Nematology, 2009, Vol. 11(1), 23-38

Short-term nematode population dynamics as influenced by the quality of exogenous organic matter

Ben L.M. LEROY [1,*], Nancy DE SUTTER [2], Howard FERRIS [3], Maurice MOENS [2,4] and Dirk REHEUL [5]

[1] *Ghent University, Department of Soil Management and Soil Care, Coupure Links 653, 9000 Ghent, Belgium*
[2] *Institute for Agricultural and Fisheries Research, Burg. Van Gansberghelaan 96, 9820 Merelbeke, Belgium*
[3] *University of California, Davis, Department of Nematology, One Shields Ave, Davis, CA 95616, USA*
[4] *Ghent University, Department of Crop Protection, Coupure Links 653, 9000 Ghent, Belgium*
[5] *Ghent University, Department of Plant Production, Coupure Links 653, 9000 Ghent, Belgium*

Received: 10 March 2008; revised: 10 April 2008
Accepted for publication: 11 April 2008

Summary – The food specificity of nematodes, their high number of species and high abundance in every habitat where decomposition takes place, indicate that the structure of the nematode assemblage has a high information content. Since nematodes respond quickly to changes in soil management and since the nematode fauna can be efficiently analysed, the structure of the nematode assemblage offers an interesting instrument to assess changes in soil conditions. We studied the effect of five organic amendments on the short-term nematode population dynamics and compared them to minerally fertilised and unfertilised plots. The experiment was started in 2005, and samples were taken in spring and autumn 2006 and spring 2007. In spring 2006, no clear differences among treatments in the diversity of free-living nematodes were observed, probably since the organic amendments were applied only twice, of which the last application was carried out 7 months before the sampling. At the second and third sampling, the enrichment index in the organically amended plots was higher than in the unamended plots, owing to the organic matter application. However, in plots amended with farmyard manure and cattle slurry the number of bacterivores increased significantly, while in the compost plots the fungivorous nematodes tended to be higher. This resulted in a low channel index for the manure and slurry plots, indicating a predominant bacterial decomposition pathway, and a higher channel index in the compost plots, suggesting a greater proportion of fungal decomposition. These assumptions on the decomposition of the applied organic matter were strongly supported by the composition of the soil microbial community, determined through PLFA analysis: in the compost plots the bacteria to fungi ratio was lower than in the manure and slurry plots. At all sampling occasions there was a remarkably lower abundance of plant-parasitic nematodes in plots amended with slurry and manure, indicating a negative impact of both amendments on plant-parasitic nematodes. We can conclude from this study that the fertiliser regimes affected the nematode assemblage, but that more samplings in the future are certainly necessary to assess adequately the impact of the different organic amendments.

Keywords – compost, fertiliser, nematode faunal indices, phospholipid fatty acids, quality.

Nematodes are the most abundant multi-cellular organisms in terrestrial and aquatic ecosystems (Bongers & Bongers, 1998). Although nematodes represent a relatively small amount of biomass in soil, their key positions at most trophic levels in soil food webs are vitally important in soil environments and ecosystem processes (Barker & Koenning, 1998). Nematode assemblage analyses are useful in assessing soil ecosystem status and function since nematodes are ubiquitous and easy to sample and classify into feeding groups or functional guilds, and they are sensitive to environmental changes. Hence, nematode faunal analysis is evolving as a powerful bioindicator of soil condition and of structural and functional attributes of the whole soil food web (Bongers & Ferris, 1999; Yeates & Bongers, 1999; Neher, 2001; Berkelmans *et al*., 2003; Yeates, 2003).

The structure of the nematode assemblage is affected by natural and anthropogenic disturbances. In response to these disturbances, the nematode assemblage becomes dominated by fast growing, bacterivorous nematodes (cp-1; *sensu* Bongers, 1990), and is then generally transformed to a more diverse community that includes slower

* Corresponding author, e-mail: ben.leroy@UGent.be

DOI:10.1163/156854108X398381

growing bacterivores and fungivores (cp-2) and, ultimately, predator nematodes and omnivores (cp-3 to cp-5) (Ferris *et al*., 1996; Yeates *et al*., 1999). This evolution of complexity can be monitored by the maturity index (MI) as defined by Bongers (1990), which has been used successfully to distinguish between unstressed ecosystems and heavily disturbed systems. However, more subtle differences among, for example, differently managed agroecosystems, could not be detected using the MI (Bongers & Bongers, 1998; Neher, 1999; Neher & Olson, 1999; Yeates & Bongers, 1999). An integration of trophic groupings and life strategies into functional guilds (Bongers & Bongers, 1998) allowed definition of several indices that describe structure, function and condition of the investigated soil food web relative to disturbance or stress. Ferris *et al*. (2001) defined the enrichment index (EI) as a measure of the nutritional level or resource availability, the structure index (SI) as a measure of the number of trophic layers and food web development, and the channel index (CI) as a measure to predict the decomposition pathway and distinguish between fungi- and bacteria-based food web structures (Berkelmans *et al*., 2003). These indicators may also be useful to characterise the soil quality or health.

Although a lot of research has been done on the effects of organic soil amendments on plant-parasitic nematode dynamics (Akhtar & Malik, 2000), there has been much less research on the effects of various kinds or qualities of organic amendments and mineral fertilisers on nematode assemblages and nematode trophic group dynamics (Bulluck *et al*., 2002). Moreover, in most of the recent studies on nematode assemblages the effect of only a small number of fertiliser treatments was investigated and compared (Bulluck *et al*., 2002; Forge *et al*., 2005; Wang *et al*., 2006; Okada & Harada, 2007). Therefore, the aim of the present study was to assess if eight different fertiliser regimes, of which five were organic amendments often used in Belgian agriculture, would cause shifts in the nematode population densities and community structure in the short term. We used the indices described by Bongers (1990) and Ferris *et al*. (2001) to characterise the community structure. Furthermore, some researchers have linked the nematode community with the microbial population (Yeates *et al*., 1997; Ferris & Matute, 2003; Ferris *et al*., 2004; Wardle *et al*., 2005; Williamson *et al*., 2005). Therefore, we also characterised the changes in the soil microbial community by phospholipid fatty acid (PLFA) analysis as the basic food source for bacterivorous and fungivorous nematodes.

Materials and methods

Experimental design

The experimental field, located in Melle, Belgium (experimental site of Ghent University, 50°59′N, 03°49′E, 11 m a.s.l.) is a sandy loam soil with the following granulometric composition: 11.7% 0-2 μm, 52.0% 2-50 μm and 36.3% >50 μm. Prior to the experiment it was cropped with monoculture maize for 8 years with mineral fertilisation only. Table 1 summarises the meteorological data of the experimental period at Melle.

The field experiment, started in 2005, was a randomised complete block design with four replicates and compared eight treatments: farmyard manure (FYM), cattle slurry + crop residues (CSL), vegetable, fruit and garden waste compost (VFG), two types of farm compost (CMC1 and CMC2), mineral fertiliser (MIN N) and two treatments without fertilisation (one with a crop (NF+) and one without (NF−), to assess the impact of the presence or absence of a crop). The two types of farm compost differed in the composition of the starting materials. CMC1 was composed of mostly woody, C rich materials resulting in a final C/N ratio of *ca* 20-40, while CMC2 was made of green, N rich materials and had a final C/N ratio of 10-20 (Table 2).

Organic amendments and fertilisers were applied on four occasions (Table 2). The first application took place on 21/04/05 and fodder beet (*Beta vulgaris* L.) was sown the day after. The second fertilisation was on 06/10/05 followed by the sowing of winter wheat (*Triticum aestivum* L.) the next day. One month after harvest of the winter wheat, the organic amendments and fertilisers were applied for the third time (07/09/06) and a catch crop of *Phacelia* (*Phacelia tanacetifolia* Benth.) was sown. On 02/05/07 the fourth application took place and red cabbage (*Brassica oleraceae* L. var. *rubra*) was planted 3 weeks later. Amounts of organic amendments were calculated in order to supply all plots (8×6 m^2) receiving organic amendments with an equal amount of organic C. This amount of organic C was 4000 kg C ha^{-1} in applications one and two; 1500 kg C ha^{-1} in application three and 2000 kg C ha^{-1} in application four. In all cases, the organic amendments were incorporated to a depth of 20 cm using a rotary tiller. During the experimental period, the NF-plots were kept fallow by removing weeds manually.

To correct for differences in the plant available N content of the different organic amendments, extra mineral N (ammonium nitrate 27%) was applied on organically

Table 1. *Total precipitation (mm) and average monthly air temperature (°C) at Melle, Belgium.*

	Month												Total
	1	2	3	4	5	6	7	8	9	10	11	12	
Precipitation (mm)													
2005	36.7	63.4	24.0	68.2	59.3	39.2	118.6	98.4	43.8	40.5	82.1	50.6	724.8
2006	16.2	96.6	70.3	52.4	112.6	45.7	21.6	292.7	19.2	106.3	79.4	107.6	1020.6
2007	78.6	108.4	55.6	0	108.2	102.8	177.7	84.7	84.3	63.0	–	–	–
Norm*	51.0	42.0	46.0	50.0	59.0	65.0	72.0	74.0	72.0	72.0	64.0	59.0	
Average air temperature (°C)													
2005	5.2	2.8	6.8	9.7	12.2	18.2	18.2	16.3	16.0	14.1	6.8	3.9	
2006	1.9	2.8	5.1	9.1	14.2	16.3	21.8	16.9	18.0	13.8	9.6	5.8	
2007	7.4	6.4	8.2	12.8	14.3	17.5	17.3	16.9	14.1	10.2	–	–	
Norm*	2.4	3.1	5.2	8.4	12.1	15.1	16.8	16.7	14.4	10.3	6.2	3.2	

* Norm = average over the last 30 years.

amended plots where needed to achieve equal levels of plant available N in all treatments and to attempt to support equal crop growth. For the fodder beet, the catch crop and the red cabbage, the mineral N was applied together with the organic amendments, while, for the winter wheat, the extra mineral N was split-applied on 23/03/06 and 26/04/06. For the calculation of the amount of extra mineral N to be added, the mineralisation rates of the soil and of the organic fertilisers, both determined by laboratory incubation, were taken into account together with the amount of mineral N (NO_3^- and NH_4^+) present in the soil at the time of fertilisation. On the CSL plots, part of the organic C was applied as crop residues (except before the catch crop and the red cabbage), since applying 4000 kg C ha^{-1} as cattle slurry would result in the application of too high an amount of mineral N. The first time (21/04/05) the crop residue used was straw, while the second time (06/10/05) it was fodder beet leaves.

At each fertilisation, except before the *Phacelia*, on the minerally fertilised plots and on the plots receiving less than 300 kg ha^{-1} K_2O and 100 kg ha^{-1} P_2O_5 out of the organic amendments, an extra amount of K_2O (muriate of potash 40% K_2O) and P_2O_5 (as triple superphosphate 45% P_2O_5) was applied to achieve equal minimum levels of plant available K_2O (300 kg ha^{-1}) and P_2O_5 (100 kg ha^{-1}).

Soil chemistry

Soil chemical properties of the experimental field (0-20 cm) were assessed at the start of the experiment and after 2.5 years of different fertiliser regimes. Composite soil samples of five cores per plot were taken to a depth of 20 cm, using a 1.8 cm diam. auger. These samples were mixed thoroughly and air-dried. Prior to analysis, the soil samples were passed through a 2 mm sieve.

The pH was measured potentiometrically in a 1 : 2.5 soil/KCl extract. In soils where the pH-KCl is lower than 6.5, the amount of organic C is equal to the amount of total C as no free carbonates are normally present. In these soil samples, total C, and hence organic C, and total N were measured by dry combustion at 850°C using an elemental analyser (Vario MAX CNS; Elementar, Hanau, Germany). K, Na, Ca, Mg and available P were assessed by extraction of the soil with ammonium lactate-acetic acid (extraction ratio 1 : 20) in dark polyethylene bottles, shaken for 4 h and the suspension was filtered in dark polyethylene bottles that were stored cool (4°C) until analysis. The P concentration was measured colorimetrically by the Mo blue method (Scheel, 1936) at 700 nm with a photometer (Universal Photometer; Vitatron, Dieren, The Netherlands). The concentration of K and Na was measured with a flame photometer (Elex 6361; Eppendorf, Hamburg, Germany) in an air-propane flame at 768 nm and 589 nm, respectively, while for the Ca concentration an air-acetylene flame was used at 623 nm. The concentration of Mg was determined by atomic absorption spectrometry (SpectrAA Atomic Absorption Spectrometer; Varian, Palo Alto, CA, USA) at 285 nm.

Soil sampling and analysis of nematodes

Soil samples were taken on 05/05/06, on 09/10/06 and on 08/05/07. Composite soil samples of 25 cores

Table 2. *The amounts of organic fertilisers and their C and N content, and extra mineral N applied on 21/04/05, 06/10/05, 07/09/06 and 02/05/07 (FYM = farmyard manure, VFG = vegetable, fruit and garden waste compost, CMC1 = farm compost 1 with high C/N ratio, CMC2 = farm compost 2 with low C/N ratio, CSL = cattle slurry, MIN N = mineral fertiliser).*

Treatment (fertiliser)	C content (g (kg fresh matter)$^{-1}$)	N content (g (kg fresh matter)$^{-1}$)	Applied amount (kg ha^{-1})	Extra mineral N to be added (kg ha^{-1})	
21/04/05 4000 kg C ha^{-1}					
FYM	62.2	4.7	64 329	105	
VFG	179.4	15.2	22 303	114	
CMC1	71.4	1.7	56 007	165	
CMC2	59.7	2.8	67 058	165	
CSL	26.7[1]	3.9[1]	77 382[2]		
+ crop residues (straw)	378.0	5.5	4704	–	
MIN N	–	–	–	165	
06/10/05 4000 kg C ha^{-1}				23/03/06	26/04/06
FYM	106.8	6.8	37 453	81	97
VFG	175.7	14.5	22 770	88	98
CMC1	71.8	3.1	55 718	91	99
CMC2	77.9	7.2	51 348	89	97
CSL	20.4[1]	2.8[1]	74 698[2]		
+ crop residues (beet leaves)	49.1	3.8	53 636	74	94
MIN N	–	–	–	91	98
07/09/06 1500 kg C ha^{-1}					
FYM	104.2	6.7	14 398	66	
VFG	183.2	15.5	8188	67	
CMC1	77.6	4.1	19 330	86	
CMC2	63.1	3.4	23 757	86	
CSL	26.4[1]	3.8[1]	56 754[2]	–	
MIN N	–	–	–	86	
02/05/07 2000 kg C ha^{-1}					
FYM	104.6	6.1	19 125	106	
VFG	139.6	9.1	14 329	103	
CMC1	192.0	3.6	10 417	170	
CMC2	91.0	6.0	21 986	162	
CSL	28.06[1]	3.2[1]	71 287[2]	–	
MIN N	–	–	–	162	

[1] In g l^{-1}.
[2] In l ha^{-1}.

were taken randomly to a depth of 20 cm in each plot, using a 1.8 cm diam. auger. The composite samples were mixed thoroughly and stored overnight at 4°C. From each sample 100 ml was taken for nematode analysis. The extraction of nematodes was conducted with an automatic zonal centrifuge, following Hendrickx (1995). For each sample all nematodes present were counted using a dissecting microscope and fixed with 4% formaldehyde. From each sample 250 randomly chosen specimens were identified to species or genus level according to the taxonomic keys provided in Bongers (1988), using a compound microscope with Nomarski DIC observation at a magnification of 400× and 1000×. All 250 nematodes were assigned to one of five trophic groups: bacterivores, fungivores, omnivores, predators or herbivores (Yeates *et al.*, 1993). Species of the Tylenchidae were classified as plant feeders (Ferris & Matute, 2003; Ferris *et al.*, 2004), but a difference was made between facultative plant feeders (*i.e.*, Tylenchidae) and obligate plant feeders (*e.g.*, *Paratylenchus*, *Rotylenchus*). The genus *Filenchus*

of the Tylenchidae was considered fungal feeding (Okada *et al*., 2005). The total number and the percentage of every trophic group in the community were calculated.

Each nematode taxon was also assigned to a functional guild defined using a combination of feeding group and life history traits expressed as cp scores ranging from 1 (r-strategist) to 5 (K-strategist) (Bongers, 1990; Bongers & Bongers, 1998). The maturity index as defined by Bongers (1990) was calculated based on this 1-5 cp scale. The nematode fauna was also analysed by a weighing system for nematode functional guilds in relation to the enrichment and structure of the soil food web and the decomposition pathway in the soil food web by calculating the enrichment index (EI), structure index (SI) and channel index (CI) according to Ferris *et al*. (2001).

Phospholipid fatty acids

Soil samples for PLFA analysis were taken on 25/04/06, on 29/11/06 and on 05/05/07. Composite soil samples of 15 cores were randomly taken to a depth of 10 cm in each plot, using a 1.8 cm diam. auger. The samples were processed for assessment of fungal and bacterial fatty acid markers. PLFAs were extracted from the freeze-dried soil samples, identified and measured by GC-MS as described by Leroy (2008). The weights of individual PLFAs were measured as ng g^{-1} dry soil. The fatty acids i15:0, a15:0, 15:0, i16:0, i17:0, a17:0, 17:0, cy17:0 and cy19:0 were chosen to represent bacterial PLFAs, while 18:2ω6, 9c was used as indicator of fungal biomass (Frostegård *et al*., 1993; Pennanen *et al*., 1996; Bossio & Scow, 1998; Marschner *et al*., 2003).

Statistical analysis

All data (nematode abundance and PLFAs) were subjected to analysis of variance (ANOVA) test using S-Plus software and significant differences at a significance level of $P < 0.05$ between means were determined by Tukey's test.

Results

Soil chemistry

Table 3 summarises the soil chemical properties of the 0-20 cm soil layer of the experimental plots before the start and at the end of the experimental period. The four applications of organic amendments significantly increased the soil organic C content. All organically amended plots had a similar organic C content, except for the CSL plots in which a slightly lower value was recorded. All organically amended plots had a significantly higher total N content than the unamended plots, but significant differences could also be observed between the CMC1 and the CSL plots on the one hand and the VFG plots with the highest total N content on the other. Both the organic C and the total N content were similar on the unamended plots (MIN N, NF+ and NF−).

The other soil chemical properties showed small differences or trends among the treatments. Significant differ-

Table 3. *Soil chemical properties of the experimental field (0-20 cm), before the start of the experiment (26/10/04) and at the end of the experimental period (15/10/07). FYM = farmyard manure, VFG = vegetable, fruit and garden waste compost, CMC1 = farm compost 1 with high C/N ratio, CMC2 = farm compost 2 with low C/N ratio, CSL = cattle slurry, MIN N = mineral fertiliser, NF+ = no fertiliser, crop, NF− = no fertiliser, no crop. All values in mg (100 g dry soil)$^{-1}$, except where indicated.*

	pH-KCl	C (%)	Total N (%)	P	Na	K	Ca	Mg
26/10/04	5.90	1.01	0.086	20.8	1.6	19.7	122.4	32.7
15/10/07								
FYM	6.10ab	1.16a	0.103ab	28.6	2.22	24.3	146.2abc	36.7
VFG	6.22b	1.19a	0.109b	26.0	2.16	18.5	158.6bc	34.7
CMC1	5.98abc	1.11a	0.095a	23.2	1.89	19.5	141.4abc	35.0
CMC2	6.04ab	1.13a	0.103ab	25.4	2.04	20.2	150.1c	35.8
CSL	6.08ab	1.09ac	0.095a	25.0	2.14	24.6	127.1a	36.0
MIN N	5.82c	0.96b	0.083c	25.0	1.79	18.9	127.7a	35.0
NF+	5.86ac	0.98bc	0.085c	24.6	1.6	11.6	131.4ac	35.1
NF−	5.97abc	0.98bc	0.084c	24.7	1.50	16.1	132.8ac	35.8

* Data within one column without letters are not significantly different according to Tukey's test ($P < 0.05$).

ences among treatments could only be observed for the pH-KCl and the Ca content.

Nematode populations

Forty-six genera of nematodes were identified in the soil samples, a few of which were not common for all sampling occasions (Tables 4, 5, 6). Total numbers of nematodes differed significantly among treatments at all samplings, with fewest nematodes in the NF− plots. In spring and autumn 2006, the nematode abundance in all fertilised plots tended to be higher than in the NF+ and NF− plots; however, these differences were not significant. Besides the greatest number of nematodes found in the CSL plots at both sampling times in 2006, there was no unequivocal trend over time in the total nematode number for the five organic amendments.

Bacterivorous nematodes were predominant in all soil samples and constituted between 39 and 84% of the total nematode abundance in spring 2006, between 34 and 72% in autumn 2006 and between 25 and 63% in spring 2007. At all sampling times, the highest absolute number (Tables 4, 5, 6) and relative abundance (Table 7) of all bacterivorous nematodes (active bacterivores and inactive dauer juveniles) were found in the FYM and CSL plots. However, in spring 2006 only the effect of CSL was significant, while in autumn this difference was significant for both treatments. In spring 2007, both fertiliser treatments had a significant impact on the relative abundance of bacterivorous nematodes, but not on the absolute amount. The high abundance of bacterivorous nematodes in the FYM and CSL plots was mostly due to the very high number of dauer juveniles on these plots. For the other treatments, there were no obvious trends or differences in the relative abundance of bacterivores.

In spring 2006 no differences were observed in the absolute number of fungivorous nematodes, except for the slightly higher numbers in the VFG plots. The relative abundance was similar for all treatments with a tendency for lowest values in the CSL plots, although the difference was not significant. In the samplings of autumn 2006 and spring 2007, there was a trend in the abundance of fungivorous nematodes among the five organic amendments. In the compost amended plots (VFG and CMC) the absolute number as well as the relative abundance of fungivores trended higher as compared to the FYM and CSL plots. None of these differences was, however, significant. In the unamended plots (MIN N and NF) the abundance of fungivorous nematodes was similar to the plots amended with compost.

The abundance of omnivorous and predator nematodes in the soil samples was low at all samplings and no trends or differences among treatments could be found. In many soil samples, no omnivores or predators were found at all.

In plots amended with VFG compost the absolute number of plant-parasitic nematodes was significantly higher than in the NF− plots for the sampling of spring 2006. In autumn 2006, no significant differences could be observed among the treatments, while in spring 2007, the number of the plant-parasitic nematodes was significantly higher in the MIN N plots than in the CSL and NF− plots. However, at all sampling dates, the absolute amount of plant-parasites tended to be slightly lower in the CSL plots, and in spring 2006 and 2007 this was also true in the FYM plots (Tables 4, 5, 6). The relative abundance of herbivore nematodes followed the same trend, but here significant differences were recorded (Table 7). In spring 2006, the relative abundance of all plant-parasitic nematodes was lower in the plots amended with CSL than in the other treatments. In autumn 2006 and spring 2007, this relative abundance was lower in both CSL and FYM plots. Almost all plant-parasitic nematode species (facultative and obligate) were suppressed by the application of CSL (spring 2006 and 2007, and autumn 2006) and FYM (autumn 2006 and spring 2007).

Nematode faunal indices

There were no trends or differences among treatments in the samples taken in spring 2006 for the maturity index (MI) and the enrichment index (EI) (Table 7). For the samples taken in autumn 2006, again there were no significant differences in the MI and EI. However, a trend was observed: on plots where organic amendments were applied, the MI was lower while the EI was higher. Moreover, the lowest MI and highest EI were found in plots amended with FYM and CSL. In contrast to the two other samplings, in spring 2007 significant differences were found in the MI and EI, with again the lowest MI and highest EI in the FYM and CSL plots. The MI and EI of the compost plots were similar to those of the unamended (MIN N and NF) plots, while in autumn 2006, the values of these indices were intermediate between the unamended and the FYM and CSL plots.

Except for the sampling in spring 2006, significant differences in the channel index (CI) were recorded. In general, in plots amended with compost, the CI was considerably higher compared to the FYM and CSL plots and lower than the unamended plots.

Table 4. *Mean nematode abundance per 100 ml soil of each identified taxon on 05/05/06 (for abbreviations of treatments, see Table 3).*

Nematode	cp	FYM	VFG	CMC1	CMC2	CSL	MIN N	NF+	NF−
Bacterivores									
Diploscapter coronatus	1	0	5	0	0	0	0	0	0
Diplogaster	1	11	0	5	0	13	10	7	0
Cuticularia	1	48	30	0	0	0	0	5	0
Rhabditidae	1	354	481	235	263	236	246	233	216
Dauer juveniles	1	1104	781	568	602	5681	362	420	320
Acrobeloides nanus	2	260	346	265	242	196	148	136	95
Eucephalobus oxyuroides	2	138	117	96	205	94	97	89	42
Eucephalobus striatus	2	0	11	32	31	25	28	10	5
Cephalobus	2	0	0	0	0	0	5	0	0
Cervidellus serratus	2	0	0	0	6	0	0	0	0
Heterocephalobus longicaudatus	2	42	6	47	24	17	27	37	5
Acrobelophis minimus	2	0	0	0	75	0	0	0	0
Acrolobus emarginatus	2	0	0	0	0	6	0	0	0
Plectus tenuis	2	108	62	24	60	55	67	79	43
Total bacterivores		2065a*	1839a	1272a	1508a	6323b	990a	1016a	716a
Fungivores									
Aphelenchus avenae	2	65	53	16	13	0	41	42	17
Aphelenchoides bicaudatus	2	13	34	17	6	0	38	17	11
Aphelenchoides asterocaudatus	2	0	11	0	12	0	6	0	3
Ditylenchus	2	32	72	53	81	101	56	32	15
Filenchus	2	12	0	15	0	0	0	0	5
Total fungivores		122	170	101	112	101	141	91	51
Omnivores									
Eudorylaimus centrocercus	4	0	14	22	0	86	2	5	10
Dorylaimoides limnophilus	4	0	0	0	0	0	5	0	3
Oxydirus oxycephaloides	5	0	0	0	0	0	0	10	0
Total omnivores		0	14	22	0	86	7	15	13
Predators									
Clarkus	4	0	0	10	8	0	5	5	1
Coomansus parvus	4	0	0	0	8	0	8	0	0
Total predators		0	0	10	16	0	13	5	1
Herbivores									
Tylenchus davainei	2	24	6	23	0	0	6	7	0
Basiria	2	0	0	27	0	0	19	7	8
Malenchus bryophilus	2	447	705	355	551	245	402	256	151
Psilenchus hilarulus	2	8	0	0	0	0	2	16	0
Psilenchus terextremus	2	30	36	0	109	51	48	45	28
Paratylenchus nanus	2	299	287	473	299	198	562	181	114
Pratylenchus crenatus	3	240	465	338	232	311	221	255	167
Pratylenchus penetrans	3	45	8	9	0	0	10	0	0
Tylenchorhynchus	3	198	196	249	234	204	142	143	129
Rotylenchus robustus	3	0	11	0	0	17	0	0	2
Meloidogyne naasi	3	14	16	0	0	0	0	15	7
Trichodorus	4	0	0	0	0	0	5	0	0
Total herbivores		1305ab	1730b	1474ab	1425ab	1026ab	1417ab	925ab	606a
Total		3492ab	3753b	2879ab	3061ab	7536c	2568ab	2052ab	1387a

* Data in row, per trophic group, without letters are not significantly different according to Tukey's test ($P < 0.05$).

Table 5. *Mean nematode abundance per 100 ml soil of each identified taxon on 09/10/06 (for abbreviations of treatments, see Table 3).*

Nematode	cp	FYM	VFG	CMC1	CMC2	CSL	MIN N	NF+	NF−
Bacterivores									
Diploscapter coronatus	1	0	8	0	3	4	2	0	0
Metadiplogaster	1	17	0	0	9	0	0	0	0
Butlerius filicaudatus	1	22	12	28	8	24	4	0	5
Cuticularia	1	40	6	0	11	0	7	4	0
Rhabditidae	1	233	233	221	172	182	162	65	124
Dauer juveniles	1	1714	566	452	734	2509	590	432	352
Acrobeloides nanus	2	98	161	153	66	86	103	59	83
Eucephalobus oxyuroides	2	70	93	111	58	63	90	43	22
Eucephalobus striatus	2	192	89	57	111	121	132	117	52
Cephalobus	2	0	0	0	0	0	12	0	0
Heterocephalobus longicaudatus	2	23	61	65	48	23	34	51	33
Acrobelophis minimus	2	0	0	0	5	0	0	0	0
Plectus tenuis	2	99	46	43	61	40	67	53	19
Teratocephalus terrestris	3	0	0	0	0	0	21	0	0
Total bacterivores		2508a*	1275b	1130b	1286b	3052a	1224b	824b	690b
Fungivores									
Aphelenchus avenae	2	64	92	44	50	27	44	57	210
Aphelenchoides bicaudatus	2	42	98	96	68	51	174	89	52
Aphelenchoides asterocaudatus	2	19	8	44	26	27	39	22	13
Ditylenchus	2	32	77	97	60	40	28	21	12
Filenchus	2	0	6	0	8	0	0	6	2
Total fungivores		157	281	281	212	145	285	195	287
Omnivores									
Eudorylaimus centrocercus	4	80	18	25	51	44	48	38	45
Dorylaimoides limnophilus	4	0	14	4	9	0	21	0	10
Oxydirus oxycephaloides	5	0	0	0	0	0	12	0	0
Total omnivores		80	32	29	60	44	81	38	55
Predators									
Clarkus	4	38	18	19	14	57	35	44	35
Coomansus parvus	4	0	0	0	3	0	0	0	0
Total predators		38	18	19	17	57	35	44	35
Herbivores									
Tylenchus davainei	2	0	9	0	5	0	13	15	0
Basiria	2	8	13	0	8	0	0	0	0
Malenchus bryophilus	2	227	391	349	258	191	279	321	153
Aglenchus	2	23	31	11	13	4	9	6	0
Psilenchus hilarulus	2	5	6	0	0	0	0	4	0
Psilenchus terextremus	2	28	67	87	44	14	31	114	44
Paratylenchus nanus	2	200	100	215	112	109	225	155	212
Pratylenchus crenatus	3	420	434	460	539	397	523	367	228
Pratylenchus penetrans	3	115	68	87	48	36	101	44	54
Tylenchorhynchus	3	377	336	469	400	207	354	264	123
Meloidogyne naasi	3	0	0	0	7	0	14	33	0
Trichodorus	4	9	0	0	2	0	4	0	0
Total herbivores		1412	1455	1678	1436	958	1553	1323	814
Total		4195a	3061ab	3137ab	3011ab	4256a	3178ab	2424ab	1881b

* Data in row, per trophic group, without letters are not significantly different according to Tukey's test ($P < 0.05$).

Table 6. *Mean nematode abundance per 100 ml soil of each identified taxon on 08/05/07 (for abbreviations of treatments, see Table 3).*

Nematode	cp	FYM	VFG	CMC1	CMC2	CSL	MIN N	NF+	NF−
Bacterivores									
Diploscapter coronatus	1	0	3	0	4	0	0	4	7
Metadiplogaster	1	0	0	0	0	0	0	0	5
Butlerius filicaudatus	1	19	0	7	0	5	0	0	0
Paroigolaimella	1	6	0	0	0	0	0	0	0
Cuticularia	1	18	0	13	0	6	4	6	0
Rhabditidae	1	178	93	70	61	213	62	75	49
Dauer juveniles	1	701	339	197	219	688	255	248	200
Acrobeloides nanus	2	101	153	73	73	70	41	148	54
Eucephalobus oxyuroides	2	30	78	42	38	44	29	20	26
Eucephalobus striatus	2	257	159	151	160	310	85	116	106
Heterocephalobus longicaudatus	2	56	13	67	41	22	21	13	33
Cervidellus serratus	2	0	10	0	0	0	0	0	0
Chiloplacus	2	0	0	0	0	0	0	0	3
Plectus tenuis	2	21	45	44	34	19	29	65	31
Teratocephalus terrestris	3	0	0	0	6	0	4	8	0
Prismatolaimus	3	12	0	11	19	15	9	39	0
Total bacterivores		1399a*	893ab	675ab	655ab	1392a	539b	742ab	514b
Fungivores									
Aphelenchus avenae	2	25	80	34	54	42	35	66	87
Aphelenchoides bicaudatus	2	6	41	52	20	26	72	38	41
Aphelenchoides asterocaudatus	2	11	5	17	18	0	3	12	13
Ditylenchus	2	11	34	50	52	5	76	24	4
Filenchus	2	0	0	0	4	18	12	18	3
Total fungivores		53	160	153	148a	91	198	158	148
Omnivores									
Eudorylaimus centrocercus	4	25	30	31	25	29	39	19	10
Dorylaimoides limnophilus	4	2	9	9	5	0	17	0	8
Dorylaimoides	4	6	5	14	4	6	29	18	19
Total omnivores		33	44	54	34	35	85	37	37
Predators									
Clarkus	4	37	31	7	44	36	30	25	31
Mylonchulus	4	6	3	0	9	0	6	0	0
Anatonchus	4	3	0	0	6	0	12	0	0
Total predators		46	34	7	59	36	48	25	31
Herbivores									
Tylenchus davainei	2	0	0	11	6	0	17	37	11
Basiria	2	10	0	16	7	23	21	0	0
Malenchus bryophilus	2	131	236	237	244	262	238	426	133
Aglenchus	2	30	73	51	84	5	93	51	12
Psilenchus hilarulus	2	3	0	0	3	0	0	0	3
Psilenchus terextremus	2	24	36	71	58	17	55	155	73
Paratylenchus nanus	2	88	56	113	27	58	163	75	142
Pratylenchus crenatus	3	237	458	339	394	201	333	408	128
Pratylenchus penetrans	3	7	18	42	23	7	24	6	15
Tylenchorhynchus	3	181	262	221	292	82	275	318	95
Rotylenchus robustus	3	0	0	0	0	0	0	0	8
Meloidogyne naasi	3	5	0	5	0	6	21	4	3
Heterodera	3	4	0	0	0	0	0	0	0
Trichodorus	4	0	0	0	0	0	6	0	0
Total herbivores		720ab	1139ab	1106ab	1138ab	661a	1246ab	1480b	623a
Total		2251a	2270a	1995a	2034a	2215a	2116a	2442a	1353b

* Data in row, per trophic group, without letters are not significantly different according to Tukey's test ($P < 0.05$).

Table 7. *Effects of the different fertiliser applications on nematode community indices on 05/05/06, 09/10/06 and 08/05/07 (for abbreviations of treatments, see Table 3).*

Nematode index	FYM	VFG	CMC1	CMC2	CSL	MIN N	NF+	NF−
05/05/06								
Bacterivores (%)	27.52a*	28.19a	24.45a	29.60a	8.52b	24.45a	29.04a	28.55a
Dauer juveniles (%)	31.62a	20.81ac	19.73ac	19.67ac	75.38b	14.10c	20.47ac	23.07ac
Total bacterivores (%)	59.14a	49.00ac	44.18ac	49.27ac	83.90b	38.55c	49.51ac	51.62ac
Fungivores (%)	3.49	4.56	3.50	3.63	1.34	5.50	4.43	3.71
Omnivores (%)	0.00	0.37	0.76	0.00	1.14	0.30	0.72	0.99
Predators (%)	0.00	0.00	0.34	0.55	0.00	0.50	0.22	0.09
Facultative herbivores (%)	13.48a	18.93a	14.08a	18.00a	3.26b	16.59a	13.14a	11.48a
Obligate herbivores (%)	23.89ab	27.16ab	37.10a	28.55a	10.35b	38.51a	31.91a	32.15a
Total herbivores (%)	37.37a	46.09a	51.18a	46.55a	13.61b	55.10a	45.05a	43.63a
MI	1.62	1.61	1.79	1.78	1.91	1.73	1.72	1.61
EI	72.60	75.87	65.23	60.67	68.93	69.38	70.86	79.03
CI	6.88	7.65	9.51	9.54	9.23	12.13	8.45	5.63
SI	0.00	7.29	18.33	8.16	41.06	13.91	18.37	19.92
09/10/06								
Bacterivores (%)	18.93	23.16	21.61	18.33	12.76	19.95	16.17	17.97
Dauer juveniles (%)	40.86a	18.49b	14.41b	24.38b	58.95c	18.57b	17.83b	18.71b
Total bacterivores (%)	59.79a	41.65b	36.02b	42.71b	71.71a	38.52b	34.00b	36.68b
Fungivores (%)	3.75a	9.17ab	8.92ab	7.01a	3.42a	8.98ab	8.07ab	15.31b
Omnivores (%)	1.92	1.07	0.94	1.98	1.02	2.56	1.55	2.93
Predators (%)	0.91	0.60	0.61	0.56	1.34	1.09	1.82	1.84
Facultative herbivores (%)	6.13a	14.54b	11.47ab	9.46ab	4.58a	9.49ab	14.12ab	8.11ab
Obligate herbivores (%)	27.54ab	33.00ab	42.03a	38.27a	17.94b	39.41a	40.44a	35.17a
Total herbivores (%)	33.67a	47.54b	53.50b	47.73b	22.52a	48.90b	54.56b	43.28b
MI	1.93	1.85	1.85	1.94	1.99	2.09	2.14	2.07
EI	68.71	64.29	64.23	64.61	67.33	57.63	47.65	61.79
CI	11.21a	21.35ab	21.98ab	20.63a	14.75a	29.02ab	41.46b	35.88ab
SI	42.60	21.94	21.55	35.68	45.68	42.60	38.98	42.09
08/05/07								
Bacterivores (%)	31.01ac	24.41abc	23.96abc	21.44abc	31.78a	13.42b	20.23bc	23.21abc
Dauer juveniles (%)	31.14a	14.93b	9.87b	10.77b	31.06a	12.05b	10.16b	14.78b
Total bacterivores (%)	62.15a	39.34b	33.83b	32.21b	62.84a	25.47b	30.39b	37.99b
Fungivores (%)	2.37a	7.03ab	7.66ab	7.31ab	4.09ab	9.33b	6.46ab	10.97b
Omnivores (%)	1.52	1.94	2.74	1.67	1.56	4.06	1.52	2.74
Predators (%)	2.05	1.51	0.36	2.88	1.63	2.27	1.01	2.26
Facultative herbivores (%)	7.61a	13.61abc	15.81abc	16.72abc	13.09ab	17.43b	21.06c	11.53ab
Obligate herbivores (%)	24.42ab	36.60a	39.66a	39.21a	16.75b	41.45a	39.59a	34.55a
Total herbivores (%)	32.03ac	50.21b	55.47b	55.93b	29.84a	58.88b	60.65b	46.08bc
MI	1.94a	2.08ab	2.07ab	2.21ab	1.92a	2.35b	2.12ab	2.14ab
EI	64.47b	46.91a	49.10ab	45.34a	64.21b	53.52ab	48.93ab	49.42ab
CI	5.69a	29.26ab	29.94ab	35.51ab	7.54a	41.22b	29.16ab	37.44ab
SI	40.21	33.67	33.95	46.40	37.00	59.14	41.31	40.40

* Data within one row without letters are not significantly different according to Tukey's test ($P < 0.05$).

The structure index (SI) was highly variable in all plots and sampling times due to the variable abundance, and sometimes even absence of the structure-indicator (cp 3-5) nematodes.

Table 8. *Total amount of phospholipids fatty acids (PFLA), amount of bacterial and fungal PLFAs (in ng (g soil)$^{-1}$) and their ratio, sampled on 25/04/06, 29/11/06 and 05/05/07 (for abbreviations of treatments, see Table 3).*

	FYM	VFG	CMC1	CMC2	CSL	MIN N	NF+	NF−
25/04/06								
Total amount of PLFAs	9487a*	6700bc	6169bc	6077bc	8081ac	5888bc	5541b	4530b
Bacterial marker PLFAs	2035a	1242ab	1246ab	1253ab	1463ab	1104b	1135b	976b
Fungal marker PLFA	691a	472b	408bc	414bc	486b	382bc	339c	204d
Bacteria/fungi ratio	2.97ab	2.64a	3.09ab	3.05ab	3.06ab	2.91ab	3.39ab	4.76b
29/11/06								
Total amount of PLFAs	8599	7631	8304	7697	7558	7515	6733	5859
Bacterial marker PLFAs	1972a	1659abc	1748ab	1594abc	1694abc	1503b	1434b	1292c
Fungal marker PLFA	641	608	873	730	511	774	676	573
Bacteria/fungi ratio	3.13	2.79	2.10	2.86	3.49	2.18	2.16	2.53
05/05/07								
Total amount of PLFAs	7988ab	8644a	7700ab	7779ab	8940a	6568b	7129ab	6169b
Bacterial marker PLFAs	2154ab	2408bc	1959ab	2115ab	2565b	1786ac	1958ac	1732a
Fungal marker PLFA	231	280	248	238	218	206	274	196
Bacteria/fungi ratio	9.41	8.73	8.02	9.15	11.67	8.99	7.29	8.84

* Data within one row without letters are not significantly different according to Tukey's test ($P < 0.05$).

PHOSPHOLIPID FATTY ACID ANALYSIS

The total amount of PLFAs is an indicator of the mass of microbial cell membranes and hence a measure of the total microbial biomass (White *et al*., 1979; Bossio & Scow, 1998). At all samplings, in the fertilised plots the total amount of PLFAs was clearly higher than in the unfertilised plots (NF), but differences were only significant in spring 2006 and 2007 (Table 8). There was no trend in the ratios of PLFA markers of bacterial and fungal biomass for the various treatments in spring 2006. However, in autumn 2006 and spring 2007, the bacteria to fungi ratio of the CSL, and, to a lesser extent, of the FYM plots, tended to be higher compared to the compost (VFG and CMC) and the unamended plots (MIN N and NF). None of these differences was significant.

Discussion

Both the presence of a crop and the application of organic amendments and mineral fertiliser affected the nematode populations, not only in composition but also in abundance. The absence of a crop on the NF− plots, and hence absence of organic matter input or root exudation, resulted in a smaller microbial population (Leroy, 2008) and fewer bacterial- and fungal-feeding nematodes. Furthermore, in the absence of a crop, there is a greater variability in (surface) soil temperature and moisture regimes (Balesdent *et al*., 1988), which are likely to affect the nematode population adversely on these plots. This assumption was supported by the low nematode abundance in spring 2007: the lowest abundance was again found in the NF− plots, but all other plots, amended or not, had rather low nematode numbers. This was undoubtedly due to the extremely dry (no rain in 30 days) and warm month of April (Table 1), during which the field was not covered or protected by a crop. Since nematodes require a water film around soil particles in which they move, feed and reproduce (Bardgett, 2005), this extreme drought will have logically affected the nematode population adversely.

The higher nematode abundance in the MIN N plots than in the NF+ plots in spring and autumn 2006, which in autumn 2006 was comparable to the plots amended with compost, is probably the result of an indirect effect of the mineral fertilisation. Following fertilisation, the crop performance on the MIN N plots was superior to that on the NF+ plots (Leroy, 2008), resulting in a higher crop and root biomass and a better supply of labile organic materials in the rhizosphere through root exudation. The consequent increase in microbial biomass provides resources for bacterivore and fungivore nematodes. These assumptions regarding the microbial communities were supported by the total amount of PLFAs (Table 8), which

is believed to be a good measure of microbial biomass (White *et al*., 1979; Bossio & Scow, 1998).

No trend could be observed in the total number of nematodes among the five organic amendments, except for the clearly higher nematode abundance on the CSL plots in spring and autumn 2006 and, only in autumn 2006, on the FYM plots. This was undoubtedly due to the very high number of dauer juveniles in these soil samples. Despite the similar nematode abundance in all fertilised plots in spring 2007, the number of dauer juveniles was also considerably higher in the FYM and CSL plots. Dauer juveniles are considered inactive stages of the enrichment opportunists (families Rhabditidae, Panagrolaimidae and Diplogastridae). These bacterivorous nematodes are classified as cp-1 organisms in the cp scale of Bongers (1990) and characterised by short generation time, small eggs and high fecundity. They feed continuously in enriched media and are able to enlarge their population immediately following the enrichment of the environment, but survive periods of resource limitation in a metabolically reduced dauer juvenile alternative life stage (Ferris *et al*., 2001; Ferris & Matute, 2003).

The dauer juveniles of enrichment opportunists are excluded from the calculation of the MI (Bongers & Bongers, 1998) and of the EI and CI (Ferris & Bongers, 2008) since their presence does not provide information about the present functioning of the soil food web. An abundance of dauer juveniles indicates a system that has been enriched in the (recent) past and has now declined to a less enriched phase. The ratio of dauer juveniles to active stages of rhabditids, as an indicator of resource availability, was introduced and tested by Sohlenius (1969, 1973), and comparisons of that ratio over time may provide insights into the resource dynamics of the system. However, a difficulty with such an approach would be the problem of identifying dauer juveniles of different nematode taxa, since animal parasites such as mermithids and entomopathogenic nematodes also have dauer juveniles. Dauer juveniles of entomopathogenic nematodes, for example, are often found in soil but are not indicators of food web enrichment.

Soils fertilised with organic amendments have a higher EI and a lower MI compared to unfertilised or mineral fertilised soils (Neher & Olson, 1999; Ferris *et al*., 2001; Berkelmans *et al*., 2003) due to an increased abundance of enrichment opportunists. In spring 2006, we observed no such trend of a higher EI and lower MI on plots with organic amendments. Furthermore, the differences in absolute and relative abundance of the various trophic groups of the free-living nematodes and the calculated indices (MI, EI and CI) were very small. This was possibly due to the fact that only two OM applications had been carried out, and particularly because the most recent application (06/10/05) was 7 months before the sampling (05/05/06). By contrast, in autumn 2006 and spring 2007 there were clear trends and differences, although not always significant, in the abundance of trophic groups and the calculated indices. In autumn 2006, the nematode sampling was carried out only 1 month after the application of the amendments (07/09/06 *vs* 09/10/06) and in spring 2007, this was less than 1 week (02/05/07 *vs* 08/05/07). The resulting bloom of the enrichment opportunists (cp-1), accompanied and followed by those of the general opportunists (cp-2), was noticeable at both sampling dates. The trend of a higher EI and lower MI on organically amended plots was observed in the data of autumn 2006. In spring 2007, this trend was less clear for the compost plots, having similar values for the MI and EI as the unamended plots. However, for both samplings the MI and EI of the FYM and CSL plots were, respectively, lower and higher compared to the three compost treatments. In general, in plots amended with FYM and CSL, the abundance of bacterivorous nematodes and dauer juveniles as their inactive stages was higher than in the other treatments. Numbers of bacterivorous nematodes tend to increase after applications of organic amendments to soil since bacterial populations are greater after application of organic amendments (Ferris *et al*., 1996; McSorley *et al*., 1998; Bongers & Ferris, 1999). Application of organic matter to the soil is also expected to increase the fungal population and hence the amount of fungivorous nematodes. However, this will mostly be the case: *i*) when, following bacterial decomposition, the remaining organic matter is more recalcitrant; *ii*) when organic amendments that are less easily decomposed are added to the soil; or *iii*) when soil conditions are not favourable for bacteria mediated decomposition, *e.g*., low pH or lower nutrient concentrations (Chen & Ferris, 2000). While the absolute amount and relative abundance of bacteria-feeding nematodes was in autumn 2006 and spring 2007 the highest in the FYM and CSL plots, the abundance of fungivorous nematodes (absolute and relative) tended to be higher in the compost plots (not significant).

These results were also supported by the values of the CI, which provides an indication of the relative flow of substrate along bacterial and fungal decomposition pathways (Ferris *et al*., 2001; Ruess, 2003). The higher

the value of the CI, the higher the proportional flow along the fungal decomposition pathway. Plots amended with FYM and CSL had a lower CI (Table 7), indicating a predominant bacterial decomposition pathway, while the CI was higher for the compost treatments, suggesting a higher proportion of fungal decomposition. Although the differences in CI among the five organic matter treatments were not significant, the observed trends can probably be linked with the quality or decomposability of the applied amendments. The composts with a usually higher C/N ratio contain more recalcitrant compounds remaining after the composting process over several months, which are mainly decomposed by fungi, while readily decomposable compounds, such as organic acids and carbohydrates present in manure and slurry with a lower C/N ratio, are preferentially utilised by soil bacteria (Marschner *et al*., 2003). In this study, relatively fresh FYM and cattle slurry that had not been subjected to composting were used. In the unamended plots, with no input of fresh exogenous organic matter and hence more recalcitrant remaining organic matter, the higher CI also suggested a more fungi-dominated decomposition pathway. This assumption was strongly supported by the results of the PLFA analysis. In autumn 2006 and spring 2007 the bacteria/fungi ratio was, although not significantly, higher in the FYM and CSL plots compared to the compost and unamended plots. Furthermore, a significant ($P < 0.01$) correlation was found ($r = 0.85$) between the bacteria/fungi ratio and the bacterial/fungal feeding nematode ratio (results not shown) for the data of autumn 2006. This correlation ($r = 0.69$) was not significant ($P = 0.06$) for the data of spring 2007 but still indicates a strong link between the microbial population and the nematode community feeding on these microbes.

It can be suggested that the observed changes in the nematode population are due to the nematodes living and reproducing in the organic amendments added to the soil, rather than that the soil-inhabiting nematodes were affected by the amendments. While we assume that this will certainly have partly influenced the results presented above, we suppose that this effect should not be overestimated. We rely for this on the analysis of the nematodes present in the organic amendments (unpubl.), which were determined in two of the four OM applications. The results of these analyses were very variable. For example, in 100 ml farmyard manure 280 nematodes were found at one analysis, while this was 3410 in the other. For the farm composts, similar results were found (*e.g*., for CMC2 3464 nematodes 100 ml^{-1} at the first analysis and 103 at the second). Moreover, the amount of bacterivorous nematodes present in the farm composts was, for both analyses, comparable to the amount of fungivores. For the VFG composts, the analyses were even more striking, since for both analyses not one living nematode was found in this type of compost. This may be due to the high temperatures (70°C+) reached during the VFG composting process. Based on these data, we think we can state that the nematodes present in the organic amendments were not the main factor influencing the (changes in the) soil nematode population.

The SI is primarily determined by omnivorous and predatory nematode populations, which are sensitive to disturbance and need much more time to establish than the more rapidly growing fungivorous and bacterivorous nematodes (Ferris *et al*., 2001). At all sampling periods, the presence of omnivores and predators was infrequent and variable, resulting in low and highly variable SI values. The SI values of disturbed arable agricultural systems are characteristically low due to repeated tillage and other soil disturbances (Ferris *et al*., 2001; Berkelmans *et al*., 2003; Ferris & Matute, 2003). In our field experiment all plots were tilled and hence disturbed with the same frequency (once or twice a year) and in the same way, whether they were fertilised or amended or not. After each crop, the plots were tilled to prepare the application of the amendments and mineral fertiliser, and afterwards a rotary tiller was used on all plots to incorporate the applied amendments. These practices probably resulted in the low and variable SI.

Finally, the clear impact of CSL, and, to a lesser degree of FYM, on the absolute and relative abundance of plant-parasitic nematodes, is remarkable. Moreover, the impact of both organic amendments was not constrained to one or a few herbivore genera, since all plant-parasitic nematode genera (facultative and obligate) were less abundant on these plots. Miller *et al*. (1973) stated that the availability of more nitrogen, due to a lower C/N ratio of the organic amendment, enhances the ability of the amendment to control parasitic nematodes. Mian and Rodriguez-Kabana (1982) also reported that the parasitic nematode management potential of an organic soil amendment is positively related to the N content or inversely to the C/N ratio. Although the cattle slurry had the lowest C/N ratio of all organic amendments, this cannot explain the negative impact of the CSL on the plant-parasitic nematodes. As described earlier, we corrected for the different amount of plant available N of the various organic amend-

ments by applying extra mineral N (ammonium nitrate), so the total amount of available ammonia and nitrate during the growing season should have been almost equal. This was supported by similar crop performance and yield in all fertilised plots. The effects of organic amendments on the population dynamics of plant-parasitic nematodes have been investigated many times before, but the results are not at all unequivocal (Leroy *et al*., 2007). For example, in contrast to our results, Forge *et al*. (2005) reported increased population densities of *P. penetrans* due to the sustained use of dairy manure slurry, but noted that their results contrasted with many previous studies. Akhtar and Malik (2000) concluded that disease control in amended soils is probably not the result of one specific factor, but of several factors, *e.g*., changes in soil properties, increase in predators and parasitic micro-organisms, nutrients or toxic metabolites released from the organic amendments, *etc.* However, several plant-parasitic species mentioned in Tables 4, 5 and 6, *e.g*., the Tylenchidae, considered as facultative plant feeders, are not considered as very important plant-parasitic nematodes (Decraemer & Hunt, 2006). Moreover, the number of some important plant-parasitic species in this experiment, *e.g*., *Trichodorus*, *Rotylenchus* and *Meloidogyne*, is rather low. Further analyses will be necessary to determine whether effects of organic amendments on the plant-parasitic nematodes will disappear or become more pronounced.

Conclusion

We can conclude that the different fertiliser regimes influenced the nematode fauna and that the indices proposed by Ferris *et al*. (2001) can be used to monitor adequately these fertiliser-induced changes. However, based on the different results in spring 2006 on the one hand and autumn 2006 and spring 2007 on the other, we hypothesise that the nematode population needs time to adapt to the specific treatments and, hence, that more samplings may be necessary to assess the long-term impacts of exogenous organic matter.

Acknowledgements

We are grateful to Franky Van Peteghem and Jean-Pierre Van Maerke for their much appreciated assistance with the field work, and Luc Deboosere, Mathieu Schatteman, Tina Coddens and Sophie Schepens for their practical assistance on the field and in the lab. The authors thank AgriVet for the use of its experimental fields.

References

AKHTAR, M. & MALIK, A. (2000). Roles of organic soil amendments and soil organisms in the biological control of plant-parasitic nematodes: a review. *Bioresource Technology* 74, 35-47.

BALESDENT, J., WAGNER, G.H. & MARIOTTI, A. (1988). Soil organic matter turnover in long-term field experiments as revealed by carbon-13 natural abundance. *Soil Science Society of America Journal* 52, 118-124.

BARDGETT, R. (2005). *The biology of soil, a community and ecosystem approach.* Oxford, UK, Oxford University Press, 256 pp.

BARKER, K.R. & KOENNING, S.R. (1998). Developing sustainable systems for nematode management. *Annual Review of Phytopathology* 36, 165-205.

BERKELMANS, R., FERRIS, H., TENUTA, M. & VAN BRUGGEN, A.H.C. (2003). Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. *Applied Soil Ecology* 23, 223-235.

BONGERS, T. (1988). *De Nematoden van Nederland.* Utrecht, Koninklijke Nederlandse Natuurhistorische Vereniging, 408 pp.

BONGERS, T. (1990). The maturity index: an ecological measure of environmental disturbance based on nematode species composition. *Oecologia* 83, 14-19.

BONGERS, T. & BONGERS, M. (1998). Functional diversity of nematodes. *Applied Soil Ecology* 10, 239-251.

BONGERS, T. & FERRIS, H. (1999). Nematode assemblage structure as a bioindicator in environmental monitoring. *Trends in Ecology and Evolution* 14, 224-228.

BOSSIO, D.A. & SCOW, K.M. (1998). Impacts of carbon and flooding on soil microbial communities: phospholipid fatty acid profiles and substrate utilization patterns. *Microbial Ecology* 35, 265-278.

BULLUCK, L.R., BARKER, K.R. & RISTAINO, J.B. (2002). Influences of organic and synthetic soil fertility amendments on nematode trophic groups and community dynamics under tomatoes. *Applied Soil Ecology* 21, 233-250.

CHEN, J. & FERRIS, H. (2000). Growth and nitrogen mineralization of selected fungi and fungal-feeding nematodes on sand amended with organic matter. *Plant and Soil* 218, 91-101.

DECRAEMER, W. & HUNT, D.J. (2006). Structure and classification. In: Perry, R.N. & Moens, M. (Eds). *Plant nematology*. Wallingford, UK, CABI Publishing, pp. 3-32.

FERRIS, H. & BONGERS, T. (2008). Indices for analysis of nematode assemblages. In: Wilson, M. & Kakouli-Duarte, T.

(Eds). *Nematodes as environmental bioindicators.* Wallingford, UK, CABI Publishing, in press.

FERRIS, H. & MATUTE, M.M. (2003). Structural and functional succession in the nematode fauna of a soil food web. *Applied Soil Ecology* 23, 93-110.

FERRIS, H., VENETTE, R.C. & LAU, S.S. (1996). Dynamics of nematode communities in tomatoes grown in conventional and organic farming systems, and their impact on soil fertility. *Applied Soil Ecology* 3, 161-175.

FERRIS, H., BONGERS, T. & DE GOEDE, R.G.M. (2001). A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. *Applied Soil Ecology* 18, 13-29.

FERRIS, H., VENNETTE, R.C. & SCOW, K.M. (2004). Soil management to enhance bacterivore and fungivore nematode populations and their nitrogen mineralisation function. *Applied Soil Ecology* 25, 19-35.

FORGE, T.A., BITTMAN, S. & KOWALENKO, C.G. (2005). Impacts of sustained use of dairy manure slurry and fertilizers on populations of *Pratylenchus penetrans* under tall fescue. *Journal of Nematology* 37, 207-213.

FROSTEGÅRD, A., TUNLID, A. & BAATH, E. (1993). Phospholipid fatty acid composition and activity of microbial communities from two soil types experimentally exposed to different heavy metals. *Applied and Environmental Microbiology* 59, 3605-3617.

HENDRICKX, G. (1995). An automatic apparatus for extracting free-living nematode stages from soil. *Nematologica* 41, 308. [Abstr.]

LEROY, B.L.M. (2008). *Soil food web C and N transformations and soil structure: interactions and feedback mechanisms as a function of the quality of exogenous organic matter.* Ph.D. Thesis, Ghent University, Ghent, Belgium, 246 pp.

LEROY, B.L.M.M., BOMMELE, L., REHEUL, D., MOENS, M. & DE NEVE, S. (2007). The application of vegetable, fruit and garden waste (VFG) compost in addition to cattle slurry in a silage maize monoculture: effects on soil fauna and yield. *European Journal of Soil Biology* 43, 91-100.

MARSCHNER, P., KANDELER, E. & MARSCNER, B. (2003). Structure and function of the soil microbial community in a long-term fertilizer experiment. *Soil Biology and Biochemistry* 35, 453-461.

MCSORLEY, R., STANSLY, P.A., NOLING, J.W. & OBREZA, T.A. (1998). Impact of organic soil amendments and fumigation on plant-parasitic nematodes in a southwest Florida vegetable field. *Nematropica* 27, 181-189.

MIAN, I.H. & RODRIGUEZ-KABANA, R. (1982). Organic amendments with high tannin and phenolic contents for control of *Meloidogyne arenaria* in infested soil. *Nematropica* 12, 221-234.

MILLER, P.M., SANDS, D.C. & RICH, S. (1973). Effects of industrial residues, wood fibre wastes, and chitin on plant parasitic nematodes and some soil-borne disease. *Plant Disease Reporter* 57, 438-443.

NEHER, D.A. (1999). Nematode communities in organically and conventionally managed agricultural soils. *Journal of Nematology* 31, 142-154.

NEHER, D.A. (2001). Role of nematodes in soil health and their use as indicators. *Journal of Nematology* 33, 161-168.

NEHER, D.A. & OLSON, R.K. (1999). Nematode communities in soils of four farm cropping management systems. *Pedobiologia* 5, 430-438.

OKADA, H. & HARADA, H. (2007). Effects of tillage and fertilizer on nematode communities in a Japanese soybean field. *Applied Soil Ecology* 35, 582-598.

OKADA, H., HARADA, H. & KADOTA, I. (2005). Fungal feeding habits of six nematode isolates in the genus *Filenchus*. *Soil Biology and Biochemistry* 37, 1113-1120.

PENNANEN, T., FRÖSTEGÅRD, A., FRITZE, H. & BAATH, E. (1996). Phospholipid fatty acid composition and heavy metal tolerance of soil microbial communities along two heavy metal-polluted gradients in coniferous forests. *Applied and Environmental Microbiology* 62, 420-428.

RUESS, L. (2003). Nematode soil faunal analysis of decomposition pathways in different ecosystems. *Nematology* 5, 179-181.

SCHEEL, K.C. (1936). Colorimetric determination of phosphoric acid in fertilizers with the Aulfrich photometer. *Zeitschrift für Analytische Chemie* 105, 256-259.

SOHLENIUS, B. (1969). The monoxenic cultivation of some rhabditid nematodes. *Oikos* 20, 287-293.

SOHLENIUS, B. (1973). Structure and dynamics of populations of Rhabditis (Nematodes: Rhabditidae) from forest soil. *Pedobiologia* 13, 368-375.

WANG, K.-H., MCSORLEY, R., MARSHALL, A. & GALLAHER, R.N. (2006). Influence of organic *Crotalaria juncea* hay and ammonium nitrate fertilizers on soil nematode communities. *Applied Soil Ecology* 31, 186-198.

WARDLE, D.A., WILLIAMSON, W.M., YEATES, G.W. & BONNER, K.I. (2005). Trickle-down effects of aboveground trophic cascades on the soil food web. *Oikos* 111, 348-358.

WHITE, D.C., BOBBIE, R.J., HERON, J.S., KING, J.D. & MORRISON, S.J. (1979). Biochemical measurements of microbial mass and activity from environmental samples. In: Costerton, J.W. & Colwell, R.R. (Eds). *Native aquatic bacteria: enumeration, activity, and ecology.* Philadelphia, PA, USA, American Society for Testing and Materials, pp. 69-81.

WILLIAMSON, W.M., WARDLE, D.A. & YEATES, G.W. (2005). Changes in soil microbial and nematode communities during ecosystem decline across a long-term chronosequence. *Soil Biology and Biochemistry* 37, 1289-1301.

YEATES, G. (2003). Nematodes as soil indicators: functional and biodiversity aspects. *Biology and Fertility of Soils* 37, 199-210.

YEATES, G.W. & BONGERS, T. (1999). Nematode diversity in agroecosystems. *Agriculture, Ecosystems and Environment* 74, 113-135.

YEATES, G.W., BONGERS, T., DE GOEDE, R.G.M., FRECKMAN, D.W. & GEORGIEVA, S.S. (1993). Feeding habits in soil nematode families and genera – an outline for soil ecologists. *Journal of Nematology* 25, 315-331.

YEATES, G.W., BARDGETT, R.D., COOK, R., HOBBS, P.J., BOWLING, P.J. & POTTER, J.F. (1997). Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes. *Journal of Applied Ecology* 34, 453-470.

YEATES, G.W., WARDLE, D.A. & WATSON, R.N. (1999). Responses of soil nematode populations, community structure, diversity and temporal variability to agricultural intensification over a seven-year period. *Soil Biology and Biochemistry* 31, 1721-1733.