ELSEVIER

Soil Biology & Biochemistry 39 (2007) 1410–1417

Soil Biology & Biochemistry

www.elsevier.com/locate/soilbio

Nematode migration and nutrient diffusion between vetch and barley material in soil

Søren Christensen[a,*], Jörn Alphei[b,1], Mette Vestergård[a], Peter Vestergaard[a]

[a]*Biological Institute, University Copenhagen, Ø. Farimagsgade 2D, DK 1353 Copenhagen, Denmark*
[b]*Institut für Zoologie, Universität Göttingen, Berliner Strasse 28, D 37073 Göttingen, Germany*

Received 20 July 2006; received in revised form 10 October 2006; accepted 27 November 2006
Available online 18 January 2007

Abstract

This paper deals with migration of nematodes along nutrient gradients in soil. Portions of barley straw and green vetch leaves were mixed with soil and buried at 6, 12, 18, and 50 mm distance from each other in soil. During the following 12 weeks respiration activity, microbial (SIR) biomass, nitrogen limitation of respiration activity in soil slurries all indicated that nitrogen was transferred in the soil from the nutrient rich vetch to the nutrient poor barley at least during the first 3 weeks of the experiment. Twelve out of 39 taxonomic groups of nematodes showed different growth in the two plant material–soil mixtures. Only one of these taxonomic groups (long rhabditid larvae) suggested that migration could have contributed to population development; for three other groups (short rhabditid larvae, Aphelenchoides, and *Bursilla*) nutrient transport through the soil was the likely mechanism for a distance-dependant population development. We suggest that for most microbivorous nematodes, except larvae of fast growing bacterivores, migration over distances exceeding one centimetre does not contribute markedly to population development even when cues such as nutrient gradients to stimulate the activity exist.

Keywords: Concentration gradient; Nematodes; N limitation; Organic resource; Respiration activity; Soil crumb

1. Introduction

Soil is characterised by a high spatial variability in environmental factors and distribution of organisms at all scales from the region to the soil crumb. The physical separation of the organisms in soil as well as the limited diffusion of water soluble compounds through soil are probably the main reasons for the high diversity of soil organisms with apparently similar functions since the chances that organisms interact are low (Giller, 1996). Studies on the migration of microfauna in soil have shown that whereas populations of microbivorous protozoa and nematodes grew within an added resource, only nematodes increased in the surrounding soil, but only within 2 mm distance (Rønn et al., 1996). In a similar study nematodes migrated up to 12 cm from the resource, however (Griffiths et al., 1998). Soil moisture is an important regulator of nematode movement being higher at field capacity compared to lower moisture contents in soil (Griffttths et al., 1995) and this factor may be involved in the different distances observed in the two abovementioned studies. In accordance with the study of Rønn et al. (1996) migration of nematodes but not protozoa seemed to occur during colonisation of organic resources in soil (Griffiths and Caul, 1993). In a more detailed study Anderson et al. (1997) found that individuals of the nematode *Caenorhabditis elegans* moved more linear towards a localised bacterial food source (*E. coli*) when present. The importance of distance between contrasting organic resources in soil for microbial activity and the factors limiting activity as well as for root development was demonstrated in an elegant experiment by Jingguo and Bakken (1997). The study showed low accumulation of inorganic *N* in soil with

*Corresponding author. Tel.: +45 3532 2156; fax: +45 3532 2321.
E-mail address: schristensen@bi.ku.dk (S. Christensen).
[1]Present address: Evaluationsagentur Baden-Württemberg M7 9a-10, D 68161 Mannheim, Germany.

0038-0717/$ - see front matter © 2007 Elsevier Ltd. All rights reserved.
doi:10.1016/j.soilbio.2006.11.026

N-rich clover leaves and N-poor barley straw placed in soil at distances below 6 mm whereas clover and straw placed at more than 6 mm distance resulted in larger accumulation of inorganic N in soil during decomposition. This strongly suggests that N diffused from the N-rich to the N-poor resource when these were situated at or below 6 mm distance in soil. Inspired by Jingguo and Bakken the purpose of the present study is to investigate how varying physical separation (e.g. N diffusion) between contrasting residues will affect the functioning and composition of the nematode communities. The rationale is that N supply in a nutrient poor organic resource increase because of N diffusion form a nutrient rich organic resource located at decreasing distance. At decreasing distance between the contrasting resources chemical cues to stimulate migration of nematodes through soil should therefore become stronger, and we therefore hypothesise that population development will become increasingly dependant on migration compared to local growth at decreasing distances. A technique similar to Jingguo and Bakken (1997) was used to identify at what distances between contrasting resources nutrients are transferred, thereby affecting microbial activity. We then want to identify if nematode population development depends on distance between food resources of different quality and to what extent that distance dependency can be ascribed to migration.

2. Materials and methods

The soil used was a sandy loam collected in the ploughing layer at Research Centre Bygholm, Horsens Denmark field B1.1, with weight fractions of sand, silt, clay, and organic matter of 0.71, 0.13, 0.13, and 0.03 (Munkholm et al., 2001). Microcosms were prepared by adding in total 320 g (d.w.) sieved ($Ø = 5$ mm) soil to plastic conduits $80 \times 57 \times 54$ mm (Fig. 1) resulting in a density of 1.30 g cm^{-3}, slightly below the field value of 1.4 g cm^{-3} (Munkholm et al., 2001). Portions of soil with N-poor and N-rich plant materials were prepared by mixing 0.2 g air-dried and ground (0.2 mm) barley straw (*Hordeum vulgare* L.) or green material of vetch (*Vicia villosa* Roth) into 20 g (d.w.) soil. The nitrogen content of the barley and vetch were 0.2% and 5.8% resulting in C to N ratios of 80 and 6.9, respectively. The soil in the conduit was arranged in layers such that there was: unamended soil; 5 mm soil + straw (20.2 g); unamended soil; 5 mm soil + vetch (20.2 g); unamended soil. The distance between the straw and vetch layers was 6, 12, 18, or 50 mm and the conduits were incubated horizontally so that the layers were aligned vertically (Fig. 1). To compensate for evaporation, water had to be added twice during the 12 week incubation. This was done carefully with a syringe, spreading the water over the whole soil surface. Respiration rate of microcosms was determined by placing them in 51 air tight glass jars two days before destructive sampling occurred. Gas samples were collected through a rubber septum at the beginning and after 48 h. The gas samples were analysed on a gas chromatograph with a TC-detector and a Haysep Q column. After 1, 3, 6, and 12 weeks three microcosms of each treatment were destructively sampled and the amended soil segments were analysed. Substrate induced respiration was measured on 1.50 g (d.w.) fresh soil after addition of 5 ml glucose solution (10 g l^{-1}) or 5 ml glucose and ammonium-nitrate solutions (10 and 4 g l^{-1}, respectively). The samples were incubated in 117 ml airtight bottles on a horizontal shaker at room temperature. CO_2 accumulated in the headspace of glucose amended bottles was measured after 0,5, 4, and 22 h incubation. The initial respiration rate between the first two samplings in glucose amended soil was used as an assay of the soil microbial biomass (SIR) as in the procedure originally suggested by Anderson and Domsch (1978). In samples amended with glucose and nitrogen headspace CO_2 was measured over a day, after 4 and 22 h. The difference in respiration rate with and without nitrogen addition between 4 and 22 h was used as an assay of N limitation of microbial activity (including growth) at conditions of sufficient available carbon as in the procedure suggested by Scheu (1993).

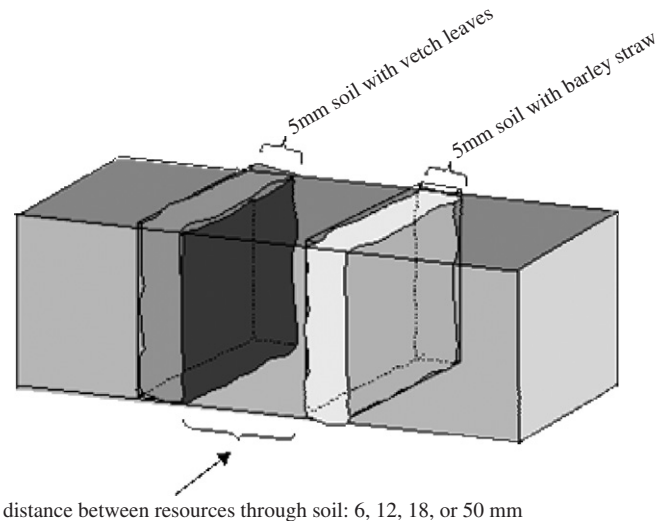

Fig. 1. The experimental set-up with boxes of soil containing layers of soil with 0.01 g g^{-1} soil of vetch leaves or barley straw placed at various distances.

Nematodes were extracted using a modified version of the Baermann funnel (Whitehead and Hemming, 1970). Seven grams soil from the amended segments was spread on paper tissues supported by a sieve and slightly submersed in a bowl of water. After 24 h the nematodes were counted live under a dissecting microscope at 30 × magnification. Following the counting samples were stored in formalin. The nematode samples from soil where the organic material was located at the minimum distance (6 mm) and the maximum distance (50 mm) from the contrasting resources were analysed for distribution on nematode taxa. These samples of largest difference in distance between resources were used because these were most likely to show distance dependant effects.

Samples were transferred into glass Petri dishes equipped with counting grids. Subsequently samples were inspected under a compound inverted microscope and nematodes were located in randomly chosen 5 × 5 mm squares until at least 100 nematodes were found. Position of nematodes in the Petri dish was listed individually. Nematodes were identified either directly under high magnification or if necessary they were picked from the Petri dish and transferred onto a glass slide to allow use of an oil immersion objective. In case of samples containing less than 100 nematodes all individuals were identified. Specimens were attributed to families or genera (Yeates et al., 1993), in some cases this proved difficult for juveniles.

3. Statistical analyses

Respiration rates in microcosms were analysed by two-way ANOVA with time and distance as variables. Respiration rates in soil + plant litter, and nematode numbers (following log transformation to attain equal variances) were analysed by three-way ANOVA with time (week 1, 3, 6, 12), material (barley, vetch), and distance (6, 12, 18, 50 mm) as variables Nematode taxa were analysed by 2-way ANOVA with material and distance (6 and 50 mm) as variables. The Tukey test was used to identify possible differences between single treatments when the ANOVA was significant. Number of nematodes of the different taxa in vetch and barley resources at distance 6 or 50 mm was analysed for the single species groups by 2-way ANOVA. We do not perform multivariate statistics or MANOVA on the interdependent nematode species groups since the focus of the paper is not to analyse nematode communities but to identify prevalence of nematode migration.

4. Results

4.1. Respiration activity

The respiration rates of the microcosms differed with time, being highest at week one, and with distance between amended soil segments ($P = <0.001$ and 0.014, respectively, 2-way ANOVA). After 3 weeks the respiration was greater in microcosms with reduced distance between the amended soil segments, the respiration being significantly higher at 6 and 12 mm than at 50 mm distance (Fig. 2, distance × time $P = 0.036$, 2-way ANOVA, Tukey, $P < 0.05$).

The microbial biomass (initial respiration rate in C-amended soil, Fig. 3) differed between materials and with time (both $P < 0.001$) and was also influenced by distance ($P = 0.005$, 3-way ANOVA). After 1 week of incubation the soil with vetch had a significantly higher microbial biomass (initial respiration rate in C-amended soil) compared to the soil with barley straw (Fig. 3). The biomass in the vetch segment was higher than the following sampling dates. In the barley soil microbial biomass peaked at three weeks (3-way ANOVA, material × time $P < 0.001$,Tukey $P < 0.05$). After one and 3 weeks microbial biomass in the barley segment was

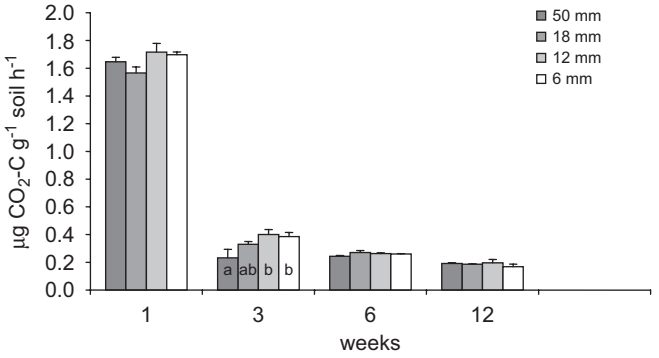

Fig. 2. Respiration rate (µg CO_2–C g^{-1} soil h^{-1}) of the intact boxes of soil. Results show the activity in the boxes of soil to be destructively sampled right after the analysis. Average ($n = 3$) and S.E. bars is shown. Different small letters on the bars indicate that these are significantly different (post 1-way ANOVA Tukey test).

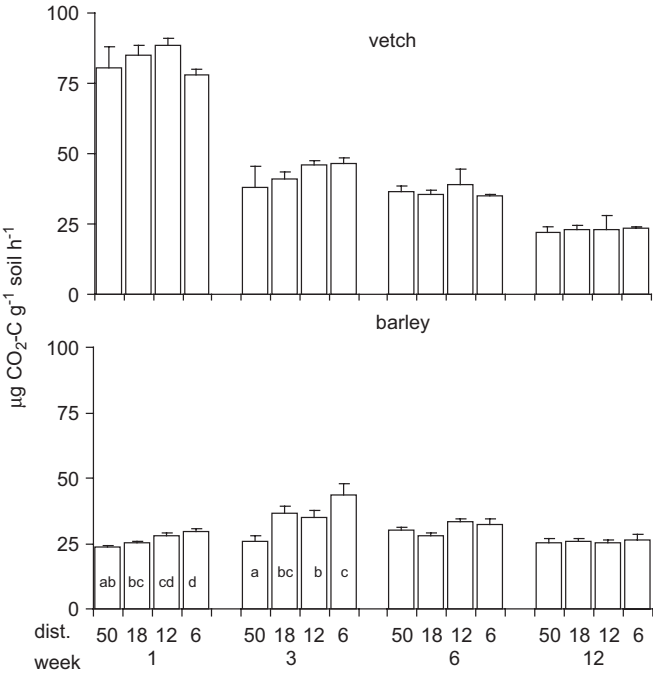

Fig. 3. Initial respiration rates (µg CO_2–C g^{-1} soil h^{-1}) in glucose-amended soil slurries measured during the first period (0.5–4 h) of incubation. Average ($n = 3$) and S.E. bars is shown. Different small letters on the bars indicate that these are significantly different (post 1-way ANOVA Tukey test).

affected by distance to the vetch, the highest values were found when located at short distance from the vetch segment (Fig. 3 bottom panel, 3-way ANOVA, time × distance $P = 0.038$, Tukey $P < 0.05$). Microbial biomass in the vetch segment did not depend on distance to the barley segment.

The respiration rates over the day (Fig. 4) depended on material and time (both $P < 0.001$, 3-way ANOVA) in C- as well as in C + N-amended soil. Without N respiration was almost significantly depending on distance (3-way ANOVA, $P = 0.053$) whereas addition of N resulted in respiration rates over the day not depending on distance

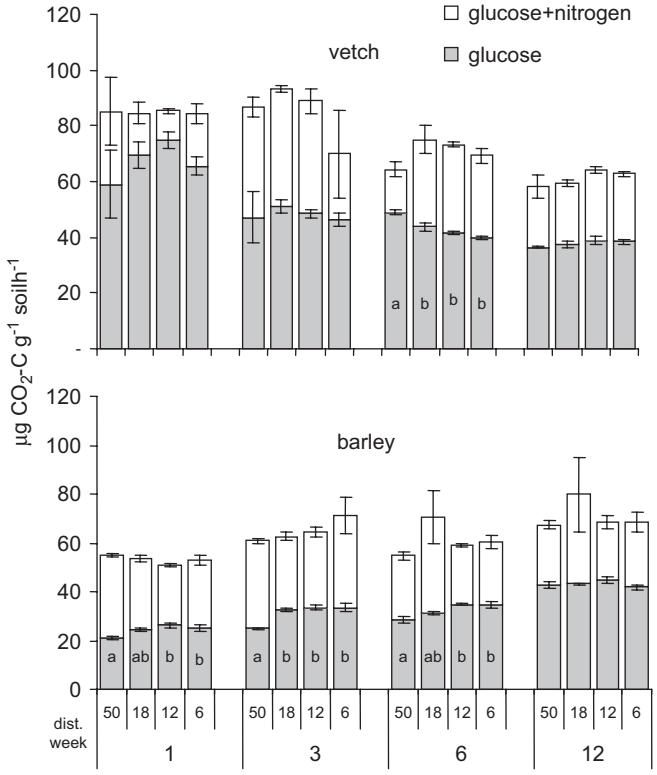

Fig. 4. Respiration rates during the day ($\mu g\, CO_2$–C g^{-1} soil h^{-1}) of glucose-amended and glucose + NH_4NO_3 amended soil slurries measured from 4 to 22 h of incubation. Bars for glucose + nitrogen as well as for glucose start at the origin of the *y*-axis. Average ($n = 3$) and S.E. bars is shown. Different small letters on the bars for C-amended soils indicate that these are significantly different (post 1-way ANOVA Tukey test).

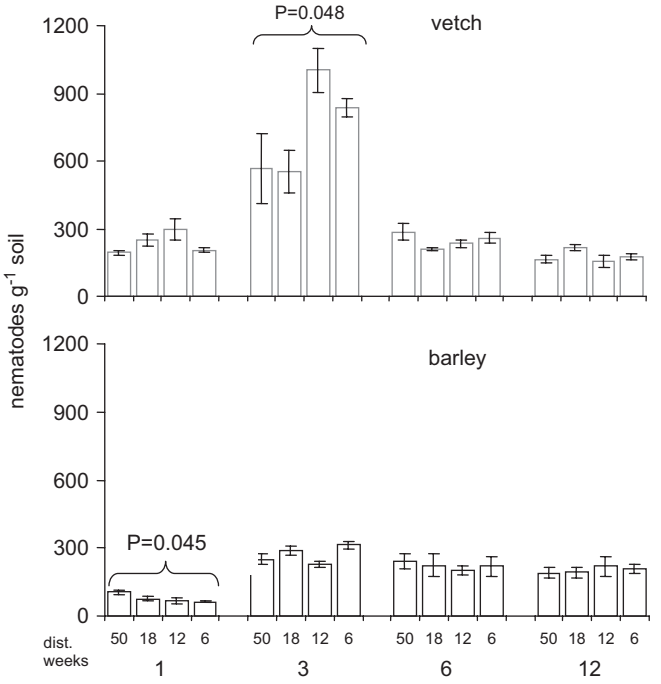

Fig. 5. Number of nematodes (g^{-1} soil) in the soil segments containing vetch or barley after 1, 3, 6, and 12 weeks of incubation at distances 6, 12, 18, and 50 mm.Average ($n = 3$) and S.E. bars is shown. *P* values are shown where 1-way ANOVA was significant but the following Tukey test did not show any differences between single treatments.

(3-way ANOVA, $P = 0.41$). The respiration rates over the day in the vetch after one week of incubation were of the same magnitude in C- and C + N-amended soil (although numerically highest in the latter) meaning that N was in surplus (Fig. 4). The following eleven weeks (three sampling dates) the respiration rates over the day of the vetch segment increased when amended with C + N compared to C so activity was apparently *N* limited in this period. In the barley segments respiration rates over the day were higher in C + N amended compared to C-amended soil at all sampling dates ($P < 0.05$) indicating N limitation throughout (Fig. 4). In vetch respiration over the day without N-amendment decreased with distance to the barley after 6 weeks (1-way ANOVA $P < 0.001$, Fig. 4, upper panel). In barley, without N addition respiration over the day was higher when placed close to the vetch segment after 1, 3, and 6 weeks (1-way ANOVA, $P = 0.028$, 0.001, and 0.004, respectively Fig. 4, lower panel).

4.2. Nematode numbers

Nematode number depended strongly on material and time (3-way ANOVA, both $P < 0.001$) whereas a distance effect varying with material and time was observed (3-way ANOVA, distance × material $P = 0.025$ and distance × time $P = 0.016$, respectively). After 1 week of incubation the segments added barley had on average 77 nematodes g $soil^{-1}$ (Fig. 5). This number increased the following sample dates ($P < 0.05$) where no less than 200 nematodes g $soil^{-1}$ were recorded. During the first 3 weeks the average nematode densities in the vetch increased from 236 to 739 nematodes g $soil^{-1}$ ($P < 0.05$) so the vetch did stimulate nematode population growth to a higher degree than did barley. The last 2 sampling dates the number of nematodes in the vetch decreased to 272 and 170 g $soil^{-1}$, respectively, whereas the number in the barley segment almost remained at the level obtained at 3 weeks. In barley, nematode number decreased marginally when closer to the vetch after 1 week (1-way ANOVA, $P = 0.048$, Fig. 5) none of the pairwise comparisons between distances were significantly different (Tukey, $P \geqslant 0.073$). Nematode number in the vetch located close to the barley segment was higher than those at large distance after 3 weeks (1-way ANOVA, $P = 0.045$, Fig. 5) but none of the distances differed from each other (Tukey, $P \geqslant 0.093$). Migration is not suggested to be the cause for these 2 distance effects since lowers numbers in the potential target is registered when close to the source (barley, 1 week) and highest number in the potential source was found when close to the target (vetch, 3 week).

4.3. Nematode taxa

In total 39 nematode taxa were encountered about half of these being bacterial feeders (Table 1). On average, 1.1%

Table 1
Taxonomic groups of nematodes observed in the vetch and barley segments

Bacterial feeders		*Omnivores*	
Short rhabditid larvae	100	Dorylaimida	10
Long rhabditid larvae	90	Qudsianematidae	5
Rhabditid dauerlarvae	30	Thornenematidae	5
Rhabditidae	5	Aporcelaimellus	<2.5
Cephalobidae	150	Microdorylaimus	<2.5
Eucephalobus	100	Pungentus	<2.5
Plectus	30	Predators	
Bursilla	20	Clarkus	10
Acrobeloides	20	Nygolaimus	<2.5
Alaimus	10	Mylonchulus	<2.5
Anaplectus	10	*Root hair/epidermal cell feeders or fungal feeders*	
Protorhabditis	5		
Cervidellus	5	Tylenchidae	250
Panagrolaimidae	5	Aglenchus	<2.5
Paramphidelus	5	Coslenchus	<2.5
Acrobelophis	<2.5	Filenchus	<2.5
Bastiania	<2.5	*Plant parasites*	
Monhysteridae	<2.5	Pratylenchus	10
Prismatolaimus	<2.5	Dolichodoridae	10
Aulolaimus	<2.5	Hoplolaimidae	5
Fungal feeders		Paratylenchus	<2.5
Aphelenchoides	80	Bitylenchus	<2.5
Aphelenchus	10		
Diphterophora	<2.5		
Tylencholaimus	<2.5		

Numbers represent the highest number of organisms per g soil encountered. When very low numbers are seen ("<2.5") it is always associated with an occasional occurrence.

(range 0–3.3%) of the nematode specimen could not be identified. The numerically dominant of the identified specimens were larvae of the bacterial feeding rhabditids, bacterial-feeding Cephalobidae and *Eucephalobus* and the fungal-feeding Tylenchidae and *Aphelenchoides*. There is some debate in the literature regarding the trophic relationships of Tylenchidae. Even though Yeates et al. (1993) regard the group as epidermal cell and root hair feeders, the group has later been found to include fungivorous nematodes (Okada et al., 2002; Wright and Coleman, 2002). Because this group of nematodes increases during incubation without plants in this investigation we regard the group as fungivorous in Table 1 and 2. Of the 39 taxa, 12 showed difference (2-way ANOVA, material and distance) between vetch and barley straw in the microcosms at least at 1 occasion during the 12 weeks study (Table 2).

In 6 occasions with significant differences between nematode densities in the materials there is also a significant distance effect (short Rhabditid larvae week 1, long Rhabditid larvae week 1, 3, and 12, *Aphelenchoides* week 1 and 6). For 4 of the taxa in question the abundance in the material with lowest number did not increase, or the abundance in the material with the highest number did not decrease, when distance between the two contrasting materials decreased. Nematode migration between the resources is therefore not suggested in these instances. Only for long Rhabditid larvae after 3 and 12 weeks the density in the potential target (barley) was higher when placed close to the source (vetch) with higher numbers than the barley. This shows that long Rhabditid larvae could have migrated between resources.

Another way to evaluate possible migration is to consider situations where nematode density differs with distance at a sampling that follows significant difference in density between the resources at the previous sampling. There are two such situations at week 3, 6, and 12. Long Rhabditid larvae only appeared in vetch at week 1, and at week 3 they had 20 times higher density in barley close to the potential source vetch compared to barley far from the vetch (Table 2) which again indicates migration from vetch to barley as a possibility for this group. *Bursilla* was found at highest density in barley at week 3 but at week 6 the number in the potential target vetch was highest when located far from the potential source barley (Table 2), so in this case migration can not explain the distance dependency of the numbers.

Taken together, the abovementioned results show that migration of nematodes does not prevail among the taxa. Out of 12 nematode taxa showing different densities between resources located down to 6 mm apart migration is only a possibility as contributor to population development for long rhabditid larvae. Other mechanisms than migration needs to be suggested for short rhabditid larvae, Aphelenchoides, and *Bursilla* that also show a distance-dependant population development.

Table 2
Number of individuals per g soil (dwt.) of the nematode taxa occasionally showing different densities between the vetch- and barley-amended soil segments (2-way ANOVA, $P(\text{mat}) < 0.05$)

Ind./g soil			Bacterial feeders									Fungal feeders		
			Rhabditid larvae		Eucephalobus	Bursilla	Acrobeloides	Anaplectus	Protorhabditis	Plectus	Monohysteridae	Tylenchidae	Aphelenchoides	Aphelenchus
			Short	Long										
1 week	50 mm	Barley	27.2 (3.8)	0.0 (0.0)	8.2 (1.1)	10.6 (3.7)	2.9 (0.6)	0.0 (0.0)	0.0 (0.0)	4.2 (0.9)	0.3 (0.3)	3.6 (1.7)	12.8 (0.8)	4.7 (1.7)
		Vetch	69.2 (2.5)	39.5 (3.2)	13.5 (4.1)	13.1 (2.9)	4.9 (1.2)	0.0 (0.0)	4.5 (1.2)	4.9 (2.0)	1.1 (0.6)	4.7 (1.6)	8.5 (1.6)	3.0 (0.9)
	6 mm	Barley	8.3 (1.6)	0.0 (0.0)	5.6 (1.5)	2.5 (0.8)	3.6 (0.5)	0.0 (0.0)	0.0 (0.0)	1.9 (0.4)	0.0 (0.0)	6.4 (1.6)	8.3 (1.5)	2.2 (0.3)
		Vetch	74.4 (4.1)	59.1 (5.9)	13.4 (1.9)	14.2 (2.6)	3.8 (1.7)	0.0 (0.0)	5.7 (0.8)	2.2 (1.0)	1.3 (0.8)	2.0 (0.8)	6.1 (0.7)	4.2 (1.8)
	P(mat)		0.001	0.001	0.041	0.020	0.276	0.581	0.001	0.655	0.058	0.344	0.022	0.966
	P(dist)		0.035	0.009	0.423	0.179	0.886	0.215	0.543	0.056	0.993	0.842	0.018	0.540
	P(mat × dist)		0.002	0.009	0.416	0.088	0.376	0.581	0.543	0.828	0.653	0.055	0.435	0.140
3 weeks	50 mm	Barley	102.3 (12.5)	1.3 (0.3)	14.3 (1.0)	4.9 (1.2)	2.9 (0.6)	0.0 (0.0)	3.2 (2.7)	6.0 (2.4)	0.3 (0.3)	8.1 (1.4)	22.3 (2.7)	4.7 (1.2)
		Vetch	75.1 (11.8)	34.1 (14.7)	8.9 (1.5)	0.0 (0.0)	3.1 (0.9)	0.0 (0.0)	0.0 (0.0)	3.5 (2.4)	0.4 (0.4)	2.3 (1.4)	17.5 (5.1)	3.6 (0.9)
	6 mm	Barley	93.8 (7.3)	26.7 (7.2)	10.9 (2.2)	4.1 (0.5)	9.2 (4.8)	0.0 (0.0)	0.7 (0.7)	4.2 (2.7)	0.6 (0.6)	12.2 (3.0)	20.4 (4.9)	6.0 (1.4)
		Vetch	54.9 (8.3)	73.0 (5.4)	9.2 (1.0)	0.0 (0.0)	1.6 (0.7)	0.0 (0.0)	0.0 (0.0)	3.3 (1.6)	0.7 (0.3)	0.9 (0.1)	16.4 (2.9)	5.2 (1.4)
	P(mat)		0.012	0.002	0.044	0.001	0.181	0.347	0.205	0.492	0.855	0.001	0.308	0.499
	P(dist)		0.198	0.006	0.331	0.541	0.377	0.347	0.414	0.677	0.492	0.478	0.710	0.265
	P(mat × dist)		0.586	0.457	0.260	0.541	0.158	0.347	0.414	0.749	0.971	0.165	0.914	0.895
6 weeks	50 mm	Barley	18.0 (4.8)	0.6 (0.6)	28.1 (4.8)	19.6 (4.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	10.4 (2.0)	0.0 (0.0)	0.0 (0.0)	82.9 (16.0)	9.6 (1.7)
		Vetch	25.4 (12.7)	11.0 (7.3)	67.4 (12.0)	22.5 (11.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	8.5 (2.7)	1.5 (0.8)	0.0 (0.0)	50.7 (1.4)	11.1 (3.0)
	6 mm	Barley	41.5 (8.8)	0.4 (0.4)	23.8 (5.2)	10.0 (2.3)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	13.7 (4.3)	0.0 (0.0)	0.6 (0.6)	47.3 (15.6)	8.6 (0.6)
		Vetch	65.0 (26.9)	0.0 (0.0)	49.4 (4.6)	0.0 (0.0)	0.5 (0.5)	0.0 (0.0)	0.0 (0.0)	8.3 (2.8)	1.5 (0.8)	0.5 (0.5)	23.0 (6.6)	12.6 (5.0)
	P(mat)		0.354	0.213	0.002	0.571	0.347			0.260	0.033	0.865	0.041	0.388
	P(dist)		0.080	0.171	0.165	0.028	0.347			0.622	0.978	0.198	0.026	0.944
	P(mat × dist)		0.621	0.180	0.379	0.316	0.347			0.593	0.978	0.865	0.740	0.674
12 weeks	50 mm	Barley	0.5 (0.5)	31.0 (1.7)	36.0 (7.3)	0.0 (0.0)	2.3 (1.2)	1.0 (1.0)	0.0 (0.0)	8.2 (1.4)	0.0 (0.0)	6.2 (2.2)	7.5 (5.1)	3.0 (1.7)
		Vetch	3.0 (3.0)	33.6 (18.3)	101.0 (26.5)	2.3 (1.5)	21.1 (6.5)	6.5 (3.3)	0.0 (0.0)	15.7 (5.5)	0.0 (0.0)	130.7 (39.5)	67.4 (18.9)	6.8 (1.8)
	6 mm	Barley	4.1 (2.1)	39.3 (6.3)	78.3 (10.8)	0.6 (0.6)	6.2 (0.9)	0.0 (0.0)	0.0 (0.0)	4.2 (0.3)	0.0 (0.0)	8.7 (2.5)	14.6 (1.1)	2.1 (0.1)
		Vetch	10.4 (2.8)	92.0 (9.5)	102.3 (3.9)	0.0 (0.0)	15.6 (8.1)	12.5 (4.8)	0.0 (0.0)	26.6 (3.8)	0.0 (0.0)	273.1 (6.8)	54.8 (5.0)	13.9 (3.0)
	P(mat)		0.092	0.034	0.017	0.333	0.027	0.016		0.002		0.001	0.001	0.004
	P(dist)		0.044	0.015	0.181	0.333	0.887	0.423		0.341		0.113	0.794	0.155
	P(mat × dist)		0.443	0.049	0.204	0.110	0.395	0.275		0.061		0.586	0.363	0.079

Only samples at 6 and 50 mm distance were analysed. Average values with S.E. ($n = 3$) in parenthesis. When numbers differed with distance (6 or 50 mm) this is indicated with a 2-way ANOVA, $P(\text{dist}) < 0.05$.

5. Discussion

In the early phase, breakdown of labile compounds in added materials gave high decomposition activity in the soil microcosms. After one week microbial biomass in the N-rich vetch was about three times that in barley and activity in the vetch was not limited by N as opposed to the barley. In vetch the easily available carbon had mineralised at week 3 and microbial biomass decreased to half of the amount at week 1 releasing N previously bound in micro-organisms. The vetch segment was therefore likely to be an N source up to week 3. The higher microbial biomass and activity without N addition in barley and microbial biomass when close to vetch was probably stimulated by nitrogen transferred through the soil. The mechanisms behind this distance effect could be: (1) increased diffusion stimulated by steeper concentration gradients, and (2) hyphae of fungi bridging the gap between vetch and barley more easily when located close to each other. This has been shown experimentally for fungi connecting blocks of wood (Lindahl et al., 2001).

In a soil very similar to the present study of soil texture (sand–silt–clay–organic matter = 0.72−0.14−0.14−0.02), bulk density (1.4 g cm^{-3}), and moisture (0.2 g g^{-1} soil) an added Cl^- tracer diffused 30 mm away from the source within a week (Oedum soil, Fig. 2 in Olesen et al., 1997) suggesting that nitrate diffusion alone could be responsible for the distance dependant changes in microbial biomass, activity, and N limitation.

The higher number of nematodes in vetch compared with those of barley up to week 3 was probably due to the higher microbial production. Total nematode numbers do not suggest nematode migration between vetch and barley to be important for population development. Nematode number in the potential target of lowest numbers (barley) did not increase when closer to the potential source of higher numbers (vetch), and numbers in vetch did not decrease when close to barley. The reduction in nematodes in the vetch far from barley at week 3 could possibly be caused by excess nutrients reaching concentrations harmful to nematodes. Although no direct evidence from the literature has been found to support this, Oka and Yermiyahu (2002) found reduced development of a plant parasitic nematode in compost and ascribed this to high concentrations of inorganic N in the compost. High local concentrations of NH_4^+ and/or NO_3^- as indicated for vetch at week 1 (Fig. 4) increase the risk for harmful concentrations of NH_3 or NO_2^- in the vetch segment.

When vetch was located closer to the N-limited barley, the enhanced nutrient export from vetch to barley suggested above could have reduced nutrient concentrations to sub-toxic levels.

Of course, the value of the data to indicate whether individual taxonomic groups have migrated improves if each recorded group only consists of 1 species. To the best of our knowledge, number of species within the families/genera listed in Table 2 seldom exceeds 2–3. When the nematode rich resource shows highest numbers being close to the nematode poor resource as for 3 groups (short rhabditid larvae, *Bursilla*, Aphelenchoides) migration is not suggested. Like for total nematodes movement of nutrients to support growth of food bacteria by diffusion or hyphal transport may be suggested as mechanism to induce distant dependant growth of nematodes within a specific site. When nematode numbers are highest in the potential target when close to the potential source and/or are lowest in the source when close to the target as for long rhabditid larvae, we infer that nematode migration potentially contributed to population development. Griffiths and Caul (1993) found strong evidence for migration of bacterivorous nematodes in soil, and in their study migrating nematodes were also predominantly rhabditids.

In model systems based on agar (Anderson et al., 1997) or sand (Young et al., 1998) bacterial feeding nematodes clearly migrated several cm in less than a day towards patches of food bacteria (*Escherichia coli*) most likely responding to gradients of chemical attractants released by the bacteria. These findings do not contradict that we only find indications of distance-dependant migrations for long rhabditid larvae, since Anderson et al. (1997) and Young et al. (1998) also tested migration potential of rhabditid larvae (*C. elegans*). Other workers indicate, however, that also cephalobid and not only rhabditid nematodes migrate (Griffiths et al., 1991, 1993).

The nematodes in our study may not have been able to follow gradients of bacterial chemical attractants for several reasons: 1. Contaminant bacteria on the body surface of nematodes may interfere with nematode ability to sense chemical attractant gradients (Young et al., 1996). In the model studies nematodes were washed free from contaminant bacterial cells before beginning the experiment 2. The release of cues from bacteria present in the barley material may also have interfered with the attractant gradient emanating from the high microbial activity of the vetch material 3. Narrow soil pores restricting nematodes following a chemical cue (Young et al., 1996).

It should be emphasised that this discussion only deals with microbivorous nematodes. Plant parasitic nematodes migrate over long distances in soil towards a root attractant— up to 8 cm d^{-1} has been reported (Pinkerton et al., 1987). Distance-dependant nitrogen transport by diffusion or hyphal growth can not be ruled out as possible mechanisms behind the distance-dependant increase in long rhabditid larvae, however: By creating a more favourable (N rich) environment nitrogen transport can mediate a faster nematode growth in a N-poor site (Georgieva et al., 2005).

In conclusion, even though cues such as gradients of nitrogen and possibly CO_2 exist, migration is not a widespread phenomenon among nematode taxa between resources only separated by a few mm in soil. Distance dependant population development only suggests migration along the nutrient gradient indicated for one out of 12 taxonomic groups, the rhabditid larvae. For three other

taxonomic groups nutrient transfer along the nutrient gradient-induced distance-dependant population development locally at the site in the soil. These results may suggest that the migration of nematodes observed in previous studies (e.g. Griffiths and Caul, 1993) will mainly be due to fast juvenile stages of growing bacterivores.

References

Anderson, J.P.E., Domsch, K.H., 1978. A physiological method for the quantitative measurement of microbial SIR-biomass in soils. Soil Biology & Biochemistry 10, 215–221.

Anderson, A.R.A., Young, I.M., Sleeman, B.D., Griffiths, B.S., Robertson, W.M., 1997. Nematode movement along a chemical gradient in a structurally heterogenous environment. 1. Experiment. Fundamental and Applied Nematology 20, 157–163.

Georgieva, S., Christensen, S., Andersen, K., 2005. Nematode succession and microfauna-microorganism interactions during plant residue decomposition. Soil Biology & Biochemistry 37, 1763–1774.

Giller, P.S., 1996. The diversity of soil communities, 'the poor man's rainforest'. Biodiversity and Conservation 5, 135–168.

Griffiths, B.S., Caul, S., 1993. Migration of bacterial-feeding nematodes, but not protozoa, to decomposing grass residues. Biology and Fertility of Soils 3, 207–210.

Griffiths, B.S., Young, I.M., Boag, B., 1991. Nematodes associated with the rhizosphere of barley (*Hordeum vulgare*). Pedobiologia 35, 265–272.

Griffiths, B.S., Ekelund, F., Rønn, R., Christensen, S., 1993. Protozoa and nematodes on decomposing barley roots. Soil Biology & Biochemistry 25, 1293–1295.

Griffttths, B.S., Young, I., Caul, C.S., 1995. Nematode and protozoan population dynamics ion decomposing barley leaves incubated at different soil matric potentials. Pedobiologia 39, 454–461.

Griffiths, B.S., Wheatley, R.E., Olsen, T., Henriksen, K., Ekelund, F., Rønn, R., 1998. Dynamics of nematodes and protozoa following the experimental addition of cattle or pig slurry to soil. Soil Biology & Biochemistry 30, 1379–1387.

Jingguo, W., Bakken, L.R., 1997. Competition for nitrogen during decomposition of plant residues in soil: effect of spatial placement of N-rich and N-poor plant residues. Soil Biology & Biochemistry 29, 153–162.

Lindahl, B., Finlay, R., Olsson, S., 2001. Simultaneous, bidirectional translocation of P-32 and P-33 between wood blocks connected by mycelial cords of *Hypholoma fasciculare*. New Phytologist 150, 189–194.

Munkholm, L.J., Schjønning, P., Rasmussen, K.J., 2001. Non-inversion tillage effects on soil mechanical properties of a humid sandy loam. Soil and Tillage Research 62, 1–14.

Oka, Y., Yermiyahu, U., 2002. Nematology 4, 891–898.

Okada, H., Tsukiboshi, T., Kadota, I., 2002. Mycetophagy in *Filenchus misellus* (Andrássy, 1958) Lownsbery & Lownsbery, 1985 (Nematoda: Tylenchidae), with notes on its morphology. Nematology 4, 795–801.

Olesen, T., Moldrup, J., Henriksen, K., 1997. Modelling diffusion and reaction in soils: VI. Ion diffusion and water characteristics in organic manure amended soil. Soil Science 162, 399–409.

Pinkerton, J.N., Mojtahedi, H., Santo, G.S., O'Bannon, J.H., 1987. Vertical migration of *Meloidogyne chitwoodi* and *M. hapla* under contolled temperature. Journal of Nematology 19, 152–157.

Rønn, R., Griffiths, B.S., Ekelund, F., Christensen, S., 1996. Spatial distribution and successional pattern of microbial activity and microfaunal populations on decomposing barley roots. Journal of Applied Ecology 32, 662–672.

Scheu, S., 1993. Analysis of the microbial nutrient status in soil microcompartments: earthworm faeces from a basalt–limestone gradient. Geoderma 56, 575–586.

Whitehead, A.G., Hemming, J.R., 1970. A comparison of some quantitative methods of extraction small vermiform nematodes from soil. Annals of Applied Biology 55, 25–38.

Wright, C.J., Coleman, D.C., 2002. Responses of soil microbial biomass, nematode trophic groups, N-mineralization, and litter decomposition to disturbance events in the southern Appalachians. Soil Biology & Biochemistry 34, 13–25.

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.

Young, I.M., Griffiths, B.G., Robertson, W.M., 1996. Continuous foraging by bacterial-feeding nematodes. Nematologica 42, 378–382.

Young, I.M., Griffiths, B.S., Robertson, W.M., McNicol, J.W., 1998. Nematode (*Caenorhabditis elegans*) movement in sand as affected by particle size, moisture and the presence of bacteria (*E. coli*). European Journal of Soil Science 49, 237–241.