Food Webs 9 (2016) 39–45

Contents lists available at ScienceDirect

Food Webs

journal homepage: www.journals.elsevier.com/food-webs

Incorporation of root C and fertilizer N into the food web of an arable field: Variations with functional group and energy channel

Nicole Scheunemann [a,*], Johanna Pausch [b], Christoph Digel [c], Susanne Kramer [d], Anika Scharroba [e], Yakov Kuzyakov [b], Ellen Kandeler [d], Liliane Ruess [e], Olaf Butenschoen [a], Stefan Scheu [a]

[a] J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Germany
[b] Department of Soil Science of Temperate Ecosystems, Georg August University Göttingen, Germany
[c] German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany
[d] Institute of Soil Science and Land Evaluation, University of Hohenheim, Germany
[e] Institute of Ecology, Humboldt University Berlin, Germany

ARTICLE INFO

Article history:
Received 2 June 2015
Received in revised form 9 January 2016
Accepted 8 February 2016
Available online 16 March 2016

Keywords:
Macrofauna
Mesofauna
Nematodes
Pulse labeling
Stable isotopes
Saprotrophic fungi
Trophic level

ABSTRACT

Agroecosystems occupy large areas of the land surface and arable soil food webs are of significant importance for global cycling of carbon (C) and nitrogen (N). In a field experiment we labeled maize plants (*Zea mays* L.) in $^{13}CO_2$ atmosphere and by $K^{15}NO_3$ fertilization. During 25 days, the incorporation of ^{13}C and ^{15}N was traced in plant compartments, soil and soil arthropods, as well as ^{13}C in microbial phospholipid fatty acids (PLFAs) and nematodes. Highlighting the importance of root-derived resources in agroecosystems, ^{13}C was incorporated into all food web compartments, including microorganisms (PLFAs), nematodes and arthropods. The amount of incorporated ^{13}C (as compared to unlabeled samples) markedly decreased along the food chain with $\Delta^{13}C$ decreasing from 500‰ in plant roots and 900‰ in microbial PLFAs, to less than 40‰ in nematodes and arthropods. Incorporation of ^{13}C into fungal PLFAs considerably exceeded that into bacterial PLFAs, highlighting the importance of soil fungi as compared to bacteria in C cycling. Fertilizer-derived ^{15}N uniformly increased with time in plant compartments and soil arthropods, indicating that N is distributed homogeneously in the soil food web. High channeling of both root-derived ^{13}C and fertilizer-derived ^{15}N to higher trophic levels by fungi, and intensive feeding on fungi by soil animals highlight the central role of saprotrophic fungi in C and nutrient fluxes in soil food webs of arable ecosystems.

1. Introduction

At a global scale, soil contains nearly twice as much carbon (C) as both the atmosphere and vegetation combined, comprising an approximate amount of 2500 Gt (Lal, 2004a). The fluxes of C between the soil and atmosphere play a crucial role in regulating the concentration of carbon dioxide in the atmosphere and in turn the Earth's climate (Lal, 2004b; Raich and Schlesinger, 1992). Ample information is available on the total amount of soil C, the different fractions and their residence time (Gaudinski et al., 2000), whereas surprisingly little is known on how the accessibility and complexity of organic C interact with the soil food web and determine the fate of C in soil. Plant-derived organic C enters the soil food web either belowground via roots and rhizodeposits or aboveground via leaf litter, which differ markedly in their quantity, quality and spatio-temporal accessibility (De Deyn et al., 2008; Kramer et al., 2013; Moll et al., 2015). Rhizodeposits, including sloughed root cells as well as mucilage and root exudates, contain labile C compounds which are easily available to decomposers (Balasooriya et al., 2014; Leake et al., 2006). Leaf litter, in contrast, is rich in structural compounds resisting decomposition (Bahri et al., 2006). The importance of root- and litter-derived resources for the decomposer community has been intensively debated and plant litter has long been considered to be the primary resource of soil food webs (Moore et al., 2004; Schneider et al., 2012). However, evidence is mounting that root-derived resources may be of similar or even higher importance for most soil organisms including microorganisms (Drigo et al., 2010) and meso- and macrofauna (Eissfeller et al., 2013; Pollierer et al., 2007; Ruf et al., 2006). This is especially the case in agroecosystems, where aboveground plant residues are removed at harvest and roots and root exudates remain as the major pathway of plant C to soil biota. Despite the importance of the root channel, little is known on the translocation and flux of root C within arable soil food webs.

Nitrogen (N) is the most important plant nutrient limiting primary production in agroecosystems. To meet nitrogen demands of crop plants inorganic fertilizer is applied to agroecosystems to increase productivity (Robertson and Vitousek, 2009). However, fertilizer not only increases plant productivity but also impacts the soil food web by

* Corresponding author at: J.F. Blumenbach Institute of Zoology and Anthropology, Georg August University Göttingen, Berliner Str. 28, 37073 Göttingen, Germany.
E-mail address: nscheun@gwdg.de (N. Scheunemann).

http://dx.doi.org/10.1016/j.fooweb.2016.02.006
2352-2496/

decreasing C fluxes within the soil food web, and thereby feeding back on energy fluxes within the whole ecosystem (Lemanski and Scheu, 2014a). Surprisingly, detailed knowledge on the fate and pathways of inorganic fertilizer N in arable soil food webs is lacking, but may help to increase fertilizer efficiency and to reduce the amounts applied to arable fields on a global scale.

Pulse labeling of plants with $^{13}CO_2$ allows tracking the flux of root-derived C into soil animal food webs (Drigo et al., 2010; Ruf et al., 2006). Previous pulse labeling studies have improved the understanding of spatio-temporal incorporation of root C into soil microorganisms (Leake et al., 2006), soil organic matter pools (Loya et al., 2002) and soil arthropods (Gilbert et al., 2014; Högberg et al., 2010). However, most previous studies on the flux of C from roots into soil arthropods were conducted in simplified laboratory systems neglecting biotic interactions and the complexity of decomposer food webs (Crotty et al., 2011; Högberg et al., 2010). Incorporation of root C likely differs within and between taxonomic groups as even closely related species differ in their feeding strategy and trophic level (Berg et al., 2004; Klarner et al., 2013; Schneider et al., 2004), resulting in the need to group species according to functional relationships such as feeding guilds rather than taxonomic affiliation. Although natural abundances of C and N stable isotopes allow separation of food web compartments according to their feeding strategy, the incorporation and fluxes of C through the soil food web can only be traced using isotope labeling.

Most previous studies investigating the flux of root-derived C into soil food webs were conducted in forest ecosystems (Bradford et al., 2012; Eissfeller et al., 2013; Pollierer et al., 2012), whereas little is known on the role of root-derived C for soil animal food webs and possible consequences for C sequestration in arable soils. This is surprising given that 40% of the global ice free land surface is currently used for agriculture (Foley et al., 2005) and the substantial increase of land area used for food production due to the rapidly growing human population (Tilman et al., 2011). Understanding the flux of C into food webs of arable soils and its consequences for C mineralization and sequestration therefore is essential for predicting the fate of C in the terrestrial realm.

We conducted a short-term pulse labeling experiment to follow the fluxes of C and N into the soil animal food web via belowground inputs. We pulse labeled maize plants (*Zea mays* L.) by adding $^{13}CO_2$ to the atmosphere and $K^{15}NO_3$ to the soil, and measured the incorporation of ^{13}C and ^{15}N into plant tissue, soil and the soil food web over a period of 25 days. We focused on C and N fluxes through soil arthropods, but in addition measured the incorporation of ^{13}C into soil microorganisms (bacteria and fungi) and nematodes as both channel plant-derived C and fertilizer-derived N to higher trophic levels. Despite their different origin we expected ^{13}C and ^{15}N to follow similar incorporation patterns into the soil food web due to soil microorganisms incorporating both and thereby forming a central node for the propagation of these elements into higher trophic levels. In more detail we hypothesized that (1) root-derived C and fertilizer-deriver N are incorporated into all dominant groups of the soil animal food web including meso- and macrofauna of low and high trophic level, (2) lower trophic levels incorporate ^{13}C and ^{15}N earlier than higher trophic levels due to the delay in channeling C and N, and (3) the incorporation of ^{13}C and ^{15}N decreases with increasing trophic level as the diet of predators include prey species not associated with the rhizosphere and rhizosphere microorganisms.

2. Materials and methods

2.1. Experimental design

The experimental arable field site is characterized as a loamy haplic Luvisol located in the vicinity of Göttingen (Lower Saxony, Germany) on a plain of the river Leine 160 m a.s.l. (51°33′37″N, 9°53′46″E). Göttingen is located in the temperate climate zone of central Europe with a mean annual precipitation of 645 mm and mean annual temperature of 8.7 °C. As part of a long-term experiment the crop was switched from C3 crops to maize (C4) in 2009 with maize roots remaining in the soil after harvest and maize residues being returned to the field after removal of cobs. The subsection of the arable field we used for the present labeling experiment covered an area of 24 × 24 m, on which four labeling chambers were installed in July 2010. The chambers were installed at randomly selected positions, each containing nine maize plants. Control samples were taken at the day of labeling at a distance of 1.5 m from the chambers. Labeling chambers consisted of a stainless steel frame base of 1 × 1 m size that was inserted into the soil to a depth of 10 cm as base of the chamber, and an aluminum frame (height 2 m) that was covered with translucent LDPE foil. Before closing the chambers, ^{15}N was added to the plots by watering the soil with a solution containing 0.7 g $K^{15}NO_3$ m^{-2} (99% ^{15}N) dissolved in 600 ml H_2O. The annual amount of N added to the field by fertilization was 11.2 g N m^{-2} (Kramer et al., 2012), the added ^{15}N therefore was assumed to only little affect the labile N pool in soil, but allowed investigating the incorporation of mineral N added as fertilizer into the soil food web. After ^{15}N labeling the soil inside the chambers was covered with plastic foil to ensure that ^{13}C only enters the soil via plant roots. ^{13}C labeling of the plants was achieved after closing the chambers airtight by addition of H_2SO_4 to a tracer solution of 16 g $Na_2^{13}CO_3$ (99% ^{13}C) in 100 ml H_2O and 4 ml of 1 M NaOH using a syringe. The emerging $^{13}CO_2$ was circulated in the chambers by a fan for 4 h. After the labeling, the foils and aluminum frames were removed from the field, while the steel frame bases remained in the soil to prevent animals from escaping from the labeled area. Further details on the experimental site and labeling method are given in Kramer et al. (2012) and Riederer et al. (2015), respectively.

2.2. Sampling

Soil samples were taken at days 2, 5, 10 and 25 (referred to later as d2, d5, d10 and d25) after labeling to analyze dynamics of the incorporation of ^{13}C and ^{15}N into soil microorganisms (^{13}C only), nematodes (^{13}C only), soil arthropods, plant shoots, roots, and bulk soil. Samples taken at adjacent plots at the day of the labeling served as control for analyzing ^{13}C and ^{15}N natural abundance. In each labeled plot, two soil samples to a depth of 10 cm were taken at each sampling date using a stainless steel soil corer (diameter 20 cm) for the extraction of soil arthropods, and a soil corer of 2.5 cm diameter for the extraction of nematodes. Soil arthropods were extracted by heat (Kempson et al., 1963), stored in saturated NaCl solution at −10 °C and identified to the highest taxonomic resolution possible under a dissecting and a light microscope using Schaefer (2010) for identification of macrofauna, and Hopkin (2007), Weigmann (2006) and Karg (1993) for identification of Collembola, Oribatida and Gamasida, respectively. Nematodes were extracted using a modified Baermann method (Ruess, 1995), fixed in cold 4% formaldehyde solution and separated into trophic groups (plant feeders, bacterial feeders, fungal feeders, omnivores and predators) according to Yeates et al. (1993). In addition, at each sampling date, samples of maize shoots, roots and bulk soil from the uppermost 10 cm were taken, dried at 60 °C for 72 h, milled to powder using a ball mill (MM 400; Retsch GmbH, Haan, Germany), and analyzed for ^{13}C and ^{15}N. Wheat shoots were sampled from an adjacent experimental field site and analyzed for ^{13}C and ^{15}N.

2.3. PLFA analysis

Incorporation of ^{13}C into soil microbial groups was analyzed in phospholipid fatty acids (PLFAs) of bulk and rhizosphere soil samples. For collection of rhizosphere soil we cut one maize plant per sampling and excavated the roots; soil attached to maize roots was taken as rhizosphere soil and collected by carefully shaking the excavated roots. Bulk soil was collected between the maize rows to a depth of 10 cm using a Riverside auger (diameter 5 cm, Eijkelkamp, Giesbeek, The Netherlands).

PLFAs from rhizosphere and bulk soil were extracted from 6 g fresh weight soil according to Frostegard et al. (1991), transformed to fatty acid methyl esters and measured by gas chromatography as described by Kramer et al. (2013). Incorporation of ^{13}C into PLFAs was analyzed after fractionation of fatty acid methyl esters with Ag^+ cartridges (6 ml, Supelco, Palo Alto, USA; Kramer et al., 2008), using a gas chromatograph (6890 series, Agilent Technologies, USA) equipped with a capillary column VS-23MS (Varian Medical Systems, Palo Alto, USA; 30 m × 250 μm, film thickness of 0.25 μm), coupled via a gas chromatography–combustion III interface (Thermo Finnigan, Waltham, USA) to a Delta Plus XP mass spectrometer (Thermo Finnigan MAT, Bremen, Germany). Fatty acids i15:0, a15:0, i16:0 and i17:0 were used as indicators for Gram positive ($Gram^+$) bacteria and cy17:0 for Gram negative ($Gram^-$) bacteria. The fatty acid marker 18:2ω6,9 was used as an indicator for soil fungi (Ruess and Chamberlain, 2010).

2.4. Stable isotope analysis and soil animal food web

Soil arthropods with a collective body weight of at least 0.05 mg dry weight, plant material and soil were analyzed for $^{13}C/^{12}C$ and $^{15}N/^{14}N$ with a coupled system of an elemental analyzer (NA 1500, Fisons-Instruments, Rodano, Milan, Italy) and an isotope ratio mass spectrometer (Delta V Plus, Thermo Fisher Scientific, Bremen, Germany; Reineking et al., 1993). Except of *Necrophloeophagus longicornis*, *Scopaeus* sp., Paederinae, Aleocharinae and Elateridae larvae, individuals of different labeling chambers had to be pooled to obtain a sufficient amount of body tissue for stable isotope analysis. For some species the limited material available only allowed single measurements. In addition, some arthropod species were not found at each sampling date in sufficient numbers to allow stable isotope analysis. Nematodes were analyzed for $^{13}C/^{12}C$ using an Eurovector elemental analyzer (Eurovector EA3000, Eurovector S.p.A., Milano, Italy) coupled to a Delta V Plus isotope ratio mass spectrometer (Thermo Fisher Scientific, Bremen, Germany; Langel and Dyckmans, 2014). The elemental analyzer was fitted with smaller oxidation and reduction reactor tubes (ID 7.8 mm, length 450 mm) to allow lower carrier gas flow and increase sensitivity.

For ^{13}C V-PDB and for ^{15}N atmospheric nitrogen was used as standard. Acetanilide (C_8H_9NO, Merck, Darmstadt, Germany) was used for internal calibration. Isotope natural abundance was expressed using the delta notation with $\delta^{13}C$ or $\delta^{15}N$ (‰) = $[(R_{sample} - R_{standard}) / R_{standard}] \times 1000$ with R_{sample} and $R_{standard}$ referring to the $^{13}C/^{12}C$ or $^{15}N/^{14}N$ ratio in samples and standard, respectively.

Natural abundance of ^{15}N was used to separate arthropod species into trophic levels. ^{15}N signatures of wheat and maize litter were used for baseline construction and individual species were ascribed to the position along the baseline assuming no shift in ^{13}C signatures between resources and consumers (Fig. S1). Soil arthropod species with a ^{15}N signature >1.7‰ above the base line were designated as species of high, others as species of low trophic level. The 1.7‰ threshold was chosen as it has been shown that decomposer invertebrates typically are less enriched than the common trophic level enrichment of 3.4‰ (Vanderklift and Ponsard, 2003). This approach bears the risk of oversimplification, but was used as objective way to group species affiliated to different trophic levels. We assume that low trophic level species mainly comprise primary decomposers feeding on leaf litter and root resources, while species grouped as high level species comprise a mixture of fungi feeding secondary decomposers, predators as well as omnivores (Scheu and Falca, 2000; Vanderklift and Ponsard, 2003). Body size was used to separate species into meso- and macrofauna with species <2 mm body length being assigned to mesofauna and those >2 mm to macrofauna, resulting in four trophic groups: low trophic level meso- and macrofauna as well as high trophic level meso- and macrofauna.

2.5. Calculations and statistical analyses

Incorporation of ^{13}C and ^{15}N ($\Delta^{13}C$ and $\Delta^{15}N$) into soil arthropods, nematodes (only ^{13}C), microbial PLFAs (only ^{13}C), maize shoots, maize roots and bulk soil was calculated as shift in the isotopic signature as

$$\Delta^{13}C \text{ or } \Delta^{15}N[‰] = R_{\text{labeled sample}} - R_{\text{unlabeled sample}},$$

with R the $\delta^{13}C$ or $\delta^{15}N$ signature of the respective taxa, microbial PLFAs, plant tissues or soil, given in ‰ ± standard error of the mean (SEM). Prior to statistical analyses $\Delta^{13}C$ and $\Delta^{15}N$ values were $\log_{10}$-transformed to improve homogeneity of variances; means presented in text, figures and tables represent back-transformed data.

Incorporation of ^{13}C and ^{15}N into shoots and roots of maize plants and into bulk soil with time was analyzed by linear regression with sampling date (d2, d5, d10, d25). Changes in the incorporation of ^{13}C into soil microorganisms with time were analyzed using double repeated analysis of variance (ANOVA) with microbial group (fungi, $Gram^+$ bacteria, $Gram^-$ bacteria) and sampling date as repeated factors and soil (bulk, rhizosphere) as independent factor. Differences in ^{13}C and ^{15}N incorporation between labeling chambers were accounted for by using chamber number as block (1, 2, 3, 4).

Incorporation of ^{13}C and ^{15}N into nematodes (only ^{13}C) and meso- and macrofauna was analyzed by linear mixed effects models fit by maximum likelihood, with chamber number (block) and species identity as random effect for nematodes and soil arthropods, respectively. Three linear mixed effects models were calculated with $\Delta^{13}C$ as dependent continuous variable and (1) nematodes (plant feeders, bacterial feeders, fungal feeders, omnivores and predators) or meso−/macrofauna (low and high trophic level, respectively) as additional random factor to account for effects of sampling date, (2) sampling date as additional random factor to account for effects of nematodes and meso−/macrofauna, and (3) sampling date and nematodes or meso−/macrofauna as independent factor to inspect for interactions of sampling date and nematodes or sampling date and meso-/macrofauna, i.e. for differences in incorporation of ^{13}C with time. Differences between means were inspected using Tukey's HSD test at $p < 0.05$.

Statistical calculations were performed using R Version 3.1.1 (R Core Team, 2013) and the packages Multcomp (Hothorn et al., 2008), NLME (Pinheiro et al., 2013) and Effects (Fox, 2003).

3. Results

3.1. Incorporation of ^{13}C and ^{15}N into plant tissue and soil

Enrichment of ^{13}C in maize shoots significantly decreased with time from 352.4 ± 66.2‰ at d2 to 207.4 ± 58.9‰ at d25 ($F_{1,14} = 6.78$, $p = 0.021$, $r^2 = 0.326$), and from 522.6 ± 64.5‰ at d2 to 104.4 ± 20.4‰ at d25 in maize roots ($F_{1,14} = 46.27$, $p < 0.0001$, $r^2 = 0.768$; Fig. 1a). ^{13}C enrichment of bulk soil did not significantly change with time ($F_{1,14} = 0.36$, $p = 0.558$) and averaged 2.1 ± 0.4‰ across sampling dates (Fig. S2).

In contrast to ^{13}C, ^{15}N enrichment increased with time in maize shoots ($F_{1,14} = 5.56$, $p = 0.033$, $r^2 = 0.284$) and roots ($F_{1,14} = 6.06$, $p = 0.027$, $r^2 = 0.302$), with an increase from 182.0 ± 41.5‰ at d2 to 694.9 ± 126.8‰ at d25 in shoots and from 316.1 ± 110.9‰ at d2 to 727.8 ± 66.0‰ at d25 in roots (Fig. 1b). In bulk soil, ^{15}N enrichment did not change significantly with time ($F_{1,14} = 0.01$, $p = 0.957$) and averaged 31.8 ± 7.4‰ across sampling dates (Fig. S2).

3.2. Incorporation of ^{13}C into soil microorganisms

Across all sampling dates, incorporation of ^{13}C into microbial PLFAs was strongly affected by soil ($F_{1,6} = 20.56$, $p = 0.004$) and averaged 170.5 ± 53.8‰ in the rhizosphere and 35.5 ± 19.0‰ in bulk soil. This was consistent in all microbial groups (microbial group × soil effect:

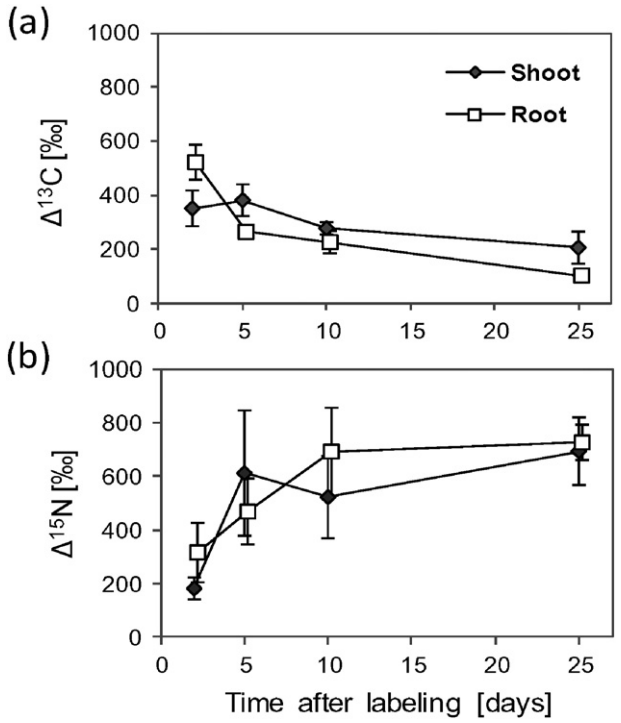

Fig. 1. Changes in the incorporation of (a) ^{13}C and (b) ^{15}N into shoots (black diamonds) and roots (white squares) of maize plants labeled with $^{13}CO_2$ and $K^{15}NO_3$ during 25 days after labeling (means ± SEM, n = 4).

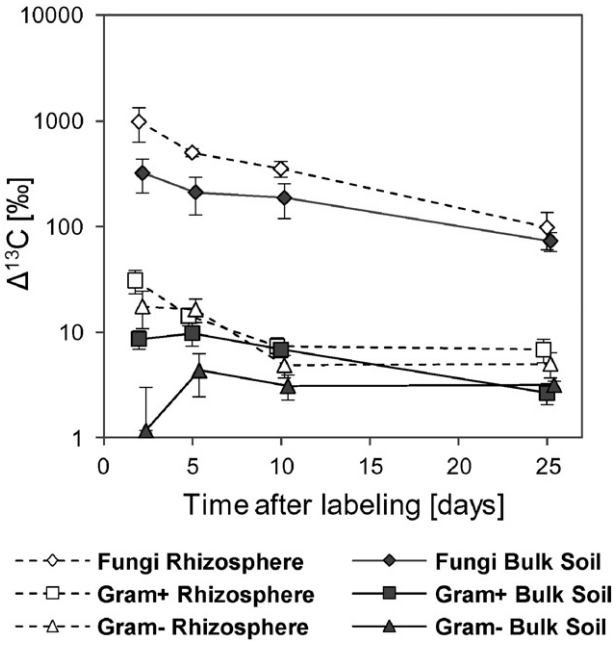

Fig. 2. Changes in the incorporation of ^{13}C into microbial PLFAs of the rhizosphere (white symbols) and bulk soil (black symbols) during 25 days after labeling (means ± SEM, n = 4).

$F_{2,12} = 0.29$, $p = 0.752$). Incorporation varied significantly between microbial groups ($F_{2,12} = 823.74$, $p < 0.0001$), with fungi incorporating higher amounts of ^{13}C than $Gram^+$ and $Gram^-$ bacteria, averaging 341.2 ± 65.7‰, 11.3 ± 1.9‰ and 8.1 ± 1.4‰ across sampling dates, respectively. ^{13}C enrichment significantly decreased with time ($F_{3,18} = 4.31$, $p = 0.018$) and this did not differ significantly in rhizosphere and bulk soil ($F_{3,18} = 1.49$, $p = 0.250$). Changes in the ^{13}C incorporation with time varied between microbial groups, and strongly decreased in fungi, while remained more constant in $Gram^+$ and $Gram^-$ bacteria (microbial group × sampling date interaction; $F_{6,36} = 7.50$, $p > 0.0001$) in both rhizosphere and bulk soil ($F_{6,36} = 1.60$, $p = 0.215$; Fig. 2).

3.3. Incorporation of ^{13}C into nematode trophic groups

When averaged across sampling dates, incorporation of ^{13}C differed between nematode trophic groups ($F_{4,54} = 3.43$, $p = 0.014$), with higher incorporation into fungal feeders, plant feeders and omnivores (9.4 ± 1.9‰, 9.0 ± 1.7‰ and 9.0 ± 3.3‰, respectively) than into bacterial feeders and predators (3.8 ± 0.9‰ and 5.6 ± 2.0‰, respectively).

Over all nematode trophic groups, mean incorporation increased with time ($F_{3,51} = 3.20$, $p = 0.031$; Fig. 3), most evident in fungal feeders and omnivores, with highest incorporation of 16.8 ± 5.8‰ and 21.8 ± 9.8‰ at day 25, respectively. In bacterial feeders and predators incorporation of ^{13}C was constant at all sampling dates with only slightly higher enrichment at day 25 than at the other sampling dates, reaching 5.3 ± 3.7‰ and 8.7 ± 6.1‰, respectively. In contrast, the flux of plant C was fast into plant feeders, with highest incorporation of 13.0 ± 4.6‰ at day 10, but decreasing incorporation afterwards. Nevertheless, incorporation dynamics did not differ significantly between nematode trophic groups (nematodes × sampling date interaction; $F_{12,51} = 1.03$, $p = 0.440$).

3.4. Incorporation of ^{13}C and ^{15}N into soil arthropods

Based on unlabeled stable isotope signatures from the control samples, we constructed the food web of the present arable field (Fig. S1), and separated soil arthropod taxa into trophic groups (see Section 2.4), with low trophic level macrofauna species including six taxa with average natural abundance $\delta^{15}N$ of 3.3 ± 0.6‰, high trophic level macrofauna species including six taxa with average $\delta^{15}N$ of 9.1 ± 1.4‰, low trophic level mesofauna species including three taxa with $\delta^{15}N$ of 6.0 ± 1.0‰, and high trophic level mesofauna species including ten taxa with average $\delta^{15}N$ of 10.1 ± 1.2‰.

Each of the species studied incorporated root-derived ^{13}C and fertilizer-derived ^{15}N, but the enrichment differed between taxa,

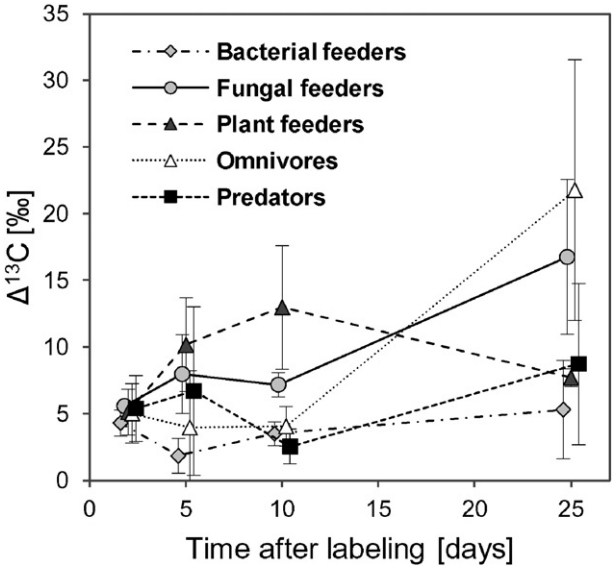

Fig. 3. Changes in the incorporation of ^{13}C into nematodes during 25 days after labeling (means ± SEM, n = 4).

sampling date and element (Tables S3 and S4). The incorporation of ^{13}C into meso- and macrofauna averaged 12.3 ± 1.4‰ across sampling dates and increased during the experiment ($F_{3,143} = 3.66$, $p = 0.014$), with the enrichment being significantly higher at d25 than at d2, d5 and d10. Generally, ^{13}C incorporation did not differ between trophic groups ($F_{3,72} = 0.66$, $p = 0.587$), but increased with time in high trophic level taxa, whereas it remained more constant in low trophic level taxa (sampling date × meso-/macrofauna interaction; $F_{9,134} = 3.19$, $p = 0.006$; Fig. 4).

In general, ^{15}N incorporation increased during the experiment across trophic groups and averaged 36.9 ± 6.7‰ at day 2 and 158.6 ± 51.1‰ at day 25 ($F_{3,143} = 11.42$, $p < 0.0001$). The increase was similar in each of the trophic groups (sampling date × meso-/macrofauna interaction; $F_{9,134} = 1.33$, $p = 0.229$), while average incorporation was higher in low trophic level mesofauna than low trophic level macrofauna, with high trophic level macrofauna and mesofauna displaying intermediate ^{15}N enrichment ($F_{3,72} = 4.52$, $p = 0.006$; Fig. 5).

4. Discussion

4.1. Incorporation of ^{13}C and ^{15}N into the soil food web

Root-derived C rapidly propagated through the soil food web from basal trophic levels including bacteria and fungi to higher trophic levels including nematodes and arthropods, confirming our first hypothesis. Since previous studies performed in microcosms (Ruf et al., 2006) and forest ecosystems (Pollierer et al., 2007) yielded similar results, we conclude that root-derived C is an important resource for the soil food web across ecosystems (Balasooriya et al., 2014; Strickland et al., 2012).

Notably, incorporation of root-derived C into fungi strongly exceeded that into bacteria, particularly at day 2 after labeling, followed by a rapid loss of ^{13}C until day 25. This is in contrast to the general assumption of a slower fungal metabolism and therefore higher C storage in soil fungi than bacteria (Six et al., 2006; Strickland and Rousk, 2010), but reflects the high activity of soil fungi as compared to bacteria in the present arable field (Pausch et al., 2015). The low fungi-to-bacteria ratio at the study site (Scharroba et al., 2012) and other arable fields (Esperschütz et al., 2007; Ngosong et al., 2010), and therefore higher C pool size of bacteria may have resulted in dilution of the label in bacteria. However, Pausch et al. (2015) showed the net incorporation of ^{13}C into fungi to exceed that into bacteria, despite the smaller C pool size of the former. Further, decreasing ^{13}C signatures in fungal PLFAs suggests that recently assimilated plant C quickly passes through the saprotrophic fungal community and leaves the soil system via respiration (Pausch et al., 2015), pointing to a low microbial growth efficiency of saprotrophic fungi in arable fields.

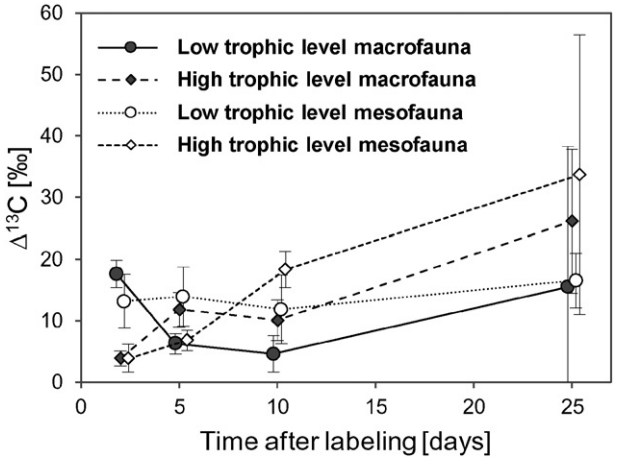

Fig. 4. Changes in the incorporation of ^{13}C into meso- and macrofauna of low and high trophic level during 25 days after labeling (means ± SEM, number of replicates varied between n = 3 for low trophic level macrofauna at day 25 to n = 18 for high trophic level macrofauna at day 5).

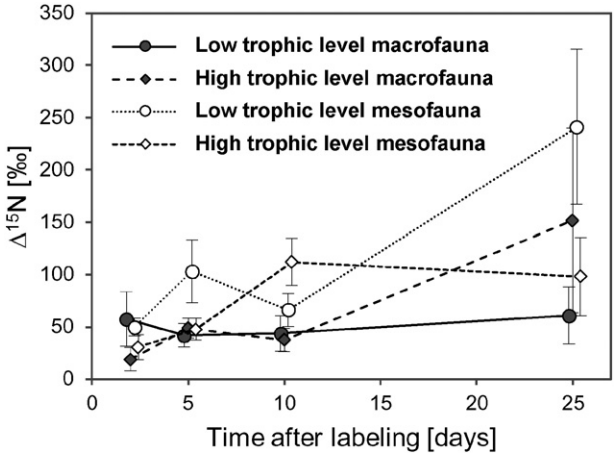

Fig. 5. Changes in the incorporation of ^{15}N into meso- and macrofauna of low and high trophic level during 25 days after labeling (means ± SEM, number of replicates varied between n = 3 for low trophic level macrofauna at day 25 to n = 18 for high trophic level macrofauna at day 5).

The occurrence of mycorrhizal fungi was very low at our field site as assigned by molecular analyses (J. Moll, pers. comm.), indicating that mainly saprotrophic fungi accounted for the high ^{13}C enrichment. Saprotrophic fungi are assumed to predominantly rely on aboveground litter resources (Ruess and Ferris, 2004), but our results suggest that they took over the role of arbuscular mycorrhiza fungi that are considered to be the major conduit in transfer of plant C into arable soils (Drigo et al., 2010). Our results support earlier findings by Kramer et al. (2012) who also found high contribution of saprotrophic as compared to mycorrhizal fungi to fungal biomass at our field site. Furthermore, the results are in line with recent studies in arable and grassland systems stressing the key role of saprotrophic fungi in channeling C to higher trophic levels (Lemanski and Scheu, 2014a, 2014b; Tavi et al., 2013). Fast incorporation of ^{13}C into high trophic level taxa, i.e. fungal feeders and predators, and high incorporation of root-derived ^{13}C into saprotrophic fungi in the present study underpin the importance of the fungal energy channel for soil animal food webs and suggest that C flux via saprotrophic fungi is more important than previously assumed (Moore et al., 2005; Ngosong et al., 2009).

Fertilizer-derived N was incorporated into each of the taxa of meso- and macrofauna proving that mineral nutrients in soil are channeled rapidly into the soil food web. The combined incorporation of root-derived ^{13}C and fertilizer-derived ^{15}N into soil meso- and macrofauna suggests that saprotrophic microorganisms function as major control point in channeling N from inorganic resources and C from root-derived resources to higher trophic levels. Both types of resources are available for meso- and macrofauna via the fungal energy channel, since fungal hyphae are the main food resource of many species (Scheu and Falca, 2000), and earlier studies suggest that soil arthropods readily incorporate fungal N as well as C (Eissfeller et al., 2013).

4.2. Temporal dynamics

Different incorporation patterns of ^{13}C and ^{15}N into the soil food web indicate that the fluxes of root-derived C and inorganic nutrients varied markedly. This contrasts our expectations and suggests that root derived resources function as short term pulse in fueling soil food webs, whereas fertilizer-derived N is incorporated more continuously.

In plant tissue and rhizosphere soil microorganisms, the enrichment in ^{13}C was highest at day 2, while ^{13}C incorporation into nematodes and meso- and macrofauna increased with time or remained constant. Thus,

root C rapidly enters basal trophic levels, while incorporation into higher trophic levels is delayed, confirming our second hypothesis. This is in line with studies that found plant derived C entering the microbial soil food web within a few days (Leake et al., 2006; Pausch et al., 2013). However, at higher trophic levels, i.e. within low trophic level meso- and macrofauna, ^{13}C incorporation did not increase rapidly, but was constant throughout the sampling dates, while it increased with time in high trophic level taxa.

Whereas the constant ^{13}C signatures of low trophic level taxa suggest that they quickly incorporated root C, the low amount of incorporated ^{13}C points to unlabeled litter residues as an additional important resource. Consequently, increasing incorporation of ^{13}C into high trophic level taxa in time can most likely be explained by relying on nematode prey rather than arthropod decomposers. Supporting this assumption, Collembola and Gamasida made up the majority of fungal feeding and predatory species in the present study, and have both been found to intensively feed on nematodes (Heidemann et al., 2014; Read et al., 2006). Similar to high trophic level meso- and macrofauna, ^{13}C in fungivorous nematodes generally increased with time, pointing to the possibility that high trophic level meso- and macrofauna included omnivorous species that rely on soil fungi as well as animal prey. The role of nematodes as prey for decomposer soil invertebrates has been discussed recently with molecular gut content analyses indicating high feeding rates (Heidemann et al., 2014; Read et al., 2006), but the extent to which decomposers rely on nematodes as food remains controversial (Kudrin et al., 2015). Due to the lack of nematode ^{15}N data we cannot prove their role as prey for higher trophic levels in the studied soil food web, but high ^{15}N signatures in many mesofauna taxa indicate feeding on other soil animals, most likely nematodes.

In contrast to root-derived ^{13}C, incorporation of fertilizer-derived ^{15}N increased with time in plant tissue and soil arthropods. This suggests that inorganic nutrients are incorporated increasingly into soil microorganisms, presumably fungi, and channeled in a proportional way into higher trophic levels of the soil food web (Eissfeller et al., 2013). Notably, ^{15}N changes with time did not significantly differ between trophic groups of meso- and macrofauna, indicating that N flows in a homogeneous way through the soil food web. Uptake of N by soil arthropods mainly occurs via microorganisms (Caner et al., 2004). In the arable field studied saprotrophic fungi showed much higher activity than bacteria (Pausch et al., 2015), suggesting that the former incorporated ^{15}N more rapidly. Preferential feeding on fungi as compared to bacteria in most soil arthropods further points to a central position of saprotrophic fungi in channeling N to higher trophic levels of soil meso- and macrofauna, supporting earlier findings for forest soil food webs (Eissfeller et al., 2013).

4.3. Extent of ^{13}C enrichment in different trophic levels

The incorporation of root-derived ^{13}C decreased markedly along the food chain. Little incorporation into nematodes and meso- and macrofauna suggests that root-derived C is locked up in rhizosphere microorganisms, quickly leaves the soil system via respiration (Pausch and Kuzyakov, 2012; Pausch et al., 2013), and does not reach higher trophic levels. Nevertheless, all food web compartments incorporated ^{13}C rapidly after labeling, underlining the importance of root-derived C as major C source in arable soils.

Higher incorporation of root-derived C into fungivorous and omnivorous nematodes as compared to other nematode trophic groups suggests that they allocated plant C directly from saprotrophic fungi, as those very efficiently captured plant C (Pausch et al., 2015; Riederer et al., 2015). Obviously, fungal feeders achieved the ^{13}C enrichment by their direct trophic linkage to fungi, while the high incorporation of ^{13}C into omnivores suggests a considerable proportion of fungal tissue as diet, besides feeding on other (labeled) nematodes.

Later in the experiment, soil animal predators incorporated higher amounts of ^{13}C than decomposers, contradicting our third hypothesis. Nematodes form an important part of the diet of soil fauna predators (Heidemann et al., 2014; Koehler, 1997; Read et al., 2006), but the similar incorporation patterns of soil fauna predators and fungivorous nematodes suggest direct feeding on soil fungi as the main ^{13}C source for most species grouped as high trophic level taxa, and nematodes as supplementary diet, resulting in omnivory as the main feeding strategy. Nematode feeding likely diluted the incorporation of ^{13}C into high trophic level meso- and macrofauna due to the high contribution of less labeled bacterial feeders to the nematode community at the investigated field site (Scharroba et al., 2012). However, nematodes were extracted from bulk soil and incorporation of root-derived ^{13}C into rhizosphere nematodes, in particular bacterial and plant feeders, presumably was underestimated.

The efficiency of plants in incorporation of CO_2 and releasing C via roots may have affected the incorporation of labeled C into the soil food web, as indicated by the high variability of ^{13}C incorporation between replicates, i.e. labeling chambers. Nonetheless, our results suggest that the incorporation of root-derived C and fertilizer-derived N decreases at higher trophic levels, as also suggested by Pausch et al. (2015).

5. Conclusions

The dual ^{13}C and ^{15}N labeling approach allowed following the flux of energy and nutrients through an arable soil food web. The root-derived resources are of essential importance for arable soil food webs, and root-derived C is channeled to higher trophic levels concurrently with fertilizer-derived N, predominantly via saprotrophic fungi. Increasing amounts of root-derived C and fertilizer-derived N with time suggest that the bottom up transfer of resources is shaped by high connectivity within the food web, i.e. high degrees of omnivory in higher trophic levels. Rapid incorporation of root-derived C into rhizosphere microorganisms and lower incorporation into micro-, meso- and macrofauna suggest that in arable systems the majority of root-derived C remains locked up at the base of the soil food web.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.fooweb.2016.02.006.

Acknowledgments

We thank Reinhard Langel at the Kompetenzzentrum Stabile Isotope (KOSI), University of Göttingen, for stable isotope measurements. Thanks to Stephanie Wolf for her work on the identification of taxa, to Bernhard Klarner and Verena Eißfeller for help in the identification of Gamasida and Oribatida, respectively, and to David Ott for advice in using R. Financial support was provided by the German Research Foundation (DFG) within the Research Unit "Carbon flow in belowground food webs assessed by isotope tracers" (FOR 918).

References

Bahri, H., Dignac, M.-F., Rumpel, C., Rasse, D.P., Chenu, C., Mariotti, A., 2006. Lignin turnover kinetics in an agricultural soil is monomer specific. Soil Biol. Biochem. 38, 1977–1988.

Balasooriya, W.K., Denef, K., Huygens, D., Boeckx, P., 2014. Translocation and turnover of rhizodeposit carbon within soil microbial communities of an extensive grassland ecosystem. Plant Soil 376, 61–73.

Berg, M.P., Stoffer, M., van den Heuvel, H.H., 2004. Feeding guilds in Collembola based on digestive enzymes. Pedobiologia 48, 589–601.

Bradford, M.A., Strickland, M.S., DeVore, J.L., Maerz, J.C., 2012. Root carbon flow from an invasive plant to belowground foodwebs. Plant Soil 359, 233–244.

Caner, L., Zeller, B., Dambrine, É., Ponge, J.-F., Chauvat, M., Llanque, C., 2004. Origin of the nitrogen assimilated by soil fauna living in decomposing beech litter. Soil Biol. Biochem. 36, 1861–1872.

Crotty, F.V., Blackshaw, R.P., Murray, P.J., 2011. Tracking the flow of bacterially derived ^{13}C and ^{15}N through soil faunal feeding channels. Rapid Commun. Mass Spectrom. 25, 1503–1513.

De Deyn, G.B., Cornelissen, J.H.C., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. Ecol. Lett. 11, 516–531.

Drigo, B., Pijl, A.S., Duyts, H., Kielak, A.M., Gamper, H.A., Houtekamer, M.J., 2010. Shifting carbon flow from roots into associated microbial communities in response to elevated atmospheric CO_2. PNAS 107, 10938–10942.

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.

Esperschütz, J., Gattinger, A., Mäder, P., Schloter, M., Fließbach, A., 2007. Response of soil microbial biomass and community structures to conventional and organic farming systems under identical crop rotations. FEMS Microbiol. Ecol. 61, 26–37.

Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G.B., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574.

Fox, J., 2003. Effect displays in R for generalised linear models. J. Stat. Softw. 8, 1–27.

Frostegard, A., Tunlid, A., Baath, E., 1991. Microbial biomass measured as total lipid phosphate in soils of different organic content. J. Microbiol. Methods 14, 151–163.

Gaudinski, J.B., Trumbore, S.E., Davidson, E.A., Zheng, S., 2000. Soil carbon cycling in a temperate forest: radiocarbon-based estimates of residence times, sequestration rates and partitioning of fluxes. Biogeochemistry 51, 33–69.

Gilbert, K.J., Fahey, T.J., Maerz, J.C., Sherman, R.E., Bohlen, P.J., Dombroskie, J.J., Groffman, P.M., Yavitt, J.B., 2014. Exploring carbon flow through the root channel in a temperate forest soil food web. Soil Biol. Biochem. 76, 45–52.

Heidemann, K., Hennies, A., Schakowske, J., Blumenberg, L., Ruess, L., Scheu, S., Maraun, M., 2014. Free-living nematodes as prey for higher trophic levels of forest soil food webs. Oikos 123, 1199–1211.

Högberg, M.N., Briones, M.J.I., Keel, S.G., Metcalfe, D.B., Campbell, C.D., Midwood, A.J., Thornton, B., Hurry, V., Linder, S., Näsholm, T., Högberg, P., 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. New Phytol. 187, 485–493.

Hopkin, S.P., 2007. A key to the Collembola (Springtails) of Britain and Ireland. first ed. Field Studies Council.

Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. Biom. J. 50, 346–363.

Karg, W., 1993. Die Tierwelt Deutschlands 59 - Raubmilben. second ed. Gustav Fischer Verlag, Jena-Stuttgart-New York.

Kempson, D., Lloyd, M., Ghelardi, M., 1963. A new extractor for woodland litter. Pedobiologia 3, 1–21.

Klarner, B., Maraun, M., Scheu, S., 2013. Trophic diversity and niche partitioning in a species rich predator guild — natural variations in stable isotope ratios ($^{13}C/^{12}C$, $^{15}N/^{14}N$) of mesostigmatid mites (Acari, Mesostigmata) from Central European beech forests. Soil Biol. Biochem. 57, 327–333.

Koehler, H.H., 1997. Mesostigmata (Gamasina, Uropodina), efficient predators in agroecosystems. Agric. Ecosyst. Environ. 62, 105–117.

Kramer, J.K.G., Hernandez, M., Cruz-Hernandez, C., Kraft, J., Dugan, M.E.R., 2008. Combining results of two GC separations partly achieves determination of all cis and trans 16:1, 18:1, 18:2 and 18:3 except CLA isomers of milk fat as demonstrated using Ag-ion SPE fractionation. Lipids 43, 259–273.

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

Kramer, S., Marhan, S., Haslwimmer, H., Ruess, L., Kandeler, E., 2013. Temporal variation in surface and subsoil abundance and function of the soil microbial community in an arable soil. Soil Biol. Biochem. 61, 76–85.

Kudrin, A.A., Tsurikov, S.M., Tiunov, A.V., 2015. Trophic position of microbivorous and predatory soil nematodes in a boreal forest as indicated by stable isotope analysis. Soil Biol. Biochem. 86, 193–200.

Lal, R., 2004a. Soil carbon sequestration impacts on global climate change and food security. Science 304, 1623–1627.

Lal, R., 2004b. Soil carbon sequestration to mitigate climate change. Geoderma 123, 1–22.

Langel, R., Dyckmans, J., 2014. Combined ^{13}C and ^{15}N isotope analysis on small samples using a near-conventional elemental analyzer/isotope ratio mass spectrometer setup. Rapid Commun. Mass Spectrom. 28, 1019–1022.

Leake, J.R., Ostle, N.J., Rangel-Castro, J.I., Johnson, D., 2006. Carbon fluxes from plants through soil organisms determined by field $^{13}CO_2$ pulse-labelling in an upland grassland. Appl. Soil Ecol. 33, 152–175.

Lemanski, K., Scheu, S., 2014a. Fertilizer addition lessens the flux of microbial carbon to higher trophic levels in soil food webs of grassland. Oecologia 176, 487–496.

Lemanski, K., Scheu, S., 2014b. Incorporation of ^{13}C labelled glucose into soil microorganisms of grassland: effects of fertilizer addition and plant functional group composition. Soil Biol. Biochem. 69, 38–45.

Loya, W.M., Johnson, L.C., Kling, G.W., King, J.Y., Reeburgh, W.S., Nadelhoffer, K.J., 2002. Pulse-labeling studies of carbon cycling in arctic tundra ecosystems: contribution of photosynthates to soil organic matter. Glob. Biogeochem. Cycles 16, 1–8.

Moll, J., Goldmann, K., Kramer, S., Hempel, S., Kandeler, E., Marhan, S., Ruess, L., Krüger, D., Buscot, F., 2015. Resource type and availability regulate fungal communities along arable soil profiles. Microb. Ecol. 70, 390–399.

Moore, J.C., Berlow, E.L., Coleman, D.C., Ruiter, P.C. De, Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K.J., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J., Wall, D.H., 2004. Detritus, trophic dynamics and biodiversity. Ecol. Lett. 7, 584–600.

Moore, J.C., McCann, K.S., Ruiter, P.C. De, 2005. Modeling trophic pathways, nutrient cycling, and dynamic stability in soils. Pedobiologia 49, 499–510.

Ngosong, C., Raupp, J., Scheu, S., Ruess, L., 2009. Low importance for a fungal based food web in arable soils under mineral and organic fertilization indicated by Collembola grazers. Soil Biol. Biochem. 41, 2308–2317.

Ngosong, C., Jarosch, M., Raupp, J., Neumann, E., Ruess, L., 2010. The impact of farming practice on soil microorganisms and arbuscular mycorrhizal fungi: crop type versus long-term mineral and organic fertilization. Appl. Soil Ecol. 46, 134–142.

Pausch, J., Kuzyakov, Y., 2012. Soil organic carbon decomposition from recently added and older sources estimated by $\delta^{13}C$ values of CO_2 and organic matter. Soil Biol. Biochem. 55, 40–47.

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.

Pausch, J., Kramer, S., Scharroba, A., Scheunemann, N., Butenschoen, O., Kandeler, E., Marhan, S., Riederer, M., Scheu, S., Kuzyakov, Y., Ruess, L., 2015. Small but active — pool size does not matter for carbon incorporation in belowground food webs. Funct. Ecol. (available online).

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Team, The R.D.C., 2013r. NLME: linear and nonlinear mixed effects models. R Package Version 3, pp. 1–111.

Pollierer, M.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.

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.

R Core Team, T., 2013. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing.

Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus 44B, 81–99.

Read, D.S., Sheppard, S.K., Bruford, M.W., Glen, D.M., Symondson, W.O.C., 2006. Molecular detection of predation by soil micro-arthropods on nematodes. Mol. Ecol. 15, 1963–1972.

Reineking, A., Langel, R., Schikowski, J., 1993. ^{15}N, ^{13}C-on-line measurements with an elemental analyzer (Carlo Erba, NA 1500), a modified trapping box and a gas isotope mass spectrometer (FINNIGAN, MAT 251). Isot. Environ. Health Stud. 29, 169–174.

Riederer, M., Pausch, J., Kuzyakov, Y., Foken, T., 2015. Partitioning NEE for absolute C input into various ecosystem pools by combining results from eddy-covariance, atmospheric flux partitioning and $^{13}CO_2$ pulse labeling. Plant Soil 390, 61–76.

Robertson, G.P., Vitousek, P.M., 2009. Nitrogen in agriculture: balancing the cost of an essential resource. Annu. Rev. Environ. Resour. 34, 97–125.

Ruess, L., 1995. Studies on the nematode fauna of an acid forest soil: spatial distribution and extraction. Nematologica 41, 229–239.

Ruess, L., Chamberlain, P.M., 2010. The fat that matters: soil food web analysis using fatty acids and their carbon stable isotope signature. Soil Biol. Biochem. 42, 1898–1910.

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

Ruf, A., Kuzyakov, Y., Lopatovskaya, O., 2006. Carbon fluxes in soil food webs of increasing complexity revealed by ^{14}C labelling and ^{13}C natural abundance. Soil Biol. Biochem. 38, 2390–2400.

Schaefer, M., 2010. Brohmer - Fauna von Deutschland. 23rd ed. Quelle & Meyer Verlag, Wiebelsheim.

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.

Schneider, K., Migge-Kleian, S., Norton, R.A., Scheu, S., Langel, R., Reineking, A., Maraun, M., 2004. Trophic niche differentiation in soil microarthropods (Oribatida, Acari): evidence from stable isotope ratios ($^{15}N/^{14}N$). Soil Biol. Biochem. 36, 1769–1774.

Schneider, T., Keiblinger, K.M., Schmid, E., Sterflinger-Gleixner, K., Ellersdorfer, G., Roschitzki, B., Richter, A., Eberl, L., Zechmeister-Boltenstern, S., Riedel, K., 2012. Who is who in litter decomposition? Metaproteomics reveals major microbial players and their biogeochemical functions. ISME J. 6, 1749–1762.

Six, J., Frey, S.D., Thiet, R.K., Batten, K.M., 2006. Bacterial and fungal contributions to carbon sequestration in agroecosystems. Soil Sci. Soc. Am. J. 70, 555–569.

Strickland, M.S., Rousk, J., 2010. Considering fungal:bacterial dominance in soils — methods, controls, and ecosystem implications. Soil Biol. Biochem. 42, 1385–1395.

Strickland, M.S., Wickings, K., Bradford, M.A., 2012. The fate of glucose, a low molecular weight compound of root exudates, in the belowground foodweb of forests and pastures. Soil Biol. Biochem. 49, 23–29.

Tavi, N.M., Martikainen, P.J., Lokko, K., Kontro, M., Wild, B., Richter, A., Biasi, C., 2013. Linking microbial community structure and allocation of plant-derived carbon in an organic agricultural soil using $^{13}CO_2$ pulse-chase labelling combined with ^{13}C-PLFA profiling. Soil Biol. Biochem. 58, 207–215.

Tilman, D., Balzer, C., Hill, J., Befort, B.L., 2011. Global food demand and the sustainable intensification of agriculture. Proc. Natl. Acad. Sci. U. S. A. 108, 20260–20264.

Vanderklift, M.A., Ponsard, S., 2003. Sources of variation in consumer-diet delta ^{15}N enrichment: a meta-analysis. Oecologia 136, 169–182.

Weigmann, G., 2006. Die Tierwelt Deutschlands Teil 76 - Hornmilben (Oribatida). first ed. Goecke & Evers, Keltern.

Yeates, G.W., Bongers, T., De Goede, R.G., Freckman, D.W., Georgieva, S.S., 1993. Feeding habits in soil nematode families and genera—an outline for soil ecologists. J. Nematol. 25, 315–331.