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Beech trees fuel soil animal food webs via root-derived nitrogen

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Abstract

Root-derived resources are receiving increased attention as basal resources for soil animal food webs. They predominantly function as carbon and energy resources for microbial metabolism in the rhizosphere, however, root-derived nitrogen may also be important. We explored both the role of root-derived carbon (C) and nitrogen (N) for the nutrition of soil animal species. Using ^{13}C and ^{15}N pulse labeling we followed in situ the flux of shoot-derived C and N into the soil animal food web of young beech (*Fagus sylvatica*) and ash (*Fraxinus excelsior*) trees. For labeling with ^{13}C, trees were exposed to increased atmospheric concentrations of $^{13}CO_2$ and for labeling with ^{15}N leaves were immersed in a solution of $Ca^{15}NO_3$. Twenty days after labeling root-derived N was detected in each of the studied soil animal species whereas incorporation of root-derived C was only detected in the ash rhizosphere. More root-derived N was incorporated into soil animals from the beech as compared to the ash rhizosphere, in spite of the higher ^{15}N signatures in fine roots of ash as compared to beech. The results suggest that soil animal food webs not only rely on root C but also on root N with the contribution of root N to soil animal nutrition varying with tree species. This novel pathway of plant N highlights the importance of root-derived resources for soil animal food webs.

Keywords: Basal resources; Mycorrhiza; Pulse labeling; Rhizodeposits; Stable isotopes

Introduction

The close interrelationship between the decomposer system and plants is mediated by leaf litter input and rhizodeposition (Wardle 2002). As up to 90% of net primary plant

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production enters the soil as detritus (Cebrian 1999), litter has long been assumed to function as the main food source for soil animals, however, recent work has shown that other resources such as those derived from roots may be more important (Ruf, Kuzyakov, & Lopatovskaya 2006; Pollierer, Langel, Körner, Maraun, & Scheu 2007; Eissfeller, Beyer et al. 2013). A variety of substances are released actively or passively from roots into the soil as rhizodeposits (Curl & Truelove 1986; Jones, Nguyen, & Finlay 2009). Rhizodeposits are divided into exudates, leakages, secretions, mucilages, mucigel and lysates (Rovira, Foster, & Martin 1979; Curl & Truelove 1986), and include both carbon (C) and nitrogen (N) containing compounds with C compounds being most important. As nitrogen typically is transferred from soil to roots and incorporated into plants, the opposite pathway with nitrogen being transferred from plants into the soil is assumed to be only of significant importance in N fixing plants such as legumes (Ayres, Dromph, Cook, Ostle, & Bardgett 2007), but the role of this pathway in other plants has received little attention (Wichern, Eberhardt, Mayer, Joergensen, & Müller 2008). In addition to fueling microorganisms and fostering microbial biomass in the rhizosphere, rhizodeposits affect mutualistic and antagonistic interactions between soil microorganisms and plants (Bais, Weir, Perry, Gilroy, & Vivanco 2006).

Soil animal communities of deciduous forests are remarkably diverse (Anderson 1975; Schaefer 1991; Scheu 2005) and form complex food webs (Digel, Curtsdotter, Riede, Klarner, & Brose 2014; Ehnes et al. 2014). These food webs span a wide range of trophic levels including primary and secondary decomposers, and first, second and third order predators (Ponsard & Arditi 2000; Scheu & Falca 2000). Soil animals are affected by soil properties (Langenbruch, Helfrich, & Flessa 2012), plant species (Scheu 2005; Eissfeller, Langenbruch, Jacob, Maraun, & Scheu 2013) and soil microorganisms (Esperschütz et al. 2009; Koranda et al. 2011), with the latter two being mediated by rhizodeposits. Plant allocation of C to roots and into the rhizosphere received considerable attention in trees (Högberg et al. 2008; Subke et al. 2009; Kuzyakov & Gavrichkova 2010), but N allocation to roots and into the rhizosphere has been investigated for herbaceous plants in particular legumes (Ayres et al. 2007; Wichern et al. 2008), whereas information on trees is lacking.

To investigate the flux of C and N from plants into the belowground system stable isotopes are increasingly used (Hertenberger & Wanek 2004; Högberg et al. 2008). Adopting this approach we conducted a pulse labeling experiment in the field. By exposing trees to increased atmospheric $^{13}CO_2$ concentrations and by immersing leaves in a $Ca^{15}NO_3$ solution we followed the flux of C and N into the soil animal food web. ^{13}C labeling by exposing trees to increased atmospheric $^{13}CO_2$ concentrations is widely used (Högberg et al. 2008; Eissfeller, Beyer et al. 2013; Goncharov, Tsurikov, Potapov, & Tiunov 2016). For aboveground ^{15}N labeling, leaf feeding is commonly used (Wichern et al. 2008). Besides urea (Høgh-Jensen & Schjoerring 2000), nitrate has been used in leaf feeding (Brumme, Leimcke, & Matzner 1992; Sierra, Daudin, Domenach, Nygren, & Desfontaines 2007; Jalonen, Nygren, & Sierra 2009). Using European beech (*Fagus sylvatica*) and common ash (*Fraxinus excelsior*) we examined if the effect of trees on the soil animal food web via rhizodeposits varies between tree species. Beech and ash were chosen as they differ in nutrient allocation patterns and mycorrhiza types. Beech roots are associated with ectomycorrhizal (EM) and ash roots with arbuscular mycorrhizal (AM) fungi. The following hypotheses were investigated: (1) incorporation of root-derived carbon into the soil animal food web varies between tree species and is more pronounced in EM beech than AM ash trees, and (2) root-derived nitrogen is of minor importance for soil animal nutrition and therefore, incorporation into the soil animal food web varies little with tree species.

Materials and methods

Study site

The experiment was conducted in a temperate deciduous beech forest in the Hainich National Park (Thüringen, Germany) near Weberstedt (51°05′N, 10°28′E) at 300 m asl. Mean annual precipitation is 670 mm and mean annual air temperature 7.5 °C. With 16,000 ha the Hainich National Park is the largest continuous deciduous forest in Germany and has been declared World Heritage Nature Site in June 2011. The forest predominantly consists of beech (*F. sylvatica*) stocking on Luvisol developed on loess underlain by Triassic Shell Limestone. The forest floor is classified as mull-like moder and the mean thickness of the litter layer is 2.8 ± 0.1 cm (Jacob, Viedenz, Polle, & Thomas 2010; Langenbruch, Helfrich, Joergensen, Gordon, & Flessa 2014). The topsoil (0–10 cm) is rather acidic with a pH_{KCl} of 3.3 (Mölder, Bernhardt-Römermann, & Schmidt 2006; Guckland, Jacob, Flessa, Thomas, & Leuschner 2009).

Labeling

In August 2011 eight young trees, four beech and four ash, were selected for labeling. Two beech trees and two ash trees served as controls. Trees were 2.5–4.0 m in height and 5 m or more apart from each other. The young trees grew in the understory of a closed-canopy beech forest. Around each tree used for labeling an area of 1 × 1 m was trenched by inserting polyethylene (PE) panels (thickness: 3 mm). The panels extended 10 cm into the soil and 10 cm above the soil surface to avoid immigration of animals.

For ^{15}N labeling 36 g $Ca^{15}NO_3$ (99.23 atom% ^{15}N, Campro Scientific GmbH, Berlin, Germany) was dissolved in 1200 ml sterile water resulting in a 0.18 M solution. Leaves were fed with this solution by inserting three leaves of beech or three leaflets of the compound leaves of ash into a vial con-