



Impacts of earthworms on nitrogen acquisition from leaf litter by arbuscular mycorrhizal ash and ectomycorrhizal beech trees



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ABSTRACT

Earthworms (EWs) and mycorrhizal fungi are key components of soil biota participating in N recycling from leaf litter. The extent to which their interactions impact leaf litter-derived N uptake by tree species colonized by different mycorrhizal types and the variation of these interactions with leaf litter quality is unknown. We used a greenhouse experiment to investigate the effects of EWs on plant acquisition of N from ¹⁵N enriched ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*) leaf litter. We employed arbuscular mycorrhizal (AM) ash and ectomycorrhizal (EM) beech trees. EW presence did not affect the overall root mycorrhizal colonization, but in the beech leaf litter treatment it caused a shift in the EM fungal community, favoring species with a ruderal life strategy at the expense of more specialized species able to degrade organic compounds. No differences in ¹⁵N capture were found between EM and AM plants. Generally, 2–7% of the N released from leaf litter was taken up by the plants. EWs uniformly increased plant acquisition of N from leaf litter. This effect was more pronounced in treatments with ash than in those with beech leaf litter, presumably because of higher degradability of ash than of beech litter. The results suggest that leaf litter quality dominates the impact of EWs on plant N acquisition from leaf litter while the mycorrhizal type is of minor importance.

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1. Introduction

In temperate forests that are less exposed to industrial and agricultural nitrogen (N) loads, plant litter decomposition is a key factor controlling N recycling and availability (Schimel and Bennett, 2004; Rennenberg et al., 2009). N release from plant litter is important as N availability typically limits plant growth in these ecosystems (Vitousek et al., 2002). Symbiotic association with mycorrhizal fungi have been invoked as one of the main strategies used by plants to improve N acquisition (Read and Perez-Moreno, 2003; Helmisaari et al., 2009).

Mycorrhizal fungi colonize the root tips and grow either within root cortical cells as arbuscular mycorrhiza (AM) or between the root cells and ensheathing root tips as ectomycorrhiza (EM). Their hyphae spread out from the roots into the surrounding soil forming a mycelial network that increases root foraging capacities, soil exploitation, and subsequently the nutrient capture (Smith and

Read, 2008). In spite of uncertainties about the effective contribution of EM fungi (Franklin et al., 2014) or AM fungi (Smith and Smith, 2011) to plants' N budget, it is assumed that EM fungi access organic and inorganic N sources while AM fungi proliferate in organic patches but rely on inorganic N (Hodge and Fitter, 2010). EM plants are thought to have a greater access to organic N compared to AM and non-mycorrhizal plants (Schimel and Bennett, 2004) due to their capabilities to secrete hydrolytic and oxidative enzymes that cleave N-containing complex polymers into smaller, more bio-accessible compounds (Lindahl et al., 2007; Talbot et al., 2008; Cullings et al., 2008; Koide et al., 2008; Rineau et al., 2012; Talbot et al., 2013; Phillips et al., 2013; Bödeker et al., 2014).

It is well recognized that the composition of soil microbial communities, including mycorrhizal fungi, influence litter decomposition while, in turn, microbial community composition is shaped by the quantity and quality of leaf litter (Berg and McClaugherty, 2008). Hence, EM fungi are predominantly associated with an “organic nutrient economy” dominated by slowly decomposing leaf litter tree species, while AM fungi are related to “inorganic nutrient economy,” which is characterized by high

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quality leaf litter species with fast decomposition and mineralization rates (Phillips et al., 2013; Read and Perez-Moreno, 2003).

Mobilization of N from the leaf litter is influenced beside mycorrhizal fungi by earthworms (EWs) as major detritivores in soil, consuming and transforming leaf litter (Edwards and Bohlen, 1996). They are recognized as “ecosystem engineers” (Lavelle, 1997; Jouquet et al., 2006) able to alter their habitat, litter decomposition and mineralization (Scheu, 1987; Bohlen et al., 2004; Blouin et al., 2013; Jouquet et al., 2014). EW activity results in the enhancement of bioavailable N affecting overall plant nutrition and growth (Scheu, 2003; Barot et al., 2007; Van Groenigen et al., 2014).

The interaction of EWs with mycorrhizal fungi likely affects plant nutrient acquisition (Milleret et al., 2009; Li et al., 2011; Li et al., 2013). However, in the literature, contrasting evidences are reported. For example, in a field experiment, the amount of N mobilized from straw litter and taken up by maize plants increased in the presence of both EWs and AM fungi (Li et al., 2013), while in experiments using grass litter, the effect of EWs on plant N uptake in the presence or absence of AM was not significant (Wurst et al., 2004; Eisenhauer et al., 2009). The extent to which the impact of interaction between EWs and mycorrhizal fungi on N nutrition depends on habitat conditions, such as soil and litter quality (Milcu et al., 2008; Holdsworth et al., 2012) is unknown.

EWs may impact soil fungi either directly, by disruption of hyphal networks through burrowing and casting (Bohlen et al., 2004), and by selective grazing on fungal hyphae (Brown, 1995; Bonkowski et al., 2000), or indirectly via alteration of soil physical and chemical properties (Schaefer, 1991; Ekschmitt et al., 2005). However, predictions about detrimental or beneficial impacts of EWs on mycorrhization of trees are difficult to make as litter quality, and particularly mycorrhizal type were not considered in a systematic way in previous studies. For example, a study conducted in a sugar maple forest indicated that EWs decreased AM colonization rate (Lawrence et al., 2003), while another study showed that EM colonization of white spruce remained unaffected by EWs (Cameron et al., 2012).

We investigated the impact of EWs on the acquisition of leaf litter-derived N by young trees via AM and EM in the presence of beech (*Fagus sylvatica*) or ash (*Fraxinus excelsior*) litter in a greenhouse experiment. We used beech, an EM plant that produces recalcitrant leaf litter with a high C-to-N ratio and high lignin content, and ash, an AM tree species whose leaf litter is characterized by a low C-to-N ratio and low lignin content and, compared with beech litter, decomposes much faster (Jacob et al., 2010). Young EM beech and AM ash trees were planted in containers filled with undisturbed forest soil, in which natural litter layer was replaced by ^{15}N enriched ash and beech leaf litter to allow the tracing of the uptake of litter-derived N by the plants. Half of the containers were equipped with EWs, while the other half were kept without. We selected the anecic vertically burrowing EW species *Lumbricus terrestris* and the endogeic geophagous EW species *Aporrectodea caliginosa*, which are dominant components of the detritivore community in deciduous forests. Our study addressed the following hypotheses: (1) EWs impact mycorrhizal colonization, community structure, and root tip ^{15}N accumulation, with the effect varying with the leaf litter type and AM and EM fungi. (2) EM plants acquire more leaf litter N than AM plants in the absence of EWs, while the pattern is reversed in the presence of EWs. (3) EWs facilitate plant capture of N from fast-decomposing ash but not that from recalcitrant beech leaf litter.

2. Materials and methods

2.1. Plant material and experimental set up

Plants and soil were collected in a mature deciduous forest in the National Park Hainich, Thuringia, Germany (51°05'28"N

10°31'24"E, about 350 m a.s.l.). The area was declared National Park in 1997; before that time it was used for military purposes for 30 years with reduced forest management.

The forest stands are predominantly composed of beech (*F. sylvatica* L.) and ash (*F. excelsior* L.) in mixtures with species of the genera *Tilia*, *Acer* and *Carpinus* (Leuschner et al., 2009). At the sampling site, the mean annual temperature is 7.5 °C, and the mean annual precipitation is 670 mm (Leuschner et al., 2009). The soil profiles are classified as Luvisol derived from Triassic mineral soil texture is sand 1.8%, silt 80.2% and 18.1% clay (Guckland et al., 2010).

In March 2011, intact soil blocks of 0.9 × 0.03 m comprising O_n, A_n, A_i, and B_t horizons were excavated at 0.6 m depths and placed in containers that were further freeze treated (stored at −18 °C for 14 days) to kill soil fauna. The containers were planted with 15 saplings of beech and 15 saplings of ash of about 0.2 m height. The plants were collected in the vicinity of soil sampling site. Each container contained one beech and one ash plant.

The O_i layer was replaced by 4.0 g of ^{15}N labeled leaf litter. The labeled litter was obtained from young ash and beech trees grown for one growth season in a greenhouse; during this time the plants were watered with nutrient solution containing $^{15}\text{NO}_3^{15}\text{NH}_4$ (both 99 atom%, Euriso-Top, Saint-Aubin, Essonne, France, for details see Cesarz et al., 2013). In seven containers, beech leaf litter (17.5 mg N g^{−1} dry mass with an enrichment of ^{15}N of 2.31 atom%), and in eight containers, ash leaf litter (17.3 mg N g^{−1} dry mass with an enrichment of ^{15}N of 8.15 atom%) was used. Further 4 g of the same set of ^{15}N labeled leaf litter were added in June 2012. The containers were placed in a greenhouse with ambient light of 200 μmol m^{−2} s^{−1} photosynthetic photon flux density (PPFD), achieved by additional illumination (MT400DL/BH, Iwasaki Electric Co., Tokyo, Japan), at 14 h day length and 20 °C in summer and 10 h and 10 °C in winter and maintained at 80% relative air humidity. The plants were watered with tap water.

At the beginning of the experiment, in half of the containers, a total of eight earthworms (i.e., four individuals of each *A. caliginosa* and *L. terrestris*) were added per container. The surface of the containers was covered with a mesh to prevent EWs from escaping.

Four treatments were established in a two-factorial design: ash leaf litter and EWs (AE), ash leaf litter without EWs (A), beech leaf litter and EWs (BE), and beech leaf litter without EWs (B).

2.2. Harvest

Four beech and four ash plants were used in each of the treatments A, AE and BE and three plants in the B treatment (beech leaf litter without EWs) since the total number of containers was 15. The plants were harvested after twenty months in October 2013. Roots were rinsed with deionized water to remove adhering soil particles. Leaves, stems, fine and coarse roots were separated, and the fresh biomass of each part was determined. The fine roots were kept at 4 °C in plastic bags. The remaining plant material was dried at 60 °C for one week and used for measurements of dry mass, C, N, and ^{15}N concentrations. For measuring the natural stable isotope abundance of nitrogen five beech and five ash plants were harvested in Hainich Natural Park in March 2012.

2.3. Mycorrhizal analysis

The root systems of ash and beech plants were analyzed using a dissecting microscope system (Leica M205 FA, Wetzlar, Germany) equipped with a digital camera (Leica DFC 420C, Wetzlar, Germany). Root tips were classified after Pena et al. (2010) and Agerer (1987–2012) Agerer (1987–2012). For EM morphotype characterization, basic characters such as shape, mantle color and texture, branching pattern, hyphal structure and external

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