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Effects of forest management history on fine roots and mycorrhizal colonization in Norwegian boreal spruce forests

Martina Vårdal
Master of Science in Environment and Natural resources

Acknowledgements

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Abstract

Fine roots play critical roles in carbon cycling in boreal forests. However, they are poorly represented in the studies of forest management effects on forest soil, likely due to the labour-intensive methods of soil sample collecting and time-consuming root sorting. Thus, measurements of fine root biomass and mycorrhizal colonization in near-natural and clear-cut stands, based on the soil core sampling, represent an important contribution to the understudied belowground biomass of boreal forests.

We collected 144 soil samples in 12 pairs of near-natural and clear-cut forests of South-East Norway. After dividing collected soil samples into soil layers, roots were sorted out and classified according to the type and size. Fine roots (diameter <2mm) were further analysed with the WinRhizo root analysis system to obtain data on the average root diameter, root length, and number of root tips. In the final stage, roots were dried and weighed to determine dry weight.

There were no significant differences in any of the analysed root traits, average root diameter, root biomass per surface area, specific root length, and number of root tips per surface area, between the two forest types. The non-significant observation may be explained by relatively low number of samples, the development of clear-cuts over time, high variability among the root traits and soil depth. Further analysis of collected soil samples resulting in a larger number of replicates, would increase the accuracy and reliability of the results. The obtained results on fine root biomass and mycorrhizal colonization provide a valuable contribution to the estimates of belowground carbon storage in Norwegian boreal forest.

Keywords: boreal forest, carbon storage, forest management, fine root biomass, forest soil, mycorrhiza, root diameter, root tips, specific root length

Contents

Introduction

The rising concentration of carbon dioxide in the Earth's atmosphere contributes to global warming causing significant threats to life on Earth such as more frequent and more intense extreme weather events, rising sea level, changes in the range and distribution of plant and animal species, acidification of oceans, public health impacts and increased frequency and intensity of wildfires. These threats emphasize the need for measures to mitigate the carbon dioxide emissions and increase the carbon sequestration.

The largest anthropogenic source of carbon into the atmosphere is fossil fuel combustion, thus reducing emissions from these sources is critical. Forests play a significant part in removing carbon dioxide from the atmosphere. With proper forest management, protection of forests, and restoration of degraded areas we would achieve a higher potential for carbon sequestration in forests and slow the pace of global warming.

Estimations of global forest carbon stock vary. Prentice et al. (2001) reported terrestrial carbon stock of 1240 Pg, where 553 Pg C is stored in tropical forests, 292 Pg C in temperate forests and, 395 Pg C in boreal forests. A huge proportion, 86% (338 Pg C) of boreal forest carbon stock is stored in soil and only 14% in plants (Prentice et al., 2001). A similar percentage, up to 80% of the forest carbon, stored in the boreal forest soil, was reported also by Scharlemann et al. (2014). According to the world resource institute, the world's forests store approximately 861 Pg of carbon (Pan et al., 2011) and the most recent estimation of the global forest C stock, 662 Pg was reported by FAO (FAO, 2020). Compared to the amounts of anthropogenic CO_2 emission, cumulative anthropogenic CO_2 emissions for 1850-2020 totalled 660 ± 65 Pg C. Bartlett et al. (2020) reported estimations of the carbon budgets within Norway's mainland ecosystems and found out that the largest stores of terrestrial carbon in Norway, as well as globally (Bradshaw & Warkentin, 2015), are in the boreal forests ecosystems. According to the (Grønlund et al., 2010), the Norwegian forest holds 2 Pg of carbon.

Human activities and forest management have an important impact on forest C sequestration and C storage potential. After a disturbance, such as clear-cut or forest fire, a forest stand is expected to be a source of carbon to the atmosphere, due to the disturbance effect on sequestration potential and direct effects on the tree stand (James & Harrison, 2016). It takes

several years before young forest turns into a carbon sink (Valentini R. et al., 2000). The discussion on carbon balance in forests after clear-cutting has been particularly intensive in the Nordic countries where clear-cutting represents common forest management.

A review on management effects on soil C sequestration and greenhouse gas fluxes in forests (Mäkipää et al., 2023) has shown that intensive thinning and harvesting decrease soil C stock, but the effects depend on soil type. In contrast, high stocking density and enhanced productivity by fertilization increase soil C stock.

Recent studies on forest management strategies have shown reduced carbon storage in forests that have been intensively managed (Ameray et al., 2021; Mayer et al., 2020). Clear-cut harvesting resulted in lower C-stocks compared to old-growth forest conservation and partially cut stands. Less intensive forest management cause lower disturbances in the soil and consequently higher potential for C-sequestration. Ameray et al. (2021) identified silvicultural practices such as partial cuttings as one solution for increasing biomass and soil C content. On the other hand, a recent study on carbon balance in young forests in Sweden (Grelle et al., 2023) revealed that forest stand turned into sinks in only 8-13 years after the disturbance and suggest that regenerated stand reach a neutral carbon balance after approximately 30% of the rotation period.

Clear-cut forests have, compared to near-natural forests, lower biodiversity, water quality, and soil preservation, increased risk of soil erosion and nutrient depletion, which may all lower ability to sequester carbon in the soil (Lindenmayer & Franklin, 2002). Even though some of the negative impacts of forest harvesting on soil carbon are known, there is still a need for further research on the effects of forest management history on fine root biomass.

While most climate change mitigation studies focus on carbon stored in the aboveground biomass, the mitigation potential of soil is less often studied, although soil plays an important role in carbon sequestration. Global soil carbon pool has been estimated to approximately 2344 Pg of C, compared to plant vegetation that stores around 615 Pg of C (Schlesinger, 2020). As a part of belowground biomass, tree roots represent an important component of the carbon cycle. In addition to the ability to stabilize soil particles which results in reducing soil erosion and preventing the loss of soil organic matter, roots contribute to the carbon storage. When aboveground biomass absorbs carbon dioxide from the atmosphere during photosynthesis

and produces organic matter, some of it is allocated to the roots, where it is stored as belowground biomass. The roots also release organic compounds that stimulate microbial activity in the soil. Microbes break down and decompose these organic compounds and in turn, release CO_2 back to the atmosphere. Some of the carbon from the organic compounds however remains stored in the soil.

In forest carbon studies, roots have been understudied or are poorly represented due to the methodological challenges and uncertainties about root dynamics (Addo-Danso et al., 2016). Studies of belowground biomass face also a common challenge on how to divide and classify roots and which category or entity would be most applicable for the analysis of a specific research topic (Freschet et al., 2021). The physiologically most active part of the root system are fine roots, technically defined as roots with root diameter below 2 mm. Roots with a diameter larger than 2 mm are defined as coarse roots and live considerably longer than fine roots. These roots are lignified, and their main functions are to provide anchorage to the trees, store, and transport resources (Guo et al., 2008; Pregitzer, 2002). In contrast, fine roots are more dynamic and have a higher turnover rate, meaning that they develop, grow and die more rapidly than coarse roots. Although coarse roots also eventually contribute to the C storage in soils, their C input is smaller than that of fine roots due to their static nature. Thus, fine roots with their dynamic nature represent the main drivers of C accumulation in forest soils (Freschet et al., 2021). Consequently, focusing on fine roots only, may bring certain advantages and address the research questions of this study. Limiting measurements to a specific root segment, in this case fine roots, may help us make more comprehensive comparisons of root traits across different forest types. Besides the direct measure of dry root biomass, average root diameter and specific root length may be the most descriptive variables to explain the possible effects of different forest types on fine root biomass.

Average root diameter is the basis of simple classification (Freschet et al., 2021). Not only is it used for technically distinguishing between fine roots and coarse roots, but it can provide insights into general information about plant growth and development. Measuring and analyzing the average root diameter can be a valuable tool for understanding plants' reponses to various biotic and abiotic stressors and can also be used to estimate other root traits such

as root length, root biomass, and root surface area and calculate root volume and root surface area.

The length of roots is essential for plants to absorb nutrients, especially when they are competing with other plants for resources. The amount of dry mass in roots indicates the amount of energy plants invest in the production of this root length. Combining these two important traits provides a valuable indicator of environmental changes, the specific root length (SRL), which is the length of a root per unit of dry root mass (Freschet et al., 2021). Specific root length is often considered to be a fundamental characteristic related to the root analysis as it reflects the potential extent of soil exploration per unit cost. Plants with higher SRL values generally have more and thinner roots per unit of root mass, which allows them to explore a larger soil volume and access resources more efficiently. However, higher SRL can also increase the cost of root construction and maintenance for the plant and may be associated with lower root lifespan and turnover rates.

To obtain a more accurate estimation of how C stock in boreal forests may respond to different management practices not only roots should be included in the overall assessment, but also associated microorganisms. It has been estimated that in boreal forests up to 50-70% of the soil C stock may originate from roots and associated mycorrhizal fungi (Clemmensen, 2013).

Mycorrhiza is a symbiotic relationship between roots and fungi, in which plants provide the fungi with photosynthetically derived carbohydrates and lipids, while fungi provide plants with vital nutrients and water (Freschet et al., 2021; Smith & Read, 2008). Mycorrhizas have strong impact on the soil carbon cycle and stock in the soil and affect carbon allocation of plants, growth rate, litter quality, and decomposition. The understanding of functional differences of mycorrhizal types and their underlying mechanisms is challenging (Brundrett & Tedersoo, 2019). Based on the morphological characteristics and identity of mycorrhizal partners, four main categories of mycorrhizas are recognized: arbuscular, ectomycorrhiza, ericoid, and orchid mycorrhiza. The most widespread mycorrhizal type in boreal forests is the ectomycorrhiza. In forest soils, the majority of fine tree roots are commonly more than 95% colonized by mycorrhizal fungi (Helmisaari et al., 2009). These fungi can in boreal forest soil compose 47-84% of fungal biomass (Bååth et al., 2004) and play a significant role in the storage of soil carbon.

In contrast to the saprotrophic fungi, ectomycorrhizal fungi do not depend on soil organic carbon, instead they derive carbon from their living hosts (Smith & Read, 2008). Thus, mycorrhizal fungi have a strong impact on belowground C allocation (Soudzilovskaia et al., 2015). Ectomycorrhizal colonization occurs exclusively in fine roots and the extent of its colonization is often measured by the number of root tips colonized by the fungi (Guo et al., 2008; Soudzilovskaia et al., 2015). This is the best available measurement to determine the "strength" of the plant-fungi relationship on the site. Consequently, the amount of fine root tips can be used as an indication of nutrient and carbon flow between plants and fungi (Soudzilovskaia et al., 2015). In addition, the number of root tips can be used in conjunction with other root traits such as root diameter, specific root length, and root biomass to characterize the functional and ecological roles of roots in plant growth and nutrient acquisition.

My master thesis is a part of the EcoForest project that aims to assess the long-term effect of clear-cut forest management practices on biodiversity and carbon stocks by comparing near-natural (NN) and mature but previously clear-cut (CC) forests. Twelve paired plots of NN and CC stands were established in South-East Norway in 2021-2022. Near-natural stands are defined as old forests, that have never been impacted by clear-cutting but might have been selectively logged at different intensities. Clear-cut stands are defined as mature stands that have gone through one cycle of clear-cutting.

The main objective of this master project was to investigate the effect of forest management on fine root biomass and ectomycorrhizal colonization by answering two main research questions. First, is there any significant variation in average diameter of fine roots, root biomass, and specific root length between NN and CC forests? And second, does historical clear-cutting affect ectomycorrhizal colonization, i.e. is there any significant variation in number of root tips in response to forest type and soil layer?

Materials and methods

Study area description

The study area included twelve locations in South-East Norway (*Fig. 1*), that were established by the Ecoforest project in 2021. At each location one previous clear-cut (CC) and one near-natural (NN) stand were identified (*Table 1*). The pair of plots were established under several criteria. CC and NN should be close, but not direct neighbours and should have the same site index, vegetation type, soil type, soil depth, exposition, and slope. The goal was to localize forests dominated by spruce on site index (H40) G17 that should not be very steep, be clearly convex or have small streams or areas with standing water throughout the year. The previous clear-cuts should have no signs of thinning, ditching or larger pest-attacks. The basal area as measured by a relascope should be minimum 20 m²/ha at G17. The near-natural stands should have no recent signs of human activity or removal of dead wood.

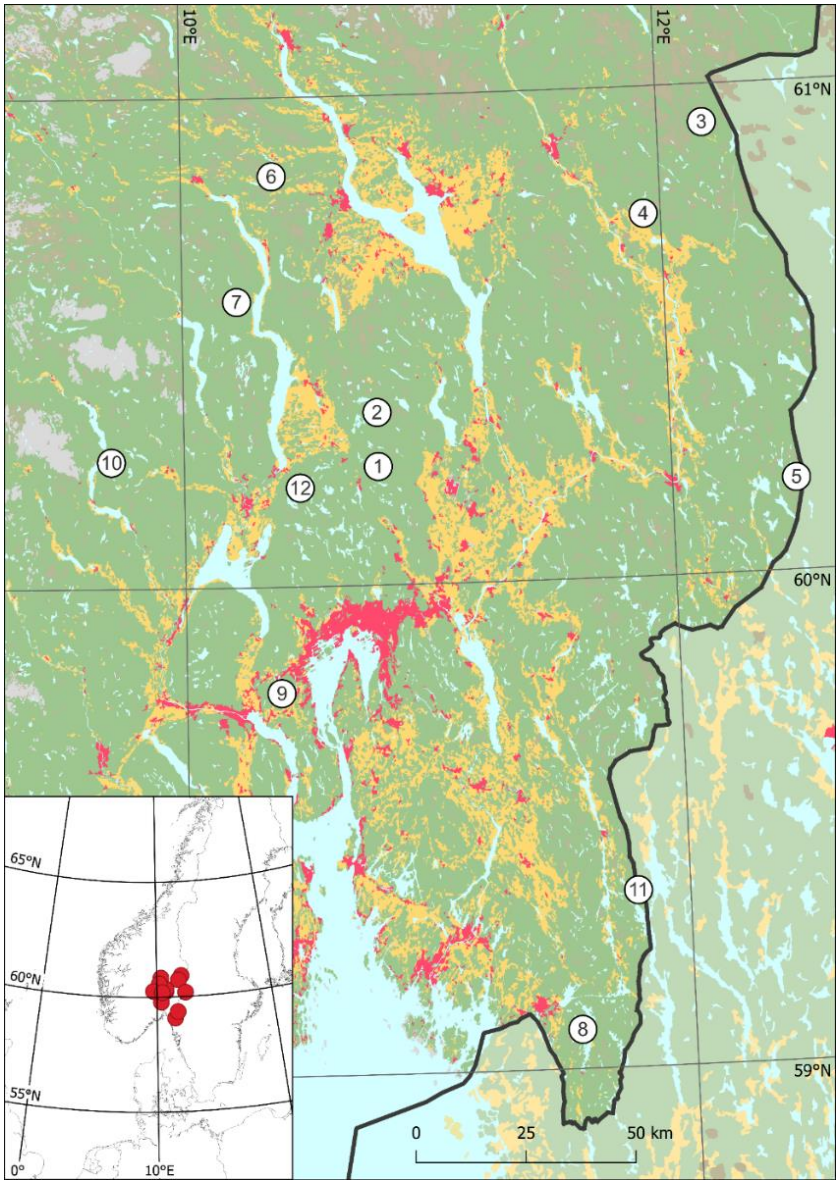


Figure 1: Map of South-East Norway showing the 12 sites (1 – Skotjernfjell, 2 – Gullenhaugen, 3 – Hemberget, 4 – Braskereidfoss, 5 - Särkilampi, 6 – Øytjern, 7 – Tretjerna, 8 – Halden, 9 – Blåfjell, 10 – Storås, 11 – Marker, 12 – Langvassbrenna) (Made by Johan Asplund)

Table 1: Plot numbers of the NN and CC fields at 12 locations with temperature and precipitation information.

Plot number	Location name	Forest type	Mean temperature of the warmest quarter (°C)	Annual mean precipitation (mm)
1	Skotjernfjell	NN	13.6	974
2	Skotjernfjell	CC	13.6	972
3	Gullenhaugen	NN	13.3	867
4	Gullenhaugen	CC	13.5	854
5	Hemberget	NN	13.4	766
6	Hemberget	CC	13.4	764
7	Braskereidfoss	NN	14.2	684
8	Braskereidfoss	CC	14.4	683
9	Särkilampi	NN	13.8	761
10	Särkilampi	CC	13.8	762
11	Øytjern	NN	12.7	818
12	Øytjern	CC	12.9	819
13	Tretjerna	NN	13.7	821
14	Tretjerna	CC	13.6	821
15	Halden	NN	16.2	1056
16	Halden	CC	16.2	1051
17	Blåfjell	NN	15.6	1041
18	Blåfjell	CC	15.6	1049
19	Storås	NN	13.6	888
20	Storås	CC	13.8	884
21	Marker	NN	15.8	971
22	Marker	CC	15.8	960
23	Langvassbrenna	NN	13.4	868
24	Langvassbrenna	CC	13.7	883

The data for mean temperature of the warmest quarter and annual mean precipitation are obtained from an observational gridded dataset over Norway, that is updated daily and presented on a high-resolution grid (1 km of grid spacing) (Lussana, 2018).

Field study design

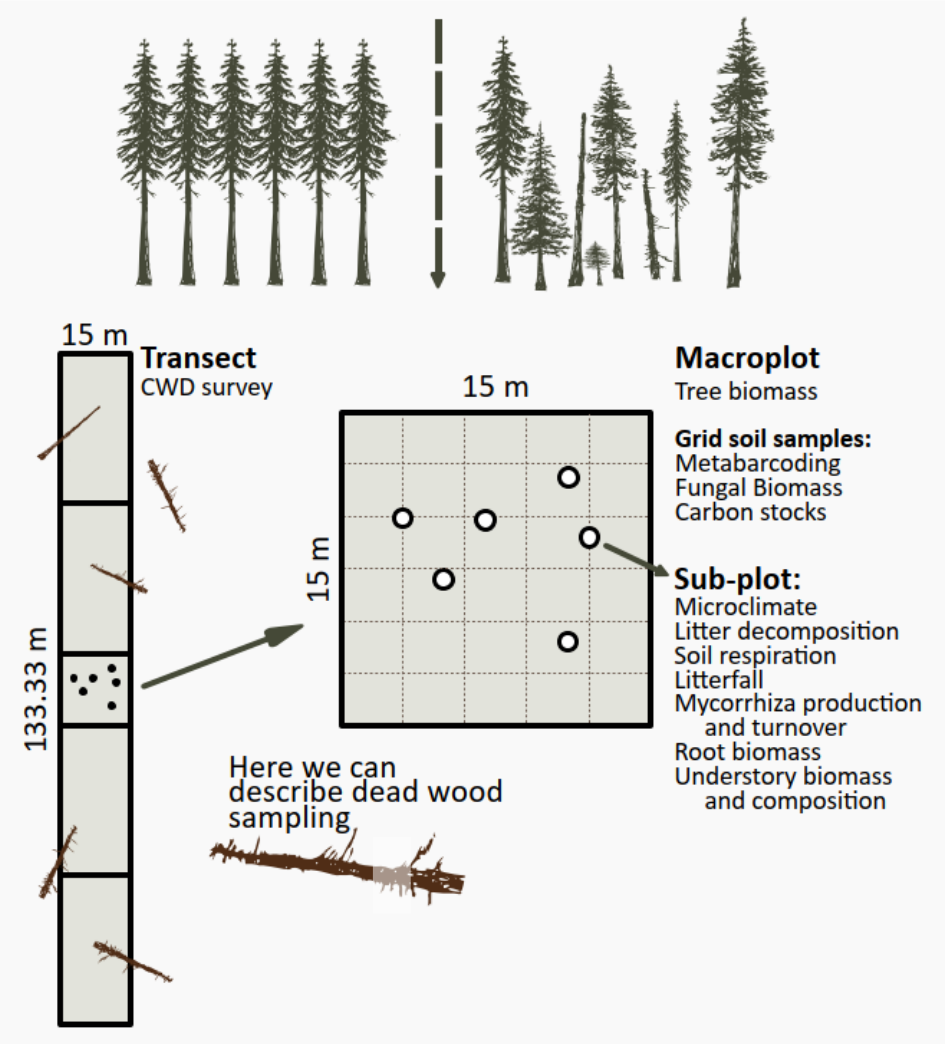


Figure 2: NN and CC with the central sampling plot with 6 subplots (Design: Johan Asplund)

Soil sampling

Soil samples were taken in June 2022. Inside each of six sub-plots (*Fig. 2 and 3*), one soil sample was collected, in total 144 soil samples (*Fig. 4*). Soil samples were obtained with a ø 6.7 cm stainless-steel soil corer. The hole depth varied between 5 cm and 23 cm with an average value of 12 cm. The core length was measured at three different core sites and varied between 5 cm and 20.5 cm with the average value of 11.5 cm. The samples were wrapped in aluminium foil and put into a plastic bag. Soil samples undergo some compression under the sampling

procedure. All plastic bags with samples were marked with the name of the location, plot, and sub-plot number.

Figure 4: An example of a plot with six sub-plots at Blåfjell (Photo: Martina Vårdal)

Figure 3: An example of a collected soil sample before wrapping (Photo: Martina Vårdal)

At each subplot also the distance to the three closest trees was measured and current weather conditions were registered.

All 144 soil samples were stored in the freezer at NMBU, Ås at -18°C.

Soil sample division into layers

A small number of samples was taken out of the freezer at a time and put to thawing in a cooling room prior to laboratory analysis in the sorting lab at NIBIO. When the samples were thawed, we measured the weight and length on four different sides to obtain the mean height of the whole soil sample. After that, we divided samples into layers according to the soil properties. All samples had a litter-fibric-humic (LFH) layer and a 2 cm long upper mineral soil layer. If the mineral layer was longer than 2 cm we separated a second mineral layer, the so-called the 2-5 cm mineral soil layer. Longer samples were divided into 4 layers (*Figure 5*). The fourth layer consisted of the lower part of the mineral soil that exceeded the 5 cm length and was labelled lower rest mineral (LRM). Each layer of soil sample was weighed separately (Mettler Toledo weighing instrument with 0.01 gram resolution).

Figure 5: One soil sample divided into four layers (*Photo: Martina Vårdal*)

Soil moisture

To obtain the information about the moisture of the soil, a small soil fraction of each layer was placed into a ceramic crucible with a known weight. A representative soil fraction was picked out from different parts of the layer, avoiding roots. The roots that might have blended in the fraction were separated and put back to the soil layer. We measured the wet weight of the fractions of soil layers immediately after the collecting to avoid the impact of drying.

Figure 6: Desiccator with soil samples (Photo: Martina Vårdal)

The crucibles with soil fractions were placed into the drying machine (Termaks TS 78042, Nordic Labtech, Norway) set to 105 °C for 24 hours. After drying, the samples were placed in a circular vacuum desiccator (*Fig. 6*) to avoid reaction with atmospheric moisture. Crucibles were cooled down after 2 hours in the desiccator and the dry soil fractions in crucibles were weighed (Mettler Toledo, MS603TS/00, 3-decimal, Switzerland) (***Error! Reference source not found.***).

To calculate a percentage moisture content (MC), we subtracted the dry weight from the wet weight and divided the result by the wet weight and multiplied it by 100.

$$MC\ (\%) = \frac{w - d}{w} \times 100$$

MC = moisture content
w = wet weight
d = dry weight

The moisture content was used later on in the calculations of dry soil mass of each soil layer.

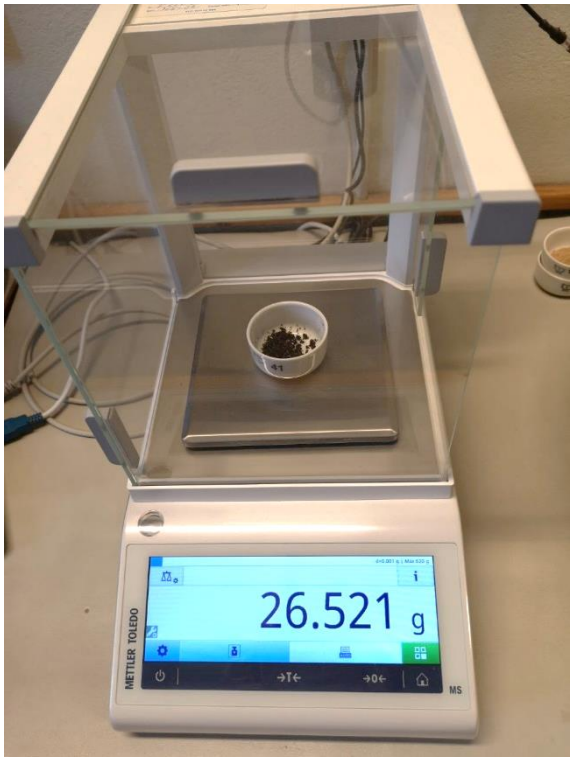


Figure 7: Mettler Toledo 3-decimal weighing instrument (Photo: Martina Vårdal)

Root sorting

Each soil layer was placed in a 1000 ml plastic container and filled with water for soil particles to loosen. A part of the sample was thereafter transferred into the laboratory sieve with a mesh size of 1x1 mm. All roots were gently washed with a cold shower. After most of the soil particles were removed and the roots became visible, roots from the sieve were then placed in water for further cleaning (*Fig. 8*). The roots were cleaned thereafter in three changes of water.

Figure 8: An example of cleaned roots of different sizes (Photo: Martina Vårdal)

When all the live roots were cleaned, they were sorted into 4 fractions according to the type and size (*Fig. 9*):

- Live tree roots with a diameter below 2 mm
- Live tree roots with a diameter between 2-5 mm
- Live tree roots with a diameter above 5 mm
- All live roots belonging to understory vegetation

Dead roots were discharged, and further analysis was performed on live tree roots only (hereafter called tree roots). Dead roots were visually identified as dead roots.

Figure 9: Four different fractions of roots (*Photo: Martina Vårdal*)

All fractions were placed into the marked storage boxes filled with water for further analysis and stored in the cooling room for further analysis.

Root scanning and drying

Fractions with roots with a diameter below 2 mm (fine roots) were scanned and analysed with WinRHlZO™ root image analysis system. The WinRHlZO™ system consists of an image acquisition scanner (EPSON Flatbed Expression 11000XL 1.8 V3.49, Regent Instruments, Canada) (*Fig. 10*), root image analysis software (WinRhizo2013d, Regent Instruments,

Figure 10: EPSON scanner with washed root sample (*Photo: Martina Vårdal*)

Canada) with a computer, root holding, and positioning trays (Pandey *et al*., 2017) (*Fig. 11*). WinRHlZO™ is an interactive system with the capacity to detect overlapping root parts generating data such as total root length, projected root area, root surface area, root length, number of root tips, branching points, and root diameter (Arsenault et al., 1995).

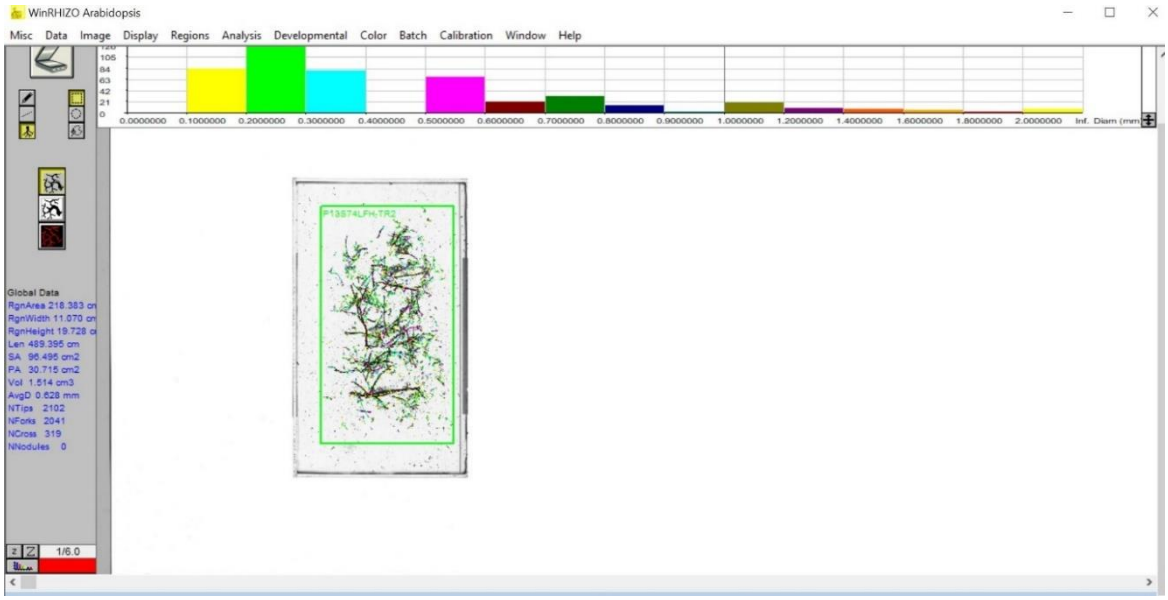


Figure 11: An example of image analysis using the WinRHIZO software.

WinRHIZO displays the analysis over the image (*Fig. 11*). The color used to draw the root skeleton indicates into which diameter class the part of the root has been classified. The same color is used for drawing the root distribution graphic. Measurement data of the sample under analysis are summarized on the left of the screen and are available in detail in data files.

After the scanning process was completed, and data were securely stored, the root samples were placed into paper bags and dried in a drying cabinet (Termaks TS 9430, Nordic Labtech) at 30 °C for one week.

The final step of the laboratory analysis was to weigh the dried samples (Mettler Toledo 2-decimal weighing instrument) to determine the dry biomass. Fine root biomass may be expressed per volume of soil or per dry mass of soil, but the most common and comparable unit to estimate it, is per surface area. The data obtained during the field and laboratory work were compiled and rearranged in Microsoft® Excel® (Microsoft 365, Version 2303). The data that were used in further statistical analysis are described in the section below.

Statistical analysis

RStudio (R version 2022.02.0) was used to analyse the data. We fitted linear mixed-effects models using the lmer function in lme4-package (Bates et al., 2015) for each response variable (average diameter, root biomass per surface area, specific root length, and number of root tips per surface area). Explanatory variables in the study were forest type (NN and CC) and soil layer (LFH layer, 0-2 cm mineral soil layer, and when avaiable also 2-5 cm mineral soil layer, and lower rest mineral layer (LRM)), and their interaction. The random effects in the study were site (12 different sites are described in Fig.1) and series (Series 1 and Series 2).

We also tested the effect of the temperature of warmest quarter and annual precipitation on each response variable. The random effects, in this case, were forest type, site, and series.

We acquired Type III Analysis of Variance Table with Satterthwaite's method with F and P values (*Tables 2,4,6 and 8*) using the lmerTest package. The confidence interval is 0.95. F-value is used to test if the fixed effects are statistically significant. Large F-value indicates that variation between fixed effects is larger than what would be expected by chance, meaning that they have an effect on the response variable (Kim, 2014). P-value is used to determine if the difference between fixed effects is statistically significant. P-value lower than 0.05 indicates statistically significant effect.

Results

Root biomass per surface area

Average root biomass per surface area of fine roots in all analysed soil samples from the near-natural forest sites was 285.5 g and 288.9 g per m² from the clear-cut sites, respectively, but this difference was not statistically significant. However, there was a significant variation in fine root biomass per surface area in response to the soil layer (*Table 6*). The upper soil layers (LFH) had much higher root biomass per surface area compared to the lower ones (*Table 7*, *Fig. 15*). These patterns were consistent between forest types, as shown by the non-significant interaction term (*Table 6*).

Table 2: Type III Analysis of Variance Table with Satterthwaite's method with root biomass per surface area as a response variable.

Explanatory variable	***F value***	***P***
Forest type	<0.01	0.968
Soil layer	59.57	<0.001
Forest type: Soil layer	0.82	0.487

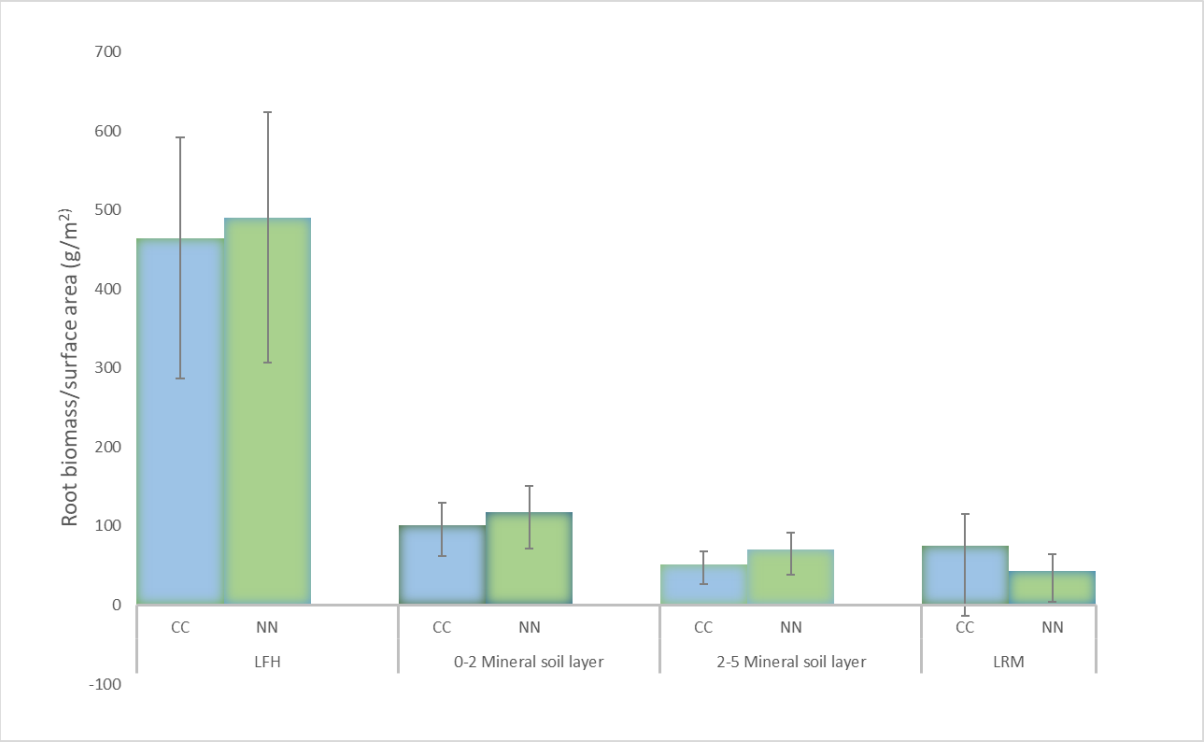
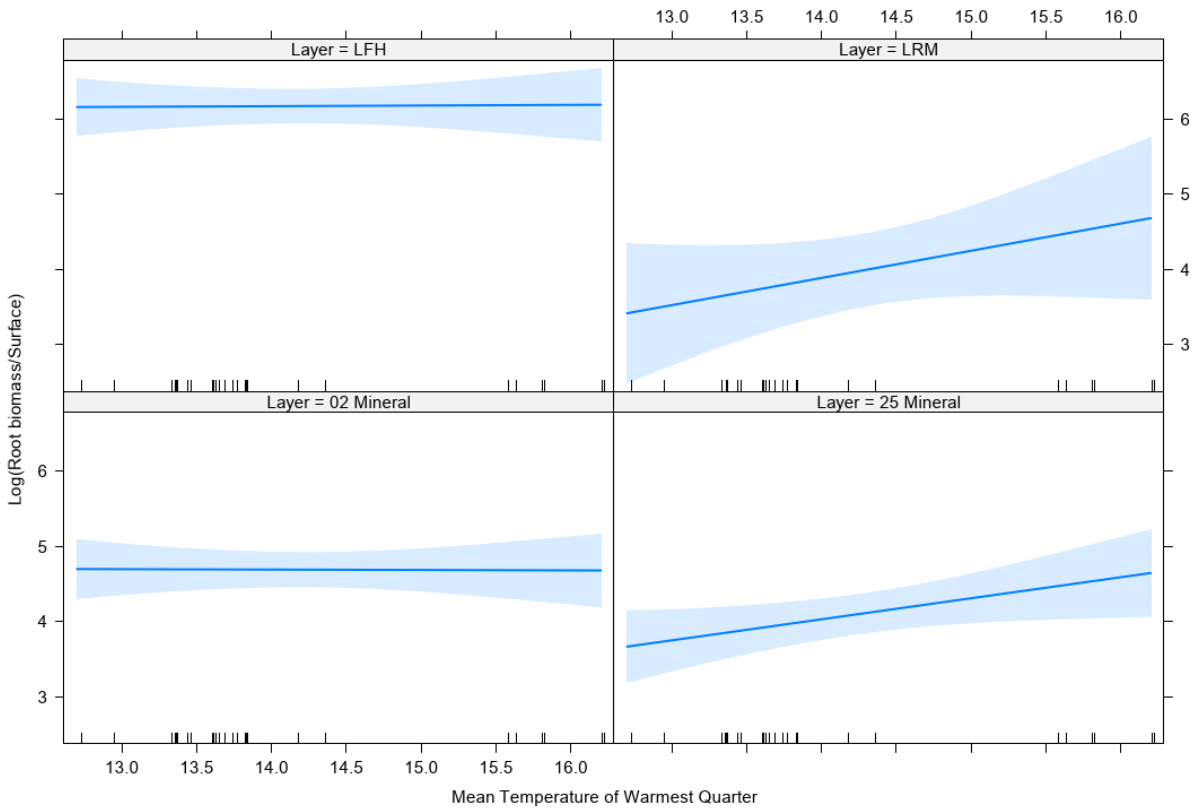


Figure 12: Root biomass/surface area (g/m²) in mature previously clear-cut (CC; blue bars), near-natural (NN; green bars) forests and in different soil layers (litter-fibric-humic layer [LFH], 0-2 cm mineral soil, 2-5 cm mineral soil, and lower rest mineral [LRM])

Table 3: ANOVA analysis table with forest type and soil layer as explanatory variables and root biomass per surface area as response variable. SE= standard error, df= degree of freedom, CL=confidence limit

Forest type	Layer	Mean	SE	df	lower.CL	upper.CL
CC	02 Mineral	101.3	16.5	100.7	73.3	140.1
NN	02 Mineral	117.8	19.7	102.7	84.6	164
CC	25 Mineral	51	10	114.8	34.5	75.2
NN	25 Mineral	69.9	12.9	109.2	48.4	100.8
CC	LFH	463.9	75.7	100.7	335.6	641.4
NN	LFH	490.7	78.6	98.3	357	674.4
CC	LRM	75.1	29.7	127.9	34.3	164.4
NN	LRM	43.4	14.1	125.2	22.9	82.4

Figure 13: The effect of mean temperature of warmest quarter on root biomass per surface area in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).



Root biomass per surface area in the 2-5 cm mineral soil layer increased with annual precipitation of the locations (*Fig. 17, Table 9*). This pattern was observed also in the lower rest mineral layer, but the low number of this layer samples resulted in large confidence intervals, and thus no significant trend. The same tendency was observed also with temperature of the warmest quarter, but it was not significant (*Fig. 16, Table 8*).

Table 4: Type III Analysis of Variance Table with Satterthwaite's method with root biomass per surface area as a response variable and soil layer and mean temperature of warmest quarter as random effects.

Random effects	***F value***	***P***
Layer	2.83	0.041
Mean Temperature	3.60	0.072
Layer: Mean Temperature	1.55	0.205

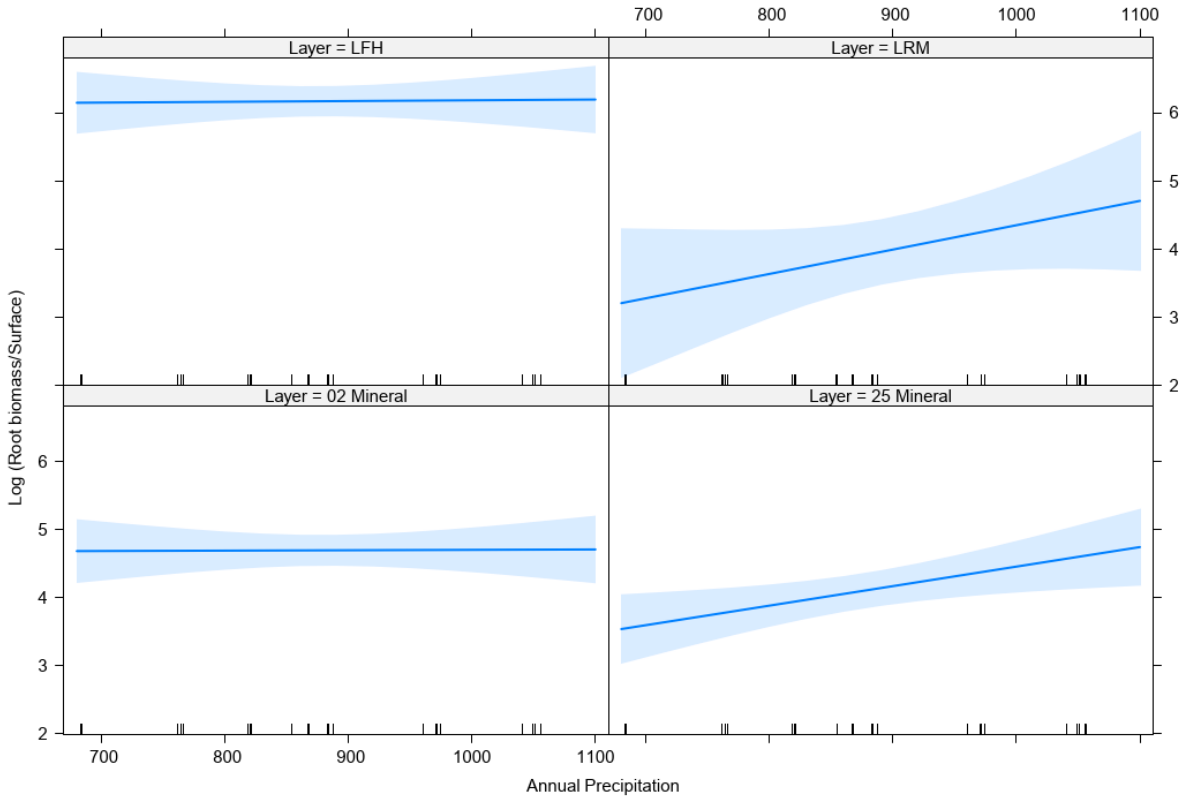


Figure 14: The effect of annual precipitation on root biomass per surface area in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 5: Type III Analysis of Variance Table with Satterthwaite's method with root biomass per surface area as a response variable and soil layer and annual precipitation as random effects.

Random effects	***F value***	***P***
Layer	4.78	0.004
Annual Precipitation	4.92	0.039
Layer: Annual Precipitation	1.89	0.135

Average diameter

Average diameter of fine roots in all analysed soil samples did not vary significantly between the two forest types and was on average 0.70 mm and 0.71 mm in the near-natural and clear-cut stands, respectively (*Table 2, Fig. 12*). However, the average diameter differed significantly with soil layers, being highest in the upper layers (*Table 2-3*, *Fig.12*). These patterns were consistent between forest types, as shown by the non-significant interaction term (*Table 2*).

Table 6: Type III Analysis of Variance Table with Satterthwaite's method with average diameter as a response variable and forest type and soil layer as explanatory variables.

Explanatory variable	***F value***	***P***
Forest type	0.44	0.510
Soil layer	4.63	0.004
Forest type: Soil layer	0.10	0.959

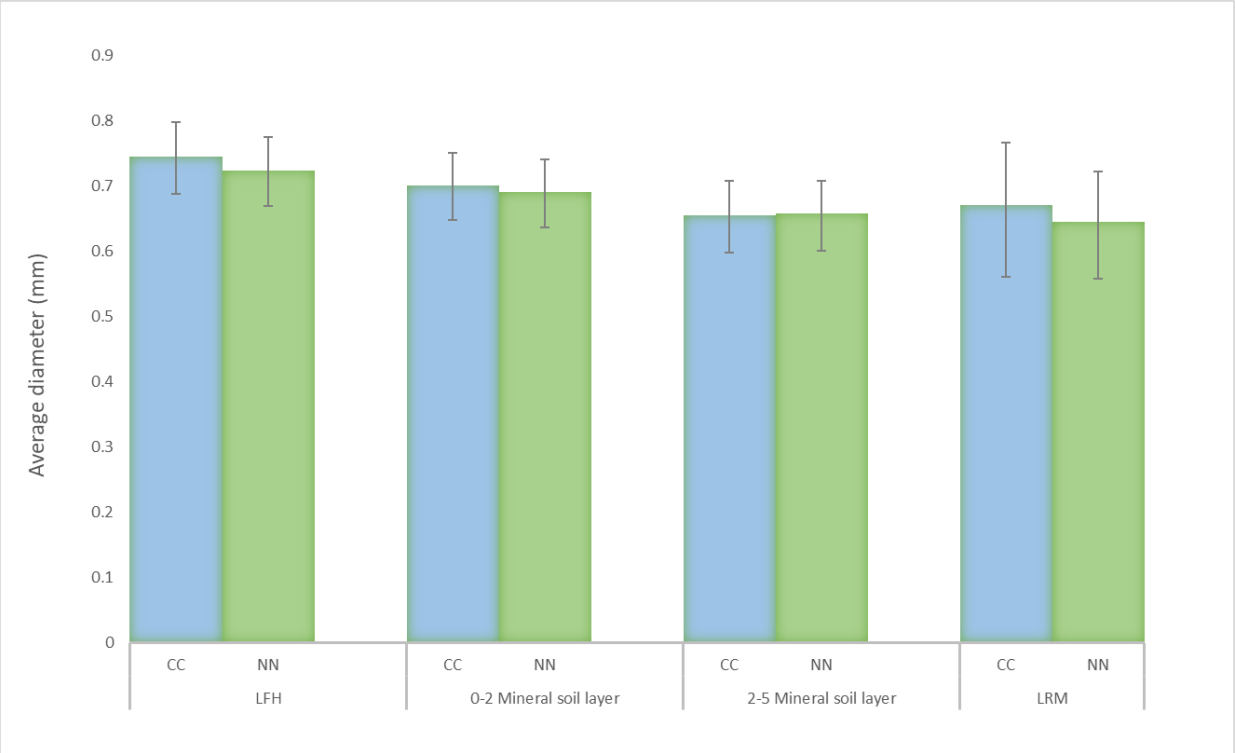


Figure 15: Average diameter (mm) in mature previously clear-cut (CC; blue bars), near-natural (NN; green bars) forests and in different soil layers (litter-fibric-humic layer [LFH], 0-2 cm mineral soil, 2-5 cm mineral soil, and lower rest mineral [LRM])

Table 7: ANOVA analysis table with forest type and soil layer as explanatory variables and average diameter as the response variable. SE= standard error, df= degree of freedom, CL=confidence limit

Forest type	Soil layer	Mean	SE	df	lower.CL	upper.CL
CC	LRM	0.671	0.0518	119.9	0.576	0.782
NN	LRM	0.645	0.0414	110.5	0.568	0.732
CC	25 Mineral	0.655	0.0276	61.9	0.602	0.713
NN	25 Mineral	0.657	0.0265	54.6	0.606	0.713
CC	02 Mineral	0.701	0.0257	42.1	0.651	0.754
NN	02 Mineral	0.69	0.0258	44.2	0.64	0.744
CC	LFH	0.745	0.0274	42.1	0.692	0.802
NN	LFH	0.724	0.0263	40.4	0.673	0.779

Average diameter was not significantly affected by either the mean temperature of warmest quarter (*Fig. 13, Table 4*) or annual precipitation (*Fig. 14, Table 5*).

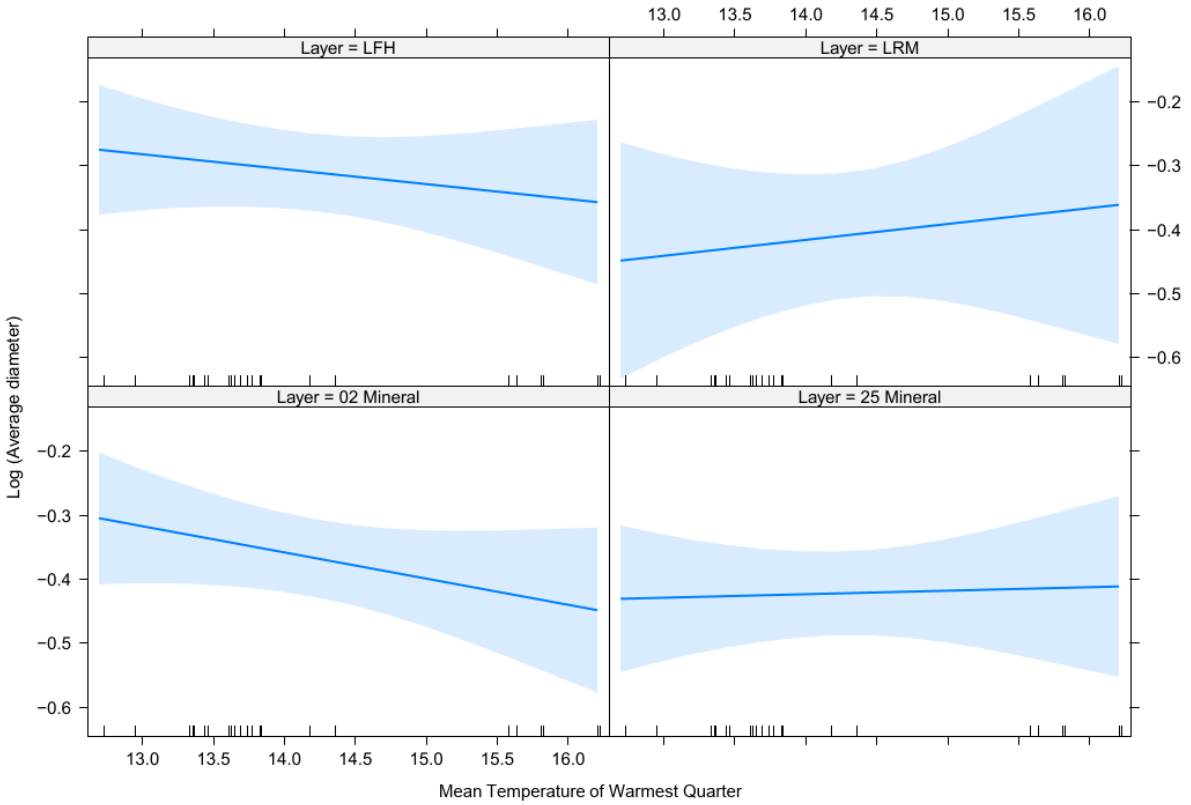


Figure 16: The effect of temperature of warmest quarter on average diameter in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 8: Type III Analysis of Variance Table with Satterthwaite's method with average diameter as a response variable and mean temperature of warmest quarter and soil layer as random effects.

Random effects	***F value***	***P***
Layer	1.43	0.240
Mean Temperature	0.10	0.756
Layer: Mean Temperature	1.22	0.308

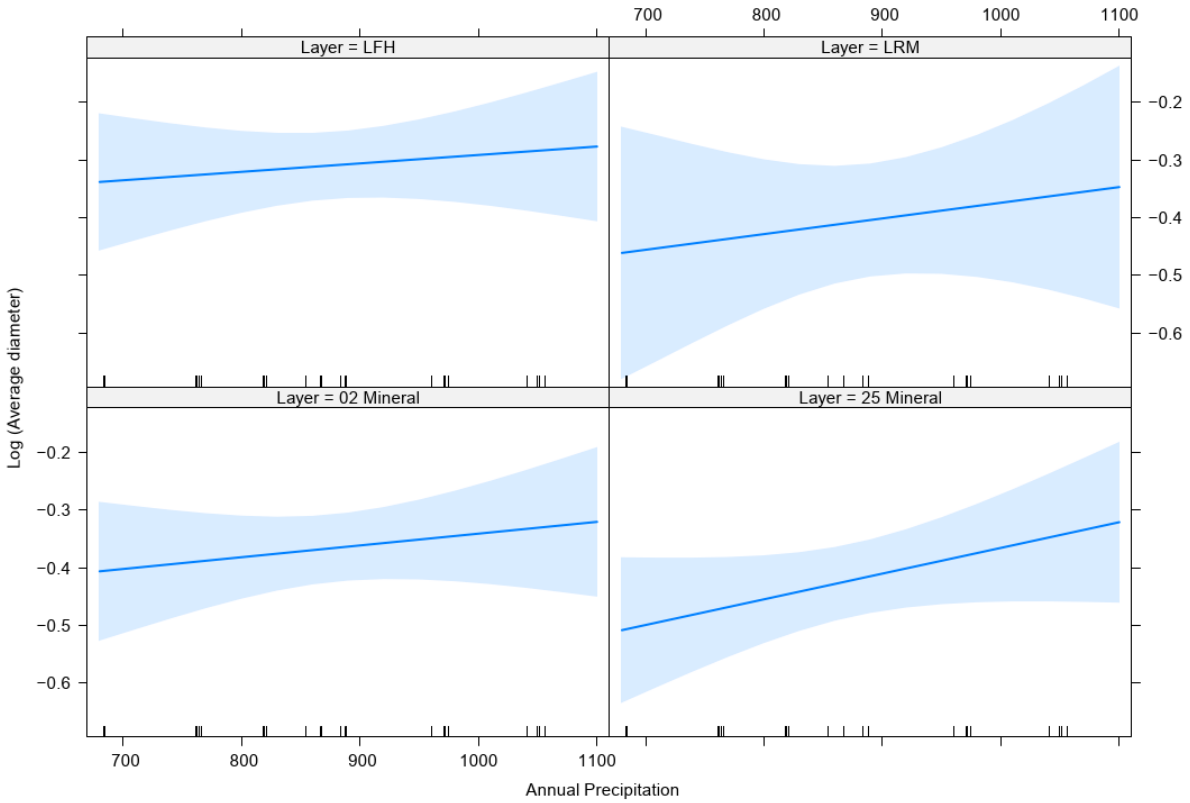


Figure 17: The effect of annual precipitation on average diameter in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 9: Type III Analysis of Variance Table with Satterthwaite's method with average diameter as a response variable and annual temperature and soil layer as random effects.

Random effects	***F value***	***P***
Layer	0.95	0.420
Annual Precipitation	1.21	0.291
Layer: Annual Precipitation	0.50	0.684

Specific root length

Average specific root length of fine roots in all analysed soil samples from the near-natural forest sites was 7.16 m/g and 6.78 m/g from the clear-cut sites, respectively, and did not vary significantly between the forest types (*Table 10, Fig.18*). However, specific root length differed significantly with soil layers, being largest at the topsoil layers (*Table 11, Fig.18*). These patterns were consistent between forest types, as shown by the non-significant interaction term (*Table 10*).

Table 10: Type III Analysis of Variance Table with Satterthwaite's method with specific root length per surface area as a response variable.

Explanatory variable	***F value***	***P***
Forest type	2.45	0.120
Soil layer	5.79	0.001
Forest type: Soil layer	0.36	0.783

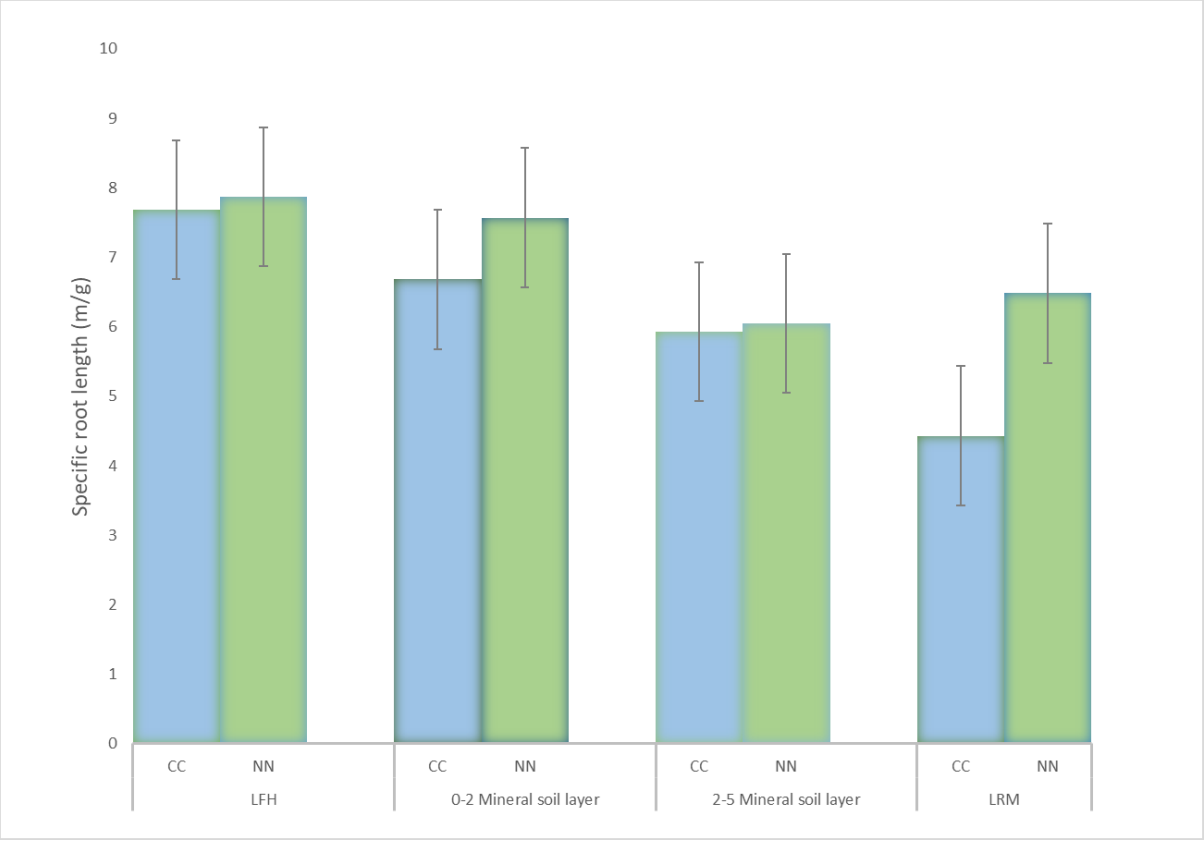


Figure 18: Specific root length (m/g) in mature previously clear-cut (CC; blue bars), near-natural (NN; green bars) forests and in different soil layers (litter-fibric-humic layer [LFH], 0-2 cm mineral soil, 2-5 cm mineral soil, and lower rest mineral [LRM])

Table 11: ANOVA analysis table with forest type and soil layer as explanatory variables and specific root length as response variable. SE= standard error, df= degree of freedom, CL=confidence limit

Forest type	Layer	Mean	SE	df	lower.CL	upper.CL
CC	02 Mineral	6.15	0.562	46.9	5.12	7.39
NN	02 Mineral	6.82	0.634	49.3	5.66	8.22
CC	25 Mineral	5.25	0.554	68.3	4.25	6.48
NN	25 Mineral	5.52	0.556	60.5	4.51	6.75
CC	LFH	7.25	0.662	46.9	6.03	8.71
NN	LFH	7.52	0.679	45.1	6.27	9.02
CC	LRM	4.56	0.894	121.6	3.09	6.72
NN	LRM	6.14	0.998	113.7	4.44	8.47

Specific root length was not significantly affected by either the mean temperature of warmest quarter (*Fig. 19, Table 12*) or annual precipitation at the locations (*Fig. 20, Table 13*).

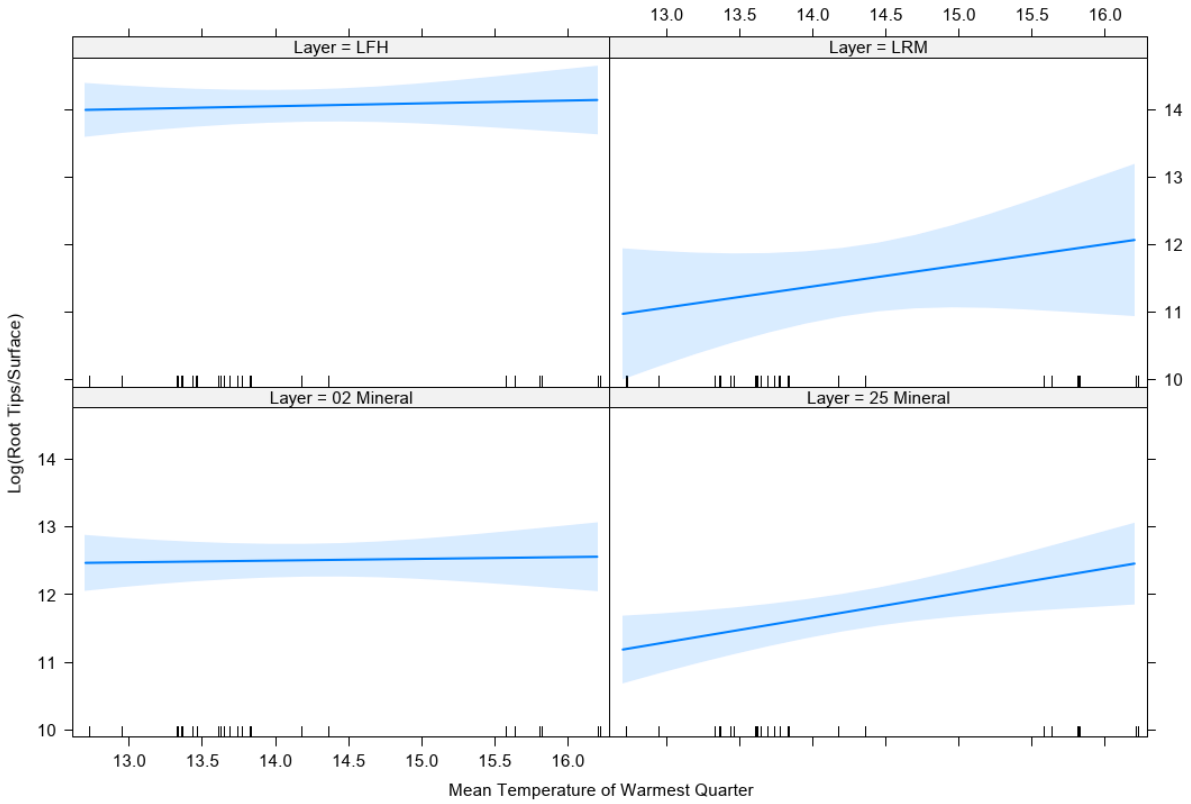


Figure 19: The effect of mean temperature of warmest quarter on specific root length in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 12: Type III Analysis of Variance Table with Satterthwaite's method with specific root length as a response variable and soil layer and mean temperature of warmest quarter as random effects.

Random effects	***F value***	***P***
Layer	0.16	0.924
Mean Temperature	0.30	0.593
Layer: Mean Temperature	0.24	0.869

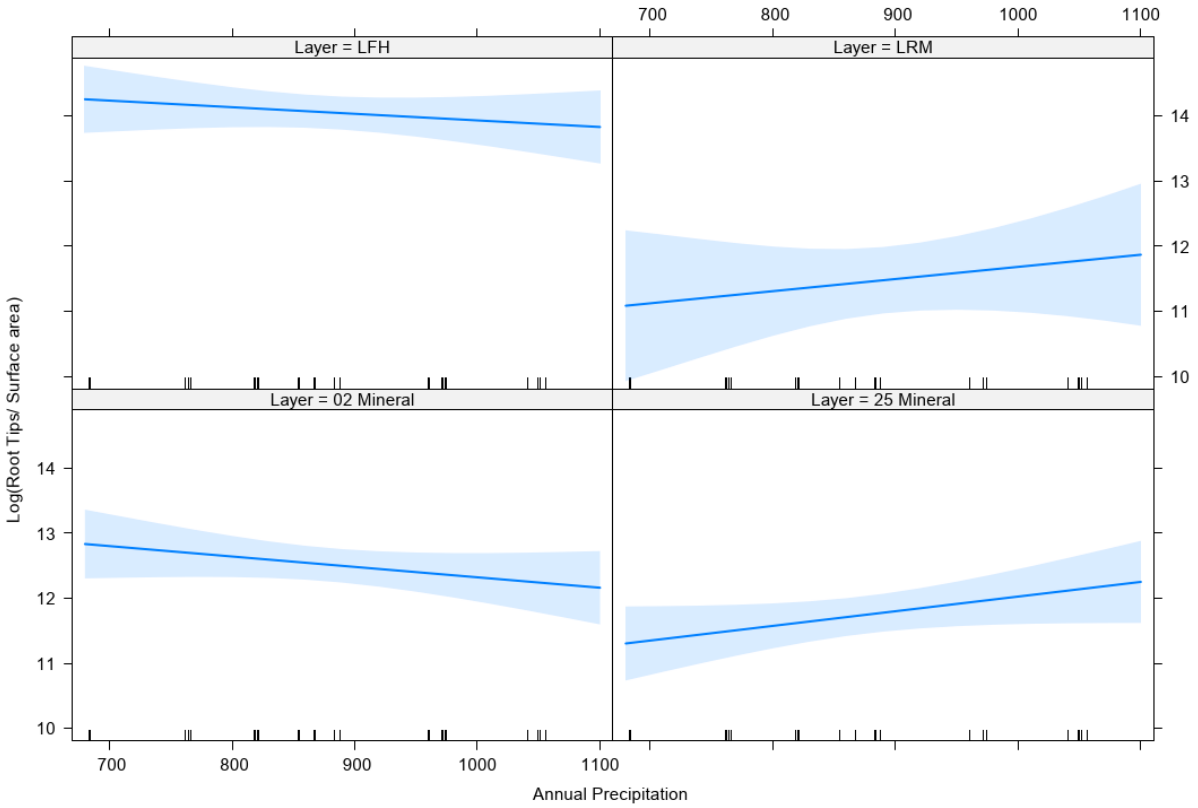


Figure 20: The effect of annual precipitation on specific root length per surface area in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 13: Type III Analysis of Variance Table with Satterthwaite's method with specific root length as a response variable and soil layer and annual precipitation as random effects.

Random effects	***F value***	***P***
Layer	0.52	0.670
Annual Precipitation	0.58	0.459
Layer: Annual Precipitation	0.21	0.890

Number of root tips per surface area

Average number of roots tips per surface area of fine roots in all analysed soil samples from the near-natural forest sites was 760533 and 692169 from the clear-cut sites, respectively, and did not vary significantly between the forest types (*Table 14*, *Fig.21*). However, there was a significant variation in number of root tips per surface area in response to soil layer (*Table 14*). The highest numbers of root tips were measured in LFH soil layer (*Table 15.*, *Fig. 21*).

Table 14: Type III Analysis of Variance Table with Satterthwaite's method with number of root tips per surface area as a response variable

Explanatory variable	***F value***	***P***
Forest type	0.33	0.568
Soil layer	72.44	<0.001
Forest type: Soil layer	0.51	0.679

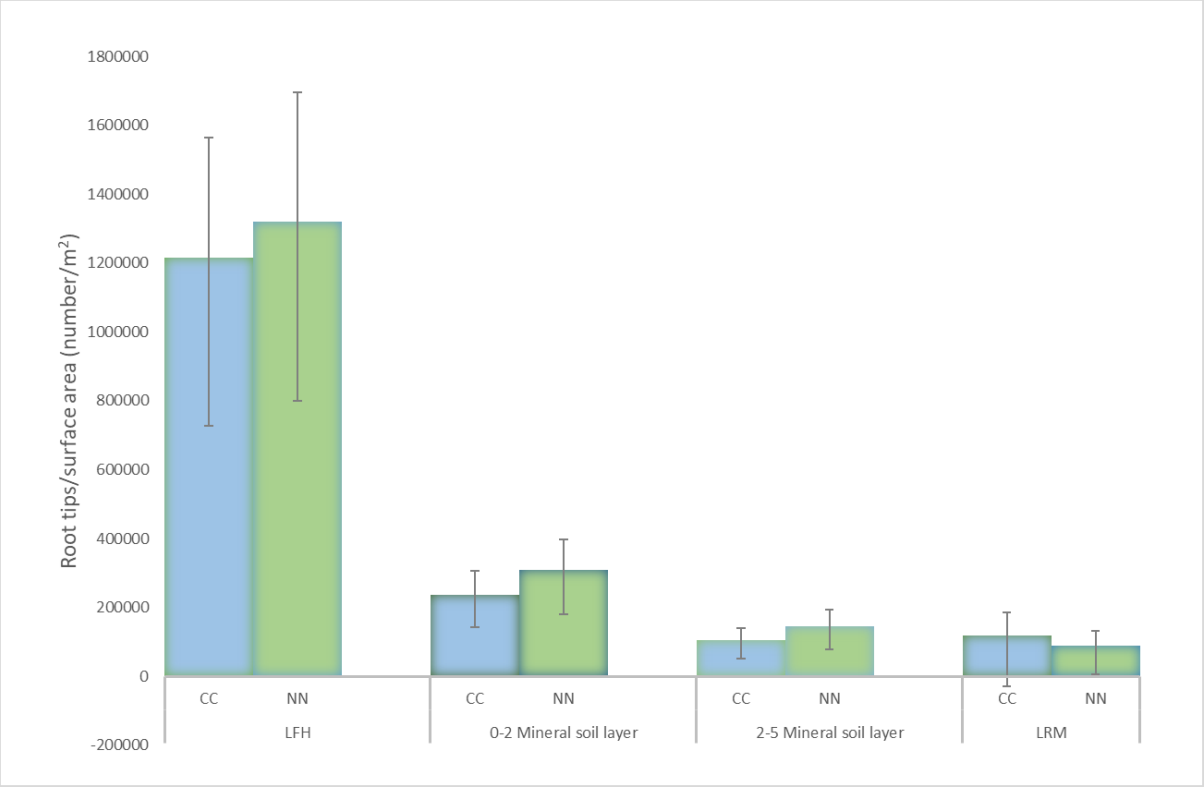


Figure 21: Number of root tips/surface area (number/m²) in mature previously clear-cut (CC; blue bars), near-natural (NN; green bars) forests and in different soil layers (litter-fibric-humic layer [LFH], 0-2 cm mineral soil, 2-5 cm mineral soil, and lower rest mineral [LRM])

Table 15: ANOVA analysis table with forest type and soil layer as explanatory variables and number of root tips per surface area as response variable. SE= standard error, df= degree of freedom, CL=confidence limit

Forest type	Layer	Mean	SE	df	lower.CL	upper.CL
CC	02 Mineral	237716	40430	86.9	169529	333330
NN	02 Mineral	308535	53658	89.5	218394	435881
CC	25 Mineral	105097	21424	105.8	70156	157441
NN	25 Mineral	146605	28189	98.9	100104	214707
CC	LFH	1216030	206820	86.9	867219	1705138
NN	LFH	1321183	220926	84	947431	1842377
CC	LRM	119483	48522	124.9	53488	266905
NN	LRM	88738	29480	121.8	45972	171288

Number of root tips per surface area increased with temperature of the warmest quarter in the upper layers (*Fig. 22, Table 16*), but there was no significant trend, and it is not significantly affected by annual precipitation either.

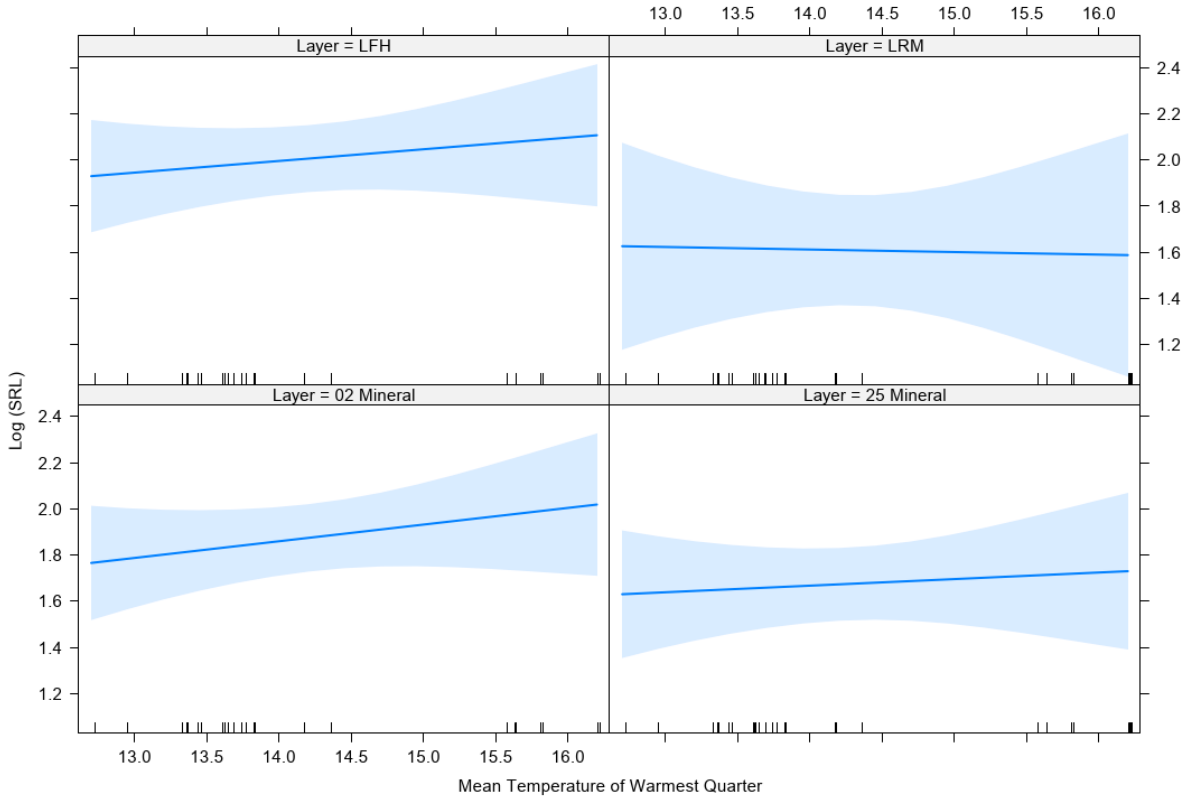


Figure 22: The effect of mean temperature of warmest quarter on number of root tips per surface area in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 16: Type III Analysis of Variance Table with Satterthwaite's method with number of root tips as a response variable and soil layer and mean temperature of warmest quarter as random effects.

Random effects	***F value***	***P***
Layer	3.26	0.025
Mean Temperature	4.16	0.056
Layer: Mean Temperature	1.72	0.167

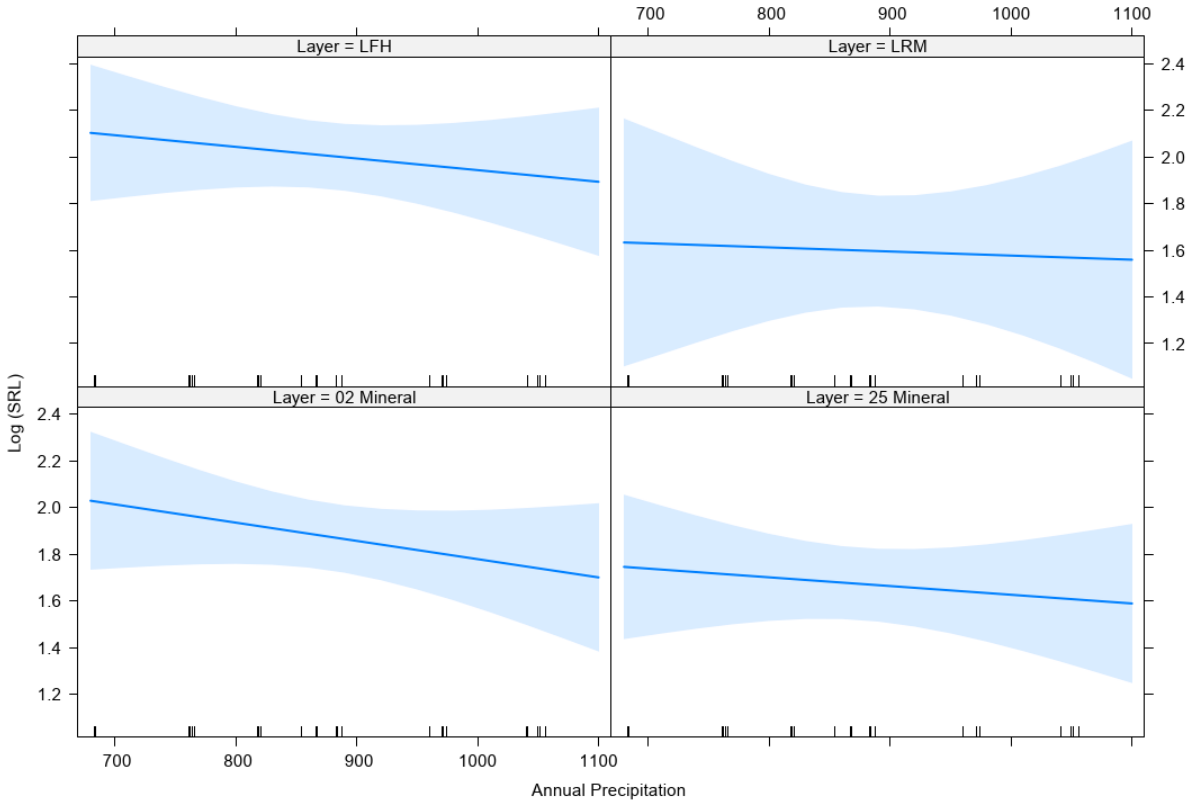


Figure 23: The effect of annual precipitation on the number of root tips per surface area in four different soil layers. The blue line is the trend line, and the light blue area is representing the confidence interval (95%).

Table 17: Type III Analysis of Variance Table with Satterthwaite's method with number of root tips as a response variable and soil layer and annual precipitation as random effects.

Random effects	***F value***	***P***
Layer	6.16	<0.001
Annual Precipitation	0.16	0.694
Layer: Annual Precipitation	2.68	0.051

Discussion

The focus of this thesis was to investigate the effect of clear-cutting on fine root biomass and mycorrhizal colonization in the boreal forest of South-East Norway. The results revealed that there is no significant difference in average diameter, root biomass per surface area, specific root length, and the number of root tips per surface area in the near-natural forests compared to clear-cuts.

One of the possible explanations for the non-significant variation among forest types may be the relatively small size of the dataset. Due to the time-consuming and labour-intensive method for root washing and sorting, we were only able to analyse two of the six sampled subplots for each plot (46 of 144 soil samples). A detailed description of the process, where in total 326 different fractions of roots were obtained, is given in the method chapter. Fractions of fine tree roots (142 in total) were included in a scanning process with detailed analysis to obtain extensive results. A larger dataset may possibly provide more precise data for statistical analysis that could result in significant variation. Freschet et al. (2021) mentiones that, taking a larger number of core samples often is not feasible, however to get a representative sample, the number of replicates cores should be larger than three. Even though this method indeed was extremly time-consuming and labourious we still considered it as the most appropriate one in order to get as accurate results of root biomass as possible in the given timeframe. The assesement of other possible methods is discussed further down.

Another explanation could be connected to the large variation between the mean values of different root traits among the pair of plots, which may be explained by climate conditions. Testing the effect of mean temperature of warmest quarter and the annual precipitation showed tendencies of some response variables, but there was little significant response on the climate. Among the analysed response variables, root biomass per surface area was the only one to show a significant response on the annual precipitation (*Table 9*, $P<0,05$). This may not be surprising, since in natural ecosystems high variability is expected.

According to some studies, response of fine roots to the disturbances, such as clear-cutting, may be detected only in the short period of time right after the disturbance occurred (Palviainen et al., 2005; Taskinen et al., 2003). The study in the boreal forests of Northern

Ontario revealed, that effects of stand origin on fine roots tend to converge after a specific period of time (Yuan & Chen, 2013). The absence of a significant correlation between forest type and studied variables could potentially be explained by the development of clear-cut sites, that may be in a certain time period, achieving the state of mature stand and thus not revealing significant difference from the near-natural stand. However, this is only an assumption, that cannot be supported by the obtained data. Although the initiation of forest history studies with dendrochronology is being planned as a part of the EcoForest project, the results will not be available until the next spring.

However, results revealed a significant variation of response variables among the soil layers (*Tables 2,6,10,14*) with the highest mean values of analysed root traits in the upper soil layers. These results were expected and supported by other studies. The review of published data on tree fine root biomass (Finér et al., 2007) revealed, that in boreal forests 80-90% of roots are in the top 30 cm, or even top 20 cm. The results of the study of fine root biomass in Norway spruce and Scots pine stands (Helmisaari et al., 2007) showed, that majority of fine roots was located in the upper soil layers.

As mentioned in the introduction, fine roots are understudied, despite their critical role in carbon cycling, mainly due to the methodological issues (Addo-Danso et al., 2016). We encountered some challenges regarding the choice of the most appropriate method for soil sampling and root sorting. We decided that manual soil coring would be the best option since it provides the best possible results on fine root biomass and can be easily scaled across plots. There was a risk of substantial disturbances, as it is expected by root sampling, and we had some challenges with coring on the high stone density plots. But it was an effective, cheap, and relatively simple way to collect the samples. However, other studies describe soil coring as a labour-intensive and time-consuming method (Brunner et al., 2013; Freschet et al., 2021). Other fine root biomass assessment techniques, such as in-growth core, soil trench, rhizobox, rhizotron, camera systems, and ground-penetrating radar, were considered less appropriate for the purposes of this research, due to the possible disturbances, difficult access to deeper roots, expensive utilization, inefficiency, calibration requirements, and lower accuracy (Addo-Danso et al., 2016; Freschet et al., 2021).

Another challenge, we faced during measurements, was the choice of a proper approach to study the roots. There are many different techniques and some studies suggested collecting and measuring the whole root system (e.g. Freschet & Roumet, 2017), which may provide data for the whole-plant functioning. Since the main purpose of this research was to study the effects on fine roots and their traits, we considered the division of soil core into soil layers followed by the classification of roots according to the size and type, as the most appropriate method. All fractions were dried and weighed, but only tree roots with a diameter below 2 mm (fine roots) were scanned and included in further analysis of average diameter, root biomass per surface area, SRL, and number of root tips per surface area. Limiting the scope of research to a specific root size and type provided more specific comparisons across soil layers and forest types.

Root cleaning and sorting were challenging processes as well. There are several possible ways to clean the roots and the most recommended option is to clean the roots immediately after the collection to minimize losses by respiration (Freschet et al., 2021). Due to the large number of samples and the time-consuming method for root sorting, we processed a low number of samples at a time. In the meantime, other soil cores were stored in the freezer at -18°C, that slowed down the respiration and decomposition. That allowed us to adjust the number of samples to be analysed to the capacity of sorting. The negative consequence of freezing the roots is that they become more fragile after thawing and are more likely to break or get damaged in the sorting process (Freschet et al., 2021). To minimize the chance of damaging the roots, we limited the use of sieve and when necessary, used additional change of water.

The lack of response and the large variation between samples could have occurred due to the large variation in sampling depth (varying from 5 cm to 23 cm), and unequal lengths of soil layers. The goal by root sampling was to reach the maximum root-depth limit, but that was not always possible. A similar challenge was mentioned also by Park et al. (2007) while root coring for estimating fine root biomass. However, reanalysing root biomass per soil mass showed similar results as the per area measurements, suggesting that this was not a viable explanation. Still, the shallow root samples only represent a fraction of the rooting zone, and any possible difference in deeper layers are not covered by this study.

In overall perspective, expanding the knowledge on the belowground parts of boreal forest, benefits the increasing interest for understanding the carbon sequestration in terrestrial ecosystems. Due to the limited research and little available data on fine root biomass in boreal near-natural and clear-cut forests, the data and results from this study provide an important contribution to the study of forest management effects on fine roots and consequently the carbon storage potential of forest soil. Furthermore, the need for multidisciplinary research is still crucial for answering complex challenges and advancing our understanding of plant responses to different environmental and anthropogenic impacts.

Conclusion

To conclude, the main findings of this study revealed that there was no significant variation in average diameter, root biomass per surface area, specific root length, and number of root tips per surface area of fine roots between near-natural and clear-cut boreal forests of South-Eastern Norway. Due to the relatively small number of analysed samples and great variation among the studied root traits, there was no distinct trend. Increasing the number of replications may provide more reliable results. The non-significant variation can partly be explained by climate factors, such as mean temperature and annual precipitation, spatial variability, and varying sampling depth. The development of clear-cut sites over time could also eliminate some of the potential differences between the two forest types. From this point of view, we cannot conclude that clear-cutting significantly affects fine roots and mycorrhizal colonization in Norwegian boreal spruce forest, nevertheless, this finding does not exclude the need for further investigation of these research topics.

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Appendix

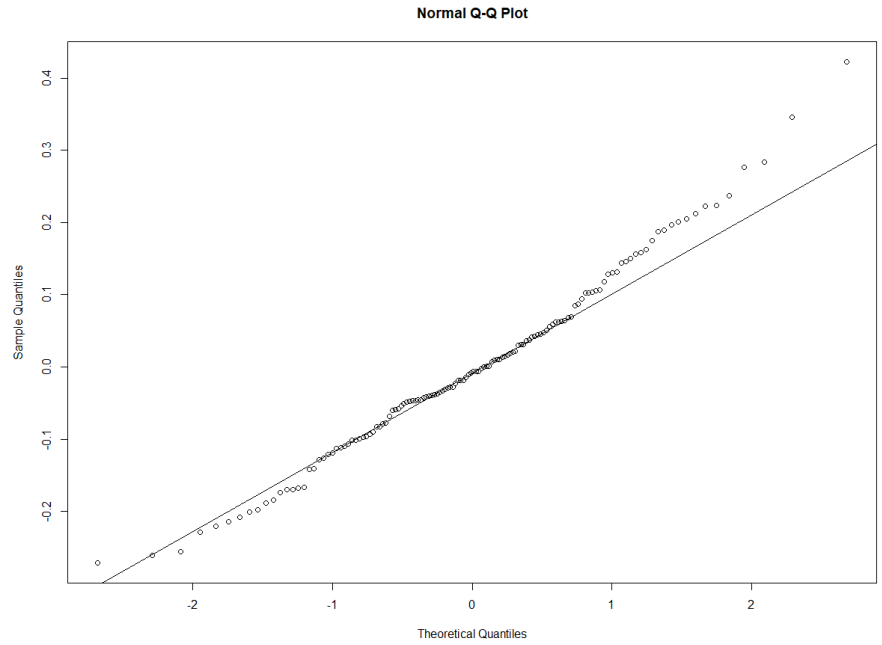


*Figure A1: Residual plots for average diameter log(AvgDiam_mm)~Skogtype*Layer+(1|Site/Serie)*

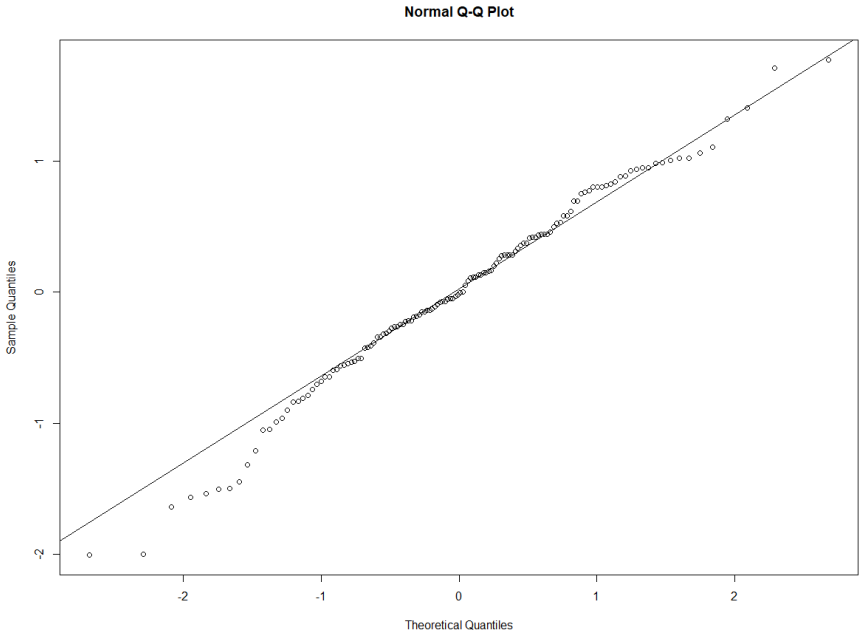


*Figure A2: Residual plots for root biomass per surface area log(Root_biomass_Surface_g_m2)~Skogtype*Layer+(1|Site/Serie)*

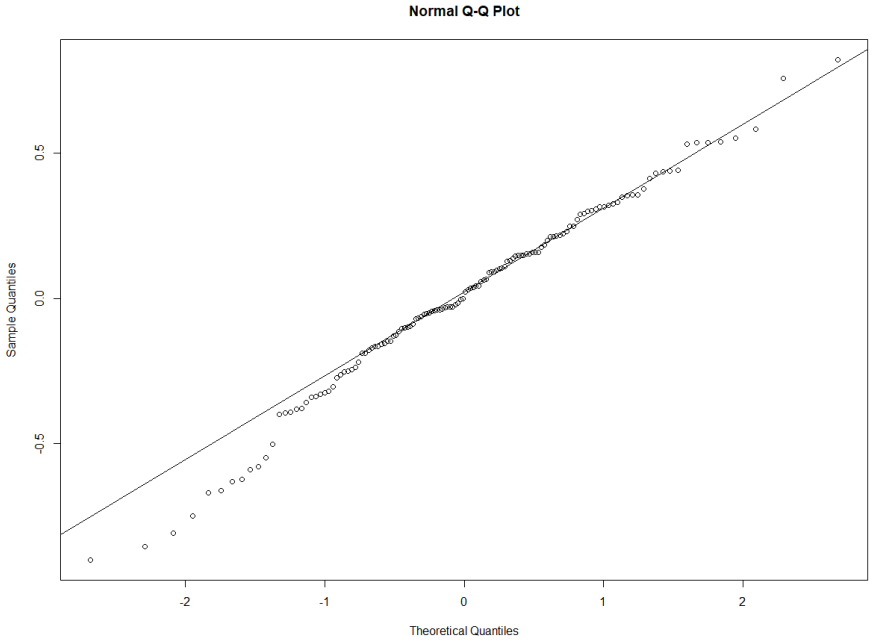


*Figure A3: Residual plots for SRL per surface area log(SRL_m_g)~Skogtype*Layer+(1|Site/Serie)*

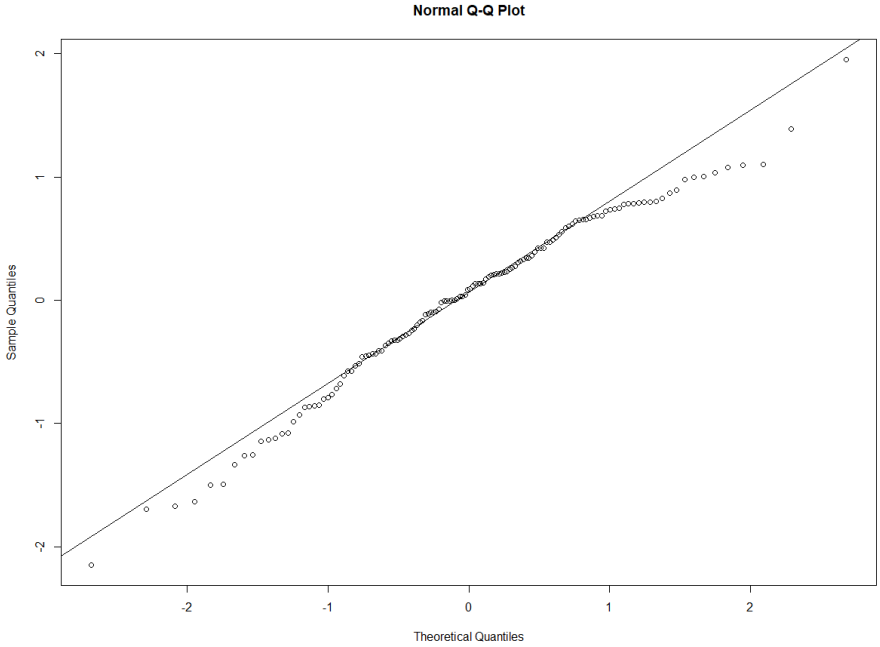


*Figure A4: Residual plots for number of root tips per surface area log(Root_Tips_area_m2)~Skogtype*Layer+(1|Site/Serie)*

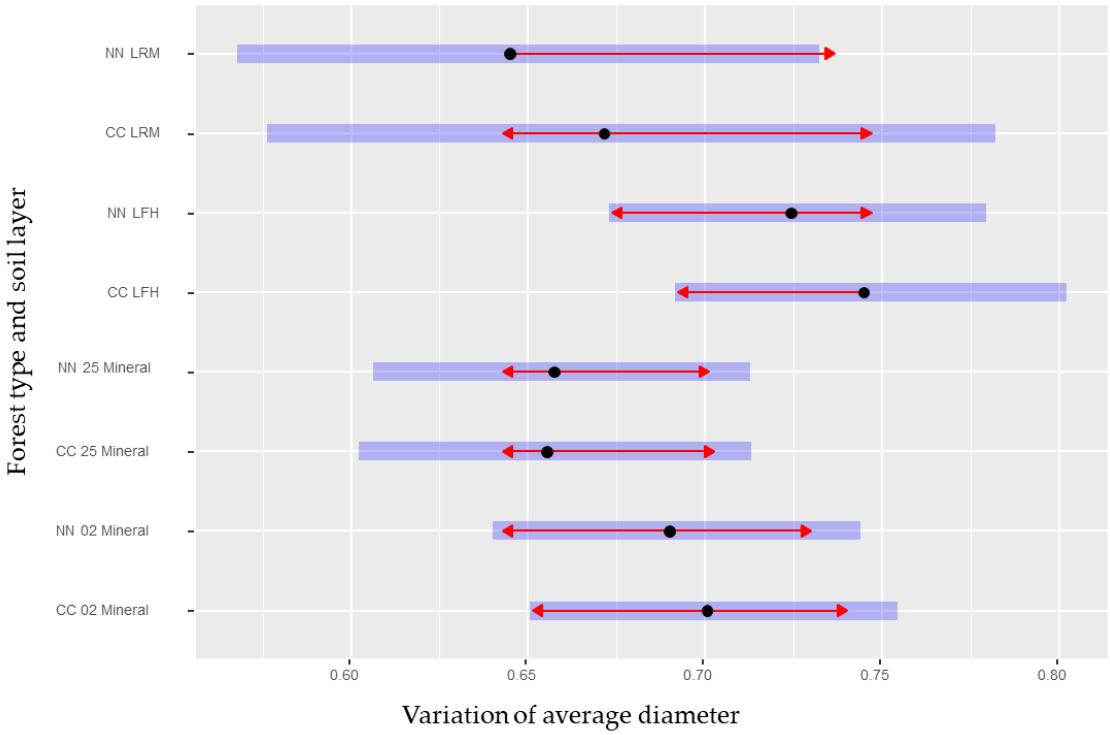


Figure A5: Variation of average diameter in response to forest type (CC and NN) and soil layer (LFH, LRM, 0-2cm mineral soil layer, 2-5 cm mineral soil layer). The confidence interval is represented by the blue line and the actual values by the red arrows. Overlapping red arrows indicate non-significance.

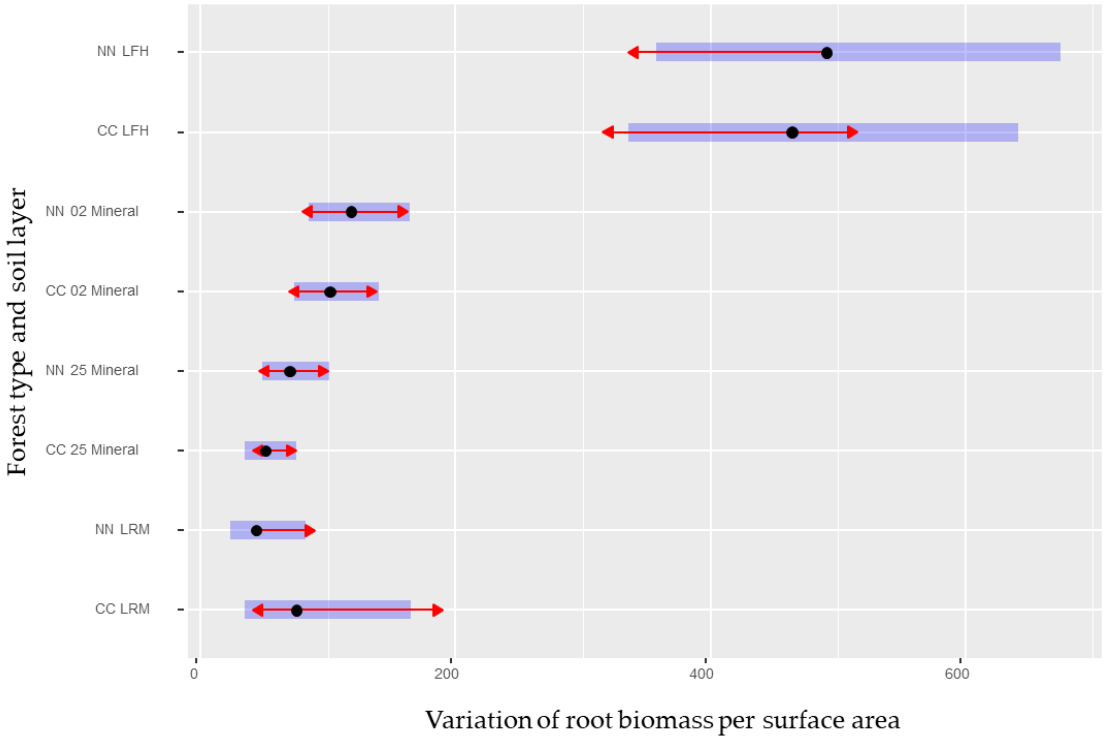


Figure A6: Variation of root biomass per surface area in response to forest type (CC and NN) and soil layer (LFH, LRM, 0-2cm mineral soil layer, 2-5 cm mineral soil layer). The confidence interval is represented by the blue line and the actual values by the red arrows. Overlapping red arrows indicate non-significance.

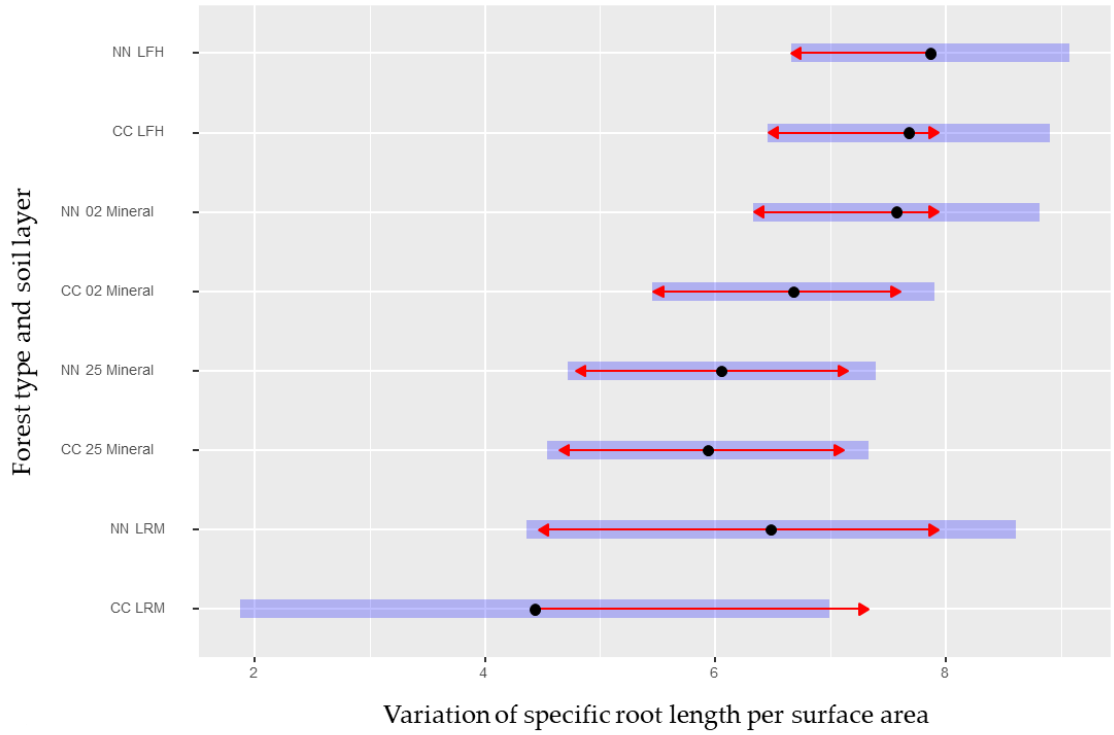


Figure A7: Variation of root specific root length in response to forest type (CC and NN) and soil layer (LFH, LRM, 0-2cm mineral soil layer, 2-5 cm mineral soil layer). The confidence interval is represented by the blue line and the actual values by the red arrows. Overlapping red arrows indicate non-significance.

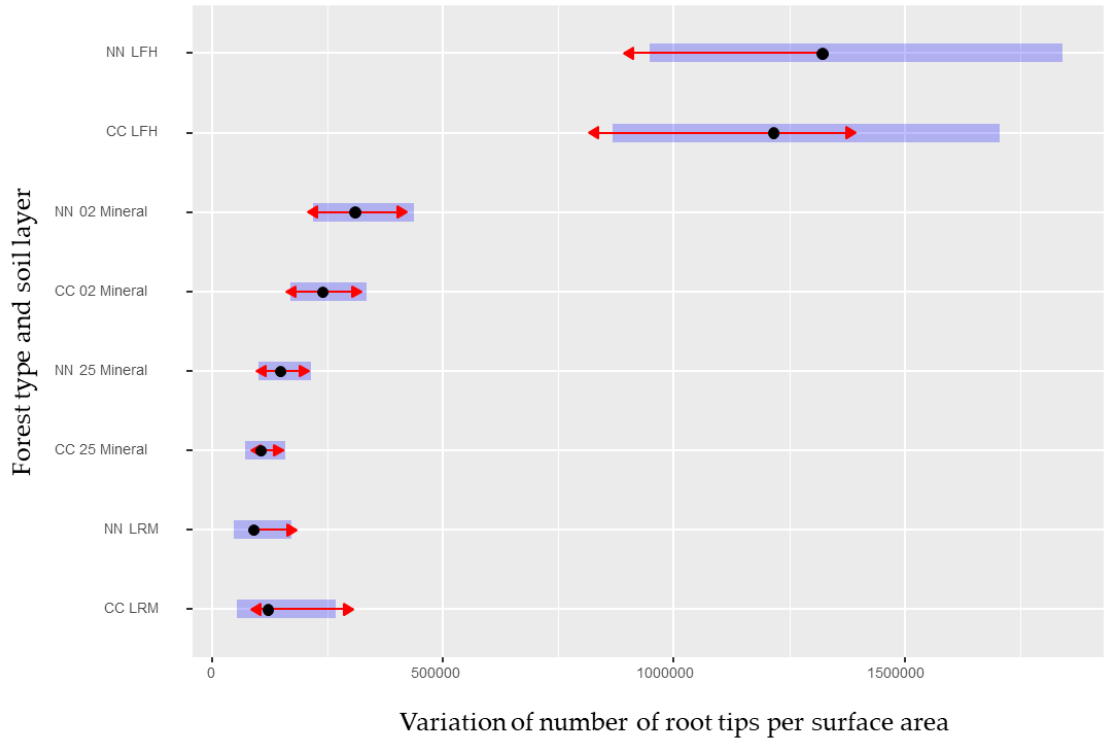
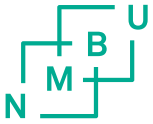


Figure A8: Variation of number of root tips per surface area in response to forest type (CC and NN) and soil layer (LFH, LRM, 0-2cm mineral soil layer, 2-5 cm mineral soil layer). The confidence interval is represented by the blue line and the actual values by the red arrows. Overlapping red arrows indicate non-significance.



Norges miljø- og biovitenskapelige universitet
Noregs miljø- og biovitskapelege universitet
Norwegian University of Life Sciences

Postboks 5003
NO-1432 Ås
Norway