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Linking soil properties and nematode community composition: effects of soil management on soil food webs

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Summary – The purported benefits of conservation tillage and continuous cropping in agricultural systems include enhancement of soil ecosystem functions to improve nutrient availability to crops and soil C storage. Studies relating soil management to community structure allow the development of bioindicators and the assessment of the consequences of management practices on the soil food web. During one year (December 2003-December 2004), we studied the influence of continuous cropping (CC), intermittent fallow (F), standard tillage (ST) and no tillage (NT) on the nematode assemblage and the soil food web in a legume-vegetable rotation system in California. The most intensive systems included four crops during the study period. Tillage practices and cropping pattern strongly influenced nematode faunal composition, and the soil food web, at different soil depths. Management effects on nematode taxa depended on their position along the coloniser-persister (cp) scale and on their trophic roles. At the last sampling date (December 2004), *Mesorhabditis* and *Acrobeloides* were positively associated with NH_4^+, while *Panagrolaimus* and *Plectus* were negatively correlated with certain phospholipid fatty acids (PLFA). Microbial-feeders were in general associated with both bacterial and fungal PLFA, microbial biomass C (MBC) by chloroform fumigation-extraction, total C and N, NH_4^+ and NO_3^-, and were most abundant in the surface soil of the NTCC treatment. Fungal-feeders were more closely related to PLFA markers of fungi than to ergosterol, a purported fungal sterol. *Discolaimus*, *Prionchulus*, *Mylonchulus* and Aporcelaimidae, in contrast, were associated with intermittent fallow and deeper soil layers. The organisms in the higher levels of the soil food web did not respond to the continuous input of C in the soil and a long recovery period may be required for appropriate taxa to be reintroduced and to increase. At the end of the experiment, each treatment supported quite different nematode assemblages and soil food webs.

Keywords – cover crops, fallow, nematode sensitivity, soil food web, tillage.

Composition and abundance of the nematode fauna have been used as soil health indicators in many different environments (Neher, 2001). Nematodes are functionally diverse and ubiquitous, and respond readily to environmental changes. The tight relationships between soil characteristics and abundance of nematode in different functional guilds (Fiscus & Neher, 2002) have been used to develop soil assessment criteria. In agricultural fields, nematode abundance and diversity are used to infer soil process rates (Ettema, 1998; Porazinska *et al*., 1999), soil functions (Ekschmitt *et al*., 2003; Yeates, 2003) and effects of disturbance on soil fauna (Wardle *et al*., 1995). Both in natural areas and under experimental conditions, nematode assemblages are used to assess the effects of pollution (Korthals *et al*., 1996; Gyedu-Ababio *et al*., 1999), as indicators of enrichment and disturbance (Bongers, 1990; Ferris *et al*., 2001; Berkelmans *et al*., 2003) and to study food webs dynamics (Mikola & Setälä, 1998b; Wardle *et al*., 2005).

Reduced tillage practices are used to minimise soil disturbance, with benefits that include improved soil structure, positive effects on soil fauna, increase in water storage and reductions of fuel cost, soil erosion and airborne dust. Under some established no-tillage systems, crop production can reach similar levels to those achieved in conventional tillage systems (Thiagalingam *et al*., 1996).

Tillage and cropping patterns cause profound changes in populations of soil organisms (Kladivko, 2001). Studies of the effects of tillage and cropping patterns on nematode assemblages have been focused mainly on plant-parasitic nematodes (Yamada, 2001; Bulluck *et al*., 2002; Smiley

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et al., 2004; Adediran *et al.*, 2005; Roberts *et al.*, 2005) but important information on soil health and quality can be derived from the entire nematode fauna (Urzelai *et al.*, 2000; Neher, 2001).

The positive effects of limiting physical disturbance may include increases in abundance of the nematode fauna (Nakamoto *et al.*, 2006). Most organisms are more abundant in no tillage than in conventional tillage systems and larger-bodied organisms are especially sensitive to soil disruption (Kladivko, 2001). Thus, earthworms are usually more abundant in non-tilled than in tilled soils, although some species react positively to tillage due to the rapid incorporation of organic matter into the soil (Chan, 2001).

In a review of tillage effects on soil organisms, Wardle (1995) reported that bacterial-feeding nematodes were at least slightly stimulated by tillage in 65% of the studies. However, in some studies, total nematode density was reduced after the first tillage, with bacterial feeders dominating in tilled plots and herbivores more abundant in no-tilled plots (Lenz & Eisenbeis, 2000). In other studies, the density of herbivore nematodes was independent of the tillage system (Bulluck *et al.*, 2002). Where nematode densities are greater in conventional than in no tillage soils, it is mainly due to greater abundances of bacterial and fungal feeders (Liphadzi *et al.*, 2005).

Fiscus and Neher (2002) developed a methodology for distinguishing distinctive responses of nematode genera to agricultural management practices. They concluded that the nematode taxa most sensitive to tillage were *Aphelenchoides*, *Discolaimus*, *Eucephalobus*, *Eudorylaimus*, *Heterocephalobus* and *Wilsonema*, whilst *Achromadora*, *Mylonchulus*, *Plectus* and *Prismatolaimus* were among the most resistant to tillage effects.

The maintenance of agricultural fields under bare fallow conditions leads usually to a reduction in abundance of plant-parasitic nematodes (Cadet *et al.*, 2003). The effects of bare fallow on free-living nematodes are not well studied, but they include reductions in abundance of some taxa (Pankhurst *et al.*, 2005) and greater nematode abundance in the higher volumes of run-off water (Villenave *et al.*, 2003). Compared with natural areas, cropped fields support lower nematode diversity. When cropping is abandoned and fields are allowed to revert to natural conditions, nematode diversity can increase significantly (Háněl, 2003).

In a previous study (Minoshima *et al.*, 2006), we found significant effects of tillage and continuous cropping systems on C storage and other soil properties. C storage was higher in no-tillage than in standard tillage and with continuous cropping than in plots which had intermittent fallow periods. Above ground plant biomass, including crop yields, was lower under no tillage than standard tillage.

Our working hypotheses were based on the following ideas: *i*) higher trophic levels of soil organisms, including nematodes, are susceptible to disturbance; *ii*) conventional cropping systems that include periods of bare fallow do not supply sufficient C to the soil to sustain omnivores and predators since C is respired by metabolically-active bacterivore opportunists; *iii*) omnivores and predators may increase with continuous cropping since C will be available to support higher trophic levels; *iv*) omnivores and predators, which are susceptible to disturbance, should be more abundant under no-tillage; and *v*) soil food web structure will be up-regulated by C inputs, and slower degradation of soil C will occur in the no tillage continuous cropping treatments.

Some of these questions have been addressed in a previous paper (Minoshima *et al.*, 2006). Therefore, the objectives of the present study were to: *i*) determine the sensitivity of nematode taxa to tillage and intermittent fallow treatments at different soil depths in agricultural fields; *ii*) relate soil properties and nematode assemblage composition to soil management; and *iii*) determine whether different agricultural practices establish and maintain different nematode assemblages and soil food webs.

Materials and methods

STUDY SITE

The experiment was performed in the companion plot area of the Long Term Research in Agricultural Systems (LTRAS) site at the University of California, Davis. The experimental plots were conventionally farmed for many decades, *e.g.*, for oat hay. The soil is classified as Rincon silty clay loam (fine, montmorillonitic, thermic Mollic Haploxeralfs). The four treatments were combinations of intermittent fallow (F) or continuous cropping (CC) with standard tillage (ST) and no-tillage (NT). In the NT plots, there were no tillage operations during the study and crop residues were spread on the top of the beds. In the ST plots, crop residues were disked and incorporated to a depth of 20 cm between crops. The cropping sequence in CC was a tomato (*Lycopersicon esculentum*) crop (planted in spring, 2003), sudan-sorghum (*Sorghum bicolor*) cover crop (planted in late summer) and a garbanzo (*Cicer* *arietinum*) crop (planted in late autumn). In 2004, the summer crop was cowpeas (*Vigna unguiculata*). In the F treatments, only tomato and garbanzo were planted and the plots were fallow in autumn 2003 and summer 2004. Four treatments were established as combinations of both cropping pattern and tillage system: NTCC (no-tillage + continuous cropping), STCC (standard tillage + continuous cropping), NTF (no-tillage + intermittent fallow) and STF (standard tillage + intermittent fallow).

SOIL SAMPLING AND NEMATODE IDENTIFICATION

Soil was sampled in December 2003, June 2004, September 2004 (only two treatments) and December 2004. Soil samples were taken at three depths: 0-5 cm, 5-15 cm and 15-30 cm. Nematodes were extracted from a subsample of 350 g using a combination of decanting and sieving and Baermann funnel methods. All nematodes in each sample were counted at low magnification and then 100 nematodes (200 at the last sampling date) from each sample were identified to genus or family at higher magnification.

Nematodes were classified by trophic habit (Yeates *et al.*, 1993) and by coloniser-persister (cp) groups (Bongers, 1990). The cp scale classifies nematode families in five groups, from microbial feeders with short life cycles (cp 1 and 2) to predators and omnivores with long life cycles and greater sensitivity to environmental perturbations (cp groups 4 and 5). Soil food web indices were calculated after Ferris *et al.* (2001) based on the abundance of functional guilds (Bongers & Bongers, 1998). The Structure Index (SI) is based on the relative abundance of higher trophic level nematodes and indicates soil food web length and soil resilience. The Channel Index (CI) is calculated as the proportion of fungal-feeding nematodes compared to enrichment-opportunistic bacterial feeders, and is an indicator of activity in the predominant decomposition channels in the soil, fungal mediated (higher values) or bacterial mediated (lower values). The Basal Index (BI) is an indicator of the prevalence of the general opportunistic nematodes that are tolerant of soil perturbation. Finally, the Enrichment Index (EI) is an indicator of enrichment opportunistic nematodes, both fungal and bacterial feeders, which respond rapidly to increases in food resources. The resilience of nematode trophic groups to tillage was calculated according to Wardle (1995).

SOIL PROPERTIES

Microbial organic carbon (MBC), NH_4^+, NO_3^- and ergosterol were measured at all sampling dates. Phospholipid fatty acids (PLFA) were used as indicators of bacterial and fungal biomass in the soil. Bacterial PLFA markers were: *iso* 15:0, *anteiso* 15:0, 15:0, *iso* 16:0, 16:1ω5c, *iso* 17:0, *anteiso* 17:0, 17:0cy, 17:0 and 19:0cy. Fungal PLFA markers were 18:2ω, 6, and 9c (Bossio *et al.*, 1998; Mikola & Setälä, 1998a). Bulk density was measured once, in samples collected in February 2005. For details of measurements of soil properties, see Minoshima *et al.* (2006). Soil physicochemical analyses (total N, total C, soil pH, K and plant available (Olsen) P) were performed by the University of California's Agriculture and Natural Resources Analytical Laboratory (http://danranlab.ucanr.org).

STATISTICAL ANALYSES

The influence of treatments on the nematode assemblage across the four sampling dates was determined by Correspondence Canonical Analysis (CCA) and by the methodology of Fiscus and Neher (2002). Nematode identification at higher resolution was used to relate nematode taxa with soil chemistry at the last sampling date (December 2004). All variables were transformed as $ln(x + 1)$ to normalise data before the analyses. ANOVA was used to check the influence of categorical variables on nematode abundances and soil food web indices. Correlation analysis was used to check relationships between variables. Analyses were performed using STATISTICA software (StatSoft, 1996).

Direct effects of tillage system, cropping pattern and depth

Differences in abundances of nematode taxa and food web indices were tested using General Linear Models. All the nematological variables (nematode taxa abundances and soil food web indices) and three categorical factors (tillage system, cropping pattern and soil depth) were subjected to CCA using data from the four sampling periods (December 2003, June 2004, September 2004, December 2004, n = 126).

In CCA bi-plots, environmental axes are represented by arrows. The length of the arrow indicates the importance of the environmental variable for the ordination roots. Its direction indicates the correlation of the variable with other variables; arrows in the same direction are positively correlated, while arrows pointing in opposite directions are negatively related. Dependent variables (nematode taxa and food web indices) located near an environmental (independent) variable suggest a positive effect of the latter on the former.

Indirect effects of tillage system, cropping pattern and depth

Data from the last sampling date were subjected to ANOVA to test differences in the soil properties among treatments. Nematode abundances and soil properties were used to perform multivariate analyses (CCA) of the state of the nematode assemblage at the end of the cropping cycle (December 2004, n = 36). In these analyses, nematode data were expressed at the highest level of taxonomic resolution available.

Results

DIRECT EFFECTS OF TILLAGE SYSTEM, CROPPING PATTERN AND DEPTH

Cropping pattern, tillage system and depth affected the composition of the nematode fauna and food web indices across the four sampling dates. Tylenchidae, Rhabditidae, *Acrobeloides* and *Pratylenchus* were more abundant in continuously cropped plots, while Dorylaimidae were more abundant in the intermittent fallow treatments (Table 1). Consequently, number of nematodes was lower and the SI was higher under intermittent fallow (Table 2).

Tillage directly affected *Aphelenchus* and Rhabditidae, which were more abundant in ST plots, and Tylenchidae, more abundant in the NT treatments. Depth affected *Aphelenchus*, Tylenchidae, *Panagrolaimus* and Dorylaimidae, which were more abundant in the upper soil layers (0-15 cm). The CI was higher in NT plots. Both BI and CI were lower in the upper soil, where EI was higher (Table 2).

Following Wardle's methodology to infer the resilience of soil organisms to tillage (Wardle, 1995), nematodes as a whole were *mildly stimulated by tillage* (V index = 0.14). In fact, the response of nematodes varied depending on their trophic group; bacterial-feeders and fungal-feeders were *mildly stimulated by tillage* (V = 0.29 and 0.03, respectively) and herbivores and predators and omnivores were *mildly inhibited by tillage* (V = −0.06 and −0.004, respectively). By the same logic, bacterial, fungal and plant feeders were inhibited and predators and omnivores stimulated by intermittent fallow (Fig. 1).

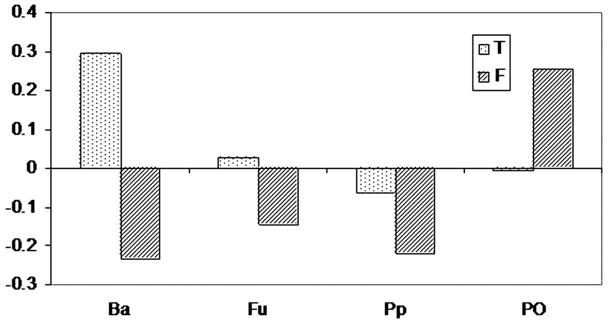


Fig. 1. *V index values for nematode trophic groups (Ba = bacterial-feeders, Fu = fungal-feeders, Pp = plant parasites, PO = predators and omnivores) sensitivity to tillage (T) and fallow (F). Positive values indicate stimulation; negative values indicate inhibition (after Wardle, 1995).*

Direct effects of cropping intensity, tillage system and depth on the nematode faunal data across the four sampling dates were analysed and expressed in a CCA bi-plot. Tylenchidae were associated with CC and negatively affected by the F treatments, while *Aphelenchus*, *Acrobeloides,* Rhabditidae and *Panagrolaimus* were positively associated with ST and negatively affected by soil depth; they were most abundant in the upper soil layers.

For the four sampling dates, the CI and the SI were higher in the 15-30 cm depth, and were associated with NT and F. The EI was associated positively with upper soil and the BI with medium depths and F (Fig. 2).

Following Fiscus and Neher (2002), the analysis of the direct effects of tillage, cropping pattern and depth on the nematode assemblage along the four sampling dates allowed classification of nematode taxa and food web descriptors as functions of their associations with each variable. Nematodes were classified as tolerant to tillage if positioned in the bi-plot area defined by ST, and sensitive if positioned in the opposite half, indicating association with NT. The same logic was used to score each nematode taxon as sensitive or resistant to fallow and to infer associations with different soil depths (Table 3).

INDIRECT EFFECT OF TILLAGE AND COVER CROPS

Relationship between environmental variables and management

On the last sampling date (December 2004) soil pH, NO_3^- and bulk density varied among the treatments. pH and bulk density were higher in the NT treatments. NO_3^- was significantly higher in STCC. Total C, total N, pH, ergosterol and bulk density were all significantly affected by tillage system and were higher in NT (Table 4).

Soil properties were, in general, strongly correlated. Soil pH and C, N, P and K concentrations were positively

Table 1. *Effects of cropping pattern, tillage system and soil depth on abundance of nematode taxa (number of nematodes/ 100 g soil). F values and level of significance are indicated (ns = not significant). Data are from the four sampling dates (n = 126).*

	Cropping $F = 5.29$; $P<0.0001$		Tillage $F = 5.75$; $P<0.0001$		Depth $F = 1.98$; $P<0.01$			Univariate effects		
	Continuous cropping	Fallow	No-till	Standard	0-5 cm	5-15 cm	15-30 cm	Cropping	Tillage	Depth
Aphelenchus	127.84 ± 10.49	116.88 ± 12.11	100.07 ± 9.21	144.65 ± 13.33	126.51 ± 15.47	167.63 ± 15.41	75.29 ± 6.72	ns	$P<0.01$	$P<0.05$
Tylenchidae	233.71 ± 15.39	132.10 ± 17.77	209.73 ± 18.85	156.08 ± 16.60	180.23 ± 21.18	238.02 ± 26.52	152.25 ± 16.39	$P<0.001$	$P<0.05$	$P<0.01$
Acrobeloides	133.55 ± 16.22	73.95 ± 18.73	63.29 ± 11.54	144.20 ± 23.47	112.88 ± 17.60	131.10 ± 26.88	80.03 ± 21.74	$P<0.05$	ns	ns
Panagrolaimus	141.08 ± 34.50	123.28 ± 39.84	113.35 ± 33.48	151.01 ± 40.32	313.43 ± 67.07	58.00 ± 18.27	28.92 ± 7.55	ns	ns	$P<0.001$
Rhabditidae	135.08 ± 20.30	57.76 ± 23.44	49.93 ± 12.43	142.91 ± 32.24	126.05 ± 26.94	124.82 ± 39.03	54.95 ± 16.00	$P<0.05$	$P<0.01$	
Tylenchorhynchus	19.29 ± 4.98	28.47 ± 5.75	26.15 ± 4.17	21.61 ± 6.53	16.89 ± 6.58	34.46 ± 8.47	18.32 ± 2.93	ns	ns	ns
Dorylaimidae	27.57 ± 5.76	48.78 ± 6.65	37.40 ± 6.58	38.94 ± 5.64	48.10 ± 11.67	37.49 ± 4.70	24.38 ± 2.99	$P<0.05$	ns	$P<0.05$
Small Dorylaimidae	1.97 ± 0.67	1.08 ± 0.78	2.51 ± 0.90	0.54 ± 0.24	1.64 ± 0.96	2.59 ± 1.10	0.54 ± 0.30	ns	ns	ns
Plectus	8.13 ± 1.75	4.40 ± 2.02	7.41 ± 2.26	5.12 ± 1.10	10.24 ± 3.33	4.93 ± 1.55	4.43 ± 1.30			
Pratylenchus	30.50 ± 5.85	12.48 ± 6.75	15.76 ± 3.48	27.22 ± 8.83	4.36 ± 1.24	21.58 ± 5.66	42.38 ± 11.62	$P<0.05$	ns	$P<0.05$
Tylencholaimus	1.01 ± 0.43	0.36 ± 0.50	0.70 ± 0.26	0.66 ± 0.64	0.42 ± 0.25	0.93 ± 0.87	0.84 ± 0.38	ns	ns	ns

Table 2. *Effects of cropping pattern, tillage system and soil depth on soil food web indices (EI = Enrichment index, SI = Structure index, BI = Basal index, CI = Channel index), total number of nematodes (N) and taxa richness (S). F values and level of significance are indicated (ns = not significant). Data are from the four sampling dates (n = 126).*

	Cropping $F = 4.52$; $P<0.0001$		Tillage $F = 2.69$; $P<0.05$		Depth $F = 5.34$; $P<0.0001$			Univariate		
	Continuous cropping	Fallow	No-tillage	Standard	0-5 cm	5-15 cm	15-30 cm	Cropping	Tillage	Depth
N	859.72 ± 64.35	599.53 ± 80.03	626.31 ± 66.25	832.94 ± 87.81	940.76 ± 106.65	821.56 ± 96.04	482.32 ± 61.25	$P<0.05$	ns	$P<0.01$
S	7.61 ± 0.15	7.85 ± 0.12	7.81 ± 0.12	7.65 ± 0.15	7.45 ± 0.15	7.74 ± 0.17	7.95 ± 0.17	ns	ns	$P<0.05$
EI	65.66 ± 2.01	66.64 ± 1.72	64.77 ± 1.52	67.53 ± 2.20	73.58 ± 1.79	60.63 ± 2.20	64.03 ± 2.30	ns	ns	$P<0.01$
SI	26.29 ± 3.15	43.62 ± 2.09	34.33 ± 2.59	35.57 ± 3.00	29.11 ± 3.64	29.77 ± 2.83	42.27 ± 3.32	$P<0.001$	ns	$P<0.01$
BI	29.76 ± 1.72	26.41 ± 1.49	29.14 ± 1.37	27.02 ± 1.86	22.90 ± 1.61	33.50 ± 2.02	28.56 ± 1.91	ns	ns	$P<0.05$
CI	40.85 ± 3.71	43.26 ± 3.20	47.17 ± 3.28	36.93 ± 3.48	23.93 ± 2.33	53.34 ± 4.17	48.37 ± 4.28	ns	$P<0.001$	$P<0.01$

Table 3. *Direct effects of tillage (ST = standard tillage, NT = no-till), cropping pattern (F = fallow, CC = continuous cropping) and soil depth (0-5, 5-15 and 15-30 cm) on abundance of nematode taxa and on soil food web indices (S = taxa richness, N = total number of nematodes, EI = Enrichment index, SI = Structure index, BI = Basal index, CI = Channel index). Trophic group (Ba = bacterial feeders, Fu = fungal feeders, Pp = plant parasites, P = predators, O = omnivores) of nematode taxa are indicated.*

	Trophic group	Cp	Tillage	Cropping pattern	Depth (cm)
Aphelenchus	Fu	2	ST	CC	0-5
Tylenchidae	Pp,Fu	2	NT	CC	5-15
Acrobeloides	Ba	2	ST	CC	0-5
Panagrolaimus	Ba	1	ST	CC	0-5
Rhabditidae	Ba	1	ST	CC	0-5
Tylenchorhynchus	Pp	3	NT	F	5-15
Dorylaimidae	O	4	ST	F	5-15
Small Dorylaimidae	O	4	NT	CC	5-15
Plectus	Ba	2	NT	CC	5-15
Pratylenchus	Pp	3	NT	CC	5-15
Tylencholaimus	Fu	4	NT	CC	5-15
N			ST	CC	0-5
S			NT	F	5-15
EI			ST	CC	0-5
SI			ST	F	15-30
BI			NT	CC	5-15
CI			NT	F	15-30

related (r between 0.49 and 0.83, $P < 0.05$). NH_4^+ was associated with intermittent fallow and correlated with ergosterol and MBC (r between 0.49 and 0.52, $P < 0.05$). PLFA of fungal markers were correlated with ergosterol ($r = 0.35$, $P < 0.05$) and with PLFA of bacterial markers ($r = 0.95$, $P < 0.05$).

Influence of environmental variables on nematode taxa and soil food web descriptors

In December 2004, at the end of the experiment, in the ordination of the nematode taxa in the multivariate space defined by the environmental variables, positive values for most of the soil properties grouped together, indicating soil enrichment and high biological activity (Fig. 3a, b). The PLFA biomarkers of both bacteria and fungi were related with the abundance of *Acrobeloides*, *Mesorhabditis* and *Tylenchorhynchus*. *Panagrolaimus* and *Acrobeles*, both bacterial feeders, were not correlated with either group of PLFAs and ordered in the opposite part of the graph. Tylenchidae was associated with pH ($r = 0.47$, $P < 0.05$). *Aphelenchoides* was associated with NO_3^-.

The abundance of all the omnivores and predators (*Discolaimus*, Aporcelaimidae, Qudsianematidae and *Mylonchulus*), except *Prionchulus*, were inversely correlated with almost all soil properties. The EI was negatively correlated with the CI ($r = -0.93$, $P < 0.05$), BI ($r = -0.95$, $P < 0.05$), taxa richness ($r = -0.56$, $P < 0.05$), bulk density ($r = -0.40$, $P < 0.05$) and PLFA of bacterial markers ($r = -0.35$, $P < 0.05$). It was positioned in the opposite part of the graph than BI and CI (Fig. 3). CI was positively correlated with bulk density and PLFA of fungal markers ($r = 0.37$ and 0.34, respectively, $P < 0.05$). SI was negatively correlated with NO_3^-, pH and K ($r = -0.37$, -0.33 and -0.34, $P < 0.05$). Taxa richness and number of nematodes were negatively correlated ($r = -0.36$, $P < 0.05$). Number of nematodes was associated with total C and taxa richness with bulk density. CI and BI were positively correlated ($r = 0.86$, $P < 0.05$).

Discussion

The aim of this study was to evaluate the relationships between nematode faunal composition and soil properties as determined by agricultural management. It is generally accepted that nematodes are strongly influenced by their microenvironment and provide a useful reflection of soil health status and several soil functions (Mulder *et al.*, 2005). The use of multivariate statistics, especially Canonical Analysis, has improved the understanding of the complex relationships between different groups of soil fauna and between organisms and soil physical-chemical properties (Popovici & Ciobanu, 2000; Wardle *et al.*, 2001; Fiscus & Neher, 2002).

As expected from previous studies (*e.g.*, Wardle, 1995), total nematode abundance was not strongly influenced by tillage due to the varied responses of different taxa. Nematode responses to tillage and cropping intensity varied with their trophic group; bacterial feeders and fungal feeders were stimulated by tillage and reduced under intermittent fallow; plant-feeders were generally inhibited by both tillage and intermittent fallow; and predators and omnivores were stimulated by intermittent fallow and did not respond clearly to tillage practices. In fact, the few omnivores and predators in this and most agricultural fields probably represent the more tolerant taxa within these trophic levels. Taxa intolerant to disturbance may no longer be present in arable soils. These observations agree with Lenz and Eisenbeis (2000), who found no changes in total nematode abundance and an increase of

Table 4. *Average values (± SE) of soil properties in the four different treatments across three depths. Significant effects of treatments (NTCC, STCC, STF, NTF), crop pattern (CC and F) and tillage (ST and NT) are indicated by level of significance. Data are from the last sampling date (December 2004, $n = 36$). Data from Minoshima* et al. *(2006).*

	NTF	STF	NTCC	STCC	Treatment	Crop	Tillage
Total C (%)	1.06 ± 0.03	0.99 ± 0.01	1.07 ± 0.04	1.03 ± 0.02			$P < 0.05$
Total N (%)	0.12 ± 0.00	0.11 ± 0.00	0.12 ± 0.00	0.12 ± 0.00			$P < 0.05$
pH	7.07 ± 0.03	6.86 ± 0.03	7.08 ± 0.06	6.90 ± 0.04	$P < 0.01$		$P < 0.001$
K (mg l^{-1})	7.00 ± 0.49	5.91 ± 0.13	7.86 ± 1.32	7.34 ± 0.80			
P (μg g^{-1})	17.38 ± 0.88	15.78 ± 0.31	19.08 ± 2.17	15.98 ± 0.83			
NO_3 (μg N g^{-1})	4.54 ± 1.06	5.50 ± 1.48	6.46 ± 0.92	12.03 ± 2.53	$P < 0.05$	$P < 0.05$	
NH_4 (μg N g^{-1})	2.36 ± 1.31	1.27 ± 0.54	1.16 ± 0.27	1.06 ± 0.16			
MBC (μg C g^{-1})	171.23 ± 26.23	148.16 ± 19.05	262.75 ± 63.98	171.58 ± 18.23			
Ergosterol (ng g^{-1})	999.32 ± 168.46	575.94 ± 36.31	2246.91 ± 829.75	1218.20 ± 256.85			$P < 0.05$
Bulk density (g/cm^3)	1.34 ± 0.02	1.25 ± 0.03	1.32 ± 0.02	1.25 ± 0.02	$P < 0.05$		$P < 0.01$
PLFAba (mg/m^2)	1907.53 ± 505.29	1445.40 ± 351.85	2301.27 ± 558.33	2086.76 ± 312.40			
PLFAfu (mg/m^2)	246.62 ± 120.47	142.95 ± 43.81	557.85 ± 262.61	272.08 ± 76.51			

bacterial-feeder nematodes after the first tillage treatment. Our results indicate that the response of total nematode abundance to management depends on the assemblage composition, so no general patterns can be discerned without analysing separately the taxa and functional group responses. For example, Liphadzi *et al.* (2005) found general increase in nematode abundance in tilled plots due to the predominance of fungal feeders and bacterial feeders (up to 90%) in the assemblages they studied.

Throughout the four sampling dates of this study, most of the microbial feeders (*Panagrolaimus*, Rhabditidae, *Aphelenchus* and *Acrobeloides*) were positively associated with standard tillage, indicating the stimulatory effect on microbes of incorporating organic matter into the soil. The nematodes less responsive to incorporated organic matter were the higher cp taxa (*Tylenchorhynchus*, *Tylencholaimus, Pratylenchus* and some Dorylaimidae), which were associated with no-tillage. Even though a greater number of taxa (especially of upper trophic levels), and higher resolution identification, would be desirable to infer relationships more reliably (Yeates, 2003; Mulder *et al.*, 2005), we observed significant relationships between sensitivity to tillage and trophic or cp groups, as similarly reported by Fiscus and Neher (2002).

Plectus was the only bacterivore associated with the soil properties of the NT treatments, suggesting a higher sensitivity to tillage practices. While Fiscus and Neher (2002) suggested that *Plectus* is an indicator of disturbance due to the concordance between its cp value (2) and its tolerance to chemical and mechanical perturbations, we found it to be more sensitive to tillage than expected from its cp value. Different responses among genera in the same trophic group are common (Porazinska *et al.*, 1999), and nematode genera within the same trophic group can exhibit asymmetric competition, negatively influencing the abundance of other genera (Postma-Blaaw *et al.*, 2005), so responses to perturbation may be influenced by the presence of other nematode taxa. Greater taxonomic resolution may be necessary to resolve differences in response to environmental variables among nematodes within higher taxonomic groupings (Yeates, 2003), especially for taxa that have numerous species and a broad size range (*e.g.*, *Plectus*).

Bacterial feeders are usually abundant in cultivated soils while predators and omnivores often disappear with cultivation (Wardle *et al.*, 1995). Microbivorous nematodes belonging to the cp 1 group (*e.g.*, *Panagrolaimus* or Rhabditidae, enrichment-opportunistic nematodes) and those with longer life cycles in the cp 2 group (*e.g.*, *Aphe-*

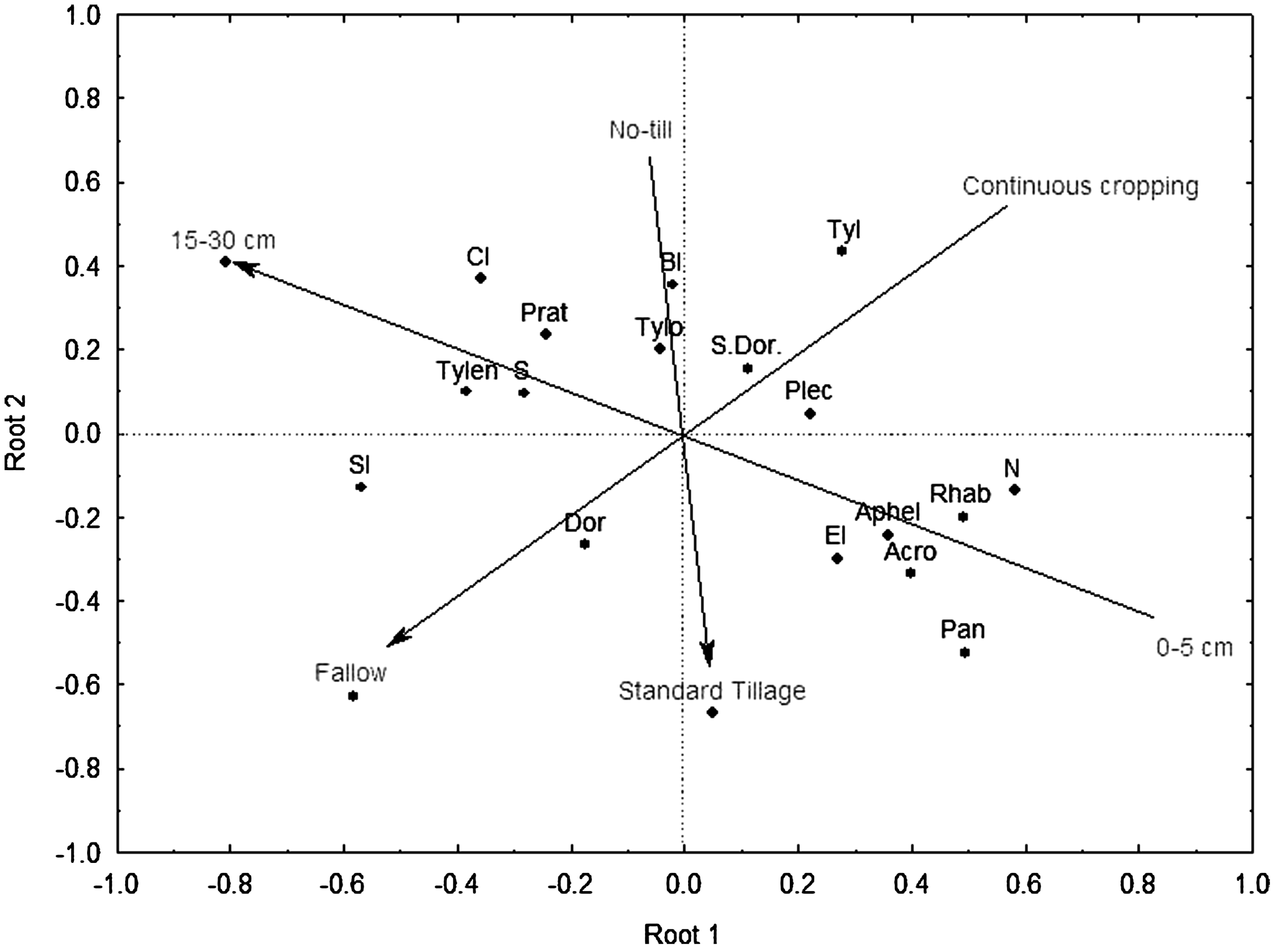
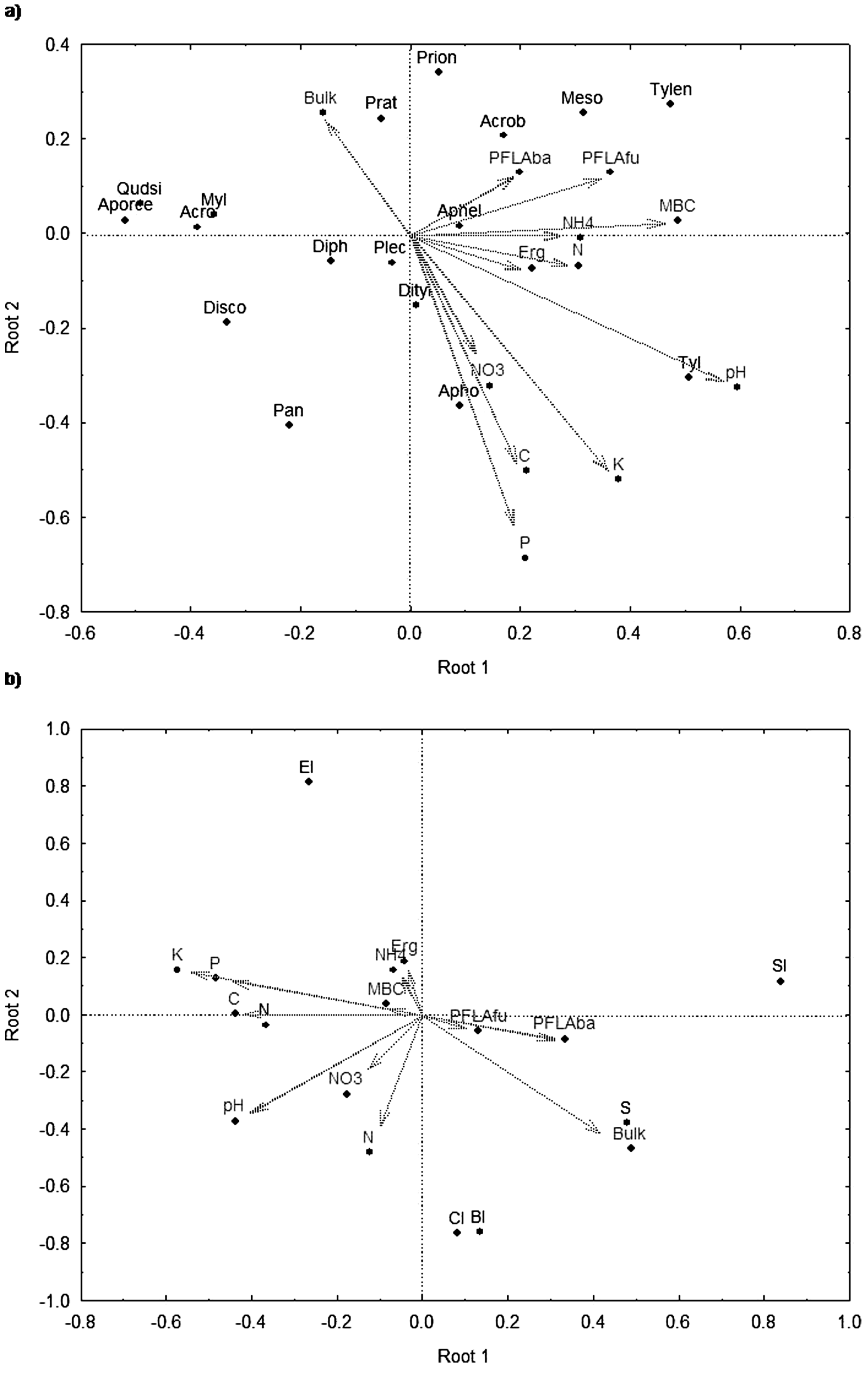


Fig. 2. *Canonical correspondence analysis bi-plot of effects of tillage system, crop pattern and depth on nematode abundances and soil food web indices. Environmental variables are marked by arrows. Aphel:* Aphelenchus, *Tyl: Tylenchidae, Acro:* Acrobeloides, *Pan:* Panagrolaimus, *Rhab: Rhabditidae, Tylen:* Tylenchorhynchus, *Dor:* Dorylaimidae, *S.Dor.: Small* Dorylaimidae, *Plec:* Plectus, *Prat:* Pratylenchus, *Tylo:* Tylencholaimus, *N: Total number of nematodes, S: Taxa richness, EI: Enrichment index, SI: Structure index, BI: Basal index, CI: Channel index. Eigenvalues were 0.568 and 0.362 for the first and the second root, respectively. Percentage of variance explained was 33.0% for both root 1 and root 2.*

lenchus and *Acrobeloides*), were also associated with continuous cropping. The combined effect of standard tillage and continuous cropping significantly enhanced the abundance of nematodes at the entry level of the soil food web. Bacterial-feeding nematodes influence C- and N-mineralisation by feeding on bacteria, excreting NH_4^+ and by spreading bacteria through the soil (Bouwman *et al.*, 1994, Fu *et al.*, 2005). *Mesorhabditis* and *Acrobeloides*, two of the most abundant bacterial-feeders in our plots, were positively associated with NH_4^+, a reasonable expec-

Fig. 3. *Scatter plot of CCA ordination showing relationships between soil properties and nematode taxa abundance (a) and soil food web indices, taxa richness and total number of nematodes (b). Acro:* Acrobeles, *Acrob:* Acrobeloides, *Aphel:* Aphelenchus, *Apho:* Aphelenchoides, *Aporce: Aporcelaimidae, Diph:* Diphtherophora, *Disco:* Discolaimus, *Dity:* Ditylenchus, *Meso:* Mesorhabditis, *Myl:* Mylonchulus, *Pan: Panagrolaimus, Plec:* Plectus, *Prat:* Pratylenchus, *Prion:* Prionchulus, *Qudsi: Qusianematidae, Tyl: Tylenchidae, Tylen:* Tylenchorhynchus. *Eigenvalues were 0.97 and 0.96 (a) and 0.80 and 0.58 (b) for roots 1 and 2, respectively. Percentages of explained variance for roots 1 and 2 were 10.7 and 11.0% (a) and 11.4 and 6.4% (b), respectively.*


a)
Prion
Bulk
Prat
Acrob
Meso
Tylen
PFLAba
PFLAfu
Qudsi
Myl
Aporce
Acro
Aphel
NH4
MBC
Diph
Plec
Erg
N
Dityl
Disco
Tyl
pH
NO3
Apho
Pan
C
K
P
Root 1
Root 2
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
b)
El
K
P
Erg
NH4
MBC
SI
C
N
PFLAfu
PFLAba
NO3
pH
N
S
Bulk
Cl
Bl
Root 1
Root 2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
-1.0
-0.8
-0.6
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
1.0

tation for the group associated with increased N mineralisation (Ferris *et al.*, 1997, 2004). By contrast, *Panagrolaimus* and *Plectus* ordered in an opposite position due to their negative relationship with PLFA biomarkers of fungi and bacteria and with bulk density. *Panagrolaimus* has a high metabolic rate and a broad, non-selective microbial feeding habit (De Mesel *et al.*, 2004). It may decrease bacterial populations (as indicated by lower PFLA from bacterial markers) to a greater extent than other bacterial feeders in our plots. When microbivorous nematodes predominate in soils, they enhance N mineralisation and thus the availability of N for plants (Ferris *et al.*, 2004). Total soil N may be correlated with abundance of certain nematodes (Nakamoto *et al.*, 2006), but potentially mineralisable N is a better indicator of N availability. That might explain why total soil N was associated only with abundance of Tylenchidae in this study. Total C, on the contrary, was more strongly associated with total nematode abundance.

Surprisingly, the abundance of fungal-feeding nematodes such as *Aphelenchus* and some Tylenchidae was not related as strongly with ergosterol as expected, suggesting that fungal biomass may not determining the size of fungal feeder populations. Villenave *et al.* (2004) found differing responses of fungal feeders to ergosterol content; fungal feeders in cp groups 2 and 4 were positively related with ergosterol but fungal feeders in the cp 5 group were not.

The discrimination between responses of nematodes in the higher and the lower levels of the soil food web was evident in the CCA ordination, revealing a link between lower trophic levels and MBC, NH_4^+, ergosterol, total N, total C and certain PLFA. Bacterial-, fungal- and plant-feeding taxa with low cp values ordered opposite to predatory and omnivore nematodes, such as *Prionchulus,* Qudsianematidae, Aporcelaimidae, *Discolaimus* and *Mylonchulus.* With the only exceptions of the plant-feeder *Tylenchorhynchus* (cp 3), which ordered close to *Mesorhabditis* (cp 1), and *Acrobeles* (cp 2), which scored close to the predators (cp 4, 5), nematodes belonging to cp groups 1 and 2 showed an opposite response to environmental variables than those in cp groups 3, 4 and 5.

Predatory and omnivore nematodes are in higher coloniser-persistent groups ($\geqslant$3) and are more sensitive to soil perturbation. Intermittent fallow and standard tillage supported higher abundances of most of the predators and omnivores; *Mylonchulus*, Qudsianematidae, *Prionchulus* and Aporcelaimidae. It is generally accepted that nematode functional diversity decreases with increasing management intensity (Mulder *et al.*, 2003); predatory nematodes were, in our case, much more affected by the cropping pattern (being enhanced in the intermittent fallow treatment) than by standard tillage. Our results thus suggest that even though predatory nematodes are sensitive to soil physical perturbation, other soil forces can drive their abundance. In some studies, 25 years of tillage did not strongly affect predators but reduced fungal-feeder nematodes (Wang *et al.*, 2004).

Table 5. *Summarized effects of treatments on nematode trophic groups (Ba = bacterial-feeders, Fu = fungal-feeders, Pp = plant-feeders, PO = predators and omnivores).*

	Standard tillage	No-tillage
Fallow	Small increase of Ba	Decrease of Ba
	Small decrease of Fu	Decrease of Fu
	Decrease of Pp	Small decrease of Pp
	Increase of PO	Increase of PO
	Increase of SI values	Increase of CI values
Continuous cropping	Increase of Ba	Small decrease of Ba
	Small increase of Fu	Increase of Fu
	Increase of Pp	Increase of Pp
	Decrease of PO	Decrease of PO
	Increase of EI values	Increase of BI values

An increase in predator and omnivore nematodes was expected in CC treatments as a result of the continuous incorporation of C into the soil, but was not found (Table 5). Minoshima *et al.* (2006) found that nematodes in the higher trophic levels were not significantly associated with the C pools in the soil. Previous studies found omnivore and predatory nematodes much more abundant in recently abandoned fallow fields than in cultivated or seminatural, meadow lands (Háněl, 2003). Polis *et al.* (2000) suggest that trophic cascades produced by complex trophic interactions are abundant in soil systems, but bottom-up regulation is difficult to demonstrate in soil trophic levels due to the high complexity of the soil biota interactions. In forest soils, Salomon *et al.* (2006) found more abundant microbial grazers when abundant resources were added to the soil, but the effects did not extend into higher trophic levels of the soil food web, leading to the conclusion that the availability of resources plays a minor role structuring soil food webs.

Responses of plant-parasites and root feeders to tillage are usually difficult to interpret and are more closely related to plant status and phenology than to soil properties. The association between *Pratylenchus* (endoparasite) and standard tillage might be explained by the release of the nematodes from the roots as a result of tillage (Lenz & Eisenbeis, 2000).

Ammonium, MBC, C, K, P and ergosterol were positively related with total number of nematodes and the EI. The EI is based on the weighted abundance of bacterial feeding nematodes enrichment-opportunistic relative to longer life cycle bacterial-feeders, indicating highly active bacterial-mediated decomposition channels. When the field is organically enriched, these nematodes exploit the abundant resources (fungi and bacteria), and increase rapidly in abundance due to their short life cycles and high fecundity (Bongers, 1990). On the contrary, high values of the CI indicate slower, fungal-mediated, decomposition pathways, so a significant relationship between CI and ergosterol was expected but not found. CI was positively correlated with PLFA of fungal biomarkers, and EI was negatively correlated with PLFA of bacterial markers but not correlated with MBC. Thus, the relationship between PLFA and microbial grazers may reflect the strength of the grazing pressure at the sampling time. The prevalence of opportunistic bacterial feeders over other microbial feeders (as expressed by the EI) may decrease bacterial biomass (indicated by PLFA of bacterial markers) more obviously than the effect of fungal feeders on fungal biomass, as indicated by the positive association between the CI, indicator of the prevalence of fungal-feeding nematodes over bacterial feeders, with fungal biomass (inferred from PLFA of fungal markers). The absence of correlation between MBC and nematode populations may thus indicate that the grazing pressure affects only certain microbes and not the total microbial community.

CI and BI were strongly correlated and associated with deeper soil layers and no tillage across all sampling dates. High BI values indicate a nematode assemblage composed of perturbation-resistant nematodes mainly of lower trophic levels. The community structure was, in this case, associated with fungal-dominated organic matter decomposition pathways. The SI was associated with deeper soil layers and intermittent fallow, suggesting a negative relationship between predator abundance and the high physical disturbance and biological activity present at the soil surface and in the continuous cropping plots.

Conclusions

Different tillage practices and cropping systems determine soil properties and thus nematode abundance. These effects vary with nematode trophic and functional group. By the end of the experiment, each treatment supported different nematode assemblages and soil food webs.

Each soil food web index describes a model nematode assemblage (Ferris *et al.*, 2001). Our four treatments structured four different nematode assemblages. The combination of standard tillage and continuous cropping (STCC) was associated with high EI values reflecting an assemblage predominantly composed of bacterial-feeding nematodes with short life cycles. This enriched assemblage was especially characteristic of the upper soil layer. Perhaps not surprisingly for a long-disturbed agricultural system, we did not find the relationships we expected between continuous cropping and the abundance of predator and omnivore nematodes. The organisms in the higher levels of the soil food web did not respond to the continuous input of C in the soil and a long recovery period may be required for appropriate taxa to be reintroduced and to increase. Intermittent fallow (especially STF) supported a longer, more structured soil food web (high SI values), especially in the deeper soil layers. The combination of no tillage and intermittent fallow (NTF) supported a fungal-based community, with slower organic matter decomposition rates, especially below the upper 5 cm of soil. The accumulation of plant residues on the soil surface may result in slower incorporation of C into the food web and exploitation by fungi. Indeed, the absence of tillage, and thus of physical perturbation, would not disrupt fungal hyphae. Finally, the combination of no tillage and continuous cropping (NTCC) supported a less well-defined assemblage, dominated by basal, perturbation-resistant nematodes.

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