

AZADEH REZAPOUR

The impact of climate change
on fine root trait responses of
deciduous and coniferous trees



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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are referred to in the text by their Roman numerals:

- I** Sell, M., Ostonen, I., Rohula-Okunev, G., Rusalepp, L., **Rezapour, A.**, Kupper, P. 2021. Responses of fine root exudation, respiration and morphology in three early successional tree species to increased air humidity and different soil nitrogen sources. *Tree Physiology*, 42(3), pp. 557–569.
- II** **Rezapour, A.**, Maddison, M., Rohula-Okunev, G., Tullus, A. Truu, M., Uri, V., Mander, Ü., Ostonen, I. 2022. Morphological variation in absorptive roots in downy birch (*Betula pubescens*) and Norway spruce (*Picea abies*) forests growing on drained peat soils. *Forests*, 13(1), p. 112.
- III** **Rezapour, A.**, Labbafi, M., Oja, T. 2023. The impact of soil warming on fine root trait responses of trees, deciduous vs. coniferous: a meta-analysis. *Forestry Studies*, 77(1), pp. 67–75.

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Author's contribution to each paper:

- I** The author contributed to the experimental measurements and data analysis.
- II** The author is primarily responsible for methodology, field data collection and processing, data analysis, interpretation, and manuscript writing.
- III** The author is primarily responsible for conceptualization and methodology, including data extraction, analyses, interpretation, and manuscript writing.

LIST OF TERMS AND ABBREVIATIONS

C	carbon
N	nitrogen
NO ₃ ⁻	nitrate
NH ₄ ⁺	ammonium
RH	relative air humidity
mRH	moderate relative air humidity
eRH	elevated relative air humidity
P _{net}	net photosynthesis rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
E	transpiration rate ($\text{g m}^{-2} \text{h}^{-1}$)
gl	leaf (shoot) conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)
Ex _{C_area}	fine root carbon exudation per root surface area ($\mu\text{g C cm}^{-2} \text{day}^{-1}$)
Ex _{C_mass}	fine root carbon exudation per root dry weight ($\text{mg C g}^{-1} \text{day}^{-1}$)
R _{root_area}	fine root respiration per root surface area ($\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$)
R _{root_mass}	fine root respiration per root dry weight ($\mu\text{mol CO}_2 \text{g}^{-1} \text{s}^{-1}$)
D	fine/absorptive root diameter (mm)
L	fine/absorptive root length (mm)
W	fine/absorptive root dry weight (mg)
BI _L	branching intensity per unit of fine/absorptive root length (no cm^{-1})
BI _w	branching intensity per unit of fine/absorptive root dry weight (no mg^{-1})
SRA	specific root area ($\text{m}^2 \text{kg}^{-1}$)
SRL	specific root length (m g^{-1})
RTD	root tissue density (kg m^{-3})
FRB	fine root biomass (g m^{-2})
FRP	fine root production ($\text{g m}^{-2} \text{yr}^{-1}$)

1. INTRODUCTION

1.1. The impact of climate change on forest ecosystems

Global climate change is increasing air and soil temperature, altered precipitation patterns, and rising anthropogenic nitrogen (N) deposition, which poses substantial risks to the world's forest ecosystems in exceptionally high latitudes (Hyvönen et al., 2007; IPCC, 2013). This is of concern since about 59% of soil's carbon (C) and associated peat deposits are located in high-latitude forests (Dixon et al., 1994). A minor increase in global mean temperature can alter these forest ecosystems' C and nutrient cycles (Leppälammil-Kujansuu et al., 2013). Forest ecosystem functioning highly depends on belowground processes, mainly regulated by trees' fine roots and their functional traits (Freschet et al., 2017). However, studies on belowground characteristics are often limited due to methodological sampling difficulty compared to aboveground studies. Available research methods for below-ground estimation are subject to uncertainties and possible errors (Addo-Danso et al., 2016). Knowledge about tree belowground adaptations to various environmental conditions is crucial for evaluating the resilience of different tree species to climate change and predicting forest C and nutrient fluxes.

Soil warming is one of the principal controlling factors on root growth and functions (Pregitzer, 2000; Kwatcho Kengdo et al., 2022). Shifts in soil temperature may determine the initiation and cessation of trees' root growth, cell elongation, root length, and diameter extension, regulating the rates of nutrient and water uptake (Lyr and Garbe, 1995; Pregitzer, 2000). Besides, the response of fine root systems to soil warming is linked to other soil conditions, such as moisture and nutrient availability, which can differ among tree species (Wang et al., 2021). Consequently, an improved understanding of how forest trees respond to soil temperature is crucial to develop strategies for preserving forest tree growth and survival in the face of the ongoing soil warming episode.

High-latitude peatlands store one-third of the global soil C and are thought to be particularly susceptible to climate change (van der Velde et al., 2021). Water table depth in peatlands is a vital soil variable in plant growth and C cycling (Holden et al., 2011). Peatlands in boreal and hemiboreal zones have been commonly drained to lower the water table level and promote aeration of the root zone (Becker et al., 2018). Estonia is among the most peatland-rich countries in the world, with 20% (9,150 km²) of its forests growing on peat soils, from which 14% are drained (Paal and Leibak, 2011; Raudsaar et al., 2016). Tree growth in many boreal coniferous forests was improved due to peatland drainage (Gustavsen et al., 1998; MacDonald and Yin, 1999). Besides, several researchers reported that tree growth improved at sites near the ditches (Miina, 1994; Hökkä et al., 2021). Because the decomposition rate of organic matter, aeration of the substrate, and nutrient availability are increased, caused by lowered water table levels at distances near ditches (Miina, 1994; Roy et al., 2000). Previous studies showed shifts in the soil bacterial and fungal communities with a distance gradient from

the ditch (Qui et al., 2013; Truu et al., 2020). At the same time, knowledge about fine root response characteristics of trees at drained peatlands is still required to elucidate the drained peatland forest's functioning and help better peatland management strategies under ongoing climate change.

In high latitudes, an increase in air temperature and precipitation frequency co-occurs with a rise in relative air humidity (RH) (Oksanen et al., 2018). High RH may improve the growth rate by lowering the plant's evaporative demand, promoting stomatal opening, and enhancing photosynthesis (Dai et al., 1992; Fanourakis et al., 2020). But reduced transpiration flux due to elevated RH limits the mass flow of soluble minerals in the soil and hinders the transport of mineral nutrients from roots to leaves, thus negatively affecting plant growth and productivity (Sellin et al., 2017; Tegeder and Masclaux-Daubresse, 2018). Reduced transpiration flux under elevated RH can increase soil moisture, influencing roots' growth environment and morphological and physiological traits (Hansen et al., 2013). In silver birch trees, fine root systems, particularly absorptive roots, reflected morphological adjustments to high air humidity (Parts et al., 2013; Godbold et al., 2014). Compared with fine root morphological traits, far less is known about fine root physiological traits such as carbon exudation and respiration – C efflux processes from roots- (Jakoby et al., 2020) in response to air humidity changes.

Over the past century, N availability in forest ecosystems has increased via increased deposition of inorganic N forms, such as nitrate (NO_3^-) and ammonium (NH_4^+) (Galloway et al., 2003). Inorganic N forms- NO_3^- or NH_4^+ – participate in plants' physiological and biochemical processes, such as photosynthesis and water and mineral nutrient absorption (Ding et al., 2018). It has been shown that the deposition of inorganic N forms affects photosynthesis and ultimately enhances forest growth; however, the overload of N deposition leads to a decline in forest productivity (Aber et al., 1998). The uptake of either NO_3^- or NH_4^+ by tree roots often depends on plant species and their growth strategy (Templer and Dawson, 2004). The soil's inorganic N forms may also influence C efflux processes from roots, such as exudation and respiration (Bloom et al., 1992). Also, fine root morphology was shown to be highly variable to soil N dynamics (Guo (a) et al., 2008); although the degree of many fine root morphological responses to N deposition is still controversial and may be ascribed to plant species, and soil environment (Zhu et al., 2021).

1.2. Fine roots and their contribution to soil C cycle

Fine roots (i.e., diameter < 2 mm) are an essential component of plants for resource acquisition and mediate biogeochemical soil cycles (Gill and Jackson, 2000). However, tree fine root biomass (FRB) accounts for a small portion (about 5%) of the total root biomass, in forest ecosystems, plants may allocate C up to 75% of annual net primary production (NPP) to fine roots (Vogt et al., 1995; Finér et al., 2011). Fine root production (FRP) is defined as the new fine root biomass

under 2 mm diameter accumulated per unit of ground surface area per unit of time (Huaraca Huasco et al., 2021). FRP has important implications for forest ecosystem productivity and belowground C dynamics, representing a significant source of soil C through root death and rhizodeposition (Jones et al., 2004; Finér et al., 2011). In addition to the soil C transferred through fine root turnover, rhizodeposition is another process of release of C compounds from living plant roots into the rhizosphere (Jones et al., 2004). For example, root exudation transfers about 5–21% of total photosynthetically fixed C into the rhizosphere (Haichar et al., 2014), which can comprise up to 10% of NPP in forests (Phillips et al., 2011). Fine root respiration is another source of CO₂ efflux from forest soils, in which more than 50% of photosynthetically fixed C is released into the soil (Reich et al., 1998; Högberg et al., 2002).

It is highly argued that root-mediated C estimates are subject to uncertainties (Addo-Danso et al., 2016). Thus, accurate estimation of FRB, FRP and turnover are especially needed for reliable understanding of forest ecosystem C pools and fluxes. Ingrowth core (IC) is one of the most commonly used methods to measure fine root biomass and production in situ, based on soil pits with or without a mesh bag filled with root-free soil (Makkonen and Helmisaari, 1998; Kubisch et al., 2016). However, the reliability of this method is impaired by several limitations. For instance, the IC installation causes soil disturbance and root cuttings that may initiate extensive new growth of fine roots from callus tissue, leading to higher estimates of FRP (Cameron and Thomson, 1969; Lukac, 2012). In addition, root-free soil may alter the soil's physical and chemical properties inside the core (Makkonen and Helmisaari, 1998). Furthermore, root growth proceeds faster inside the core due to the lack of competition compared to the surrounding soils, resulting in the overestimation of FRP (Lukac, 2012). Ingrowth mesh (IM) is an alternative method based on a more effortless installation procedure, placing a sheet of mesh vertically into the forest soil for a specific period, causing minimal soil disturbance (Godbold et al., 2007; Hirano et al., 2009). It has been shown that the IM method can underestimate FRP (Andreasson et al., 2016) due to measuring only living fine roots or biomass. Measuring the amount of root death or necromass is impossible with the IM method. Besides, a small mesh size (1 mm) in the IM method can prevent pioneer roots (i.e., apical diameter > 1mm) from passing through the mesh, causing shifts in lateral roots morphology through root clustering or bending root growth, leading to underestimation of FRP (Montagnoli et al., 2014). Therefore, using different root research methods could lead to under-or over-estimating fine root-mediated C rates.

1.3. Functional traits of fine roots: biomass, morphology, and physiology

The fine root systems are composed of individual roots of different morphology and size, implying heterogeneous physiological traits and functions (Eissenstat et al., 2000). According to their functions, fine roots can be divided into absorptive and transport roots (McCormack et al., 2015). Absorptive roots, defined as first- and second-order roots, exhibit primary development and, with their ectomycorrhizal (ECM) fungal associates, constitute the most active parts of the fine root system that are responsible for soil resource acquisition (McCormack et al., 2015). In boreal and temperate forests, absorptive roots prevalently form ECM symbioses with higher fungi, which are involved in multiple functions of the plant host roots (Pritsch and Garbaye, 2011). Conversely, transport roots, or so-called pioneer roots, occur in the higher orders (i.e., \geq third-order roots) and, with their secondary growth, have the function of transporting water and mineral nutrients (Sutton and Tinus, 1983; Guo (b) et al., 2008; Bagniewska-Zadworna et al., 2012; McCormack et al., 2015).

Fine root systems modify their biomass allocation and morphological and physiological functions to acclimate to environmental changes and optimize resource acquisition (Wang et al., 2016; Nikolova et al., 2020). For instance, an increase in biomass partitioning to roots may promote the uptake of mineral substances (Oleksyn et al., 1998). A higher investment in FRB is tightly associated with extensive foraging strategies under nutrient-poor conditions (Helmisaari et al., 2007). Specific root area (SRA) and specific root length (SRL) are linked to root functioning and determine the rates of resource uptake (Fitter, 1985; Makita et al., 2012). Fine roots with higher SRA or SRL mean a higher surface area per root biomass which may result in higher resource acquisition efficiency and intensive plant growth (Weemstra et al., 2016). A reduction in either root tissue density (RTD) or root diameter (D) leads to a higher SRA and SRL (Weemstra et al., 2016). Fine roots with larger root D usually live longer (McCormack et al. 2012). RTD is commonly associated with many critical aspects of root lifespan and survival (McCormack et al., 2012; Weemstra et al., 2016). Fine roots with high RTD are expected to live longer and to be more conservative with soil resources (Eissenstat et al., 2000; Reich, 2014). Branching intensity (BI) is a key root functional trait for soil resource acquisition, and the BI of absorptive roots indicates the plasticity of absorptive roots to nutrient patches (Liese et al., 2017). Increased BI is associated with a higher proportion of absorptive root tips per length or mass unit and higher resource uptake capacity (Guo et al., 2008 (b); McCormack et al., 2015). Besides, fine roots, through the exudation of a wide variety of primary and secondary metabolites, may regulate soil microbial community, nutrient cycling, and soil enzyme activity (Jones et al., 2004; Shi et al., 2011; Haichar et al., 2014). Root respiration influences root functions, providing driving force for growth, maintenance, and ion uptake (Högberg et al., 2002; Lambers et al., 2008). Root exudation and respiration significantly contribute to the belowground C dynamics, but how they related to branching fine root system and functional root orders is less well known.

1.4. Variability of fine root traits

Variations in fine root morphological and chemical traits of individual root segments can explain the high variability in exudation and respiration rates within a root system (Rewald et al., 2014; Sun et al., 2021). For example, Sun et al. (2021) found a negative correlation between root morphological conservative trait – RTD – and fine root exudation. A positive correlation was observed between N content and root respiration (Pregitzer et al., 1998). There is also growing evidence that root respiration rate varies with root diameter (Pregitzer et al., 1998; Chen et al., 2010), and it was highest at first-order roots (Jia et al., 2011). Similarly, the root exudation rate increased with decreasing root diameter, reflecting a close relationship between the physiological function of fine roots concerning the shift between root orders (Akatsuki and Makita, 2020). Despite this, the role of the proportion of the functionally different root orders within fine root systems, including absorptive, pioneer, and transport roots, in determining both C-release processes- exudation and respiration- remains relatively unknown.

Global studies reported that fine root traits vary widely along with soil and climatic gradients (Comas et al., 2002; Meier et al., 2020). For example, in warmer soils, FRB increased (Wang et al., 2021) and decreased (Melillo et al., 2011). Oleksyn et al. (1999) found that harsh edaphic environments existing in Northern pine populations stimulated proportional distribution of biomass to fine roots. Soil temperature increased root exudation rate and affected absorptive root morphological traits, resulting in a higher SRA, SRL, and a lower RTD in coniferous tree species (Yin et al., 2013; Parts et al., 2019). Root exudation may respond to soil pH, although past studies have found contradictory results (Meharg and Killham, 1990; Meier et al., 2020). RTD was negatively correlated with soil pH (Freschet et al., 2017). It has been suggested that the root exudation rate depends on atmospheric CO₂ concentration, N availability, and soil moisture conditions (Kuz'yakov, 2002; Phillips et al., 2009; Meier et al., 2020). Fine root respiration rates strongly depended on soil factors, such as temperature, N availability, and moisture (Zogg et al., 1996; Jarvi and Burton, 2013). However, the conflicting results in fine root traits are primarily related to the species identity and plant functional groups. Yet further studies are required to understand how and to what extent soil and climate conditions drive fine root trait responses among various tree species.

Moreover, climatic variations, especially air temperature and precipitation, affect fine root growth and its production patterns interannually and geographically (Pregitzer et al., 2000; Olesinski et al., 2012; Fukuzawa et al., 2013). Several field experiments using interannual variation and latitudinal transects revealed significant relationships between FRP rate and temperature (Pregitzer et al., 2000; Yuan and Chen, 2010; Olesinski et al., 2012). Ruess et al. (1998) suggested that the FRP rate will increase during warmer and drier years. Also, it has been hypothesized that roots grow faster at higher temperatures (Pregitzer et al., 2000). Identifying temporal and spatial patterns of fine root production is essential for generalizing FRP characteristics and its growth dynamics under changing climate.

In addition, fine root production patterns differ among species (Fukuzawa et al., 2013), and considering the role of different plant species on C dynamics in forest ecosystems is necessary.

1.5. Aims of the thesis

The overall objective of this doctoral thesis was to analyze the acclimation strategies of fine roots of different tree species (deciduous vs. coniferous) to changing climate and soil conditions. Comparing deciduous and coniferous trees in fine root trait responses will contribute to a better understanding of the resilience of various forest trees under predicted climate scenarios. We primarily examined a set of fine root functional traits such as biomass, morphological, and physiological traits of trees with some aboveground characteristics, including photosynthesis, transpiration rate, and leaf N concentrations under environmental shifts. We also investigated the relationships between fine root characteristics and various climate and soil factors depending on functional root orders such as absorptive, pioneer, and transport roots.

The specific aims were:

- 1) To analyze the effect of elevated RH and inorganic N forms (NO_3^- , NH_4^+) on fine root C fluxes such as exudation and respiration, morphology, and aboveground traits (photosynthesis, transpiration, and foliar [N]) within and between tree species, including hybrid aspen, silver birch, and Scots pine. We also assessed how differences in proportions of fine root functional groups such as absorptive, pioneer, and transport roots affect fine root C exudation rate (I).
- 2) To investigate the morphological variation of absorptive roots across distance gradient from the ditch in drained peatland forests in Estonia dominated by Downy birch and Norway spruce to identify the most responsive absorptive root morphological traits in acclimation strategies of investigated tree species (II).
- 3) To evaluate the global patterns in the responses of fine root biomass and morphology of trees (deciduous and coniferous) to soil warming. In addition, we assessed the impact of warming magnitude, soil depth, and tree species in our meta-analysis (III).

The main hypotheses were:

- 1) lower transpiration rate limits N uptake, particularly for nitrate-fertilized trees. Elevated RH increases fine root C exudation rate depending on fine root functional distribution.
- 2) The effect of distance from the ditch on absorptive root morphological variation is similar between birch and spruce, which concurs with an increase in the mean SRA and SRL and a decrease in the mean RTD towards far away distances.

2. MATERIAL AND METHODS

2.1. Description of study sites

The measurements of the belowground traits (fine root C exudation and respiration, fine root morphology) and aboveground traits (photosynthesis, transpiration, foliar [N]) were carried out in controlled climate chamber experiments. In this experiment, three different tree species- hybrid aspen (*Populus × wettsteinii* Hämet-Ahti), silver birch (*Betula pendula* Roth.), and Scots pine (*Pinus sylvestris* L.) – were included, which are characterized by different growth potentials, water- and nutrient-use strategy (Publication I).

Morphological variation of the absorptive roots was studied in 6 drained peatland forests with a long drainage history growing on Histosol in the Järvelja experimental forest area in the eastern part of Estonia (Truu et al., 2020). Three stands dominated by Downy birch (*Betula pubescens*), and three stands dominated by Norway spruce (*Picea abies*) were under investigation, and the stands were coded as B1–B3 for birch and S1–S3 for spruce stands (Table 1).

Table 1. Geographical coordinates and means ± standard errors of fine root biomass and soil characteristics of the four sampling plots per each stand (B1–B3, birch stands; S1–S3, spruce stands) and of the three replicate stands per birch and spruce in drained peatland forests (Truu et al., 2020) (Publication II).

Replicate Stands	Geographical coordinates	Fine root biomass (g m ⁻²)	Peat depth (cm)	pH _{-H₂O}	Soil temperature-10cm (°C)	Soil water content-10cm (m ³ m ⁻³)
B1	N 58°18'24,8 E 27°15'23,1	222±33	43±2	4.38±0.05	11.76±0.04	0.21±0.02
B2	N 58°17'21,4 E 27°19'3,2	206±50	87±1	5.68±0.05	12.00±0.21	0.23±0.03
B3	N 58°18'37,0 E 27°21'11,8	251±25	77±3	4.85±0.03	11.86±0.08	0.30±0.06
Means for birch		226±20	69±6	4.97±0.16	11.87±0.07	0.25±0.03
S1	N 58°18'6,3 E 27°16'54,0	242±40	49±2	5.08±0.13	11.68±0.18	0.32±0.03
S2	N 58°17'49,3 E 27°14'53,4	289±71	36±5	4.93±0.30	10.76±0.10	0.24±0.03
S3	N 58°15'14,5 E 27°17'44,2	140±42	65±6	4.04±0.05	11.23±0.07	0.19±0.02
Means for spruce		217±33	51±4	4.63±0.16	11.23±0.12	0.25±0.02

In each stand, a gradient with four sampling plots at distances of 5, 15, 40, and 80 m from the ditch was selected. In one of the spruce stands (S3), the most distant plot from the ditch was at 40 m, and plots at 5 m and 15 m were duplicated toward the next ditch at the same stand (Publication II).

A meta-analysis was performed with 149 paired observations from 43 publications between 1999 and 2020 that investigated fine root biomass and morphology of tree species (deciduous vs. coniferous) to global soil warming experiments across the world's biomes (Publication III).

For all the studied stands in this doctoral thesis, comprehensive background data of the climate variables, stand, and soil characteristics were described more thoroughly in the corresponding publications.

2.2. Controlled climate chamber experiments

The impact of elevated RH and inorganic N sources (NO_3^- , NH_4^+) on above- and belowground parameters of trees (Publication I) were studied on 20 one-year-old micro-propagated hybrid aspen saplings, 20 two-year-old silver birch saplings, and 32 five-year-old Scots pine saplings. Tree saplings were kept in two double-sided Percival AR-95 HIL (Percival Scientific Inc., USA) growth chambers with constant temperature (~ 21.6 °C) and light intensity ($\sim 600\text{--}800$ $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the top of the saplings) for four months (see the publication I for a detailed description).

Two chamber experimental units were conducted for air humidity treatments: 1) moderate (mRH), where the RH was set at 80% and 65% during night and day, respectively. 2) elevated (eRH), where the chamber RH was set at 80% during both night and day. The air RH and temperature were measured with HMP45A sensors (Vaisala, Helsinki, Finland) located at the height of the tree canopies inside the chambers. For N treatments, half of the trees of each species were fertilized with nitrate (NO_3^-), and the other half of the trees were fertilized with ammonium (NH_4^+). The soil surface of the pots was sealed with aluminum foil to prevent soil evaporation. Tree saplings were weighed and watered every morning to compensate for the water loss during transpiration and to maintain the upper limit of the soil water content at 60% of the field capacity. From the pot weight and leaf area data, the whole tree transpiration rate (E , $\text{g m}^{-2} \text{h}^{-1}$) was calculated in the third month of the experiments, when the leaf area of the trees was highest.

2.3. Fine root carbon exudation and respiration measurements

For fine root carbon exudates collection (Publication I) followed by the culture-based cuvette method (Phillips et al., 2008), one branched fine root segment (approximately 10 cm long) that remained attached to the target trees was chosen

for each sapling. The intact root system, including absorptive, transport, and pioneer root tips, was carefully washed with water, and soil particles were removed entirely. Each root sample was placed into a sterile plastic 30 mL syringe tube containing approximately 20 mL of sterile glass beads ($\text{\O} 0.5\text{--}1.25$ mm) and sealed with rubber septum covered with parafilm, with a wedge cut to accommodate the protruding root. C-free nutrient solution (0.5 mM NH_4NO_3 , 0.1 mM KH_2PO_4 , 0.2 mM K_2SO_4 , 0.2 mM MgSO_4 , and 0.3 mM CaCl_2) was added to the syringes to maintain humid conditions. After 24 h stabilization, the root systems were flushed three times with a fresh carbon-free solution to remove soluble C and incubated for the next 24 h with a fresh carbon-free solution. Solutions containing exudates were collected from syringes, kept in 40 mL glass vials with silicon caps, and stored at 4 °C until further measurement of total organic carbon (TOC, mg C l^{-1}), used by a Vario TOC analyzer (Elementar GmbH, Germany). All analyses were done within 24 h after collection. TOC was multiplied by the quantity of the solution, and the exudation rate was calculated by dividing the carbon content by the surface area ($\text{Ex}_{\text{C_area}}$, $\mu\text{g C cm}^{-2} \text{ day}^{-1}$) and the dry mass of fine root segments ($\text{Ex}_{\text{C_mass}}$, $\text{mg C g}^{-1} \text{ day}^{-1}$).

Fine root respiration rates (Publication I) were measured using CIRAS-2 equipped with a conifer cuvette. The fine root samples were rinsed to remove soil particles, and the clean roots were immediately placed into the conifer cuvette. The fine root respiration rates were recorded after ~ 5 min when the readings had stabilized and determined at a constant cuvette temperature (22 °C), external CO_2 concentration (~ 400 ppm), and with a high RH ($> 90\%$) to avoid any dehydration of root samples during respiration measurements. Fine root surface area was measured with WinRHIZO™ Pro (Regent Instruments Inc. 2003) to calculate fine root respiration per unit fine root surface area ($\text{R}_{\text{root_area}}$, $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), and dry weight was used to calculate the per-unit fine root dry mass ($\text{R}_{\text{root_mass}}$, $\mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$).

2.4. Gas exchange, leaf area, and nitrogen measurements of aboveground components

In controlled climate chamber experiments (Publication I), the leaf conductance (g_l) and net photosynthesis (P_{net}) were measured in three fully developed sample leaves per tree for aspen and birch inside growth chambers with a portable gas analyzer CIRAS-2 (PP-Systems, Amesbury, MA) equipped with a standard leaf cuvette in the second month of study. Leaves at higher canopy positions were randomly sampled in aspen and the 3rd, 5th, and 7th leaves from the top of the upper canopy branch were measured in birch. The shoot conductance (g_{shoot}) and P_{net} in one previous and two current year shoots (each bearing ~ 60 needles) of pine trees were measured inside a growth chamber with CIRAS-2 provided with a conifer cuvette. The gas exchange measurements of aspen and birch trees were conducted once in the middle of the experiment. For pine trees, an average of four measurements taken at two-week intervals in the second and third months was

used. In aspen and birch, the daytime gas exchange measurements of leaves were carried out at constant irradiance ($800 \mu\text{mol m}^{-2} \text{s}^{-1}$) using the external light unit of the cuvette. In pine, the external light unit was not used, and the daily measurements were conducted at the sample shoot position inside the growth chamber at an irradiance level $\sim 400 \mu\text{mol m}^{-2} \text{s}^{-1}$. All gas exchange measurements were conducted at a constant temperature ($22 \text{ }^\circ\text{C}$), and external CO_2 concentration ($\sim 400 \text{ ppm}$), and the ambient RH was $\leq 70\%$ inside the cuvette to avoid water vapor condensation in the measuring unit.

For aspen and birch trees, the total leaf area at the end of the experiment was measured with an area meter LI-3100C (LI-COR Biosciences, USA). The projected area of a subsample of 100 needles from previous and current years was measured for Scots pine. The biomass (stem/branches, leaves/needles) was dried separately at $65 \text{ }^\circ\text{C}$ for at least 48 h, and the dry mass was measured. The total needle area was calculated based on the sample needle area and dry mass and the total needle dry mass. The N concentrations of leaves and needles were determined using a Kjeltec Auto 1030 Analyzer (FOSS Tecator AB, Höganäs, Sweden). Specific leaf/needle area (SLA, $\text{m}^2 \text{kg}^{-1}$) was calculated by dividing the leaf/needle area by dry mass (Publication I).

2.5. Fine and absorptive root morphology: sampling and measurements

For absorptive root morphology (publication II), root samples were collected at the end of the growing season (September–October 2018) from the 20 cm deep topsoil layers with a spade at random locations in drained peatland forests in Estonia. We collected five root samples per sampling plot at distances of 5, 15, 40, and 80 m from the ditch. 125 root samples were totally collected from three birch and three spruce stands, packed in plastic bags, transported to the lab, and stored at $4 \text{ }^\circ\text{C}$ until further processing in the lab. Subsequently, five to six approximately 10 cm long fine root segments were removed from each root sample. Tree fine roots were separated from the fine roots of understory vegetation visually according to their morphology and color. Fine root segments of each sample were washed free of soil particles, kept with water in plastic containers, and stored in the freezer ($-18 \text{ }^\circ\text{C}$) until further absorptive root morphological analysis. First- and second-order roots, defined as absorptive roots (Pregitzer et al., 2002; McCormack et al., 2015), were assessed in publication II. Four random subsamples were created from fine root segments of a sample. Absorptive roots of each subsample (about 20–40 tips) were randomly taken from fine root segments and counted under the microscope. In controlled climate chamber experiments (Publication I), fine roots ($< 2\text{mm}$ in diameter) morphology of aspen, birch, and pine trees were analysed. Fine and absorptive roots were washed with tap water and were cleaned with a small soft brush to remove all soil and organic debris (Publication I and II). Fine and absorptive roots of each subsample were placed

in a transparent water-filled tray with minimum overlap and scanned (Publication I and II).

The following characters for fine and absorptive roots were measured with WinRHIZO™ Pro (Regent Instruments Inc. 2003) (Publication I and II): the length (L, cm), surface area (SA, cm²), and mean root diameter (D, mm), and root volume (V, cm³). The root subsamples were oven-dried at 65 °C for 4 hours (for absorptive roots) and 48 hours (for fine roots), and subsequently, the dry weight was measured. Different parameters were calculated: specific root area (SRA= surface area/mass, m² kg⁻¹), specific root length (SRL= length/mass, m g⁻¹), root tissue density (RTD= mass/volume, kg m⁻³), branching intensity per unit of length (BI_L= tips/length, no cm⁻¹) or branching intensity per unit of dry weight (BI_W= tips/dry weight, no mg⁻¹). Additionally, 9 aspen, 10 birch, and all 32 pine tree root samples were divided into absorptive (first and second-order roots), pioneer (long root tips with primary structure as early-stage transport roots), and transport roots (long woody roots), and measured separately with WinRHIZO™ Pro (Publication I). Absorptive (absorb), pioneer (pioneer), and transport (transp) root proportion (%) of total fine root sample area (SA), length (L), and dry weight (DW) were calculated (Publication I).

2.6. Data extraction of soil warming impacts on fine root trait response: a meta-analysis

We searched peer-reviewed publications between 1999 and 2020 that investigated the effect of soil warming on fine root (diameter < 2 mm) trait responses using the Web of Science, Google Scholar, and FRED database (Publication III). The following fine root traits were extracted from each study: fine root biomass (FRB, g m⁻²), and fine root morphological indicators, including diameter (D, mm), specific root length (SRL, m g⁻¹), and specific root area (SRA, m² kg⁻¹). We used the following combination of keywords for our systematic search such as “fine roots biomass”, “fine roots morphology or fine root diameter, or D, specific root length or SRL, and specific root area or SRA”, “soil warming or soil temperature” (Appendix, Publication III). We applied the following criteria to select appropriate publications: only soil warming manipulation (with control and treatment) data were chosen; control and treatment had the same initial conditions and were reported for the same tree species; only publications from studies that reported the warming magnitude as well as the means, the number of sample sizes/replications, and the standard deviations or standard error of fine-root traits were included. Present data were directly compiled from tables or extracted from figures by PLOT DIGITIZER (<http://plotdigitizer.com>) (Wang et al., 2021) from the original publications. We also extracted the studied site information, including continent, latitude (°), longitude (°), mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), the studied biome, tree species (deciduous and coniferous), warming magnitude (°C), and soil depth (cm) from each study (Supplementary data, Publication III).

2.7. Statistical analyses

Statistical analyses were carried out using the STATISTICA 7.1 software (Stat-Soft Inc., Tulsa, Ok, USA) (Publications I, II) and Comprehensive Meta-Analysis (CMA) statistical software, version 3 for the meta-analysis study (Publication III). The statistical significance level was accepted as $p < 0.05$ for all the analyses. The normality of the variable distribution was verified using the Shapiro–Wilk, and Kolmogorov–Smirnov tests. Fine root C exudation rates per root area were log-transformed, and the homogeneity of variance was tested using F and Levene tests and for the C exudation between species and treatments, Kruskal–Wallis multiple comparison analysis was used (Publication I). In publications I and II, one-way analysis of variance (ANOVA), followed by Tukey’s HSD, were used to determine the effects of air humidity on fine root exudation, respiration, morphological traits, and aboveground measurements within and between tree species (I), also the impacts of distance from the ditch, replicate forest stands and tree species on absorptive root morphological traits (II). A correlation matrix (Pearson’s r ; $p < 0.05$) was constructed in publication II to observe the correlations between the stand and soil characteristics and between absorptive root morphological traits and stand and soil properties. Multiple stepwise regression analysis was used to determine which soil and root-related properties influenced the absorptive root morphology of the trees (II). In publications I and II, linear regression analyses were used to determine the relationship between root C exudation rates and fine root morphology (I), and the relationship between absorptive root morphological traits and the significant factors of the stand and soil characteristics (II). Generalized linear models (GLM: Type III SS) were used to assess the effects of tree species, RH and N treatments, and the proportional distribution of absorptive, pioneer, and transport roots within fine roots on C exudation rates (I). The same GLM was applied to assess the impact of forest stand and distance from the ditch on absorptive root morphological traits in tree species (II).

Redundancy analysis (RDA) (CANOCO program; ter Braak and Smilauer, 2002) was used in publication I to detect the relationships between fine root morphological characteristics, including C exudation, and the proportional length, surface area, and mass of absorptive, pioneer, and transport roots; tree species, RH, and N source as descriptive factors. Partial canonical analysis was performed to assess the effect of each explanatory data set (Legendre and Legendre, 1998) (I). The significance of the RDA results was tested with a permutation test (Monte Carlo test (999); $P < 0.01$) (I). In publication II, RDA was applied to describe relationships between absorptive root morphological traits, tree species, forest stands, sampling plots, stands, and soil characteristics.

The meta-analysis (Publication III) was conducted by calculating the effect size for each study using the standardized mean differences method and determining the sum of the effect sizes. I^2 was calculated for quantifying inconsistency (Higgins and Thompson, 2002):

$$I^2 = \left(\frac{Q - df}{Q} \right) \times 100\%$$

Q is the chi-squared statistic used to assess the statistical heterogeneity in the meta-analyses, and df indicates its degrees of freedom (Higgins and Thompson, 2002). If the I^2 index was insignificant, the fixed effects model was used. Sensitivity analysis was used to detect unfitting effect sizes in the meta-analysis; if outliers and extreme effects were identified and removed, the analysis was repeated. In this meta-analysis, a statistical index (classic fail-safe N) was used to investigate the publication bias. If the publication bias was detected and non-significant findings were reported, the results of that study were not included in the meta-analysis (if there is no publication bias, the graph is symmetrical, and the amount of scatter around the intervention effect size decreases with increasing sample size). Tree species (deciduous and coniferous) were considered the discrete moderator variable, and soil depth and warming magnitude were used as continuous moderator variables for the meta-regression model. Data compiled for meta-analysis were taken from either experimental warming or natural gradients; thus, the impact of geographic regions was not considered for further statistical analyses.

3. RESULTS AND DISCUSSION

3.1. Experimental air humidity and nitrogen source impacts on above- and belowground traits

In the controlled climate chamber experiment (Publication I), the eRH significantly decreased the transpiration flux (E) in all tree species, such as aspen, birch, and pine (Figure 1, D and Table 2 in I). The cause of this reduced transpiration rate is due to the reduced driving force for transpiration at elevated RH, which affects plant growth and productivity (Tegeader and Masclaux-Daubresse, 2018). Nevertheless, increasing RH might also lead to an increase in leaf or canopy conductance, and to a consequent rise in the transpiration rate, which has been shown earlier in birch (Kupper et al., 2017). However, a higher leaf and shoot conductance in aspen and pine under elevated RH did not increase the transpiration rate in our study (Table 2, I). The soil nitrogen source affected the E, and this effect was species-specific. In birch, the E was higher in nitrate-fertilized trees than in ammonium-fertilized trees (Table 2, Figure 2a, in I). The possible reasons arise rather from the increased mobility of NO_3^- than NH_4^+ in soil solution, leading to a high NO_3^- mass flow under a higher transpiration flux (Cramer et al., 2009). Evidence also showed that nitrate sources enhanced aquaporin expression in root cells leading to a higher water flux (Gao et al., 2018). Similarly, a previous study in birch saplings revealed higher whole tree and root system conductance in nitrate-fertilized trees (Kupper et al., 2020). Also, foliar N concentrations were significantly lower at eRH than at mRH in birch (Figure 1, F), and this was evident only in nitrate-fertilized trees (Figure 2b, I). Our results indicate that E did not affect the uptake of NH_4^+ since the two humidity treatments revealed similar foliar N concentrations (Figure 2b, I). However, we observed that the uptake of NH_4^+ is more favored than NO_3^- at higher air humidity when the E is limited. The air humidity treatments significantly affected P_{net} in pine only (Figure 1, C), whereas greater net photosynthesis was found at eRH than mRH. This higher photosynthesis at higher air humidity is probably linked to a twofold increase in g_{shoot} of pine at eRH (Table 2, I), resulting in increased CO_2 diffusion to the chloroplast and metabolic constraints. Increased stomatal and mesophyll resistance are the leading cause of decreased CO_2 diffusion from the atmosphere to the site of carboxylation and reduced photosynthesis under water limitation (Grassi and Magnani, 2005; Chaves et al., 2009). However, photosynthetic capacity varies among species (Hikosaka and Shigeno, 2009). It has been shown that in evergreen conifers, the share of mesophyll resistance in the total resistance of CO_2 diffusion is higher than in deciduous tree species (Tomás et al., 2013). Moreover, in pine trees, the total biomass increased at eRH coincided with a two-fold lower C exudation rate (Table 1 in I), implying faster growth due to increased photosynthetic assimilation of CO_2 at higher humidity. While in deciduous trees (e.g., aspen and birch), the air humidity did not affect the P_{net} (Figure 1, C).

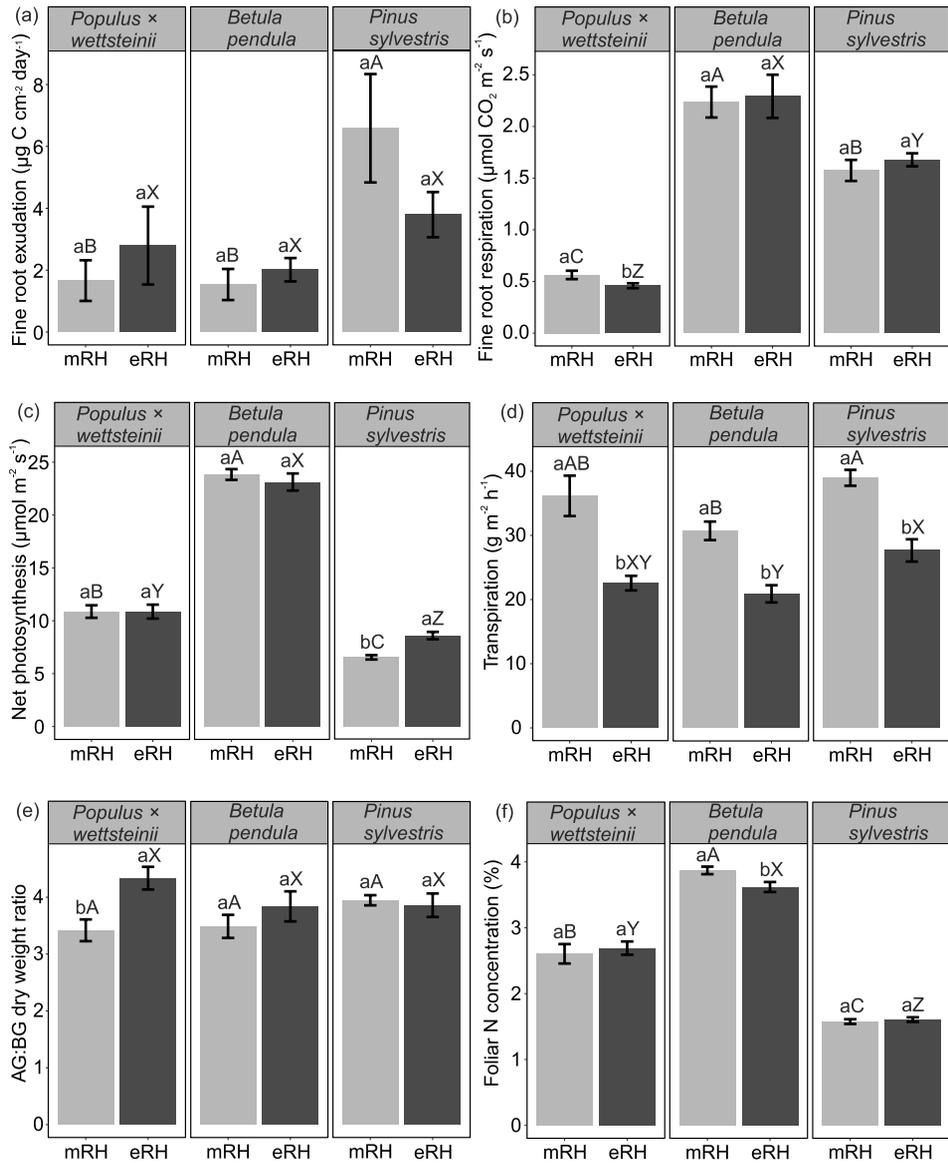


Figure 1. Average \pm standard error of fine root carbon exudation rate per fine root surface area (a); fine root respiration rate per fine root surface area (b); net photosynthesis rate (c); transpiration rate (d); above: belowground biomass dry weight ratio (e) and leaf or needle [N] (f) of *Populus* \times *wettsteinii*, *Betula pendula* and *Pinus sylvestris*. Lower case letters indicate the species-specific effects between air humidity treatments. Capital letters “ABC” indicate the differences between species at moderate relative air humidity (mRH), and capital letters “XYZ” indicate the differences between species at elevated relative air humidity (eRH) ($P < 0.05$).

However, in aspen, the g_i increased at eRH, and the overall highest P_{net} found in birch was related to the higher foliar N concentrations and leaf conductance (Table 2, I). Elevated RH increased specific leaf area (SLA) in deciduous trees (e.g., aspen and birch), while soil NH_4^+ fertilization increased SLA in pine saplings (Table 2, I). A previous study revealed that birch saplings acclimated to humidification through adjustment in aboveground morphology, including a rise in SLA, to maintain tree growth under diminished mineral nutrition and photosynthesis (Sellin et al., 2015). Also, the plastic response of specific leaf area to nitrogen fertilization indicated previously coupled up with leaf functional traits (Sun et al., 2022).

It has been shown that nutrient deficiency (Neumann and Romheld, 2000), rates of C assimilation (Hill et al. 2007), and increased soil and air temperature (Yin et al., 2013; Yang et al., 2020) may increase C exudation. While in our study, neither changes in air humidity nor differences in the soil N source increased the C exudation in all investigated tree species, which indicates sufficient resource uptake for trees. However, at the eRH treatment, we observed a decreased C exudation in pine and a weak tendency of enhanced exudation in aspen and birch (Figure 1A, Table 1 in I). Enhanced root exudation is a typical response for plants exposed to stress conditions (Karst et al., 2017). Stress-induced C exudation may alter soil microbial communities and fertility, positively affecting plant growth and survival (Yin et al., 2014). Moreover, many exogenous factors were shown to influence root respiration rates. For example, fine root respiration is highly sensitive to soil water availability, temperature (Zogg et al., 1996; Jarvi and Burton, 2013), soil fertility (Li et al., 2017), and atmospheric CO_2 concentration (Clinton and Vose, 1999). In our study, fine root respiration rates were affected by air humidity treatments which were only evident in aspen; lower respiration was found at eRH than at mRH (Figure 1B, Table 1 in I). We revealed that below-ground carbon fluxes had some species-specificity, varying highly between deciduous and coniferous species. One explanation for species differences in the rate of C fluxes observed in our study may be related to differences in species strategies for responding to environmental shifts. In present study, pine had the highest fine root C exudation, while birch had the highest fine root respiration rates (Figures 1, A, and B). Correspondingly, several studies revealed that deciduous trees had much higher respiration rates than coniferous species (Reich et al., 1998; Han and Zhu, 2021).

3.2. Air humidity impact on fine root morphological acclimation and functional distribution

Air humidity treatment caused a species-specific response in the fine root morphological traits of studied trees. At higher RH, the mean SRA increased in birch, while it decreased in pine, due to significantly lower RTD in birch and higher root D in pine at eRH (Table 1, I). Similar to our findings, free air humidity manipulation experiments (FAHM) revealed the longer and thinner fine roots with

higher SRA of birch in response to the rise in air humidity, indicating fine root morphological adjustments to enhance resource acquisition (Parts et al., 2013). Variations in fine root morphological traits may affect the belowground C fluxes (Sun et al., 2021). The present study observed a positive correlation between SRA and SRL of deciduous trees and the C exudation rate at eRH. The higher SRA and SRL increase the root-soil connections, corresponding to the increase in the average C exudation rate (Tüchmantel et al., 2017). Besides, we found that the lower SRA and SRL of pine coincided with the lower C exudation rates. Previous studies reported that fine roots with lower RTD exude more intensively because of higher shares of younger and metabolically active fine roots (Akatsuki and Makita, 2020). Indeed, the functional distribution of fine roots and the proportion of different root orders, such as absorptive, pioneer, and transport roots in a fine root system, affect the C-release processes, such as exudation and respiration rates. At the same time, the C exudation flux has been so far measured as a sum of exuded C from all three functional root orders, including absorptive, pioneer, and transport roots (Phillips et al., 2008). Our results indicated that the amount of fine root C exudation depended on different proportions of functional root orders. For example, the higher amount of C released by actively growing pioneer roots since the greater Ex_{C_mass} was linked to a higher share of pioneer roots (Figure 2). A seasonal trend in C exudation flux previously found, indicating more significant fluxes in early summer and mid-autumn corresponded with the fine root C allocation pattern (Pritchard et al., 2008). The higher shares of pioneer and absorptive roots were reported in beech and spruce during early and late summer (Nikolova et al., 2020). Evidence also showed a positive correlation between root respiration rate and root diameter (Pregitzer et al., 1998; Chen et al., 2010), reflecting a close connection between fine root functional distribution and its metabolic activity. The respiration rate was higher in absorptive than transport roots (Trocha et al., 2017).

Our results indicated that the functional distribution of fine roots adjusted in a species-specific manner varied among deciduous and coniferous species. We observed a higher proportion of pioneer and transport roots in aspen and pine trees, respectively (Figure 2), corresponding with previous research (Nikolova et al., 2020). Beyond the effect of tree species on C-release fluxes, in the present study, a considerable variation in fine root C exudation and morphological traits was explained by the functional distribution of absorptive, pioneer, and transport roots. However, shifts in climatic conditions can remarkably affect this functional distribution of fine roots. Across a latitudinal gradient, the proportional biomass of absorptive roots of deciduous and coniferous species increased towards the northern boreal forest (Ostonen et al., 2017). Therefore, we can assume that differences in the functional distribution of different fine root orders can cause the observed variability in the C exudation rate of diverse forest ecosystems. In our controlled climate chamber experiment (Publication I), the tree saplings were grown at different humidity and soil fertilization treatments, which could affect the fine root functional distribution and their morphological traits, leading to variation in C exudation fluxes. Nevertheless, the proportion of functionally different root orders

of trees measured in this lab experiment was comparable to those reported in natural forest conditions, implying the applicability of lab-measured fine root C exudation rates for estimating total belowground forest C budgets. However, species-specific exudation rates exist in different fine root orders responding to environmental shifts.

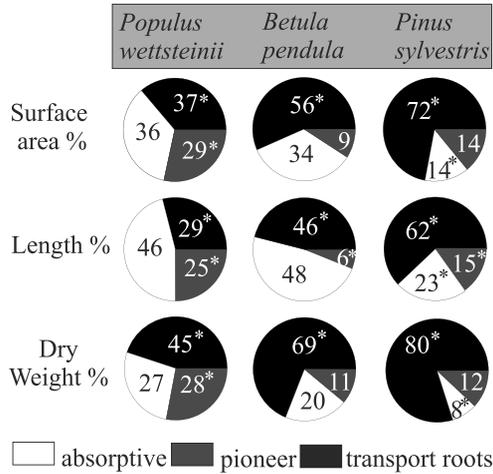


Figure 2. Pie charts showing the distribution of absorptive, pioneer, and transport roots within fine root samples (%) for *Populus wettsteinii*, *Betula pendula*, and *Pinus sylvestris*. The first row shows the distribution of functional groups per surface area, the second for length, and the third for dry mass. Asterisks denote significant differences within one functional group (per surface area, length, or dry mass, respectively) between the tree species ($P < 0.05$).

3.3. Absorptive root morphological acclimation of trees associated with ditch distance

In studied drained peatland forests, different tree species (i.e., deciduous vs. coniferous) exhibited different absorptive root morphology (Table 2), which determine the contrasting nutrient foraging strategies among tree species (Liu et al., 2015; Yang et al., 2021). Similar to the earlier study performed in the alkaline soils (Ostonen et al., 2006), our study at peatland forests with organic soils showed that the mean absorptive root D and RTD were lower in birch than those in spruce, which led to a higher mean SRA and SRL in birch than spruce (Table 2, Table S1 in II). BI_L and BI_w were 2 and 3 times higher in birch than spruce, respectively (Table 2). However, the mean SRA and SRL of birch studied in drained peat soils were lower than those previously measured in alkaline soils, but the similar values of spruce did not differ between alkaline and organic soils (Ostonen et al., 2006).

Distance from the ditch affected absorptive root morphological traits, such as mean SRA and SRL, in a similar direction in both tree species (Table 2). From a distance of 5 to 80 m from the ditch, mean SRA increased by about 10 and 5% in

birch and spruce, respectively; the mean RTD reduced by about 10% in both trees (Table 2). This uniform response found among birch, and spruce contradicts several reported species-specific root morphological responses to adverse soil conditions (Zhou et al., 2019; Lozano et al., 2020). However, consistent root morphological responses among several grassland species to wind intensity were also found (Werger et al., 2020).

In this study, shifts in absorptive root morphological traits, including SRA and RTD, can reflect shifts in nutrient foraging and the morphological adjustments of absorptive roots to the local soil condition along with different distances from the ditch. An increase in SRA and a decrease in RTD towards spatially higher distances from the ditch highlights the more efficient acquisition of soil resources. Increasing absorptive surface area per unit mass is linked to more root resource uptake efficiency (Weemstra et al., 2016). We also observed that FRB per stand basal area at the spruce stands tended to be lower at nearer distances to the ditch highlighting the more advanced foraging efficiency close to the ditch than far away distances (Figure 3B). This is because fewer roots in the belowground supported the same basal area unit in the aboveground at near distances to the ditch. However, the soil physical and chemical properties in drained peatland forests were not dependent on the distance gradient from the ditch (Table 1). For example, a similar soil water content was observed along with distances from the ditch ranging from 0.22 to 0.27 m³ m⁻³ from plot 5 to plot 80, respectively (Figure S2 in II). This is in contrast with previous studies that showed specific soil properties depending on the distance gradient from the ditch; poor soil properties were found towards higher distances from the ditch (Miina, 1994; Roy et al., 2000). A higher water table level at sites located far from the ditch leads to less aeration of the substrate and a lower decomposition rate of organic matter resulting in limited soil resources (Miina, 1994). However, several studies mentioned the effects of other factors than ditch distances on peat soil hydrology, such as topography, vegetation characteristics, tree stands, meteorological conditions, and peat hydraulic properties (Young et al., 1997; Leppä et al., 2020). Previous studies showed that ditch distance led to an apparent change in soil microbial communities (Fang et al., 2017; Truu et al., 2020). For example, Qiu et al. (2013) mentioned that the soil fungal communities were more diverse at a 5-m distance with relatively good drainage conditions than those at other distances with relatively poor drainage conditions. Changes in the root-associated mycorrhizal fungi may be related to changes in their growing environment. According to previous studies, ECM fungi contribute substantially to soil nutrient availability, and exhibit contrasting foraging strategies with varying enzyme activities, nutrient uptake capacities (Pritsch and Garbaye, 2011; Tedersoo et al., 2012). Therefore, considering the roots and the root-associated microbial acclimation particularly ECM fungi in peat soils would help better to identify tree growth responses and peatland forest functioning.

Table 2. Means \pm standard errors of absorptive root morphological traits of the three replicate stands per sampling plot at the distances of 5, 15, 40, and 80 m from the ditch and of the four sampling plots per birch and spruce. D – diameter (mm), L – length (mm), W – dry weight (mg), BL – branching intensity per length (cm^{-1}), BL_w – branching intensity per mass (mg^{-1}), SRA – specific root area ($\text{m}^2 \text{kg}^{-1}$), SRL – specific root length (m g^{-1}), and RTD – root tissue density (kg m^{-3}). Small letters indicate a statistically significant difference (one-way ANOVA, followed by Tukey's HSD; $p < 0.05$) of the mean absorptive root morphological traits between four sampling plots within birch and spruce. Capital letters denote a statistically significant difference (one-way ANOVA, followed by Tukey's HSD; $p < 0.05$) of the mean absorptive root morphological traits of four sampling plots between birch and spruce.

Root Traits	Stands	Sampling plots at distances from the ditch (m)				Means of Plots
		5	15	40	80	
D (mm)	Birch	0.227 \pm 0.013	0.231 \pm 0.012	0.221 \pm 0.003	0.229 \pm 0.011	0.227 \pm 0.002 ^B
	Spruce	0.278 \pm 0.007 ^{ab}	0.265 \pm 0.004 ^c	0.272 \pm 0.005 ^{abc}	0.281 \pm 0.009 ^{ab}	0.274 \pm 0.003 ^A
L (mm)	Birch	1.12 \pm 0.14 ^{abc}	1.27 \pm 0.09 ^a	1.01 \pm 0.19 ^c	1.16 \pm 0.13 ^{abc}	1.14 \pm 0.05 ^B
	Spruce	1.90 \pm 0.06	1.82 \pm 0.07	1.86 \pm 0.07	1.78 \pm 0.02	1.84 \pm 0.02 ^A
W (mg)	Birch	0.0124 \pm 0.0035 ^{abc}	0.0141 \pm 0.0026 ^a	0.0105 \pm 0.0025 ^c	0.0123 \pm 0.0027 ^{abc}	0.0124 \pm 0.0007 ^B
	Spruce	0.0339 \pm 0.0021 ^a	0.0301 \pm 0.0012 ^c	0.0324 \pm 0.0020 ^{abc}	0.0305 \pm 0.0016 ^{abc}	0.0317 \pm 0.0009 ^A
BL (cm^{-1})	Birch	9.58 \pm 1.10 ^{bc}	8.45 \pm 0.67 ^{bc}	11.26 \pm 1.90 ^a	9.40 \pm 1.15 ^{bc}	9.67 \pm 0.58 ^A
	Spruce	5.44 \pm 0.12	5.60 \pm 0.23	5.53 \pm 0.23	5.73 \pm 0.03	5.58 \pm 0.06 ^B
BL _w (mg^{-1})	Birch	99.0 \pm 22.9 ^{abc}	82.2 \pm 15.4 ^c	121.4 \pm 24.6 ^{ab}	106.3 \pm 26.8 ^{ab}	102.2 \pm 8.1 ^A
	Spruce	31.1 \pm 1.6 ^c	34.3 \pm 1.4 ^a	32.5 \pm 2.3 ^{abc}	34.6 \pm 1.6 ^{abc}	33.1 \pm 0.8 ^B
SRA ($\text{m}^2 \text{kg}^{-1}$)	Birch	69 \pm 6 ^{abc}	68 \pm 4 ^c	71 \pm 4 ^{abc}	75 \pm 6 ^a	71 \pm 2 ^A
	Spruce	50 \pm 1 ^{bc}	51 \pm 1 ^{abc}	50 \pm 1 ^{bc}	53 \pm 2 ^a	51 \pm 1 ^B
SRL (m g^{-1})	Birch	100 \pm 14 ^{abc}	95 \pm 11 ^c	105 \pm 4 ^{abc}	108 \pm 14 ^a	103 \pm 3 ^A
	Spruce	57 \pm 2 ^c	62 \pm 1 ^a	59 \pm 2 ^{abc}	60 \pm 3 ^{abc}	59 \pm 1 ^B
RTD (kg m^{-3})	Birch	262 \pm 11 ^{ab}	262 \pm 4 ^{ab}	264 \pm 17 ^{ab}	242 \pm 10 ^c	258 \pm 5 ^B
	Spruce	295 \pm 6 ^{ab}	300 \pm 7 ^{ab}	300 \pm 4 ^{ab}	276 \pm 1 ^c	293 \pm 6 ^A

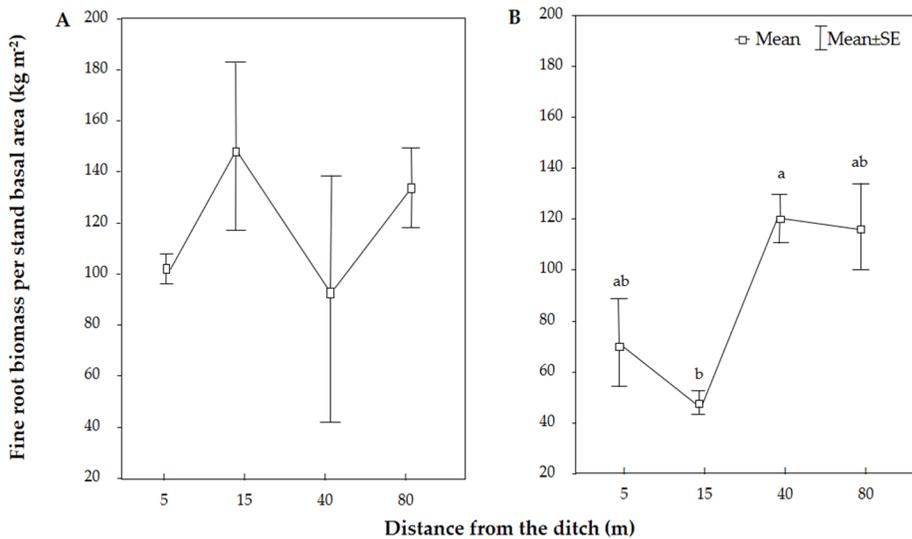


Figure 3. Means of the fine root biomass per stand basal area (FRB/BA, kg m⁻²) with the standard error bars of three replicate stands per sampling plot at the distances of 5, 15, 40, and 80 m from the ditch in Downy birch (A) and Norway spruce (B). Small letters indicate a statistically significant difference (one-way ANOVA, followed by Tukey's HSD; $p < 0.05$) of the mean spruce FRB/BA between four sampling plots.

3.4. Absorptive root morphology in relation to stand and soil properties

According to redundancy analysis, absorptive root morphological parameters correlated significantly with tree species, forest stands (B1 and S2), sampling plots located at 15 and 80 m distances from the ditch, stand density, BA, FRB, soil N and P concentration, and soil water content (Figure 4). Altogether, these factors accounted for 65.4% of the total variation in morphological traits (Figure 4A).

Soil physical and chemical properties, such as peat depth, pH, and temperature, significantly affected trees' absorptive root morphological traits, and this effect was species-specific (Figure 5). Similar to our findings, previous studies showed that the impact of soil conditions on absorptive root morphology varies among plant species (Lozano et al., 2020). In addition to soil factors, forest stand affected the variation of absorptive root morphological traits, including L , BI_L , and RTD only in birch (Table S3 in II). Peat depth in birch stands varied from 43 cm at B1 to 57 cm at B2 stand, negatively affecting the mean RTD of birch stands (Figure 5A). In spruce, absorptive roots were thinner and had higher RTD in the most acidic soils (Figures 5 B, and C). Since soil pH is negatively correlated with peat depth in spruce stands (Table S2 in II), we assume that the peat layer is becoming more profound in more acidic soils, leading to a lower decomposition rate and limited nutrient availability.

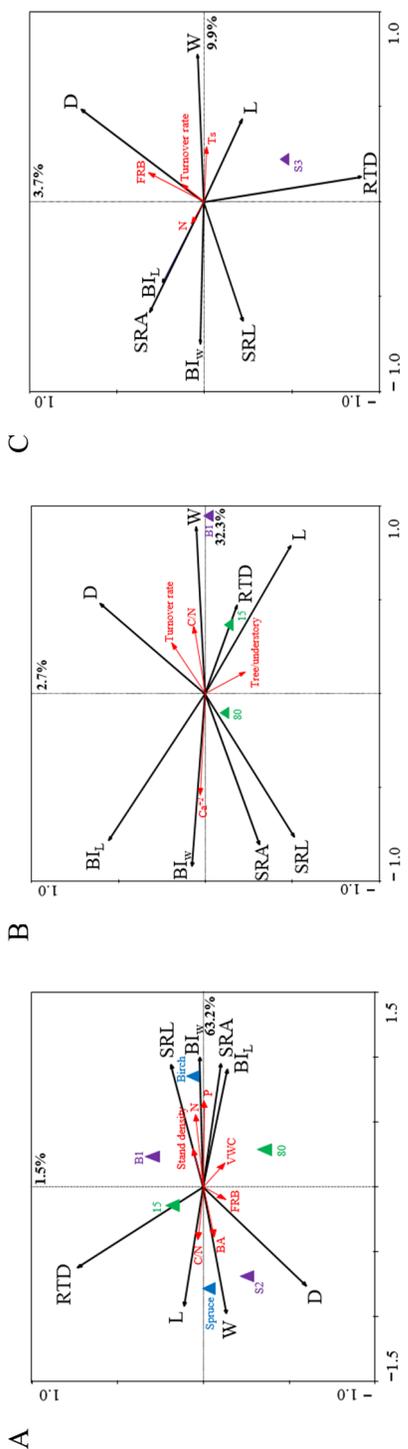


Figure 4. The ordination biplot is based on redundancy analysis (RDA, manual forward selection) of absorptive root morphological traits, including D – diameter (mm), L – length (mm), W – dry weight (mg), BI_L – branching intensity per length (cm⁻¹), BI_W – branching intensity per mass (mg⁻¹), SRA – specific root area (m² kg⁻¹), SRL – specific root length (m g⁻¹), and RTD – root tissue density (kg m⁻³) (black arrows) for both studied tree species, Downy birch, and Norway spruce (A), and separately for birch (B) and spruce (C). In all figures, absorptive root morphological traits were shown in relation to the tree species (blue triangles), forest stands (purple triangles), and studied stand and soil characteristics (red arrows). The relative eigenvalues of axis 1 and axis 2 were 63.2% and 1.5%, respectively, and in total, the model described 65.4% of the variation in absorptive root traits (Figure 1A, $p < 0.05$).

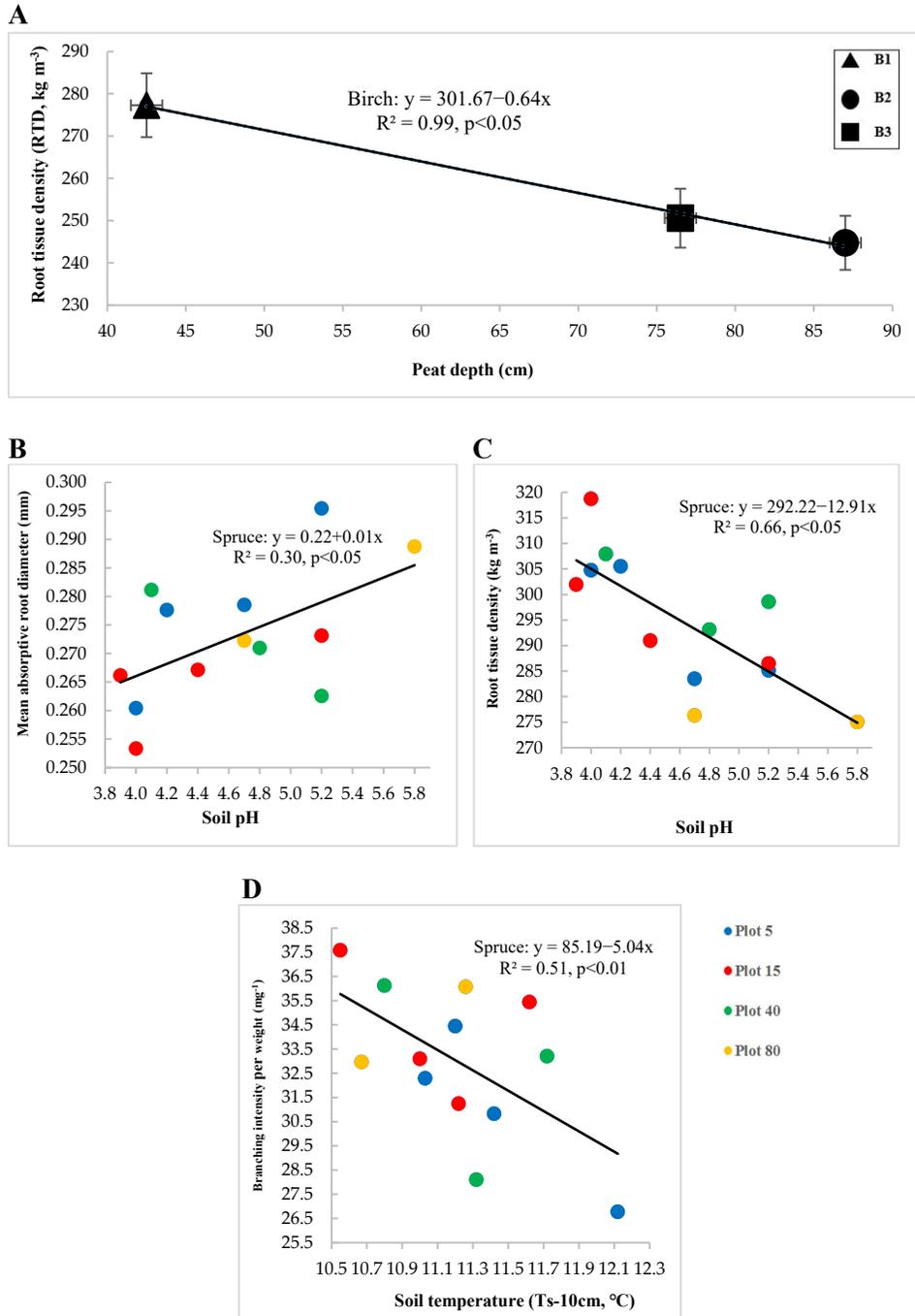


Figure 5. Relationships between absorptive root morphological traits of studied stands in birch (A) and all sampling plots (5, 15, 40, and 80) in spruce with the soil characteristics (B–D). The soil temperature was measured from a depth of 10 cm.

Therefore, the thinner absorptive roots with high RTD in acidic soils could be linked to a higher resource acquisition efficiency aligning with an earlier study (Doi et al., 2020). Soil temperature in spruce stands significantly affected root branching intensity: in warmer soils, less-branched absorptive roots were evident (Figure 5D). Correspondingly, it has been revealed that soil warming reduced the root branching intensity of spruce (Parts et al., 2019). We assume that the mineralization rates and nutrient availability are reduced in less warm soils; thus, the high BI can support the rapid and extensive proliferation to enhance nutrient uptake (Liese et al., 2017).

3.5. The impact of soil warming on fine root biomass and morphology: a meta-analysis

Present meta-analysis (III) revealed an increase in FRB with increased soil warming ($p=0.001$, Figure 6), which was consistent with previous studies (Wang et al., 2021; Lin et al., 2010). This may be attributable to the photosynthesis stimulation and extension of growing season at higher temperatures, enhanced fine root growth (Malhotra et al., 2020). However, our results showed that with increasing warming magnitude the effect size for FRB significantly decreased ($p=0.00$, Table 3), which can be due to an increase in root mortality at elevated temperatures as suggested previously (Wang et al., 2021).

In contrast to FRB, fine root morphological traits such as SRL, SRA, and D were unresponsive to soil warming in the current meta-analysis (Figure 6, Table 3). This result is in contradiction with previous studies that found fine root morphological shifts as a consequence of soil warming (Björk et al., 2007; Parts et al., 2019). Besides, we suggest that different responses of fine root traits to warming could have been affected by the limited sample size used for morphological traits (SRL, $n=12$; SRA, $n=6$; D, $n=5$), compared to FRB observations ($n=42$).

At the tree species level, the effect of soil warming and depth on FRB differed significantly between deciduous and coniferous species (Figure 6, Table 3). Our finding aligns with previously reported species-specific root morphological responses to adverse soil conditions (Lozano et al., 2020; Förster et al., 2021). Also, the heterogeneity of fine root responses to soil warming changes at a global scale may be the result of the interactions of different experimental factors and climatic conditions. Soil depth affected fine root morphological traits, including SRA and D, and warming effects on SRA and D increased in deeper soil horizons (Table 3). In this regard, we propose that warming magnitude and soil depth probably interact with each other to impact fine root traits, and such interactions may vary with other soil environmental factors (e.g., moisture, acidity, and soil structure) and tree species. For example, deciduous trees (e.g., beech stand) produced higher SRA and SRL, enhanced resource uptake in the organic layer than in the mineral soils (Kirfel et al., 2019), while coniferous trees (e.g., pine stand) exhibited similar fine root morphology in both soil layers (Försetr et al., 2021).

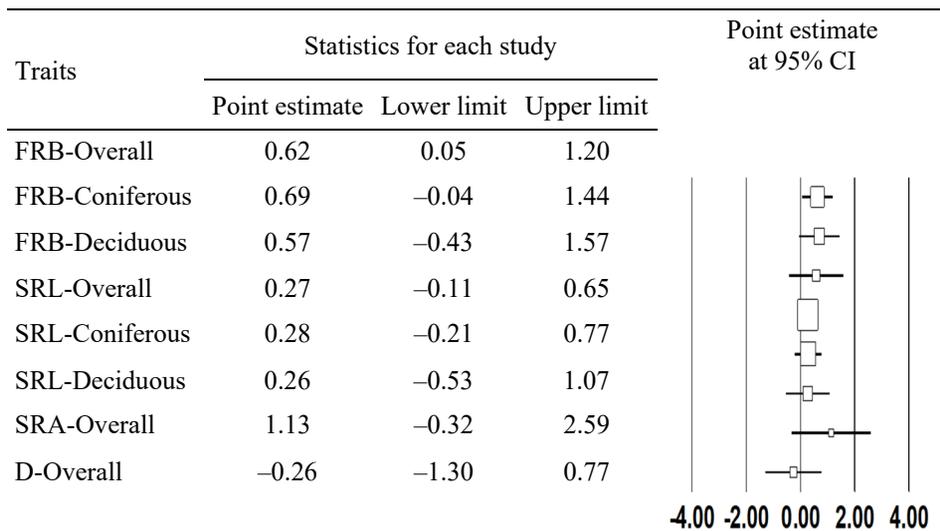


Figure 6. Effect sizes of fine root traits, including fine root biomass (FRB), and fine root morphological traits such as specific root length (SRL), specific root area (SRA), and diameter (D) of coniferous and deciduous trees to soil warming. Error bars represent 95% confidence intervals (CI). The central vertical line shows an effect size of zero. The effect of soil warming on fine root traits was considered significant if the 95% CI of effect size for a variable did not overlap zero.

Table 3. Summary of the Meta-regression model, P values <0.05 are significant.

Fine root traits	Moderator variables	Tree species	Covariate	Coefficient	Standard Error	95% Lower	95% Upper	Z-value	Two-tailed P-value	R ²
	Warming magnitude	Overall	Intercept	2.13	0.581	0.99	3.27	3.67	0.00	0.28
			Warming magnitude	-0.53	0.178	-0.87	-0.18	-2.99	0.00	
	Warming magnitude	Coniferous	Intercept	3.21	0.796	1.64	4.77	4.03	0.00	0.56
			Warming magnitude	-0.84	0.235	-1.30	-0.38	-3.59	0.00	
FRB		Deciduous	Intercept	1.02	0.733	-0.41	2.46	1.40	0.16	0.01
			Warming magnitude	-0.11	0.255	-0.61	0.38	-0.44	0.66	
		Overall	Intercept	-0.00	0.58	-1.16	1.14	-0.01	0.98	0.07
			Soil depth	0.05	0.04	-0.02	0.13	1.38	0.16	
	Soil depth	Coniferous	Intercept	0.21	0.96	-1.67	2.10	0.22	0.82	0.08
			Soil depth	0.05	0.05	-0.06	0.16	0.85	0.39	
		Deciduous	Intercept	-0.34	0.93	-2.18	1.49	-0.37	0.71	0.20
			Soil depth	0.12	0.09	-0.06	0.32	1.28	0.20	
SRA	Warming magnitude	Overall	Intercept	-1.06	1.78	-4.55	2.42	-0.60	0.54	0.42
			Warming magnitude	0.73	0.46	-0.18	1.64	1.57	0.11	
	Soil depth		Intercept	-1.03	1.36	-3.70	1.63	-0.76	0.44	0.65
			Soil depth	0.14	0.07	0.00	0.29	1.99	0.04	
SRL	Warming magnitude	Overall	Intercept	-1.06	1.78	-4.55	2.42	-0.60	0.54	0.42
			Warming magnitude	0.73	0.46	-0.18	1.64	1.57	0.11	
	Soil depth		Intercept	-1.03	1.36	-3.70	1.63	-0.76	0.44	0.65
			Soil depth	0.14	0.07	0.00	0.29	1.99	0.04	
D	Warming magnitude	Overall	Intercept	0.49	0.51	-0.52	1.50	0.95	0.34	1.00
			Warming magnitude	-0.13	0.06	-0.25	-0.00	-2.06	0.03	
	Soil depth		Intercept	-2.82	0.95	-4.68	-0.95	-2.97	0.00	1.00
			Soil depth	0.16	0.05	0.04	0.27	2.77	0.00	

4. CONCLUSIONS

This thesis demonstrates how different climate- and soil-change factors affect fine root functional traits of deciduous (e.g., silver birch, Downy birch, and Hybrid aspen) and coniferous (e.g., Scots pine and Norway spruce) tree species to identify the most plastic fine root traits in response to environmental change for both species. The focus of this study was on trees' belowground traits including fine root biomass, morphological acclimation, C flux variability associated with fine root functional distribution responding environmental shifts.

Deciduous and coniferous tree species responded to the different environmental factors through alterations in a number of fine root traits, and their acclimation responses were largely species-specific.

In response to increased RH, transpiration rate was reduced in all studied tree species, potentially hindering the nutrient acquisition by mass flow. The transpiration rate also depended on the prevailing soil N source in birch, in which water flux was higher in nitrate-fertilized soils than in ammonium-fertilized soils. The foliar N concentration of nitrate-fertilized birch trees was lower at eRH than mRH, while it was similar between air humidity treatments for ammonium-fertilized trees. This finding suggests that in deciduous trees (e.g., silver birch), the reduced transpiration flux due to elevated RH decreases nitrate uptake more than ammonium acquisition, this was in agreement with our hypothesis. The higher RH affected fine root C fluxes, decreased fine root mass-specific exudation rate in pine, and decreased fine root respiration in aspen, which contradicted our hypothesis, stating that elevated air humidity increases fine root C exudation and respiration. Although exudation rates in birch and aspen tended to be higher at eRH compared to mRH, but the increased pattern remained insignificant. Soil N treatment did not significantly affect fine root carbon processes such as exudation and respiration rates in any of the studied trees. Moreover, any significant relationship between fine root C exudation and the leaf net photosynthesis rate was not observed. We showed that functionally different fine root proportions, such as absorptive, pioneer, and transport roots, determined the C exudation rate and fine root morphological traits, supporting our hypothesis. However, species differed in the C exudation rates and morphology, suggesting a species-specific response to environmental change. The eRH significantly increased the proportion of absorptive roots in deciduous trees (aspen and birch), corresponding to a higher SRA, SRL, and increased C exudation rate, in contrast to coniferous trees (pine).

In this work, fine and absorptive root morphology was highly plastic to environmental changes. Increased air humidity caused contrasting shifts in fine root morphology for birch and pine. Contrasting root morphology among species may exhibit distinctive acclimation processes and nutrient-foraging strategies of trees. The increase in SRA in birch was due to a decrease in RTD, while thicker fine roots drove a decline in SRA in pine at eRH. At drained peatland forests, similarly, absorptive root morphological traits differed between tree species, birch absorptive roots were significantly thinner, and had a higher SRA, SRL, and BI with a lower RTD compared to those of spruce absorptive roots. However, in this work, the overall morphological reaction of absorptive roots to a distance gradient

from the ditch at drained peat soils was uniform between species. Irrespective of tree species, SRA increased while RTD decreased toward higher ditch distances, indicating an acclimation in absorptive roots to the local soil properties at different distances from the ditch and a potential shift in nutrient foraging. Although, the studied ditch distance gradient did not exert any significant change on soil properties, except a tendency of higher soil moisture towards far away distances. It is also notable that considering factors other than distance gradients, such as topography, vegetation characteristics, tree stands, climate, and peat properties, can contribute better to the local soil hydrology. In the same study, soil physical and chemical properties such as peat depth, pH, and soil temperature influenced the species-specific responses of absorptive root morphology in birch and spruce. Among studied root morphological traits, RTD was the most sensitive below-ground trait at drained peatland birch, and spruce stands. High RTD indicates trees' adaptation to the more acidic soil with thicker peat depth where the decomposition of organic matter and nutrient availability were limited. On the other hand, thinner absorptive root D was produced toward acidic soils only in spruce stands, attributed to higher nutrient absorption efficiency. Besides, root branching intensity (per mass unit) was responsive to soil temperature change at spruce-drained peat soils. Higher branched root system was observed in less warm soils, reflecting the plasticity of absorptive root systems for extensive proliferation at cooler soils, with limited mineralization capacity and scarce resources.

In our meta-analysis, on the other hand, fine root morphology of trees remained unchanged under increased soil warming at the global scale. These nonsignificant results when testing the warming effects on trees' fine root morphology might be the result of limited data available on different root morphological traits. A more comprehensive examination of these root morphological characteristics in response to global climate warming is required in the future studies. Instead, we found that trees allocate more biomass to fine roots toward soil warming, depending on the magnitude of warming. The effect size of FRB decreased with increasing warming magnitude, indicating that root growth of trees is limited under higher warming environments due to soil water stress.

This thesis thoroughly explains the responses of trees' fine root functional traits and the prospective acclimation capacities of deciduous and coniferous species to changing climate and soil conditions. Our findings have potential implications for future investigations into the adaptation mechanisms of different species to environmental shifts and future forest ecosystem modeling. Our results underline the importance of fine root partitioning on morphology and C-release functioning of fine roots. Despite interspecific differences in absorptive root morphology, we detected a similar morphological acclimation pattern in deciduous and coniferous species in drained peatland forests. Our global meta-analysis proposes that warming condition enhances trees' biomass allocation to belowground, modulated by warming magnitude. However, there is a crucial need for future investigations on the interactive effects of global change factors on the acclimation processes of fine roots along with root-associated microbial communities, particularly on ECM fungi, to better predict the forest belowground feedback to climate change.

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SUMMARY

The rising global temperature associated with precipitation shifts, rising air relative humidity (RH), and nitrogen (N) deposition pose challenges to the world's forest ecosystem functioning, especially high-latitude forests. Of particular concern are northern peatland forests which represent globally significant stores of soil carbon (C) and will experience dramatic changes due to ongoing climate change. Peatlands in boreal and hemiboreal forests have extensive drainage ditch networks to lower the water table and improve tree growth by increasing nutrient availability via the decomposition of organic matter. Tree growth response may vary across distances from the drainage ditch causing shifts in local site properties. However, we lack sufficient understanding of the resilience of forest ecosystems, particularly drained peatlands affected by various environmental stressors.

Tree species have evolved various functional and structural traits in above and belowground components to resist environmental stresses. However, studies on belowground characteristics are often limited due to methodological sampling difficulty compared to aboveground studies. Belowground components, especially fine roots, and their functional traits are highly responsive to varying environmental conditions and are critical to the maintenance of many tree functions. Fine roots (i.e., <2 mm in diameter) contribute significantly to forest ecosystems' C, water, and nutrient fluxes through soil resource acquisition, turnover, and rhizodeposition processes such as respiration and exudation. Fine roots are functionally divided into absorptive and transport roots. Absorptive roots (i.e., first and second orders) have a strong potential for soil resource acquisition as transport roots or so-called pioneer roots (i.e., \geq third-order roots), enhance transportation function. Fine root systems based on their functional root orders, such as absorptive and transport roots, may exhibit different reactions to environmental shifts.

Trees can optimize resource acquisition and acclimate to environmental changes by modifying fine root biomass and several morphological and physiological traits. For instance, higher investment in fine root biomass (FRB) is commonly associated with extensive foraging strategies under nutrient-poor conditions. High specific root area (SRA) and specific root length (SRL) mean a higher surface area per lower biomass investments, reflecting higher resource acquisition efficiency and intensive plant growth. Fine roots with larger root diameters (D) usually live longer. Fine root tissue density (RTD) is commonly associated with many critical root lifespan and survival aspects. Fine roots with high RTD are expected to live longer and to be more conservative with soil resources. Increased branching intensity (BI) is associated with a higher proportion of root tips per length or mass unit and higher resource uptake capacity. In addition to the morphological adjustments, fine roots exude primary and secondary metabolites into the soil, which may regulate soil microbial community, nutrient cycling, and soil enzyme activity. About 5–21% of total photosynthetically fixed C is exuded into

the rhizosphere. Fine root respiration is another source of CO₂ efflux from forest soils, which accounts for 50% of total soil respiration.

Several global studies indicate that climatic and soil variables are often substantial drivers of fine-root trait variation. Soil warming has increased FRB and root exudation rates, resulting in higher SRA and SRL and lower RTD in several coniferous species. Variations in soil factors such as moisture, temperature, and N availability strongly influenced fine root respiration rates. Under elevated air humidity, FRB increased, and thinner, and longer absorptive roots were formed, while RH-induced root physiological responses remained underrepresented. Moreover, inter-annual or geographical fluctuations in meteorological parameters, especially air temperature, and precipitation, may substantially affect fine root production dynamics. Fine root growth rate increased towards warmer years or regions. Besides, different tree species may exhibit varying nutrient uptake capacities and distinctive fine root dynamics under climate shifts. Therefore, knowledge of fine root responses of different tree species to various environmental variables is crucial for evaluating tree species' resilience and predicting the patterns of C allocation and N cycling in forest ecosystems under ongoing projected climates.

This doctoral thesis aimed to analyze the fine root acclimation strategies of different tree species (deciduous and coniferous) to varying climate and soil conditions.

The main objectives were:

- 1) To evaluate fine root C fluxes such as exudation and respiration, fine root morphological variation along with aboveground traits such as photosynthesis, transpiration, and leaf N concentration of tree species (hybrid aspen, silver birch, and Scots pine) in response to elevated RH and soil inorganic N sources (NO₃⁻, NH₄⁺). Moreover, we analyzed the role of different fine root functional groups (absorptive, pioneer, and transport roots) on fine root C exudation rate (I).
- 2) To investigate the morphological variation of absorptive roots across distance gradient from the ditch in drained peatland forests in Estonia dominated by Downy birch and Norway spruce to identify the most plastic traits in fine root acclimation strategies of tree species (II).
- 3) To assess the response patterns of fine root traits, including biomass and morphology of trees (deciduous and coniferous), to soil warming at a global scale study. In addition, we assessed the impacts of warming magnitude, soil depth, and tree species in this meta-analysis (III).

The measurements for above- and belowground traits were carried out in controlled climate chamber experiments, where trees grown at moderate (mRH) and elevated air humidity (eRH) and also fertilized with nitrate and ammonium (I). Morphological variation of the absorptive roots was studied in 6 drained

peatland forests growing on Histosol in the Järvelja experimental forest area in the eastern part of Estonia. In each stand, a gradient with four sampling plots at distances of 5, 15, 40, and 80 m from the ditch was selected (II). We performed a meta-analysis with 149 paired observations from 43 publications between 1999 and 2020 that studied fine root biomass and morphology of tree species (deciduous vs. coniferous) responding to various soil warming magnitudes across the global biomes (III).

The current study showed tree species-specific responses to climate change and soil nutrient availability affecting soil C balances. In climate chamber experiments (I), transpiration was reduced in all studied trees under eRH. Soil N sources also influenced the transpiration rate, and it increased in nitrate-fertilized birch saplings. Unlike ammonium-fertilized trees, we observed a lower foliar N concentration in nitrate-fertilized birch trees at eRH than mRH. We suggest that the uptake of NO_3^- is more diminished than NH_4^+ under eRH, where the transpiration flux and mass flow slow down. Pine photosynthesis rate increased under eRH, associated with elevated leaf (shoot) conductance. Regarding belowground traits, eRH significantly decreased C fluxes. Root mass-specific exudation in pine and root respiration in aspen reduced at higher air humidity treatments. Fine root morphology was also influenced by air humidity treatments; specific root area increased in birch but decreased in pine at eRH. Our result suggested that fine roots with higher specific SRA and SRL and lower RTD, with a higher share of thinner, younger, and metabolically active roots, can exudate more C into the soil. We highlight a strong connection between fine root morphology and C-fluxes depending on root partitioning (I). In drained peatland forests (II), absorptive roots morphologically adjusted to the local soil condition across ditch distances. The absorptive root morphological responses were uniform between birch and spruce. With increased distance from the ditch, the mean SRA increased, while the mean RTD decreased in both trees, reflecting a potential shift in nutrient foraging in relation to spatially different distances from the ditch. Although soil properties (e.g., peat depth, pH, and temperature) influenced the species-specific responses of absorptive root morphological traits, the corresponding soil factors did not vary across distance gradient. We can assume that other factors (e.g., tree stands, climate conditions, peat, and subsoil hydraulic properties) might influence the local soil hydrology rather than distance to ditch (II). In the current meta-analysis (III), soil warming increased fine root biomass (FRB), which differed between deciduous and coniferous species. We observed that the warming effects on fine root biomass decreased with greater warming magnitude. We suggested that a rise in soil temperature could initially stimulate fine root growth, probably caused by enhanced photosynthesis. In contrast, fine root biomass is diminished under elevated temperatures, which can be due to low soil water levels. Fine root morphological traits, by contrast, were unresponsive to the global soil warming magnitudes. Meanwhile, insignificant responses of fine root morphological traits in our study can be linked to the limited available sample sizes. Thus, future studies should prioritize further examining these critical fine root morphological traits in response to global warming. Our meta-analysis suggested that trees

allocate more biomass to fine roots under warmer conditions, while fine root morphological plasticity is less influenced.

This study focused on trees' above- and below-ground acclimation, especially fine root functional traits to climate and soil changes. We outlined specific acclimation capacities for tree species, such as deciduous and coniferous, under environmental shifts. Our results underline the importance of root partitioning and functional orders on fine root trait responses such as morphology and C fluxes. The findings indicated morphological plasticity in fine and absorptive roots when trees acclimate to a changing climate. We suggest evaluating more comprehensive analyses of fine root traits along with other soil microbiomes, especially root-associated ectomycorrhizal fungi, and under multifactorial environmental conditions.

SUMMARY IN ESTONIAN

Kliimamuutuste mõju leht- ja okaspuude peenjuurte omadustele

Globaalse temperatuuri tõus koos kaasnevate muutustega sademetes, suhtelises õhuniiskuses ja lämmastiku depositsioonis mõjutab oluliselt maailma metsaökosüsteemide toimimist, märgatavamad on muutused kõrgetel laiuskraadidel kasvavates metsades. Enim ohustatud on metsad turbasel mullal, kus on talletunud ülemaailmselt tähtis süsinikuvaru ning kus toimuvad kliimast tingitud olulised muutused. Turbamullal kasvavates boreaalsetes ja hemiboreaalsetes metsades on ulatuslikud kuivenduskraavide võrgud, et alandada veetaset ja parandada puude juurdekasvu. Tänu orgaanilise aine lagunemisele paraneb toitainete kättesaadavus. Puude kasv võib erineda sõltuvalt kaugusest kuivenduskraavist, täheldatav on lokaalne varieeruvust kasvukoha omadustes. Paraku puudub meil piisav arusaam metsaökosüsteemide, eriti kuivendatud turbaalade vastupidavusest mitmesugustele keskkonnastressidele.

Puuliikidel on keskkonnamõjude talumiseks välja kujunenud erinevad funktsionaalsed ja struktuursete tunnused nii maapealsetes kui maa-alustes osades. Sageli piiravad maa-aluste näitajate uuringuid võrreldes maapealsete uuringutega meetoodilised raskused proovide võtmisel. Maa-alusteks uuringuteks kasutatavaid meetodeid mõjutavad mitmed määramatused ja võimalikud vead. Puude maa-alused komponendid, eriti peenjuured ja nende funktsionaalsed omadused reageerivad erinevatele keskkonnanähtudele ning on mitmete funktsioonide tagamisel kesksel kohal. Hoolimata sellest, et peenjuured moodustavad vaid umbes 5% puude biomassist, võib nende toodang ulatuda kuni 75%ni metsaökosüsteemide aastasest esmasest netotoodangust. Peenjuured aitavad mullaressursside omandamise, käibe ja risosfääri depositsiooniprotsesside nagu hingamine ja eksudatsioon kaudu oluliselt kaasa metsaökosüsteemide süsiniku, vee ja toitainete voogudele. Peenjuured on juured läbimõõduga alla 2 mm ning need jagatakse funktsionaalselt imi- ja transpordijuurteks. Imijuurteil (esimest ja teist järku juurteil) on oluline roll mullaressursside omandamisel, samas kui transpordijuured ehk nn pioneerjuured (\geq kolmandat järku juured) tagavad toitainete ja vee transpordi. Peenjuured eristatuna vastavalt funktsionaalsele juurjärjekorrale – imi- ja transpordijuured, võivad keskkonnamuutustele reageerida erinevalt. Puud saavad optimeerida ressurside omandamist ja kohaneda keskkonnamuutustega, muutes peenjuurte biomassi ja mitmeid morfoloogilisi ning füsioloogilisi tunnuseid. Näiteks seostatakse suuremaid investeeringuid peenjuurte biomassi ulatuslike toitumisstrateegiatega toitainevaestes tingimustes. Kõrge juure eripindala ja juure eripikkus tähendavad suuremat pindala väiksemate biomassiinvesteeringute korral, mis tagab suurema ressursi omandamise efektiivsuse ja intensiivsema kasvu. Suurema läbimõõduga peenjuured elavad tavaliselt kauem. Peenjuure kudede tihedust seostatakse tavaliselt juure eluea ja ellujäämise kriitiliste aspektidega.

Suure kudede tihedusega peenjuured elavad eeldatavasti kauem ja on mulla-ressursside suhtes tundlikumad. Suurenenud hargnemise intensiivsus on seotud suurema juuretippude osakaaluga pikkus- või massiühiku kohta ja suurema ressursi omastamisvõimega. Lisaks morfoloogilistele kohastumistele eritavad peenjuured pinnasesse primaarseid ja sekundaarseid metaboliite, mis võivad reguleerida mulla mikroobikooslust, toitainete ringlust ja mulla ensüümide aktiivsust. Umbes 5–21% kogu fotosünteesiliselt fikseeritud süsinikust eritub rissfääri. Peenjuurte hingamine on üks CO₂ metsamuldadest väljumise allikas, mis moodustab 50% kogu mullahingamisest.

Nagu näitavad mitmed ülemaailmsed uuringud, mõjutavad kliima- ja pinnasemuutujad sageli peenjuurte omaduste plastilisust. On näidatud, et mulla soojenemine suurendas peenjuurte biomassi ja juurte käivet ning põhjustas mitmetel okaspuuliikidel juurte suuremat eripinda ja -pikkust ning madalamat juurekoe tihedust. Mullategurite, nagu niiskus, temperatuur ja lämmastiku kättesaadavus, kõikumised mõjutasid oluliselt peenjuurte hingamismäära. Kõrgendatud õhuniiskuses suurenes juurte biomass ning moodustusid õhemad ja pikemad imijuured, samas kui suhtelisest õhuniiskusest tulenevad juurte füsioloogilised reaktsioonid jäid alaesindatuks. Veelgi enam, meteoroloogiliste parameetrite, eriti õhutemperatuuri ja sademete aastatevahelised või geograafilised kõikumised võivad oluliselt mõjutada peenjuurte juurdekasvu dünaamikat. Positiivne seos peenjuurte produktiooni määra ja õhutemperatuuri vahel on leidnud kinnitust; peenjuure kasvukiirus suureneb soojematel aastatel või piirkondades. Lisaks võib erinevatel puuliikidel olla erinev toitainete omastamise võime ja iseloomulik peenjuure tootlikkus kliimamuutuste ajal. Seetõttu on ülioluline uurida puude peenjuurte omaduste reaktsioone erinevatele keskkonnatingimustele, et hinnata erinevate liikide vastupidavust ning prognoosida süsiniku eraldumise ja lämmastiku tsükli mustreid metsaökosüsteemides prognoositava kliima tingimustes.

Doktoritöö eesmärk oli analüüsida erinevate puuliikide (leht- ja okaspuud) peenjuure aklimatiseerumisstrateegiaid erinevates kliima- ja mullatingimustes.

Peamised eesmärgid olid:

- 1) Hinnata puuliikide (hübriidhaab, hõbekask ja harilik mänd) peenjuurte süsinikuvoogusid nagu eksudatsioon ja hingamine, peenjuurte morfoloogilist varieeruvust koos maapealsete tunnustega, nagu fotosüntees, transpiratsioon ja lehtede lämmastiku kontsentratsioon, vastusena mulla suhtelise niiskuse ja mulla anorgaaniliste lämmastikuallikate (NO₃⁻, NH₄⁺) suurenemisele. Lisaks analüüsisin erinevate peenjuurte funktsionaalrühmade (imi-, pioneer- ja transpordijuured) rolli süsiniku eksudatsiooni kiiruses peenjuurtest (I).
- 2) Uurida imijuurte morfoloogilist varieerumist kraavist lähtuval kaugusgradiendil Eesti kuivendatud turbametsades, kus domineerivad kask ja kuusk, et teha kindlaks kõige plastilisemad tunnused puuliikide peenjuurte aklimatiseerumisstrateegiates (II).

- 3) Hinnata peenjuurte tunnuste, sealhulgas puude (leht- ja okaspuu) biomassi ja morfoloogia reageerimismustreid mulla soojenemisel globaalses mastaabis. Lisaks hindasin selles metaanalüüsis (III) soojenemise ulatuse, pinnase sügavuse ja puuliikide mõju.

Maapealsete ja maa-aluste tunnuste mõõtmised tehti kontrollitud kliimakambriga katsetes, kus puud kasvasid mõõdukas ja kõrgendatud õhuniiskuses ning neid väetati ka nitraadi ja ammooniumiga (I). Imijuurte morfoloogilist varieerumist uuriti kuues kuivendatud metsas, mis kasvavad Järvelja katseala turbamullal Ida-Eestis. Igas puistus valiti nelja proovitükiga gradient 5, 15, 40 ja 80 m kaugusel kraavist (II). Tegin metaanalüüsi 149 paarisvaatlusega 43st publikatsioonist aastatest 1999–2020, milles uuriti puuliikide (leht- ja okaspuu) peenjuurte biomassi ja morfoloogiat, nende reageerimist mulla soojenemisele globaalsetes bioomides (III).

Uuring näitas puuliigispetsiifilisi reaktsioone kliimamuutustele ja mulla toitainete kättesaadavusele, mis mõjutavad mulla süsinikutasakaalu. Kliimakambri katsetes (I) vähenes kõrgenenud suhtelise õhuniiskuse tingimustes transpiratsioon kõigil uuritud puuliikidel, mida on ka varem täheldatud. Pinnase lämmastikuallikad mõjutavad ka transpiratsiooni kiirust ja see suurenes nitraadiga väetatud kaskedes, mida tõenäoliselt stimuleerib nitraadi mõjul suurenenud akvaporiooni ekspressioon juurerakkudes. Erinevalt ammooniumiga väetatud puudest täheldasin nitraadiga väetatud kaskedel madalamat lehtede lämmastikusisaldust mõõduka õhuniiskuse juures kui kõrgenenud suhtelise õhuniiskuse korral, mis on kooskõlas varasemate uuringutega. Tuleb arvata, et suurema suhtelise õhuniiskuse tingimustes, kus transpiratsioonivoog ja massivool aeglustuvad väheneb nitraadi omastamine ammooniumi omastamisest enam. Männi fotosünteesi kiirus suurenes kõrgenenud suhtelise õhuniiskuse tingimustes, mis on seotud lehtede (võrsete) suurenenud juhtivusega. Maa-aluste tunnuste osas vähendas kõrgenenud suhteline õhuniiskus märkimisväärselt süsiniku vooge. Kõrgema õhuniiskuse tingimustes vähenes juuremassispetsiifiline eksudatsioon männil ja juurehingamine haaval. Teisalt on näidatud, et abiootiliste stressoritega kokku puutunud puud suurendasid juureeksudaatide hulka. Oletame, et kasvuks ja ellujäämiseks võis puudel olla toitainete varu (I). Peenjuurte morfoloogiat mõjutas ka õhuniiskuse muutumine; kõrgenenud suhtelise õhuniiskuse tingimustes suurenes juure eripind kasel, kuid vähenes männil. Leidsime peenjuured, millel on kõrgem juure eripind ja -pikkus ning madalam koetihedus, mis viitab peenemate, nooremate ja metaboolset aktiivsete juurte suuremale osakaalule, suurendades juure-mulla ühendusi ja eritades pinnasesse rohkem süsinikku, tuues esile tugeva seose peenjuure süsinikuvoogude ja sellest sõltuva juurte hargnemise morfoloogia vahel (I). Kuivendatud turbametsades (II) kohanesid kase ja kuuse imijuured (s.o. esimest ja teist järku juured) morfoloogiliselt kohaliku mulla seisundiga vastavalt kaugustega kraavist sarnaselt, kauguse kavades suurenes keskmine juure eripind, samas kui keskmine koe tihedus vähenes mõlemal liigil, tuues esile võimaliku kohanemise toitainete leidmisel. Kuigi mulla omadused, nagu turba sügavus, pH ja temperatuur, mõjutasid neelduvate juuremorfoloogiliste tunnuste liigispetsiifilisi

reaktsioone, ei muutunud vastavad mullategurid kaugusgradiendil (II). Erinevalt minu tulemustest näitasid varasemad uuringud nihkeid mulla omadustes (nt niiskus, toitainete kontsentratsioon) ja mikroobikooslustes seoses ruumiliselt erinevate kaugustega kraavist. Kohalikku pinnase hüdroloogiat võivad mõjutada ka muud tegurid (nt puistud, kliimatingimused, turvas ja aluspinnase hüdraulilised omadused), mitte pelgalt kaugust kraavist. Metaanalüüs (III) näitas, et mulla soojenemine suurendas peenjuurte produktsiooni, mis erines leht- ja okaspuuliikidel. Eelkõige vähendas soojenemine peenjuurte biomassi, mis on kooskõlas teiste uuringutega. Mullatemperatuuri tõus tingib alguses peenjuurte kasvu kiirenemise ja tootlikkuse suurenemise, mis on põhjustatud fotosünteesist. Samas väheneb peenjuurte kasv soojemas mullas niiskuse vähenemise tõttu.

Globaalne metaanalüüs ei tuvastanud peenjuurte morfoloogiliste tunnuste reageerimist mulla soojenemisele samas suurjärgus. Samas teised uuringud täheldasid olulisi nihkeid peenjuurte morfoloogias soojemas keskkonnas, et optimeerida mullaressursse ja säilitada juurdekasvu. Seejuures saab meie uuringus peenjuurte morfoloogiliste tunnuste (st imijuurte eripikkus, eripind ja diameeter) ebaolulisi reaktsioone seostada piiratud valimiga. Seega peaks tulevaste uuringute prioriteet olema kriitiliste peenjuurte morfoloogiliste tunnuste edasine uurimine vastusena globaalsele soojenemisele. Praegune metaanalüüs viitab, et soojemates tingimustes kasvatavad puud rohkem peenjuurte biomassi, samas kui peenjuurte morfoloogilist plastilisust mõjutatakse vähem.

See uuring keskendus puude maapealsele ja maa-alusele aklimatiseerumisele, eriti peenjuurte funktsionaalsetele tunnustele seoses kliima ja pinnase muutustega. Selgitasin leht- ja okaspuuliikide spetsiifilisi kohanemisvõimeid keskkonna muutudes. Tulemused rõhutavad juurte hargnemise ja funktsionaalse järgu tähtsust peenjuurte omaduste reaktsioonides. Töö annab ülevaate peenjuuretoodangu täpsemast hindamisest, võttes arvesse uurimismeetodite mõju ning ajalisi ja ruumilisi kliimakõikumisi, et minimeerida metsaökosüsteemide süsinikuringe ebamäärasust. Otstarbekas oleks teha peenjuurte tunnuste põhjalikumaid analüüse koos teiste mulla mikroobioomidega, eriti juurtega seotud ektomükoriisa seentega ja multifaktoriaalsetes keskkonnatingimustes.

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PUBLICATIONS

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A list of publications and patents:

Sell, M., Ostonen, I., Rohula-Okunev, G., Rusalepp, L., Rezapour, A., Kupper, P. 2021. Responses of fine root exudation, respiration and morphology in three early successional tree species to increased air humidity and different soil nitrogen sources. *Tree Physiology*, 42(3), pp. 557–569.

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Research grants and scholarships

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Peamised uurimvaldkonnad:

Puude peen- ja imijuurte aklimatiseerimisstrateegiad seoses keskkonnamuutustega. Peenjuurega seotud ektomükoriisaseente juuretunnuste mõõtmine, sealhulgas morfoloogia ja süsinikuvood (hingamine ja eksudatsioon) ning molekulaarne mõõtmine. Peenjuureproduktiooni hindamine uurimismeetoditega nagu sissekasvusüdamik ja sissekasvuvõrk.

Teadsupublikatsioonid ja patendid:

- Sell, M., Ostonen, I., Rohula-Okunev, G., Rusalepp, L., Rezapour, A., Kupper, P. 2021. Responses of fine root exudation, respiration and morphology in three early successional tree species to increased air humidity and different soil nitrogen sources. *Tree Physiology*, 42(3), pp. 557–569.
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Uurimistoetused

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DISSERTATIONES GEOGRAPHICAE UNIVERSITATIS TARTUENSIS

1. **Вийви Руссак.** Солнечная радиация в Тыравере. Тарту, 1991.
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