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Incorporation of plant carbon and microbial nitrogen into the rhizosphere food web of beech and ash

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ABSTRACT

We labeled tree saplings of beech and ash with ^{15}N and ^{13}C in a greenhouse. Carbon (C) was applied as $^{13}CO_2$ to plants and nitrogen (N) was added as $^{15}NH_4^{15}NO_3$ to the soil. We hypothesized that C will be transferred from plants to the rhizosphere, subsequently in beech to ectomycorrhiza (EM), in ash to arbuscular mycorrhiza (AM) and finally to soil animals. We expected the C signal to be more effectively transferred to soil animals in EM as compared to AM systems since EM forms more extensive extramatrical mycelia as compared to AM. For ^{15}N we hypothesized that it will be taken up by both saprotrophic microorganisms and mycorrhizal fungi and then channeled to soil animals. After five month, $\delta^{13}C$ and $\delta^{15}N$ signatures of soil animals, EM and fine roots of beech and ash were measured. Litter and soil were hardly enriched in ^{15}N whereas fine roots of beech and ash were highly enriched suggesting that nitrogen in $^{15}NH_4^{15}NO_3$ was predominantly taken up by plants and mycorrhizal fungi but little by saprotrophic microorganisms. Roots of beech and ash were highly enriched in ^{13}C with maximum values in EM proving that ^{13}C was translocated into roots and mycorrhizal fungi. Soil animals were a priori assigned to primary decomposers, secondary decomposers and predators. Generally, signatures of soil animals did not significantly vary between beech and ash and therefore were pooled. Primary decomposers had low $\delta^{13}C$ and $\delta^{15}N$ signatures similar to litter and soil confirming that rhizosphere C and microbial N are of limited importance for primary decomposer taxa. $\delta^{13}C$ and $\delta^{15}N$ signatures of secondary decomposers were higher than those of primary decomposers and spanned a large gradient indicating that certain secondary decomposers rely on root derived C and microbial N, however, none of the secondary decomposers had signatures pointing to exclusive feeding on EM. Unexpectedly, $\delta^{13}C$ and $\delta^{15}N$ signatures were highest in predators suggesting that they heavily preyed on secondary decomposer species such as the litter dwelling Collembola species *Lepidocyrtus cyaneus* and species not captured by the heat extraction procedure used for capturing prey taxa, presumably predominantly root associated nematodes. Overall, the results highlight that in particular higher trophic levels rely on carbon originating from other resources than litter with these resources channeled to dominant predators via litter dwelling Collembola species.

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1. Introduction

In forest ecosystems most of the net primary production enters the decomposer community as detritus. This dead organic material usually is assumed to be the main source of nutrients for soil microbes (Swift, 1979; Berg and McClaugherty, 2008) and decomposer animals (Hättenschwiler and Gasser, 2005; Scheu, 2005). However, this view has been challenged recently by documenting that soil animals strongly rely on root-derived carbon (Ruf et al., 2006; Albers et al., 2006; Pollierer et al., 2007, 2012). In fact, a large fraction of plant fixed carbon enters the belowground system via roots and root exudates (Bardgett et al., 2005; Leake et al., 2006) and this carbon is more easily available for soil organisms than the recalcitrant carbon in plant litter since it comprises predominantly amino acids, sugars and peptides (Bais et al., 2006; Dennis et al., 2010).

Most plant roots are closely associated with mycorrhizal fungi channeling plant carbon to the outer rhizosphere (Smith and Read,

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1997; Wallander et al., 2009). In temperate forest ecosystems ectomycorrhizal fungi (EMF) dominate (e.g., in beech, oak, lime and hornbeam), but some tree species are associated with arbuscular mycorrhizal fungi (AMF; e.g., ash and acer; Lang and Polle, 2011; Lang et al., 2011). The transfer of carbon from the plant to the rhizosphere likely is more effective in the well-dispersed extramatrical mycelium of the EMF (Högberg et al., 2008; Cairney, 2012) than in AMF which do not form intensive extramatrical mycelia (Smith and Read, 1997).

Nitrogen is of crucial importance for soil microorganisms and plants. During decomposition of litter material and for microbial growth in general microorganisms immobilize mineral nutrients in soil thereby competing with plants for these resources (Chapman et al., 2006; Geissler et al., 2010). Tree roots take up nitrogen from soil, but in temperate forests most nitrogen is channeled to plants via EMF (Hobbie and Hobbie, 2006; Van der Heijden et al., 2008). In soil food webs carbon is channeled along two main energy pathways, the fungal and bacterial energy channel (Moore and Hunt, 1988; Moore et al., 2005; Crotty et al., 2011). In temperate forests litter quality typically is low and litter is mainly processed by saprotrophic fungi (Wardle et al., 2004). Together with EMF saprotrophic fungi form the main source of N for the fungal energy channel of soil food webs (Moore-Kucera and Dick, 2008). In contrast, bacteria predominantly consume root exudates and serve as source for N (and other elements) for the bacterial energy channel (Crotty et al., 2011).

From a trophic level point of view the soil food web might be separated into primary decomposers, secondary decomposers and predators (Scheu and Falca, 2000; Scheu, 2002). Primary decomposers, such as Diplopoda, and certain species of Oribatida and Lumbricidae, are assumed to feed mainly on litter material (Pollierer et al., 2009). Secondary decomposers, such as most Oribatida, Collembola and certain species of Isopoda and Lumbricidae, are assumed to feed predominantly on fungi and microbial residues (Maraun et al., 1998; Scheu and Falca, 2000). Predators, such as Lithobiidae or Araneida, have been assumed to rely predominantly on secondary decomposers as food (Scheu, 2002; Pollierer et al., 2012; Ferlian et al., 2012).

Natural variations in stable isotope ratios of carbon ($^{13}C/^{12}C$) and nitrogen ($^{15}N/^{14}N$) have been shown to be a powerful tool for investigating nutrient fluxes and trophic interactions in soil food webs (Scheu and Falca, 2000; Illig et al., 2005; Tiunov, 2007; Pollierer et al., 2009). However, labeling experiments with enriched ^{13}C and ^{15}N compounds are indispensable for tracing carbon and nitrogen fluxes through decomposer systems (Ruf et al., 2006; Pollierer et al., 2007; Sticht et al., 2008; Högberg et al., 2010).

We conducted a $^{13}CO_2$ labeling experiment in the greenhouse to follow the flux of carbon from plant shoots to the rhizosphere and into the soil animal food web. In parallel, we used ^{15}N labeled mineral nitrogen (NH_4NO_3) to follow the flux of nitrogen via saprotrophic microorganisms and mycorrhiza into the soil animal food web. Saplings of European beech and European ash were excavated in the field, potted into mesocosms including rhizosphere soil and the associated soil animal community. After five months of labeling i.e., after one vegetation period, $\delta^{13}C$ and $\delta^{15}N$ signatures of beech and ash roots, ectomycorrhiza and soil animals were measured.

We investigated the following hypotheses: (1) Plant carbon is translocated via roots and mycorrhiza into fungal feeding soil invertebrates. (2) Carbon as well as nitrogen is transferred mainly to lower trophic levels and is diluted toward higher trophic levels due to predators incorporating prey relying in part on root and in part on litter carbon. (3) Carbon and nitrogen transfer into the soil animal food web is more pronounced in beech than in ash due to the more extensive extramatrical mycelium in EMF than in AMF. (4) Mineral nitrogen is translocated to higher trophic levels via both saprotrophic microorganisms and mycorrhizal fungi and subsequently into soil animals.

2. Material and methods

2.1. Study site and experimental setup

Tree saplings were collected at two locations (Thiemsburg and Lindig) in the south east of the Hainich National Park, Thuringia, Germany (51°05′28″N, 10°31′24″E). The Hainich is the largest cohesive deciduous forest in Germany and was declared National Park in 1997. In the sampling area, forest cover was present since the mid 18th century. In the last four decades, the area was used for military training and has been managed little (Schmidt et al., 2009). The dominating tree species at the study sites is beech (*Fagus sylvatica* L.), but ash (*Fraxinus excelsior* L.), maple (*Acer pseudplatanus* L.) and lime (*Tilia platyphyllos* Scop. and *Tilia cordata* P. Mill.) are interspersed. The herb layer of the Hainich is dominated by *Allium ursinum* (L.), *Anemone nemorosa* (L.) and *Galium odoratum* (L.) (Vockenhuber et al., 2011). The mean annual temperature ranges from 7.5 to 8.0 °C and the mean annual precipitation is 600 mm (Leuschner et al., 2009). The area represents a slightly sloping plateau of the Triassic Upper Limestone formation covered by Pleistocene loess (Leuschner et al., 2009).

At the study sites 15 saplings of *F. sylvatica* and 14 saplings of *F. excelsior* (height ca. 60 cm) were excavated together with the surrounding intact soil (depth 25 cm and 2–3 cm litter layer) and placed into containers (diameter 25 cm, height 45 cm) equipped with drainage at the bottom. For ^{13}C labeling tree saplings were exposed to $^{13}CO_2$ enriched atmosphere (maximum CO_2 concentration 1200 ppm) in a greenhouse for five months at 23 °C and 70% humidity. For ^{15}N labeling the mesocosms were irrigated daily with a Hoagland-based nutrient solution containing 0.1 mM $^{15}NO_3^{15}NH_4$ and 0.6 mM $CaCl_2$, 0.4 mM $MgSO_4$, 0.01 mM $FeCl_3$, 0.4 mM K_3PO_4, 1.8 μM $MnSO_4$, 0.064 μM CuCl, 0.15 μM $ZnCl_2$, 0.1 μM MoO_3, 0.01 mM H_3BO_3 and 5 mM NO_3NH_4 (Euriso-top, Saint-Aubin, Essonne, France). The soil was moistened at regular intervals by adding tap water.

2.2. Sampling of soil, litter, plants and ectomycorrhiza

At the end of the experiment the soil was divided into two horizons, 0–10 cm (A1 horizon including litter) and 10–25 cm (A2 horizon). Aliquots of soil material for stable isotope analyses were collected from the A1 horizon, dried and stored in plastic bags until analysis. From the litter layer and A1 horizon large soil animals were picked by hand. From the A1 and A2 layer roots were washed, divided in coarse (>2 mm) and fine roots (<2 mm), dried (48 h, 70 °C) and weighed. Aliquots of the litter were taken, dried and stored in plastic bags until stable isotope analysis. Root caps of beech with EMF were collected and twenty samples were analyzed for stable isotope ratios.

2.3. Sampling of soil animals

Animals of the litter and A1 layer were extracted by heat using a high-gradient canister method effectively extracting mobile soil animals such as arthropods and (non-dormant) earthworms (Kempson et al., 1963). Soil animals were transferred into 70% ethanol and sorted to groups. Individuals were counted and determined to family, genus or species level (see Appendix). Based on natural variations in stable isotope ratios ($^{15}N/^{14}N$), feeding experiments, analyses of fatty acids and gut content analyses soil animal species were classified into primary decomposers, secondary decomposers and predators (see Appendix). Primary

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