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Temporal variations of phosphorus uptake by soil microbial biomass and young beech trees in two forest soils with contrasting phosphorus stocks

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ABSTRACT

The objective of this study was to determine temporal variations of phosphorus (P) uptake by young beech trees (Fagus sylvatica L.) and soil microorganisms in two forests with contrasting P stocks with the aim to better understand P dynamics in forest ecosystems. For this purpose, we conducted a mesocosm experiment and determined P uptake by F. sylvatica, total soil microbial biomass (SMB) and ectomycorrhizal fungi (EMF) at the root tip based on ³³P labeling at five times during the year. Furthermore, we measured EMF community composition, potential acid phosphatase activity (APA), and abundance of bacterial acid phosphatase (phoN) genes. The results showed that plant P uptake was elevated in summer and autumn in the mesocosms from the P-poor site, while it was elevated only in autumn in the mesocosms from the P-rich site. P uptake by SMB was higher in the organic layer at the P-poor site than in the organic layer at the P-rich site throughout the year, underlining the importance of the microbial P pool in the organic layer of P-poor forests. The finding shows that the SMB was able to compensate for the lower P availability in the soil of the P-poor site. The EMF community composition was very variable over the year, and plant P uptake seemed to be independent of EMF community composition. Despite the high species turnover in the EMF community, the potential APA was high throughout the year, indicating functional redundancy of the microbial community with respect to P mineralization. Taken together, our results show important differences in temporal patterns of P uptake by F. sylvatica and the SMB as well as in the total partitioning of P between the SMB and F. sylvatica across the sites. Moreover, decreasing P availability in forests would not only change the size of P stocks and of P cycling rates, but would also affect temporal dynamics of P uptake and the overall partitioning of P between different biotic compartments.

1. Introduction

Despite the importance of phosphorus (P) for plant nutrition, little is known about the temporal patterns of plant P uptake in forest ecosystems and about the factors that control them (Vance et al., 2003; Plassard and Dell, 2010). During the last decades, foliar P concentrations of several tree species in temperate forests have decreased, and the reasons for this decrease are not yet known (Flückiger and Braun, 1998; Duquesnay et al., 2000; Ilg et al., 2009; Braun et al., 2010; Crowley et al., 2012; Jonard et al., 2015; Talkner et al., 2015). This calls for a better understanding of P dynamics in the interplay of soil, and microbial activities in temperate forests.

trix, only a small proportion of the total soil P is plant available. Thus, plants, bacteria and especially EMF have developed several mechanisms to solubilize bound inorganic P by releasing organic acid anions, protons and siderophores (Jones and Oburger, 2011; Jansa et al., 2011; Smits et al., 2012). Furthermore, they can mineralize organic P by releasing extracellular phosphatases, which renders P plant available (Plassard and Dell, 2010; Nannipieri et al., 2011). Microbial organic

ectomycorrhizal fungi (EMF), soil microbial biomass (SMB), and plant

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P availability in soil is largely affected by sorption (Hinsinger, 2001; Giesler et al., 2002). Since phosphate is rapidly sorbed to the soil ma-

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Table 1

Properties of the soils of the P-poor site LUE and the P-rich site BBR together with the soil chemical features of soil in the mesocosms from the two sites, and the average soil mass, fine root abundance, and water content during the experiment. Different letters indicate significant differences (p < 0.05) in soil chemical parameters between all four soil layers.

	Luess (LUE)		Bad Brueckenau (BBR)	
Soil order (WRB) Parent material Humus form Depth of the organic layer [cm]	Cambisol Glacial sands Mor-like Moder 12		Dystric Skeletic Cambisol Basalt Mull-like Moder 7	
	Organic layer	Mineral soil	Organic layer	Mineral soil
Dry weight per mesocosm [g]* Relative fine root abundance [×] Average water content [%]* Total C [g kg ⁻¹] [×] Total N [g kg ⁻¹]* Labile P [mg kg ⁻¹]* Soil pH _{H20} [×]	276 (±133) 0.64 (±0.05) 18.8 (±4.6) 223.6 (±19.1) ^c 8.96 (±0.76) ^c 0.5 (±0.2) ^b 52.7 (±37.8) ^b 4.3 ^b	$\begin{array}{c} 1226 \ (\pm 391) \\ 0.36 \ (\pm 0.05) \\ 50.3 \ (\pm 4.6) \\ 48.4 \ (\pm 4.9)^a \\ 1.75 \ (\pm 0.19)^a \\ 0.1 \ (\pm 0.0)^a \\ 5.9 \ (\pm 4.2)^a \\ 3.8^a \end{array}$	$180 (\pm 76) 0.32 (\pm 0.02) 33.9 (\pm 6.7) 141.5 (\pm 7.6)b 7.88 (\pm 0.36)c 2.8 (\pm 0.3)c 120.0 (\pm 81.9)c 5.1c$	$788 (\pm 184) 0.68 (\pm 0.03) 42.4 (\pm 10.8) 62.7 (\pm 2.7)^a 3.79 (\pm 0.12)^b 2.8 (\pm 0.4)^c 11.9 (\pm 37.8)^a 4.3^b$

 $n = 100, \times n = 5.$

phosphorus mineralization in the vicinity of the root can increase the plant available inorganic P concentration (Richardson et al., 2009; Spohn et al., 2013). Besides mobilizing P, EMF can be very efficient in P uptake from soil because their hyphae reach micropores that are not accessible to roots and have a very high surface area-to-volume ratio (Jansa et al., 2011).

Only few studies explored P uptake kinetics of ectomycorrhizalforming tree species (Van Tichelen and Colpaert, 2000; Brandtberg et al., 2004; Jonard et al., 2009; Desai et al., 2014; Kavka and Polle, 2016). Tracer studies with ³³P showed that P uptake systems of nonmycorrhizal roots are limited because their Michaelis-Menten constants (K_m) are higher than typical concentrations of free P_i in the soil solution (Van Tichelen and Colpaert, 2000; Desai et al., 2014; Kavka and Polle, 2016). In mycorrhizal trees, the K_m is strongly decreased and the uptake rate drastically enhanced (Van Tichelen and Colpaert, 2000; Desai et al., 2014), which underpins the relevance of EMF for plant P uptake. It is not known yet, whether high plant P uptake is associated with a specific EMF community or whether there is a functional redundancy in EMF communities with respect to P mobilization. Moreover, since previous experiments (Van Tichelen and Colpaert, 2000) were conducted in hydroponic solutions in the absence of soil bacteria and saprotrophic fungi, which may strongly affect tree nutrient uptake, the environmental factors that influence P acquisition of EMF and their host trees are still unknown.

Microbial biomass P can represent a substantial fraction of the total soil P. In temperate coniferous and broadleaf forests it amounts on average to 4.3 and 8.6% of the total P in the mineral soil, respectively (Xu et al., 2013). In the organic layer of beech forests, about 22–47% of the total P is sequestered in the microbial biomass (Zederer et al., 2017). Especially in relatively nutrient poor temperate forests with the humus form moder, a large proportion of the total soil P is stored in the SMB (Zederer et al., 2017).

While there are only few studies that explored P uptake kinetics of trees and microorganisms using ³³P, uptake kinetics have been studied more intensively for nitrogen (N) using ¹⁵N. In many studies, in which N uptake by trees and SMB was compared, it was found that initially the SMB took up a significantly larger percentage of the added ¹⁵N than the tree. This was documented for *Acer saccharum* in northern hardwood forests (Zogg et al., 2000), for *Quercus douglasii* in California (Cheng and Bledsoe, 2004), for birch forests in subarctic Sweden (Grogan and Jonasson, 2003), for *Fraxinus excelsior* in France (Bloor et al., 2009), and for *Fagus sylvatica* in Germany (Pena et al., 2013; Leberecht et al., 2015; Dannenmann et al., 2016). ¹⁵N immobilized in the SMB was only very slowly released during the following months (Zogg et al., 2000; Grogan and Jonasson, 2003).

In ecosystems with pronounced seasonality, such as temperate and

alpine ecosystems, plant N uptake and microbial N uptake are often anticyclical in the way that plants take up N mostly during the growing season, while microbial N uptake is highest in autumn, stimulated by high inputs of leaf litter during this time of the year (Jaeger et al., 1999; Lipson et al., 1999; Kaiser et al., 2011). At the end of winter, microbial N decreases again due to thawing-and-freezing events that induce microbial cell lysis (Jaeger et al., 1999; Lipson et al., 1999; Kaiser et al., 2011). It is not known yet, whether such dynamics also occur in temperate forest soils with respect to P uptake.

The objective of this study was to determine temporal variations of P uptake by SMB and by young beech trees (Fagus sylvatica) along with the root-associated EMF assemblage, potential acid phosphatase activity (APA) and abundance of the bacterial acid phosphatase (phoN) genes in two forests differing in total P stocks. For this purpose, young beech trees were extracted with intact soil cores from two forest sites that differ in total soil P stocks and P availability (Zavišić et al., 2016), and were exposed to ambient conditions in a common garden study. We hypothesized, first, that uptake of P by beech trees is higher in summer, when the trees are photosynthetically more active than in autumn (Yang et al., 2016), while P uptake by the SMB is highest in autumn due to inputs of plant detritus during this time of the year. Second, we hypothesized that a larger proportion of P is taken up by the SMB in the P-poor forest compared to the P-rich forest throughout the year. Third, we hypothesized that P uptake by F. sylvatica is independent of specific EMF species due to a high diversity and functional redundancy of EMF species.

2. Materials and methods

2.1. Study site

Soils and juvenile trees were collected at two sites with contrasting soil P availability (Table 1). The site Bad Brueckenau (BBR) that has a high soil P availability is located in the Rhoen Mountains, close to the city of Fulda, Germany (N 50° 21.38′, E 9° 55.71′) at 825 m above sealevel. The mean annual rainfall is 1031 mm and the mean annual temperature is 5.8 °C. The soil is a Dystric Skeletic Cambisol derived from basalt, and the prevailing tree species is European beech (*Fagus sylvatica* L.). The site Luess (LUE) that has a low soil P availability is located in the Lueneburg Heath, close to the city of Hamburg, Germany (N 52° 50.32′, E 10° 16.06′) at 115 m above sea-level. The mean annual rainfall amounts to 730 mm and the mean annual temperature is 8 °C. The soil is a Hyperdystric Folic Cambisol developed from sandy Pleistocene sediments, and the dominant tree species is also *Fagus sylvatica* L. More details have been reported by Zavišić et al. (2016). Download English Version:

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