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Fluxes of root-derived carbon into the nematode micro-food web of an arable soil

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ABSTRACT

Organic carbon (C) released from living roots forms a major resource for microorganisms controlling energy, C pathways and, hence, food web structure and dynamics. However, knowledge on quantitative C fluxes into food web compartments is scarce. Nematodes, with functional groups at each trophic level, served as a model community for assessing root C fluxes into the micro-food web. Maize, grown on soil cores from an arable field, was pulse-labeled with $^{14}CO_2$ followed by sampling 2, 5, 10 and 16 days after labeling. Nematode population density, community structure, trophic groups and their ^{14}C activities were analyzed.

Overall, 55 genera of 22 families were detected. Plant-feeders, which had the highest density, showed the fastest and highest incorporation of root C. Bacterial-feeders incorporated more root-derived ^{14}C than fungal-feeders. This was consistent with a bacterial- to fungal-feeder-ratio of 0.63 and a moderate to low Channel Index (average 38), a nematode faunal index that assigns the magnitude of carbon flow via the bacterial or fungal channel, both indicating a major energy flux in the bacterial decomposition pathway. Predators and omnivores showed low incorporation of root-derived C, pointing to a basal food web structure with short food chains and low energy transfer to higher trophic levels.

Combining ^{14}C tracing with taxonomic identification of nematodes allowed quantification of root C fluxes into food web compartments. The incorporation of root C into nematodes was small (~0.1% of that in microbial biomass), yet forms an important part of belowground C channeling as it links microbial and faunal food web.

1. Introduction

The input of organic carbon (C) from plants, either as shoot and root litter after plant death or as C released from living roots (rhizodeposits), is the main determinant of soil food web structure and dynamics. While the C and energy flux from slowly decomposing plant litter into soil food webs has been intensively studied, little is known about the belowground C transfer of easily available rhizodeposits, especially root exudates, with most studies focusing on forest ecosystems (Pollierer et al., 2012; Eissfeller et al., 2013). It has, however, been suggested that the majority of soil animals rely on root-derived sources rather than on litter (Albers et al., 2006; Pollierer et al., 2007). This is especially important for agroecosystems, where aboveground plant biomass is removed at harvest, thereby disrupting the internal soil C cycle and intensifying the dependency of the soil food web on root-derived resources.

To measure the trophic transfer of root-released C through the soil food web, nematodes are ideal model organisms because they occur at great densities with several million per square meter, are highly diverse, and comprise functional groups at each trophic level (Yeates et al., 1993a; Yeates, 2010). The dominant trophic groups of nematodes in arable soil are plant-, fungal- and bacterial-feeders (Yeates and Bongers, 1999). Plant-feeders play a major role in agriculture as they can cause severe damage to plant tissue, resulting in reduced crop biomass (Neher, 2010). However, moderate feeding activity leads to leakage of cell metabolites, predominantly labile C, which can increase soil microbial biomass and, in turn, nutrient mineralization (Yeates et al., 1998; Poll et al., 2007). Grazing by bacterial-feeders fosters microbial activity, again enhancing mineralization and nutrient availability for plants (Ingham et al., 1985; Neher, 2010). Saprophytic fungi, which degrade plant litter and detritus, as well as mycorrhiza-forming taxa, constitute the food source for fungal-feeding nematodes (Ruess et al., 2000). Omnivores have considerable influence on soil C fluxes due to their broad range of nutritional sources (Neher, 2010). They not only consume plant tissue, bacteria, fungi or other nematodes, but also feed on algae and enchytraeids (Yeates et al., 1993a, 1993b). Finally, predatory nematodes play an important role within the food web as top down regulators, as well as in the nutrient cycle via released excess nitrogen (Ferris, 2010).

Analyses of the natural abundance of stable carbon ($^{12}C/^{13}C$) or nitrogen ($^{14}N/^{15}N$) isotopes have given detailed insight into soil food

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webs and essential knowledge about trophic linkages (Gannes et al., 1997, 1998; Post, 2002; Crawford et al., 2008; Martínez del Rio et al., 2009). $\delta^{15}N$ reflects the relative trophic levels, whereas $\delta^{13}C$ corresponds to the respective food sources (Ponsard and Arditi, 2000; Scheu and Falca, 2000; Tiunov, 2007). However, nematodes as important representatives of the soil microfauna, have seldom been studied. The few stable isotope data available are mainly on whole communities or single well defined species (Neilson and Brown, 1999; Crotty et al., 2011; Darby and Neher, 2012), giving no insight into food web structure. Only recently, methodological advances were made in obtaining C stable isotope ratios of low organismic biomass (Crotty et al., 2013), and first empirical investigations under field conditions studying nematode trophic groups were performed (Pausch et al., 2015).

Beside stable isotope measurements of nematodes, a few experiments have been carried out employing the radioactive isotope ^{14}C as tracer to follow the C flux from pulse-labeled plants to nematodes. Fu et al. (2000) used ^{14}C-labeled corn and showed higher ^{14}C incorporation from plant residues into nematode biomass in conventional tilled compared to no-tillage soil. Further, Fu et al. (2001) determined the impact of aboveground grazers, namely grasshoppers, and revealed that the ^{14}C activities in nematode populations are highest with intensive grazing and without tillage. Yeates et al. (1998) analyzed the C transfer from plants to plant-feeders by inoculation of white clover with *Heterodera trifolii*, after plants were labeled with ^{14}C-CO_2. The study strikingly showed that the C uptake by plant-feeders caused considerable leakage of root cell metabolites into the rhizosphere. A comparable experiment with five plant-feeding taxa revealed distinct differences in root C incorporation between the species (Yeates et al., 1999). However, with the focus on plant-feeders only, these experiments did not take into account the whole nematode community and their food web linkages.

To address root-derived C incorporation at food-web level and to establish a budget of root C flux to nematodes, a $^{14}CO_2$ pulse labeling experiment with maize (*Zea mays*) was conducted in undisturbed soil cores from an arable field. To gain a comprehensive picture of the nature of C flux and allocation to the soil micro-food web, the ^{14}C activity of trophic groups of nematodes was examined. By using undisturbed soil cores the study aimed to establish a representative endogenous nematode community as prerequisite for modeling plant C flux to the below-ground fauna. As nematodes are key drivers of the soil micro-food web and mirror major functional changes, their population dynamics, structure and faunal indices serve as image for the entire micro-food web. This plant-soil system was used to test the following hypotheses: *i*) ^{14}C is predominantly incorporated into plant-feeding nematodes as they directly feed on labeled roots, *ii*) leakage induced by plant-feeders fosters ^{14}C flux into the rhizosphere and to rhizosphere bacteria, resulting in *iii*) a fast and high incorporation of ^{14}C in bacterial-feeding nematodes and, hence, into the bacterial energy channel of the food web.

2. Material and methods

2.1. Experimental set-up

The soil (Luvisol) for the experiment was taken from an arable field cropped with wheat in the north-west of Göttingen, Germany, in November 2010. The sampling site and soil properties are described in detail by Kramer et al. (2012). Twenty undisturbed soil cores were taken with a soil corer (inner diameter 12 cm, height 30 cm) and directly transferred into Plexiglas pots (inner diameter 13 cm, height 30 cm) covered with dark foil. Maize seeds (*Zea mays* L. cv. Ronaldinio) were germinated on wet filter paper for 3 days and afterwards 3 seeds were planted in each soil cores. The pots were then covered with Plexiglas lids, with holes for the plant shoots. The soil water content was gravimetrically adjusted daily to 70% of the water holding capacity. Plants were grown at a temperature of 26 to 28 °C during the day and 22 to 23 °C at night and a light intensity of ~400 μmol m^{-2} s^{-1}.

Of the labeled maize plants (see Section 2.2) four pots were destructively harvested on days 2, 5, 10, and 16 after labeling. In addition, unlabeled control pots were sampled at day 0, i.e. before labeling. Maize shoots were cut at their base and the roots were carefully picked from the soil with tweezers. Plant and soil material was dried (60 °C for 3 days) and pulverized in a ball mill. The remaining soil was stored at 4 °C until further analysis.

2.2. $^{14}CO_2$ pulse labeling

Maize plants were labeled at the tillering stage, 25 days after planting. One day before labeling, the holes in the lids were sealed with a silicon paste (NG 3170, Thauer & Co., Germany). The labeling procedure was done 2 times with 8 pots each in a Plexiglas chamber ($48.1 \times 48.1 \times 158$ cm^3). The chamber was connected to a flask containing the labeling solution (5 ml of $Na_2^{14}CO_3$; ARC Inc., USA) with a ^{14}C activity of 1.2 MBq per pot. The $^{14}CO_2$ was released into the chamber by addition of an excess (10 ml) of 5 M H_2SO_4. Plants were exposed to the label for 4 h. Afterwards, the air inside the chamber was pumped through 15 ml of 1 M NaOH solution for 2 h to remove the unassimilated $^{14}CO_2$. After labeling, the chamber was opened and the plants were further grown under the conditions described above. Four pots with plants were kept unlabeled as control.

2.3. ^{14}C analyses of plant tissue, microbial biomass, soil and CO_2 efflux

To assess plant tissue and soil ^{14}C activity, 50 mg of shoots and roots, and 500 mg of soil per replicate were combusted in an oxidizer unit (Feststoffmodul 1300, AnalytikJena, Germany). The released CO_2 was trapped in 10 ml of 1 M NaOH. For 4 pots, starting directly after labeling, the soil CO_2 efflux was continuously trapped using 15 ml of 1 M NaOH solution. The NaOH solution was changed every 2 h after labeling for the first day, then twice daily, then once every 2 days until 16 days after labeling.

The ^{14}C activity of microbial biomass C (MBC) and of extractable organic C (EOC) was determined for day 16 after labeling by the chloroform fumigation extraction method of Vance et al. (1987). Briefly, 5 g fresh soil were shaken with 20 ml of 0.05 M K_2SO_4 for 1 h at 200 rev min^{-1}, centrifuged at 3000 rev min^{-1} for 10 min, and filtrated. Another 5 g fresh soil were fumigated with chloroform for 24 h and extracted in the same way. The extracts were analyzed for total organic carbon by means of an N/C analyzer (Multi N/C 2100, AnalytikJena, Germany) (Pausch et al., 2013).

The ^{14}C activity of shoots, roots, soil, unassimilated CO_2 after labeling, C remaining in the tracer solution, and soil CO_2 efflux were measured in 2 ml aliquots of sample added to 4 ml Rothiscint scintillation cocktail (Roth, Germany) with a liquid scintillation counter (LS 6500 Multi-Purpose Scintillation Counter, 217 Beckman, USA) after the decay of chemiluminescence. The K_2SO_4 extracts of non-fumigated and fumigated soil for MBC and EOC analysis were measured in the same way in 1 ml aliquots added to 6 ml Rothiscint scintillation cocktail. The ^{14}C counting efficiency was about 92% and the ^{14}C activity measurement error did not exceed 2%. Total C of all samples were analyzed by an N/C analyzer (Multi N/C 2100, AnalytikJena, Germany).

2.4. Nematode extraction and ^{14}C analyses

Nematodes were extracted from 50–80 g fresh soil using a modified Bearman method after Ruess (1995), fixed in 4% formaldehyde, and stored at 7 °C in a refrigerator. Nematodes were counted and 10% or a minimum of 100 individuals per sample were identified to genus level (Bongers, 1994; Brzeski, 1998; Andrássy, 2007). For ^{14}C measurements, individuals were assigned to bacterial-, fungal-, and plant-feeders, omnivores and predators according to Yeates et al. (1993a) using an inverted microscope and sorted with a Pasteur pipette into scintillation vials. The Dauerlarvae of Rhabditidae were assigned to the group of

bacterial-feeders. All nematodes within a sample were sorted and identified. The ^{14}C activity of trophic groups was measured after volatilization of formaldehyde solution in 6 ml Rothiscint scintillation cocktail (Roth, Germany) using a liquid scintillation counter as described above. To obtain exact ^{14}C activity of nematodes, the duration of scintillation counting of each group was at least 3 h. We also measured the ^{14}C activity of trophic groups of nematodes sampled at day 0 (before labeling). These ^{14}C activities were set as natural background and were subtracted from the ^{14}C activities of all nematode groups sampled after labeling (day 2, 5, 10, and 16 after labeling).

2.5. Nematode indices

To assess whether the carbon flow is predominantly via the bacterial or fungal channel the bacterial- to fungal-feeder ratio (b/f) according to Yeates et al. (1993b) and the Channel Index (CI) according to Ferris et al. (2001) were calculated. The following equations were used:

$$\frac{b}{f} = \frac{\text{proportion of bacterial feeders}}{(\text{proportion of bacterial feeders} + \text{proportion of fungal feeders})} \quad (1)$$

$$CI = 100 \cdot \frac{0.8Fu_2}{3.2Ba_1 + 0.8Fu_2} \quad (2)$$

where the coefficients (0.8 and 3.2) are weightings for the functional nematode guilds after Ferris et al. (2001), and Ba_1 represents the bacterial-feeders with a colonizer-persister (*c-p*) value of 1 and Fu_2 fungal-feeders with a *c-p* value 2. Nematodes life strategy was ascribed to colonizers (*c*) and persisters (*p*) that are extremes on a scale from 1 to 5, respectively (Bongers, 1990). Nematode families classified as *c-p* 1 represented colonizers or *r*-strategists, whereas, families, *c-p* 5 are persisters or *K*-strategists. Opportunists are characterized as *c-p* 2, while *c-p* 3 have an intermediate life strategy and *c-p* 4 can be assigned to moderate *K*-strategists (Bongers, 1990).

Note that the Rhabditidae Dauerlarvae are non-feeding stages and, therefore, they have not been taken into consideration for the calculation of CI and b/f.

2.6. Nematode biomass and carbon content

The length and width of individuals within a nematode genus are relatively constant and can be used as a reliable morphometric trait. The biomass (fresh weight) of the nematodes was calculated according to Andrássy (1956), with the following equation:

$$\text{Nematode biomass } (\mu g) = a^2 * b/16 * 100,000 \quad (3)$$

where *a* is the body width and *b* the body length. The correction factor 16 was derived from Andrássy and multiplication by 100,000 converts biomass data to μg.

The biomass was calculated for each genus and the C content assigned as 12.5% of the fresh weight, based on the assumption that the dry weight is 25% of the fresh weight and has a carbon content of 50% (Schmidt et al., 2000).

2.7. Calculations

Activity of ^{14}C in various trophic groups of nematodes over time ($r(^{14}C)_{nematode}$; %) was expressed relative to the total belowground ^{14}C activity at each sampling date ($a(^{14}C)_{belowground}$; kBq pot^{-1}), i.e. as a percentage of the sum of ^{14}C in roots, soil, and soil CO_2:

$$r(^{14}C)_{nematode}(\%) = a(^{14}C)_{nematode}/a(^{14}C)_{belowground} * 100 \quad (4)$$

where $a(^{14}C)_{nematode}$ is the ^{14}C activity of the individual nematode trophic group (kBq pot^{-1}).

The ^{14}C budget was compiled for day 16 after labeling on the basis that the ^{14}C allocation between above- and belowground pools is completed at that time. It was shown that the allocation of recent assimilates between above- and belowground C pools is mainly completed within the first 2 days after labeling (Pausch et al., 2013).

The percentage of ^{14}C recovered in a C pool ($r(^{14}C)_{pool}$; %) was calculated by relating the ^{14}C activity of the respective C pool ($a(^{14}C)_{pool}$; kBq pot^{-1}) to the total ^{14}C recovery at day 16 ($a(^{14}C)_{total}$; kBq pot^{-1}), i.e. to the sum of the ^{14}C activity in shoot, root, soil, and CO_2:

$$r(^{14}C)_{pool}(\%) = a(^{14}C)_{pool}/a(^{14}C)_{total} * 100 \quad (5)$$

Specific ^{14}C activities (kBq g^{-1} C) of the individual nematode groups were calculated by dividing the measured activity of the respective group by its C content. The specific ^{14}C activity allowed to compare the various trophic groups of nematodes independently of their C pool size.

2.8. Statistics

Means and standard deviations (SD) are presented in figures and tables.

A one-way analysis of variance (ANOVA) in combination with post hoc Tukey's HSD tests was performed for each sampling date to determine if the trophic groups of nematodes (independent variable) varied significantly ($P \le 0.05$). A one-way ANOVA in combination with post hoc Tukey's HSD tests was also performed for each trophic group of nematodes to determine significant differences ($P \le 0.05$) over time (the sampling date was the independent variable).

3. Results

3.1. Nematode population density and community structure

The population density of nematodes was ~590 Ind. 100 g^{-1} DW at day 0 and increased significantly until the end of the experiment (day 16) with ~1800 Ind. 100 g^{-1} DW (Fig. 1). In total, 55 nematode genera belonging to 22 families were detected (Table 1, Appendix 1). Of these, nine families were classified as bacterial-feeders, whereas plant-feeders

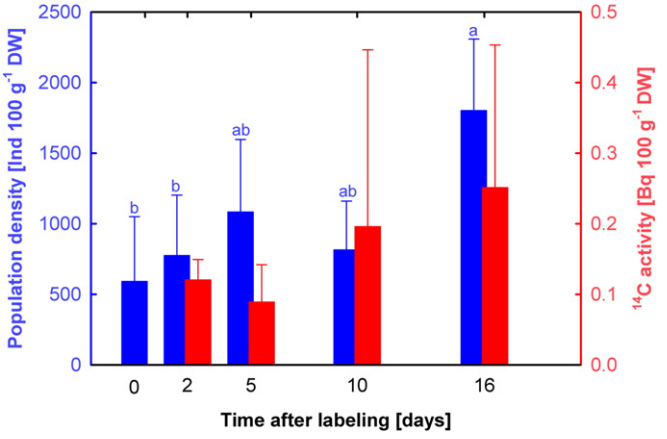

Fig. 1. Population density (individuals 100 g^{-1} DW ± SD, blue bars) and ^{14}C activity (Bq 100 g^{-1} DW ± SD, red bars) for the sum of all trophic groups 0, 2, 5, 10, and 16 days after $^{14}CO_2$ pulse labeling. Bars with the same or no letters are not significantly different over time according Tukey's HSD tests at $P < 0.05$.

Table 1
Nematode families within different trophic groups (individuals 100 g^{-1} DW ± SD) at day 0, and 2, 5, 10 and 16 days after $^{14}CO_2$ pulse labeling and colonizer-persister (*c-p*) values according to Bongers (1990). Values followed by different letters indicate significant differences over time according to Tukey's HSD tests at $P < 0.05$. Values without letters are not significantly different over time. For information to nematode genera see Appendix A1.

Trophic group	Nematode family	Time after labeling [days]					*c-p* value
		0	2	5	10	16	
		[Ind 100 g^{-1} DW]					
Plant-feeders		*340 ± 325*	*484 ± 416*	*501 ± 229*	*229 ± 151*	*785 ± 495*	
	Dolichodoridae	17 ± 13	12 ± 7	24 ± 25	38 ± 15	67 ± 53	3
	Heteroderidae	19 ± 38	1 ± 3	0	0	0	3
	Paratylenchidae	0	0	0	0	1 ± 2	2
	Pratylenchidae	0	0	0	0	2 ± 4	3
	Tylenchidae	304 ± 284	470 ± 120	477 ± 226	190 ± 137	715 ± 525	2
Bacterial-feeders		*163 ± 144*	*192 ± 79*	*410 ± 309*	*410 ± 161*	*507 ± 126*	
	Alaimidae	3 ± 3	6 ± 8	8 ± 15	0	6 ± 11	4
	Cephalobidae	92 ± 81	100 ± 9	192 ± 129	220 ± 46	260 ± 122	2
	Diploscapteridae	19 ± 38	25 ± 35	24 ± 14	2 ± 3	10 ± 8	1
	Panagrolaimidae	5 ± 8	4 ± 9	4 ± 5	2 ± 3	1 ± 2	1
	Plectidae	3 ± 4	12 ± 5	29 ± 48	9 ± 16	18 ± 25	2
	Prismatolaimidae	17 ± 10	14 ± 10	32 ± 28	47 ± 48	79 ± 56	3
	Rhabditidae	26 ± 22	14 ± 9	79 ± 92	130 ± 58	125 ± 36	1
	Rhabditidae DL	67 ± 49	28 ± 33	77 ± 70	75 ± 48	43 ± 17	
	Rhabdolaimidae	0	0	0	1 ± 2	0	3
	Teratocephalidae	0	0	1 ± 3	0	0	3
Fungal-feeder		*78 ± 29*	*94 ± 39*	*163 ± 99*	*161 ± 41*	*503 ± 147*	
	Anguinidae	3 ± 4	0	2 ± 3	9 ± 12	8 ± 14	2
	Aphelenchidae	29 ± 20	23 ± 11	35 ± 23	58 ± 17	46 ± 18	2
	Aphelenchoididae	47 ± 12	71 ± 44	125 ± 76	94 ± 67	451 ± 127	2
Predators		*2 ± 3*	*1 ± 3*	*4 ± 5*	*2 ± 3*	*5 ± 7*	
	Anatonchidae	0	0	1 ± 2	0	0	4
	Aphelenchoididae	0b	0b	0b	0b	2 ± 3a	2
	Mononchidae	2 ± 3	1 ± 3	3 ± 5	2 ± 3	3 ± 6	4
Omnivores		*8 ± 3*	*5 ± 4*	*7 ± 4*	*15 ± 9*	*2 ± 2*	
	Aporcelaimidae	0	0	3 ± 3	0	1 ± 2	5
	Qudsianematidae	3 ± 2b	2 ± 3b	3 ± 3b	12 ± 7a	0b	4
	Thornenematidae	5 ± 4	2 ± 3	2 ± 5	2 ± 4	1 ± 2	5

DL: Dauerlarvae.

were represented by five families. Fungal-feeders, omnivores and predators comprised three families each.

Plant-feeders were the most abundant trophic group with a mean density across time of 468 Ind. 100 g^{-1} DW (Table 1), equaling 42.6% of all nematodes. Bacterial- and fungal-feeders accounted on average for 323 and 200 Ind. 100 g^{-1} DW, representing 32.5% and 18.2% of the nematode community, respectively. Both, bacterial- and fungal-feeders showed a slight increase (not statistically significant) in density over the experimental period. Omnivores and predators were scarce with 7 and 3 Ind. 100 g^{-1} DW, respectively, representing a minor portion of the nematode fauna with an average of 1% for omnivores and 0.3% for predators.

The Channel Index (CI) did not differ significantly between the sampling dates. The CI was below 50, with an overall average of 38, indicating a modest dominance of the bacterial decomposition channel (data not presented). Correspondingly, the number of bacterial-feeders was higher than that of fungal-feeders, leading to a b/f-ratio with an average of 0.63. Values for both indices did not differ significantly between the sampling days (data not presented).

3.2. ^{14}C allocation to various trophic groups of nematodes

The nematodes in the soil were successfully labeled with ^{14}C derived from the maize plants as they had significant higher ^{14}C activities compared to the background samples from the unlabeled control (data not shown). All functional groups of nematodes already showed a ^{14}C signal at day 2 after labeling with ^{14}C activities for the whole nematode population ranging from 0.09 ± 0.05 Bq 100 g^{-1} DW at day 5 to 0.25 ± 0.2 Bq 100 g^{-1} DW at day 16 (Fig. 1). The ^{14}C activity increased with time (not significant), which is in accordance with the higher population density at day 16 after labeling (Fig. 1).

The ^{14}C activity of various trophic groups of nematodes through time is given as percentage of total belowground ^{14}C (Fig. 2). Among the trophic groups, the plant-feeders showed the highest ^{14}C activity across the entire experimental period. Incorporation of root C into plant-feeders was significantly higher compared to the other trophic groups at day 2 and 16 after labeling. The ^{14}C activity of plant-feeders increased

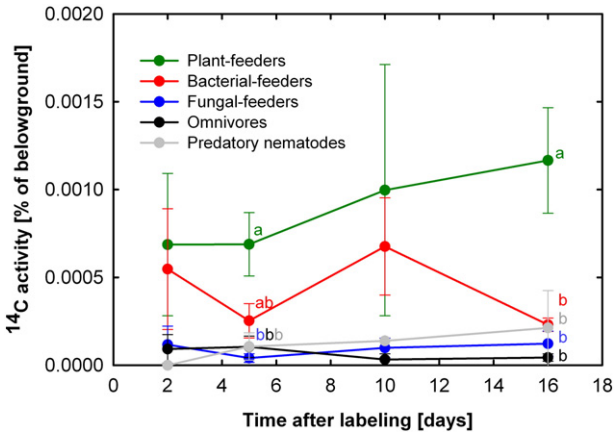

Fig. 2. ^{14}C activities of each trophic group as percentage of total belowground ^{14}C (i.e. sum of root, soil, and soil CO_2 efflux ± SD) at days 2, 5, 10, and 16 after $^{14}CO_2$ pulse labeling. Significant differences ($P < 0.05$) between the trophic groups of nematodes at one sampling date are indicated by different letters. Values with the same or no letters are not significantly different according Tukey's HSD tests at $P < 0.05$.

with time from about 0.7×10^{-3}% of total belowground ^{14}C at day 2 to a maximum of 1.2×10^{-3}% at day 16 after labeling (Fig. 2). The ^{14}C activity for bacterial-feeders ranged from 0.3×10^{-3}% at day 5 to 0.7×10^{-3}%$^{-1}$ at day 10 after labeling, and that of fungal-feeders between 0.04×10^{-3}% at day 5 and 0.1×10^{-3}% at day 16 after labeling. The ^{14}C transferred to higher trophic levels (omnivores and predators) was always below 0.2×10^{-3}%.

The specific ^{14}C activity gives a relative measure of root C allocated to nematodes per gram of biomass C. Two days after labeling, with maximum ^{14}C recovery belowground, root-derived C was uniformly distributed between the herbivore food chain (12.9 kBq g^{-1} C) in plant-feeders and the detritivore food chain with 5.8 and 1.4 kBq g^{-1} C for bacterial- and fungal-feeders, respectively (data not presented). In comparison, omnivores had approximately 10 to 30 times higher specific ^{14}C activity, with 126.4 kBq g^{-1} C, whereas that in predators was negligible and not significantly different from unlabeled controls.

3.3. ^{14}C budget of the plant-soil-nematode system

To place the ^{14}C data of nematodes in a broader perspective, we compared the ^{14}C recovery in trophic groups at day 16 to the respective ^{14}C in plant and soil pools (data from Pausch et al., 2013). The end of the experiment was chosen to consider the flux of root-derived C through the entire nematode micro-food-web. Half of the ^{14}C tracer remained in the shoots, while 28% was detected in roots. About 5% of ^{14}C remained in the soil and 16% had been lost via root-derived respiration after 16 days (Table 2). The microbial biomass and extractable organic C contained 1% and 0.05% ^{14}C, respectively. Among the trophic groups of nematodes, the plant-feeders incorporated the highest amount of ^{14}C, with 0.68×10^{-3}% (according to Eq. (5)). Even though the bacterial- and fungal-feeders had identical population densities at day 16 after labeling (Table 1), the ^{14}C content of bacterial-feeders, at 0.12×10^{-3}% of total recovered ^{14}C was about twice as high as that of fungal-feeding nematodes. The omnivores and predatory nematodes incorporated 0.02×10^{-3} and 0.07×10^{-3}% ^{14}C, respectively.

4. Discussion

4.1. Development of endogenous nematode populations

At the beginning of the experiment, the endogenous nematode community in the undisturbed soil cores (0–30 cm depth) had a population density of 6.6 Ind. g^{-1} DW. This corresponds to a report from the same field site by Scharroba et al. (2012) with 7.7 Ind. g^{-1} DW at 0–10 cm depth under maize during the growing season (July). Such low nematode densities are common in arable soils due to frequent disturbance by management practices. Studies with other crops (barley, wheat, soybean, maize) have reported between 7 and 10 Ind. g^{-1} DW (Sohlenius and Sandor, 1987; Neher et al., 2005; Liang et al., 2009; Hu and Qi, 2010).

The population density of nematodes in an arable field varies with season depending on alterations in soil moisture, agricultural practice and crop root development (Freckman and Ettema, 1993; Yeates and Bongers, 1999). The environmental conditions in the present experiment were kept constant, i.e. the nematode population was predominantly affected by the growing maize root. The associated enhanced resource supply, with both living root tissue as well as rhizodeposits, resulted in a strong increase of the nematode population density from 6.6. to 18.4 Ind. g^{-1} DW. Similar densities were observed in the field under maize crop with litter amendment, where 15.1 Ind. g^{-1} DW were recorded (Scharroba et al., 2012).

The nematode communities in the incubated soil displayed a diversity level and composition comparable to the arable site where the undisturbed cores were taken (Scharroba et al., 2012). However, a noteworthy difference was observed for Tylenchidae, with densities of 1.9–4.8 and 0.9 Ind. g^{-1} DW in pot-incubated and field soil, respectively. These nematodes can either act as root- or fungal-feeders (Yeates et al., 1993a, 1993b; Okada et al., 2005), thereby serving quite different food web functions. Their distinctly higher density in pot compared to field soil, as well as the increase along with plant growth during the experimental period, assigns roots as predominant carbon source. Thus, in the present study Tylenchidae can be considered as plant-feeding opportunists that respond quickly to an increase in root biomass, which is in line with Ferris and Bongers (2006).

In contrast to plant-feeding Tylenchidae, the Rhabditidae were more frequent while their Dauerlarvae were less in the field (1.7 and 2.3 Ind. g^{-1} DW, respectively) than in the laboratory (0.2–1.3 and 2.8–7.7 Ind. g^{-1} DW, respectively). As *r*-strategists, Rhabditidae multiply fast with food enrichment, but enter dauerstage when nutrients diminish (Ferris and Matute, 2003). This suggests a moderate and continuous resource supply for the micro-food web during the experiment.

4.2. Composition of the nematode micro-food web

In arable soils, plant-feeding nematodes are key biota in the primary production-based (herbivory) food chains (Cohn et al., 2002) and are the most abundant trophic group, making up 46 to 69% in soils under maize (Li et al., 2009; Hu and Qi, 2010). In the investigated soil this functional group was dominated by ectoparasites, particularly epidermal cell and root hair feeders (i.e. Tylenchidae), whereas endoparasites (i.e. Heteroderidae, Pratylenchidae) with strong negative effect on plant performance were scarce. This has implications for root C flux into the food web, as predominantly ectoparasites promote the release of C into the soil by causing leakage of labile plant metabolites from epidermal cells, whereas endoparasites mainly act as strong nutrient and carbon sinks (Yeates et al., 1999; Williamson and Gleason, 2003). The release of root C into the soil by leakage was shown to result in enhanced microbial biomass (Yeates et al., 1998; Poll et al., 2007), yet microbial biomass C did not change in the present investigation. As bacterial feeders were the second abundant trophic group within the community, a potential "bloom" of bacteria could have been rapidly exploited by these nematodes.

The second dominant C pathway in soil is the detritivore food chain comprising fungal- and bacterial-feeders as basal groups. The latter were frequent in the investigated soil (average 33%), whereas fungal-feeders were less (average 18%), a pattern generally observed in arable soil (Ruess, 2003; Ruess and Ferris, 2004). Likely maize rhizodeposits, as easily decomposed and fast available C source, promoted the bacterial decomposition channel within the detritivore food chain. Scharroba et al. (2012) report a CI of 22 under fodder maize at the arable field site the undisturbed soil cores were derived from. Compared to that, the observed CI of up to 38 is fairly high (Ferris et al., 2001), in particular as no aboveground maize litter, the major resource for fungal degraders, entered the soil due to coverage of pots by lids. This suggests that root-derived resources supported the fungal carbon pathway to some extent.

Omnivores and predators, with an average proportion of 1% each, represented a minor fraction of the community, suggesting no "long" food chains with substantial biomass at higher trophic levels, pointing

Table 2
^{14}C budget calculated as % of ^{14}C recovered (i.e. sum of shoot, roots, soil, soil CO_2 efflux) 16 days after labeling (±SD). The data of plant and soil pools were taken from Pausch et al. (2013).

Plant and soil pools	^{14}C [% recovery]	Nematode trophic group	^{14}C [% recovery] $\times 10^{-3}$
Shoot	50.9 ± 7.3	Plant-feeders	0.68 ± 0.55
Root	28.0 ± 10.8	Bacterial-feeders	0.12 ± 0.07
Soil	5.3 ± 0.6	Fungal-feeders	0.07 ± 0.1
Soil CO_2 efflux	16.2 ± 3.8	Omnivores	0.02 ± 0.01
MBC	1.0 ± 0.3	Predatory nematodes	0.07 ± 0.1
EOC	0.05 ± 0.02	*Total nematodes*	*0.96 ± 0.57*

to a micro-food-web regarded as bottom-heavy, with only slow growth of predator populations.

4.3. Root carbon allocation to nematode trophic groups and ^{14}C budget

Plant-feeders showed the strongest incorporation of root-derived C among the nematodes, likely because they feed directly on the roots. However, a ^{13}C pulse labeling of maize in the field revealed a higher uptake of plant-derived C by the detritivore food chain (Pausch et al., 2015). This divergence is explained by the up to 5 times higher densities of plant-feeders, namely Tylenchidae, in the undisturbed soil cores compared to field soil, increasing the significance of the root energy channel. Accordingly, at day 16 after labeling, the root biomass in the 30 cm high soil core was 8 times higher than in the field (considering the upper 30 cm; Pausch et al., 2013). This indicates that shifts in C flux through herbivore and detritivore food chains are likely to take place during the growing season, when plant parasites are fostered by the increased root biomass of crops. The ^{14}C incorporation in plant-feeding nematodes nearly doubled over 16 days, yet not statistically significant. Nevertheless, the constant increase with time suggests a continuous flow of root-derived C into the herbivore food chain. As the dominant Tylenchidae are migratory ectoparasites, moving freely in soil between host plants, they may act as an important link between herbivore and detritivore food chain via higher level predators, merging the flux of root C in the soil food web.

Plant C uptake by bacterial- and fungal-feeders was lower over time compared to plant-feeders due to the intervening trophic level, the microorganisms as primary decomposers. The ecological rule of thumb gives about 10% energy allocation per consumer level in the trophic cascade (Smith and Smith, 2006). However, only 1% of root-derived ^{14}C was recovered in microbial biomass at day 16 after labeling, as about 62% was lost by respiration as CO_2 (Pausch et al., 2013). Although not significant, bacterial feeders allocated 2 to 7 times more ^{14}C than fungal feeders, which reflects rhizosphere bacteria as the major functional group allocating and processing plant root C, whereas fungi rely more on recalcitrant and complex plant C such as cellulose or lignin (Strickland and Rousk, 2010). The loss at the next trophic level was even greater, with only 0.2% of the ^{14}C in microbial biomass allocated to the bacterial- and fungal-feeding nematodes. This indicates either a high loss via respiration or a low efficiency of energy transfer between trophic levels, e.g. nematode predators and bacterial/fungal prey in the decomposer food chain. In particular, C loss by respiration could have been enhanced by the experimental incubation temperature between 22 and 28 °C, as many bacterial-feeders show highest metabolic rates (10–20 ng CO_2 μg nematode^{-1} h^{-1}) at temperatures around 25 °C (Ferris et al., 1995). In this case, C transfer to higher trophic levels such as predators and omnivores is limited (Ferris and Bongers, 2006), which is in accordance with the low ^{14}C activity of these trophic groups. Shortly after labeling, omnivores had 10 to 30 times higher specific ^{14}C activity (i.e. C allocation in biomass) than bacterial- and fungal-feeders, whereas that in predators was negligible but increased within 16 days. This suggests that omnivores rely directly on rhizosphere resources, either animal- or microbial-based, whereas predators range the bulk soil for their prey.

At day 16 after labeling, about 0.96×10^{-3}% of total ^{14}C recovered was incorporated into nematodes. This value is in accordance with results from the $^{13}CO_2$ pulse labeling experiment in the field, showing that minimum fluxes of root-derived C through the nematodes micro-food-web ranged between 0.1×10^{-3} and 1.6×10^{-3}% (Pausch et al., 2015). Plant-feeders showed the highest ^{14}C recovery with 0.68×10^{-3}%, however, Yeates et al. (1999) calculated even higher ^{14}C recovery rates ranging from 0.02–0.09%. The latter study mainly investigated endoparasites, predominantly cyst and root-knot nematodes, which modify plant gene expression and alter physiological processes to shift photoassimilate C directly to the nematode parasite (Williamson and Gleason, 2003; Davis et al., 2004). Endoparasites might have been underrepresented in the present study, as Yeates et al. (1999) used Whitehead trays, more efficient than Bearman funnels for those nematodes. However, free ranging larvae of *Heterodera* (cyst nematode) were scarce and *Meloidogyne* (root-knot nematode) not detected in the arable field likely due to maize as common crop (Scharroba unpub.). The dominant plant-feeders in the present study were external epidermal cell and root hair feeding Tylenchidae with low impact on plant carbon transfer, likely resulting in less ^{14}C recovery compared to the findings of Yeates et al. (1999), despite the high ^{14}C activity of roots (28% ^{14}C recovery). This indicates that in arable systems the host plant and its associated nematode plant parasites are of predominant importance for the level of plant C flux into the soil food web.

5. Conclusions

The present study demonstrated that $^{14}CO_2$ pulse labeling of plant shoots and the subsequent ^{14}C tracing in trophic groups of nematodes is a promising approach to disentangle root-derived C fluxes through the soil microfauna and individual food web levels. Dynamics of ^{14}C activity and recovery allow the C share in the herbivore and detritivore food chains to be distinguished, as well as assignment of their linkage at higher trophic levels. Shifts between these two major soil food chains likely occur during a crop cycle, and are modulated by plant root growth. The high ^{14}C activity in plant-feeders underlines the role of nematodes as strong and direct root C sinks and their contribution to C and energy transfers within soil food webs in agricultural ecosystems.

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Appendix A

Table A1
Nematode taxa detected in the pot soil across the whole experimental period. Trophic groups were assigned according to Yeates et al. (1993a, 1993b).

Family	Genus	Trophic group
Alaimidae	*Alaimus*	Bacterial-feeders
	Amphidellus	Bacterial-feeders
Anatonchidae	*Anatonchus*	Predators
Anguinidae	*Ditylenchus*	Fungal-feeders
Aphelenchidae	*Aphelenchus*	Fungal-feeders
	Paraphelenchus	Fungal-feeders
Aphelenchoididae	*Aphelenchoides*	Fungal-feeders
	Seinura	Predators
Aporcelaimidae	*Aporcelaimellus*	Omnivores
	Aporcelaimus	Omnivores
Cephalobidae	*Acrobeloides*	Bacterial-feeders
	Acrobelophis	Bacterial-feeders
	Cephalobus	Bacterial-feeders
	Chiloplacus	Bacterial-feeders
	Eucephalobus	Bacterial-feeders
	Heterocephalobus	Bacterial-feeders
Diploscapteridae	*Diploscapter*	Bacterial-feeders
Dolichodoridae	*Amplimerlinius*	Plant-feeders
	Bitylenchus	Plant-feeders
	Merlinius	Plant-feeders
	Nagelus	Plant-feeders
	Tylenchorhynchus	Plant-feeders
Heteroderidae	*Heterodera*	Plant-feeders
Mononchidae	*Clarkus*	Predators
Panagrolaimidae	*Panagrellus*	Bacterial-feeders
	Panagrolaimus	Bacterial-feeders
Paratylenchidae	*Paratylenchus*	Plant-feeders
Plectidae	*Anaplectus*	Bacterial-feeders

(continued on next page)

Table A1 (*continued*)

Family	Genus	Trophic group
	Plectus	Bacterial-feeders
Pratylenchidae	*Hirschmanniella*	Plant-feeders
	Pratylenchus	Plant-feeders
Prismatolaimidae	*Prismatolaimus*	Bacterial-feeders
Qudsianematidae	*Epidorylaimus*	Omnivores
	Eudorylaimus	Omnivores
	Microdorylaimus	Omnivores
	Thonus	Omnivores
Rhabditidae	*Mesorhabditis*	Bacterial-feeders
	Protorhabditis	Bacterial-feeders
	Rhabditis	Bacterial-feeders
Rhabdolaimidae	*Rhabdolaimus*	Bacterial-feeders
Teratocephalidae	*Teratocephalus*	Bacterial-feeders
Thornenematidae	*Laimydorus*	Omnivores
	Mesodorylaimus	Omnivores
Tylenchidae	*Aglenchus*	Plant-feeders
	Basiria	Plant-feeders
	Boleodorus	Plant-feeders
	Coslenchus	Plant-feeders
	Filenchus	Plant-feeders
	Lelenchus	Plant-feeders
	Malenchus	Plant-feeders
	Neopsilenchus	Plant-feeders
	Tylenchus	Plant-feeders

References

Albers, D., Schaefer, M., Scheu, S., 2006. Incorporation of plant carbon into the soil animal food web of an arable system. Ecology 87, 235–245.

Andrássy, I., 1956. Die Rauminhalts-und Gewichtsbestimmung der Fadenwürmer (Nematoden). Acta Zool. Hung. 2, 1–5.

Andrássy, I., 2007. Free-living nematodes on Hungary II (Nematoda errantia). In: Csuzdi, C., Mahunka, S. (Eds.), Pedozoologica Hungarica 4. Hungarian Natural History Museum, Budapest (496 pp).

Bongers, T., 1990. The maturity index, an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83, 14–19.

Bongers, T., 1994. De Nematoden van Nederland. second ed. Natuurhistorische Bibliotheek 4. Koninklijke Nederlands Natuurhistorische Vereniging, Utrecht (408 pp).

Brzeski, M.W., 1998. Nematodes of Tylenchina in Poland and temperate Europe. Muzeum i Instytut Zoologii Polska Akademia Nauk (PAN) (395 pp).

Cohn, E., Koltai, H., Sharon, E., Spiegel, Y., 2002. Root-nematode interactions: recognition and pathogenicity. In: Waisel, J., Eshel, A., Kalkaf, U. (Eds.), Plant Roots - The Hidden Half I. Dekker, New York, pp. 783–796.

Crawford, K., Mcdonald, R.A., Bearhop, S., 2008. Applications of stable isotope techniques to the ecology of mammals. Mammal Rev. 38, 87–107.

Crotty, F.V., Blackshaw, R.P., Murray, J., 2011. Tracking the flow of bacterially derived ^{13}C and ^{15}N through soil faunal feeding channels. Rapid Commun. Mass Spectrom. 25 (1530–1513).

Crotty, F.V., Stocki, M., Knight, J.D., Adl, S.M., 2013. Improving accuracy and sensitivity of isotope ratio mass spectrometry for $\delta^{13}C$ and $\delta^{15}N$ values in very low mass samples for ecological studies. Soil Biol. Biochem. 65, 75–77.

Darby, B.J., Neher, D.A., 2012. Stable isotope composition of microfauna supports the occurrence of biologically fixed nitrogen from cyanobacteria in desert soil food webs. J. Arid Environ. 85, 76–78.

Davis, E.L., Hussey, R.S., Baum, T.J., 2004. Getting to the roots of parasitism by nematodes. Trends Parasitol. 20, 134–141.

Eissfeller, V., Beyer, F., Valtanen, K., Hertel, D., Maraun, M., Polle, A., Scheu, S., 2013. Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash. Soil Biol. Biochem. 62, 76–81.

Ferris, H., 2010. Contribution of nematodes to the structure and function of the soil food web. J. Nematol. 42, 63–67.

Ferris, H., Bongers, T., 2006. Nematode indicators of organic enrichment. J. Nematol. 38, 3–12.

Ferris, H., Matute, M.M., 2003. Structural and functional succession in the nematode fauna of a soil food web. Appl. Soil Ecol. 23, 93–110.

Ferris, H., Bongers, T., De Goede, R.G.M., 2001. A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl. Soil Ecol. 18, 13–29.

Ferris, H., Lau, S., Venette, R., 1995. Population energetics of bacterial-feeding nematodes: respiration and metabolic rates based on CO_2 production. Soil Biol. Biochem. 27, 319–330.

Freckman, D.W., Ettema, C.H., 1993. Assessing nematode communities in agroecosystems of varying human intervention. Agric. Ecosyst. Environ. 45, 239–261.

Fu, S., Coleman, D.C., Schartz, R., Potter, R., Hendrix, P.F., Crossley Jr., D.R., 2000. ^{14}C distribution in soil organisms and respiration after the decomposition of crop residue in conventional tillage and no-till agroecosystems at Georgia Piedimont. Soil Tillage Res. 57, 31–41.

Fu, S., Kisselle, K.W., Coleman, D.C., Hendrix, P.F., Crossley Jr., D.A., 2001. Short-term impacts of aboveground herbivory (grasshopper) on the abundance and ^{14}C activity of soil nematodes in conventional tillage and no-till agroecosytems. Soil Biol. Biochem. 33, 1253–1258.

Gannes, L.Z., Del Rio, C.M., Koch, P., 1998. Natural abundance variations in stable isotopes and their potential uses in animal physiological ecology. Comp. Biochem. Physiol. A Mol. Integr. Physiol. 119, 725–737.

Gannes, L.Z., O'Brien, D.M., del Rio, C.M., 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. Ecology 78, 1271–1276.

Hu, C., Qi, Y., 2010. Effect of compost and chemical fertilizer on soil nematode community in a Chinese maize field. Eur. J. Soil Biol. 46, 230–236.

Ingham, R.E., Trofymow, J.A., Ingham, E.R., Coleman, D.C., 1985. Interactions of bacteria, fungi, and their nematode grazers: effects on nutrient cycling and plant growth. Ecol. Monogr. 55, 119–140.

Kramer, S., Marhan, S., Ruess, L., Armbruster, W., Butenschoen, O., Haslwimmer, H., Kuzyakov, Y., Pausch, J., Schoene, J., Scheunemann, N., Schmalwasser, A., Totsche, K.U., Walker, F., Scheu, S., Kandeler, E., 2012. Carbon flow into microbial and fungal biomass as a basis to understand the belowground food web in an agroecosystem. Pedobiologia 55, 111–119.

Li, Q., Jiang, Y., Liang, W.J., Wang, H., Jiang, S.W., 2009. Nematode diversity in phaeozem agroecosystems of Northeast China. Pedosphere 19, 597–605.

Liang, W., Lou, Y., Li, Q., Zhong, S., Zhang, X., Wang, J., 2009. Nematode faunal response to long-term application of nitrogen fertilizer and organic manure in Northeast China. Soil Biol. Biochem. 41, 883–890.

Martínez del Rio, C., Wolf, N., Carleton, S.A., Gannes, L.Z., 2009. Isotopic ecology ten years after a call for more laboratory experiments. Biol. Rev. 84, 91–111.

Neher, D.A., 2010. Ecology of plant and free-living nematodes in natural and agricultural soil. Annu. Rev. Phytopathol. 48, 371–394.

Neher, D.A., Wu, J., Barbercheck, M.E., Anas, O., 2005. Ecosystem type affects interpretation of soil nematode community measures. Appl. Soil Ecol. 30, 47–64.

Neilson, R., Brown, D.J.F., 1999. Feeding on different host plants alters the natural abundances of $\delta^{13}C$ and $\delta^{15}N$ in Longidoridae (Nemata). J. Nematol. 31, 20–26.

Okada, H., Harada, H., Kadota, I., 2005. Fungal-feeding habits of six nematode isolates in the genus *Filenchus*. Soil Biol. Biochem. 37, 1113–1120.

Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen, O., Kandeler, E., Marhan, S., Riederer, M., Scheu, S., Kuzyakv, Y., Ruess, L., 2015. Small but active – pool size does not matter for carbon incorporation in below-ground food webs. Funct. Ecol. http://dx.doi.org/10.1111/1365-2435.12512.

Pausch, J., Tian, J., Riederer, M., Kuzyakov, Y., 2013. Estimation of rhizodeposition at field scale: upscaling of a ^{14}C labeling study. Plant Soil 364, 273–285.

Poll, J., Marhan, S., Haase, S., Hallmann, J., Kandeler, E., Ruess, L., 2007. Low amounts of herbivory by root-knot nematodes affect microbial community dynamics and carbon allocation in the rhizosphere. FEMS Microbiol. Ecol. 62, 268–279.

Pollierer, M.M., Dyckmans, J., Scheu, S., Haubert, D., 2012. Carbon flux through fungi and bacteria into the forest soil animal food web as indicated by compound-specific ^{13}C fatty acid analysis. Funct. Ecol. 26, 978–990.

Pollierer, M., Langel, R., Körner, C., Maraun, M., Scheu, S., 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecol. Lett. 10, 729–736.

Ponsard, S., Arditi, R., 2000. What can stable isotopes ($\delta^{15}N$ and $\delta^{13}C$) tell about the food web of soil macro-invertebrates? Ecology 81, 852–864.

Post, D.M., 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83, 703–718.

Ruess, L., 1995. Nematode fauna in spruce forest soils: a qualitative/quantitative comparison. Nematologica 41, 106–124.

Ruess, L., 2003. Nematode soil faunal analysis of decomposition pathways in different ecosystems. Nematology 5, 179–181.

Ruess, L., Ferris, H., 2004. Decomposition pathways and successional changes. Nematol. Monogr. Perspect. 2, 547–556.

Ruess, L., Garzía Zapata, E.J., Dighton, J., 2000. Food preferences of the fungal feeding nematode *Aphelenchoides* sp. Nematology 2, 223–230.

Scharroba, A., Dibbern, D., Hünninghaus, M., Kramer, S., Moll, J., Butenschoen, O., Bonkowski, M., Buscot, F., Kandeler, E., Koller, R., Krüger, D., Lueders, T., Scheu, S., Ruess, L., 2012. Effects of resource availability and quality on the structure of the micro-food web of an arable soil across depth. Soil Biol. Biochem. **50**, 1–11.

Scheu, S., Falca, M., 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro-and a mesofauna-dominated community. Oecologia 123, 285–296.

Schmidt, I.K., Ruess, L., Baath, E., Michelsen, A., Ekelund, F., Jonasson, S., 2000. Long-term manipulation of the microbes and microfauna of two subarctic heaths by addition of fungicide, bactericide, carbon and fertilizer. Soil Biol. Biochem. 32, 707–720.

Smith, T., Smith, R., 2006. Elements of Ecology. Pearson, San Francisco, p. 447.

Sohlenius, B., Sandor, A., 1987. Vertical distribution of nematodes in arable soil under grass (*Festuca pratensis*) and barley (*Hordeum distichum*). Biol. Fertil. Soils 3, 19–25.

Strickland, M.S., Rousk, J., 2010. Considering fungal: bacterial dominance in soils- methods, controls, and ecosystem implications. Soil Biol. Biochem. 9, 1385–1395.

Tiunov, A.V., 2007. Stable isotopes of carbon and nitrogen in soil ecological studies. Biol. Bull. 34, 395–407.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707.

Williamson, V.M., Gleason, C.A., 2003. Plant-nematode interaction. Curr. Opin. Plant Biol. 6, 327–333.

Yeates, G.W., 2010. Nematodes in ecological webs. Enclycl. Life Sci. 1–11.

Yeates, G.W., Bongers, T., 1999. Nematode diversity in agroecosystems. *Agric. Ecosyst. Environ.* 74, 113–135.

Yeates, G.W., Bongers, T., De Goede, R.G.M., Freckman, D.W., Georgieva, S.S., 1993a. Feeding habits in soil nematode families and genera - an outline for soil ecologists. J. Nematol. 25, 315.

Yeates, G.W., Saggar, S., Denton, C.S., Mercer, C.F., 1998. Impact of clover cyst nematode (*Heterodera trifolii*) infection on soil microbial activity in the rhizosphere of white clover (*Trifolium repens*) - a pulse-labelling experiment. Nematologica 44, 81–90.

Yeates, G.W., Saggar, S., Hedley, C.B., Mercer, C.F., 1999. Increase in ^{14}C-carbon translocation to the soil microbial biomass when five species of plant-parasitic nematodes infect roots of white clover. Nematology 1, 295–300.

Yeates, G.W., Wardle, D.A., Watson, R.N., 1993b. Relationships between nematodes, soil microbial biomass and weed-management strategies in maize and asparagus cropping systems. Soil Biol. Biochem. 25, 869–876.