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Effects of Cover Crops on *Pratylenchus penetrans* and the Nematode Community in Carrot Production

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Abstract: Cover cropping is a common practice in U.S. Midwest carrot production for soil conservation, and may affect soil ecology and plant-parasitic nematodes—to which carrots are very susceptible. This study assessed the impact of cover crops—oats (*Avena sativa*), radish (*Raphanus sativus*) cv. Defender, rape (*Brassica napus*) cv. Dwarf Essex, and a mixture of oats and radish—on plant-parasitic nematodes and soil ecology based on the nematode community in Michigan carrot production systems. Research was conducted at two field sites where cover crops were grown in Fall 2014 preceding Summer 2015 carrot production. At Site 1, root-lesion (*Pratylenchus penetrans*) and stunt (*Tylenchorhynchus* sp.) nematodes were present at low population densities (less than 25 nematodes/100 cm^3 soil), but were not significantly affected ($P > 0.05$) by cover crops. At Site 2, *P. penetrans* population densities were increased ($P \leq 0.05$) by 'Defender' radish compared to other cover crops or fallow control during cover crop growth and midseason carrot production. At both sites, there were few short-term impacts of cover cropping on soil ecology based on the nematode community. At Site 1, only at carrot harvest, radish-oats mixture and 'Dwarf Essex' rape alone enriched the soil food web based on the enrichment index ($P \leq 0.05$) while rape and radish increased structure index values. At Site 2, bacterivore abundance was increased by oats or radish cover crops compared to control, but only during carrot production. In general, cover crops did not affect the nematode community until nearly a year after cover crop growth suggesting that changes in the soil community following cover cropping may be gradual.

Key words: Avena sativa, *Brassica napus*, carrot, cover crop, *Daucus carota*, ecology, management, nematode community, oats, oilseed radish, oilseed rape, *Pratylenchus penetrans*, *Raphanus sativus*, root-lesion nematode, stunt nematode, *Tylenchorhynchus*.

Carrot (*Daucus carota* var. *sativus*) production, including freshmarket and processing carrots, is a nearly $800 million industry spanning over 35,000 ha in the United States (NASS-USDA, 2016). The upper Midwest produces about a tenth of the United States' carrots, and is the largest production area outside of California (NASS-USDA, 2014). This makes the Midwest a key region for broadening the geographic range of carrot production which reduces the risk of supply issues due to localized adverse growing conditions (Tendall et al., 2015). Carrot production in the upper Midwest relies heavily on maintaining soil that has proper biological and physicochemical properties. In particular, carrots are high-value root crops that require a consistent supply of nutrients and water (Batra and Kalloo, 1990; Brainard and Noyes, 2012) and prefer well-drained soils not prone to compaction—soils that are often prone to erosion (Millette and Broughton, 1992; Johansen et al., 2015).

In addition, soil-borne diseases have large impacts on carrot root yield and value. Root defects caused by soil-borne diseases deter consumers in freshmarket production and may be incompatible with the machinery used in the processing industry. Plant-parasitic nematodes are a major cause of carrot disease as they can cause stunting or forking of carrot roots, reduce water and nutrient uptake efficiency, and decrease crop growth (Greco and Brandonisio, 1980; Vrain and Belair, 1982; Vrain, 1982). Despite this high potential for economic loss caused by plant-parasitic nematodes, no nematode-resistant cultivars are commercially available and pesticide options are extremely limited. Therefore, optimizing other aspects of carrot production for maximum management of plant-parasitic nematodes is vital.

Cover cropping is a common management practice in carrot production for conserving soil and maintaining soil conditions conducive for carrot growth. In particular, cover cropping can help retain nutrients, reduce soil erosion, increase soil organic matter, manage water runoff, and increase water infiltration (Joyce et al., 2002; Fageria et al., 2005; Kleinman et al., 2005; Snapp et al., 2005). Cover cropping can also impact plant-parasitic nematode populations. Growing cover crops that are nonhosts or poor hosts of the plant-parasitic nematodes at a given site can decrease nematode populations such as growing oats for root-knot nematode (*Meloidogyne* spp.) management (Opperman et al., 1988; Wang et al., 2004). Cover cropping may also increase plant-parasitic nematode population densities if the crop or cultivar is a good host for the nematodes present such as some leguminous winter cover crops in fields infested by *Meloidogyne incognita* (Mercer and Miller, 1997; Timper et al., 2006).

Cover crops can also serve as trap crops—crops that stimulate nematode hatch or activity but do not allow nematode reproduction (Scholte, 2000; Smith et al., 2004). The trap crop could be a nematode-resistant cultivar such as a resistant oilseed radish or mustard used to manage sugarbeet cyst nematode, *Heterodera*

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schachtii (Smith et al., 2004; Hafez and Sundararaj, 2009). A nematode-susceptible cultivar terminated or removed before a nematode generation can be completed may serve as a trap crop such as growing potato trap crops for potato cyst nematode (*Globodera* spp.) management (Halford et al., 1999; Scholte, 2000). Some cover crops, particularly those in the Brassicaceae family, act as biofumigants (Wang et al., 2001; Matthiessen and Kirkegaard, 2006) because they contain compounds that are toxic to nematodes and other organisms (Gimsing and Kirkegaard, 2009; Oka, 2010). Cover crops may also help control plant-parasitic nematodes by stimulating organisms that are predatory or antagonistic to nematodes (Oka, 2010).

In addition to impacting physicochemical soil properties and pathogen populations, cover crops can also impact biological aspects of soil ecosystems such as microbial, mesofaunal, and macrofaunal communities (Reeleder et al., 2006; McSorley et al., 2009; Treonis et al., 2010). Organisms in these communities provide services such as nutrient cycling (Ferris et al., 1998; Chen and Ferris, 1999), residue decomposition (Chauvin et al., 2015; Holajjer et al., 2016), pest or pathogen suppression (Noel et al., 2010; Timper et al., 2012), and improved soil aggregation (Oades, 1993). The soil nematode community provides these services (Ferris et al., 1998; Holajjer et al., 2016) and is a dynamic bioindicator of soil ecology (Villenave et al., 2010; Grabau and Chen, 2016) since nematodes occupy a wide range of ecological niches (Bongers and Korthals, 1993; Ferris et al., 2001).

While cover crops are used in carrot production in the Midwestern United States, there is minimal information on the value of these cover crops for plant-parasitic nematode management or their impacts on the nematode community in this system. The objectives of this study were to investigate the influence of common cover crops in the Midwestern United States including oats (*Avena sativa*), oilseed radish (*Raphanus sativus*), oilseed rape (*Brassica napus* var *oleifera*), and a mixture of oats and oilseed radish on 1) soil ecology based on the nematode community, and 2) plant-parasitic nematodes in Michigan carrot agroecosystems.

Materials and Methods

Experimental sites and design: Research was conducted at two sites in the lower peninsula of Michigan that were in commercial carrot production. Site 1 was located in Fremont, MI, on Pipestone sand (92% sand, 2% silt, 6% clay). Site 2 was located in Walkerville, MI, on Grattan Sand (94% sand, 1% silt, 5% clay). At both sites, the experiment was arranged in a randomized complete block design with four replicates, and cover crop treatment was the only experimental factor. The five cover crop treatments were 1) fallow control, 2) oats, 3) oilseed radish cv. Defender, 4) a mixture of oats and 'Defender' radish, and 5) oilseed rape cv. Dwarf Essex. Treatments of cowpea (*Vigna unguiculata*) cv. Iron Clay as well as a mixture of cowpea and oats were initially included in the study, but were removed because cowpea did not establish. The oats-radish mixture was included because growers commonly plant a mixture of cover crops to capitalize on the advantages of both crops—such as robust radish root growth and relatively tall oat stubble. Cover crops were sown at 56 kg/ha for oats alone, 9 kg/ha for radish alone, 9 kg/ha for 'Dwarf Essex' rape alone, and 28 kg/ha of oats and 4.5 kg/ha for radish in the mixed treatment. Treatments were established in 6.1 m by 30.5 m plots.

Site maintenance: Research sites were managed uniformly according to each grower's conventional practices including fertilizer and herbicide applications. Nematicides were not applied at either site. At Site 1, peas (*Pisum sativum*) were grown in Summer 2014 and harvested in early July. The field was tilled in July 2014 and sprayed with glyphosate herbicide and disked for weed control in August 2014 before cover crops were planted. Cover crops were planted on 21 August 2014. Oats were broadcast-planted across the whole site as a windbreak at the time of carrot planting in the spring. All cover crops except 'Dwarf Essex' rape died during the winter. The site was strip tilled and planted to processing carrot on 5 May 2015. Herbicides including linuron and sethoxydim were sprayed in accordance with standard grower practices for weed control and to control both the oats windbreak and 'Dwarf Essex' rape regrowth (Zandstra, 2015). Herbicide application on 14 May 2015 killed oats. 'Dwarf Essex' rape was injured, but survived that herbicide application and was successfully terminated by herbicide application on 25 June 2015.

At Site 2, wheat was grown in Summer 2014 and terminated prior to establishment of cover crops. Cover crops were planted on 14 August 2014 at Site 2. Some volunteer wheat from the preceding wheat crop also became established within cover crop treatments. The field was strip tilled on 17 April 2015. Cover crops died over the winter except 'Dwarf Essex' rape and some volunteer wheat. A combination of the earlier strip tillage and an herbicide application on 7 May 2015 effectively terminated the wheat and 'Dwarf Essex' rape. Processing carrots were planted on 24 April 2015. Herbicides including linuron and sethoxydim were sprayed in accordance with standard grower practices (Zandstra, 2015).

Nematode assays: Soil samples were collected from each plot (18 cores to 20 cm deep, with 3-cm diam. probe) approximately 2 mon after planting cover crops (22 October 2014 at both sites), before planting carrots (22 April 2015 at both sites), at midseason (20 July 2015 at both sites), and at harvest (17 September and 6 October 2015 at Sites 1 and 2, respectively). Soil samples were homogenized thoroughly and vermiform (wormshaped stages) nematodes were extracted from 100-cm^3 soil subsamples. Nematodes were extracted using a semiautomatic elutriator followed by centrifugation (Byrd et al., 1976). Following extraction, nematodes were fixed at 70°C in double triethanolamine (2%)-formalin (7%) solution. The entire nematode community was enumerated and identified to genera morphologically. Population densities of individual genera of plant-parasitic nematodes and nematode trophic groups including herbivores, bacterivores, fungivores, and omnivores/predators (Yeates et al., 1993) were calculated for nematode community analysis. Colonizer-persister (c-p) values, ranging from 1 for extreme colonizers to 5 for extreme persisters, were assigned for each genus as previously established (Bongers, 1990).

Feeding types and c-p values were used to calculate nematode community indices—including the maturity index, structure index, channel index, and enrichment index (Bongers, 1990; Ferris et al., 2001). The maturity index measures soil community disturbance based on average c-p values of free-living nematodes in the soil (Bongers, 1990). The enrichment and structure indices measure the enrichment and structure conditions, respectively, of the food web based on weighted abundance of indicator nematode guilds (Ferris et al., 2001). The channel index measures whether fungal or bacterial decomposition pathways are more predominant in a system based on weighted ratios of fungal- and bacterial-feeding nematodes (Ferris et al., 2001). Separately at each site, the frequency and relative abundance for each genus was calculated as overall values across all sample dates and plots. Frequency was calculated as percent of total samples ($n = 80$, 20 plots each at four sample dates) in which the genus was detected. Relative abundance was also calculated as average density of the genus divided by average density for the total nematode population of all genera at the given site and expressed as a percent.

Cover crop establishment: Cover crop dry biomass was recorded at each site on 22 October 2014. Aboveground cover crop biomass and, at site 2, aboveground volunteer wheat biomass was measured in two sectors of 0.25 m^2 in each plot. Radish root biomass was also measured in radish or oats + radish plots.

Statistical analysis: The impacts of cover crop treatments on nematode population densities, nematode community indices, total cover crop biomass, and volunteer wheat biomass at Site 2 were calculated using one-way analysis of variance (ANOVA) for each individual season when data was collected. Data from the two sites at each sampling date were analyzed separately because there were significant ($P \leq 0.1$) treatment by site interactions for some variables in certain seasons and the two sites did not have the same genera of plant-parasitic nematodes. Data from each sampling date were analyzed separately because there were sampling dates by treatment interactions ($P \leq 0.1$) for most variables with significant treatment effects. The ANOVA models were evaluated for homogeneity of variance using Levene's test and for normality of residuals graphically and response variables were transformed as necessary to meet these assumptions (Levene, 1960; Cook and Weisburg, 1999). For variables with significant cover cropping effects ($P \leq 0.05$), cover crop treatment means were separated using Fischer's protected least significant difference test ($\alpha = 0.05$).

Results

Site 1: Cover crops, except for cowpea treatments, established well at the site in Fall 2014 (Table 1). Cowpea aboveground biomass was 1.8 and 0.24 g/m^2 in the cowpea only and oats with cowpea treatments, respectively, both of which were removed from the study due to poor cowpea establishment. Total cover crop biomass was significantly greater ($P \leq 0.05$) for all cover crop treatments than the untreated control (Table 1).

At Site 1, 48 genera of nematodes were identified. Genera present in at least 5% of samples are listed in Table 2. Bacterivores from 17 genera were present at the site and constituted 66.9% of total nematode abundance across all plots and sample dates (relative abundance). Herbivores, from 14 genera and totaling 18.4% relative abundance, and fungivores, from six genera and totaling 12.0% relative abundance, constituted most of the rest of the community. Omnivores, from six genera and totaling 1.9% relative abundance, and predators, from four genera and totaling 0.8% relative abundance, made up a small portion of nematodes at the site. *Pratylenchus penetrans* (root-lesion nematode) and *Tylenchorhynchus* sp. (stunt nematode) were the only major plant-parasitic nematodes at the site present in large enough population densities to analyze statistically. *Criconemoides* sp. (ring nematode), *Meloidogyne hapla* (northern root-knot nematode), *Paratrichodorus* sp. (stubby-root nematode), *Paratylenchus* sp. (pin nematode), and *Xiphinema* sp. (dagger nematode) were present, but at population densities less than 1 nematode/100 cm^3 soil on average across sample dates.

Table 1. Cover crop establishment at Site 1 on October 22, 2014.[a]

Cover crop	Total aboveground cover crop dry biomass (kg/ha)	Radish root dry biomass (kg/ha)
Control	0 b	0
Oats	2,620 a	0
Oats + radish	2,460 a	1,090
Radish	2,200 a	1,100
Oilseed rape	2,310 a	0

[a] Values are the average of four replications.
[b] Total aboveground biomass followed by the same letter are not significantly different based on Fischer's protected least significant difference ($P \leq 0.05$).

TABLE 2. Nematodes identified at Site 1 classified by feeding type. Only nematodes that were present in 5% or more of samples are listed.

Nematode	C-p value	Frequency (%)[a]	Relative abundance (%)[b]
1. Bacterivores			
Cephalobus	2	97	13.84
Rhabditis	1	97	19.51
Mesorhabditis	1	96	12.81
Acrobeles	2	95	8.49
Eucephalobus	2	83	3.83
Prismatolaimus	3	69	3.00
Plectus	2	63	1.64
Alaimus	4	42	1.37
Heterocephalobus	2	28	0.66
Chiloplacus	2	26	0.67
Cervidellus	2	21	0.26
Panagrolaimus	1	15	0.56
Eumonhystra	2	12	0.14
2. Fungivores			
Aphelenchus	2	97	8.72
Filenchus	2	72	2.24
Aphelenchoides	2	26	0.69
Ditylenchus	2	14	0.17
Diphtherophora	3	8	0.14
3. Herbivores			
Pratylenchus	3	78	7.69
Tylenchorhynchus	3	77	9.12
Tylenchus	2	15	0.20
Criconemoides	3	14	0.31
Paratrichodorus	4	14	0.36
Meloidogyne	3	13	0.17
Basiria	2	10	0.12
Psilenchus	2	10	0.18
Paratylenchus	2	8	0.14
4. Omnivores			
Thonus	4	53	1.25
Aporcelaimellus	5	24	0.37
Eudorylaimus	4	14	0.17
Paraxonchium	5	5	0.06
5. Predators			
Clarkus	4	29	0.52
Discolaimus	5	21	0.26

[a] The percent of samples in which the given nematode was detected.
[b] The percent of total nematode abundance for a given nematode.

Among nematode trophic groups, only omnivore-predators were significantly ($P \leq 0.05$) affected by cover crops at any sampling date (Table 3). Before carrot planting (April 2015), omnivore-predator population densities were significantly increased after oats than oats with radish or fallow control cover crop treatments ($P \leq 0.05$; Table 3). Neither root-lesion nematode nor stunt nematode were significantly ($P > 0.05$) affected by cover crops at any sampling date (Table 3).

Neither channel index nor maturity index was significantly ($P > 0.05$) affected by cover crops at any sampling date (Table 4). At carrot harvest (October 2015), enrichment index values were significantly greater after oats with radish or 'Dwarf Essex' rape than fallow control or oats only cover crop treatments ($P \leq 0.05$; Table 4). At carrot harvest, structure index values were significantly greater after radish or 'Dwarf Essex' rape than oats only cover crop treatments.

Site 2: Cover crops, except for cowpea treatments, established well at the site (Table 5). In Fall 2014, there was no measureable cowpea biomass in most of the cowpea only or oats plus cowpea treatments, both of which were removed from the study. Volunteer wheat biomass varied significantly by cover crop treatment ($P \leq 0.05$) with biomass greatest in control plots where no cover crops were planted (Table 5). In each cover crop treatment, wheat represented a relatively small portion (2% to 23%) of the aboveground cover crop biomass. Despite volunteer wheat growth, total aboveground biomass was significantly greater in any treatment where cover crops were grown than the untreated control (Table 5).

At Site 2, 47 genera of nematodes were identified. Genera present in at least 5% of samples are listed in Table 6. Bacterivores from 15 genera were present at the site and constituted 61.9% of total nematode abundance across all plots and sample dates (relative abundance) while fungivores, from six genera, constituted 13.1% relative abundance. Herbivores (11 genera, 3.1% relative abundance), omnivores (9 genera, 3.1% relative abundance), and predators (5 genera, 1.8% relative abundance) made up the remainder of the nematode community. *Pratylenchus penetrans* (root-lesion nematode) was the only major plant-parasitic nematode present at the site in population densities large enough to evaluate statistically and constituted 92% of herbivores. *Criconemoides* sp. (ring nematode), *Helicotylenchus* sp. (spiral nematode), *Meloidogyne hapla* (northern root-knot nematode), *Paratylenchus* sp. (pin nematode), and *Xiphinema* sp. (dagger nematode) were present, but at population densities less than 1 nematode/100 cm^3 soil on average across sampling dates.

Among nematode trophic groups, neither fungivores nor omnivore-predators were significantly ($P > 0.05$) affected by cover crops for any sampling date (Table 7). During cover crop (October 2014) and carrot (July 2015) growth, total herbivore and root-lesion nematode population densities were significantly greater with radish-only than most other cover crop treatments. During carrot production (July 2015), bacterivore population densities were significantly greater in radish only and oats only treatments ($P \leq 0.05$; Table 7). Maturity Index was also smaller for radish than oats-radish mixture and untreated control in July 2015 (Table 8) and caused in part by increased bacterivore population densities, which have low c-p values of 1 or 2. Structure, enrichment, and channel indices were not affected by cover crops at any time at Site 2 (Table 8).

DISCUSSION

Pratylenchus penetrans was the only major plant-parasitic nematode consistently present in plots at both sites. *Pratylenchus penetrans* is very common in Midwest soils and can reduce yield and value of carrots due

TABLE 3. Nematode abundances at Site 1 as affected by cover crop treatments at four sampling dates.

	Bacterivores				Fungivores			
Cover crop	October 2014[a]	April 2015	July 2015	October 2015	October 2014	April 2015	July 2015	October 2015
	Nematodes/100 cm^3 soil							
Control	39 ± 7	24 ± 2	46 ± 30	64 ± 12	9 ± 5	7 ± 2	7 ± 2	13 ± 5
Oats	69 ± 22	37 ± 17	37 ± 9	68 ± 27	10 ± 3	6 ± 2	12 ± 6	15 ± 3
Oats + radish	73 ± 14	53 ± 13	78 ± 16	154 ± 65	12 ± 2	11 ± 3	10 ± 4	23 ± 2
Radish	50 ± 14	53 ± 25	52 ± 11	43 ± 8	9 ± 2	12 ± 5	6 ± 1	10 ± 1
Oilseed rape	71 ± 20	30 ± 10	39 ± 10	50 ± 8	7 ± 2	10 ± 4	5 ± 1	7 ± 2
	Herbivores				Omnivores and predators			
Control	21 ± 11	12 ± 5	3 ± 2	16 ± 11	2 ± 1	1 ± 1 b	2 ± 1	2 ± 1
Oats	32 ± 10	25 ± 12	11 ± 9	16 ± 6	2 ± 1	4 ± 1 a	1 ± 1	2 ± 1
Oats + radish	6 ± 2	11 ± 5	5 ± 2	4 ± 0	1 ± 1	1 ± 0 b	2 ± 1	2 ± 0
Radish	19 ± 13	11 ± 5	7 ± 2	15 ± 8	5 ± 1	2 ± 1 ab	1 ± 0	5 ± 2
Oilseed Rape	28 ± 11	24 ± 12	6 ± 5	22 ± 9	4 ± 3	2 ± 1 ab	3 ± 1	4 ± 2
	Root-lesion nematode				Stunt nematode			
Control	3 ± 2	3 ± 1	1 ± 1	12 ± 9	16 ± 9	8 ± 5	2 ± 1	3 ± 2
Oats	6 ± 2	8 ± 6	2 ± 1	12 ± 5	24 ± 9	15 ± 7	10 ± 9	3 ± 2
Oats + radish	4 ± 2	6 ± 3	2 ± 1	3 ± 1	2 ± 1	4 ± 3	2 ± 1	0 ± 0
Radish	7 ± 5	5 ± 3	3 ± 1	13 ± 8	10 ± 7	5 ± 3	3 ± 1	1 ± 0
Oilseed rape	5 ± 2	10 ± 5	2 ± 2	17 ± 7	20 ± 11	12 ± 10	3 ± 3	3 ± 1

[a] Values are means ± standard errors (n = 4). Different letters in the same column of the same nematode type indicate significant differences based on Fischer's protected least significant difference ($P \leq 0.05$). Mean separation is only shown if cover crop treatment effect was significant based on analysis of variance ($P \leq 0.05$).

to symptoms such as stunting, galling, and root forking (Olthof and Potter, 1973; Vrain and Belair, 1982; Berney and Bird, 1992). Selecting cover crops to manage *P. penetrans* is difficult as it has a very wide host range which includes oats, radish, and oilseed rape (Miller, 1978; Belair et al., 2002) although susceptibility is known to vary by cultivar (Townshend, 1989; Webb, 1996).

In this study, *P. penetrans* was unaffected by the cover crops tested at Site 1, but its population densities were increased compared to fallow by 'Defender' radish at Site 2 where *P. penetrans* population densities were numerically greater than at Site 1. This suggests 'Defender' radish was a good host for the *P. penetrans* population at Site 2 and better than oats or 'Dwarf Essex' rape. In other studies, *P. penetrans* responses to crops also varied by location (Miller, 1978; Kimpinski and Sanderson, 2004; LaMondia, 2006) suggesting that the environment, population variation, or both can affect their responses. *Pratylenchus penetrans* population densities were relative low in this study, particularly at Site 1, which may have impeded the ability to detect if any of the cover crops reduced *P. penetrans* densities compared to the fallow control.

Soil densities of *P. penetrans*, which was the only measure of population densities taken in this study, is a reliable measure for *P. penetrans* although measuring root abundance of this endoparasitic nematode as well as soil abundance gives a more complete assessment of its population. In a study at Prince Edward Island, *P. penetrans* carrot root and soil abundances were roughly proportional and soil abundances were more responsive to treatments (Kimpinski and Sanderson, 2004). In Tasmania, *Pratylenchus crenatus* root and soil densities decreased after taproot formation and nematode densities in roots were a better predictor of carrot

TABLE 4. Nematode community indices at Site 1 as affected by cover crop treatments at four sampling dates.

	Enrichment Index				Structure Index			
Cover crop	October 2014[a]	April 2015	July 2015	October 2015	October 2014	April 2015	July 2015	October 2015
Control	74 ± 4	82 ± 3	66 ± 12	61 ± 4 b	20 ± 6	26 ± 15	42 ± 11	41 ± 11 ab
Oats	70 ± 4	58 ± 10	78 ± 5	60 ± 6 b	19 ± 8	53 ± 10	31 ± 6	23 ± 6 b
Oats + radish	77 ± 5	79 ± 3	83 ± 9	77 ± 6 a	14 ± 5	52 ± 14	39 ± 6	28 ± 5 ab
Radish	70 ± 5	78 ± 5	89 ± 3	67 ± 3 ab	42 ± 8	44 ± 17	28 ± 5	49 ± 11 a
Oilseed rape	69 ± 5	69 ± 4	80 ± 5	76 ± 6 a	25 ± 8	48 ± 8	44 ± 17	52 ± 12 a
	Channel Index				Maturity Index			
Control	10 ± 4	10 ± 3	22 ± 13	14 ± 5	1.70 ± 0.09	1.66 ± 0.13	1.92 ± 0.19	2.02 ± 0.11
Oats	9 ± 1	19 ± 5	13 ± 5	20 ± 5	1.74 ± 0.07	2.15 ± 0.22	1.68 ± 0.08	1.88 ± 0.05
Oats + radish	9 ± 2	12 ± 4	8 ± 6	9 ± 4	1.61 ± 0.07	1.94 ± 0.23	1.56 ± 0.17	1.68 ± 0.14
Radish	10 ± 1	12 ± 5	4 ± 1	15 ± 4	1.89 ± 0.09	1.87 ± 0.15	1.40 ± 0.06	2.05 ± 0.08
Oilseed rape	7 ± 1	19 ± 8	8 ± 3	8 ± 2	1.77 ± 0.03	2.01 ± 0.09	1.76 ± 0.20	1.92 ± 0.16

[a] Values are means ± standard errors (n = 4). Different letters in the same column of the same index indicate significant differences based on Fischer's protected least significant difference ($P \leq 0.05$). Mean separation is only shown if cover crop treatment effect was significant based on analysis of variance ($P \leq 0.05$).

TABLE 5. Cover crop establishment at Site 2 on 22 October 2014.[a]

	Aboveground		Root
Cover crop	Wheat[b]	Total (cover crops and wheat)	Radish
		Dry biomass (kg/ha)	
Control	400 a	400 e	0
Oats	60 c	2,680 a	0
Oats + radish	160 bc	2,200 b	500
Radish	50 c	1,650 c	860
Oilseed rape	250 b	1,050 d	0

[a] Values are the average of 4 replications.
[b] Means in the same column followed by the same letter are not significantly different based on Fischer's protected LSD ($P \leq 0.05$).

yield than nematode population densities in soil (Hay and Pethybridge, 2005). In other crops, *P. penetrans* population densities in soil and roots tend to be roughly proportional to each other and of similar value for predicting yield (MacGuidwin and Bender, 2016).

Tylenchorhynchus was present at Site 1, but was unaffected by cover crop treatments, suggesting that all cover crops were similarly efficient hosts. *Tylenchorhynchus* is associated with many crops (Ferris and Bernard, 1971; Hallmann et al., 2007) and has a wide host range which includes oats, radish, and oilseed rape (Sharma, 1968). *Tylenchorhynchus* population densities were near minimum detectable levels by carrot harvest which suggests carrots were a poor host for *Tylenchorhynchus* as reported elsewhere (Sharma, 1968; Castro and Ferraz, 1989).

Oilseed radish and oilseed rape shoots applied as green manures contain glucosinolates which convert to isothiocyanates in the soil and are known to suppress plant-parasitic nematodes including *Meloidogyne javanica* (McLeod and Steel, 1999) and *Pratylenchus neglectus* (Potter et al., 1998). In this study, these crops had no impact on or increased plant-parasitic nematode population densities compared to fallow. As host crops for lesion nematode, any nematicidal effects of oilseed radish and oilseed rape may have been outweighed by nematode reproduction, particularly for radish, as has been observed in previous studies (McLeod and Steel, 1999). Cover crops were not incorporated into the soil before winter in this study and were only incorporated with strip tillage in the spring. This left residue to reduce erosion, a common grower practice, but may have reduced the nematode-suppressing potential of oilseed radish and oilseed rape because *Brassica* shoots can have more nematicidal activity than roots (Potter et al., 1998).

The neutral or density-increasing effects of cover crops on plant-parasitic nematodes in this study suggest that oats, oilseed radish, and oilseed rape are unlikely to help with lesion or stunt nematode management under the conditions of the study, although tests under greater nematode pest pressure may be useful. Oilseed radish may be more detrimental than other cover crops for lesion nematode management. Altering the length of cover cropping to facilitate trap cropping or incorporating radish and oilseed rape shoots to increase nematicidal activity could make these crops useful for plant-parasitic nematode management. Further research would be needed to determine whether these changes would be effective.

The current study also documented the importance of determining the plant-parasitic nematodes present in a given field and choosing appropriate management strategies for those nematodes. This is even more important when using biological management options such as cover crops where host status varies by species. For example, sugarbeet cyst (*Heterodera schachtii*) and root-knot (*Meloidogyne* spp.) nematodes do not reproduce well on 'Defender' radish and it can be

TABLE 6. Nematodes identified at Site 2 classified by feeding type. Only nematodes that were present in 5% or more of samples at the given site are listed.

Nematode	C-p value	Frequency (%)[a]	Relative abundance (%)[b]
1. Bacterivores			
Cephalobus	2	100	10.56
Rhabditis	1	99	19.78
Acrobeles	2	96	12.82
Plectus	2	95	7.11
Mesorhabditis	1	89	4.66
Eucephalobus	2	81	2.28
Eumonhystra	2	81	2.60
Prismatolaimus	3	46	0.71
Cervidellus	2	36	0.37
Wilsonema	2	36	0.56
Panagrolaimus	1	25	0.31
Alaimus	4	5	0.03
Bunonema	1	5	0.08
Chiloplacus	2	5	0.04
Heterocephalobus	2	5	0.04
2. Fungivores			
Aphelenchus	2	96	7.50
Filenchus	2	80	2.61
Aphelenchoides	2	68	1.39
Ditylenchus	2	26	0.42
Diphtherophora	3	23	0.57
Paraphelenchus	2	19	0.45
Tylencholaimus	4	13	0.10
3. Herbivores			
Pratylenchus	3	100	18.60
Xiphinema	5	24	0.31
Meloidogyne	3	19	0.60
Criconemoides	3	18	0.19
Tylenchus	2	15	0.15
Axonchium	5	9	0.10
Paratylenchus	2	6	0.05
Basiria	2	5	0.04
Lelenchus	2	5	0.07
4. Omnivores			
Thonus	4	74	1.63
Aporcelaimellus	5	48	0.55
Eudorylaimus	4	38	0.50
Microdorylaimus	4	20	0.25
Pungentus	4	10	0.11
5. Predators			
Discolaimus	5	35	1.21
Clarkus	4	29	0.51

[a] The percent of samples in which the given nematode was detected.
[b] The percent of total nematode abundance for a given nematode.

TABLE 7. Nematode abundances at Site 2 as affected by cover crop treatments at four sampling dates.

	Bacterivores				Fungivores			
Cover crop	October 2014[a]	April 2015	July 2015	October 2015	October 2014	April 2015	July 2015	October 2015
	Nematodes/100 cm^3 soil							
Control	98 ± 25	29 ± 2	45 ± 10 c	43 ± 9	22 ± 7	3 ± 2	15 ± 6	12 ± 3
Oats	95 ± 12	60 ± 5	102 ± 14 ab	72 ± 18	25 ± 11	7 ± 2	27 ± 6	18 ± 6
Oats + radish	92 ± 10	48 ± 14	71 ± 2 abc	89 ± 40	22 ± 5	7 ± 2	18 ± 1	18 ± 7
Radish	97 ± 11	51 ± 13	118 ± 21 a	55 ± 15	9 ± 2	10 ± 3	16 ± 1	24 ± 6
Oilseed rape	94 ± 10	64 ± 24	56 ± 20 bc	62 ± 24	19 ± 7	6 ± 2	11 ± 1	13 ± 2
	Herbivores				Omnivores and predators			
Control	12 ± 3 b	3 ± 0	8 ± 4 b	22 ± 8	14 ± 4	3 ± 1	5 ± 2	4 ± 3
Oats	18 ± 4 b	6 ± 2	22 ± 7 b	37 ± 10	11 ± 2	2 ± 1	3 ± 1	3 ± 1
Oats + radish	26 ± 8 b	2 ± 1	30 ± 5 b	51 ± 17	15 ± 7	4 ± 1	7 ± 3	6 ± 2
Radish	45 ± 10 a	5 ± 1	59 ± 15 a	36 ± 9	14 ± 1	2 ± 0	2 ± 1	4 ± 1
Oilseed rape	29 ± 5 ab	7 ± 3	15 ± 2 b	35 ± 7	8 ± 4	1 ± 0	3 ± 1	4 ± 0
	Root-lesion nematode							
Control	12 ± 3 b	2 ± 0	7 ± 4 b	20 ± 7				
Oats	17 ± 3 b	5 ± 1	21 ± 6 b	35 ± 10				
Oats + radish	25 ± 9 ab	2 ± 1	28 ± 5 b	50 ± 17				
Radish	43 ± 10 a	4 ± 1	57 ± 15 a	34 ± 9				
Oilseed rape	26 ± 5 ab	6 ± 3	15 ± 2 b	24 ± 6				

[a] Values are means (nematodes per 100 cm^3 soil) ± standard errors ($n = 4$). Different letters in the same column of the same nematode type indicate significant differences based on Fischer's protected LSD ($P \leq 0.05$). Mean separation is only shown if cover crop treatment effect was significant based on analysis of variance ($P \leq 0.05$).

beneficial for control of these nematodes (Hafez and Sundararaj, 2009; Teklu et al., 2014). However, based on this study and others (Miller, 1978; Belair et al., 2002), radish is a host for *Pratylenchus* and may increase its population densities. Other cover crops that are compatible with Midwest carrot production and can contribute to lesion nematode management, such as sorghum, sorghum-sudangrass, or rye, which have been beneficial in vegetable systems in the Northeastern United States (Abawi and Widmer, 2000; Everts et al., 2000), could be the focus of future research.

Cover crops had relatively few impacts on the nematode community in this study. Enrichment opportunist nematodes were enhanced by certain cover crops at both sites suggesting cover crops enriched the soil food web, but this only occurred in single seasons at each site toward the end of the study. However, the cover crops driving enrichment differed between sites with 'Dwarf Essex' rape and oats-radish mixture the drivers at Site 1, but radish the driver at Site 2. Impacts of cover crops on soil food web maturity or structure—while only occurring in single seasons—also differed between sites as radish and 'Dwarf Essex' rape matured the soil food web at Site 1, but radish disturbed the food web at Site 2. Cover crops are known to enrich the soil food web based on the nematode community as additional organic matter is incorporated into the soil (Gruver et al., 2010; Ferris et al., 2012). Cover crops generally have a neutral or negative (Ferris et al., 2012; Hinds et al., 2013) effect on soil food web structure, particularly in the early years of a new system, although long-term cover cropping may improve soil food web structure as demonstrated in long-term experiments conducted by Villenave et al. (2009).

TABLE 8. Nematode community indices at Site 2 as affected by cover crop treatments at four sampling dates.

	Enrichment Index				Structure Index			
Cover crop	October 2014[a]	April 2015	July 2015	October 2015	October 2014	April 2015	July 2015	October 2015
Control	57 ± 2	61 ± 6	72 ± 6	72 ± 4	47 ± 10	36 ± 8	46 ± 14	36 ± 10
Oats	43 ± 8	75 ± 6	72 ± 3	76 ± 4	39 ± 6	25 ± 10	20 ± 3	22 ± 2
Oats + radish	48 ± 6	71 ± 7	71 ± 4	80 ± 4	42 ± 11	31 ± 5	31 ± 11	44 ± 9
Radish	42 ± 6	63 ± 13	84 ± 3	69 ± 7	47 ± 2	23 ± 5	19 ± 2	38 ± 13
Oilseed rape	43 ± 4	66 ± 6	78 ± 2	73 ± 4	29 ± 6	12 ± 5	29 ± 5	34 ± 6
	Channel Index				Maturity Index			
Control	18 ± 3	11 ± 6	15 ± 6	14 ± 5	2.15 ± 0.12	1.94 ± 0.06	1.96 ± 0.14 a	1.87 ± 0.16
Oats	27 ± 7	8 ± 3	12 ± 2	11 ± 3	2.13 ± 0.09	1.66 ± 0.05	1.73 ± 0.05 ab	1.67 ± 0.06
Oats + radish	25 ± 5	10 ± 3	13 ± 2	10 ± 4	2.19 ± 0.17	1.77 ± 0.10	1.82 ± 0.05 a	1.76 ± 0.12
Radish	16 ± 5	19 ± 11	6 ± 1	18 ± 4	2.19 ± 0.03	1.78 ± 0.12	1.51 ± 0.07 b	1.90 ± 0.13
Oilseed rape	24 ± 7	11 ± 8	10 ± 3	13 ± 4	2.06 ± 0.03	1.74 ± 0.09	1.69 ± 0.05 ab	1.82 ± 0.08

[a] Values are means ± standard errors ($n = 4$). Different letters in the same column of the same index indicate significant differences based on Fischer's protected LSD ($P \leq 0.05$). Mean separation is only shown if cover crop treatment effect was significant based on analysis of variance ($P \leq 0.05$).

Based on the faunal profile developed by Ferris et al. (2001), nearly all treatments from both sites and seasons were categorized as a disturbed, but enriched, food web condition (enrichment index greater than 50 and structure index less than 50) which is typical of agricultural systems (Ferris et al., 2001; Grabau and Chen, 2016). At carrot harvest at Site 2, a couple of treatments (radish only and 'Dwarf Essex' rape) were on the boundary between disturbed and maturing (enrichment and structure indices greater than 50) food web conditions due to the increased structure index mentioned above. Similarly, Site 2 in fall after cover crop growth was classified as a degraded food web condition (enrichment and structure indices less than 50), but these values were near 50 for most treatments which is on the boundary between all four food web conditions.

At both sites, cover crops only affected the nematode community nearly a year after cover crops were grown. This suggests that nematode community changes may have been relatively gradual after cover cropping. Although cover crops can influence soil ecology while they are still growing or the year after they are grown (Hinds et al., 2013; Chauvin et al., 2015), impacts can be more substantial after multiple years of rotating cash crops with cover crops (Villenave et al., 2009; Hooks et al., 2011).

The amount of cover crop biomass produced at the sites may have also influenced the degree of impacts on the nematode community since input of organic material is a major reason cover crops impact soil biology (Ferris et al., 2012; Chauvin et al., 2015). Cover crop biomass at the sites was within the range of values that are typically observed in the Midwestern United States for fall cover crops (Stute and Posner, 1993; Andraski and Bundy, 2005). However, fall cover crop growth is highly variable in the region and cover crop growth can be substantially greater than that observed in this study (Wang et al., 2008; Björkman et al., 2015). Fall mustard cover crop biomass is positively correlated with growing degree-days (Björkman et al., 2015), so earlier planting dates and warmer weather generally increase biomass. Thus, in years or at sites where conditions are more favorable, cover crop growth may be greater than that observed in this study possibly leading to more substantial impacts on the nematode community and the soil food web (Ferris et al., 2012; Chauvin et al., 2015). Further investigation would be needed to confirm this.

Additionally, cover crop residues were not well incorporated into the soil in this study which reduced the amount of organic matter added to the system. There were also alternate sources of organic matter at the sites, such as spring windbreaks. While these practices are used at the commercial farms where the experiments were conducted and are relatively common, the impact of cover cropping may be more substantial in different systems or for carrot producers that use slightly different production practices.

In summary, radish was detrimental for *P. penetrans* management at one site, highlighting the risks of growing a cover crop that is susceptible to the plant-parasitic nematodes present at a given site. Oats and 'Dwarf Essex' rape were similar to fallow for short-term impacts on *P. penetrans* but low population densities of this nematode at the sites could have obscured differences between these practices. Cover crops had minimal impacts on the nematode community suggesting they may have few short-term impacts on the soil food web in Midwest carrot production. This may be due in part to common production practices that reduce the amount of cover crop organic matter incorporated into the soil and practices that provide alternative sources of organic matter. Certain cover crops did shift the soil web to more enriched, as indicated by enrichment index values and bacterivore abundances, or structured conditions, but not until nearly a year after cover crop growth. Additionally, the crops that caused these changes differed by site. The delay between cover crop growth and detection of differences in soil ecology suggests changes in soil ecology from cover cropping may occur gradually over time in this system, although further investigation would be needed to confirm this.

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