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Fine root traits in European beech and Norway spruce forests in Southern Norway and their impact on carbon storage

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Front page photo: Fine roots of Beech (*Fagus Sylvatica*) with ectomycorrhizal fungi. Photo by Julia F. Brendehaug

Abstract:

With a warmer climate, temperate tree species like beech may become more widespread towards Norden latitudes, because of the less favorable conditions for spruce trees. Boreal forest trees form ectomycorrhiza, a symbiotic relationship between plants and fungi, with key importance for global carbon and nutrient cycling. Despite the broad recognition of the importance of fine roots and mycorrhizae for carbon acquisition, we do not know how the amount of fine root traits in different tree species may reflect their potential for carbon storage. The aim of my thesis was to quantify the fine root traits in beech and spruce forests and interpret the results as the potential for carbon storage belowground. I considered the mycorrhization, the root biomass, and fine root production as a indicator for carbon storage in spruce and in beech.

To quantify the fine root traits, I sampled soil cores in spruce and beech forest stands in southeast Norway, then extracted and scanned live fine roots. I measured fine root traits such as root branching (number of root tips and forks), root length, root diameter, root surface area and root biomass. By considering all fine root tips to be mycorrhizal I estimated the mycorrhization level in beech and spruce in different soil layers. To estimate the amount of fine root production (over one growing season) I extracted and weighed all fine roots from root meshes, which I installed at the beginning of the growing season, and then evaluated three months later.

Visual inspection showed almost 100% of all root tips to be ectomycorrhizal. Beech had significantly more root tips (mean $n = 1.1$ million tips/m²), than spruce (mean $n = 0.4$ million tips/m²). The total number of root forks was also significantly higher in beech. Average fine root diameter was significantly larger in spruce than in beech. I found no significant difference in specific root area (SRA) among beech and spruce. The average fine root biomass was significantly higher in beech (mean = 662 g/m²) compared with spruce (mean = 367 g/m²). Fine root production was significantly higher in the beech forest than in the spruce forest.

My results indirectly indicate beech forests to potentially store more belowground carbon than spruce forests. How beech forests, which potentially store more carbon belowground, will change in the context of a warmer climate with longer growing seasons, remains to be seen. More research is needed to test if these results can be generalized to wider forest ecosystems in the future.

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1. Introduction

Carbon (C) is one of the most abundant elements in all living organisms (Hessen et al., 2004). The C content in vegetation is usually calculated by considering the C content in plants to be 50% of plant biomass (de Vries et al., 2009; Ma et al., 2018). Plant photosynthesis captures the atmospheric CO₂ and transfers it into C to form biological compounds for building and maintaining the biological structures (Hessen et al., 2004). In this process a vast organic C pool is created in terrestrial vegetation, both above and belowground.

The largest terrestrial pool of organic carbon (C) is found in soils (Batjes, 1996). Especially boreal forests are efficient in storing belowground C and about 60% of their C is stored belowground (Pan et al., 2011). The ultimate C storage in forest soils is determined by the balance between C input (litter, photosynthesis) versus C output (respiration, decomposition), recalcitrance of the C-compounds, also affected by climate, vegetation, soil properties, and land use (Batjes, 1996).

Tree roots play a crucial role in acquiring and storing the belowground C (Clemmensen et al., 2013). Fine roots, usually defined as < 2mm in diameter (Figure 1) (Pregitzer, 2002), are mainly involved in water and nutrients resource uptake and, C storage created from the tree photosynthesis (Ostonen et al., 2013). Although fine roots constitute only a fragment of the total root biomass, they consume substantial amounts of C during their growth and maintenance (Deans, 1981; Guo et al., 2013). They make up a considerable part of the global terrestrial carbon cycle and are a major constituent of carbon belowground (Jackson et al., 1997). Therefore, they play an essential role in soil carbon, nutrient, and water cycles (Soudzilovskaia et al., 2015b).

While fine roots are the short-lived, physiologically active part of the root system, coarse roots live considerably longer. Coarse roots, defined as roots larger than 2 mm in diameter, are lignified and mainly have a function in resource transportation and stability (Persson, 2002). Although coarse roots eventually contribute to the C storage in soils, their contribution to C input is smaller than fine roots because of their static nature (Bolte et al., 2004). Consequently, fine roots are more dynamic in nature than coarse roots, and constantly grow, die, and decompose.

Fine root branching, or number of root tips and forks, reflects the absorptive potential of the root system (Soudzilovskaia et al., 2015a; Soudzilovskaia et al., 2015b). The fine root length along with root surface area, indicate the potential of fine roots to explore the soil in the search for and acquisition of water and nutrients, and these traits have a high relevance for ecosystem functioning (Ostonen et al., 2007b). Root diameter is used for technically distinguishing among the fine roots and coarse roots and for calculating other traits, such as root volume or root surface area (Bauhus & Messier, 1999). Root area is used to estimate the area of the roots available for absorption of nutrients and water as

well as attachment of symbiotic fungi (Børja et al., 2008; Ostonen et al., 2013). Biomass of fine roots, expressed as dry weight of fine roots per square meter of soil, is the total amount of fine roots. Root production, on the other hand, is a dynamic measure, reflecting the amount of fine roots (n/m^2) produced during a given time period (Ekblad et al., 2013; Lukac & Godbold, 2010) (see extended definitions in Appendix A, table 7.1).

The assessment of different root traits may provide a promising basis for a more quantitative and predictive global change research (Kattge et al., 2011), such as their use in models and in databases. Plant traits in general, or root traits in particular, are defined as morphological, anatomical, or phenological features measurable at the individual species level (Violle et al., 2007). Root traits, such as tips, forks, length, diameter, area, biomass, and production reflect the evolutionary adaptation of the root system and respond dynamically to abiotic and biotic environmental factors (Valladares et al., 2007), and thus the effect of environmental changes, such as warming (Wilson et al., 2017), elevated CO₂ (Staddon et al., 1999) or nitrogen enrichment (Jumpponen et al., 2005) on ecosystem functioning. Therefore, the quantification of root traits provides indirect information about their nutrient absorbing efficiency or carbon storage. Many of the of fine root traits are relatively sparsely represented in different databases (Kattge et al., 2011), which reflects their laborious assessment and methodological challenges.

1.1 Mycorrhiza:

In forest soils, the majority of fine tree roots are commonly more than 95% colonized by mycorrhizal fungi (Helmisaari et al., 2009; Ma et al., 2018; Taylor, 2002). Mycorrhiza is a symbiotic interaction where plant fine roots and specialized soil fungi exchange carbon and nutrients (Smith & Read, 2008). While plant roots provide carbohydrates from their photosynthesis to their fungal partners, mycorrhizal fungi provide nutrients and water to plants. Therefore, the mycorrhizal short root, or root tip, is considered a symbiotic functional unit where exchange of nutrients, carbon, and water between the symbiotic partners takes place (Smith & Read, 2008). Because mycorrhizal fungi (unlike saprotrophic fungi) derive carbon from their living hosts, this strategy frees them from the competition with saprotrophic soil fungi which derive their carbon from dead organic material (Kyaschenko et al., 2017; Smith & Read, 2008). Therefore, mycorrhizal fungi can strongly affect plant nutrient uptake, biomass, and carbon allocation (Soudzilovskaia et al., 2015a; Soudzilovskaia et al., 2015b). In many ecosystems, mycorrhizae, together with fine roots, provide the largest input of carbon into soils (Clemmensen et al., 2013; Verbruggen et al., 2016). Mycorrhizal symbionts and fine roots are therefore also of major importance to the carbon flow on global scales (Kattge et al., 2011).

The most abundant mycorrhizal association in temperate and boreal forests is ectomycorrhiza (ECM), which occurs in 2% of trees globally (Brundrett, 2002; Maherali et al., 2016). Ectomycorrhizal colonization takes place primarily, if not exclusively, in fine roots (Guo et al., 2008), meaning not the

total root biomass, but rather the fine root fraction, needs to be examined in mycorrhizal studies. Therefore, the intensity of plant root colonization by ectomycorrhiza is usually expressed as the number of root tips colonized by the fungi (Soudzilovskaia et al., 2015a). This is the best available measurement quantifying the “strength” of the plant–fungi relationship at the site. Therefore, the amount of fine root tips (or colonization by mycorrhizal fungi) can be used as an indicator of nutrient and carbon flow between plants and fungi (Soudzilovskaia et al., 2015b).

Ectomycorrhizal fungi cause the fine root tips to swell and develop into a “Christmas tree”-like structure on the surface of the fine root (Figure 1) (Smith & Read, 2008). Ectomycorrhizal hyphae expand into an extensive belowground network which can cover a considerable area. Because the amount of mycorrhization can be species-specific, it can be used in ecological analyses (Soudzilovskaia et al., 2015a; Soudzilovskaia et al., 2015b).



Figure 1. Beech fine roots (left) and spruce fine roots (right) with ectomycorrhiza. Observation during lab work in the autumn of 2021. Photo: Julia F. Brendehaug

The amount of mycorrhization connected to fine roots varies with species and depth due to their nutrient and water requirements in their forest ecosystems. For example, two different tree species can have a difference in fine roots depth, and thus where the mycorrhization is located. Possibly, fine roots and mycorrhization can together say something about where carbon is stored belowground (Meier et al., 2018; Soudzilovskaia et al., 2015b). Therefore, there is a connection between fine root traits, mycorrhization, and carbon storage in tree species which is important to assess further.

1.2 Spruce and beech in boreal forests of Norway

Looking at tree species located in Norway, spruce (*Picea abies* (L. Karst)) is currently the dominant species in the amount of biomass, especially on nutrient rich soils (Moen & Lillethun, 1999). The tree species with the lowest distribution is beech (*Fagus sylvatica* L.), which is restricted to a few locations: Larvik and a few other locations in southeast and western Norway (Myking, 2020) (Figure 2). These populations of beech are regarded as the northernmost distribution in Europe (Myking et al., 2011).



Figure 2: Current beech distribution in Scandinavia, restricted to Vestfold, Larvik, and a few trees in the northwestern part of the Hardanger fjord (Seim). (Source: www.nibio.no) (Myking, 2020).

Current beech distribution is low in Norway, as beech has a temperature disadvantage compared to spruce because of a cool climate and short growing seasons. Possibly, climate warming and prolonged growing season can contribute to more beech forests in Norway. A slow shifting process in species from the current spruce forest domination to more beech and deciduous species may be seen as we approach the year 2100 (Figure 3), together with a decrease in spruce, following the higher

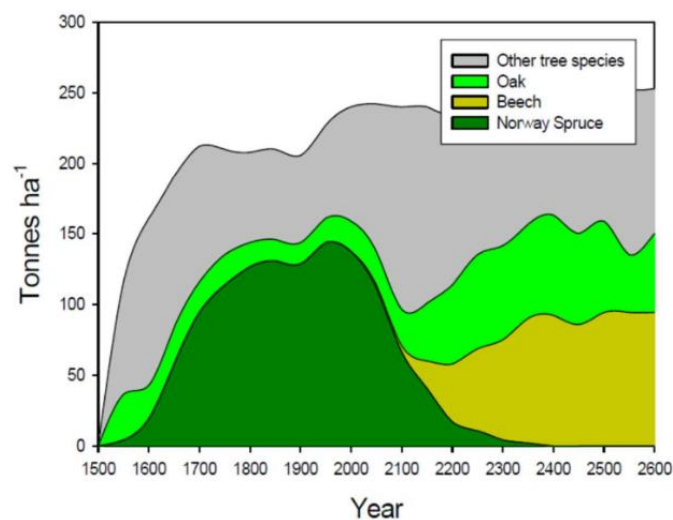


Figure 3: Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model (Source: Hickler et al., 2012).

temperatures. However, how a species shift from coniferous to deciduous species may affect carbon storage belowground is still very uncertain, due to many variables affecting C storage in tree roots (Hickler et al., 2012).

Research by Ransedokken (2016, 2019) in boreal forests (in Brånakollane), who looked at the soil carbon below spruce and beech, showed the amounts of soil carbon between the species to be similar. However, according to research by Kirfel et al. (2019) and Ostonen et al. (2013), beech and spruce fine root traits and mycorrhization are heterogeneous due to their differences in root architecture, which is defined as the shape and the structure of the roots (Freschet et al., 2021a). Kirfel et al. (2019) reports a higher amount of fine roots in beech subsoil (10-15 cm), due to the species root architecture (Figure 4). Spruce, on the other hand, is believed to have a shallow root architecture with most fine roots in the topsoil (5-10 cm), which is where most of the previous research is concentrated (Ostonen et al., 2013).

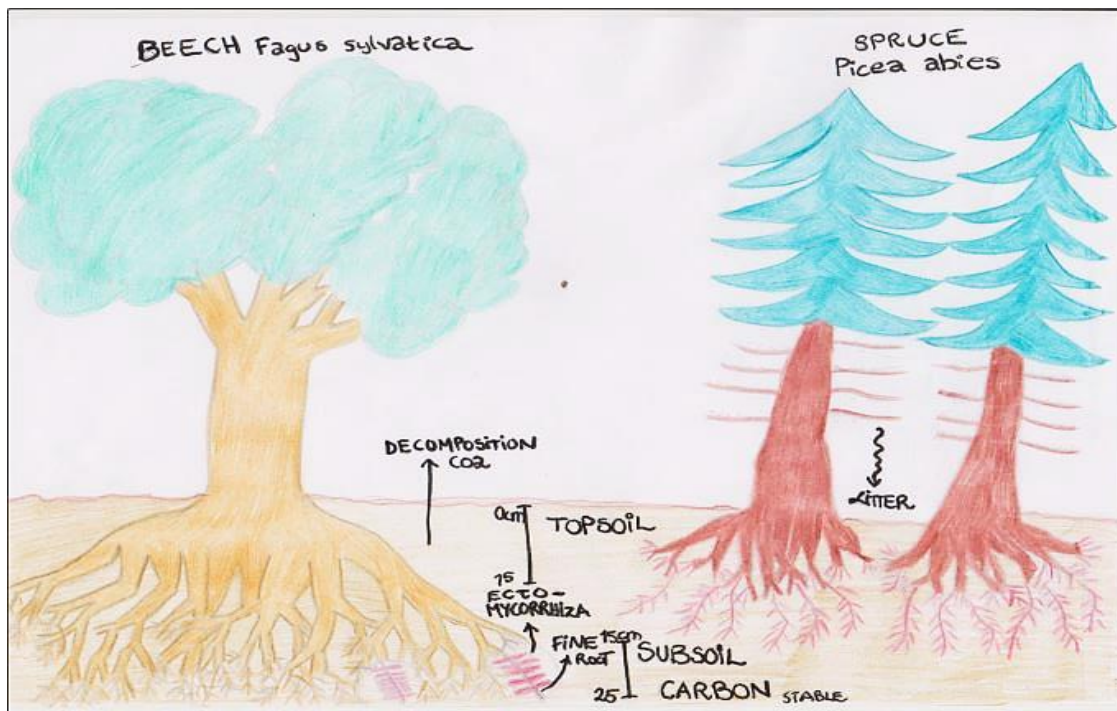


Figure 4: Beech and spruce tree root characteristics with topsoil (0 -15 cm) and subsoil (15-25 cm) at a site. Drawing by Julia F. Brendehaug

The number of fine roots varies with species and depth according to previous literature. For example, Helmisaari et al. (2009) reports a high concentration of fine roots in spruce topsoil. Further, studies by Børja et al. (2008) and also found high amounts of fine roots in spruce in the upper layers. Previous studies therefore suggest the proportion of C to be larger in coniferous forests than in deciduous forests (Gower et al., 1997). However, in a review analysis of over 140 sites in Europe, Finér et al. (2007) showed fine root biomass to be greater belowground in beech than spruce. Due to this

difference in opinion, comparisons between fine roots in deciduous species (beech) and conifer species (spruce) needs to be further studied in boreal forests.

Helmisaari et al. (2009), Vogt (1998) and Ostonen et al. (2005) also reported a higher number of studies on spruce in boreal forest in Scandinavia, compared to beech. Beech has not been extensively researched in boreal forests, especially on fine roots. However, it may be explained by a lack of comparisons between beech and spruce in boreal forests, but also due to its scattered appearance (Figure 2). Therefore, beech and other deciduous trees needs to be recognized in boreal forests due to their possible increased distribution in the future (Figure 3).

1.2 Knowledge gaps and previous research:

To date, only a few studies have looked into fine root traits and ectomycorrhizal fungi in beech in boreal forest, using fine root tips and other fine root traits (Helmisaari et al., 2009), especially how the quantified root traits may be interpreted; regarding the belowground carbon storage and mycorrhization (Soudzilovskaia et al., 2015b). For example, the traits of root tips/forks, length, diameter, and root area have only been studied and measured in some previous studies by Soudzilovskaia et al. (2015a; 2015b). The present research is far from complete (Chen et al., 2004; Freschet et al., 2021b; Meier et al., 2018). Obtaining these data is cumbersome, as any attempt to quantify the roots is destructive and methods of estimation and assessment are energy and time consuming (Finér et al., 2011a; Finér et al., 2011b). Fine roots are hard to work with due to their small size (Cornelissen et al., 2003), and therefore the workload needed is often not prioritized.

Ectomycorrhizal fungi have to a lesser extent been included in the models of carbon storage of the roots (Soudzilovskaia et al., 2015b), and little of mycorrhiza's important contribution to carbon storage has been used in ecological analysis.

1.3 Aim of the study

The aim of this study was to quantify the fine root traits in beech and spruce forests and interpret the results with the amount of mycorrhization, as their potential for carbon storage belowground. I considered the increase in mycorrhization, root biomass, and production as a relative measurement to increase in carbon storage in spruce and beech.

To quantify the fine root traits, I took soil cores in spruce and beech forest stands in southeast Norway, then extracted and scanned live fine roots. I measured fine root traits such as root branching (number of root tips and forks), root length, root diameter, root surface area and root biomass. By considering all fine root tips to be mycorrhizal I estimated the mycorrhization level in beech and spruce and different soil layers. To estimate the amount of fine root production over one growing season I extracted and weighed all fine roots from root-meshes I installed at the beginning of the growing season and evaluated three months later.

2. Materials and Methods

2.1 Site characteristics

I established two study sites: one in a beech forest (Brånakollane, nature reserve, (59.1954, 10.0502) and one in the nearby spruce forest, outside the nature reserve (59.1890, 10.0436) (Figure 5). Both sites were situated about 20 km north of Larvik in Vestfold and Telemark County, in the boreonemoral bioclimatic zone. Other research projects were performed in the same nature reserve (Asplund et al., 2018; Ransedokken, 2016). The beech site at Brånakollane was established as a nature reserve in 1980 (Norwegian Ministry of Climate and Environment, 1980). The nature reserve is protected as a natural and wild beech forest, together with its associated wildlife, insects, and soil fungi (Naturbase, 2022). While the beech forest has not been affected by forest logging or other forest activity since 1837, the spruce forests surrounding the beech forest are managed regularly (Ransedokken et al., 2019).

The general area belongs to the Oslo Rift geological bedrock, consisting of syenite, granite, and monzonite (Solli & Nordgulen, 2007). The specific study sites are on a monzonite bedrock covered with a thin layer of weathering material (NGU, 2022).

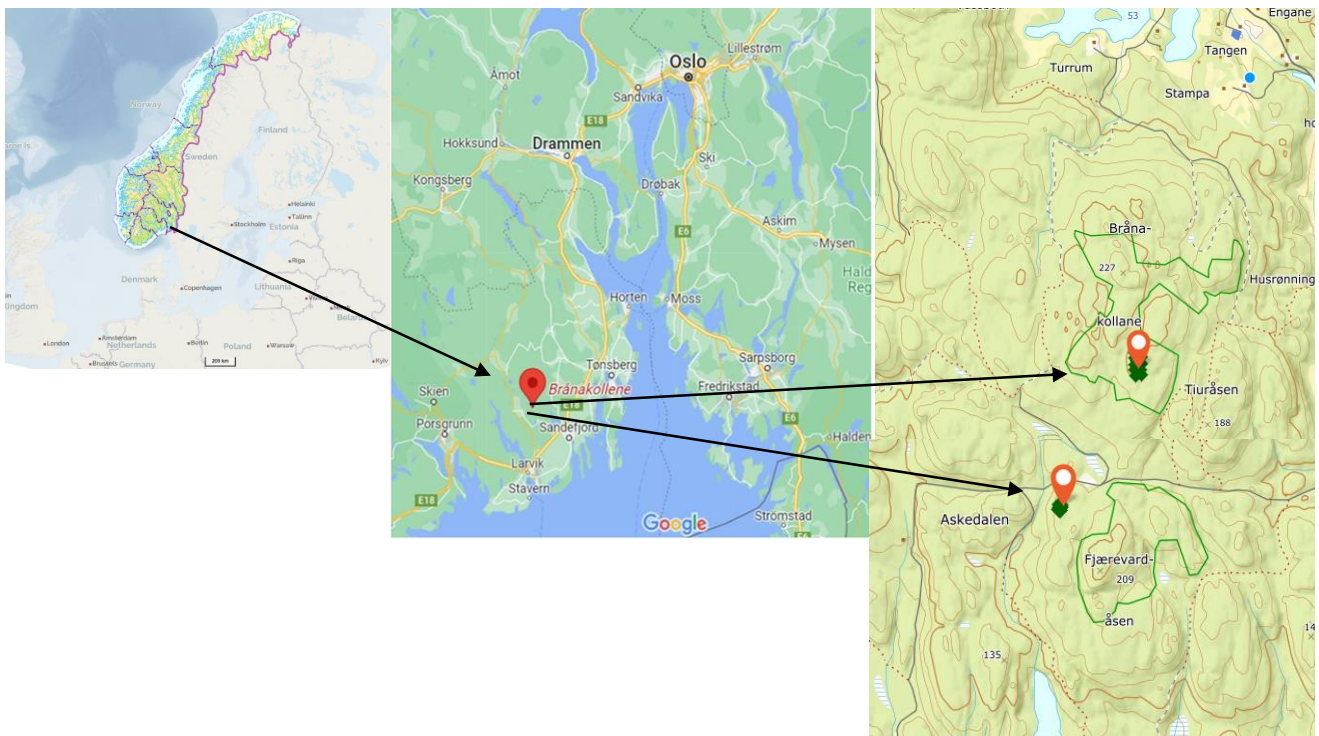


Figure 5: Map over the locations in Norway, Brånakollane in Larvik (marked with a drop). The two locations of beech (upper arrow) and spruce (lower arrow) are marked with arrows. The green boundaries represent nature reserves. Source: www.norgeskart.no (Norgeskart, 2022).

2.2 Vegetation description:

In the spruce forest the ground was covered with mosses like Splendid feather moss (*Hylocomium splendens*), Greater Feather wort (*Plagiochila asplenioides ssp. asplenioides*) and, also small plants like White wood sorrel (*Oxalis acetosella*) and Common polypody (*Polypodium vulgare*). During the field season the ground vegetation in the beech forest was sparse and mostly covered with beech leaves (Figure 6), and only some grasses, like Bunch grass (*Calamagrostis arundinacea*) (Naturbase, 2022).



Figure 6: Beech site vegetation and tree composition at Brånakollane. Photo: Julia F. Brendehaug

European beech is a shade-tolerant species, and forms a dense canopy, which produces a large amount of leaf litter while the extensive root system reaches from shallow to intermediate depths (Wühlisch, 2008). The evergreen, coniferous, Norway spruce is a shallow rooted, shade-tolerant species, but more light-demanding than beech. Its needle litter accumulates on soil surface and with time forms a thick organic layer (humus), creating soil conditions with low pH (Asplund et al., 2018) (Figure 4).

At both the sites the soil was stony, observed to increase at about 10 cm depth. It consisted of weathered rock with a thin layer of organic matter and mineral layers, which was also observed by Ransedokken (2016). Our soil cores were relatively shallow due to stoniness, reaching to about 20 cm depth (Table 1).

Table 1: Site and sampling characteristics for beech and spruce forests.

Site	Beech reserve	Spruce forest
Number of plots	3	3
Number of replicates at each plot	5	5
Longitude (°E)	59.1954	59.1954
Latitude (°N)	10.0502	10.0502
Elevation (m.a.s.l)	190	188
Number of soil cores topsoil and subsoil each)	15	15
Mean subsoil depth ± SD (cm)	13.5±4.50	13.9±3.56
Mean topsoil depth ± SD (cm)	3.3±1.6	6.3±1.8
Annual rainfall (mm)*	17.2	17.2
Mean precipitation (mm)*	7.5	7.5
Mean temperature	14	14.2
Organic Soil pH **	4.40	4.05

* Hedrum metrological station in Kvelde, Norway.

** Measured by Ransedokken (2016)

2.3 Sampling design

I selected three plots in the beech forest and three plots in the nearby spruce forest. Each plot was about 30 x 30 m in size and plots were about 50 m in distance from each other. Within each plot I selected 5 trees with approximately the same size and age; one tree in the center surrounded by 4 trees around it (3 plots with 15 trees in total for each site). At the southeast side of each selected tree, I took soil cores for fine root analysis. At the northwest side of each tree, I installed root meshes to estimate the fine root production.

I took soil cores about 1,5-2 m from the stem of each of the selected trees in beech and spruce sites; 30 soil cores in total from both sites, 15 in each. To take soil cores I used an auger (10 cm in diameter) and took a soil sample until I reached the solid bedrock. The soil core depths were ranging from 8-20 cm. I placed each soil core on a rounded tray and measured the depth of the whole core (Figure 7). Then I divided each core into topsoil and subsoil part, measured the length of each fraction and placed them into separate plastic bags (60 samples altogether: 30 from topsoil and 30 from subsoil). The bags were kept cool during transportation. In the lab, the soil cores were stored at -80 °C until further processing.



Figure 7: Field work with soil core extraction showing the different soil layers. Photo: Julia F. Brendehaug

2.4 Fine root extraction and scanning

To estimate fine root traits and biomass I thawed each soil core and extracted the fine roots from each soil core manually and by using water stream and soil sieve of 1 mm mesh size. All live tree roots < 2 mm in diameter were picked out. Tree roots were distinguished morphologically from those of understory vegetation and all dead or understory roots were discarded. Clean roots were kept in water at 4 °C until further scanning. Roots from each sample (60 samples altogether) were scanned for root characteristics/traits. I used a 400 dpi Epson Expression 800 transmitting light scanner. To scan the fine roots, I positioned all roots in water on a glass tray.

The images obtained from the scanner were analyzed by using the software WinRHIZO (Version 2013d, Regent Instruments, Quebec City, Canada). From the digitized images the number of fine roots, their length, diameter, and branching (number of root tips and forks) were obtained. Root tips

were recognized as all root endings, while forks were identified as points where three lines intersect. The data obtained from WinRHIZO were exported to an Excel spreadsheet for further analysis (Appendix A, table 7.2, 7.3). Based on the assumption that all the fine root tips were mycorrhizal, I used the data of number of fine root tips to estimate the mycorrhization level expressed as number of tips per unit soil area (tips/m²).

Forks, defined in the WinRHIZO software as root crossing of three lines (Richner et al., 2000; Smit et al., 2013), were also expressed as number of forks per unit soil area (forks/m²). To calculate the specific root length (SRL) the length of fine roots was divided by their biomass dry weight (dw), expressed as m/g. Specific root area (SRA) was calculated as root area/surface per root biomass dry weight (dw), expressed as cm²/g. After scanning, I gathered all roots from one sample, placed them in marked paper bags, dried them at 60 °C for 3 days, and weighed their dry matter biomass. Fine root biomass was expressed as biomass dry weight per unit soil area, g/m². Since all of fine roots were considered to be mycorrhizal and 50% of the biomass is carbon (Lukac & Godbold, 2010), I can estimate the mycorrhization level from number of root tips and carbon from the biomass fraction.

2.5 Fine root production

To estimate the fine root production at both sites during the vegetation period I installed one nylon mesh about 1.5-2 m from the trunk of each selected tree, at the north-west side, as described by Lukac & Godbold (2010) and Hirano et al. (2009). Briefly, each root-mesh (23 x 6 cm, with 1 mm² mesh size) was inserted into the soil vertically by using a custom-made metal plate with a blunt edge. I coated the metal plate with a nylon mesh and used a rubber hammer to insert the mesh into the soil, retrieving the metal plate after the mesh insertion. At the beech site the meshes were installed on 28th of June 2021. In the spruce forest, the meshes were installed 16-18th of July 2021. All installed meshes were marked with colored sticks for better visibility at the retrieval timepoint. The meshes then remained in the soil for the whole vegetation period until September 2021. The fine roots entangled in the meshes during the vegetation period were considered as new roots produced during this period.

All meshes were removed from the soil on the 18th of September 2021. Each mesh was extracted from the soil by using a spade, leaving about 1 cm soil layer at each side. Fine roots trapped in the mesh, protruding 1 cm from the netting surface on each side, were included. Soil samples were then transported to the laboratory and stored at -80 °C until further analysis. To estimate the fine root production, all roots entangled into the meshes were picked out, cleaned, dried, and weighed (dw). Root production was calculated as weight of fine roots (dw) per soil area unit.

2.6 Statistical methods

Data from the two sites were analyzed in R (R Development Core Team 2011). The quantitative root traits and the nested mixed model were performed with the one way-variance analysis (ANOVA).

I performed linear mixed effect models to test for the effect of tree species (spruce vs. beech), soil layers (topsoil vs. subsoil) and their interaction on the quantitative root traits. In these models, soil cores (including both layers) nested within plot were used as random effects. Model assumptions were checked visually through residual diagnostics. In cases where residuals were not normally distributed, the response variable was either log- or square root-transformed (Appendix, figure 7.1-7.6). I used results from an ANOVA table to test (F - and P -values) for the linear mixed effect models, which were calculated using Satterthwaite's approximation of degrees of freedom.

Fine root production was not divided by layers and thus I instead performed a linear mixed effects model testing for the effect tree species only. Here, I also used soil core nested within plot as random effect. For this model, transformations of the response variable did not improve the distribution of the residuals. Therefore, I performed a permutation test for mixed effects models, with 1000 permutations, using the function `perm.lmer` in the R package `permutes`.

This provided the results of F - and P -values in an ANOVA-table (Table 2). I set the significance level to $P < 0,05$.

3. Results

3.1 Number of root tips – mycorrhization level

Beech had significantly more root tips (total mean $n = 1.1$ million tips/m²), than spruce (total mean $n = 0.4$ million tips/m²) (Figure 3.1, Table 2). This pattern was more pronounced in the topsoil, resulting in a significant interaction effect (Appendix, Figure 7.1). Beech had more root tips in the topsoil (mean $n = 1.3$ million tips/m²) compared to spruce topsoil (mean $n = 0.4$ million tips/m²) (Figure 3.1), as well as in subsoil (mean $n = 0.9$ million tips/m² vs. mean $n = 0.4$ million tips/m²) (Figure 3.1). I inspected the fine roots visually and almost 100% of all root tips was ectomycorrhizal.

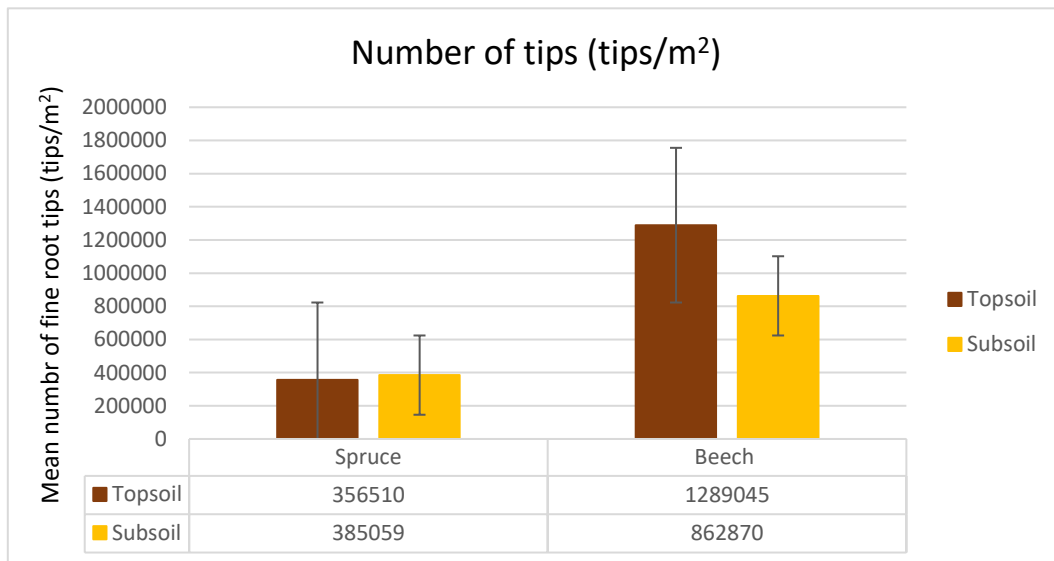


Figure 3.1: Mean number fine root tips in spruce and beech forests measured in numbers of tips (n) per square meter soil (n/m^2) with standard error bars. Data table shows mean number of tips in beech and spruce in topsoil and subsoil.

3.2. Number of fine root forks – mycorrhization level

The total number of root forks was significantly higher in beech (total mean $n = 3.9$ million forks/m²) compared to spruce (total mean $n = 1.1$ million forks/m²) (Table 2, Figure 3.2). Overall, there were no difference between layers, but the tree species effect was even larger in the topsoil resulting in a significant interaction effect (Appendix, Figure 7.2). Beech had significantly more forks in both the topsoil (mean $n = 2.5$ million forks/m²) and subsoil (mean $n = 1.4$ million forks/m²), compared to spruce (Figure 3.2.).

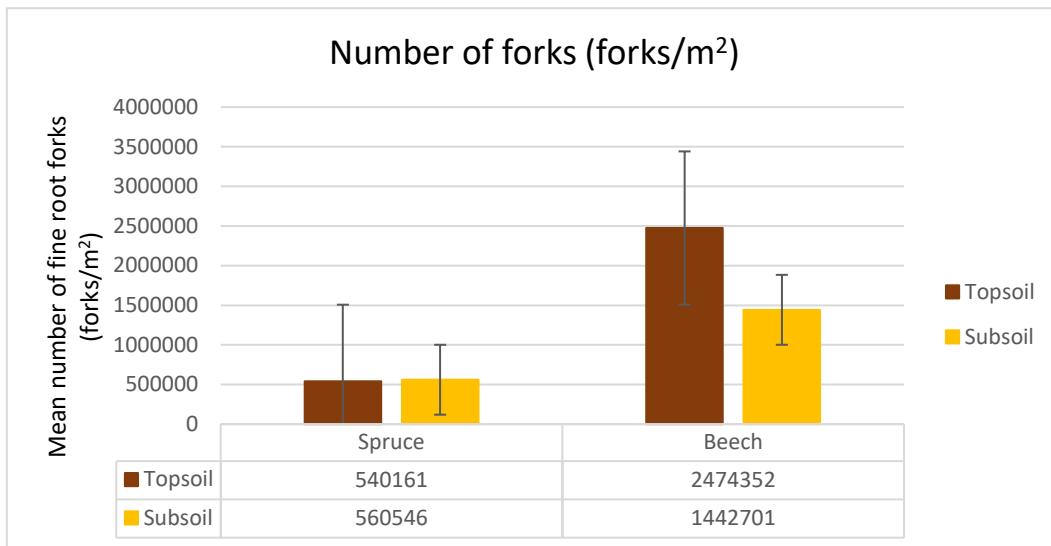


Figure 3.2: Mean number of fine root forks in spruce and beech measured in numbers per square meter (forks/m²) with standard error bars. Data table shows mean number of forks in beech and spruce in topsoil and subsoil.

3.3 Specific root length (SRL)

Overall, beech and spruce did not differ in fine root length per dry weight root mass (total mean = 24 m/g and 16 m/g, respectively (Table 2, Figure 3.3)). However, in the topsoil, beech had higher specific root length than spruce. Overall, the topsoils had longer roots per dry weight, but this effect was solely driven by beech, as shown by the significant interaction term (Appendix, Figure 7.3).

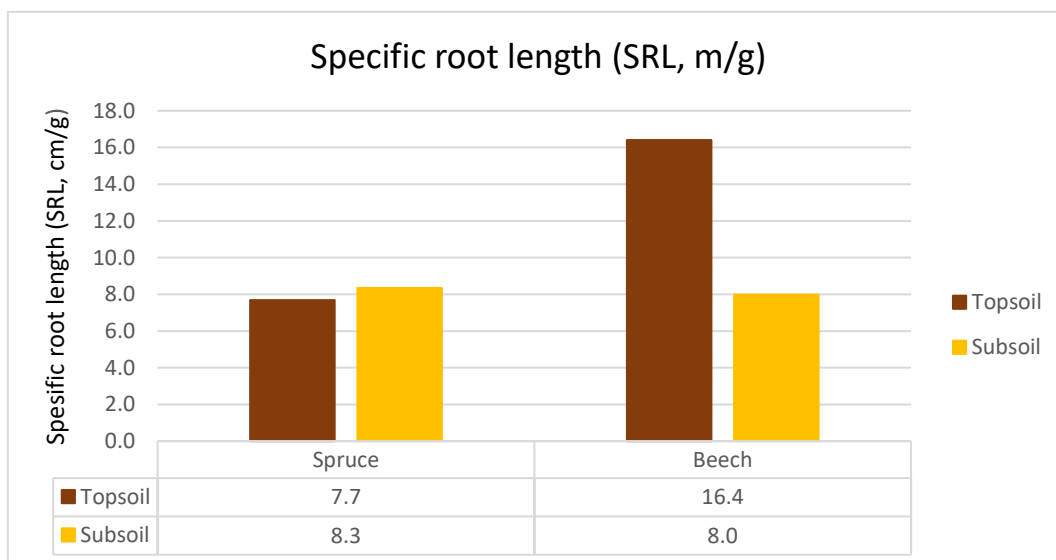


Figure 3.3: Specific root length (SL) measured in spruce and beech topsoil and subsoil in centimeters (cm) per grams (g) dry weight of fine root biomass with standard error bars. Data table shows mean specific root length in beech and spruce in topsoil and subsoil.

3.4 Fine root diameter

Overall, average fine root diameter was significantly larger in spruce (total mean = 1.21 mm) than in beech (total mean = 0.97) (Table 2, Figure 3.4). Furthermore, topsoils had overall significantly smaller diameters and both these patterns was driven by the thin roots in beech topsoils. In the spruce forest there were no difference between layers, resulting in a significant interaction term (Appendix, Figure 7.4).

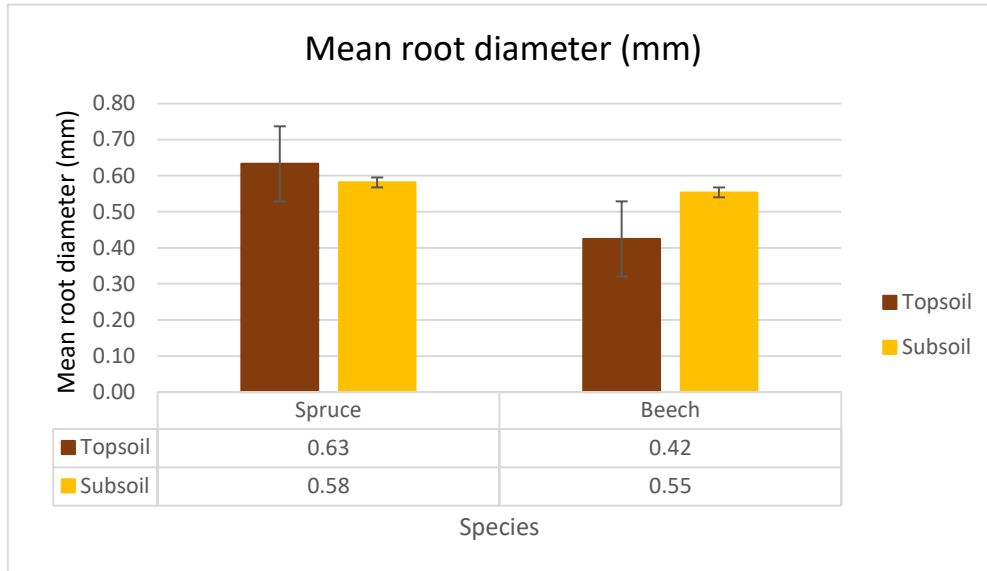


Figure 3.4: Mean root diameter measured in spruce and beech topsoil and subsoil in millimeter (mm) with standard error bars. Data table shows mean root diameter in beech and spruce in topsoil and subsoil.

3.5 Specific root area (SRA)

I found no significant difference in SRA between beech (total mean = 5103 cm²/g) and spruce (total mean = 4242 cm²/g) (Figure 3.5, Table 2). Overall, topsoils had significantly higher specific root area, but this was only true for beech resulting in a significant interaction effect (Appendix, Figure 7.5).

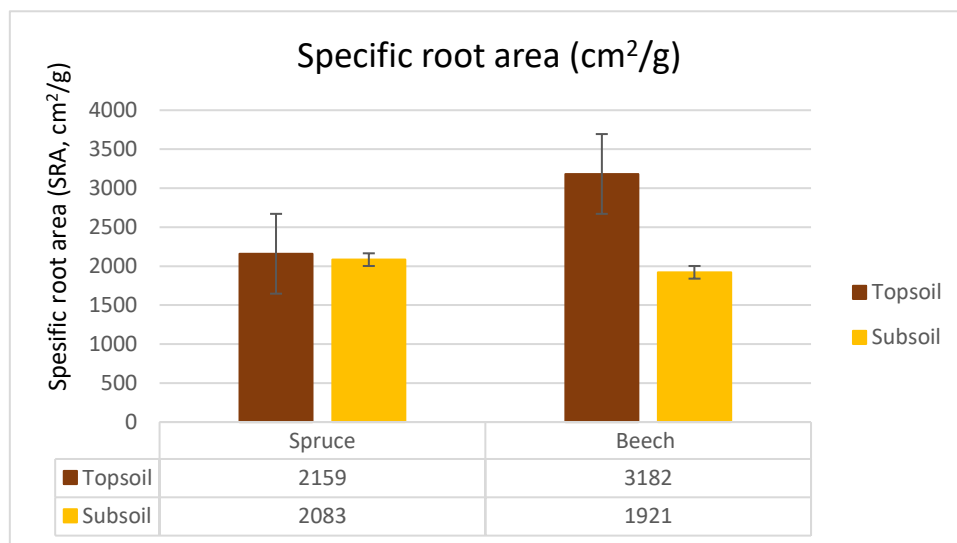


Figure 3.5: Specific root area (SRA) measured in spruce and beech topsoil and subsoil in square centimeters (cm²) per gram (g) with standard error bars. Data table shows mean specific root area in beech and spruce topsoil and subsoil.

3.6 Fine root biomass

Overall, fine root biomass was significantly higher in beech (total mean = 367 g/m²) compared with spruce (total mean = 662 g/m²) (Figure 3.6). This pattern was most pronounced in the topsoil, which had a significantly higher biomass (Table 2). On the other hand, the fine root biomass in spruce topsoil (mean = 175 g/m²) differed only little compared to the subsoil (mean = 192 g/m²), resulting a significant interaction term (Appendix, Figure 7.6).

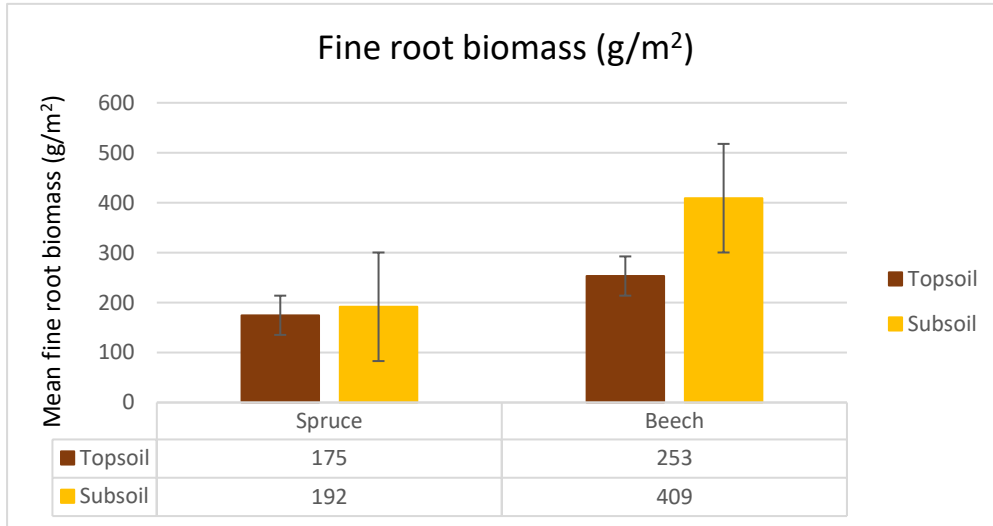


Figure 3.6: Mean biomass of fine roots in spruce and beech in topsoil and subsoil. Biomass is expressed in gram (g) per square meter (m²) root biomass dry weight with standard error bars. Data table shows mean fine root biomass in beech and spruce.

3.7 Fine root production

Fine root production was significantly higher in the beech forest (mean = 114 g/m²) than in the spruce forest (mean = 45 g/m²). In beech forest the fine root production was more than twice as high, as in the spruce forest (Table 2, Figure 3.7, Figure 7.7 in Appendix).

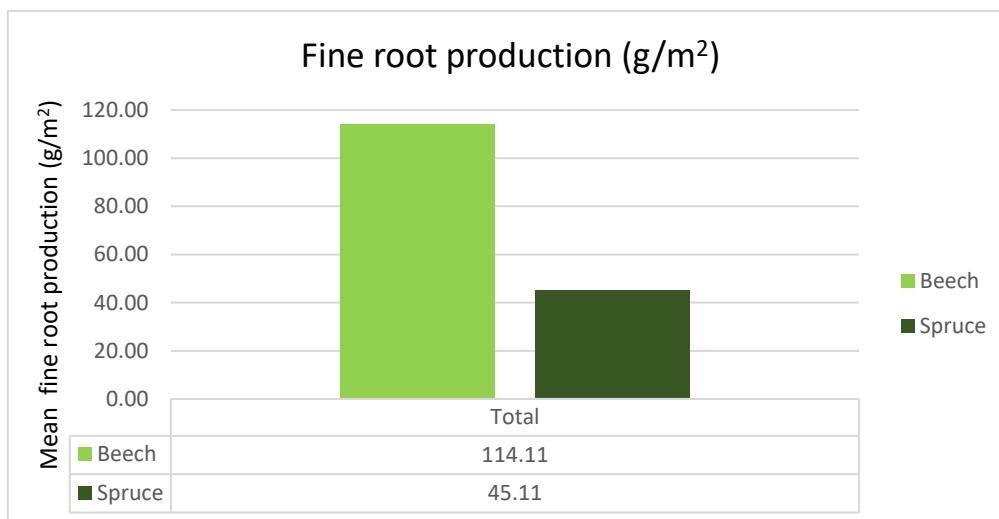


Figure 3.7: Mean fine root production in spruce and beech in grams (g) per square meter (m²). Data table shows mean fine root production in beech and spruce in topsoil and subsoil.

Table 2: Summary of linear mixed effect models (F and P-values) with block as a random factor testing for the effect of forest type (with dominant species, DS, beech vs. spruce) and soil layer (L, topsoil vs. subsoil) on fine root traits.

Root Characteristics	Dominant species (DS)	Layer (L)	L×DS
	F (P)	F (P)	F (P)
Fine root forks (n/m ²)*	49.86 (<0.001)	0.72 (0.401)	5.19 (0.027)
Fine root tips (n/m ²)*	53.76 (<0.001)	0.48 (0.491)	4.81 (0.033)
Specific root length (m/g) *	3.46 (0.138)	10.04 (0.003)	20.47 (<0.001)
Average fine root diameter (mm/m ²)*	9.94 (0.035)	5.84 (0.022)	18.06 (<0.001)
Specific root surface area (cm ² /g)*	0.89 (0.400)	10.55 (0.002)	17.62 (<0.001)
Fine root biomass (g/m ²)*	10.73 (0.031)	7.45 (0.011)	4.75 (0.038)
Fine root production (g/m ²)*	2.86 (0.041)		

Values in bold are significant at $P < 0.05$

* = log transformed

The order of the other root traits presented is a consequence of the mapping order instrument WinRHIZO software gives in their output. In the software the fine root traits is given in an order from smaller root traits (tips and forks) to larger root traits (fine root biomass). The following root traits with soil core extraction are measured in this order; root length (m/g), root diameter(mm), root surface (cm²/g) and root biomass (g/m²). On the other hand, fine root production (g/m²) is given last, as it is measured with root meshes opposed to the other root traits.

4. Discussion

4.1 Number of tips and forks - mycorrhization level

The visual observation of cleaned fine roots from Norway spruce and European beech sites showed most of the fine roots, close to 100%, to be ectomycorrhizal. This agrees with other studies reporting on high mycorrhization level of fine roots in boreal forests, ranging from 90-100% (Børja & Nilsen, 2009; Helmisaari et al., 2009; Taylor et al., 2000) (Soudzilovskaia et al., 2015b).

In my study I only investigated indirect data on the presence of fungi in the roots (root tips), while the presence of external mycelium in the soil is not assessed here. Currently, we do not know how the amounts of external and internal mycelium within an ecosystem are related (Soudzilovskaia et al., 2015b). However, it may be fair to assume, because the carbon and nutrient transfer takes place within fine roots, the root colonization intensity (number of mycorrhizal fine root tips) is probably a more direct predictor of mycorrhizal involvement in belowground carbon transfer processes than the extent of the external mycelium (Bever et al., 2010; Hoeksema et al., 2010; Veresoglou et al., 2012).

Branching, expressed as number of root tips or forks, indicates the mycorrhization level present (Soudzilovskaia et al., 2015b). The number of root tips and forks are correlated, with the number of forks always being higher (Brunner et al., 2009). For example, in my study the total number of root forks was always higher in both spruce and beech than the total number of tips in spruce (0.7 million tips/m² in total) and beech (2.1 million tips/m²). This is a consequence of how the mapping instrument WinRHIZO software evaluates tips and forks. In the software the root tips are seen as all root endings, while forks are seen as where three lines meet in all fine root branching and root crossings (Richner et al., 2000). Therefore, the number of forks in the same material will always be higher than number of tips (Brunner et al., 2003; Brunner et al., 2009).

In a study on fine root tips in spruce forest in Finland, Helmisaari et al. (2009) detected somewhat higher mean numbers of root tips, ranging from 0.79 million tips/m² to 2.43 million tips/m², than in my study (0.7 million tips/m²). However, the values are still comparable when being done in boreal forests. Helmisaari et al. (2009) also reported a similar mean number of fine root tips (0.5 to 2 million tips/m²) in the topsoil (5-15 cm) of spruce compared to my study (mean = 0.4 million tips/m²) (Figure 3.1 & 3.2), which is in line with higher numbers in the topsoil compared to the subsoil. Børja et al. (2008) reported 0.3 million root tips/m² in spruce subsoil, which is also in line with my results. These results on root tips indicate higher numbers in the topsoil of spruce, which indirectly indicate more mycorrhization present in the topsoil of spruce, than in the subsoil.

In beech soil layers I found more root tips in the topsoil (mean= 1.3 million tips/m²) compared to the subsoil (mean = 0.9 million tips/m²) (Figure 3.1). Leuschner et al. (2004), who worked in temperate

beech forest, did however report on somewhat higher numbers of root tips (mean = 3 - 18 million tips/m²) in the entire soil profile. My results being similar in root tips (and forks) amounts compared to Leuschner et al. (2004), can indirectly assess the mycorrhization level present in beech.

Kirfel (2019), also from temperate beech forest, reported even higher numbers of tips, with more tips in subsoil than topsoil 25.5 and 17.5 million tips/m², respectively. The difference may be due to the sampling timepoints, but also the differences in geographical location: While my study was conducted at the site with the northernmost distribution of beech, the study by Kirfel is from the temperate forests, where beech has its optimal growth conditions (Kirfel et al., 2019).

The amount of mycorrhization has a significant effect on the shape of the root, and this could contribute to changes in carbon storage (Soudzilovskaia et al., 2015b). My data on mean number of fine root tips, all considered to be mycorrhizal, show more mycorrhizal root tips in beech forest compared to spruce forest. Thus, indirectly the mycorrhization assess the carbon storing ability of the sites (Soudzilovskaia et al., 2015a; Soudzilovskaia et al., 2015b). Therefore, the fine root trait of branching should be included to a higher degree in databases and C-models, to further improve their precision (Moore et al., 2015; Moore et al., 2020).

4.2 Specific root length (SRL)

Specific root length is probably the most frequently measured morphological parameter of fine roots (Ostonen et al., 2007b). SRL can be indicative of environmental changes and therefore SRL can be used successfully as an indicator of nutrient availability to trees. In my study the beech, with its higher SRL values, reflected the measure of the ability of roots to proliferate in the soil and take up nutrients. A higher SRL (i.e., thin roots) in beech allows rapid nutrient uptake per unit root mass and suggests higher efficiency in nutrient uptake, as compared to spruce (Schmid & Kazda, 2001). High specific root length can lead to thinner roots, which increases nutrient uptake, and also induces an efficient allocation of fine root biomass (Eissenstat & Yanai, 1997; Eissenstat et al., 2015).

The mean estimate of SRL has been reported to range from 1.4 to 196 m/g in different parts of the fine root system in different tree species (Ostonen et al., 2007b). For spruce, my data is similar to those reported by Børja et al (2008) where SLR ranged from mean = 13.4 to 19.8 m/g in spruce forests in SE Norway. While the SRL in spruce did not differ significantly among the topsoil and subsoil in my study (7.7 vs. 8.4 m/g, respectively), the SRL in beech was significantly higher in the topsoil compared to subsoil (16.4 vs. 8.0 m/g, respectively). Kirfel et al. (2019) also found longer SRL in beech topsoil (mean = 13 m/g) than in beech subsoil (mean = 6 m/g), which agrees with my data. Consequently, long, thin fine roots, often associated with mycorrhizal fungi (Pregitzer, 2002), may also indicate a larger capacity for carbon storage in beech (Kirfel et al., 2019), compared to spruce.

The SRL per fine root biomass can indirectly weight in the amount of mycorrhization, and thus their contribution to carbon storage (Bauhus & Messier, 1999; Ostonen et al., 2007b).

4.3 Fine root diameter

Although fine roots are generally quantified based on their diameter, with the common upper diameter limit being < 2 mm (Vogt et al., 1986), this limit is purely mechanical and practical, but does not reflect the physiological function of the roots. There has been a discussion about using this limit because roots < 2 mm in diameter may also include lignified conducting roots with little or no role in the absorption of nutrients and water, and do not become mycorrhizal (Pregitzer, 2002). Pregitzer et al. (2002) suggested classifying fine roots rather based on their branching order than diameter, with root tips being classified as first-order roots (Guo et al., 2004). Pregitzer et al. (2002) and Guo et al. (2004) reported fine root diameter to decrease with decreasing root order.

In my study, spruce fine roots had larger mean diameter (0.6 mm in both soil layers) than fine roots of beech with 0.4 and 0.6 mm in topsoil and subsoil, respectively. Although I extracted from the soil samples all fine roots with diameter less than 2 mm, majority of the fine roots had diameter less than 1 mm. In comparison, according to Guo et al. (2004) the first-order roots (root tips) of *Pinus palustris* had a mean diameter of 0.35 mm. Bauhaus and Messier (1999) reported only small differences (mean values of 0.24–0.34 mm) in the diameters of fine roots of *Abies balsamea* and *Picea glauca* (Bauhus & Messier, 1999). The mean diameter of Norway spruce and Scots pine fine roots in Estonian and Finnish stands varied from 0.3–0.5 mm (Ostonen et al., 2007a), with all of them being < 1 mm in diameter. In fact, majority of fine roots in boreal forests seem to be < 1 mm in diameter (Ostonen et al., 2005; Persson, 1978), which is in agreement with my measurements. Consequently, nutrient uptake and carbon storage studies, separating roots < 1 mm in diameter and their ECM short root tips from other fine roots, could be functionally the most meaningful classification of the fine root system in boreal forests (Pregitzer, 2002).

4.4. Specific root area (SRA)

I found higher total SRA in beech (total mean = 5103 cm²/g) than in spruce (total mean = 4242 cm²/g) for the entire soil profile, but the differences among species were not significant (Table 2).

While some studies support my results and report on higher SRA values in beech compared to spruce (Jackson et al., 1997), others report the opposite tendency (Helmisaari et al., 2009). These contradicting results may reflect the different geographical and soil conditions.

At the root level, trees can increase root surface area by producing thinner roots which have a larger specific surface area (surface area per unit mass) at a given investment of carbon (Leuschner et al., 2004). Thus, water and nutrient uptake per unit root mass will also be higher at a larger SRA (Freschet

et al., 2021a). Furthermore, uptake rates of nutrients and water may depend on other associated root traits, such as the number of mycorrhizal root tips per root mass. As higher SRA means higher potential for establishment of ectomycorrhiza (Kirfel et al., 2019), beech with its higher SRA values can therefore indirectly store higher amount of carbon and nutrients and water compared to spruce.

The extent of SRA may be indicative of the capacity of the fine roots to accommodate the ectomycorrhizal fungi, which in turn absorb carbon from the tree (Soudzilovskaia et al., 2015b). A higher SRA gives the fungi more space to attach on the root surface area, which can increase the amount of biomass and carbon allocated to fine roots (Smith & Read, 2008). An increase in carbon storage is possible due to the abilities of ectomycorrhizal fungi to colonize fine roots (Helmisaari et al., 2009; Ostonen et al., 2007a). Therefore, a higher SRA in beech could indicate more carbon stored in the soil, due to more available root surface area for mycorrhization, compared to spruce with a lower SRA.

The mean estimates of all assessed fine root traits in this study (number of root tips and forks, SRL, SRA) in beech forest were always significantly higher in the topsoil than in subsoil. On the other hand, for spruce roots I did not observe any significant differences in the same traits among the soil layers. My soil samples did not contain the entire rooting depth of the trees, because of the stony bedrock, and therefore the amount of fine roots in both species may be underestimated, which is also seen in other studies by Finér et al. (2007). Moreover, another limitation which may have impacted the result is in measuring root traits I did not include environmental conditions such as pH, stoniness, and tree age, however, I used numbers from Ransedokken (2016).

4.5 Fine root biomass

I found almost twice as high fine root biomass in beech (total mean 662 g/m²) than in spruce. A review study of Finér et al. (2011a), based on data from 517 forest stands across the world, which estimated fine root biomass as 526 ± 321 g/m² and 775 ± 474 g/m² in boreal and temperate forests, respectively, agrees with my results. Another review from Finér et al. (2007), also found a higher amount of fine root biomass in beech (mean = 389 g/m²) compared to spruce (mean = 294 g/m²). Thus, my results showing higher root biomass in beech compared to spruce are supported in previous literature.

I detected in the entire spruce profile (topsoil and subsoil) a total mean of 367 g/m², which is similar to results from spruce stands in SE Norway, where the mean fine root biomass ranged from 49 to 398 g/m² (Børja et al., 2008). In addition, Ostonen et al. (2013) found mean fine root biomass in spruce and pine in Estonia ranging from 120 - 935 g/m² in the finest roots (<1 mm), and Lukac & Godbold (2010) found mean fine root biomass in spruce of 914 g/m² in the entire sampled soil profile, which is in line with my results. My results support the previous studies on spruce generated from boreal

forests. In boreal forests spruce are studied extensively compared to beech, whereas in temperate forests beech are studied much more frequently than at Northern latitudes.

Fine root biomass in beech stands in central Europe ranged between 320 and 470 g/m² (Leuschner et al., 2004), which is at somewhat lower values than in our study. However, the different environmental factors, especially drought, are reported to strongly influence the beech fine root biomass (Leuschner et al., 2004). Moreover, my results have higher fine root biomass in beech subsoil, compared to the topsoil (Figure 3.6). Konôpka (2009) also found higher beech fine root biomass in the subsoil (mean = 360 g/m²) than in the topsoil (mean = 250 g/m²) which is also in agreement with my data, although being lower. The lower values in my study could also be due to different geographical locations: I did my study in boreal forests, where beech has a temperature disadvantage compared to spruce and other beech forests in temperate forests.

Although I did not quantify the ECM mycelia in this study, the results of Wallander (2001) et al. (2001) and Nilsson et al., (2005) suggested ECM mycelial biomass and production to be strongly correlated with tree fine root biomass. Their statement agrees with the interaction pattern found in my results on root biomass (Table 2). According to Karst et al. (2008) the biomass of trees with mycorrhized fine roots can indirectly be considered as 50% carbon. This suggests plant biomass of an individual plant species indirectly indicate the amount of carbon stored in their fine roots less than < 1 mm (Soudzilovskaia et al., 2015b). Therefore, it may be fair to assume increasing fine root biomass to lead to increased mycorrhization and therefore to increased carbon storage in soils.

4.6. Fine root production

In my study the production of fine roots in beech was more than twice as large (mean = 114 g/m²) than in the spruce forest (mean = 45 g/m²). Lukac & Godbold (2010) study in temperate forests reported a mean root production in spruce of 70 g/m². They measured fine root production with root meshes and used an incubation time of one year, which gave them higher results (mean = 70 g/m²), compared to my estimates (mean = 45 g/m²). However, this difference is logical when taking my short incubation time of three months compared to one year of their study into consideration.

To measure the fine root production, I used the method of nylon meshes embedded in the soil during the vegetation period. By using meshes, the number of fine roots protruding through the meshes was assessed by the naked eye, and roots were easily extracted from the meshes for further estimation of fine root production. If only a rapid comparison of root production under contrasting treatments or conditions is needed, the mesh method can be used in the forest to take fine root production samples (Lukac & Godbold, 2010). Nevertheless, this method has its limitations, as it may cause differential thickening of fine roots once they have grown through the mesh and the cutting of roots when it is placed into the soil (Hirano et al., 2009; Lukac & Godbold, 2010).

Some previous studies have lower fine root production results than mine, which could be due to the measurements of fine root production being done with meshes instead of ingrowth cores. For example, Ostonen et al. (2013) also showed a higher root production (mean = 182.87 g/cm²) than my study in spruce. The author used soil ingrowth cores and sequential coring, methods different to mine, which may be the cause of the result discrepancy. The ingrowth cores can often give lower quantifications than root meshes, due to their cylindrical form changing the nutrient and water availability within the core (Hirano et al., 2009). Therefore, more knowledge is needed to understand the measurement advantages and disadvantages of root meshes and ingrowth cores.

It was difficult to compare our fine root production data to other studies, because of the different timespans, used for incubation either of meshes or ingrowth cores. While my meshes were embedded in the soil for three months only, other studies often report values for at least the whole year, where fine roots had longer time to establish and grow (Lukac & Godbold, 2010). Such a limited soil sampling and timespan may have favored the growth of fine roots in the deciduous beech forests, due to the shorter growing season for spruce forests (McCormack et al., 2015).

4.7 Future research

To my knowledge, currently, there are no data on mycorrhization level and fine root traits included in models for calculating/predicting of carbon storage in forest soils. Although several databases on root traits already exist (Kattge et al., 2011), the data are not implemented in the models.

Fine roots and ectomycorrhiza quantification could be beneficial for the predicting power of C-models (Soudzilovskaia et al., 2015b), due to their crucial role in C cycle. Root biomass and mycorrhization level (number of fine root tips) may contribute to improving the models used for predicting the future C sequestration in forest soils (Kattge et al., 2011; Soudzilovskaia et al., 2015a). Fine root biomass and the number of fine root tips are therefore indirect indicators of each species-specific contribution to belowground carbon storage (Soudzilovskaia et al., 2015b). In addition, my data on root traits may be used to find out how plants respond to environmental factors (drought, nutrient status), or influence ecosystem processes and services (carbon sequestration) (Kattge et al., 2011).

My study, because it was conducted only once and the production was measured during one vegetation period, may be considered as a “snapshot” of the root traits, describing the situation at the given time and place, but unable to describe the dynamics over time. Long term studies are in the position to help with this uncertainty (Finér et al., 2011a; Freschet et al., 2021b). Firstly, in order to see the effects of fine root biomass and carbon storage it would be helpful to include fine root traits in modeling of carbon belowground (Finér et al., 2011a). Secondly, it would be useful to understand better the relationship between fine root traits and carbon storage in both deciduous and conifer species (Finér et al., 2007). An approach such as this could improve the quantification when measuring carbon pools across different ecosystems (Soudzilovskaia et al., 2015b). Thirdly, the belowground measurements must be conducted over a longer time to capture the dynamic changes (Finér et al., 2011b), to come up with suggestions on how beech and spruce forests may help mitigate the effects of climate change (Finér et al., 2007).

5. Conclusions

I here provide a quantitative comparison among the root traits in beech and spruce forests, related to belowground carbon sequestration. My results on amounts of root tips (and forks) in spruce and beech forests can be used to indirectly assess the mycorrhization level, and thus indicate the carbon storing ability of the sites. The results indirectly indicate beech forest potential to storage more carbon than spruce. To summarize, I suggest that beech, which have a higher amounts of fine root tips (mycorrhization level), higher fine root biomass and production compared to spruce, may potentially contribute to higher amounts of belowground carbon. More research is needed to test if these results can be generalized to wider forest ecosystems.

6. References

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7. Appendix

Table 7.1: Overview over fine root traits and measurements. All definitions are modified from the Freschet et al., (2021 a).

Fine root traits overview	Description
Root	An axis made by one sub-apical meristem and an anatomical structure distinct from other plant organs. It usually has a monopodial structure, but by extension it can have a sympodial construction when it is made by successive equivalent meristems.
Fine root	Root with a relatively small diameter, often operationally defined as all roots ≤ 2 mm in diameter, though other diameter thresholds are used as well. These roots are generally lacking a lignified structure and are expected to be more active in resource acquisition than coarse roots.
Mycorrhizal root:	Roots forming a symbiotic association with a fungus; most frequently used for ectomycorrhizal root forming a hyphal mantle.
Root tip:	Apical portion of the root includes the root apical meristem (and root cap).
Root tips and forks	Considered to vary among different trees within the same species. Have a strong impact on the mycorrhizal hyphae distribution. Usually about 98% of all fine root tips are mycorrhizal.
Specific root length (SRL)	Reflects the potential of fine roots to explore the soil in the search and acquisition of water and nutrients. One of the most studied root traits, high relevance for ecosystem functioning.
Root diameter	Technically, roots are defined as fine roots if their diameter is < 2 mm. Root diameter is used when calculating other traits, such as root volume or root surface area.
Specific root area (SRA)	Used to estimate the area of the roots available for absorption of nutrients and water. SRA is calculated by considering each root as cylinder with a measured length and diameter.
Fine root biomass	Biomass of fine roots is the amount of fine roots (dry weight) per ground area unit (g d.w. m ⁻²).
Root production	Root production is a fine root growth during one season. I measured root production by inserting nylon meshes in the soil at the beginning of growing season and extracting all fine roots entangled in the meshes at the end of the season.

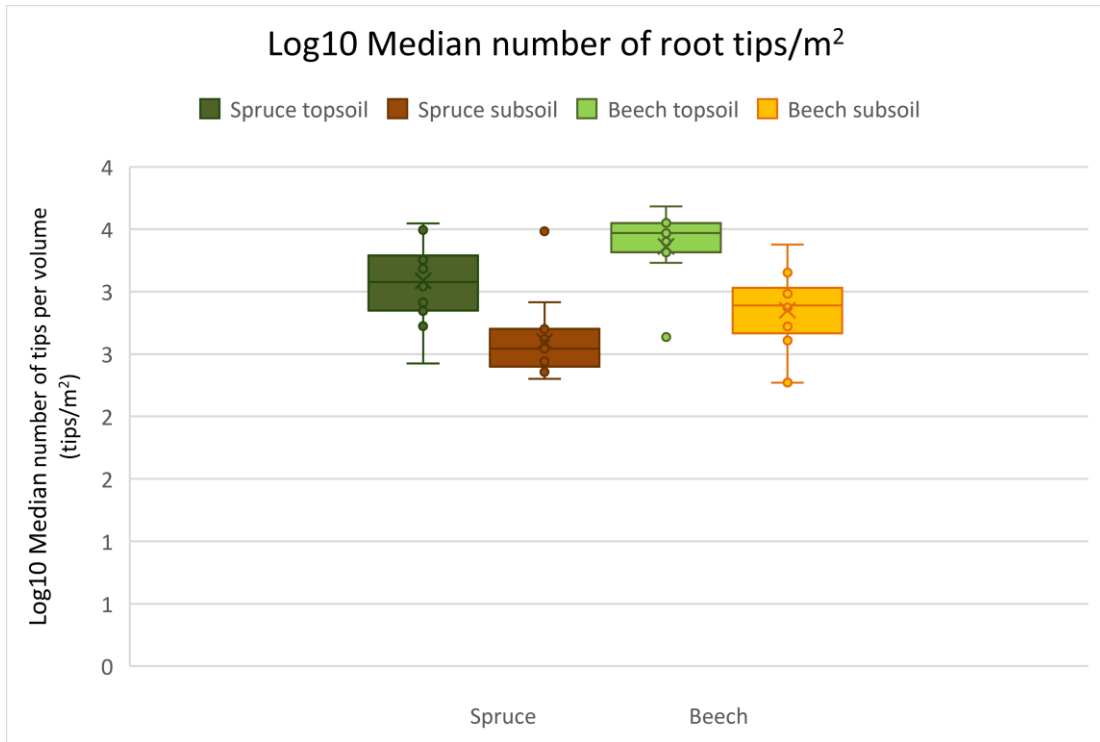


Figure 7.1: Median number fine root tips in beech and spruce forests measured in logarithmic scales (Log10) per square meter (m²).

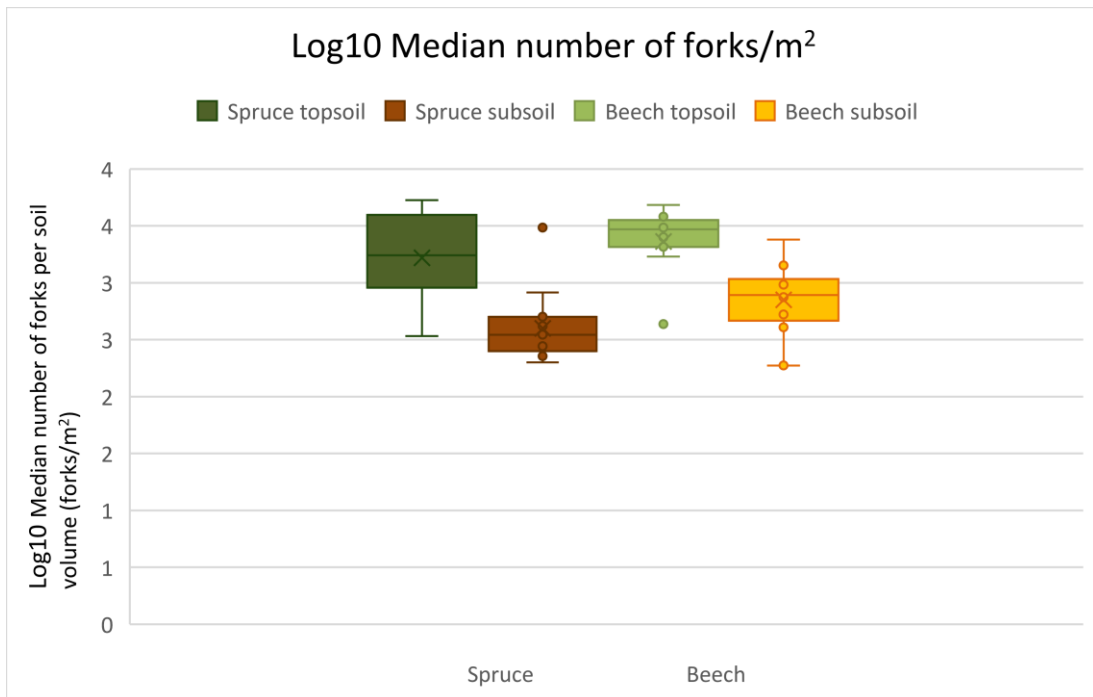


Figure 7.2: Median number fine root forks in beech and spruce forests measured in logarithmic scales (Log10) per square meter (m²).

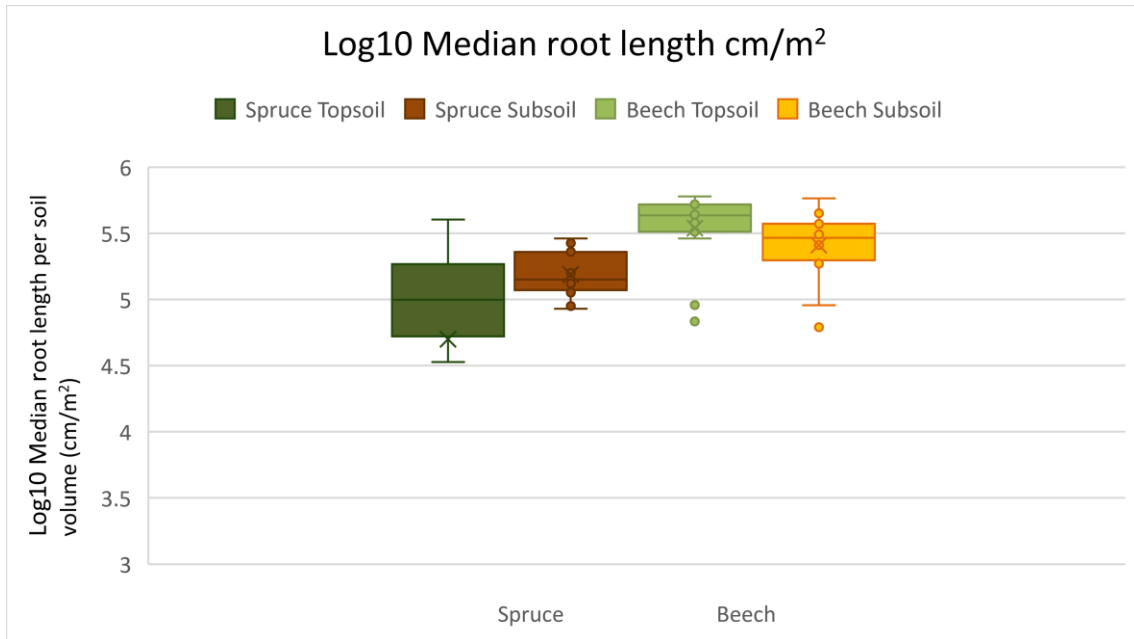


Figure 7.3: Median fine root lengths measured in mm in logarithmic scales (Log10) per square meter (cm/m²).

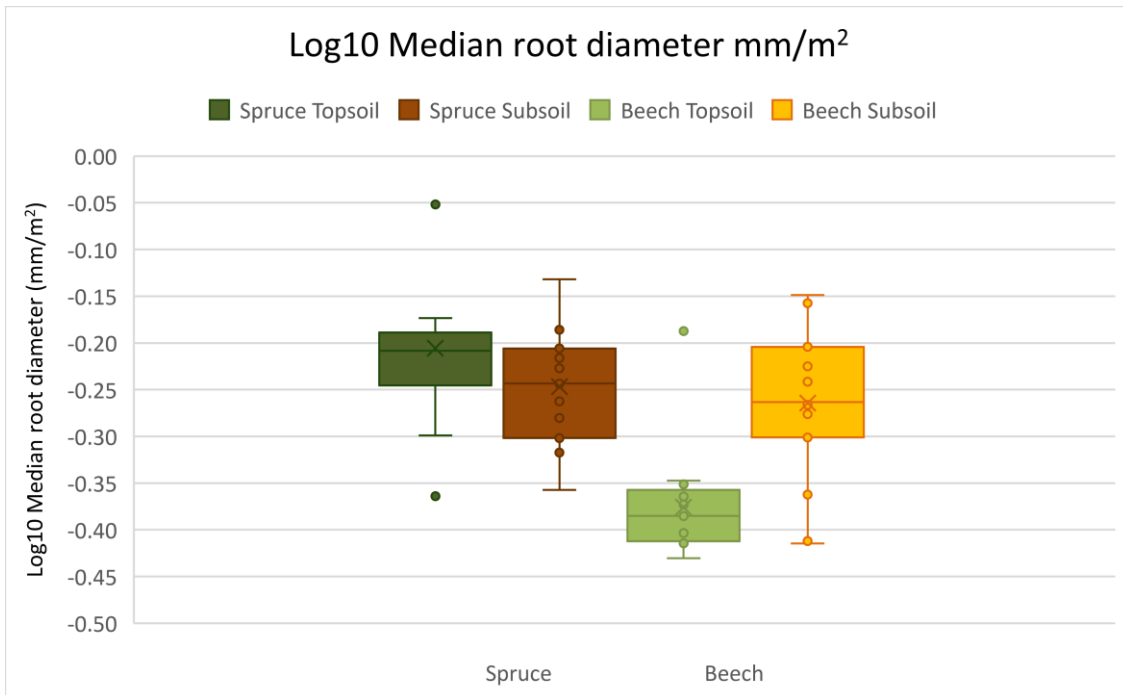


Figure 7.4: Median average root diameter in spruce and beech measured in logarithmic scales (Log10) in millimeter (mm) per square meter (m²).

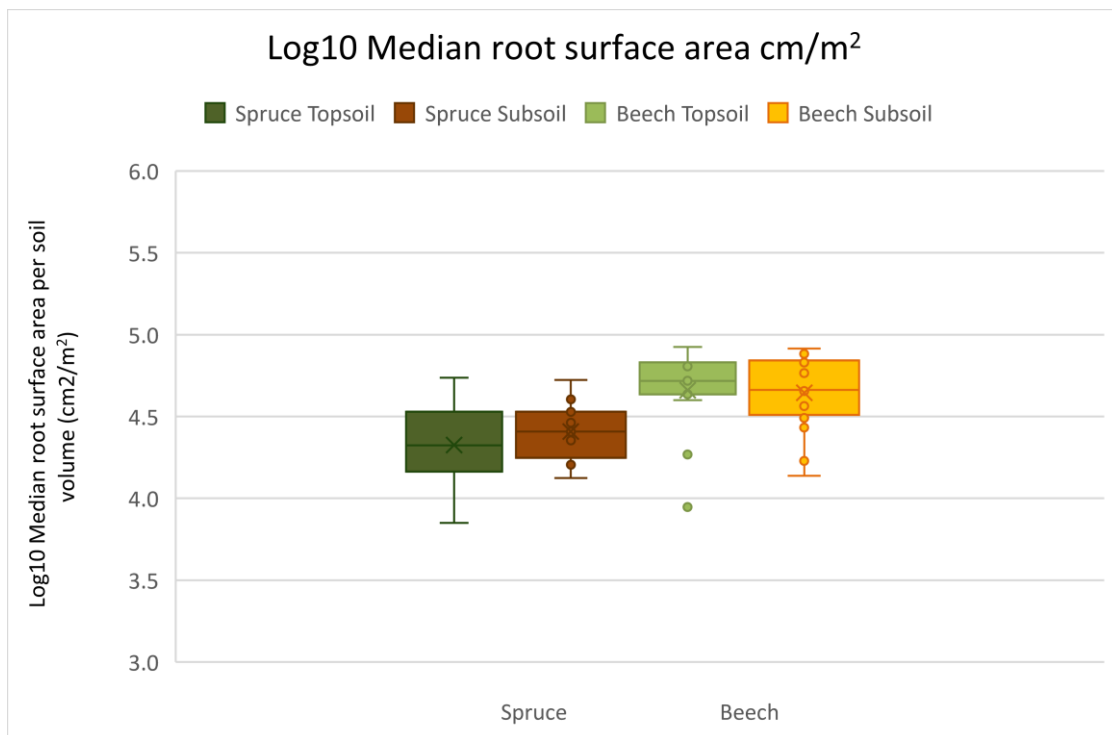


Figure 7.5: Median root surface area in beech and spruce measured in logarithmic scales (Log10) in square centimeters (cm²) per square meter (m²).

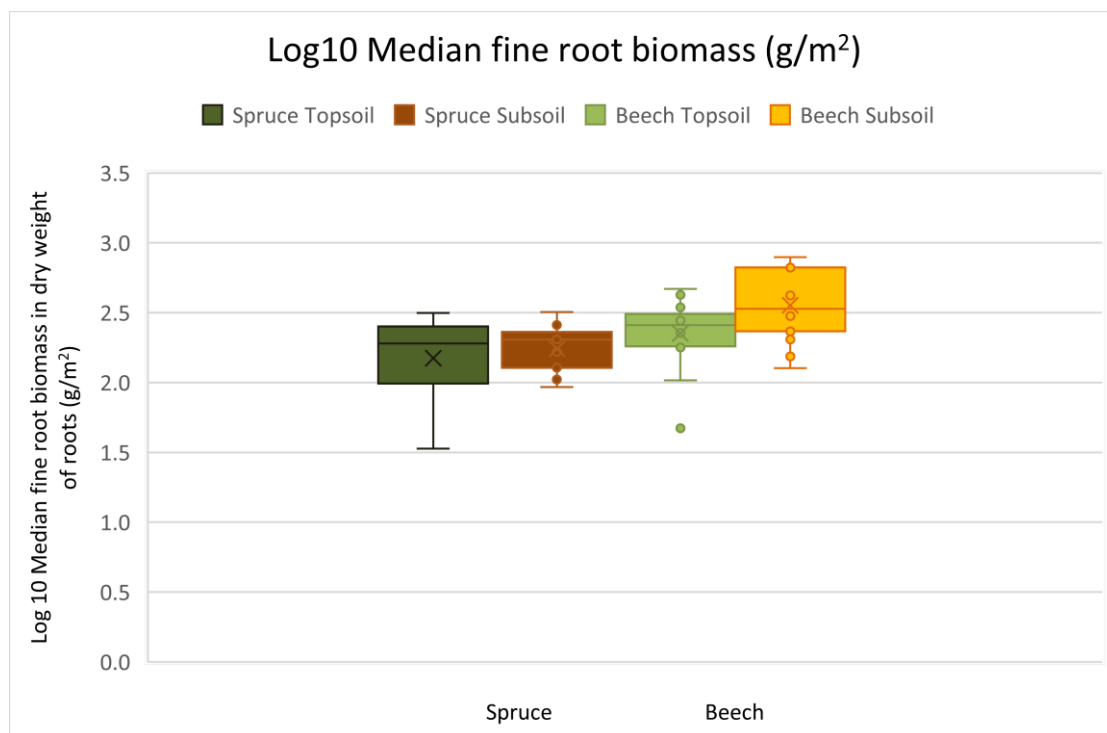


Figure 7.6: Median biomass of fine roots in spruce and beech in topsoil and subsoil measured in Log10 (logarithmic scales). Biomass is expressed in grams (g) dry weight (dw) per square meter (m²).

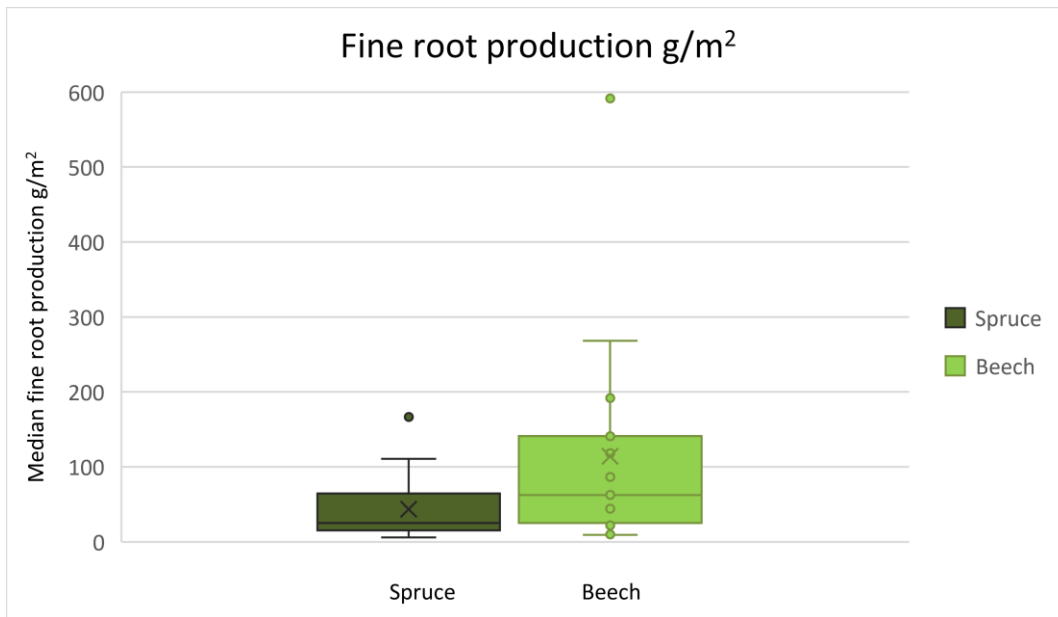


Figure 7.7: Median fine root production in spruce and beech measured in dry weight (dw) in grams (g) per square meter (m²).



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