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Roots from beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.) differentially affect soil microorganisms and carbon dynamics

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ABSTRACT

Knowledge about the influence of living roots on decomposition processes in soil is scarce but is needed to understand carbon dynamics in soil. We investigated the effect of dominant deciduous tree species of the Central European forest vegetation, European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.), on soil biota and carbon dynamics differentiating between root- and leaf litter-mediated effects. The influence of beech and ash seedlings on carbon and nitrogen flow was investigated using leaf litter enriched in ^{13}C and ^{15}N in double split-root rhizotrons planted with beech and ash seedlings as well as a mixture of both tree species and a control without plants. Stable isotope and compound-specific fatty acid analysis (^{13}C-PLFA) were used to follow the incorporation of stable isotopes into microorganisms, soil animals and plants. Further, the bacterial community composition was analyzed using pyrosequencing of 16S rRNA gene amplicons. Although beech root biomass was significantly lower than that of ash only beech significantly decreased soil carbon and nitrogen concentrations after 475 days of incubation. In addition, beech significantly decreased microbial carbon use efficiency as indicated by higher specific respiration. Low soil pH probably increased specific respiration of bacteria suggesting that rhizodeposits of beech roots induced increased microbial respiration and therefore carbon loss from soil. Compared to beech $\delta^{13}C$ and $\delta^{15}N$ signatures of gamasid mites in ash rhizotrons were significantly higher indicating higher amounts of litter-derived carbon and nitrogen to reach higher trophic levels. Similar $\delta^{13}C$ signatures of bacteria and fine roots indicate that mainly bacteria incorporated root-derived carbon in beech rhizotrons. The results suggest that beech and ash differentially impact soil processes with beech more strongly affecting the belowground system via root exudates and associated changes in rhizosphere microorganisms and carbon dynamics than ash.

1. Introduction

Soils store twice as much carbon as plants and the atmosphere together thereby forming an important component of the global carbon cycle (Schlesinger and Andrews, 2000). However, the way carbon is processed and how carbon dynamics are controlled still is not well understood. Knowledge on factors changing the flux of carbon from plants into the soil and controlling its turnover is of significant importance especially in face to global warming (McKinley et al., 2011).

In terrestrial ecosystems 90% of the annual biomass produced by plants enters the dead organic matter pool forming the basis of the decomposer system in soil (Gessner et al., 2010). Plant carbon enters the soil via two pathways, dead organic matter (leaf litter and dead roots) and root exudates. Soil chemical properties are mainly influenced by parent material and mineralogy but also by leaf litter forming the major resource of soil biota responsible for decomposition processes (Reich et al., 2005; Jacob et al., 2009; Langenbruch et al., 2012). Litter quality strongly influences soil pH, as calcium and magnesium of the litter compete with H^+ and Al^{3+} for exchange sites on soil particle surfaces or organic matter (Reich et al., 2005). As a consequence, high pH often promotes higher microbial

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biomass resulting in higher soil respiration, mineralization and decomposition (Swift et al., 1979; Wardle, 1998). Low mineralization and decomposition rates are associated with high C-to-N ratios and high lignin contents as it is typical for recalcitrant litter. In contrast, Pollierer et al. (2007) highlighted that in temperate forests carbon does not enter the soil food web predominantly via litter but rather via roots. Rhizodeposits comprise labile exudates (e.g., sugars, amino acids and organic acids), but also complex molecules (e.g., polysaccharides, mucilage and proteins). Labile exudates control both community structure and activity of rhizosphere microorganisms (Paterson et al., 2009). Summarizing results of 95 plant ^{14}C labeling studies, Jones et al. (2004) estimated the loss of carbon by exudation to be equivalent to 5–10% of the net carbon fixed by plants and 25% of the carbon plants allocate to root growth. This supply of energy increases microbial biomass (Butler et al., 2004), acts as soil organic matter (SOM) priming agent (Bird et al., 2011) and alters the physical and chemical soil environment (Gregory, 2006). Microbial communities in rhizosphere and bulk soil are therefore responsible for root exudate-mediated changes in soil processes (Söderberg et al., 2004; Paterson et al., 2007). Since plant species differ in the quality and quantity of exudates (Jones et al., 2004), soil carbon dynamics are likely affected by plant species identity and diversity (Grayston et al., 1998; Steinbeiss et al., 2008).

Decomposition studies report both effects of individual plant species (Jacob et al., 2009) and positive mixing effects (Gartner and Cardon, 2004; Hättenschwiler et al., 2005). Until today, however, studies investigating the influence of plant diversity on belowground dynamics in forests are scare (but see Meinen et al., 2009) and most often only consider the effect of aboveground plant residues (Hättenschwiler and Gasser, 2005; Jacob et al., 2009, 2010). To what extent belowground processes mediated by roots and root exudates affect soil organisms and thereby carbon dynamics remains largely unknown. This lack of knowledge is unfortunate as 60% of the terrestrial carbon is bound in forests and its contribution to global carbon cycling is of fundamental importance (McKinley et al., 2011).

To improve knowledge on carbon dynamics in forest soils from a root perspective we used the common temperate broad-leaved tree species European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.) to differentiate between general and species-specific effects of living roots on soil organisms and decomposition of litter material in soil. Beech is the dominant tree species in many Central European deciduous forests. Ash often is associated with beech and is expected to increase in dominance in a warmer and drier climate (Broadmeadow and Ray, 2005). Life history traits of beech and ash differ strongly, e.g., speed of growth, root morphology, litter quality, mycorrhizal association, and nutrient, water and light use efficiency (Grime et al., 1997; Emborg, 1998). Beech has higher specific root tip abundance, specific fine root surface area (SRA) and specific fine root length (SRL), whereas ash roots are characterized by higher mean fine root diameter (Meinen et al., 2009). Roots of beech are colonized by ectomycorrhizal (EM) fungi and those of ash by arbuscular mycorrhizal (AM) fungi which differ in nutrient acquisition strategies (Smith and Read, 2008). Beech tolerates soil pH from acid to highly alkaline, while ash is restricted to soils of high base saturation (Weber-Blaschke et al., 2002). Litter of beech at more acidic sites has high C-to-N ratio (>50) and high lignin content, while ash litter is regarded as high quality litter due to its low C-to-N ratio of about 28 and low lignin content (Jacob et al., 2010).

For allowing access to the root system and to investigate interactions between both tree species, beech and ash seedlings were planted into double split-root systems. The systems allowed dissecting root associated processes and belowground interactions between beech and ash. Carbon and nitrogen fluxes in soil were traced following the incorporation of ^{13}C and ^{15}N from labeled ash litter into soil, bacteria, fungi, soil animals and plants. Ash litter was used to follow the uptake of resources from high quality litter materials by beech and ash as compared to more recalcitrant soil resources.

We hypothesized that (1) beech and ash differentially affect the structure of the microbial community thereby modifying soil processes and plant nutrient capture. Differences in microbial community structure are expected to (2) result in differential decomposition of labeled ash litter and differential mobilization of nutrients from the litter. Further, we expected (3) modifications of the soil microorganism community and soil processes to be most pronounced in the mixed treatment with both tree species present due to complementary effects of the two tree species.

2. Material and methods

2.1. Rhizotrons

Double split-root rhizotrons were used to separate root systems of two tree seedlings into compartments with root strands of one individual seedling at each side and a shared root compartment in the center where root strands of both tree seedlings could interact (Fig. 1). We focused on the middle compartment where the two root strands grew together. The central compartment had a volume of 7.6 l and side compartments half the volume. Rhizotrons were 90 cm high and 64 cm wide, and were built from anodized aluminum covered at the front with a 10-mm Perspex plate. They were tilted at 35° to direct roots growing along the Perspex plate. The Perspex plate was covered with black scrim to ensure that roots grow in darkness. Rhizotrons were divided into six soil depth sections (I–VI). Each soil depth contained four experimental sites (ES), two in the center and two at the sides (Fig. 1). The back side of the rhizotrons was equipped with a cooling system keeping the temperature at a constant level of 20 °C over the whole soil column. Climate conditions were set to 20 °C air temperature, 70% relative air humidity and 10 h daylight in winter and 14 h in summer. The tree seedlings were illuminated (EYE Lighting, Clean Ace, Mentor, OH, USA) ensuring a minimum PPFD of 200 ± 10 μmol m^{-2} s^{-1} from June 2009 to October 2010. The experiment lasted for 475 days, i.e., plants were harvested after the second season.

2.1.1. Soil and plants

The soil was taken from a mixed temperate broadleaf forest dominated by *F. sylvatica*, *F. excelsior* and *Tilia cordata* in Central Germany (Hainich forest, 51°04′ N 10°30′ E, about 350 m a.s.l.) from a depth of 0–10 cm after removing the litter. The soil type was a Stagnic Luvisol (IUSS Working Group WRB, 2007; 1.8% sand, 80.2% silt and 18.1% clay) and free of carbonate (<0.02% of total carbon) with a pH (H_2O) of 4.56 ± 0.03 and a gravimetric water content at date of sampling of 22.7%. Initial total carbon amounted to 19.2 ± 0.3 g kg^{-1} dry weight, initial total nitrogen averaged 1.56 ± 0.01 g kg^{-1} dry weight and base saturation was 22.9 ± 1.3%. Each rhizotron was filled with 15.2 L of sieved soil (1 cm mesh) containing soil microflora and fauna. Volumetric soil water content was monitored three times a week with a TDR measurement device (Trime-FM, IMKO, Ettlingen, Germany), and kept at constant level by adding distilled water. Soil temperature was measured with NTC thermistors (Epcos, Munich, Germany), arranged vertically in the center of the rhizotrons at soil depths of 8, 20, 42.5 and 70.5 cm at a distance of 2 cm from the Perspex plate. Data were recorded in 15-min intervals with a CR1000 data logger (combined with two AM416 Relay Multiplexer, Campbell Scientific Inc., Utah, USA).