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Effects of cover crop quality and quantity on nematode-based soil food webs and nutrient cycling

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ABSTRACT

Soil food webs cycle nutrients and regulate parasites and pathogens, services essential for both agricultural productivity and ecosystem health. Nematodes provide useful indicators of soil food web dynamics. This study was conducted to determine if nematode soil food web indicators and crop yield can be enhanced by combinations of cover crops in a conservation tillage system. The effects of three cover crop treatments (vetch/pea, oat/wheat and oat/wheat/pea/vetch) with low, medium and high C:N and a bare fallow control were investigated in Davis, CA. Nematode fauna, soil properties and plant productivity were measured. Soil food web indices, including the Enrichment Index (EI), Structure Index (SI), Basal Index (BI), and Channel Index (CI), based on the composition of nematode assemblages, were calculated to infer soil food web condition. Cover cropped tomato/corn rotations had twice the number of enrichment opportunist bacterial feeding nematodes, active participants in nitrogen mineralization, than fallowed tomato/corn rotations (opportunist bacterial feeders = 163 versus 98). In winter fallowed plots food webs were basal, common in disturbed, nutrient-poor conditions (BI = 37). Total number of enrichment opportunist nematodes, soil NH_4-N levels, and inferred nitrogen mineralization, were higher in cover crop treatments with low to mid C:N ratios. Omnivore and predator nematodes were scarce, averaging less than 6 nematodes 100 g^{-1} in all treatments. In year one, plant productivity was highest after fallow. In contrast, in year two productivity was highest after cover crops with high nitrogen content and productivity significantly correlated with the structure of the soil fauna. Monitoring the abundance of enrichment opportunists may provide managers with a new tool to evaluate soil food web nitrogen mineralization and plant productivity.

1. Introduction

Mounting concerns over degradation of soil, water and air quality associated with contemporary crop production have encouraged the development of alternative cropping systems (Pimentel et al., 1995; Turner and Rabalais, 2003; Roberts et al., 2007). Currently more than 31 million hectares are under organic management in 120 countries worldwide (Willer and Yussefi, 2001). Nutrient management is a critical concern for conventional and organic systems, most of which rely heavily on the import of nitrogen rich materials. World consumption of nitrogen fertilizer is over 82 million Mg yr^{-1}. Only 35–50% of applied nitrogen is taken up by crops, the other 50–65% is lost to the environment (Cassman et al., 2003; MEA, 2006a). Identifying

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ways to manage soil biota for enhanced nutrient cycling has been proposed as an important method to maintain yields with acceptable environmental impact. The Millennium Ecosystem Assessment states ‘‘Specific forms of (soil) biodiversity are critical to performing the buffering mechanisms that ensure the efficient use and cycling of nutrients in ecosystems’’ (MEA, 2006b).

Soil biota form complex webs of organisms (Phillips et al., 2003). The abundance of soil organisms, the composition of their assemblages, and their interaction with environmental factors, determine their contribution to nutrient cycling. Bacteria and fungi may contribute a net release of nitrogen to soils as their populations turn over, or render it unavailable as immobilized biomass N. Mesofauna feeding on microbes excrete nitrogen-rich waste contributing up to 30% of mineralized N (De Ruiter et al., 1993; Griffiths, 1994), and increasing plant uptake up to 50% (Laakso et al., 2000).

Abundant and functionally diverse, nematodes provide useful indicators of soil food web dynamics (Bongers and Bongers, 1998). Nematodes directly influence soil processes and reflect the structure and function of many other taxa within the soil food web (Ferris et al., 2001; Berkelmans et al., 2003; Hohberg, 2003). Nematode indices allow us to determine the effects of environmental stress, dominant decomposition channels, and may reflect soil suppressiveness to plant parasites and pathogens (Bongers, 1990; Wardle et al., 1995; Lenz and Eisenbeis, 2000; Ferris and Matute, 2003).

Cover crops may provide agricultural managers with effective tools to regulate soil faunal composition and ecosystem services. Organic matter additions drive soil food web dynamics, N availability and plant growth (Ferris and Matute, 2003). However, most studies focus on the application of amendments such as manure, compost, sawdust and municipal waste (Yeates et al., 1993b; Bulluck et al., 2002; Okada and Harada, 2007) that may be difficult or expensive for farmers to access, contain large numbers of extant organisms, or heavy metal contaminants (Porazinska et al., 1999). Cover crops provide an attractive alternative, reducing erosion, decreasing soil compaction, and building soil organic matter, as well as influencing soil organisms (Snapp et al., 2005). However, most cover crop studies that include nematode fauna investigate nematode-suppressive green manures such as sorghum sudangrass, rye, and mustards (Abawi and Widmer, 2000; Wang et al., 2006a; Machado et al., 2007; Collins et al., 2006; Everts et al., 2006), focus only on plant-parasitic nematodes (Kimpinski et al., 2000; Wang et al., 2004a,b) are inconclusive (Sanchez et al., 2007), or compare only one cover crop to mineral fertilizers (Blanchart et al., 2006). Here we build on microcosm studies (Fu et al., 2000), and studies focused on plant-parasitic nematodes (McSorley and Gallaher, 1994) in order to determine the interactions of legume and grain cover crops, nematofauna and plant productivity.

The objectives of this study were to investigate the ability of winter cover crops to increase nematode indicators of nitrogen mineralization and the numbers of predator and omnivore nematodes associated with soil food web structure and complexity. We hypothesized that (a) Cover crop treatments with high C:N increase the structure index (SI) indicating complex soil food webs. (b) Inputs of low C:N cover crops increase the enrichment index (EI) and associated nitrogen mineralization capacity of soil food webs. (c) Moderate C:N ratios increase EI and SI.

2. Methods

2.1. Experimental site and treatment details

The experiment was conducted on the University of California at Davis Student Farm from September 2005 until August 2007. The experimental site was under organic management. The soil type is a yolo silt loam. It had not been cropped in three years and had received only periodic disking to control weeds. The 0.33 ha experimental area was organized in a randomized complete block design with four treatments and five blocks. Each plot was 111 m^2 and consisted of six 1.5 m wide raised beds.

Treatments consisted of two- to five-species cover crop mixtures, designed to produce low, medium and high C:N residue, and a fallow control. Treatments planted in 2005 were combinations of ‘Cayuse’ oats, *Avena sativa*; ‘Triticale 118’, *Triticale hexaploide*; ‘Magnus’ field peas, *Pisum sativum*; purple vetch, *Vicia benghalensis*; and ‘Lana’ woollypod vetch, *Vicia villosa* based on proportional seed weights of above species at the following rates: Grains (Gr) 1:1:0:0:0 134 kg ha^{-1}; legumes (L) 0:0:4:1:1 135 kg ha^{-1}; mixture (M) 1:1:4:1:1 135 kg ha^{-1}; and fallow control (F). In 2006 triticale was replaced by ‘Summit’ wheat, *Triticum aestivum* and purple vetch with common vetch, *Vicia sativa*. Rates were adjusted to (Gr) 1:1:0:0:0 134 kg ha^{-1}; (L) 0:0:4:1:1 140 kg ha^{-1}; and (M) 1:1:7.5:2.5:2.5 162 kg ha^{-1}.

2.2. Site preparation and cropping practices

In fall 2005 the experimental site was disked twice and permanent beds were formed with a lister and two passes each with a power incorporator and a power harrow. In May 2006 a 10 cm wide band was strip-tilled down bed centers and drip irrigation tape was buried 25 cm deep. Irrigation tape was left in place for the duration of the experiment.

Cropping systems consisted of two years of fall-planted, spring-mowed cover crops or bare fallow followed by spring-planted cash crops (tomatoes/corn). Cash and cover crops were grown with no additional fertilizers and following organic production standards (A.M.S., 2000). Cover crops were seeded into moist soil on bed tops, but not in furrows. In order to maintain low weed biomass, fallow plots were flame-weeded periodically during winter months. Cover crops were flail-mowed in the spring and the residue left on bed tops. In May 2006 plots were strip-tilled and transplanted to ‘AB2’ tomatoes (*Lycopersicon esculentum*), one row down the center of each 1.5 m wide bed. After tomato harvest in September 2006, tomato residue was mowed and cover crops were planted into the undisturbed beds in October. In March 2007 cover crop mow-down was followed by strip tillage and direct seeding to corn, *Zea mays* (Pioneer 31G98). Only one row was planted per 1.5 m wide bed, half the normal row density for corn in the region, due to placement of buried drip tape at 25 cm deep in the center of each bed. In both years cash crops were irrigated with buried drip tape. A dry soil surface was maintained and few weeds germinated in tomato or corn beds.

2.3. Cover crop sampling and analysis

Cover crop biomass was sampled from two randomly chosen 0.25 m^2 quadrats on May 2, 2006 and March 27, 2007; directly preceding mowing. Samples were weighed in the field, dried at 60 °C and weighed again. Dry samples were chopped and mixed for subsampling. Subsamples were ground to pass through a 0.833 mm screen and oven dried at 50 °C.

Total plant N and C were determined using the combustion gas analyzer method combined with gas chromatographic separation and thermal conductivity detection by the University of California Division of Agriculture and Natural Resources Analytical Laboratory (DANR) (AOAC, 1997).

2.4. Soil sampling

Soil samples were taken after major field operations in May and September of 2006. In 2007 soil sampling was increased to include samples 3, 7, 14 and 17 weeks after cover crop mow down. Twelve-core composite samples (2.5 cm diameter × 15 cm deep) were taken randomly from each plot. Samples were thoroughly mixed and divided for nematode faunal analysis (350 g) and soil moisture (50 g). Twice per year soil was also partitioned for total soil N, total soil C, NH_4-N, and NO_3-N determination.

Soil moisture for each sample was determined by weight loss after drying. Soils for N and C analysis were oven dried at 50° C and ground to pass through a .246 mm screen. Soil N (NH_4-N, NO_3-N and total N) and total C were determined by the University of California DANR laboratory using flow injection and Carlo Erba combustion methods respectively (Hofer, 2003; Knepel, 2003).

On the final sampling date, July 20, 2007, five subsamples of crop residue were collected from 95 cm^2 quadrats on the bed-top surface for nematode extraction. Residue and partially decomposed plant material was removed with only the soil which was loose on the soil crust or mixed with decomposing residue. Subsamples were bulked, mixed and 30–80 g removed for nematode enumeration and faunal analysis. Nematodes were extracted from residue using the same methods as for soil.

2.5. Inoculation with omnivore and predator nematodes

Intact cores (10 cm deep × 5 cm diameter) containing high percentages of omnivores and predators were taken from a natural forest on a creek edge, eight miles from the test site. Fifteen cores were inserted in four 1.5 m^{-2} microplots within the larger study and paired with non-inoculated microplots.

2.6. Nematode enumeration

Samples were extracted using a combination of decanting, sieving and Baermann funnel methods. Samples were sieved through a .246 mm sieve to remove larger particles and a 36 μm sieve to separate nematodes from excess water. Samples were washed into beakers and placed on Baermann funnels for 48 h. Nematodes were counted using a dissecting microscope and the first 200 nematodes encountered in the sample identified at 200× to 400× to genus or family within one week of extraction or fixed in 4% formalin until identification.

2.7. Faunal indices

Nematodes were assigned to trophic groups according to Yeates et al. (1993a) and colonizer-persister groups (cp) based on Bongers (1990) and Bongers and Bongers (1998). The cp scale classifies nematodes into five groups from microbial feeders with short life cycles and high fecundity (cp 1 and 2) to omnivores and predators with long life cycles and greater sensitivity to perturbation. Soil food web indices were calculated after Ferris et al. (2001). The Structure Index (SI) is based on the relative abundance of nematodes in higher trophic groups and cp levels and indicates soil food web length and connectance. The Channel Index (CI) is calculated as the proportional abundance of [cp 2] fungal feeders to the abundance of enrichment opportunist bacterial feeders and reflects the primary decomposition channel in the soil, fungal mediated or bacterial facilitated. The Basal Index (BI) enumerates the predominance of nematode groups that are tolerant to disturbance. The Enrichment Index (EI) measures the number of opportunistic bacterial and fungal feeders that respond quickly to the input of C and N sources.

The seasonal average total abundance of enrichment opportunists (SAb1f2) we defined as the average number of bacterial feeders 1 ($b1$) + fungal feeders 2 ($f2$) for the cropping season:

$$\mathrm{SAb1f2} = \frac{\sum(b1_1 + f2_1 + b1_2 + f2_2)/2D_\mathrm{p}}{D_\mathrm{s}}$$

where D_p is the number of days between each sampling date and D_s is the number of days in the entire cropping season. The SAb1f2 is similar to the average of $b1 + f2$ except that it uses the slope of the line between each sampling date to calculate estimated values for every date in the season. Estimates for all days in the cropping season are averaged. This normalizes for unequal spacing between sampling dates.

We calculated the aggregate enrichment index (AEI) after Ferris and Matute (2003) to provide an integral measure of the enrichment affect of organic matter during the cropping season. The AEI equals the area under the regression line for EI and time. The AEI is essentially the sum of daily EIs. Unlike the EI or average EI, it integrates small differences in the rates of EI decline over the course of the season.

2.8. Crop yield measurements

Tomato harvest for yield was calculated from two subsamples per plot, each one row wide and 3 m long. Tomato plants were cut at the base and shaken onto tarps to mimic mechanical harvest. Fresh plant biomass and tomato fruit were weighed in the field. Biomass subsamples were dried for percent moisture at 70 °C. Tomatoes not sampled for yield were hand-harvested and removed from the field site.

Corn silage was sampled from randomly chosen 3 m row sections of two center beds in each plot. Plants were weighed, and two stalks per sample were randomly chosen for subsamples. After measuring initial wet weight, subsamples were oven dried at 70 °C and reweighed.

2.9. Statistical analysis

The data for all eight sampling dates was analyzed as a randomized complete block using the proc mixed ANOVA procedure in SAS (Statistical Analysis Systems Inc., 1989). Trophic group total abundance was log transformed. Stepwise regressions were used to analyze relationships between nematode fauna and all soil/cover crop parameters measured (SAb1f2, AEI; cover crop kg ha^{-1}, N kg ha^{-1}, C kg ha^{-1}, %C, %N, C:N; soil Total N, Total C, NH_4-N, NH_3-N at mowing and harvest). Seasonal average abundance of important nematode groups in regression analysis was used due to greater number of sampling dates in nematode versus crop parameters.

3. Results

3.1. Cover crop biomass and nutrient content

Cover crop biomass and quality differed between treatments (Table 1). Grains (Gr) produced high biomass (18 Mg ha^{-1} in 2006), legumes (L) low biomass, and mixtures (M) varied between high biomass in 2006 and low in 2007 ($p < 0.05$). Consistent with study design, cover crop quality varied between treatments where C:N for Gr was greater than for L in both years ($p < 0.05$). C:N ratios for M were high in 2006 and low in 2007.

3.2. Soil properties

Soil mineral N varied depending on cover crop presence and C:N ratio. NH_4-N was significantly higher in L than in F (Fallow). Values were intermediate for M and G ($p < 0.05$, Table 2). After only two years, total soil C tended to be higher in Gr plots than in F ($p < 0.1$). NH_4-N and NO_3-N varied with sampling date ($p < 0.0001$, $p < 0.01$), but the relationship between treatments was consistent across sampling dates as indicated by no significant treatment × date interactions (Table 2).

3.3. Effect of cropping season on nematode taxa and soil food web indices

Relationships between treatments for nematode taxa and functional groups were generally consistent for all years and dates. The ANOVA across two years and eight sampling dates revealed significant treatment by date interactions. However, further analysis both by year and beginning versus end of season, showed that relationships between treatments were similar in 2006, 2007, beginning and end of season, and across all eight sampling dates. One exception is bacterial feeders cp 1 ($b1$) and fungal feeders cp 2 ($f2$). For $b1$ Gr was similar to F in 2007 versus similar to M and L across all eight dates ($p < 0.05$, Table 3). Numbers of $b1$ and $f2$ were 1.4 to 4 times as great in 2007 than 2006 ($p < 0.001$, Table 4).

Enrichment opportunist nematodes are bacterial and fungal feeding nematodes with short life cycles and high fecundity (colonizer persister scale 1 and 2). Response of enrichment opportunist nematodes $b1$ and $f2$ varied according to the number of days after cover crop mowing. After mowing in 2007, $b1$ was greater in G, M, and L than F. By the end of the season differences were no longer significant. In L, $b1$ increased quickly at mowing and dropped to below M by

Table 1 – Average values for cover crop biomass (±SE).

Cover crop	Fallow	Legume	Mix	Grain
2006				
Biomass (Mg ha^{-1})	0.4 ± 0.2a	6.5 ± 0.5b	18.5 ± 2.4c	18.9 ± 1.2c
Nitrogen (Mg ha^{-1})	0.01 ± 0.01a	0.22 ± 0.02b	0.33 ± 0.04b	0.32 ± 0.03b
Carbon (Mg ha^{-1})	0.1 ± 0.1a	2.6 ± 0.2b	7.1 ± 0.9c	7.3 ± 0.5c
C:N	13 ± 0.00a	11.8 ± 0.3a	21.8 ± 1.1b	23.3 ± 1.2b
2007				
Biomass (Mg ha^{-1})	0.9 ± 0.1a	5.8 ± 0.6b	7.3 ± 1.3b	11.5 ± 0.8c
Nitrogen (Mg ha^{-1})	0.03 ± 0.00a	0.2 ± 0.02b	0.25 ± 0.03b	0.24 ± 0.02b
Carbon (Mg ha^{-1})	0.4 ± 0.04a	2.5 ± 0.3b	3.2 ± 0.5b	5 ± 0.4c
C:N	11.9 ± 0.6a	12.7 ± 1.1a	12.9 ± 0.7a	21.6 ± 1.6b

Table 2 – Average values of soil properties (±SE) for four cover crop treatments.

	Total C (%)	Total N (%)	NH_4-N (ppm)	NO_3-N (ppm)
trt	<.1	ns	<.05	ns
Date	ns	ns	<.0001	<.01
txd	ns	ns	ns	ns
Fallow	0.94 ± 0.02a	0.1 ± 0	4.56 ± 0.55a	6.54 ± 0.79
Legume	1.00 ± 0.03ab	0.11 ± 0	5.79 ± 0.88b	7.87 ± 1.33
Mix	0.99 ± 0.02ab	0.11 ± 0	5.01 ± 0.49ab	5.21 ± 0.77
Grain	1.04 ± 0.02b	0.11 ± 0	4.99 ± 0.68ab	6.21 ± 1.47

Data are from 3 sampling dates (May 2006, September 2006, March 2007). Soil sampled to 15 cm. trt = treatment, txd = treatment × date interaction.

Table 3 – Nematode taxa and functional groups in cover crop treatments.

	Fallow	Legume	Mix	Grain	trt	Date	txd
Total abundance (nematodes 100 g^{-1} soil)							
*b*1	97.8 ± 12.0a	183 ± 19.3b	164 ± 14.8b	142 ± 15.5b	<.0001	<.0001	<.0001
Monhysteridae	1.5 ± 0.4	6.5 ± 3.7	2 ± 0.6	5.4 ± 1.8	0.042	<.0001	ns
Panagrolaimus	15.8 ± 3.5a	49.1 ± 9.6bc	46.8 ± 4.5c	32.3 ± 4.6b	<.0001	<.0001	<.0001
Dauerlarvae	12.1 ± 2.4	12.3 ± 2.9	10.7 ± 3.3	6.5 ± 1.3	0.046	<.0001	ns
Mesorhabditis	57.8 ± 9.6a	105 ± 14.7b	91.9 ± 12.0b	87.4 ± 13.4ab	0.018	<.0001	ns
*b*2	162 ± 16.2b	131 ± 13.5ab	112 ± 10.2ab	90.1 ± 12.2a	0.013	<.0001	0.005
Acrobeloides	151 ± 16.5b	119 ± 13.5ab	102 ± 10.4ab	83 ± 11.9a	0.012	<.0001	0.007
*b*3	6.8 ± 1.3	6.9 ± 1.8	7.8 ± 1.5	16.7 ± 8.5	ns	<.0001	0.065
Prismatolaimus	6.2 ± 1.2	6.5 ± 1.7	7.2 ± 1.4	15.4 ± 7.8	ns	<.0001	ns
*f*2	119 ± 12.8ab	136 ± 14.3ab	139 ± 12.7b	104 ± 14.5a	ns	<.0001	0.019
Aphelenchus	31.7 ± 3.6	22.9 ± 3.5	25.1 ± 2.5	23 ± 3.2	ns	<.0001	0.007
Aphelenchoides	42.1 ± 8.1ab	62.1 ± 8.0b	50 ± 6.6ab	35.1 ± 7.7a	0.031	<.0001	ns
pa	34.3 ± 4.5	48.3 ± 10.4	57.6 ± 9.1	41.1 ± 7.2	ns	<.0001	0.001
Tylenchidae	65.8 ± 8.9	86.5 ± 19.8	107 ± 17.5	76 ± 13.8	ns	<.0001	0.001
pp3	12.1 ± 2.1a	96.3 ± 20.4b	101 ± 11.9b	103 ± 11.4b	<.0001	<.0001	<.0001
Tylenchorhynchus	5.5 ± 1.4a	78.6 ± 18.3b	72 ± 9.5b	81.1 ± 10.1b	<.0001	<.0001	<.0001
Helicotylenchus	4.4 ± 0.9	9.4 ± 3.2	20.5 ± 5.6	13.1 ± 3.4	ns	<.0001	<.0001
o5	5.5 ± 1.3	6 ± 1.2	4.7 ± 1.0	7.1 ± 1.9	ns	<.0001	ns
Aporcelaimidae	4.6 ± 1.2	5.8 ± 1.2	4.4 ± 1.0	6.1 ± 1.7	ns	<.0001	0.02

Means (±SE) from eight sampling dates, two in the 2006 cropping season and six in the 2007 cropping season. Scarce genera are removed (<2 nem 100 g^{-1}). b = bacterial feeders, f = fungal feeders, pa = plant associates, pp = plant feeders, o = omnivores; numbers after trophic group are for cp levels 1–5; trt = treatment, txd = treatment date interaction. *p*-Values for significance are indicated (ns = not significant).

Table 4 – Average abundance of enrichment opportunist nematodes by cropping system and year.

	*b*1 (nematodes 100 g^{-1})		*f*2 (nematodes 100 g^{-1})	
	2006	2007	2006	2007
Fallow	29.8 ± 22.6	121.1 ± 10.9	48 ± 7.6	141.3 ± 12.1
Legume	124.6 ± 72	206 ± 16.2	108.8 ± 51.4	146.6 ± 13
Mix	59.1 ± 8.1	202.5 ± 12.2	74.9 ± 18.3	162.5 ± 12.5
Grain	78.1 ± 18.7	166.5 ± 16	73.3 ± 23.1	120.6 ± 16.7

Date is significant at $p < .0001$ for all treatments.

three weeks after mowing (Fig. 1). In contrast, *b*1 in G and M increased slowly and maintained higher levels over time. *f*2 did not differ among treatments at the beginning or end of the cropping season. However, *f*2 was highest in M and lowest in Gr for most of the cropping season (0–14 weeks) (Fig. 1).

3.4. *Effect of cover crop treatments on nematode populations and soil food web indices*

Cover crop treatment affected the abundance of several nematode taxa and functional groups across all eight sampling dates (Tables 3 and 5). Thirty-six genera and higher taxonomic groupings were identified, including 13 abundant groups and 23 scarce taxa (<2 nem 100 g^{-1}). Abundance of enrichment opportunists (*b*1) *Mesorhabditis* and *Panagrolaimus* was 2.2 times higher in cover crop treatments than in F ($p < 0.05$). In contrast, abundance of general opportunist (*b*2), nematodes found in most soils, primarily *Acrobeloides*, was highest in F and lowest in Gr ($p < 0.05$). Abundance of bacterial feeders (Ba) was not significantly different between treatments due to large numbers of *b*1 in cover crop treatments and *b*2 in control plots. Fungal feeders (Fu) were primarily composed of the taxa *Aphelenchoides* and *Aphelenchus* (*f*2). Abundance of *Aphelenchoides* was significantly higher in L than in Gr with intermediate levels in F and M. Total Fu was highest

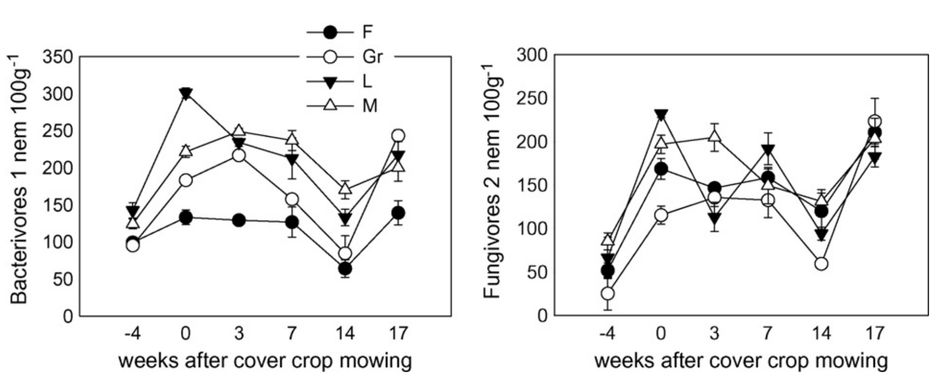

Fig. 1 – Dynamics of key functional groups of nematodes during the 2007 cropping season. F = fallow, Gr = grain, M = mix, L = legume, nem = nematodes.

Table 5 – Effect of cover crop treatment on trophic abundance and soil food web indices.

	Fallow	Legume	Mix	Grain	trt	Date	txd
Total abundance (nematodes 100 g^{-1})							
Ba	264 ± 25	324 ± 29	283 ± 21	249 ± 23	ns	<.0001	0.002
Fu	116 ± 12ab	139 ± 15ab	139 ± 13b	105 ± 15a	0.037	<.0001	0.022
PA	36 ± 5	47 ± 10	58 ± 9	41 ± 7	ns	<.0001	0.003
Pf	11 ± 2a	97 ± 20b	101 ± 12c	104 ± 11c	<.0001	<.0001	<.0001
OP	7 ± 1	10 ± 2	7 ± 1	14 ± 5	ns	<.0001	ns
Tot	435 ± 38a	617 ± 65b	588 ± 41b	512 ± 44ab	0.002	<.0001	<.0001
Indices							
EI	60 ± 2a	74 ± 2b	75 ± 2b	78 ± 2b	<.0001	<.0001	ns
SI	16 ± 2	21 ± 3	18 ± 3	27 ± 4	ns	<.0001	0.011
CI	31 ± 3b	19 ± 3a	19 ± 1a	16 ± 2a	0.001	<.0001	<.001
BI	37 ± 2b	24 ± 2a	24 ± 2a	20 ± 2a	<.0001	<.0001	ns

Means (±SE). Ba = bacterial feeders, Fu = fungal feeders, PA = plant associates, Pf = plant feeders, OP = omnivores and predators, Tot = total abundance for all trophic groups, EI = Enrichment Index, SI = Structure Index, BI = Basal Index, CI = Channel Index, trt = treatment, txd = treatment times date interaction. Significance for main effects and interactions are indicated (ns = not significant). Data are from eight sampling dates ($n = 35$).

in M and L and lowest in Gr. Plant feeders (Pf) were higher in all cover crop treatments versus F. Number of omnivores and predators (OP) was very low (average of 5 OP 100 g^{-1}) across all treatments and did not significantly respond to cover crop treatments or inoculation of soil cores from natural areas.

Crop residue sampled at harvest 2007 had high densities of nematodes (Table 6). Total abundance was significantly different between treatments with 62,000–100,000 nematodes m^{-2} in cover crop residue versus 6000 nematodes m^{-2} in F. Residue in all treatments was dominated by bacterial feeders (80–90%). Ba composed mostly of b1 *Panagrolaimus* was higher in Gr, M and L than F ($p < 0.05$). Fu, though less abundant, were higher in M and L than F. No OP were found in residue. PA composed of the family Tylenchidae and Pf (*Tylenchorhynchus*) were present in residues.

Cover crops affected soil food web indices consistently across all dates (data not shown). Cover-cropped plots had high EI ($p < 0.05$). In contrast, F had higher BI and CI. In 2007 the BI and CI increased in cover crop plots over time until L, M, Gr, and F were no longer significantly different at harvest. The SI was not different between treatments ($p < 0.05$). The significant regression ($p < 0.001$) for biomass produced versus aggregate EI explains 68.7% of the variation in EI indicating that the amount of cover crop biomass might influence the EI (Fig. 2a).

Soil food web indices calculated from nematodes present in cover crop residue were not different among treatments (Table 6). All treatments had high EI (80–91), low CI (2–8) and low BI (2–7). Upper trophic groups were absent in residue (SI = 0).

3.5. *Relationship between cover crops, nematode groups and plant productivity*

Season average of enrichment opportunists (SAb1f2) was significantly affected by cover crop quantity and quality in 2007. A stepwise regression of all cover crop properties measured (biomass kg ha^{-1}, N kg ha^{-1}, C kg ha^{-1}, %N, %C, C:N) showed that the number of SAb1f2 can be described by a linear combination of cover crop biomass (cb) and cover crop %N, as expressed by the following relationship SAb1f2 = $-55.5 + 8.02\text{cb} + 80.8\%\ \text{N}$ ($R^2 = 56.7$, $p = 0.023$) (Fig. 2c). Cover crop %N accounted for the highest variation ($R^2 = 39.7\%$). Biomass contributes an additional 17%. Gr (high cover crop

Table 6 – Effect of cover crop treatment on nematodes present in crop residue on the soil surface.

	Fallow	Legume	Mix	Grain	pdiff
Total abundance (nematodes m^{-2})					
Tot	5209 ± 3082a	62776 ± 19884b	101264 ± 19181b	64238 ± 42622b	0.001
Ba	4459 ± 3127a	52839 ± 16283b	92410 ± 20569b	51017 ± 36516b	0.001
Fu	434 ± 57a	8469 ± 3947b	6430 ± 1284b	9576 ± 6076b	0.01
PA	314 ± 112a	1393 ± 120ab	2424 ± 314b	1886 ± 877ab	0.046
Pf	0 ± 0	74 ± 74	0 ± 0	1757 ± 1419	ns
Indices					
EI	93.3 ± 2.9	96.5 ± 0.9	97.8 ± 0.91	95 ± 1.9	ns
CI	7.5 ± 3.4	3.6 ± 1	2.3 ± 1	5 ± 1.7	ns
BI	6.7 ± 2.9	3.5 ± 0.9	2.2 ± 0.9	5 ± 1.9	ns

Means (±SE). Ba = bacterial feeders, Fu = fungal feeders, PA = plant associates, Pf = plant feeders, OP = omnivores and predators, EI = Enrichment Index, BI = Basal Index, CI = Channel Index, Tot = total abundance for all trophic groups. *p*-Values for significance (pdiff) are indicated (ns = not significant). Data are from one sampling date on July 20, 2007.

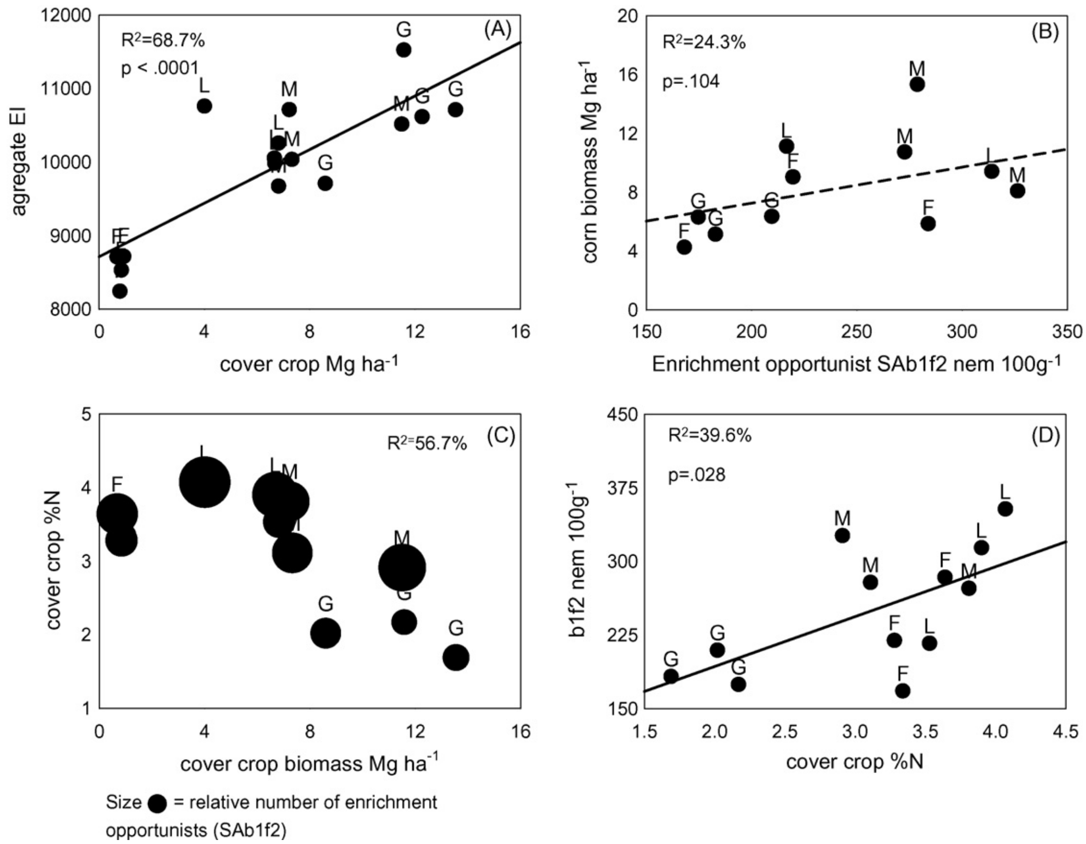

Fig. 2 – Relationships between cover crop inputs, nematode functional groups and yield. (A) Relationship between cover crop biomass and aggregate enrichment index (AEI). (B) Regression of enrichment opportunists (SAb1f2) and silage harvest Mg ha^{-1}. (C) Relationship between cover crop biomass, %N and weighted average of enrichment opportunists (SAb1f2). Size of circle indicates the relative number of nematodes at each level of nitrogen and biomass. (D) Effect of cover crop %N on enrichment opportunists (SAb1f2). F = fallow, G = grain, M = mix, L = legume, N = nitrogen.

biomass but low %N) had few SAb1f2 (average 189 nematodes 100 g^{-1} soil). L and M with medium cover crop biomass and %N had the largest number of SAb1f2, on average 293 nematodes 100 g^{-1} soil. The accumulative enrichment index (AEI) was also positively correlated with the amount of cover crop biomass (Fig. 2a).

Tomato aboveground biomass and fruit yield were highest in F in 2006 ($p < 0.05$, Table 7). In 2007 corn biomass and silage yield were higher in M than F and Gr ($p < 0.05$). Stepwise regression of 17 soil, nematode and cover crop factors in 2007 (cover crop kg ha^{-1}, N kg ha^{-1}, C kg ha^{-1}, %C, %N, C:N; SAb1f2, AEI; soil Total N, Total C, NH_4-N, NH_3-N at mowing and harvest) with plant productivity indicated that SAb1f2 and NH_4^+ (at mowing) were primary factors associated with higher plant productivity after two years ($R^2 = 47.29$, $p \leq 0.05$). SAb1f2 accounted for most of explained variation ($R^2 = 24.3$, Fig. 2b). The linear relationship is described as silage biomass dry = 2.37 + 0.0245*b1f2*. The coefficient 0.0245 suggests that yield will increase by 0.0245 Mg ha^{-1} with an increase in enrichment opportunists of one nematode 100 g^{-1} soil across all treatments.

Table 7 – Crop plant productivity, 2006 and 2007 cropping seasons.

	2006		2007	
	Tomato aboveground biomass (Mg dry wt. ha^{-1})	Tomato fruit yield (Mg ha^{-1})	Corn silage aboveground biomass (Mg dry wt. ha^{-1})	Corn silage yield (Mg ha^{-1})
Fallow	5.3 ± 0.5b	68.0 ± 6.0b	6.2 ± 1.0a	15.7 ± 1.4a
Legume	3.7 ± 0.3a	47.1 ± 4.9a	9.6 ± 0.7ab	29.6 ± 2.2b
Mix	2.7 ± 0.2a	27.3 ± 2.4a	11.4 ± 2.1b	30.9 ± 5.4b
Grain	2.3 ± 0.2a	34.3 ± 3.1a	5.8 ± 0.3a	16.3 ± 1.4a

Yield data is expressed as fresh weight for both tomatoes and corn silage. Tomato and corn above ground biomass is for oven dried plant material.

4. Discussion

This two year study indicates that legume and grass–legume cover crop mixtures can increase soil food web enrichment indicator groups (bacterial feeders 1 and fungal feeders 2) and associated nitrogen mineralization. Cover-cropped soils had high EI and low BI and CI, indicating enriched soils with sufficient resources and active bacterial decomposition channels. Plant productivity may have been influenced by nitrogen mineralization from soil food webs as indicated by a positive correlation between plant productivity and numbers of enrichment indicator nematodes. However plant productivity was positively associated with leguminous cover crops only in year two. Indicators of structured soil food webs, including omnivores, predators and the SI, were not affected by treatment. Omnivore and predator nematodes were undetectable at the beginning of the experiment (data not shown) and did not appear or increase during the two-year time course.

4.1. *Cover crop quantity and quality affect soil food webs and nutrient cycling*

The total number and biomass of organisms are factors that drive the capacity of soil to perform essential ecosystem functions such as nutrient cycling. Similar to other studies with organic amendments, total nematode abundance was significantly greater in cover crop treatments, where 475–1545 kg ha^{-1} of biomass was added to soil per year (Porazinska et al., 1999; Okada and Harada, 2007). Total nematode abundance was, on average, 72% higher in cover crop treatments containing legumes versus fallow, suggesting abundant resources in the presence of cover crops.

Cover crops affect functional diversity of soil fauna and associated nutrient cycling in soils. Cover-cropped soils had high EI and low CI and BI, suggesting bacterial-dominated systems with abundant resources and fast nutrient turnover, qualities often associated with high agricultural productivity. Our observations are consistent with past studies where organic matter (Wang et al., 2004a,b) and cover crops (Ferris et al., 1996; Berkelmans et al., 2003) increase soil food web nutrient cycling and the EI. Soil food webs in fallow plots were characterized by more abundant general opportunists adapted to adverse conditions and fungal-mediated decomposition channels (high BI and CI). In our study, as also observed by Wang et al. (2006a), fallow reduced the numbers of Rhabditidae and other enrichment opportunist bacterial feeders compared to cover crops. Without these groups the CI was higher common for agricultural soils with no organic inputs (Berkelmans et al., 2003).

Quantity of cover crop grown was an important driver of the EI. Although the EI was not different between treatments at most sampling dates, by the end of the 2007 cropping season the EI was significantly higher in Gr (high cover crop biomass) than F. L and M had intermediate values. Low EI values late in the season contributed to a lower aggregate EI (AEI) for grain plots over the entire cropping season. The AEI was positively correlated with the amount of cover crop biomass (Fig. 2a). In applications of sunnhemp hay Wang et al. (2006b) found a similar trend. Doubling the application rate of sunnhemp hay increased bacterivores and the EI. Increases in the AEI are correlated with greater seasonal release of mineral N (Ferris and Matute, 2003).

Bacterial- and fungal-feeding nematodes responded to organic matter input but their response varied by functional guild and depended on the quantity and quality of organic material. Bacterivore abundance generally increases with the incorporation of cover crop residues (Ferris et al., 1996, 2004), often attributed to the increase in bacterial biomass after cover crop additions (Ferris et al., 1996). Total abundance of bacterial feeders did not vary here because increases in general opportunists were canceled by decreases in enrichment opportunists. General opportunists (*b*2) were dominant in F, consistent with the ecological designation of *b*2 genera such as *Acrobeles* and *Acrobeloides* as bacterial scavengers predominant in highly disturbed cropping systems with few organic inputs (Ferris et al., 1996, 1997). In contrast, enrichment opportunists (*b*1) were significantly higher in cover crop treatments.

In year two a larger data set allowed correlation of cover crop properties and enrichment opportunists (Fig. 2c and d). High biomass, high C:N, grain cover crops producing 11–19 Mg ha^{-1}, supported the lowest number of enrichment opportunists. Enrichment opportunists were most abundant under legume and mixture cover crops with mid-high %N. Percent N in organic amendments may determine the diversity and abundance of nematodes groups. Ilieva-Makulec et al. (2006) found density of bacterivores and fungivores increased exponentially in response to decreasing C:N litter applications. Rhabditidae and *Panagrolaimus* (*b*1) are particularly stimulated by amendments with a C:N $<$19 (Wang et al., 2006a).

Similar to other studies, leguminous cover crops (L, M) had higher plant productivity in 2007 than fallow or high C amendments (F, Gr) (Pimentel et al., 1995). However, in this study, 2006 crop plant productivity was greatest in fallow plots. On average there were half the number of *b*1 and *f*2 in 2006 than 2007, suggesting low availability of organic material. After three years without cropping, reservoirs of available soil N may have been taken up by the cover crops and held in surface residues. Unlike tilled systems, where plant C and N can be decomposed and assimilated into microbial and nematode biomass as quickly as 31 days, very little is quickly assimilated under no-till management (Minoshima et al., 2007), particularly in an arid climate with buried drip irrigation. Data from 2007 may better reflect long term influences of cover crops on soil biota and plant productivity because winter rainfall likely resulted in decomposition of the previous winter's cover crop residues and movement of N into soils.

Abundance of enrichment opportunists may be one of multiple factors influencing plant productivity. Soil fauna can contribute significantly to N mineralization, liberating up to 30% of mineralized N (Griffiths, 1994). Enrichment opportunist bacterial and fungal-feeding nematodes respond quickly to organic amendments. Due to their high respiration rates and low N needs, they mineralize N to plant available forms (Chen and Ferris, 1999; Ferris et al., 1997). In 2007 numbers of enrichment opportunists and corn plant productivity were higher in L and M where 4–5000 kg ha^{-1} of N from cover crop biomass had been applied over two years. Regression analysis of soil, nematode and cover crop factors designated NH_4-N and SAb1f2 as important factors associated with plant productivity. However SAb1f2 alone only account for 24% of the variation in corn plant biomass in 2007. Soil N levels (NH_4-N) at cover crop mowing (corn planting) accounted for another 23% of the variation, suggesting that the level of residual N is another important factor.

Surprisingly, enrichment opportunists were abundant after cover crops even in a conservation tillage system. No-till plots often have a high CI (Minoshima et al., 2007). The accumulation of residue on the soil surface is readily exploited by fungi, resulting in slow decomposition rates and a dominance of fungivores (Sánchez-Moreno et al., 2006). In the present study, the CI in soil was less than 20 after both high and low C:N cover crops and only reached 31 in control plots. Unexpected levels of bacterivores in cover crop residue further show that bacterial decomposition may dominate in low tillage systems in this dry Mediterranean climate. Residue samples had extremely high densities (51,000–92,000) of bacterial enrichment opportunists m^{-2} in all cover-cropped plots versus 4000 in fallow. Fungal enrichment opportunists were an order of magnitude lower than bacterial enrichment opportunists, 6–9000 nematodes m^{-2} in cover crops and 400 nematodes m^{-2} in fallow, resulting in CI < 8 for all treatments. The contribution of bacterial and fungal groups in conservation tillage is controversial. Some studies find that fungal channels are more important (Parmelee and Alston, 1986), others bacterial channels (Fu et al., 2000), or no significant differences (Stinner et al., 1984). Differences may be due to temporal dynamics under varying moisture levels, litter qualities, and faunal compositions. In order to determine contributions from soil fauna in conservation tillage systems, long term studies of dynamics at, near and below the soil surface are necessary.

Additions of mid-range C:N ratio (16–18) residues/materials may provide the highest potential to maximize faunal nutrient cycling and synchrony of N release with plant needs. R-strategist bacterivores and fungivores respond quickly to N-rich organic matter additions (Ettema and Bongers, 1993; Porazinska et al., 1999). In order to maintain high levels of beneficial, mineralizing fauna, Ferris et al. (2004) suggest multiple amendment applications or pre-season irrigation. Less cost prohibitive may be management of C:N ratios of soil inputs to favor stable decomposer populations mineralizing a steady flow of N. With high %N cover crops, *b*1 abundance peaked at cover crop mowing before seedlings emerged (Fig. 1). Abundance of *b*1 in plots after moderate N cover crops (M) grew more slowly, consistently higher than L from 3 to 14 weeks after planting the crop, suggesting temporary immobilization of N in microbial biomass. Population dynamics of enrichment opportunists associated with N mineralization imply that mid-range C:N cover crops may avoid excess net mineralization at the beginning of the season when plants need less N and excess N is more likely to be released to the environment by leaching.

4.2. *Cover crops did not increase soil food web structure*

Abundant, complex soil food webs made up of diverse interacting elements may offer biological buffering capacity, preventing individual organisms (i.e. nematode pests) from becoming dominant (Stirling and Eden, 2008), directly by predation (Yeates and Wardle, 1996; Khan and Kim, 2005) or indirectly through competition (Mazzola, 2002). Omnivores and predators predominant in complex structured soil food webs are particularly susceptible to disturbance such as tillage (Wardle et al., 1995; Kladivko, 2001). In order to track the effects of cover crop combinations on soil food web structure (SI), this case study was set under a strip tillage regime designed to minimally impact sensitive fauna.

Contrary to expectations, high and mid-range C:N inputs did not build soil food web structure and inferred plant parasite regulatory capacity. We hypothesized that in the absence of physical disturbance from tillage, steady resource availability from fungal dominated decomposition channels would stimulate top trophic level omnivores and predators. Minimal tillage was performed throughout the experiment, yet we observed only 22 predator nematodes out of more than 32,000 nematodes identified across eight sampling dates.

No difference in SI between treatments may be due to very low initial populations of omnivores and predators after previous agricultural disturbance. Slow reinvasion rates and regeneration times preclude significant increases in these groups over the two-year span of the study. One year after inoculation we were unable to detect increases in the SI even in subplots inoculated with high OP densities. Agricultural systems often have low SI values in comparison to natural areas (Ferris et al., 2001). Tillage diminishes disturbance-sensitive populations of omnivores and predators (Bongers, 1990; Kladivko, 2001) by direct abrasion and changes to soil texture. After two years, Minoshima et al. (2007) did not see significant increases in soil food web structure with conversion to no-till and suggested that it may take many years after conversion to no-till for sensitive species to re-colonize disturbed sites. In a chronosequence of 4–25 years of reduced disturbance in cotton there was some increase in the abundance of organisms (nematodes, mites and insects) during the first 8 years, but only the two older fields (8–26 years) accumulated both abundance and species richness that approached that of undisturbed sites (Adl et al., 2006). Response to conversion varies. Hanel (2003) saw increases in omnivores and predators only two years after fields were abandoned but there was little change in community structure after 5 years of no-till in a study by Parmelee and Alston (1986).

Cover crop quality as well as quantity is an important determinant of the nature and magnitude of soil food web services. Cover crops increased nutrient cycling capacity as indicated by an elevated EI. However, high biomass producing grain cover crops that increase the EI were associated with low plant productivity in 2006. In contrast, the total number of enrichment opportunist taxa was affected by both the amount and %N of cover crops grown. Monitoring the abundance of enrichment opportunists may provide managers with a new tool to evaluate soil food web nutrient cycling capacity.

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