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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.

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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 below-ground 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 belowground 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

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