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ORIGINAL PAPER

Potassium fertilization affects the distribution of fine roots but does not change ectomycorrhizal community structure

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Abstract

• ***Key message*** K fertilization led to a significant increase in fine root biomass, fine root length, and root tip number in the mineral soil layer but does not affect the ecomycorrhizal community structure in the organic horizon.

• ***Context*** Potassium (K) deficiency is common in *Picea abies* in the European Alps. Fertilization with other nutrients often influences fine root biomass and ectomycorrhizas, but less is known about the effects of K-fertilization.

• ***Aims*** The aim of the investigation was to determine the effects of K-fertilization on stem growth and fine root biomass of *Picea abies*, as well as the influence on ectomycorrhizal community structure of the fine roots.

• ***Methods*** Eight years after a single fertilization of K-deficient *Picea abies* with 200 kg K ha^{-1}, fine roots were collected from 7 control and 6 K-fertilized plots. Fine root biomass and morphology were determined. The identification of ectomycorrhizal taxa was determined by morphotyping and by amplification of the internal transcribed spacer region of the nuclear ribosomal DNA.

• ***Results*** K-fertilization did not affect the amount of fine root biomass and ectomycorrhizal community structure in the Oi + Oe and Oa layers but led to a significant increase in fine root biomass, fine root length, and root tip number in the mineral soil layer.

• ***Conclusion*** An increase in growth due to K-fertilization leads to great exploration of the mineral soil by fine roots but does not affect the ectomycorrhizal community structure in the organic horizons.

Keywords Picea abies · Radial growth · Potassium · Diversity · Abundance

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Contribution of the co-authors Lixia Wang carried out the research, determined root biomass, identified ectomycorrhizas, and co-wrote the manuscript.
Klaus Katzensteiner designed and instigated the K-fertilization study, worked on drafts of the manuscript, and advised on statistics.
Helmut Schume carried out measurements of radial growth and commented on the manuscript.
Marcela van Loo was involved in molecular determination of ectomycorrhizas and revised the manuscript.
Douglas Godbold lead the research on root and mycorrhizas, supervised Lixia Wang, and co-wrote the manuscript.

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1 Introduction

Tree growth in alpine and boreal forest is often limited by deficiency of mineral nutrients especially nitrogen (N) (Tamm 1991) and water (Bergh et al. 1999). Jonard et al. (2014) showed potassium (K) deficiencies in 36 % of spruce trees analyzed in the International Co-operative Programme, ICP Forest, and decreasing trends of the foliar K-status for this species. As a result of geological substrates low in K (Führer and Neuhuber 1998), and the remnant effects of acid deposition and biomass harvesting (Glatzel 1991), sub-optimal needle levels of K are common in montane forests in Austria. Due to the pivotal roles of many nutrients such as N, phosphorus (P), and K in photosynthesis, fertilization with these elements often results in an increase in

photosynthesis rates (Linder and Troeng 1980). For example, in eucalyptus, K-fertilization increased photosynthesis (Battie-Laclau et al. 2014) and increased aboveground biomass (Laclau et al. 2009; Epron et al 2011). In addition, K also has an important role in the movement of sucrose in and out of phloem vessels (Hermans et al. 2006); thus, K deficiency can strongly influence tree carbon (C) allocation (Epron et al 2011). In studies of *Betula pendula* seedlings, the root fraction of total seedling biomass decreased with increasing K limitation (Ericsson and Kähr 1993). Although fine roots represent a small proportion of total plant biomass (Vanninen and Mäkelä 1999), the morphology and the distribution of fine roots in the soil are very important factors for nutrient and water acquisition, which have impacts on growth (Nadelhoffer and Raich 1992). Fertilization of forest soils can result in changes in fine root biomass through direct improvement of soil chemical properties, such as after liming (Hahn and Marschner 1998). However, changes in fine root biomass can also be a consequence of greater aboveground growth or changes in allocation after fertilization (Kreutzer 1995; Helmisaari and Hallbäcken 1999). After N-fertilization, fine root biomass of *Picea abies* was increased in upper soil layers (Persson and Ahlström 1990). Investigations of the effects of K-fertilization on the fine root growth of forest trees at a stand level are rare (Tripler et al. 2006). In an old growth tropical forest, Wurzburger and Wright (2015) showed a significant reduction of fine root biomass in the surface soil (0–10 cm depth). The decrease in biomass was a consequence of reduced fine root tissue density and not a lower fine root length (Wurzburger and Wright 2015).

>Mycorrhiza is a mutualistic symbiosis between plant roots and fungi, which plays a critical role in the uptake and transport of poorly mobile soil nutrients, such as P and K (Marschner and Dell 1994). Although K can be abundant in soils, due to strong mineral adsorption, K availability can be low. Ectomycorrhizas can enhance K uptake and storage in roots by increasing the size of vacuolar pools and through increasing K influx rates and decreasing K efflux rates (Rygiewicz and Bledsoe 1984). In natural ecosystems, the fine roots of most trees are colonized by a large number of ectomycorrhizal fungal species (Erland and Taylor 1999; Courty et al. 2008). Such investigations have shown that ectomycorrhizal communities in forests can be highly diverse, but these communities tend to be dominated by a few species and have a high number of rare species (Erland and Taylor 1999; Courty et al. 2008). The ectomycorrhizal community structure is influenced by tree species (Lang et al. 2011) and also by environmental factors such as nutrients (Jones et al. 2012). In a long term study of mixed (N, P, K, magnesium (Mg), sulphur (S), and boron (B)) fertilizer application, fertilization tended to decrease species (Operational Taxonomic Units) richness of ectomycorrhizas associated with *Pinus contorta* (Hay et al. 2015). Nitrogen availability influences ectomycorrhizal species community composition in European *Pinus sylvestris* forests (Cox et al. 2010). Changes in ectomycorrhizal community structure are also common after addition of N containing fertilizer (Peter et al. 2001). Changes in community structure of ectomycorrhizas after N-fertilization can be a result of increases in tree productivity but also direct effects of N on nitrophobe ectomycorrhizal species (Peter et al. 2001). Several factors that increase tree productivity have been shown to change community structure of ectomycorrhizas; these include elevated CO_2 (Fransson et al. 2001; Godbold et al. 2015), defoliation (Pestana and Santolamazza-Carbone 2011), and stem harvesting (Jones et al. 2010). The change in ectomycorrhizal community structure through all of these factors is linked to changes in C allocation to roots (Godbold et al. 2015).

Studies of K-fertilization of forest trees are less common than studies with other nutrients (Wurzburger and Wright 2015; Ouimet and Moore 2015). Despite the negative effects of low K availability in montane forests, to the best of our knowledge, there are no published investigations of the effects of remedial K-fertilization on roots and ectomycorrhizas in European forests. In the work presented here, the influence of K-fertilization on fine root biomass and ectomycorrhizal community structure of *Picea abies* is investigated. The work tested the hypothesis that K-fertilization would lead to an increase in tree growth and subsequent increase in fine root biomass. Furthermore, we investigated whether changes in aboveground growth and fine root biomass lead to changes in ectomycorrhizal community structure.

2 Materials and methods

2.1 Study site

The research site is located at the Niederwechsel in the Southeast of Austria (47° 31′ 50″ N, 15° 59′ 20″ E). The stocking of the stand (55 years old in 2005) was dominated by Norway spruce (*Picea abies*) with additional single stems of *Larix decidua* and *P. sylvestris*. The stocking density was around 1250 stems ha^{-1}; the dominant tree height at the time of fertilizing (2005) was 16 m. The stem diameters were primarily in the distribution classes between 13 and 20 cm (Online resource 1). The site is 18 to 20 % inclined towards South to Southwest and is located between 1100 and 1200 m above sea level. The bedrock consists of Gneiss and Slate, from which a Skeletic Dystric Cambisol has developed. In terms of texture, the soil was classified as a sandy loam, while Moder constitutes the humus form (Zanella et al. 2011). The stone volume in the soil was estimated to be in total between 37 and 60 %. The volume of stones <63 mm was 12 % in the A horizon and 35 % in the B horizon. The volume of stones >63 mm was 25 % in both horizons.

Few stones were present in the organic horizons. The site has an oligotrophic character and is moderately dry. At the time of sampling in 2013, the pH of the soil was between 4.3 and 4.4 (water) and the water content of the humus layer ca. 56–58 %. There were no significant differences in soil moisture or pH between plots or treatments.

Analysis in 2004 showed that *Picea abies* trees at the site had a strong potassium deficiency, with needle values of 2.5 to 3 mg g^{-1} needle dry mass (Katzensteiner et al. 2008). Mellert and Göttlein (2012) set the lower limit of the normal range at 5.2 mg g^{-1} and the lower limit of latent deficiency at 3.5 mg g^{-1} (Mellert and Göttlein 2012). There were no significant differences in the K content between the K-fertilized plots and the control plots at the beginning of the experiment. Prior to the experiment, the cation exchange capacity was around 15 $mmol_c$ 100 g^{-1} in the topsoil (0–10 cm depth), decreasing to <2 $mmol_c$ 100 g^{-1} in the subsoil. The base saturation varied between <10 and 20 %.

2.2 Experimental design

In 2004, 18 plots of ca. 400 m^2 were established, of which 9 were fertilized in June 2005 with potassium sulphate (K + S, Kali GmbH, Kassel). The product used contained 40 % water-soluble K and was distributed by hand to the equivalent of 500 kg ha^{-1}, giving a K addition of ca. 200 kg ha^{-1}. All research plots were established in the same stand, which was homogeneous with respect to stand composition and site conditions. The plots were assigned randomly (Online resource 2). In the work described here, samples were taken from 7 control plots and 6 K-fertilized plots.

2.3 Determination of basal area and radial growth

Stand basal area increment was assessed by two complete inventories of diameters in breast height (DBH) in spring 2005 and autumn 2013 using a Pi-tape. Therefore, the given basal area increments reflect the increments of 9 growing seasons. Additionally, the diameter increment in breast height of one tree per plot was measured in intervals of approximately 1 week using dendrometer tapes. For a very high resolution in time, three trees per treatment were equipped with automatically registering dendrometers (Environmental Measuring Systems, Brno, Czech Republic). Values were recorded in 15-min intervals.

2.4 Root sampling and analysis

Five soil samples were taken from each of the seven control plots and the 6 K-fertilized plots with a stainless steel corer (7 cm diameter) to a maximum depth of 40 cm in September 2013. Sampling of soil cores and roots was restricted to the plot centers (inner squares of 10 by 10 m) in order to avoid a bias by potential fertilizer transfer via lateral water flux. The soil cores were transported on ice back to the laboratory where they were stored at 4 °C for later examination. All soil cores were analyzed within 4 weeks. For analysis of fine roots and ectomycorrhizas, the organic layer of the soil cores were divided into an Oi + Oe layer composed of non or poorly decomposed litter, and an Oa layer in an advanced stage of decomposition (Zanella et al. 2011), as well as a mineral soil layer of 15 cm length. Taking a 15 cm length of the mineral soil normalized the maximum sampling depth to ca. 30 cm. The thickness of each horizon (Oi + Oe, Oa, and mineral soil) was determined and used to calculate fine root biomass per soil volume. The thickness of Oi + Oe was 6.6 ± 0.4 cm in control plots and was 6.8 ± 0.4 cm in K-fertilized plots; the thickness of Oa was 8.2 ± 0.9 cm in the control plots and was 7.5 ± 0.8 cm in K-fertilized plots. From each horizon, roots were removed by hand sorting and categorized as dead or alive on the basis of color and tensile strength. Live roots were categorized into fine roots (<2 mm diameter) and coarse roots (>2 mm diameter). From three soil cores per plot, from the fine roots removed from each Oi + Oe and Oa horizon, a subsample was taken for ectomycorrhizal analysis. For determination of ectomycorrhizas in total, 22 soil cores (one extra core was analyzed) from control plots and 19 soil cores (one extra core was analyzed) from K-fertilized plots were analyzed. The root segments removed in the subsamples had approximately 150–300 root tips. The subsamples were then washed carefully, placed into petri-dishes filled with clean tap water, and stored at 4 °C (analyzed within three weeks). All clearly definable ectomycorrhizal root tips from each sample (22 soil cores × two soil layers = 44 samples for control plots; 19 soil cores × two soil layers = 38 samples for K-fertilized plots, respectively) were sorted into morphotypes based on the method described by Agerer (1997), using a ZEISS (Stemi 2000-CS) dissecting microscope which was connected with an AxioCam ERc5s camera. The method of Agerer (1997) is based on morphological characteristics, including branching structure, tip shape and dimensions, mantle color and texture, and emanating hyphae and rhizomorphs. This method allows identification of ectomycorrhizas to genus or species levels and is referred to as morphotypes in the following text. The final identification to genus or species level (where possible) was carried out by sequencing of DNA (see below) and after identification are referred to as taxa (Read et al. 2004). The total number of root tips colonized by each of the morphotype was counted under the dissecting microscope.

Between 1 and 10, ectomycorrhizal root tips of each morphotype were placed into micro-centrifuge tubes. The number of root tips varied from one to ten depending on the abundance of the morphotype. The samples were then stored at −20 °C until DNA extraction. The remainder of the root subsample was then scanned using the WinRHIZO program to determine the total number of fine root tips, as well as the length of the fine roots for each sample. The fine root subsamples and the remaining total fine root mass were subsequently oven dried (65 °C) and weighed. From each soil core and horizon, all root samples, both the total mass samples and the subsamples, were dried and weighed separately, and the values were used to calculate a mean for each plot.

Fine root biomass per m^2 was calculated using the surface area of the core and scaled to m^2. The values of fine root biomass in the mineral soil were corrected for the volume content of stones >63 mm. Biomass per cubic decimeter was determined by scaling the volume of the soil horizon sampled to 1 dm^3. The measurements of length, root tips, and fine root dry weight were used to calculate specific root tip number (tips g^{-1} Dwt) and specific root length (m length g^{-1} Dwt).

2.5 DNA extraction and PCR amplification

The 1.5-ml micro-centrifuge tubes containing the ectomycorrhizal root tips were placed in liquid nitrogen for 5–10 min, and the tips were ground with a sterilized glass bar. DNA from the crushed ectomycorrhizal root tips was extracted by using DNeasy Plant Mini kits (QIAGEN), and the extracted DNA was stored at −20 °C until the PCR reactions were run. For the PCR reactions, 1 μl DNA template was mixed with 12.5 μl MyTaq mix (BIOLINE), 0.5 μl ITS1F (20 μM) primer (CTTGGTCATTTAGAGGAAGTAA forward), 0.5 μl ITS4 (20 μM) primer (TCCTCCGCTTATTGATATGC reverse), and diluted with 10.5 μl distilled deionized H_2O. For the PCR, the Thermocyler (TProfessional Basic) cycling parameters were an initial denaturation at 95 °C for 1 min, a second denaturation at 94 °C for 30 s, annealing at 50 °C for 40 s, and extension at 72 °C for 30 s, followed by a final auto-extension step at 72 °C for 4.5 min. The step from the second denaturation to extension was run for 35 cycles. To check the success of the PCR amplification, electrophoresis was carried out using 1 % regular agarose gel stained with SERVA DNA Stain G in a 1 % Tris-EDTA buffer solution. The gel was then visualized under UV light. If a clear single band was visible on the gel, the PCR products were sent for sequencing. Sequencing was done by Macrogen Inc., Seoul, Korea. Sequencing reactions were performed in a MJ Research PTC-225 Peltier Thermal Cycler using a ABI PRISM® BigDyeTM Terminator Cycle Sequencing Kits with AmpliTaq® DNA polymerase (FS enzyme) (Applied Biosystems), following the protocols supplied by the manufacturer. Single-pass sequencing was performed on each template using an ITS4 primer. The fluorescent-labeled fragments were purified from the unincorporated terminators using the BigDye® XTerminator™ purification protocol. The samples were resuspended in distilled water and subjected to electrophoresis in an ABI PRISM® 3730XL sequencer (Applied Biosystems). The sequences obtained were manually checked and edited using Finch TV_1_4_0. Query sequences were compared with sequences on the UNITE and NBCI databases to identify the species of ectomycorrhiza; all but one of the sequences had a similarity of over 97 % (Online resource 3). The sequences were deposited in GenBank with Accession No. KU861471–KU861502. Four morphotypes could not be identified using the DNA analysis and were labelled as unknown.

2.6 Statistical analyses

Relative frequency was calculated as the absolute frequency of individual taxa divided by the sum of absolute frequencies for all taxa (equation 1). Relative abundance was calculated as the ectomycorrhizal root tips of individual taxa divided by the total ectomycorrhizal root tips for all taxa (equation 2). Importance values for individual ectomycorrhizal fungal taxa were calculated by summing their relative abundance and their relative frequency (equation 3) (Douglas et al. 2005). For the parameters determined, the significance of the difference between control and K-fertilized plots, and also the difference between the soil layers, were tested using two-way analysis of variance (ANOVA). The parameters determined were fine root biomass (g fine root m^{-2} soil surface area), fine root density (g fine root per cubic decimeter soil volume), fine root tips (shown as thousands of fine root tips m^{-2} soil surface area), fine root length (m fine root length m^{-2} soil surface area), specific root length, specific root tip number, and the Student–Newman–Keuls test was used for post hoc multiple comparison in SPSS. Difference in Shannon index, ectomycorrhizal root tips relative abundance and importance value between control and K-fertilized plots, and the relative frequency, ectomycorrhizal root tips abundance between different soil layers, were tested using the *t* test. Estimation of the total number of expected taxa was made with the program Estimates using the Chao estimator of taxa richness .

Equations:

$$\text{Relative Frequency} = \text{fi}/\Sigma\text{f (frequency of a given taxa (fi) as a proportion of the sum of the frequencies for all taxa)} \quad (1)$$

$$\text{Relative Abundance} = \text{ni}/\Sigma\text{ni (ni is the number of individuals of a given taxa counted)} \quad (2)$$

$$\text{Importance Value} = \text{Relative Abundance} + \text{Relative Frequency} \quad (3)$$

3 Results

In 2005, the basal area of spruce was not significantly different between the control and K-fertilized plots (Table 1). Spruce represents 82 % of the total stand basal area (Online resource 1). By 2013, the basal area had increased by 6.5 m^2 ha^{-1} in the control plots and by 8.2 m^2 ha^{-1} in the K-fertilized plots. The basal area increment was significantly different between the control and the K-fertilized plots ($P = 0.006$).

3.1 Fine root biomass

For the whole soil profile, the total fine root biomass was 670 ± 71 g m^{-2} in the control plots and 790 ± 66 g m^{-2} in the K-fertilized plots and was not significantly different. Similarly, there was no significant difference between control and K-fertilized plots in the Oi + Oe or Oa layers for the fine root biomass determined as g m^{-2} (Fig. 1a) or g dm^{-3} (Fig. 1b). In the mineral soil, the fine root biomass (Fig. 1a, b) was almost twice as high in K-fertilized plots compared to the control plots, and significant differences were shown. The number of root tips (root tips m^{-2}) was higher in the Oi + Oe layer compared to the other two layers (Fig. 1c), and the difference was significant. In the mineral soil, a significantly higher number of fine root tips were found in the K-fertilized plots. Fine root length did not differ between the treatments in the Oi + Oe and Oa layers but was significantly higher in the mineral soil of the K-fertilized plots (Fig. 1d).

3.2 The comparison of fine root characteristics between two sites

The patterns shown in fine root length and the number of root tips in the different soils layers and treatments are reflected in the specific root length and specific root tip number (Table 2). The specific root tip number (root tips g^{-1} dwt) was highest in the Oi + Oe layer compared to the other two layers (Table 2). There were no significant differences between the treatments in the Oi + Oe and Oa layers, but in the mineral layer (0–15 cm), the specific root tip number was significantly higher in the K-fertilized plots compared to the control plots ($P = 0.006$). Similarly, the specific root length was also highest in the Oi + Oe layer, and again in the mineral layer, there was a significant difference between the control and K-fertilized plots.

3.3 Frequency, abundance, and diversity patterns of identified ectomycorrhizal taxa

In the Oi + Oe and Oa soil layers, a total of 22 ectomycorrhizal fungal taxa were determined. On the control plots 15 taxa and on the K-fertilized plots, 17 ectomycorrhizal fungal taxa were determined (Table 3). These were detected after examining 2094 and 1975 root tips from the control and K-fertilized plots, respectively (Table 3). Comparison of the total number of tips and the ectomycorrhizal tips (Table 3) shows that a large percentage of the tips did not have definable

Table 1 Basal area of the *Picea abies* plots in 2005 before fertilization with 500 kg ha^{-1} K_2SO_4 and in 2013 at sampling. The basal area increment, total root biomass, and the ratio of fine root biomass to basal area of the control and the K-fertilized plots are also shown

	Control		K-fertilized	
	2005	2013	2005	2013
Basal area increment in percent		24.0 ± 1.4a		28.8 ± 1.1b
Total root biomass (g m^{-2})		670 ± 71a		790 ± 66a
Basal area in (m^2 ha^{-1})	27.2 ± 3.4a	33.7 ± 4.2a	28.4 ± 3.1a	36.6 ± 4.2b
Total root biomass/basal area (g fine root m^{-2} basal area)		20.1 ± 2a		21.7 ± 1.7a

Mean ± SE. The *t* test was used to determine the significance of difference between control and K-fertilized plots. Within a year, between control and K-fertilized plots, data points followed by different letters are significantly different ($P \leq 0.05$)

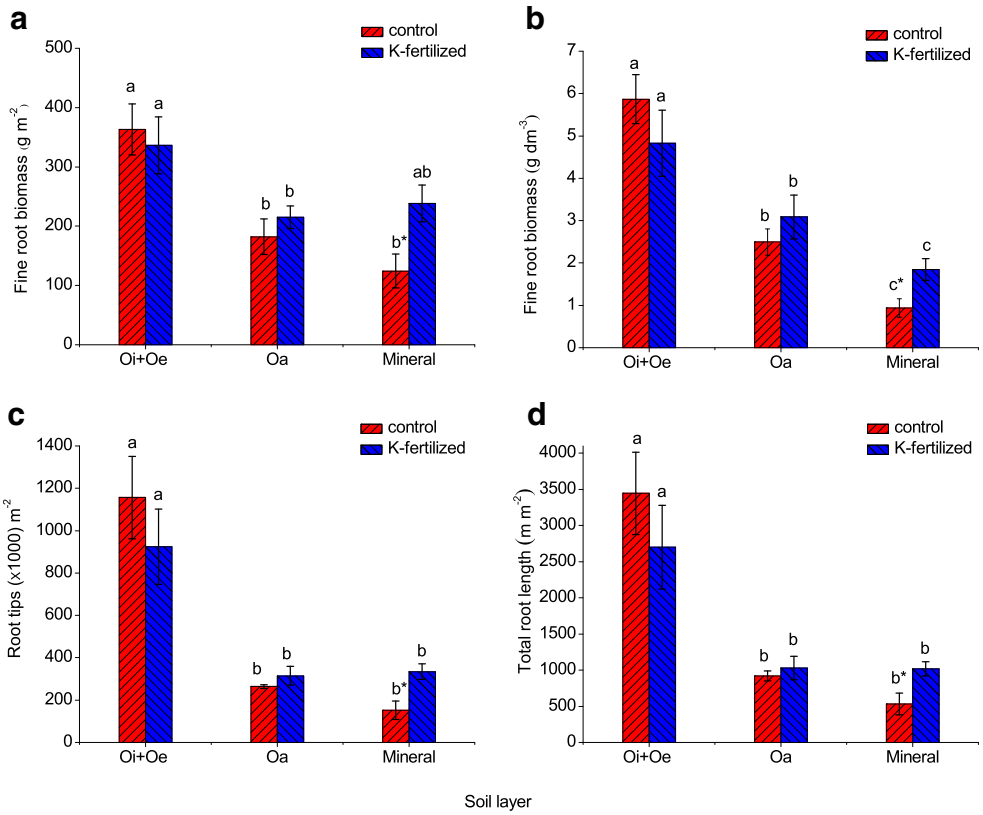

Fig. 1 **a** Fine root biomass (g fine root m^{-2} soil surface area), **b** fine root density (g fine root dm^{-3} soil volume), **c** fine root tips (1000 of fine root tips m^{-2} soil surface area), and **d** total fine root length (m fine root length m^{-2} soil surface area) in different soil layers of control and K-fertilized (500 kg ha^{-1} K_2SO_4) plots of *Picea abies*. *Bars* show means ± SE. *Bars* with different *lower case letters* indicate significant differences between different soil layers in the same treatment ($P \leq 0.05$). *Asterisks* indicate significant differences between control and K-fertilized plots for same soil layer ($P \leq 0.05$)

ectomycorrhizas. Using the program Estimates, the estimated total richness of taxa for the control and K-fertilized was 23 and 26 taxa, respectively (Online resource 4, Table 3). Hence, the observed number of ectomycorrhizal taxa was 65 % of the estimated richness in the control plots and 66 % in the K-fertilized plots. The mean number of ectomycorrhizal taxa detected in each sample was ca. 2 and did not differ between control and K-fertilized plots (Table 3).

Ten taxa were detected that were shared between control and K-fertilized plots (Table 4). *Lactarius rufus* was the dominant taxa (Table 4) in both treatments comprising 43 or 32 % of all ectomycorrhizal root tips in control and K-fertilized plots, respectively, but no significant difference was observed in relative abundance between the two sites ($P = 0.401$). However, numerically, *L. rufus* occurred in a greater number of samples and had a higher abundance value in the control plots. *Cenococcum geophilum*, *Meliniomyces variabilis*, and *Tylospora fibrillosa* were the other three most common taxa (Table 4). These taxa were similar between plots, both in the number of samples in which they were found, and in their relative abundance value (Table 4). Figure 2 shows that the two sites have a similar pattern when the importance values are ranked. For the three most important taxa, *L. rufus*, *T. fibrillosa*, and *C. geophilum*, no significant differences were found between control and K-fertilized plots ($P = 0.426$, $P = 0.922$, $P = 0.279$), respectively. Table 4 shows that *C. geophilum* comprised just over 7 % of the total ectomycorrhizal root tips in control plots and nearly 10 % of total ectomycorrhizal root tips in K-fertilized plots. *M. variabilis* comprised 3.9 % of the total ectomycorrhizal root tips in control plots and 3.6 % of the total ectomycorrhizal root tips in K-fertilized plots (Table 4). *L. rufus* and

Table 2 Specific root tip number and specific root length of the roots of *Picea abies* from different soil layers of control and K-fertilized (500 kg ha^{-1} K_2SO_4) plots

	Specific root tip number (root tips g^{-1} root)		Specific root length (m g^{-1} root)	
	Control	K-fertilized	Control	K-fertilized
Oi + Oe	3099 ± 177a	2657 ± 260a	9.30 ± 0.58a	7.72 ± 0.89a
Oa	1559 ± 33b	1474 ± 25b	5.27 ± 0.42b	4.93 ± 0.56b
Mineral	826 ± 61c*	1647 ± 17b	2.74 ± 0.61c*	4.88 ± 0.54b

Mean ± SE. Data points with different lower case letters indicate significant differences between different soil layers in the same treatment ($P \leq 0.05$). Asterisks indicate significant differences between control and K-fertilized plots for same soil layer ($P \leq 0.05$)

Table 3 The number of root tips and total number of ectomycorrhizal root tips examined per treatment and the detected and estimated number of taxa in the Oi + Oe and Oa soil layers of control and K-fertilized (500 kg ha^{-1} K_2SO_4) plots

Characteristics	Control	K-fertilized
Total taxa detected	15	17
Mean taxa per sample	2.0 ± 0.2a	1.9 ± 0.2a
Estimated richness	23	26
Shannon index	1.8 ± 0.1a	1.9 ± 0.1a
Total root tips	9944	9175
Total ectomycorrhizal root tips	2094	1975

Shown is the Mean ± SE. As indicated by the same letters, the values of mean taxa per sample and Shannon index were not significantly different between control and K-fertilized ($P \leq 0.05$)

C. geophilum together comprised almost half of the ectomycorrhizal fungal root tips at both sites (Table 4).

For the most common taxa at the site, there were no significant differences in tip abundance or importance value between the control and K-fertilized plots (Table 4, Fig. 2). The main difference between the ectomycorrhizal community structures of the treatments was in the rare taxa. In both treatments, a number of rare taxa occurred only in 1 or 2 samples (Table 4). Of the 9 or 10 taxa that occurred in 1 or 2 samples in the control and K-fertilized treatment, respectively (Table 4), and had a low importance rank (Fig. 2), four taxa occurred in both treatments, *Piloderma sphaerosporum*, *Cortinarius delibutus*, *Cortinarius neofurvolaesus*, and *Lactarius lilacinus*. Thus, of the rare taxa that were not common to both treatments, four occurred in the control and six in the K-fertilized plots. Of these, two morphotypes could not be identified in both treatments. The Shannon diversity index, calculated from values from the Estimates program, was also not significantly different between control and K-fertilized plots ($P = 0.461$).

3.4 Vertical distribution of 10 shared ectomycorrhizal fungal taxa

The distribution of the 10 shared ectomycorrhizal taxa in the Oi + Oe and Oa layer is presented in Fig. 3. Among these 10 shared ectomycorrhizal fungal taxa, *L. rufus*, *C. neofurvolaesus*, *T. fibrillosa*, and *C. delibutus* appeared

Table 4 The 22 ectomycorrhizal fungal taxa detected on the roots of *Picea abies* from control and K-fertilized (500 kg ha^{-1} K_2SO_4) plots

Control			K-fertilized		
Fungal taxa	Occurrence	Abundance	Fungal taxa	Occurrence	Abundance
Lactarius rufus	22	0.428	***Lactarius rufus***	17	0.321
Cenococcum geophilum	11	0.07	***Cenococcum geophilum***	12	0.098
Tylospora fibrillosa	8	0.122	***Meliniomyces variabilis***	7	0.036
Meliniomyces variabilis	7	0.039	***Tylospora fibrillosa***	6	0.094
Russula ochroleuca	7	0.025	***Tylospora asterophora***	4	0.063
Paxillus involutus	4	0.038	*Cortinarius subtortus*	3	0.035
Cortinarius delibutus	2	0.121	***Russula ochroleuca***	3	0.003
Tylospora asterophora	2	0.031	***Cortinarius neofurvolaesus***	2	0.147
Unknown *14*	2	0.046	***Piloderma sphaerosporum***	2	0.037
Boletus edulis	2	0.021	***Cortinarius delibutus***	2	0.104
Lactarius lilacinus	2	0.014	*Cortinarius glandicolor*	1	0.025
Cortinarius neofurvolaesus	1	0.017	Unknown 22	1	0.019
Piloderma olivaceum	1	0.022	*Clavulina* spp.	1	0.004
Piloderma sphaerosporum	1	0.004	*Rhizopogon salebrosus*	1	0.002
Unknown 11	1	0.003	Unknown 21	1	0.007
			Amanita submembranacea	1	0.003
			Lactarius lilacinus	1	0.001

Taxa common to both treatments are shown in bold typeface. Shown are the number of samples in which each taxa occurred out of a total of 44 samples (control) and 38 samples (K-fertilized), as well as the relative root tip abundance of each taxa calculated as a fraction of the total number of ectomycorrhizal root tips per treatment

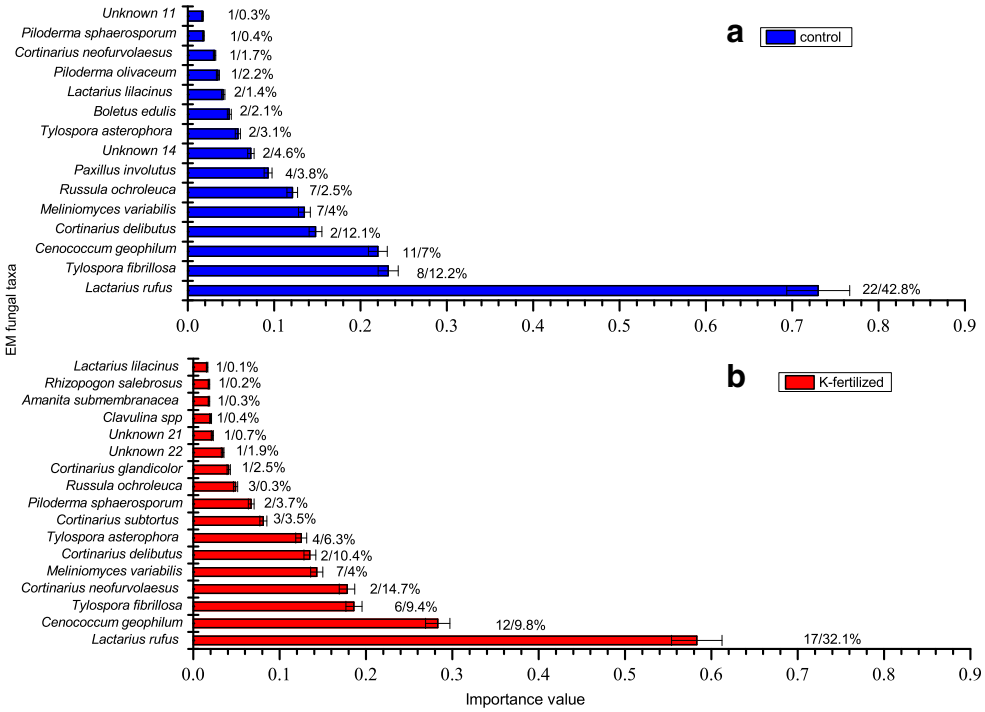

Fig. 2 **a**, **b** Ranked distributions of different ectomycorrhizal taxa according to importance values based on the sum of relative ectomycorrhizal root tip abundance and relative sample frequencies of ectomycorrhizal taxa on the roots of *Picea abies* taken from **a** control plots and **b** K-fertilized (500 kg ha^{-1} K_2SO_4) plots. *Numbers* at the end of each *bar* correspond to sample frequency for each taxa and the percent of total ectomycorrhizal root tips (see legend to Table 4)

more often and abundant in the Oi + Oe layer than the Oa layer. Significant differences were detected in the absolute abundance of *L. rufus* ($P = 0.001$) and in *T. fibrillosa* ($P = 0.048$) in the Oi + Oe layer.

4 Discussion

4.1 Comparison of fine root distribution between treated and control plots

Over the 8-year treatment period, a single K-fertilization led to a sustained increase in basal area increment of ca. 26 %. Before fertilization, the stand at Niederwechsel had low levels of K in needles and also yellowish short needles (Katzensteiner et al. 2008). In a young *Abies balsamea* stand with symptoms of chlorosis, K-fertilization led to an increase in radial growth for over 11 years (Ouimet and Moore 2015). The 26 % increase in radial growth shown at Niederwechsel after K-fertilization is of a similar value to that induced by elevated CO_2. An average increase in growth of 23 % was shown in free air carbon dioxide enrichment studies (Norby et al. 2005; Smith et al. 2013). In N-fertilization experiments in *Picea abies* stands in Sweden, the average increase in radial growth was ca. 30 % after a single addition of 150 kg N ha^{-1} (Nohrstedt 2001). In Eucalyptus, fertilization with K doubled CO_2 assimilation rates (Battie-Laclau et al. 2014). In an adjacent experiment, the K addition lead to an increase in the amount of gross primary production allocated to stem wood production (Epron et al. 2011). The increase growth under elevated CO_2 was also a direct consequence of increased rates of photosynthesis. Similarly, N-fertilization resulted in higher levels of needle chlorophyll and higher rates of photosynthesis per unit area of needles in *Picea abies* (Linder and Troeng 1980).

Addition of nutrients can result in greater fine root growth through the direct effects of changes in soil chemistry and nutrient availability (Hahn and Marschner 1998), but also via indirect effects through greater aboveground productivity, and thus greater C availability to fine roots (Norby et al. 2010). The greater productivity can be achieved as discussed above by fertilization with K, N, or CO_2; however, the effects of elevated CO_2 are only via aboveground driven changes in productivity. Thus, comparison between K- and N-fertilization and elevated CO_2 may be a useful tool to distinguish the direct and indirect effects of fertilization on fine root biomass. In an old growth tropical forest (Wurzburger and Wright 2015), K-fertilization resulted in a significant reduction in fine root biomass of the surface soil (0–10 cm depth). This is in contrast to the results of our study in which K-fertilization had no effect on roots in the upper organic soil layers but significantly increased fine root biomass in the mineral soil. As in 2006, 1 year after fertilization, fine root biomass had not changed (Katzensteiner et al. 2008); it is unlikely that these changes are due to the direct effects of changes in soil chemistry. A similar increase in fine root biomass in the mineral soil layer was shown after $MgSO_4$ fertilization of Mg deficient *Picea abies* (Raspe 1997). In comparison, fertilization with dolomitic lime resulted in an increase in fine root biomass only in the organic soil horizons (Raspe 1997).

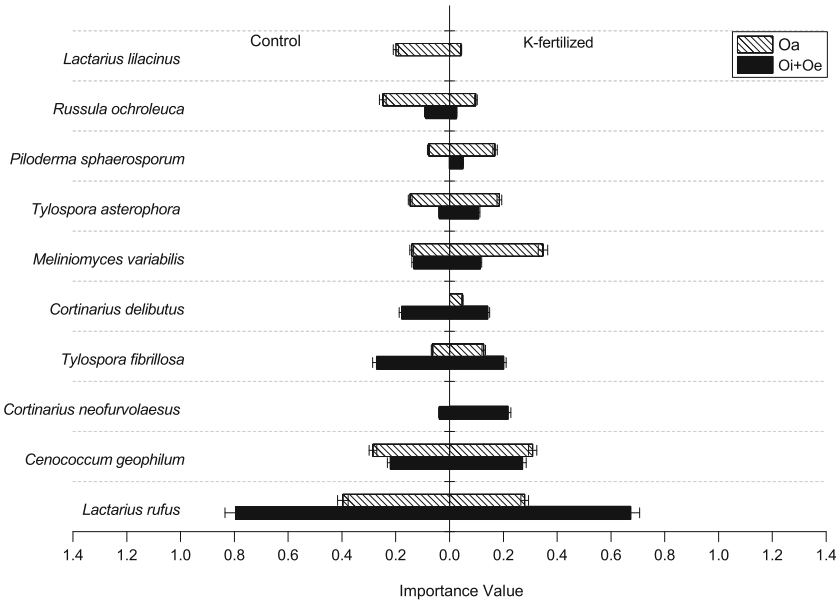

Fig. 3 Comparison of the importance value of shared ectomycorrhizal taxa on roots of *Picea abies* taken from the Oi + Oe and Oa layers in control and K-fertilized (500 kg ha^{-1} K_2SO_4) plots. Mean ± SE. The importance value was calculated from the sum of the relative ectomycorrhizal root tip abundance and relative sample frequencies

Fertilization with $MgSO_4$ led to a rapid increase in the levels of Mg in fine roots and improved Mg nutrition. Magnesium deficiency is known to decrease C translocation to roots (Fink 1992). In many studies, elevated CO_2 has also been shown to increase fine root biomass in deeper soil layers (Iversen 2010; Smith et al. 2013) and has been suggested to be the response to a greater C availability and a greater water and nutrient demand. However, the reason for the increase in root biomass in deeper soil layers is unknown (Iversen 2010).

In the mineral soil, the fine root biomass was ca. 47 % higher after K-fertilization, and the fine root length in the mineral soil was ca. 48 % greater after K-fertilization. The morphological traits of fine roots, such as root diameter and tissue density, are highly plastic in response to resource supply. This plasticity has been shown for both C (Smith et al. 2013) and soil conditions (Lõhmus et al. 1989). In other studies, addition of N and liming of soils was shown to reduce specific root length (Ostonen et al. 2007). Similarly, elevated CO_2 was also shown to either reduce specific root length (Ostonen et al. 2007) or have no influence on root morphology (Smith et al. 2013). After K-fertilization, changes in specific root tip number and specific root length were again found only in the mineral soil, emphasizing the difference in the response of roots shown in the organic and mineral soil layers.

After K-fertilization, an increase in radial growth of the trees was determined suggesting an increase in C availability within the tree. In addition, K is known to be important in both phloem loading and unloading of sucrose (Hermans et al. 2006), and K deficiency is known to impede sucrose export from leaves resulting in a decrease in allocation to roots (Hermans et al. 2006). Thus, an increase in K-status with the tree has the potential to increase C allocation to roots. However, after K-fertilization, the basal area to fine root biomass did not change which suggests that there is no major change in allocation, but rather larger trees support a larger fine root system, and that this is formed preferentially in less exploited mineral soil layers. For example, for *Picea abies*, there is a strong positive correlation between stem cross sectional area and fine root biomass per tree (Finér et al. 2007). Thus, larger trees have a higher fine root biomass, and on a stand basis, fine root biomass will be higher without changes in allocation to fine roots.

4.2 Distribution and diversity of mycorrhizas

Potassium fertilization increased the radial growth of trees, and the proliferation of fine roots into the mineral soil, two effects that also occur under elevated CO_2. The change in ectomycorrhizal community structure under high CO_2 is often shown as a change in the abundance of dominant taxa (Fransson et al. 2001; Godbold et al. 2015) and has been related to changes in the supply of C to roots (Parrent and Vilgalys 2007). Recently, Clemmensen et al. (2015) showed that productivity of *Picea abies* was a factor most strongly related to changes in fungal community composition. In the control and K-fertilized plots in total, 22 ectomycorrhizal taxa were determined, 65 % of the estimated richness. Bruns (1995) suggested that 20–35 taxa typically occur in single species forests (Bruns 1995). In a young *Picea abies* plantation, Korkama et al. (2006) detected 34 ectomycorrhizal taxa, which was 75 % of the estimated richness. In fast and slow growing clones of 11-year-old *Picea abies*, Korkama et al. (2006) showed that the faster growing clone had a more complex ectomycorrhizal community structure. Thirty taxa were detected in fast growing clones and 18 ectomycorrhizal taxa in slow growing clones (Korkama et al. 2006). The differences in

the number of taxa were related to a higher fine root tip density in some of the fast growing clones. In the expanding root systems of the 11-year-old *Picea abies*, the higher fine root tips density probably results in a higher number of root tips for ectomycorrhizal colonization (Korkama et al. 2006). As in most studies of below ground ectomycorrhizal diversity, we have focused on the upper organic horizon, where root tip density is high (Rosling et al. 2003). After K-fertilization, faster growth has not affected the ectomycorrhizal community structure. The lack of change is also related possibly to a lack of change in the number of fine root tips in the upper soil layers, even if due to fine root turnover, there must have been a considerable renewal of fine roots during the 8 years after fertilization. In the study of Korkama et al. (2006), the relative abundance of *Tylospora asteraphoa and Tylospora terrestis*, the two most abundant taxa (total 55 %) on the slow growing clones, was negatively correlated with ectomycorrhizal taxa richness (Korkama et al. 2006). In the K-fertilization plots, *T. fibrillosa* had a lower abundance, and *Tylospora asteraphoa* had a higher abundance than on the control plots, but these two taxa only had a combine relative abundance of 15 %.

The most abundant taxa in this study, *L. rufus* and *T. fibrillosa*, occurred significantly more often in the Oi + Oe layer compared to the Oa layer. As did both *C. neofurvolaesus* and *C. delibutus*, but for these two taxa, the differences were not significant. In contrast, the very abundant *C. geophilum* had no significant difference in occurrence in the Oi + Oe and Oa layers. This distribution has been shown in a number of studies (Baier et al. 2006; Courty et al. 2008) where the medium distance exploration types (*L. rufus*, *C. neofurvolaesus*, and *C. delibutus*) occur more often in the loose substrate horizons (Oi + Oe) than the more compact Oa layers. However, the short distance exploration type *T. fibrillosa* was also found preferentially in the Oi + Oe layer, suggesting that factors other than the compactness of the soil substrate may also be important, such as tolerance to fluctuations in soil temperature and moisture (Baier et al. 2006). Between the control and the K-fertilization treatment, no differences in the relative abundance of exploration types or the hydrophobicity of the ectomycorrhizal taxa were shown.

Our study shows that fertilization of K-deficient stands of *Picea abies* results in an increase in radial growth, but that higher growth rates do not automatically result in a change in relative abundance and taxa richness of ectomycorrhizas. However, an increase in growth due to K-fertilization leads to great exploration of the mineral soil by fine roots.

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Compliance with ethical standards

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