Plasticity of Pine Tree Roots to Podzolization of Boreal Sandy Soils

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Abstract

**Aims** The morphological traits of fine roots change with forest succession and soil weathering. However, low tree species diversity in boreal forests may limit plastic responses of the roots to soil nutrient loss. We tested whether pine trees (*Pinus sylvestris* L.) have root plasticity to change fine root allocation to deeper soil horizons in response to varying degree of podzolization.

**Methods** We compared root biomass in two sand dune chronosequences (aluminium (Al)/iron (Fe) oxide-poor coarse-textured sand vs. oxide-rich fine-textured sand) in Estonia.

**Results** We found that faster podzolization in coarse-textured soil promotes migration of Al/Fe oxides and phosphorus (P) into deeper horizons and reshapes the depth distribution of fine root biomass. A decrease in P availability in the coarse-textured soil profile increases fine root biomass and length in both the organic and mineral horizons. In the fine-textured old soil, fine root distribution increases in the mineral soil (especially, spodic horizon) rich in oxide-bonded P.

**Conclusion** Pine roots have two plasticities in low-diversity boreal forests – changing root morphological traits and changing depth distribution of root biomass, depending on the abundance of Al and Fe oxides and the depth distribution and dominant form of P.

Introduction

Higher plants develop root systems to acquire most of their essential nutrients from the soil (Lambers et al. 2008). Soil provides nutrients to plants through weathering, but long-term weathering ultimately reduces nutrient availability as soil ages (Chapin III et al. 2011). Despite soil nutrient loss associated with weathering, high productivity is maintained in some ecosystems on highly weathered soils (Wardle et al. 2004). Roots play key roles in nutrient acquisition from nutrient-limited soils (Landeweert et al. 2001).

Morphological traits of roots can change with long-term decline in nutrient availability in soil aging (Lambers et al. 2008). Nitrogen (N) is typically the limiting nutrient in young soils (Northup et al. 1995), but phosphorus (P) is also limiting in old soils due to the decreased P supply from the bedrock and P sorption by short-range-order aluminium [Al] and iron [Fe] oxides (Turner and Condron 2013). Along with soil aging, plant species composition shifts towards communities with finer root systems with higher surface area (Landeweert et al. 2001). Finer roots could have a greater ability to acquire soil nutrients (McCormack et al. 2012), especially P bonded to oxides by releasing organic acids in the vicinity of roots or the rhizosphere (Aoki et al. 2012). However, it is still unclear whether a single plant species has root morphological plasticity in response to soil aging.

A single plant species can enlarge their root surface area or length by increasing root hairs and tips in response to water and nutrient deficiencies (López-Bucio et al. 2003). However, the range of root morphological plasticity within a single plant species is inherently limited (Tobner et al. 2013; Valverde-Barrantes et al. 2017). High phylogenetic variation of plants and a wide variation of root morphological
traits in tropical forests facilitate access to nutrients in various forms and availabilities even on highly-weathered soils (Ma et al. 2018). The low-diversity of boreal forests might lead to the limited root morphological plasticity.

On the other hand, plants have another plasticity to change depth distribution of fine root biomass (< 2 mm in diameter) (Jackson et al. 1996). Seedling roots have been shown to expand towards acquire deep water in arid soil (Butterfield et al. 2017; Canadell et al. 1996) or nutrient-rich hotspots (Hodge 2004; Smits et al. 2012). Changing depth distribution of root biomass could be an alternative strategy for plant roots to forage nutrients. Most studies have focused on changes in root traits in topsoil, because active roots are typically located in the nutrient-rich surface soil (Canadell et al. 1996; Ostonen et al. 2007; Holdaway et al. 2011). However, nutrient hotspots can migrate rapidly in sandy soil profiles under boreal forests, where podzolization typically promotes the formation of a bleached eluvial (E) horizon and the illuviation of clays (esp., short-range-order Al and Fe oxides) in the spodic B horizon (Lundström et al. 2000). The phosphate is strongly bonded to Al and Fe oxides (Turner and Condron 2013) and thus, soil P hotspots could migrate downward along with illuviation of Al and Fe oxides. If tree roots change their depth distribution in response to nutrient hotspot migration, neglecting roots in subsoil risks underestimation of root biomass and vertical root plasticity in podzolized sandy soils. Vertical root plasticity in mature trees need to be tested under field conditions.

Coastal Estonia has been uplifting since the retreat of the last glacier. Sand plains and coastal sand dune ridges have formed as a result of storm events in this area (Vilumaa et al. 2017). As the distance from coastal line increases, forest development and podzolization progress. Moreover, different storm intensities provide soil chronosequences that differ in texture and oxide content of parent materials. The podzolization, or migration of Al and Fe oxides from the E horizon to the B horizon, progresses more rapidly in the coarse-textured soil, compared to the fine-textured soil (Lundström et al. 2000). This enables us to assess vertical root plasticity associated with soil development with varying degree of podzolization. We hypothesized that (1) podzolization changes depth distribution of soil P and fine root biomass in each chronosequence and that (2) allocation of fine roots to the deeper soil horizons differs between the coarse-textured soil and the fine-textured soil, depending on availability and dominant form of soil P.

**Materials And Methods**

**Study area**

We selected two coastal sand dune chronosequences in Hiiumaa (N 59°04,’ E 022°38’) and Juminda (N 59°30,’ E 025°36’), Estonia. These sites share similar climates and vegetation types (Fig. 1a). Annual precipitation in the study area is 587–639 mm yr$^{-1}$ and mean annual air temperature is 5.7–6.8°C (Estonian Weather Service, climate normals between 1981 and 2010 in Kunda and Ristna). Vegetation is dominated by Scots pine (*Pinus sylvestris* L.) with an understory dominated by blueberry (*Vaccinium myrtillus* L.) and mosses (e.g., *Hylocomium splendens* L.). The two soil chronosequences differ in particle
size distribution. The coarser-textured soil found at Hiiumaa is dominated by ca. 80% coarse sands (0.25–2 mm), with 18% fine sands (0.05–0.25 mm) and 2% clays (< 0.002 mm), whereas the finer-textured soil found at Juminda is dominated by 87% fine sands with 10% coarse sands and 3% clays. The Hiiumaa chronosequence is located on an island shore that faces the Baltic Sea, whereas the Juminda chronosequence is located on the shore of the Juminda Peninsula facing the Gulf of Finland (Table 1). Therefore, Hiiumaa experiences greater storm surges than Juminda, which has resulted in the accumulation of coarser-textured sands due to the erosion of fine particles during storm events (Vilumaa et al. 2017). At both locations, sand plains are composed of shore-parallel beach ridges and depressions between ridges (Fig. 1a). Ridge bands are approximately 20 m in width and the two soil chronosequences include different stages of podzolization. Using a transect line, we established three sites on soils of different ages on sand dune ridges: 200, 500, and 1,500 years old at Hiiumaa and 500, 1,500, and 7,000 years old at Juminda (Fig. 1a). We referred to these three ages as young, middle, and old soils, respectively. Soil ages were estimated from peat $^{14}$C dating data obtained from adjacent areas (Vilumaa et al. 2017). The young, middle, and old soils were Arenosols, Aluveluvisols, and Podzols (Aluveluvisols in Hiiumaa), respectively, according to the World Resource Base for Soil Resources (IUSS Working Group WRB, 2015). We collected soil and fine root samples from three soil pits per site along each coastal sand dune chronosequence in August 2015. One soil pit was placed along the transect and the other two were located 10 m on each side in a perpendicular direction.

Root Biomass And Morphological Traits

Fine root biomass was assessed using block sampling at each soil pit. One soil block (width × length × depth = 10 cm × 10 cm × 10 cm) was excavated at eight soil depths (0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, 60–70 cm, and 70–80 cm). All blocks were transported to the laboratory at 4°C for further analyses. Then roots were carefully sorted from soil for each sample. Root segments were sieved through a 0.5 mm mesh and gently washed with tap and deionized water. We selected at least three intact root segments from each soil block for measuring morphological traits. Selected roots were placed into sealed polyethylene bags, labelled, and refrigerated at 4°C for up to 1 week before processing for classification and dissection. Broken root segments were brushed clean of attached soil particles, bagged, and refrigerated for sorting.

Living and dead roots were separated by visual inspection for resilience, brittleness, and bark and xylem colour. Living woody roots were separated from understory roots and sorted into two diameter classes (< 0.5 mm and 0.5–2.0 mm). Fine root biomass was represented by two diameter classes (< 0.5 mm and 0.5–2.0 mm) per unit soil area (g m$^{-2}$). For root morphology analyses, we scanned roots and calculated the total root length and volume with a WinRHIZO Pro 2013a (Regent Instruments, Québec, Canada). After scanning, samples were dried at 70°C to a constant weight and then weighed. Specific root length (SRL, m g$^{-1}$) and root tissue density (RTD, g cm$^{-3}$) were calculated using the root length and dry weight of each sample. Morphological characteristics, such as SRL and RTD, reflect resource availability and thus are an important indicator of physiology, lifespan, and foraging strategy (Ryser 1996; Ostonen et al. 2011;
Makita et al. 2015). To evaluate fine root allocation and fine root length, the fine root length of each soil horizon was calculated using fine biomass and SRL for each horizon and summed to calculate total fine root length in soil profiles.

### Chemical Analyses Of Plant And Soil Materials

To analyze changes in plant nutrient status along with soil aging, we measured N and P concentrations in Scots pine needle litter and *Hylocomium splendens* moss samples in each plot. The plant materials were dried in an oven at 70°C for 48 h and milled. Then, the concentrations of C and N were determined using a CN analyzer (Vario Max CN, Elementar Analysensysteme GmbH, Langenselbold, Germany). The concentration of P was determined using an inductively coupled plasma atomic emission spectrometer (ICP-AES, SPS1500, Seiko Instruments Inc., Chiba, Japan) following nitric-sulfuric acid wet digestion.

To evaluate the extent of podzolization and migration of nutrient hotspots, soil chemical properties were also measured. Soil samples were stored in plastic bags at 4°C prior to analyses, and sieved (< 2 mm) to eliminate litter, roots, and stones. A subsample of field-moist soil was used for soil solution extraction. A second subsample was air dried and used for measurements of physicochemical properties. Soil pH was measured using a soil-to-solution (water) ratio of 1:20 (w/v) for the organic horizon and 1:5 (w/v) for mineral soil horizons after shaking for 1 h. Total C and N concentrations were determined using a CN analyzer (Vario Max CN, Elementar Analysensysteme GmbH). Bulk density samples were collected using a 0.1 L soil core sampler and bulk density was measured after oven-drying (105°C, 24 h). To assess effects of water limitation on root biomass distribution, potential water retention in the soil profile was calculated using bulk density and water holding capacities (Öhlinger 1995). To assess extent of podzolization and depth distribution of P adsorbents, the concentrations of short-range-order Fe and Al (hydr)oxides (Fe\(_0\) and Al\(_0\), respectively) in the soil were estimated by extraction in the dark with acidic (pH 3) 0.2 M ammonium oxalate (McKeague and Day, 1966). The extent of podzolization was calculated as the ratio of short-range-order Al and Fe oxide concentration (Al\(_0\) + 1/2Fe\(_0\)) in the upper illuvial B horizon (spodic B in Juminda) relative to that in the E horizon. Concentrations of P, Fe, and Al in soil extracts were determined using the ICP-AES (SPS1500, Seiko Instruments Inc.). Oxalate-extracted P was defined as short-range-order oxide-bonded P (Pote et al. 1999). Available P concentrations were estimated using the Bray-2 extraction method (Blakemore et al. 1987). Bray-2 extractable P includes both organic and inorganic labile P and P that is weakly bonded to oxides in the soil, whereas oxalate-extractable P includes only P that is weakly bound to oxides (Pote et al. 1999). We calculated C, Bray-2 extractable P, oxalate-extractable P, and Al\(_0\)+1/2Fe\(_0\) stocks and their weighted mean concentrations in the soil horizons using the concentration and bulk density of each respective horizon.

### Rhizosphere and bulk soil fractionation, soil solution extraction, and chemical analyses

Rhizosphere acidification by organic acid exudation is required to solubilize P bonded to Al or Fe oxides in the old soils, where recalcitrant P bonded to Al or Fe oxides are a dominant P form (Jongmans et al.
To assess functional root plasticity for soil P solubilization, we compared the extent of rhizosphere acidification and the solubility of Al and Fe oxides in the old soils (upper spodic B horizon) of the Hiiumaa and Juminda chronosequences (1,500 and 7,000 years old, respectively). The old soil of each chronosequence was selected, because the distinct boundary between the E and spodic B horizons allows us to collect the rhizosphere soil from the upper spodic B horizon or the frontier of podzolization. Fresh, unsieved soil samples were separated into rhizosphere and bulk fractions using the method of Wang and Zabowski (1998). Rhizosphere soil was obtained by gently shaking the fine root systems (< 2 mm) approximately 10 times until the loosely adherent soil was removed and then carefully scraping the roots to collect closely adhering soil. The bulk fraction was collected from soil outside of the rooting area. Both rhizosphere and bulk fractions of fresh soil samples were extracted using the centrifugation-drainage technique (Giesler and Lundström, 1993). Soil solutions were extracted without adding water, by centrifugation for 30 min at a speed of 8,800 rpm (10,560 g; ~1.5 MPa; High-Speed Refrigerated centrifuge CR20G; Hitachi, Tokyo, Japan). The soil solution extracts were filtered through a 0.6 µm filter (GF/C, Whatman, Maidstone, United Kingdom) and frozen at −24°C before analyses. The concentrations of P, Fe, and Al in soil solutions were determined using the ICP-AES (SPS1500, Seiko Instruments Inc.).

Calculations And Statistics

All results are expressed on an oven-dried (105°C for 24 h for soil samples and 70°C for 48 h for plant samples, respectively) weight basis as the mean ± standard errors (SE) of three replicates. The significance of differences between mean values among groups (horizons and soil age) were assessed using analysis of variance (ANOVA) at the $P < 0.05$ significance level for fine root biomass and SRL, unless otherwise stated. The significance of differences between mean values among groups (sites) were assessed using $t$-tests at the $P < 0.05$ significance level for pH, Al, Fe, and P concentrations in the rhizosphere and bulk soil solutions. Pearson’s linear correlations were used to assess the relationships between SRL, RTD, and soil extractable P. All statistical analyses were performed using Sigmaplot version 14.0 (Systat Software, Inc., San Jose, CA, USA).

Results

Soil nutrient availability and litter nutrient concentration

Organic horizon C stocks increased with soil age in the sandier Hiiumaa soil, whereas no significant increase was observed in the finer Juminda soil (Fig. 1b). In both chronosequences, podzolization resulted in a decrease in soil pH and migration of short-range-order Al and Fe oxides from the E horizon (Table 1; Fig. 2a) to the B horizons (Fig. 2b). Potential soil water storage was greater in the fine-textured Juminda soil than in the sandier Hiiumaa soil, but there were no significant differences between soil ages within each chronosequence (Table 1). Bray-2 extractable (available) P concentrations in the mineral soil were positively correlated with soil pH ($R = 0.41$, $P < 0.05$, $N = 154$; Fig. S1a), while oxalate-extractable P
concentrations in the mineral soil were positively correlated with the abundance of short-range-order Al and Fe oxides (i.e., $\text{Al}_2\text{O}_3 + 1/2\text{Fe}_2\text{O}_3$) ($R = 0.62$, $P < 0.05$, $N = 154$; Fig. S1b). Oxide-bonded P (oxalate-extractable) was the dominant form in the fine-textured Juminda soil (Fig. 2b), whereas available P (Bray-2) was the dominant form in the sandier Hiiumaa soil (Fig. 2a). The ratios of oxide-bonded P to extractable P increased with short-range-order Al and Fe oxides ($R = 0.62$, $P < 0.05$, $N = 162$) and reached saturation with increasing short-range-order Al and Fe oxides (Fig. S2). The faster migration of oxalate-extractable P and short-range-order Al and Fe oxides in the sandier Hiiumaa soil (Figs. 2ab) is consistent with the higher extents of podzolization (Fig. S3a).

Regarding nutrient limitation along with soil development, there was no evidence of a trend in C:N ratios in either moss biomass or needle litter within either soil chronosequence (Table 1). P concentrations in both moss biomass and needle litter were positively correlated with soil Bray-2 extractable P stocks, respectively (Fig. 3).

**Fine Root Biomass In Soil Chronosequences**

There was no consistent trend in aboveground biomass along each chronosequence (Table S2), but rooting zone, fine root biomass and length, and root:shoot ratios increased with soil age in both chronosequences (Figs. 4, S3b, and S4; Table S2). The rooting zone depth increased in the initial stage of podzolization and then reached saturation (80 cm) in the both soils (Fig. 5a). In each chronosequence, a significant ($P < 0.05$) increase in fine root biomass was observed in the organic horizons of the sandier Hiiumaa soil (Fig. 2c), whereas a significant ($P < 0.05$) increase was observed in the B and C horizons in the Juminda (Fig. 2c). The ratios of fine root biomass in the mineral soil relative to the organic horizon (root allocation to the mineral soil) increase with soil age in the fine-textured Juminda soil, but not in the sandier Hiiumaa soil (Fig. 4a). The fraction of fine root biomass below the B horizon relative to the total fine root biomass (< 0.5 mm) was positively correlated with extent of podzolization in the finer-textured Juminda soil, but not in the Hiiumaa soil (Fig. 5b).

**Morphological Traits Of Fine Roots Among Soil Horizons**

Fine root biomass and morphological traits varied widely among soil horizons and ages (Figs. 4 and 6). The SRL of fine roots (diameter < 0.5 mm) decreased with soil depth in Hiiumaa (Fig. 6). By contrast, the SRL in the spodic B horizon in Juminda was as high as that found in the organic horizons (Fig. 6). The SRL of fine roots (diameter < 0.5 mm) was positively correlated with available P (Bray-2) in the sandier Hiiumaa soil (Fig. 7a), whereas SRL was positively correlated with oxalate-extractable P in the Juminda soil (Fig. 7b). In the fine-textured Juminda soil, SRL and RTD were positively and negatively correlated with short-range-order Al and Fe oxides, respectively ($R = 0.57$, $P < 0.05$, $N = 52$; Fig. 7cd) and the SRL of fine roots (diameter < 0.5 mm) was negatively correlated with RTD ($R = -0.53$, $P < 0.05$, $N = 99$). Total fine root length in the soil profile increased with soil age in both chronosequences (Fig. 4b). Most of the total fine root length was distributed in the organic horizon in Hiiumaa, whereas most of the root length was
distributed in the mineral soil in Juminda (Fig. 4b). The ratio of total fine root length in the mineral soil to that in the organic horizon was greater in old soil (7,000 years old) than in younger soils (500 and 1,500 years old) in Juminda (Fig. 4b).

**Rhizosphere And Bulk Soil Solution Composition**

As with the fine root distribution in the spodic B horizon, the extent of rhizosphere acidification differed between the old soils of two chronosequences (Table 2). The pH of the rhizosphere soil solution was significantly ($P < 0.05$) lower than that of the bulk soil solution in the fine-textured Juminda soil, but not in the sandier Hiiumaa soil ($P > 0.05$; Table 2). Consistent with pH, Al, Fe, and P concentrations in the rhizosphere soil solution were significantly ($P < 0.05$) higher than those in the bulk soil solution in Juminda, but no significant difference was found in Hiiumaa ($P > 0.05$; Table 2).

**Discussion**

**Podzolization and soil phosphorus limitation**

Sandy soil is favourable for fast development of rooting zone and developing distinct E and spodic B horizons within 500 years (Lundström et al. 2000), as seen in Hiiumaa (Fig. 1). Podzolization resulted in deeper migration of oxide-bonded P and short-range-order Al and Fe oxides in the sandier soil (Figs. 2ab and S3a). In oxide-rich soil, short-range-order Al and Fe oxides are major adsorbents of phosphate (Van Hees et al. 2003). Podzolization or soil aging increases proportion of oxide-bonded P relative to Bray-2 extractable P in the spodic B horizons (Figs. 2a and S2; Table 1). An increase in recalcitrant P fractions bonded to short-range-order Al and Fe oxides in the oxide-rich podzol (Juminda; Fig. 2a) is consistent with the long-term pedogenesis studies (Walker and Syers 1976; Turner and Condron 2013).

The P concentrations in both needle litter and moss biomass (Fig. 3) are used to characterize plant P limitation (Hidaka and Kitayama 2009). Bray-2 extractable P can be a rough indicator of soil P availability to plants (Blakemore et al. 1987). The positive correlation between soil Bray-2 extractable P and needle litter P concentrations (Fig. 3) suggests that plant P uptake is limited by soil available P in our study, as seen in long-term pedogenesis (Holdaway et al. 2011). The pattern in needle litter P concentrations along soil aging is not clear within each chronosequence (Fig. 3) due to a narrow range of soil labile P stocks over short-term pedogenesis in our study, compared to chronosequences over millennial time scales (Holdaway et al. 2011).

**Effects of podzolization on depth distribution and morphological traits of fine roots**

The rooting zone is limited by effective soil depth or breakup of bedrocks during the initial stages of pedogenesis (Uselman et al. 2007). The rooting zone depth in our study is not limited by bedrocks, as suggested by the initial high intercept of soil depth (Fig. S3b). Rather, rooting zone depth is associated with podzolization (Fig. 5a). The fine root biomass allocated to below B horizon is dependent on extent of
podzolization in the finer-textured Juminda soil, which contrasts with the consistently low allocation to the below B horizon in the sandier Hiiumaa soil (Fig. 5b). The different responses to podzolization support the hypothesis of vertical root plasticity.

Fine roots, which have high nutrient uptake ability, produce longer roots within a given mass than coarse roots (McCormack et al. 2012). An increase in SRL in older soils of chronosequence is usually the result of plant succession with mycorrhizal roots (Lambers et al. 2008), but a single tree species displayed morphological plasticity in our study (Fig. 4b). The variation in SRL of Scots pine has been reported to increase with mean annual temperature at latitudinal gradient (Zadworny et al. 2017). The longer SRL and lower RTD in the organic horizons support that root morphological traits could also vary with soil depth and soil properties (Table S1; Fig. 7), although effects of ectomycorrhizal roots can not be excluded in our study (Fritze et al. 2000).

SRL decreases with increasing soil depth and RTD increases due to an increase in lignified roots with a longer lifespan (Ryser, 1996; Makita et al. 2011; McCormack et al. 2012). However, an increase in SRL in the spodic B horizon of a fine-textured podzol is exceptional (Fig. 6). This supports the existence of root morphological plasticity (Rosling et al. 2003; Ostonen et al. 2011). In the finer-textured soil (Juminda), podzolization is slower (Fig. S3a) and the spodic B horizon is not deeper than in the coarser-textured soil (Hiiumaa) (Fig. 1a). These conditions of the finer-textured soil are favorable for high allocation of fine roots to the deeper soil in response to podzolization (Fig. 5b). However, allocation of limited resources (photosynthate) to root growth, enzyme and exudate production, and mycorrhizal association needs to be optimized by plants to acquire nutrients (Treseder and Vitousek 2001). As shown by a decrease in fine root biomass with depth (Figs. 2c and S4) and the saturation of rooting zone depth (Fig. 5a), the hotspots of oxide-bonded P in the deeper horizons (50 to 80 cm) of the sandier soil (Hiiumaa) is not accessible for most of the fine roots (Fig. S3; Table S1). Foraging behaviour of roots for nutrient hotspots has been demonstrated by seedlings of pot experiments (Smits et al. 2012). However, our data suggest that strategy of root allocation to the deeper soil is also affected by depth of nutrient hotspots as well as extent of podzolization under the field condition (Fig. 5b).

**Effects Of Soil Phosphorus Forms On Rhizosphere Acidification**

Rhizosphere acidification by releasing organic acids is one of strategies to solubilize oxide-bonded P (Lundström et al. 2000; Jones et al. 2003). In our study, rhizosphere acidification was only observed in the finer-textured podzol (Table 3). Judging from the positive correlation between SRL and oxalate-extractable P (Fig. 7b), fine roots were most likely targeting oxide-bonded P in the spodic B horizon of the finer-textured podzol. The direct or indirect effects of organic acids (e.g., chelating and acidification) could promote solubilization of oxides and oxide-bonded P (Table 2; Fujii et al. 2012). Short-range-order Al and Fe oxides are the dominant P adsorbents and acid buffers in podzols (Van Hees et al. 2003; Funakawa et al. 1993; Figs. 2bc and 3a). Finer roots can release greater amounts of organic acids along
with a shift in plant community on highly-weathered tropical soils (Aoki et al. 2012). In boreal forests, single tree species promotes different extents of rhizosphere acidification between the coarse-textured soil and the fine-textured soil (Table 2). In the sandier soil, oxide-bonded P is not a dominant P form (Fig. 2a) and thus, roots are considered to rely on more labile P that could be released without rhizosphere acidification (Fig. 7a; Table 2). In addition to the morphological traits of roots, the functional plasticity of rhizosphere acidification can change depending on target P fractions in the soil (Landeweert et al. 2001), and dominant P forms were strongly regulated by short-range-order Al and Fe oxides in our study (Figs. 2, S1; Table 3).

**Vertical Root Plasticity Driven By Plant–soil Feedback**

In the coarser-textured soil (Hiiumaa), podzolization led to faster and deeper P migration due to less sorption onto oxides, compared to the finer-textured podzols (Juminda) (Table 1). The development of the thick organic horizon in the sandier soil (Fig. 1) is partly explained by low P concentration in needle litter and moss biomass (Figs. 1b and 3) that retard microbial litter decomposition through plant–soil feedback (Vitousek et al. 2004). A gradual increase in available P in the organic horizon (Fig. 2a) could account for an increase in fine root biomass in the organic horizons of the sandier soil (Fig. 5b).

In the finer-textured soils, the higher P concentration in needle litter and moss biomass facilitates litter mineralization (Vitousek et al. 2004), which limits the development of organic horizons (Fig. 1b). Short-range-order Al and Fe oxides limit mobility of organic acids and slow podzolization in the finer-textured soils (Figs. 3 and S3a; Fujii et al. 2012, 2019). Because short-range-order Al and Fe oxides increase with soil age in the spodic B horizons of the finer-textured podzols (Fig. 2b), roots are exposed to competition for P with sorption (Bolan 1991). Allocation of fine roots to the mineral soil horizons is required for P uptake through diffusion or solubilization of oxide-bonded P in the finer-textured soils (Jones et al. 2003). The forms and availability of soil P acted to shape root architecture (Figs. 6 and 7). Soil aging thus induced vertical and morphological root plasticity in fine root systems in a boreal Scots pine community (Figs. 4 and 5b).

**Conclusion**

We tested whether a single pine species displayed morphological plasticity to nutrient limitation in boreal forests with limited phylogenetic diversity. We found that tree roots show wide vertical plasticity by changing their vertical root distribution and increasing specific root length to target different P sources. Fine roots with high specific length are allocated into the spodic B horizon to solubilize oxide-bonded P when P hotspots are located in the shallow soil horizons of fine-textured podzols. In a coarse-textured podzols with low oxide-bonded P, fine roots increase dependency to labile P in the organic horizon. Our findings enlarge the scope of plant root plasticity to ameliorate P limitation in boreal sandy soils.

**Declarations**
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**Tables**

Due to technical limitations, table 1 and 2 is only available as a download in the Supplemental Files section.

**Figures**

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![Image of Figure 1](image-url)
Relief map and a) podzolization and b) changes in soil carbon stocks (0–80 cm) within the Hiiumaa and Juminda soil chronosequences. Bars indicate standard errors (N = 3). Different letters (A, B, C) indicate that values are significantly different (P < 0.05) between soil ages. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

**Figure 2**

a) Changes in the depth distribution of Bray-2 extractable phosphorus (column) and oxalate extractable phosphorus (dot), b) short-range-order aluminium and iron minerals (Al$_{0}+1/2$Fe$_{0}$), and c) fine root biomass (<2 mm) along the sand dune soil chronosequences in Hiiumaa and Juminda. Bars indicate standard errors (N = 3). Different capital letters (A, B, C) indicate that the values of each soil horizon are significantly different (P < 0.05) between soil ages of each chronosequence. Different lowercase letters (a, b, c) indicate that the values are significantly different (P < 0.05) between soil ages of each chronosequence.
Figure 3

Relationships between moss biomass or needle litter phosphorus concentrations and soil Bray-2 phosphorus stocks (0–80 cm). Bars indicate standard errors (N = 3).
Figure 4

Allocation of a) fine root biomass and b) fine root length to the organic and mineral soil horizons along the sand dune chronosequences at Hiiumaa and Juminda. Fine root data (<2 mm) are shown. Bars indicate standard errors (N = 3). Different capital letters (A, B, C) indicate that ratios of root biomass or length in mineral horizon relative to organic horizon are significantly different (P < 0.05) between soil ages of each chronosequence. Different lowercase letters (a, b, c) indicate that root biomass or length is significantly different (P < 0.05) between soil ages of each chronosequence.
Figure 5

(a) Relationship between extent of podzolization and rooting zone depth and (b) relationship between extent of podzolization and the fraction of fine root biomass below the B horizon relative to total root biomass (< 0.5 mm). The extent of podzolization was calculated as ratio of short-range-order Al and Fe oxide concentration (Alo + 1/2Feo) in the upper spodic B horizon relative to that in the E horizon. * indicates the significant differences between the slopes of linear regressions.
Figure 6

Changes in the specific root length (diameter < 0.5 mm) in soil horizons along the sand dune chronosequences at Hiiumaa and Juminda. Bars indicate standard errors (N = 3). Different capital letters (A, B, C) indicate that the values of each soil horizon are significantly different (P < 0.05) between soil ages of each chronosequence. Different lowercase letters (a, b, c) indicate that the values are significantly different (P < 0.05) between soil ages of each chronosequence.
Figure 7

Relationships between specific root length (diameter < 0.5 mm) and a) soil available phosphorus (Bray No. 2), b) soil oxalate extractable phosphorus, and c) short-range-order Al and Fe oxides. d) Relationships between root tissue density and short-range-order Al and Fe oxides.

Supplementary Files

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