sites 3 and 4.

In conclusion, RLN was the predominant PPN at all the sites. This suggested a need for appropriate RLN management strategies to reduce its abundance in these sites. This further suggests that RLN could be predominant in other carrot fields in the area with similar cropping system, soil type, and climatic conditions. However, nematode taxa that were not recovered in these carrot fields does not necessarily mean they did not occur and infect carrots. Sites 1 and 2 had low-to-moderate soil disturbances, balanced bacterial-fungal decompositions pathway, and maturing soil food webs, suggesting better soil health conditions. Sites 3 and 4 had highly disturbed soils, bacterial decomposition pathways and disturbed soil food webs, suggesting poor soil health conditions. Overall, the study sites require management strategies that would manage both RLN and soil health condition. The high abundance of RLN in these carrot fields deserves the attention of growers, researchers, and extension agents.

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