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Brassicaceous and rye cover crops altered free-living soil nematode community composition

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ABSTRACT

Nematode community analysis was utilized to evaluate the biofumigant or allelopathic effects of brassicaceous and rye winter cover crops on non-target nematodes in three experiments (two sites) in Maryland. The cover crop treatments included mustard blend (*Sinapis alba* and *Brassica juncea*) 'Caliente', rapeseed (*B. napus*) 'Essex'/'Humus', forage radish (*Raphanus sativus*) 'Dichon', oilseed radish (*R. sativus*) 'Adagio'/'Colonel', rye (*Secale cereale*) 'Wheeler' and a no cover crop (winter weeds) control. Soil samples (0–15 cm) were collected two or three times per year and extracted nematodes were identified to genus or family. Nematode response parameters were genus, family, trophic group population density, and percent distribution of trophic groups in the entire nematode community divided into colonizer-persister ranks. The parameters refer only to free-living nematodes, however facultative hyphal-root hair feeding Tylenchidae were included. Cover crops had unique impacts on nematode communities, but these impacts appeared to be associated more with quality of organic matter inputs rather than biofumigation or allelopathy. Across all dates and seasons, and four to nine months after winter-kill, dormant bacterivore (dauer larvae) nematode populations in the forage radish (C/N shoots ~10) plots ranged from 3.5 to 15.7 times higher ($P < 0.10$) than in the control plots. Plant-associate (Tylenchidae) nematodes were 4–6.5 times higher ($P < 0.10$) in rapeseed or rye (C/N shoots ~25) plots compared to the control in June of two experiments. Across experiments fungivore nematode abundance was increased in either rapeseed 'Essex' or rye compared to radishes or the control. Correlations of nematode community groups with cover crop and soil parameters suggested that dauer larvae abundance was associated with soil moisture in radish plots, and tissue quality and quantity at the time of cover crop termination was associated with nematode community response. Canonical discriminant analysis suggested that rapeseed and rye had similar effects on the nematode community composition, as did the two radish cultivars, though distinct from the effect of rye and rapeseed. Overall, results suggest that radishes stimulated a bacterial decomposition pathway, while rapeseed and rye stimulated a proportionally greater fungal-based food web.

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1. Introduction

Brassicaceous cover crop green manures provide multiple benefits to agroecosystems, and research on their impact on free-living nematode communities may help scientists and farmers understand best management practices for optimizing ecological services. Some brassicaceous species are exceptional for nitrogen capture in fall and winter (Kristensen and Thorup-Kristensen, 2004; Kremen, 2006; Dean and Weil, 2009), or for compaction alleviation (Williams and Weil, 2004; Weil and Kremen, 2007). Brassicaceous cover crops are also well known for their biofumigation potential (Matthiessen and Kirkegaard, 2006). Rye has also received interest as a cover crop because of its multiple ecological benefits, including allelopathic effect on weeds (Ercoli et al., 2007) and plant-parasitic nematodes (McBride et al., 2000; Zasada et al., 2007).

Many studies have reported the ecological effects of biomass amendment to soil (including cover crops) on free-living nematode communities (McSorley and Frederick, 1999; Porazinska et al., 1999; Ferris and Matute, 2003; Forge et al., 2003; Ferris et al., 2004; Wang et al., 2004). A few papers have reported on the free-living nematode community after brassicaceous or rye cover crop incorporation (Lundquist et al., 1999; Georgieva et al., 2005a, 2005b), but no published studies were found that describe in detail

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the effects of brassicaceous cover crops on the free-living nematode community.

Aside from taxonomic or trophic groups, Bongers (1990) proposed grouping nematode community members into functional guilds, each weighted with a value reflecting sensitivity to disturbance. According to this protocol, individuals are ranked from 1 to 5, based on their tendency to behave like an opportunistic *r*-selected colonizer (1) or a generalist *K*-selected persister (5). This rank serves as the value for weighting relative abundances of that genus or family. During succession or maturation of a nematode community, c-p 1 enrichment opportunists decline and are replaced by c-p 2 generalists (Ettema and Bongers, 1993). As abundances of c-p 3–5 nematodes increase, c-p 2 nematodes remain as the basal part of the food web. Disturbance of a soil nematode community by addition of N-rich organic amendments is evident by an increase in the abundance of c-p 1 enrichment opportunist nematodes.

We studied the non-target effects of brassicaceous and rye cover crops on the free-living nematode community. We performed the nematode community analysis on a subset of samples from a larger study investigating the pest-suppressive potential of brassicaceous cover crops. We hypothesized that incorporation of biofumigant and allelopathic cover crops would alter the free-living nematode community by increasing the abundances of c-p 2 genera, including those particularly known to be tolerant of pollution or chemicals, while decreasing abundances of c-p 3–5 genera. We expected mustard, rapeseed, and rye cover crops to have unique effects due to purported differences in chemical properties among these species (Matthiessen and Shackelton, 2005; Zasada et al., 2007). A secondary objective of this research was to assess associations between nematode community parameters and soil or crop parameters, in order to aid interpretation of the observed changes in nematode community structure.

2. Materials and methods

2.1. Experiment 1

Experiment 1 was conducted at the University of Maryland Lower Eastern Shore Research and Education Center (LESREC) in Salisbury, MD (N38°22′, W75°39′). The soil transitioned from a Hammonton series (coarse-loamy, siliceous, semiactive, mesic, aquic Hapludult) to a Galestown series (siliceous, mesic, psammentic Hapludult) from east to west across the field. Average surface soil properties (0–15 cm) were loamy sand texture, pH 6.8, and organic matter 9.7 g kg^{-1} ($n = 4$). Sand and clay contents ranged from 83% and 5% at the eastern end to 90% and 3% on the western end. Precipitation, temperature, and supplemental irrigation are shown in Fig. 1.

Experiment 1 was initiated in August 2003, and data collection was completed in fall 2004. Prior to the experiment, the field was cropped with a soybean (*Glycine max*)-corn (*Zea mays*)-wheat (*Triticum aestivum*) rotation, using conventional tillage. Plots were 3 m × 9 m with all planting and tillage operations conducted within individual plot boundaries. The treatments evaluated in this experiment included five brassicaceous cover crops: mustard blend (*Sinapis alba* and *Brassica juncea*) 'Caliente', rapeseed (*B. napus*) 'Essex' and 'Humus', forage radish (*Raphanus sativus*) 'Dichon', oilseed radish (*R. sativus*) 'Adagio', and a weedy control (dominant weeds were chickweed (*Stellaria media*), horseweed (*Conyza canadensis*), henbit (*Lamium amplexicaule*), and pigweed (*Amaranthus* sp.)). Cover crop seeds were broadcast by hand into bare tilled soil on 25 August 2003, and cultipacked. Seeding rates were 4.5 kg ha^{-1} mustard blend, 9 kg ha^{-1} rapeseed, and 14.6 kg ha^{-1} radishes. Cover crops were fertilized with

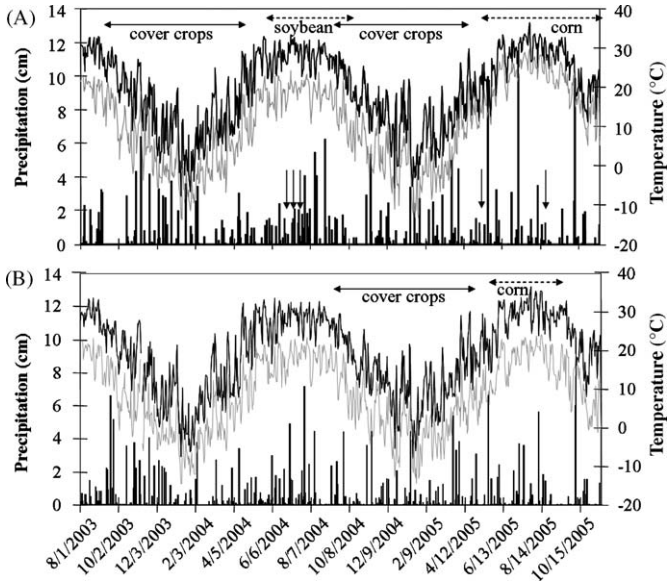

Fig. 1. Daily precipitation and daily average high and low air temperatures for 2003–2005 at (A) Lower Eastern Shore Research and Education Center (LESREC) (Exps. 1 and 2) and (B) Central Maryland Research and Education Center (CMREC) (Exp. 3). Vertical arrows indicate irrigation events (available at LESREC only).

90 kg ha^{-1} N as ammonium sulfate and ammonium nitrate on 15 September 2003, to ensure adequate nitrogen and sulfur nutrition for vigorous cover crop growth. A second application of 45 kg N ha^{-1} as ammonium sulfate was applied on 22 October. Mustard and radishes winter-killed, while rapeseed was cold-tolerant. Cover crop biomass was collected from two 0.25 m^2 quadrats per plot on 18 October 2003 (all cover crops vegetative except mustard which was in full flower) and 28 April 2004 (rye in boot stage and rapeseed in full flower) (Table 1). Winter-surviving cover crops were killed by incorporation when all plots were disked three times and cultipacked on 28 April 2004. A soybean cyst-susceptible, glyphosate tolerant soybean, cultivar 'NK/Syngenta S39Q4', was planted with 38-cm row spacing on 12 May 2004 at a seeding rate of 480,000 seeds ha^{-1}. No further cultivation was performed after cover crop incorporation. To permit data collection on weed establishment for complementary studies, application of glyphosate herbicide (N-(phosphonomethyl) glycine) at a rate of 0.96 L ha^{-1} active ingredient was delayed until 15 June 2004. The soybeans were sidedressed with 36 kg N ha^{-1}, 22 kg P ha^{-1}, and 112 kg K ha^{-1} on 29 June 2004. Soybeans were harvested by combine on 18 October 2004.

2.2. Experiment 2

Experiment 2 was also conducted at LESREC, in the unused middle portion of the same field used for Exp. 1. The experiment was a randomized complete block design with plot size 3 m × 9 m. This area had been kept fallow with repeated disking between fall 2003 and cover crop planting in August 2004. Treatment levels and seeding rates in Exp. 2 were the same as in Exp. 1, except that cold-tolerant rye (*Secale cereale*) 'Wheeler' was included (seeding rate 126 kg ha^{-1}) instead of rapeseed 'Humus'. Cover crops were broadcast by hand on 27 August 2004. Ammonium nitrate was broadcast by hand into cover crop plots on 1 September and 22 September 2004 for a total application of 100 kg N ha^{-1}. Cover crop biomass was collected from two 0.25 m^2 quadrats per plot on 8 or 15 November (all cover crops were vegetative except mustard, which was in full flower) and 13 or 14 April 2005 (rye in boot stage and rapeseed in 50% flower) (Table 1). All plots were mowed and

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Table 1
Cover crop dry matter and percentage N contents before cover crop termination for three experiments at two sites in Maryland.

Experiment	Biomass Harvest Date	Cover Crop[a]	Plant Part (root/shoot)	Dry Matter[b] (kg ha^{-1} ± SEM)	% N ± SEM[c]
Exp. 1	18 October 2003	Forage radish	R	1254 ± 120	ND
		Forage radish	S	3948 ± 651	ND
		Oilseed radish	R	913 ± 36	ND
		Oilseed radish	S	4807 ± 556	ND
		Mustard	R	736 ± 105	ND
		Mustard	S	3995 ± 70	ND
	28 April 2004	Rapeseed Essex	R	2070 ± 364	0.89 ± 0.08
		Rapeseed Essex	S	7474 ± 901	1.73 ± 0.06
		Rapeseed Humus	R	1134 ± 379	0.74 ± 0.04
		Rapeseed Humus	S	5943 ± 630	1.41 ± 0.04
		Control (weeds)	S	4637 ± 969	1.65 ± 0.13
Exp. 2	8 November 2004	Forage radish	R	2258 ± 75	2.00 ± 0.20
		Forage radish	S	3647 ± 441	4.44 ± 0.38
	15 November 2004	Oilseed radish	S	5026 ± 346	ND
	13 April 2005	Rapeseed Essex	S	4620 ± 474	2.89 ± 0.20
		Rye	S	3634 ± 676	2.24 ± 0.38
		Control (weeds)	S	894 ± 160	ND
Exp. 3	30 October 2004	Forage radish	R	2224 ± 500	3.12 ± 0.47
		Forage radish	S	3758 ± 322	3.94 ± 0.25
		Oilseed radish	R	996 ± 84	2.86 ± 0.16
		Oilseed radish	S	3139 ± 629	3.94 ± 0.28
	23 April 2005	Rapeseed Essex	R	1533 ± 788	1.42 ± 0.19
		Rapeseed Essex	S	3140 ± 406	2.66 ± 0.13
		Rye	S	4658 ± 818	1.61 ± 0.11
		Control (weeds)	S	678 ± 99	ND

[a] The cover crop planting date for Exp. 1 was 25 August 2003, and dates for Exp. 2 and Exp. 3 were 27 and 25 August 2004, respectively. Winter-kill dates for radish cover crops were early December 2004 and late December to early January 2005. Spring cover crops were terminated on the cover crop harvest dates in Exps. 1 and 2 and in Exp. 3 were herbicide-killed on 27 April 2005. Data were not available for all treatments.
[b] Values shown are the means of four replicates, except for oilseed radish shoot and forage radish root dry matter in Exp. 3, which had three replicates. ND = not determined.
[c] Values shown are the means of four replicates, except for rapeseed 'Essex' shoots in Exp. 1, which had two replicates. ND = not determined.

tilled by one pass of a chisel plow (15 cm deep) followed by two passes of a disk harrow with solid wheel cultipacker on 13 and 14 April 2005. On 9 May 2005, plots were disked twice, fertilized with 12 kg P ha^{-1}, 84 kg K ha^{-1}, 28 kg S ha^{-1}, 1 kg B ha^{-1}, and sown with glyphosate tolerant corn 'Pioneer 34B62' in 76 cm rows at a rate of 64,000 seeds ha^{-1}. On 10 June 2004, glyphosate herbicide (N-(phosphonomethyl) glycine) was applied at a rate of 0.62 L ha^{-1} active ingredient. A total of 134 kg N ha^{-1} (as a urea-ammonium nitrate solution) was applied to the corn, half on 13 June and half on 24 June 2005. In response to spider mite infestation, the pesticide cyhalothrin, lambda ((RS)-alpha-cyano-3-phenoxybenzyl 3-(2-chloro-3,3,3-trifluoropropenyl)-2,2,-dimethylcyclopropanecarboxylate) was sprayed at a rate of 0.03 L ha^{-1} active ingredient on 15 July 2004. Corn was combine-harvested on 26 September 2004.

2.3. Experiment 3

Experiment 3 was conducted at the Central Maryland Research and Education Center (CMREC) in Laurel, MD (N39°1′, W76°51′). The soils transitioned from a Rosedale series (loamy, siliceous, semiactive, mesic Arenic Hapludult) at the northern end to an Evesboro series (mesic, coated-lamellic Quartzipsamment) at the southern end of the field. Surface soil texture was a loamy sand throughout the field (86% sand, 4% clay; $n = 4$) with pH 6.5 (September 2003) and organic matter 16.9 g kg^{-1}.

Experiment 3 was initiated in August 2004, as a randomized complete block design, and completed in fall 2005. The field was no-till managed for five years prior to the experiment and remained in no-till management during the experiment. Wheat was grown in the winter of 2002–2003, and no cover crop was grown during the winter of 2003–2004. Soybeans planted in spring 2004, were mowed on 18 August 2004 (growth stage R6 or early pod fill) and the residue was left to provide an organic source of nitrogen (208 kg N ha^{-1}) to ensure adequate cover crop growth. Cover crop treatments were no-till drilled on 25 August 2004 and included rapeseed 'Essex' (8 kg ha^{-1}), forage 'Dichon' and oilseed 'Colonel' radishes (16.5 kg ha^{-1}), rye 'Wheeler' (126 kg ha^{-1}), and a weedy control (dominant weeds were henbit, chickweed, pygmy flower (*Androsace septentrionalis*), creeping veronica (*Veronica filiformis*), and unidentified winter rosettes). Plot size and orientation of operations were the same as in Exps. 1 and 2.

Cover crop plant biomass was determined from two 0.25 m^2 quadrats per plot on 30 October 2004 (all cover crops in vegetative growth stage) and on 23 April (rye in early boot stage and rapeseed in 50% flower) (Table 1). All plots were treated with herbicide (N-(phosphonomethyl) glycine) at 2.3 L ha^{-1} active ingredient on 27 April 2005, to facilitate termination of winter-surviving cover crops. Lime was surface-applied on 5 May 2005, at a rate of 1100 kg ha^{-1} based on soil test recommendations for the entire field. Corn (Pioneer '34B62') was planted on 10 May 2005 in 76-cm wide rows at a rate of 65,000 seeds ha^{-1} and a second application of the same herbicide was applied on 4 June at a rate of 1.7 L ha^{-1} active ingredient. Corn was fertilized with 146 kg ha^{-1} N using 30% urea–nitrate dribbled between the rows on 15 June 2005. Corn silage yield in each plot was determined on 12 September 2005, by hand-harvesting 3 m of each of the two center corn rows.

2.4. Soil and crop sampling and analysis

Soil samples, to a depth of 15 cm, were collected in April (select treatments), June, and September 2004 in Exp. 1; June and August 2005 in Exp. 2; and November 2004 (select treatments), June and August 2005 in Exp. 3. All soil samples were taken at least 60 cm or more distance from the plot borders and within 8 cm of the stem of cover crop or cash crop plants. Twelve, 2.3 cm-diameter subsample

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cores were collected from each plot. Samples were transported to the laboratory in coolers and kept at 6 °C for 1–5 days before nematode extraction. To determine bulk density for each sample, the entire composite soil sample was weighed prior to opening the plastic bags in which samples were sealed, and field water content was determined gravimetrically on a small subsample.

Shoot biomass was collected for all cover crop treatments, while root biomass was only collected for radishes, mustard, and rapeseed. Plants were gently pulled out of the sandy soil, washed, separated between root and shoot (all parts-leaves, stems, flowers when present), and then dried in forced draft ovens at 60 °C for 3+ days. Select samples were weighed for calculation of total dry biomass, and then ground and sieved to <1 mm. Sub-samples of select treatments were prepared for total N analysis by a LECO CHN-2000 analyzer (LECO Corporation; St. Joseph, Michigan) (Campbell, 1992).

2.5. Nematode extraction and identification

Nematode soil samples, sealed in plastic bags, were gently crumbled and mixed before a 300 cm^3 subsample was removed and weighed. Nematodes were extracted using a modified Baermann funnel technique (48 h extraction period) (Christie and Perry, 1951), with stacked 20- and 325-mesh sieves (850 μm and 45 μm, respectively). Samples were stored at 4 °C for 12–72 hrs before removing 15 ml of supernatant water from 20-ml samples. Five ml of 10% formaldehyde with 0.1% glycerol was added to the remaining 5 ml of sample at 55–65 °C (Grewal et al., 1990). Alternatively, some samples were prepared by adding 4 ml of the fixative and 1 ml of a 5% streptomycin solution (K.-H. Wang, personal communication, 2004) to the 5 ml nematode sample. Preserved samples were stored at 6 °C.

Nematode community identification was primarily conducted at 400–1000× magnification. Slides were prepared by sampling an aliquot size estimated to have at least 150 ± 15 free-living nematodes (not including dauer larvae); additional aliquots were taken if necessary. Each aliquot was centrifuged at 1700 rpm for 3 min, allowed to settle, and the supernatant removed. The remaining nematode pellet was placed on a slide and sealed with clear nail polish. Nematodes were identified to genus level when possible (Bongers, 1988). Analysis was conducted on free-living nematodes only, including facultative hyphal-root hair feeding Tylechidae. Total number of nematodes m^{-2} was calculated by using data for field soil bulk density, field soil water content, mass of soil sub-sampled in the lab (for nematode extraction), and the proportional volume of nematodes counted. Dauer larvae (Fuchs, 1915) can be identified by the presence of a double cuticle and lipid reserves in the body. In this study, the double cuticle was most noticeable in the buccal cavity or when the outer cuticle of the preserved specimen was loose.

2.6. Experimental design and statistical analysis

All experiments were randomized complete block designs, with five or six treatment levels and four replications. Cover crop treatments were explanatory variables and block was a random factor. Data were analyzed using SAS 9.1 (SAS Institute Inc., Cary, NC, USA) software. Nematode response variables, genus/family abundance and trophic group abundance, were transformed ($\ln(x + 1000)$ or $\mathrm{sqrt}(x + 1000)$) as needed to meet assumptions of normality and homogeneity of variance. Analysis of variance (ANOVA) was performed using the SAS MIXED procedure or the GLIMMIX procedure (with negative binomial distribution and logit function). Variance grouping using the REPEATED statement of the MIXED procedure was used when the Null Model Likelihood Ratio Test indicated a better fit of the model with grouped residual variances ($P < 0.10$) (Littell et al., 2006, pp. 170, 352). Pairwise multiple mean comparisons of the response variables were made after significant overall *F*-test using the Tukey (HSD) method. Analysis of covariance (MIXED procedure) with initial populations was performed for *Coslenchus*, and letter assignments in Exp. 1 reflect this analysis. Some nematode parameters were analyzed across time using repeated measures ANOVA, in the SAS MIXED procedure with REPEATED option. In cases of significant interaction between cover crop and time, data were analyzed as a split-plot in time (two dates) or separately by date.

Canonical Discriminate Analysis (CDA) was performed using the SAS CANDISC procedure. The analysis was performed first on experiments where the winter-killed mustard treatment was included and secondly from experiments where rye was included, with the response variable as percent distribution of free-living c-p trophic groups in the entire nematode community. Data from the June sampling dates were transformed ($\mathrm{arcsine}(\mathrm{sqrt}(x + 0.01))$) prior to analysis. Variables that were not normally distributed were eliminated from the CDA to prevent distortion of results. Fungivores and plant-associates were lumped into one category since plant-associates are considered facultative fungal-feeders, they share the same c-p score or guild, and their percentages were normally distributed when grouped together. Canonical variables (CANVARs) are linear functions derived by assigning coefficients to each trophic group variable such that the CANVAR will maximally discriminate between cover crop means. The importance of the response variables in the construction of the CANVARs is shown by the correlation coefficients (loadings) between the nematode responses and the canonical variable.

3. Results

3.1. Cover crop effects on nematode community composition

Cover crop dry matter quantities and percentage N contents are presented in Table 1. The free-living nematode communities were similar across the three experiments (Table 2), and cover crops had unique and lasting impacts on these communities. Canonical discriminant analysis showed the unique impacts of the cover crops on the free-living nematode community from June sampling dates (Fig. 2). Analyses of Exps. 1 and 2 showed distinct separation of the radish cover crops from the other treatments by canonical variable 1 (CANVAR 1) ($P < 0.0001$) and separation of rapeseed 'Essex' from mustard and the control by CANVAR 2 ($P < 0.03$) (Fig. 2A). Dauer larvae, c-p 2 fungivores and plant-associates, c-p 2 bacterivores, and c-p 4 omnivores contributed most to this discrimination (Table 3). Results for Exps. 2 and 3, which included a rye cover crop and not mustard, also showed distinct separation of the radish cover crops from the other treatments by CANVAR 1 ($P < 0.0001$), and separation of the control from rye and rapeseed by CANVAR 2 ($P < 0.06$) (Fig. 2B). Dauer larvae, c-p 2 fungivores and plant-associates, c-p 2 bacterivores, c-p 4 omnivores, and c-p 4 predators contributed most to this discrimination (Table 3). CANVAR 1 and 2 represented 72% and 26% of the variation in Fig. 2A and 75% and 21% of the variation in Fig. 2B, respectively.

Tables 4–6 present abundances of those genera, families, or trophic groups that were affected by cover crop treatments on at least one sampling date. Forage and oilseed radishes stimulated the abundance of dauer larvae (Tables 4–6). In June, across all experiments, dauer larvae abundance was greater in radish plots than control plots ($P < 0.01$). The effect was consistent in late summer, though less significant (Exp. 1, $P < 0.10$; Exp. 2, $P < 0.01$; Exp. 3, $P < 0.05$). In oilseed radish plots, dauer larvae abundance was 2.5–9.9 times higher than in the control plots in April or June, across experiments (Exp 1, $P < 0.01$; Exp. 2, $P < 0.10$; Exp. 3, $P < 0.05$).

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Table 2
Nematode family, genera, or subgenera identified across all dates and experiments, from two sites in Maryland.

Bacterivores[a]	Fungivores	Omnivores	Predators	Algivores	Plant-associates
Acrobeles (2)[b]	*Aphelenchoides* (2)	*Aporcelaimellus* (5)	*Anatonchus* (4)	*Achromadora* (3)	*Boleodorus* (2)
Acrobeloides (2)[c]	*Aphelenchus* (2)	Dorylaimidae (4)	*Clarkus* (4)		*Coslenchus* (2)
Alaimus (4)	*Diphtherophora* (3)	*Ecumenicus* (4)	*Discolaimus* (5)		*Ditylenchus* (2)
Amphidelus (4)	Leptonchidae (4)[g]	*Lordellonema* (4)	*Mylonchulus* (4)		*Filenchus* (2)
Anaplectus (2)	*Leptonchus* (4)	*Mesodorylaimus* (4)	*Nygolaimus* (5)		*Laimaphelenchus* (2)
Bastiana (3)	*Tylolaimophorus* (3)	*Microdorylaimus* (4)	*Paractinolaimus* (5)		*Miculenchus* (2)
Bunonema (1)			*Paraxonchium* (5)		*Psilenchus* (2)
Ceratoplectus (2)			Predator (3)[h]		Tylenchidae (2)
Cervidellus (2)			Qudsianematidae (4)[i]		
Cruznema (1)			*Seinura* (2)		
Cylindrolaimus (2)			*Thonus* (4)		
Diploscapter (1)					
Drilocephalobus (2)					
Eumonhystera (2)					
Mesorhabditis (1)					
Odontolaimus (3)					
Panagrolaimidae (1)[d]					
Plectus (2)					
Prismatolaimus (3)					
Pristionchus (1)					
Rhabditidae dauer larvae					
Rhabditidae 1 (1)[e]					
Rhabditidae 2 (1)[f]					
Rhabditis (1)					
Teratocephalus (3)					
Tylocephalus (2)					
Wilsonema (2)					
Zeldia (2)					

[a] Trophic groups assigned primarily according to Yeates et al. (1993).
[b] Numbers in parentheses signify colonizer-persister ranks assigned according to Bongers and Bongers (1998).
[c] Included some individuals of other genera such as *Cephalobus*.
[d] Included Panagrolaimus and Panagrobelus.
[e] Included Protorhabditis and Prodontorhabditis.
[f] Included other unidentified Rhabditidae.
[g] Included Tylencholaimus and Tylencholaimellus.
[h] Included c-p 3 predators.
[i] Represented an unknown nematode genera in this family.

Rapeseed and rye cover crops increased populations of the plant-associate (facultative hyphal-feeder) *Coslenchus* across sites (Tables 4–6). In Exp. 1, analysis with initial populations as a covariate revealed a greater abundance of *Coslenchus* in rapeseed 'Essex' plots compared to oilseed radish plots only in April ($P < 0.04$). In June of Exp. 2 *Coslenchus* populations in rye plots were higher than in radishes, mustard and control plots ($P < 0.04$), and populations in rapeseed plots were higher than in the radish ($P < 0.01$) and control plots ($P < 0.10$). In August of Exp. 2 the abundances of *Coslenchus* in rye and rapeseed were higher than in forage radish plots ($P < 0.02$), and populations in rye were also higher than in oilseed radish plots ($P < 0.05$). *Coslenchus* populations in the control plots were higher than those in forage radish plots ($P < 0.04$). In November of Exp. 3, during cover crop growth, *Coslenchus* populations were higher in the control than in radish and rapeseed plots ($P < 0.10$). In both June and August of Exp. 3, rapeseed and rye plots had higher *Coslenchus* populations than forage radish, oilseed radish, and the control plots ($P < 0.01$).

Fungivore abundance in rapeseed 'Essex' plots was on average 2.8 times higher than in the oilseed radish plots in Exp. 1, across time ($P < 0.10$). Abundance of cp-2 fungivores, primarily *Aphelenchoides*, contributed to this effect (Table 4), and populations

Table 3
Correlation coefficients (loadings) of trophic group variables with canonical variables (CANVARs) 1 and 2, depicted in Fig. 2.

Nematode taxa	Exps. 1 and 2 Total canonical structure		Nematode taxa	Exps. 2 and 3 Total canonical structure	
	CANVAR 1	CANVAR 2		CANVAR 1	CANVAR 2
Dauer larvae	0.82****	0.30†	Dauer larvae	0.90****	−0.26
Bacterivores cp-2	−0.42**	−0.28†	Bacterivores c-p-1	−0.03	−0.22
Bacterivores cp-4	0.09	−0.31†	Bacterivores c-p-2[a]	−0.57****	0.50***
Plant-associates and fungivores c-p 2	−0.69****	0.53***	Bacterivores c-p-4	−0.05	0.32*
Fungivores cp-3	−0.22*	−0.01	Plant-associates and fungivores c-p 2	−0.91****	−0.36*
Omnivores cp-4	−0.17	−0.41**	Fungivores c-p-4	0.14	0.14
Predators cp-5	0.10	−0.20	Omnivores c-p 4	−0.09	0.72****
			Predators c-p-4	−0.21	0.47**
			Predators c-p-5	−0.02	0.26†

[a] Data were arcsin(square root (x + 0.01)) transformed to meet the assumptions of normality except this variable which was already normally distributed.
† $P \leq 0.10$.
* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.
**** $P \leq 0.0001$.

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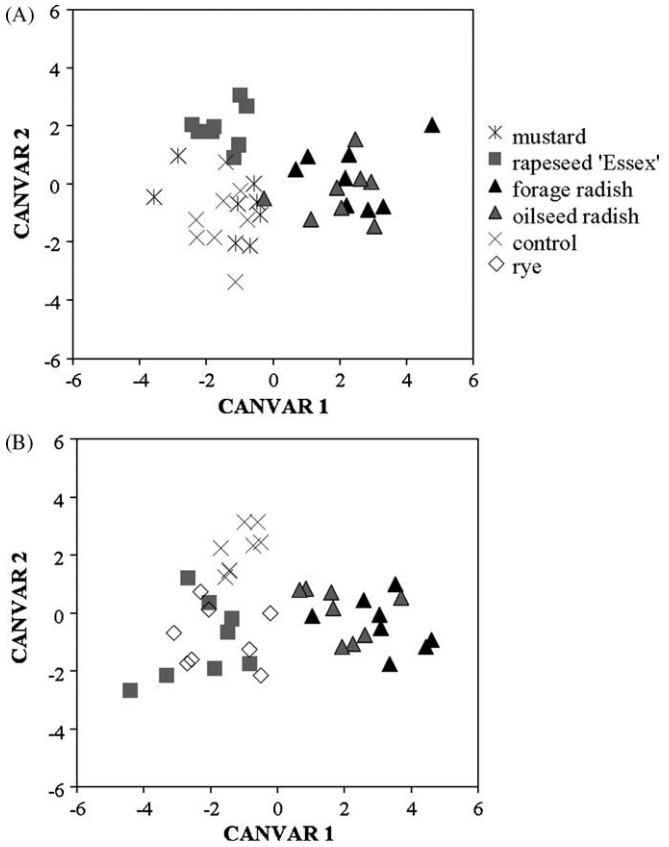

Fig. 2. Canonical discriminant analysis (CDA) of cover crop treatments, with response variable percent distribution of free-living c-p trophic groups in the entire nematode community for Exps. 1 and 2 (A) and Exps. 2 and 3 (B) sampled in June.

were higher in rapeseed 'Essex' plots across dates compared to oilseed radish ($P < 0.02$) and forage radish ($P < 0.10$) plots. In Exp. 2, total fungivore abundance was 4.0–9.8 times greater in rye plots than other treatments (except rapeseed 'Essex') in June ($P < 0.10$) and 2.6–3.7 times greater in rye plots than mustard ($P < 0.09$), forage radish ($P < 0.01$) or the control ($P < 0.05$) plots in August (Table 5). Differences in Exp. 2 were also primarily the effect of *Aphelenchoides*. In Exp. 3, abundance of fungivores in rapeseed 'Essex' plots (142×10^3 nematodes m^{-2}) was greater than in forage radish (82×10^3 nematodes m^{-2}; $P < 0.01$), oilseed radish (92×10^3 nematodes m^{-2}; $P < 0.04$), or the control plots (96×10^3 nematodes m^{-2}; $P < 0.06$) across time. Rye plots had 2.3–2.6 times more fungivores than forage or oilseed radish plots in August ($P < 0.04$) (Table 6).

3.2. Associations between cover crop or soil parameters and nematode community composition

In Exp. 1, total cover crop biomass (in October) of winter-killed cover crops was correlated positively with dauer larvae abundance in June (Fig. 3A), though not in September ($r = 0.341$, $P = 0.278$, $n = 12$). In Exp. 2, there was no correlation between dauer larvae abundance and cover crop shoot biomass in June ($r = 0.130$, $P = 0.687$, $n = 12$) or August ($r = 0.341$, $P = 0.278$, $n = 12$). However, populations of dauer larvae in June ($r = 0.672$, $P < 0.02$, $n = 12$) and August were positively correlated with cover crop shoot N biomass (kg ha^{-1}) (using samples from 8 November for radishes and 18 April for rapeseed and rye) (Fig. 3B). Correlations between dauer larvae and soil moisture content were observed in two experiments and were strongest in radish plots (Fig. 3C and D).

Table 4
Abundances (10^3 m^{-2}) of nematode genera, family, or trophic groups that were affected by cover crops on at least one of the three sampling dates in Experiment 1.

Nematode group or genera[a]	Stats[b]	21 April 2004				11 June 2004						19 September 2004					
		Rape essex	Forage radish	Oilseed radish	Control	Must	Rape essex	Rape humus	Forage radish	Oilseed radish	Control	Must	Rape essex	Rape humus	Forage radish	Oilseed radish	Control
Bacterivores																	
Cylindrolaimus (2)	ln Apr; sqrt Jun/Sep	38.4 ab[c]	64.3 a	88.3 a	20.6 b	16.0	11.9	7.6	28.5	17.6	13.4	10.8	12.6	12.7	26.0	15.4	15.4
Dauer larvae (1)	ln Apr/Jun/Sep	48.8 c	1096.7 a	338.4 b	70.0 c	254.3 c	328.8 bc	341.8 bc	752.7 ab	868.8 a	146.4 c	116.7 ab	182.1 ab	118.5 ab	330.2 a	237.3 ab	84.4 b
Panagrolaimidae (1)	nbin Apr	227.8	137.3	137.5	170.9	143.4	252.6	239.1	204.5	323.3	298.2	65.8 b	99.5 ab	165.1 a	90.3 ab	111.7 ab	86.8 ab
Fungivores																	
Aphelenchoides (2)	ln Apr/Sep	59.8 a	20.5 ab	15.0 b	42.9 ab	81.1 b	244.6 a	108.6 ab	101.7 ab	59.3 b	95.8 ab	46.9	128.9	28.8	38.8	56.8	27.9
Leptonchus (4)	sqrt Sep	101.8 a	98.7 a	56.4 ab	37.2 b	154.1	183.9	162.2	99.7	107.8	107.5	16.5	26.8	28.5	12.2	24.7	33.3
Total	ln Jun	262.7	242.2	151.7	200.3	435.9 ab	851.9 a	662.8 ab	370.8 ab	308.5 b	383.0 ab	181.2	241.8	124.1	112.1	123.2	130.5
Plant-associates																	
Coslenchus (2)	ln Apr; sqrt Jun/Sep	368.6 a	29.3 b	29.9 b	23.9 b	34.8 ab	242.1 a	228.4 ab	8.9 b	40.1 ab	17.8 b	20.4	188.2	85.1	5.9	10.0	16.3
Tylenchidae (2)	ln Jun	127.3 a	55.0 b	75.4 ab	84.3 ab	20.5	28.2	4.8	14.4	18.4	13.9	2.1	0.0	1.7	3.9	0.0	9.8
Total	ln Jun	519.8 a	104.7 b	124.3 b	131.2 b	80.5	321.7	264.8	98.0	96.1	89.9	56.0 b	202.4 a	121.0 ab	32.5 b	20.5 b	79.9 b
Omnivores																	
Ecumenicus (4)		23.5	34.4	10.8	27.7	97.6	59.4	60.0	112.8	62.9	84.5	2.9 ab	7.1 ab	15.7 a	0.0 b	0.0 b	9.3 ab

[a] Colonizer-persister scores are in parentheses according to Bongers and Bongers (1998).
[b] Data presented are untransformed means of four replications. Statistics applied are indicated by date and included: ln = ln(x + 1000), sqrt = sqrt(x + 1000), or nbin = negative binomial distribution.
[c] Means with the same letter within a single date and row are not significantly different at $P < 0.10$ (HSD).

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Table 5
Abundances (10^3 m^{-2}) of nematode genera, family, or trophic groups that were affected by cover crops on at least one of the two sampling dates in Experiment 2.

Nematode group or genera[a]	Stats[b]	4 June 2005						20 August 2005					
		Must	Rape essex	Forage radish	Oilseed radish	Control	Rye	Must	Rape essex	Forage radish	Oilseed radish	Control	Rye wheeler
Bacterivores													
Acrobeles (2)	lnJun	21.8	149.4	20.7	22.1	14.5	19.9	19.4 ab	3.1 b	32.7 a	8.4 ab	13.1 ab	6.3 b
Acrobeloides (2)		507.2 b [c]	364.9 b	350.6 b	331.6 b	466.7 b	1149.2 a	47.2	47.5	62.3	44.4	61.4	57.1
Anaplectus (2)	lnJun	70.2 a	41.1 ab	32.6 a	2.1 b	0.0 b	87.0 ab	33.8	30.2	29.4	3.8	9.3	37.4
Ceratoplectus (2)	lnJun	0.0	0.0	6.3	3.4	9.3	8.1	9.9 ab	3.2 ab	8.5 ab	11.5 a	2.0 ab	0.0 b
Dauer larvae	lnAug	328.4 c	928.6 ab	1370.5 a	981.5 a	390.6 bc	840.3 abc	196.6 bc	493.6 ab	585.3 a	266.4 abc	97.5 c	356.6 ab
Panagrolaimidae (1)		87.5 b	86.4 b	201.7 b	143.0 b	95.0 b	639.2 a	36.6	52.9	55.2	41.1	35.7	62.1
Rhabditidae 1 (1)		1.9	9.9	1.6	6.0	2.0	4.1	0.8 b	7.7 ab	0.9 b	2.4 ab	2.3 ab	14.9 a
Rhabditidae 2 (1)	lnJun	4.0 ab	7.9 ab	0.0 b	4.2 ab	0.0 b	31.7 a	0.0	0.0	0.9	2.8	1.3	1.2
Total	Aug v	1261.3 b	1930.7 b	2255.2 b	1742.2 b	1233.2 b	3388.6 a	559.6 ab	943.0 ab	962.7 ab	575.8 ab	392.5 b	795.6 a
Total (without dauer)		932.8 bc	1002.1bc	884.6 b	760.7 bc	842.6 c	2548.3 a	363.0	449.4	377.4	309.4	295.0	439.0
Fungivores													
Aphelenchoides (2)	lnJun v	151.9 bc	260.0 ab	122.3 bc	58.7 c	130.7 bc	1189.6 a	27.5 b	69.9 ab	25.0 b	19.2 b	24.1 b	167.8 a
Diphtherophora (3)	sqrt Jun	19.6	23.5	11.7	11.7	30.4	55.2	11.5 c	18.3 bc	31.1 ab	40.9 a	35.5 ab	45.3 a
Leptonchidae (4)		9.6	7.6	11.5	12.4	0.0	3.6	8.9 ab	0.9 b	0.8 b	15.4 a	5.3 ab	6.3 ab
Leptonchus (4)		33.6 ab	17.1 b	40.9 ab	15.6 b	30.5 ab	66.1 a	37.4 ab	44.0 ab	15.12 b	40.5 ab	14.4 b	63.5 a
Total	lnJun	338.3 bc	404.1 ab	211.3 bc	138.0 c	298.9 bc	1356.3 a	111.3 b	156.1 ab	77.6 b	122.8 ab	103.7 b	289.2 a
Plant-associates													
Coslenchus (2)	lnJun v; lnAug v	224.0 bc	590.7 ab	24.7 d	71.9 cd	146.2 bc	713.8 a	70.8 abc	238.5 ab	25.8 c	36.8 bc	125.0 ab	403.8 a
Total	Jun v; sqrt Aug v	276.2 ab	671.1 a	98.1 b	150.0 b	208.8 ab	773.2 a	120.9 bc	260.3 bc	42.4 c	49.7 bc	140.0 ab	443.3 a
Predators													
Mylonchulus (4)	lnJun, Aug	17.7 ab	23.3 ab	4.1 c	35.3 a	16.5 ab	8.0 bc	6.4	14.6	10.7	12.3	17.8	10.1
Total	Aug v	2245.3 b	3404.7 b	2946.2 b	2359.8 b	2221.2 b	6153.5 a	1495.5 ab	1939.9 ab	1604.5 ab	1315.2 ab	1124.2 b	1797.2 a
Total (without dauer)		1916.9 b	2476.1 b	1575.6 b	1378.2 b	1830.6 b	5313.2 a	1298.9	1446.2	1019.2	1048.9	1026.7	1440.6

[a] Colonizer-persister scores in parentheses according to Bongers and Bongers (1998).
[b] Data presented are untransformed means of four replications. Statistics applied are indicated by date and included: $ln = \ln(x + 1000)$, sqrt = sqrt(x + 1000), or v = variance grouping.
[c] Means with the same letter within a single date and row are not significantly different at $P < 0.10$ (HSD).

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Table 6
Abundances (10^3 m^{-2}) of nematode genera, family, or trophic groups that were affected by cover crops on at least one of the three sampling dates in Experiment 3.

Nematode group or genera[a]	Stats[b]	3 November 2004				11 June 2005					17 August 2005				
		Rape essex	Forage radish	Oilseed radish	Control	Rape essex	Forage radish	Oilseed radish	Control	Rye	Rape essex	Forage radish	Oilseed radish	Control	Rye
Bacterivores															
Alaimus (4)	ln Jun sqrt Aug	29.2	26.5	22.3	49.9	12.8 ab[c]	4.1 c	13.1 ab	22.3 bc	31.0 a	15.4	19.8	10.4	18.5	14.3
Acrobeloides (2)	ln Jun	128.0	65.6	123.4	98.2	66.6 ab	17.5 b	48.0 abc	27.6 ab	68.4 a	40.5	39.0	23.2	40.5	44.5
Dauer larvae	sqrt Jun; ln Aug v	113.3	80.0	98.7	76.3	66.0 c	1199.6 a	893.6 ab	90.1 c	483.9 bc	73.2 b	702.3 a	675.6 a	95.1 b	136.1 b
Tylocephalus (2)	sqrt Nov	3.2	9.2	1.3	24.6	3.9 ab	3.8 ab	4.7 ab	9.6 a	0.8 b	6.9	5.6	7.7	14.2	4.1
Wilsonema (2)	ln Jun	2.5	8.0	3.5	9.6	0.0 b	0.0 b	0.0 b	2.1 ab	8.5 a	0.0	2.0	0.0	0.0	0.0
Total		698.2	548.4	600.2	703.0	511.5 bc	1446.3 ab	1317.8 a	482.1 c	960.8 abc	410.1 b	947.0 a	854.4 ab	384.9 b	483.2 ab
Total (without dauer)	Aug v	585.0	468.5	501.5	626.7	445.5	246.7	424.3	392.0	476.9	336.9 a	244.8 ab	178.7 b	289.8 ab	347.1 a
Fungivores															
Aphelenchoides (2)	sqrt Jun	27.8 ab	28.2 ab	50.9 a	14.2 b	12.3	10.7	8.1	8.2	12.3	20.8	20.6	12.8	11.3	25.3
Diphtherophora (3)	ln Aug	59.0	29.0	41.3	39.9	40.8 ab	27.1 ab	24.6 b	29.8 ab	76.0 a	71.6 abc	41.0 c	55.4 bc	85.0 ab	164.7 a
Total		145.7	99.3	122.3	92.6	125.3	70.5	65.3	77.7	96.0	154.6 ab	75.1 b	86.9 b	125.2 ab	197.2 a
Plant-associates															
Coslenchus (2)	ln Jun v; Aug v	43.3 b	41.6 b	37.3 b	89.9 a	575.5 a	18.8 c	77.2 b	87.2 b	466.7 a	482.9 a	48.3 b	53.6 b	72.9 b	545.1 a
Total	ln Jun; Aug v	61.0	58.3	57.9	120.4	598.3 a	21.4 c	113.7 b	104.1 b	487.6 a	500.2 a	59.8 b	84.3 b	106.2 b	567.6 a
Omnivores															
Aporcelaimellus (5)		32.5	20.5	34.0	25.8	39.7 ab	33.2 b	78.8 a	68.6 ab	29.2 b	29.8	33.8	30.3	31.4	21.4
Mesodorylaimus (4)	ln Nov/Jun Jun v	21.6	17.6	7.9	22.6	38.8 ab	43.0 ab	53.6 ab	68.5 a	24.4 b	49.3 ab	26.1 b	44.9 ab	38.8 b	98.2 a
Predators															
Mylonchulus (4)	ln Jun/Aug	61.4 a	24.4 ab	13.4 b	35.9 ab	41.4	22.5	11.2	61.2	48.5	21.7	35.2	10.3	14.0	32.0
Total (without dauer)	sqrt Aug v	1295.5	1026.9	1056.1	1288.6	1608.5 ab	794.1 c	1145.8 abc	1140.3 bc	1754.4 a	1855.3	1210.4	1119.0	1340.1	1803.3

[a] Colonizer-persister scores in parentheses according to Bongers and Bongers (1998).
[b] Data presented are untransformed and are means of four replications. Statistics applied are indicated by date and included: ln = ln(x + 1000), sqrt = sqrt(x + 1000), or v = variance grouping.
[c] Means with the same letter are not significantly different within a single date and row at $P < 0.10$ (HSD).

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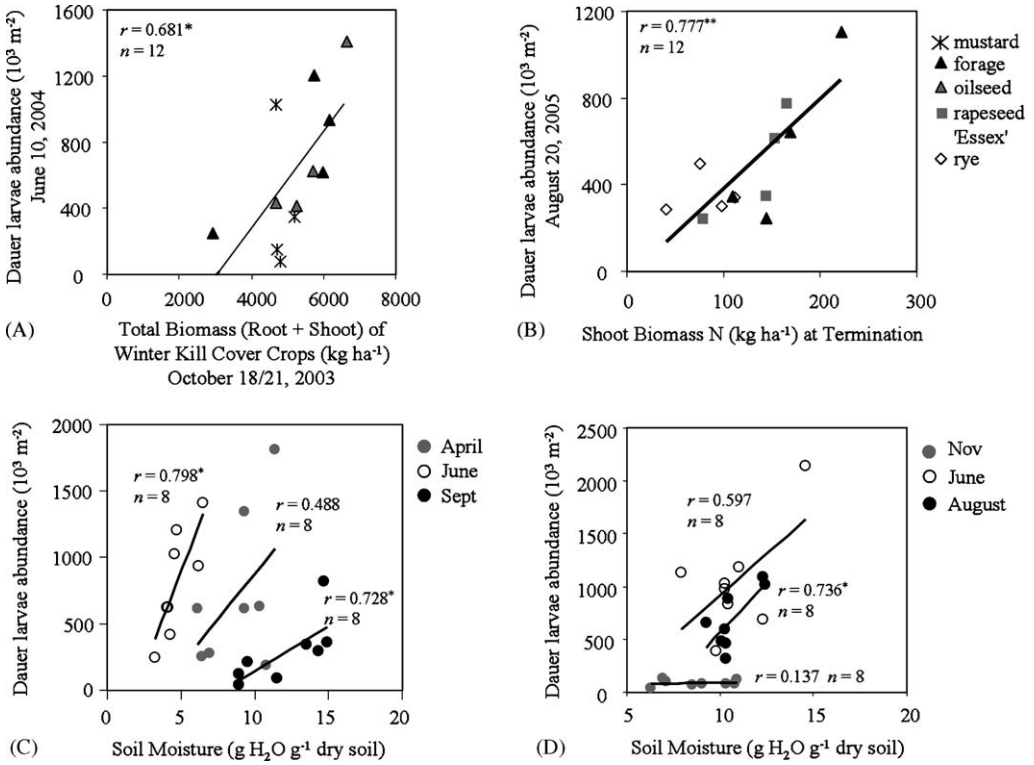

Fig. 3. Correlations between dauer larvae nematode abundances and cover crop parameters (A and B) or soil moisture (C and D) from Exp. 1 (A and C), and Exp. 3 (B and D). The words 'at termination' refer to the biomass sampling prior to winter-freeze or spring-termination. $^{*}P \leq 0.05$ and $^{**}P \leq 0.01$.

Populations of plant-associates also correlated with crop properties (Fig. 4). In Exp. 2, plant-associate abundance in June and August was negatively correlated with the N concentration in cover crop shoot tissue prior to termination (Fig. 4A and B). However, there was little correlation with cover crop shoot biomass alone in June ($r = -0.0138$, $P = 0.966$, $n = 12$) or August ($r = -0.210$, $P = 0.512$, $n = 12$). In Exp. 3, plant-associate abundances in November (Fig. 4C), June (Fig. 4D), and August

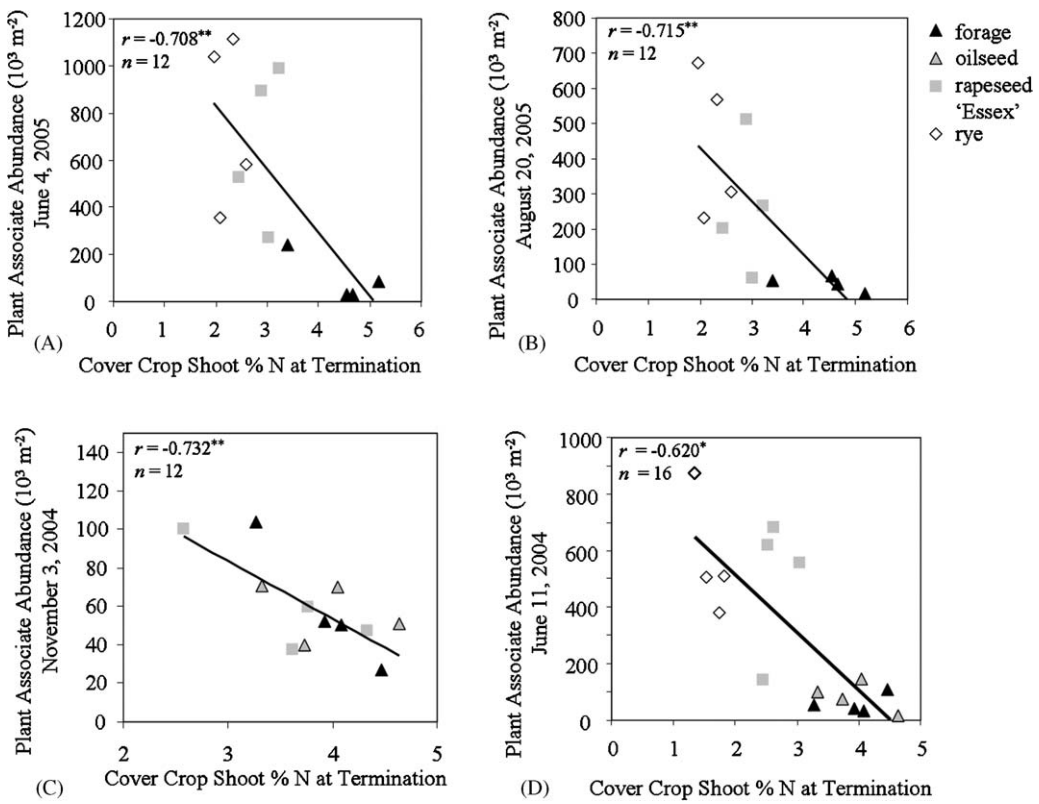

Fig. 4. Correlations between plant-associate nematode abundances and cover crop parameters from Exp. 2 (A and B) and Exp. 3 (C and D). The words 'at termination' refer to the biomass sampling prior to winter-freeze or spring-termination. $^{*}P \leq 0.05$ and $^{**}P \leq 0.01$.

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($r = -0.780$, $P < 0.001$, $n = 16$) were negatively correlated with percent N content of cover crop shoot tissue sampled in late October.

4. Discussion

4.1. Cover crop effects on nematode community composition

Free-living nematode response to cover crops was evident four to nine months after cover crop termination (Fig. 2; Tables 4–6). Other studies have shown that nematode communities can reflect plant or amendment identity (De Deyn et al., 2004; Viketoft et al., 2005; Wardle et al., 2006), and several have shown that amendments can have impacts on nematode communities detectable after months and sometimes persisting for years (Ferris and Matute, 2003; Forge et al., 2003; Ferris et al., 2004). We believe this is the first study to show in detail the impact of brassicaceous cover crops on the genera within free-living nematode communities.

Canonical discriminant analysis showed the primary influence of the cover crops was on dauer larvae and plant-associates/c-p 2 fungivores (Fig. 2). Separation of the control due to higher c-p ranked groups suggests more stability in those plots. Since plots within an experiment were treated with the same tillage regime, the disturbance effects observed were probably due to enrichment. Discrimination of mustard from radishes (Fig. 2; Table 3) suggests that mustard may have had attributes more similar to rapeseed and rye. Mustard was in full bloom prior to winter-kill and lignacious stalks remained standing through winter. In addition, lack of separation between rye and rapeseed in CDA (Fig. 2), despite strong differences in cover crop attributes (root morphology, cold tolerance, and chemistry) suggests that the influence of C/N ratio (~10 radish shoots; ~25 rye and rapeseed shoots) may be one of the strongest properties driving the biological effects of cover crops. Future studies should include a fine-rooted, high carbon cover crop such as winter-killing oats, to better evaluate the effect of termination date on the nematode community.

4.2. Biofumigant or allelopathic effects

Clear indications of biofumigant or allelopathic effects on free-living nematodes were not observed in this study. *Aphelenchoides* is known to be stress tolerant (Georgieva et al., 2002) and rapeseed or rye increased its abundance on some dates (Tables 4–6). However, one would also expect to see a decline of c-p 3–5 nematodes in conjunction with these changes, if there was a negative biological effect (Ettema and Bongers, 1993). Tables 4–6 show there were no changes in abundances of predators or omnivores as a trophic group from these treatments.

Fiscus and Neher (2002) identified *Cylindrolaimus*, *Discolaimus*, *Mesorhabditis*, *Odontolaimus*, *Prismatolaimus*, and *Protorhabditis* as the genera most sensitive to direct chemical treatment. All of these genera were present at these experimental sites; however, the only treatment effects detected were on the abundance of *Cylindrolaimus* and the Rhabditidae group that included *Protorhabditis*, and in both cases the effects were not likely to be indicators of chemical toxicity due to the treatments involved. An effect on *Acrobeles*, identified by Wang et al. (2006a) as sensitive to methyl bromide fumigation, was observed at only one sampling date under rapeseed and rye. This effect, observed four months after incorporation, is unlikely to be evidence of biofumigation, but rather that of fungal-based decomposition.

Failure to observe suppression of the free-living nematode community was consistent with effects on the plant-parasitic nematode community (Gruver, 2007). Nematode-suppressive glucosinolate degradation products are known to volatilize rapidly (Brown et al., 1991) and irrigation immediately after incorporation of macerated green manures improves biofumigation by carrying glucosinolate by-products deeper into the soil. Ideal conditions were not achieved in this study, and results suggest that a biocidal or allelopathic effect will not result from organic matter incorporation, but rather from a complex bio-chemical system requiring careful management. Future studies investigating the non-target effects of brassicaceous or rye cover crops, should be done where suppression of the targeted pest is achieved.

4.3. Associations between cover crop or soil parameters and nematode community composition

The dominant cover crop effects appeared to be related to inputs of N-rich organic matter and the subsequent flush of bacterial activity and associated nutrient mineralization. The greater abundance of dauer larvae in radish plots compared to rapeseed or rye plots (Tables 4 and 6) may have been related to the higher N content in radish tissues (Table 1) and their release of N earlier in the season after freezing (Kremen, 2006; Dean and Weil, 2009). Lower N contents in rapeseed and rye biomass (Table 1) may have been associated with relatively more fungal-mediated decomposition nearly six weeks after incorporation (Lundquist et al., 1999), and therefore fewer dauer larvae (Tables 4 and 6). Georgieva et al. (2005a, 2005b) reported larger populations of dauer larvae after burial of vetch root biomass (C/N = 8) compared to burial of rye root biomass (C/N = 22) in both field and pot studies. According to studies on *Caenorhabditis elegans*, the specific mechanism that induces dauer formation is a low ratio between a yeast-like carbohydrate cue from bacteria and a dauer pheromone released during overcrowding (Golden and Riddle, 1984a; Jeong et al., 2005). Therefore, the main cause of dauer formation in this study was probably bacterivore nematode overgrazing following periods of rapid N mineralization and bacterial population increases in late winter or early spring (Zelenev et al., 2004; Georgieva et al., 2005a; Ferris and Bongers, 2006). Correlation with winter-killing cover crop biomass or biomass N supports this conclusion (Fig. 3A and B; Table 1).

This study also points to gaps in the knowledge about the formation, persistence, and recovery of dauer larvae and the corresponding ecological implications. Fig. 3 suggests that dauer formation and/or persistence may be a biophysical interaction between available N, soil moisture, and soil texture. Laboratory studies with *C. elegans* showed that the dauer state extended the life span from 2 weeks to 8–16 weeks (Riddle and Albert, 1997). We observed dauer larvae in samples nine months after radish winter-kill, and correlations between spring or summer dauer populations and soil moisture in radish plots were strongest when these sandy soils were driest. Positive correlations were present in other cover crop plots (data not shown), but strongest in the radish plots. Future studies should include soils of finer texture and more frequent sampling, especially after winter-kill of cover crops. The temporary immobilization of N, the possibility of more efficient N mineralization in space and time, and the possibility of more efficient transfer of carbon (high lipid content) to higher trophic groups are areas of research that would help us better understand the practical implications of our results.

Additional research is needed in the laboratory on dynamics of dauer recovery from field extracted samples, including movement through filter paper in passive extraction. Observations in our study of partially molted Rhabiditdae correspond with some of the first recorded descriptions of dauer larvae, reviewed by Ferris and Bongers (2006). Specimens in this study were observed after a 48 hr passive extraction process. Georgieva et al. (2005a) observed dauer after a 24 hr passive extraction, but Wadsworth and Riddle (1988) observed dauer recovery within 16 h. The dispersal of

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entomopathogenic nematode dauer is extensive (Portillo-Aguilar et al., 1999), but little is documented about movement of Rhabditidae dauer larvae.

The effect of rapeseed and rye on plant-associates is difficult to interpret by abundance alone, given their ability to feed on more than one food source (Yeates et al., 1993). The *r*-selected response of *Coslenchus* was similar to the response of other fungal-feeders in amendment studies, including *Aphelenchoides* (Tables 4 and 5) (Porazinska et al., 1999; Wang et al., 2004) and *Filenchus* (McSorley and Frederick, 1999). In addition, other members of the Tylenchidae have been cultured on fungi (Háněl, 2003; McSorley and Frederick, 1999; Okada et al., 2005). However, some studies do support evidence for classification of *Coslenchus* or Tylenchidae as root-hair feeders (Ilmarinen et al., 2005; Viketoft et al., 2005). Neither root biomass of summer crops, nor fine-rooted cover crops (rye) were sampled in this study. Low populations of *Coslenchus* in November of Exp. 3 (Table 6), after several months of cover crop growth, suggests that the root hairs of rye or rapeseed were not a favored food source in fall. Verschoor et al. (2001) showed that root quality as a food source declined over time with a decrease in soil fertility and this favored nematodes with smaller body sizes, such as Tylenchidae. Thus, roots in spring may be higher in carbon and more suitable as a food source. Since Tylenchidae are facultative feeders, they also may be feeding on the fungi decomposing the roots that were injured by winter stress.

More attention should be given to understanding how plant-associates contribute to nutrient cycling. Correlations between plant-associate abundance and cover crop tissue percent N content, during cover crop growth (Fig. 4C) and after cover crop incorporation (Fig. 4A, B and D), suggests that plant-associates were associated with nutrient cycling, whether directly through mineralization or indirectly through mortality or causing root leakage. Verschoor (2002) estimated that herbivorous grassland nematodes (including abundant populations of Tylenchidae) contributed directly to 2–5% of N mineralization, and more through indirect means such as defecation and mortality. Additional studies have shown root-feeding nematodes contribute to N mineralization in the rhizosphere (Denton et al., 1999; Tu et al., 2003), and that root leakage plays an important role in transferring carbon to nematodes through the soil food web (Yeates et al., 1999; Ruf et al., 2006). Their niche in ecosystem functioning is probably enhanced by the adaption of some genera to feed on either root hairs or hyphae.

4.4. Practical implications of cover crops

Return of cover crop biomass to the soil provides a stimulus for soil biological activity. Rapeseed and rye cover crops stimulated more fungal-feeding nematodes compared to the radish cover crops, especially if the response by plant-associates was associated with feeding on fungi. Observations of abundant dauer larvae in radish plots indicated stimulation of greater bacterial decomposition activity. Correlations between cover crop biomass or tissue N content with populations of these nematode groups, suggests that cover crops may provide biologically derived fertility, which may result in mineralization of nitrogen more synchronously with summer crop needs. There were significant positive treatment effects ($P < 0.05$) on corn biomass and N content at the V6 (6 true leaves) stage in Exp. 2 (rapeseed > control and rye) and Exp. 3 (forage radish > control and rye) (Kremen, 2006). Ferris et al. (2004) used winter irrigation and N-rich cover crops to stimulate bacterivore nematodes and thereby enhance N mineralization later in the year for tomato production systems in California. Our study suggests winter-freeze of N-rich cover crop tissue may effectively prime bacterivore populations in cold climates. Farmers may consider selecting cover crops which prime decomposer communities suited to digest the residue of the following summer crop, and thereby reduce nitrogen immobilization in high carbon residues. Combinations of cover crops with different termination dates and favoring different decomposition pathways may optimize ecosystem functioning.

This study also suggests that weeds (average 1769 kg ha^{-1}) were not an effective winter cover for stimulating nematode activity compared to the cover crops, adapted for high biomass production, deep rooting, and consisting of more uniform physiology. The cover crops suppressed weeds, which may have additional biological benefits. Weed coverage in mid-April, across experiments in the control plots was approximately 40%, compared to cover crop plots, which had 2–5% weed coverage (Y. Lawley, personal communication, 2005). Although there were no effects on yield at harvest (Exp. 1 soybean-conventional till, Exp. 2 corn grain-conventional till, Exp. 3 corn silage-no-till) compared to the control, additional years of cover cropping or different management systems may show more benefits.

5. Conclusion

Biofumigation or negative allelopathic effects on the free-living nematode community from brassicaeous or rye cover crops were not observed in this study. These effects correspond with the lack of effects observed on plant-parasitic nematodes and may have been related to insufficient release of suppressive compounds. Instead, effects of cover crops appeared to be associated with cover crop tissue quality (C/N). There were strong positive effects of the high-N radish cover crops on bacterivores, particularly with regard to dauer larvae formation. In addition rye and rapeseed cover crops stimulated fungivores and plant-associates. This study shows that brassicaceous and rye cover crops can have lasting impacts on different decomposition pathways, as indicated by changes in nematode community composition. With more knowledge about the mechanisms stimulating these community changes and their relationship with ecosystem function, researchers could develop cover crop management plans to maximize the desirable effects associated with changes in nematode community groups.

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