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REGULAR ARTICLE

Fire-derived charcoal affects fine root vitality in a post-fire Gmelin larch forest: field evidence

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Abstract
Background and aims Fine roots are only a small part of total ecosystem biomass, but substantially contributing to soil carbon accumulation in boreal forests. Wildfires may influence fine root dynamics directly via heating and indirectly via interactions with wildfire-deposited charcoal. We tested if the presence of charcoal in a recently burned larch forest affected fine root vitality.
Methods This study was stratified across vegetation type (understorey and overstorey), soil depth (upper and lower layers), and root diameter classes: fine (≥0.5 mm but <2 mm diameter), and very fine (diameter < 0.5 mm) in a recently surface-burned Gmelin larch (*Larix gmelinii (Rupr.)* Rupr.) forest in the Russian Far East.
Results Charcoal content and fine root vitality were positively correlated for overstorey vegetation, but negatively correlated for understorey vegetation. On the other hand, total charcoal content did not significantly correlate with very fine root vitality, biomass or necromass.
Conclusions Our study provides the first field evidence that fine root dynamics are influenced by fire-derived charcoal in frequently burned boreal forest. Furthermore, the effect of charcoal on fine root vitality depends on the vegetation type, root diameter, and soil depth, which indicates the necessity of complicated modeling of soil organic carbon derived from fine roots in post-fire boreal forests.

Keywords Fine root vitality · Charcoal · Black carbon · Discontinuous permafrost · Belowground plant competition · Wildfire · Carbon sequestration

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Introduction

Boreal forest soils are large carbon (C) pools containing up to 1700 Pg C which is 84% of total C stored in boreal forest biome (Dixon et al. 1994; Anderson 1991; Deluca and Boisvenue 2012). A substantial amount of photosynthetically fixed C in forest ecosystems is directed to fine roots which influences belowground C dynamics (Högberg et al. 2001; Clemmensen et al. 2013). Fine roots (<2 mm diameter) comprise a small part of the conifer biomass (< 5%), but substantially contribute to soil C accumulation via synthesis and senescence. Fine root turnover results in belowground C input larger than C input from aboveground litter (Persson and Stadenberg 2009; Brunner et al. 2013). Thus, we need to enhance our understanding of the fine root dynamics in soil to better understand the mechanism through which C is sequestered in boreal forests.

Fine root dynamics are strongly affected by disturbances (Persson and Ahlström 2002; Yuan and Chen 2013). In boreal forests, wildfire is one of the major disturbances, and it may influence fine root dynamics. In eastern Eurasia, anthropogenic surface fires have been increasing and changing the forest structure (Goldammer and Furyaev 1996; Wang et al. 2001; Makoto et al. 2007). Surface fire influences fine root dynamics through both direct and indirect pathways. Directly, fire-derived heat substantially reduces the fine root biomass and specific root length (Swezy and Agee 1991; Hart et al. 2005; Smirnova et al. 2008). Indirectly, fires can modify soil nutrient concentrations, change C:N ratios, increase pH, increase soil bulk density and aeration, and reduce water holding capacity (Neary et al. 1999; Certini 2005; Santín and Doerr 2016), and consequently, influence fine root traits (Mei et al. 2009; Yuan and Chen 2013; Makita et al. 2016). Fine root productivity temporarily increases after surface fires because of the partial survival of the fine root and its development to utilize fire-derived nutrients, but this is only temporary (Finér et al. 1997; Day et al. 2006; Singh et al. 2008; Yuan and Chen 2013). Fire-induced changes in forest soils are also caused by the incorporation of charcoal, which is an influential and unique process, through which fire influences the belowground ecosystem (Wardle et al. 1998; Preston and Schmidt 2006; Makoto et al. 2011b). However, to better understand the mechanism through which fire disturbances influence boreal C dynamics, we also need to understand how fire-derived charcoal influences fine root dynamics after a fire.

Charcoal due to highly porous structure and a high surface area occludes nutrients and water and may enhance fine root growth (DeLuca and Aplet 2008; Makoto et al. 2010). Thus, charcoal increases soil phosphorous (P) availability and fine root biomass of larch seedlings in a microcosm experiment (Makoto et al. 2010). Furthermore, charcoal positively influences pH, water content, and available P concentration of soil in a recently surface burned Gmelin larch/Scots pine forest in the Russian Far East. These charcoal-induced changes led to more regenerated seedlings of *Pinus sylvestris* (Makoto et al. 2011b). Charcoal also adsorbs toxic compounds such as phenols (Zackrisson et al. 1996; Wardle et al. 1998), which may directly suppress fine root development or complex soil nitrogen to reduce availability (Wardle et al. 1998). However, to the best of our knowledge, no study has yet tested the interactions of charcoal content and fine root traits in post-fire forest stands.

Understorey and overstorey vegetation comprises the entire fine root pool in post-surface fire forests. Fire-derived charcoal influences fine roots differently among the species and habitats (Wardle et al. 1998; Pluchon et al. 2014). For example, charcoal promoted the fine root mass of larch seedlings in a laboratory experiment (Makoto et al. 2011a). On the other hand, charcoal suppresses the fine root mass of herbaceous species *Koeleria macrantha* grown in the laboratory (Gundale and DeLuca 2007). However, in the field, charcoal affects plant growth via chemical, physical and biological characteristics of the forest soils. These characteristics are more temporally and spatially heterogeneous than those in the microcosm, nursery and agricultural field experiments. For example, the biomass of fine roots increased when ash nutrients were added to soil, but this effect was significant only for upper soil layer; in mineral layers, there was no significant effect (Majdi et al. 2008). Furthermore, fire disturbances changed the respiration rate and morphological traits of the very fine roots, while these parameters did not change for fine roots (Makita et al. 2011; Makita et al. 2016). Very fine roots may exhibit species-specific traits and change their potential for nutrient and water uptake in different soil depths by plasticity in root biomass in response to available resources (Makita et al. 2011). These previous findings allow us to predict different fire-derived charcoal effect on fine root mass in overstorey and understorey vegetation as well as in diameter classes and soil depths in post-surface fire forests.

The ratio of living fine root biomass over the dead fine root necromass (LD ratio) is a useful proxy of root "vitality"(Persson 1983; Persson and Ahlström 2002; Persson and Stadenberg 2009; Ma et al. 2013). Previous studies have shown that decreasing LD ratio reflects root damage by drought, clear cutting, and atmospheric nitrogen deposition (Clemensson-Lindell and Persson 1995; Ma et al. 2013). However, to our knowledge, there have been no studies that test the fire and fire-derived charcoal effects on fine root vitality.

In this research, we hypothesized that there would be a positive correlation between fire-derived charcoal mass and fine root vitality as measured by the LD ratio in a Gmelin larch boreal forest in the Russian Far East. We also hypothesized that the relationship of fire-derived charcoal on fine root biomass and necromass would differ between the understorey and overstorey vegetation, at different soil depths, and across different fine root diameter classes. Our study provides an investigation of the role of charcoal in ecosystem functioning, which has been recognized broadly (Zackrisson et al. 1996; Wardle et al. 1998), as well as its importance in understanding the belowground C dynamics in fire-prone boreal forest ecosystems through fine root vitality.

Materials and methods

Site description

A field survey was conducted near the eastern border of Zeysky State Nature Reserve which spans the Tukuringra mountain range in the Russian Far East (53°50′ N, 127°10′ E). The study used Gmelin larch forest (see details below) that was located 322 m a.s.l. on a foot of mountain range on an eastward facing slope with 3–5° of inclination. This territory has regularly experienced surface fires. Latest fire occurred in the summer of 2012 and killed all of the white birch trees (*Betula platyphylla*) and up to 20% of Gmelin larch trees (*Larix gmelinii (Rupr.)* Rupr.). In 2014, the dominant woody species was larch in the post-fire forests. In this stand the average age of larch trees was 169 years with an average diameter at breast height of 38.8 ± 1.6 cm, average height of 25.5 ± 0.8 m and tree density of 132trees per ha^{-1}. Understorey vegetation was scarce and mainly consisted of perennial herbs (*Galium boreale*, *Atragene* sp., *Equisetum* sp., etc) with minor shrub coverage (*Salix* sp., *Spiraea* sp., *Sorbaria sorbifolia*sp). Soil of the study area refers to Cambisols, following World Reference Base for soils (IUSS Working Group WRB 2014). Soil texture is sandy formed from Neogene sedimentary rocks (Procopchuk and Bryanin 2007; Bryanin and Sorokina 2015). Study site is distributed in the discontinuous permafrost soil region with a mean annual temperature of −0.7 °C. The minimum temperature occurs in January (−19.3 °C) with the maximum in July (+ 19.1). The mean annual precipitation is 526.8 mm of which 77% falls as rain from July to September (Amur Center for Hydrometeorology and Environmental Monitoring 2015). Forest fires usually occur in spring (from middle of April to the beginning of July) and fall (from the middle of September to the end of October). These periods are dry, warm and windy (Amur Center for Hydrometeorology and Environmental Monitoring 2015). Most fires are human-caused surface fires with low to medium severity. The fire return interval is less than 5 years (Makoto et al. 2007).

Sampling of roots and charcoal

Fine roots and charcoal were collected at the end of July 2014, which coincided with maximum root biomass development due to favourable soil moisture and temperature. In the study area, trees were evenly spaced with an average distance between trees of approximately 8.7 m. We selected ten mature larch trees that had survived the fire with equal and representative diameters and heights. We then installed small plots (1 m by 1 m) 2 m to the south of each tree bole. There were neither trees inside these small plots nor 8.7 m to other directions from the chosen bole. Fine root biomass has a large spatial variation, which could require substantial number of soil cores (Yan and Cai 2008). Therefore, we employed 10 replicates which are more than those in the previous studies (e.g.,Gundale and DeLuca 2007; Wang et al. 2013; Palviainen and Finér 2015). We used a metal auger to extract 10 soil cores (5 cm in diameter, 30 cm in depth). The soil sample included the organic horizon and mineral soil within each plot. Fine roots 20-cm-deep account for more than 90% of the total fine root mass in this area (data not shown). Therefore, the soil cores were divided into two subsamples according to depth. The 'upper' layer was 0–10 cm and the 'lower' layer was 10–20 cm. The soil samples were put into plastic bags and transferred to the laboratory immediately, then stored at maximum for 30 days at −20 degrees C until the further processing.

In this study, we investigated roots with a diameter ≤ 2 mm. For root sorting, samples were soaked, transferred to trays, and then rubbed gently to separate roots from soil and coarse fragments. The roots were then sorted separately according to state 'alive' or 'dead'. Roots classified as 'alive' were elastic, pale on the exterior, and free of decay with a whitish cortex. The dead roots were brown or black in color, rigid and inflexible, in various stages of decay, and had a dark colored cortex (Persson 1983). In further sections, the live root mass was referred to as 'biomass' and dead root mass was considered a 'necromass'. Furthermore, the roots were separately sorted depending on the diameter class 'fine' (0.5-2 mm) and 'very fine' (<0.5 mm) and vegetation type 'overstorey' (larch trees) and 'understorey'(grass and shrub species of ground cover). After separation from soil samples, the fresh root was oven dried at 70 °C for three days to a constant weight of each fraction. Then LD ratio was calculated for each species, diameter class, and soil depth as follows:

$$LD\ \text{ratio} = \frac{\text{root biomass (grams)}}{\text{root necromass (grams)}}$$

Charcoal pieces were picked by tweezers from soil samples during the root washing process. All charcoal parts larger than 0.25 mm were picked from the water and dried at 85 °C for three days until a constant weight was measured.

Statistical analysis

All data were analysed for the normality of data distribution with Shapio-Wilk test. Data not meeting the assumption of normality were transformed using log-transformation or analysed using a permutation ANOVA followed by non-parametric multiple comparison Steel-Dwass test. The effect of soil depth, root condition (alive and dead), root diameter and their interaction on the root mass was analyzed using three-way analysis of variance (ANOVA) for each vegetation type separately. If significant effects of factors were found by ANOVA, we conducted Tukey's HSD multiple comparison test to determine the significant group differences. Correlations between charcoal contents and all root characteristics were analyzed by the generalized linear model (GLM). The response variable followed the Gaussian distribution. In all analyses, differences were considered to be significant at $p < 0.05$. All analyses used R software version 3.3.1(R Development Core Team 2016).

Results

Basic traits of roots

Mean total fine root mass (FRM) for fine and very fine roots of overstorey and understorey vegetation at layer of 0–20 cm was 506 g m^{-2}. Mainly fine roots (52% of FRM) concentrated in upper soil layer of 0–10 cm and were almost equally comprised by alive and dead roots. The rest (48%) were concentrated in lower soil layer of 10–20 cm. Under 20 cm depth fine roots tended to vanish (data not shown). Very fine roots were dominant and comprised about 64% of a FRM. More than half of roots in soil layer of 0–20 cm were overstorey dead roots (necromass) which comprised about 60% of a FRM.

For overstorey vegetation, the root mass significantly differed among root condition ($P < 0.001$), root diameter ($P < 0.05$), and soil depth ($p < 0.05$, Table 1, Fig. 1a). Very fine roots had a significantly higher mass than the fine roots ($P < 0.05$, Fig. 1a). Root mass in the lower layer was significantly higher than that in the upper layer ($P < 0.05$, Fig. 1a). Furthermore, root necromass was significantly higher than the biomass ($P < 0.001$, Fig. 1a). On the other hand, the differences between the necromass and the biomass were larger in very fine roots than fine roots (Table 1, Fig. 1a). In the lower layer, the difference between necromass and biomass was larger than that in the upper layer ($P < 0.05$, Fig.1a). However, there was no significant difference between mass of fine and very fine roots in both studied layers for both overstory and understory vegetation. Similarly, there was no significant difference between root biomass and necromass for fine and very fine roots of both vegetation types. For overstorey vegetation, the LD ratio differed significantly among root diameters ($P < 0.001$, Fig. 2a). Fine roots have higher LD ratio than very fine roots (Fig. 2a). However, the soil layer did not affect the LD ratio of roots in the overstorey vegetation.

For understorey vegetation, the root mass was significantly affected by root diameter, soil layer and root condition individually and interactively (Table 1, Fig. 1b). The fine root biomass was significantly lower than necromass in both layers, while very fine root

Table 1 Statistical results of 3-way ANOVA showing the effect of root diameter, soil depth and root condition on root mass (g m^{-2}) of understorey and overstorey vegetation

Source of variation	Overstorey		Understorey	
	F	*P*	F	*P*
Root diameter	4.37	0.04	21.63	<0.0001
Soil depth	1.79	n.s.	12.81	0.0006
Root condition	74.91	<0.0001	15.38	0.0002
Diameter: Soil depth	0.05	n.s.	3.71	n.s.
Diameter: Condition	14.33	0.0003	63.92	<0.0001
Soil depth: Condition	3.41	n.s.	2.05	n.s.
Diameter: Soil depth: Condition	0.69	n.s.	10.77	0.0015

n.s Not significant

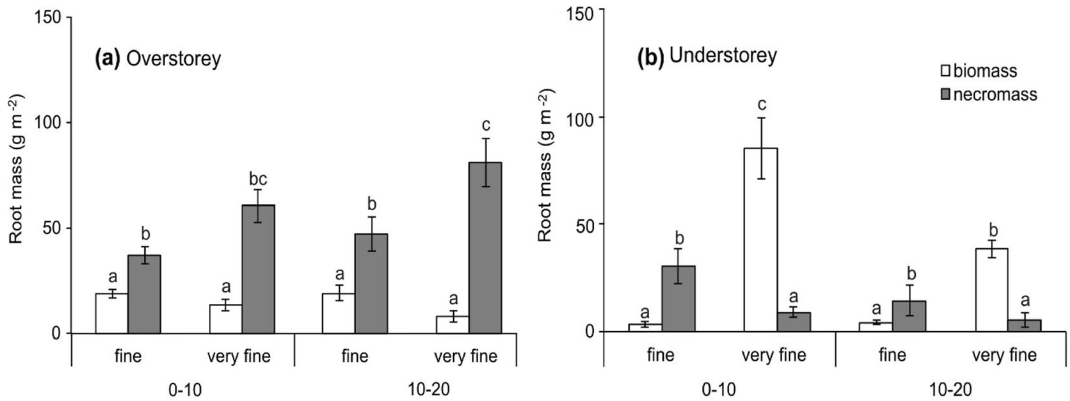

Fig. 1 Root mass of overstorey **a** and understorey **b** vegetation in soil depth of 0–10 cm and 10–20 cm. Error bars represent means ± SE for 10 replicates. Different letters above the bar plots indicate significant difference between means according to the Tukey HSD ($P < 0.05$)

biomass of understorey was significantly higher than necromass in both layers ($P < 0.05$, Fig. 1b). Furthermore, for both root diameter classes, the differences between the biomass and necromass were larger in upper layer than the lower layer. For understorey vegetation, the LD ratio differed significantly between the root diameter classes ($P < 0.001$, Fig. 2b,). Very fine roots had higher LD ratio than fine roots in both layers.

Correlation between charcoal and root traits

The charcoal content in the upper 0–10 cm and lower 10–20 cm layers was 24 ± 3.1 g m^{-2} and 190.1 ± 40.5 g m^{-2}, respectively (mean ± SE; $n = 10$). For overstorey vegetation, the LD ratio of fine roots was positively correlated with charcoal content in both upper and lower soil layers (Table 2, Fig. 3a and b). However, there was no correlation between LD ratio of very fine roots and charcoal content in either layers. The biomass of the fine roots was positively correlated with charcoal ($P < 0.05$) only in the upper layer. However, the biomass of very fine roots and charcoal content had no correlation in either layers.

Interestingly, the charcoal content correlated with root necromass in the lower layer for both fine and very fine roots (Table 2). Furthermore, this correlation was positive for very fine root necromass and negative for fine root necromass. In addition, the total mass of very fine roots and charcoal content had a strong and positive correlation in lower layer.

For understorey vegetation, the LD ratio of fine roots negatively correlated with charcoal only in upper layer (Table 2, Fig. 3c and d). No correlation was found between LD ratio of very fine roots and charcoal in both layers. The significant negative correlation between charcoal contents and fine root biomass was found only in upper layer ($P < 0.001$). However, the charcoal content did not correlate with roots in either diameter classes or root state in the lower layer.

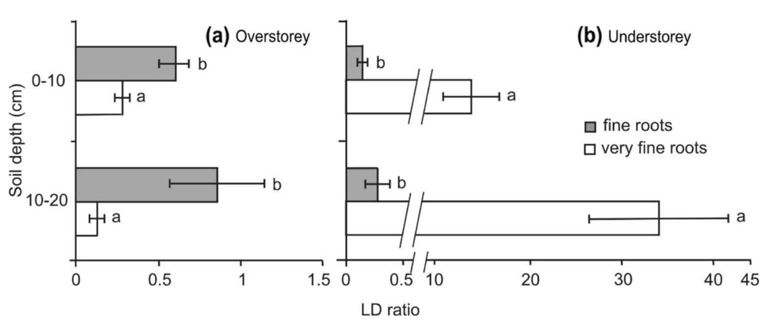

Fig. 2 Vertical distribution of biomass to necromass of roots (LD ratio): **a** for overstorey and **b** for understorey vegetation. Error bars represent means ± SE ($n = 10$). Different lowercase letters near the barplots indicate significant difference between means according to Steel-Dwass test ($p < 0.05$)

Table 2 Pearson correlation coefficients and *p*-values to test correlations between charcoal content and fine root traits in soil depth of 0–10 cm and 10–20 cm

Root trait	Overstorey				Understorey			
	fine		very fine		fine		very fine	
	r	*P*-value	r	*P*-value	r	*p*-value	r	*p*-value
0–10 cm								
Biomass	**0.822**	**0.0035**	-0.155	n.s.	**-0.918**	**0.0002**	0.119	n.s.
Necromass	-0.570	n.s.	-0.137	n.s.	-0.088	n.s.	-0.575	n.s.
Total mass	-0.218	n.s.	-0.168	n.s.	-0.207	n.s.	0.0032	n.s.
LD ratio	**0.714**	**0.015**	0.057	n.s.	**-0.810**	**0.003**	0.272	n.s.
10–20 cm								
Biomass	0.567	n.s.	-0.113	n.s.	0.055	n.s.	0.161	n.s.
Necromass	**-0.831**	**0.003**	**0.911**	**0.00025**	0.168	n.s.	-0.121	n.s.
Total mass	-0.589	n.s.	**0.927**	**0.0001**	0.171	n.s.	0.057	n.s.
LD ratio	**0.863**	**0.001**	-0.251	n.s.	0.019	n.s.	0.192	n.s.

Bold entries indicates significant correlation between tested variables.

n.s Not significant

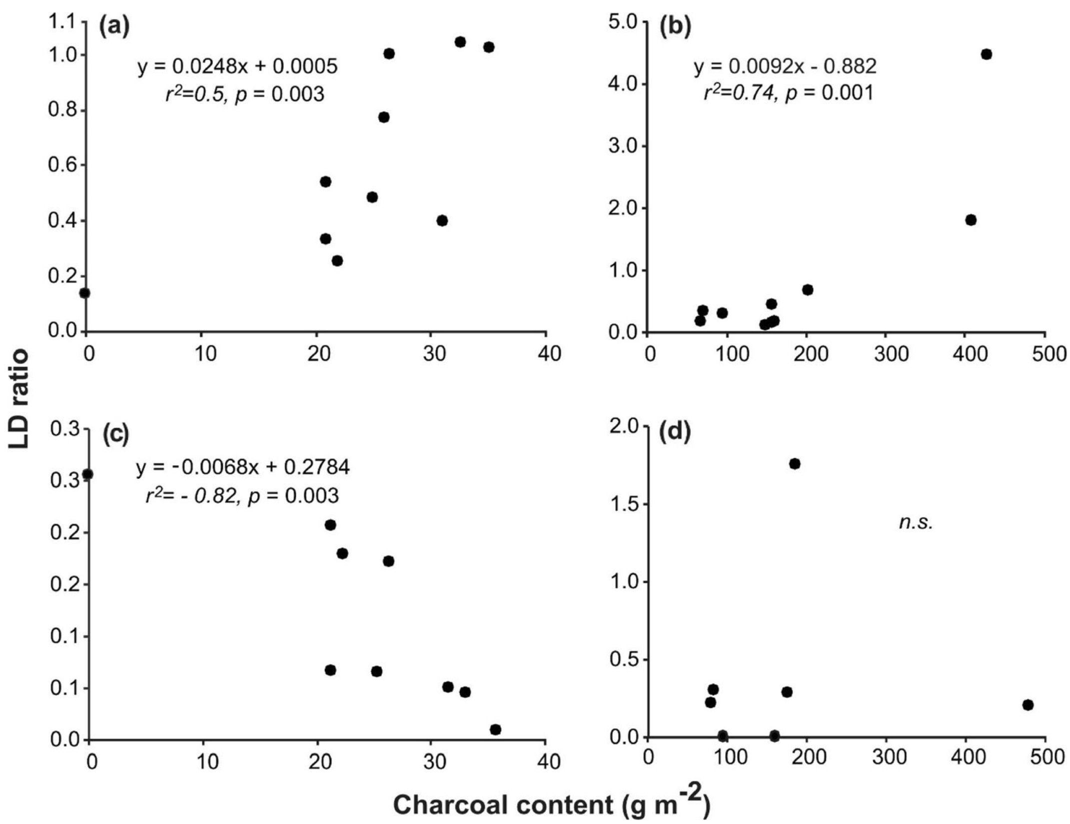

Fig. 3 Relationship between charcoal content and LD ratio of fine (≥0.5 mm but <2 mm diameter) rootsfrom overstorey vegetation at a soil depth of: **a** 0–10 cm and **b** 10–20 cm and of understorey vegetation at soil depth of: **c** 0–10 cm and **d** 10–20 cm

Discussion

The LD ratio of fine roots is a powerful metric of root vitality. It reflects the rate of fine root production and death (Persson and Ahlström 2002; Richter et al. 2007; Ma et al. 2013; Persson and Stadenberg 2010; Sun et al. 2015). We found a positive correlation between charcoal and fine root vitality for overstorey vegetation ($r = 0.82$, Fig. 3a and b). This is consistent with our hypothesis that the presence of charcoal is correlated to fine root vitality of post-surface fire forest soils. Previous research has reported that charcoal positively affects root biomass via the change in soil moisture and amount of available nutrients (Gundale and DeLuca 2007; Makoto et al. 2010; Makoto et al. 2012; Pluchon et al. 2014). In previous field study in this region we found positive correlations between charcoal contents and soil pH, water contents, and P contents (Makoto et al. 2011b). These findings suggest a positive correlation between charcoal content and Gmelin larch fine root, which could be attributed to charcoal-induced changes in soil properties.

Zackrisson et al. (1996) and Pingree et al. (2016) reported that the charcoal adsorption capacity could last up to 100 years after wildfire. Zackrisson et al. (1996) also proved that charcoal function could be reactivated after subsequent exposure to heat. In our system, fire is a regular event that frequently creates new charcoal and reactivates charcoal in the upper soil layers. In fact, a positive correlation between the charcoal and the fine root biomass and vitality of larch were found in the upper layer (Fig. 3a and b), where the previously deposited charcoal can be exposed to subsequent fire. Repeated surface fire could maintain the activity of charcoal in the soil and influence fine root biomass and root vitality of overstorey larch trees. In future studies, the mechanism of context-dependent responses in fine root biomass to charcoal should be tested experimentally.

Charcoal has a significantly negative correlation with fine root vitality of understorey vegetation (Fig. 3c, Table 1). Previous laboratory experiments showed a negative effect of charcoal on fine root biomass in a perennial grass (Gundale and DeLuca 2007). This negative influence resulted from the toxicity caused by some compounds formed during charring or by nitrogen immobilization through charcoal adsorption. In our study, another possible mechanism for the negative effects of charcoal on vitality of understorey fine roots is an indirect process including a positive charcoal effect on overstorey fine roots. If charcoal promoted the roots of overstorey vegetation, then it could have caused the consequent competitive exclusion of understorey vegetation. The upper layer is most preferable to fine roots due to nutrient abundance. In such conditions, roots are distributed close to each other and may overlap zones of nutrient uptake (Robinson et al. 2003). This could result in a competitive relationship. In future studies, the mechanism of vegetation-dependent response to charcoal should be tested experimentally.

Interestingly, the presence of charcoal was not positively correlated with very fine root mass in either soil layer (Table 1). This suggests that the charcoal effects are not only species-specific but also diameter-dependent for fine roots. It is known that fine and very fine roots are functionally different (McCormack et al. 2015; Makita et al. 2016). Very fine roots have a high absorptive function while fine roots (near 2 mm) transport absorbed materials such as water and nutrients. Charcoal promotes the root transport function of water and nutrients by positive influence on fine roots biomass but does not influence the root exploitation ability of nutrients and water. Causality and the underlying mechanism of this diameter-dependent effect should be investigated experimentally. These findings support our second hypothesis that charcoal influences the fine root parameters differently among species and root diameter class.

In our study, the LD ratio significantly differs among species and root diameters (Fig. 2). This suggests that vitality of fine root is highly heterogeneous in post-fire forests. Previous studies found high fine-root vitality in the upper soil layer due to extensive mycorrhizal infection in that layer (Persson and Stadenberg 2009; Ma et al. 2013). Mycorrhizal infection increases the uptake root area and improves the function of fine roots over a prolonged period of time (Brundrett 2002). In contrast, our results show increasing LDratio with increasing depth for both vegetation types (Fig. 3). This might implicate fire caused changes in depth-dependent differences in root vitality. In fact, some previous studies have shown that forest disturbances or environmental stress lead to a decrease in fine root vitality (Leuschner et al. 2006; Richter et al. 2007; Xiao et al. 2008), and this could decrease the vitality of fine roots in the upper layer with relatively higher vitality in the lower layers. Fine root biomass and necromass and hence LD ratio are likely to be heavily influenced by seasonal growing conditions of plants (Metcalfe et al. 2008; Janos et al. 2008). Furthermore, duration of charcoal influence on fine root dynamics in soil is indeterminate in spite of long charcoal residence time in soil. In future investigations it is important to check seasonal, spatial and amount-dependent effect of charcoal on fine root dynamics for the integrative understanding of the charcoal in situ importance for the root dynamics in boreal forests.

We found a high proportion of necromass in the very fine roots of the overstorey vegetation. This might be due to the rapid root recovery after fire and its subsequent death. Briefly, nutrient abundance increases after the surface fire. Plants that survive utilize them rapidly and increase the amount of very fine roots (Day et al. 2006). This recovery process could help refill nutrient stores by taking up nutrients immediately after the fire. However, rich nutrient conditions are ephemeral and run out in a short period. Plants, in turn, stop intensive root proliferation and superfluous very fine roots might die. At the same time, microbiota of recurrently burned boreal forests are suppressed, and this could result in a slow rate of root decomposition with abundant temporary necromass (Neary et al. 1999; Mabuhay et al. 2003; Holden et al. 2015).

Fine roots are major contributors to the soil C pool in the boreal forest. Moreover, a long-term decomposition experiment showed that the amount of soil C derived by fine roots was about 2.3-fold higher than that for aboveground plant residues (Kätterer et al. 2011). Our data suggest that fine root dynamics are highly correlated with fire-derived charcoal in frequently burned boreal forest. The charcoal effects can be substantial, but they are highly dependent on the vegetation type and root diameters as well as the soil depth. These findings suggest that models of soil organic carbon might be complicated—especially those derived from fine roots in post-fire boreal forests.

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