

MARILI SELL

The impact of environmental change  
on ecophysiology of hemiboreal  
tree species – acclimation  
mechanisms in belowground





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UNIVERSITY OF TARTU

Press

1632

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Dissertation was accepted for the commencement of the degree of *Doctor philosophiae* in plant ecology and ecophysiology at the University of Tartu on October 10, 2022 by the Scientific Council of the Institute of Ecology and Earth Sciences, University of Tartu.

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Commencement: Room 127, Liivi 2, Tartu. On 9<sup>th</sup> of December at 10.15 a.m.

Publication of this thesis is granted by the Institute of Ecology and Earth Sciences, University of Tartu

ISSN 1024-6479 (print)

ISBN 978-9916-27-066-0 (print)

ISSN 2806-2140 (pdf)

ISBN 978-9916-27-067-7 (pdf)

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University of Tartu Press  
[www.tyk.ee](http://www.tyk.ee)

## TABLE OF CONTENTS

LIST OF ORIGINAL PUBLICATIONS .....	6
LIST OF ABBREVIATIONS .....	7
1. INTRODUCTION.....	8
1.1. Climate change and available nitrogen in soil.....	8
1.2. Research frontiers in measuring plant belowground dynamics.....	9
1.3. Fine root morphology and carbon fluxes in the soil.....	10
1.4. Studied tree species .....	12
1.5. Aims of this thesis .....	12
2. MATERIAL AND METHODS .....	14
2.1. Experimental setup .....	14
2.2. Tree water flux, leaf/shoot gas exchange and nutrient concentration measurements .....	14
2.3. Fine root carbon exudation and respiration measurements .....	15
2.4. Imaging and analysis of <i>Picea abies</i> roots .....	17
2.5. Data analysis.....	18
3. RESULTS .....	20
3.1. Effects of air humidity and soil N sources.....	20
3.1.1. Water fluxes.....	20
3.1.2. Tree biomass and belowground biomass fractions .....	21
3.1.3. Leaf chemistry .....	23
3.1.4. Fine root growth dynamics .....	24
3.1.5. Fine root morphology and fine root proportioning .....	25
3.1.6. Tree C fluxes: leaf photosynthesis, fine root C exudation and respiration .....	29
3.2. Successional status vs phylogenetic relatedness.....	30
3.3. Novel tools for measuring fine root growth dynamics .....	32
4. DISCUSSION .....	33
4.1. Water flux and nutrient uptake in changing environments.....	33
4.2. Tree growth and acclimation to a changing environment .....	34
4.3. Future implications for measuring fine root growth dynamics.....	38
5. CONCLUSION .....	40
REFERENCES.....	42
SUMMARY IN ESTONIAN .....	52
ACKNOWLEDGEMENTS .....	60
PUBLICATIONS .....	61
CURRICULUM VITAE .....	139
ELULOOKIRJELDUS.....	141

## LIST OF ORIGINAL PUBLICATIONS

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

- I** Kupper, P., Rohula-Okunev, G., **Sell, M.**, Kangur, O., Sellin, A. (2020) Effects of air humidity and soil nitrogen source on diurnal water flux in hybrid aspen and silver birch. *Acta Horticulturae* 1300, 153–160.  
<https://doi.org/10.17660/ActaHortic.2020.1300.20>
- II** **Sell, M.**, Ostonen, I., Rohula-Okunev, G., Rusalepp, L., Rezapour, A., Kupper, P. (2022). 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, 557–569  
<https://doi.org/10.1093/treephys/tpab118>
- III** **Sell, M.**, Smith, A.G., Burdun, I., Rohula-Okunev, G., Kupper, P., Ostonen, I. (2022). Assessing the fine root growth dynamics of Norway spruce manipulated by air humidity and soil nitrogen with deep learning segmentation of smartphone images. *Plant and Soil*  
<https://doi.org/10.1007/s11104-022-05565-4>
- IV** **Sell, M.**, Rohula-Okunev, G., Kupper, P., Ostonen, I. 202x. Do successional status or phylogenetic relatedness of trees determine their fine root carbon exudation rate in changing environments? (manuscript)

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**The participation of the author in preparing the listed Publications is as follows:**

- Paper I – The author contributed to data collection
- Paper II – The author collected and analysed data and was leading author in writing the article
- Paper III – The author contributed to developing the idea and experimental design, collected root photos and analysed the data, and was leading author in writing the article
- Paper IV – The author collected and analysed data and was the leading author in writing the article

## LIST OF ABBREVIATIONS

- C** – carbon  
**N** – nitrogen  
**NO<sub>3</sub><sup>-</sup>** – nitrate  
**NH<sub>4</sub><sup>+</sup>** – ammonium  
**RH** – relative air humidity  
**mRH** – moderate relative air humidity  
**eRH** – elevated relative air humidity  
**P<sub>net</sub>** – net photosynthesis rate ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )  
**E** – Transpiration rate ( $\text{g m}^{-2} \text{h}^{-1}$ )  
**K<sub>l/s/r/plant</sub>** – leaf/shoot/root/whole plant hydraulic conductance ( $\text{g m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$ )  
**Ex<sub>C\_area</sub>** – fine root carbon exudation per root surface area ( $\mu\text{g C cm}^{-2} \text{day}^{-1}$ )  
**Ex<sub>C\_mass</sub>** – fine root carbon exudation per root dry weight ( $\text{mg C g}^{-1} \text{day}^{-1}$ )  
**R<sub>root\_area</sub>** – fine root respiration per root surface area ( $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ )  
**R<sub>root\_mass</sub>** – fine root respiration per root dry weight ( $\mu\text{mol CO}_2 \text{g}^{-1} \text{s}^{-1}$ )  
**AD** – average diameter of fine roots (mm)  
**SRA** – specific fine root area ( $\text{m}^2 \text{kg}^{-1}$ )  
**SRL** – specific fine root length ( $\text{m g}^{-1}$ )  
**RTD** – fine root tissue density ( $\text{kg m}^{-3}$ )  
**BI** – fine root branching intensity ( $1 \text{mg}^{-1}$ )  
**PA** – fine root projection area ( $\text{cm}^2$ )  
**M1<sub>total</sub>** – Model 1 for total fine root projection area  
**M2<sub>total</sub>** – Model 2 for white fine root projection area  
**L<sub>absorb/pioneer/transp</sub>** – the length proportion of absorptive, pioneer, transport roots (%) of total fine roots  
**SA<sub>absorb/pioneer/transp</sub>** – the surface area proportion of absorptive, pioneer and transport roots (%) of total fine roots  
**DW<sub>absorb/pioneer/transp</sub>** – the dry weight proportion of absorptive, pioneer and transport roots (%) of total fine roots

# 1. INTRODUCTION

## 1.1. Climate change and available nitrogen in soil

Global climate change scenarios predict continuously increasing CO<sub>2</sub> concentrations in the atmosphere and rising air temperatures (Lee et al., 2021). While most regions experience drought, the frequency of precipitation is predicted to increase by 5–20 in northern latitudes (Jaagus & Mändla, 2018; Kjellström et al., 2018). In Estonia, the mean annual air temperature between 1951 and 2015 significantly increased, 0.3–0.4 °C/decade, on average, in all seasons, the highest warming occurred in spring and winter (Jaagus et al., 2017). The months of January and June demonstrate increased precipitation, while April and September are drier than average (Jaagus et al., 2018). The higher frequency of rainfall prolongs the wetting of plant foliage and is tightly coupled with relative air humidity (RH) (Betts et al., 2014), which stays high in tree canopies because of the evaporation of intercepted water (Von Arx et al., 2012). On the one hand, elevated RH can improve growth due to higher water potential, enhancing leaf growth and lowering the stomatal limitation of photosynthesis (Lendzion & Leuschner, 2009; Fanourakis et al., 2020). On the other hand, high air humidity may slow down plant transpiration flux; thus, the mass flow of water and mineral nutrients in the rhizosphere can also be reduced (Cramer et al., 2009). Previous studies have shown the effect of increased air humidity on plant aboveground physiological traits, for example, in fast-growing deciduous tree species, such as silver birch and hybrid aspen, high RH reduced leaf hydraulic conductance and photosynthetic capacity in a free air experiment (Sellin et al., 2013; 2017). However, plants can acclimate to environmental changes by modifying growth or physiology and using these mechanisms to cope with stress (Lambers et al., 2008). Ecosystems' belowground at elevated RH have shown increase in fine root biomass, and thinner and longer ectomycorrhizal absorptive root tips (Parts et al., 2013; Rosenvald et al., 2014). Less is known about the changes in root physiology and functional acclimations in fine roots under elevated air humidity.

Nitrogen (N) is often the most limiting mineral nutrient for plants (Miller & Cramer, 2005). Plant growth becomes restricted when there is an N deficit in the soil (Aerts & Chapin, 2000). In addition to organic N (such as amino acids), plants can take up inorganic nitrogen in the form of nitrate (NO<sub>3</sub><sup>-</sup>) or ammonium (NH<sub>4</sub><sup>+</sup>) ions from soil (Bhatla & Lal, 2018). The efficient diffusion coefficient of NH<sub>4</sub><sup>+</sup> in the soil is up to 100-fold less than that of NO<sub>3</sub><sup>-</sup>, and when N delivery is slowed down with transpiration-driven mass flow, the preferred N form for plants might be NO<sub>3</sub><sup>-</sup> (Owen & Jones, 2001; Cramer et al., 2009). Some plant species prefer a specific nitrogen form for uptake, while others assimilate the most abundant N form from soil (Hachiya & Sakakibara, 2017). However, the uptake of nitrogen forms differs. The NO<sub>3</sub><sup>-</sup> is taken up against an electrochemical gradient and needs further reduction into NH<sub>4</sub><sup>+</sup> in the plant, which requires more energy than NH<sub>4</sub><sup>+</sup> acquisition (Bhatla & Lal, 2018). In soil the different inorganic nitrogen ions



affect the regulation of water transport channels, which determines the water uptake rate by roots (Gao et al., 2018), whereas the nitrogen ion mobility is dependent of the transpiration induced mass flow. The interactive effect of different N forms in soil and air humidity alter tree transpiration flux, but the effects on fine root growth, morphology and physiology in hemiboreal forest tree species are unknown.

## **1.2. Research frontiers in measuring plant belowground dynamics**

Plant adaptations to specific environmental changes are quite commonly investigated in growth chambers, growing plants individually under controlled and/or manipulated light, temperature, water and fertilisation regimes (Poorter et al., 2016). From a holistic perspective, continuous and direct observations of roots hidden in the soil, as well as in aboveground organs, are necessary to understand plant growth changes under different environmental conditions (Lecompte et al., 2001). The most common non-destructive methods for monitoring root growth are image-based approaches, such as rhizotrons, scanners or root windows, which allow continuous assessment of root characteristics over time. The rhizotron system consists of a transparent tube installed in soil and a tube-specific camera (Rewald & Ephrath, 2013). The required equipment, continuous imaging campaigns and image processing are costly and time consuming. Therefore, root growth imaging techniques and image analysis tools are subjects of rapid development and innovation. Mohamed et al. (2017) compared different scanners, cameras and smartphones, of which the last was the most accurate. Since smartphones today have high-quality cameras, they can be used for monitoring root growth by taking pictures with high frequency. A wide range of different programmes have been continuously developed to analyse root images; for example, RootTrace, RootNav and MyRoot have been used to record seed germination dynamics (French et al., 2009; Naeem et al., 2011; Yasrab et al., 2019; Gonzalez et al., 2020). RootFly and SegROOT are non-commercial alternatives for analysing root growth on images (Zeng et al., 2006; Wang et al., 2019). However, because of the manual root growth tracking on images, the speed of processing hundreds and (tens of) thousands of images has been a ‘bottleneck’ for obtaining plant root growth data. Recent technological innovations have focused on advancing progress in automatising image-based root trait measurements. Convolutional neural networks (CNN) are popular deep learning methods for image processing, representing a prediction based on segmentation and classification for each pixel of the original input image (Smith et al., 2022). The recently developed software RootPainter uses CNNs for plant image analysis and is freely available, open source and user friendly (Smith et al., 2022). Training a model in RootPainter marks the roots and background separately, whereas with every following segmented image, the model learns from assigned corrections (Smith et al., 2022).

However, combining imaging with smartphone and non-commercial deep learning programmes offers a very simple, efficient and rapid analysis of specific research questions (III). Further aim is to minimise errors, such as false positives, where parts of the background are identified as roots, and false positives, where parts of the root are identified as background. This depends on soil type or on how much organic material comparable to roots is on the images. Even senescing, rotting, lignifying or browning of roots can make the estimation of roots inaccurate. In addition to brown colours, young white roots can also induce false positives when reflections or white particles in soil are identified as roots.

### **1.3. Fine root morphology and carbon fluxes in the soil**

Plant roots contribute to carbon and nutrient cycling belowground, taking up water and nutrients from the soil, storing a considerable amount of carbon in belowground biomass, and transporting carbon captured in the photosynthesis process into the soil (Brunner & Godbold, 2007). Roots are commonly divided by diameter into coarse ( $> 2$  mm) and fine roots ( $< 2$  mm) (Bauhus & Messier, 1999; Tufekcioglu et al., 1999; Lucash et al., 2005; Freschet et al., 2021). Fine roots represent a very small proportion of the overall biomass belowground; for example, in boreal forests, the proportion of fine roots from total plant biomass is considered  $< 10\%$  (Vogt et al., 1995). Compared to coarse roots, fine roots are short-living and have high plasticity; therefore, fine root traits are expected to reflect their adaptation to environmental change (Löhmus et al., 1989; Ostonen et al., 2007). Fine roots loop together functionally different roots: 1) absorptive roots with primary growth and high water and nutrient acquisition ability and 2) nutrient transporting roots with secondary growth (Wells & Eissenstat, 2003; McCormack et al., 2015). However, Kubikova (1967) described heterorhizy on fine roots, separating 1) previously mentioned exploitative absorptive root tips, which are mostly mycorrhizal (Guo et al., 2008; Ostonen et al., 2017), and 2) pioneer roots, which are fast-growing exploratory root tips that spread the root system and become transport roots in their basal part (Sutton & Tinus, 1983; Bagniewska-Zadworna et al., 2012; Freschet et al., 2021). Absorptive and pioneer roots have different sensitivities and responses to environmental changes (Polverigiani et al., 2011; Ding et al., 2020).

A root morphological trait that has recently been overlooked is the colourisation of fine roots in changing environments. Roots are predominantly regarded as white when first produced, turning brown during senescence (Wells & Eissenstat, 2003). With secondary xylem thickening, the roots may change from white to brown due to suberisation (Waisel et al., 2002). The anatomy of brown roots can be primary, secondary or even transitional between primary and secondary (McCrary & Comerford, 1998). Thus, brown roots can function and be part of nutrient acquisition, however usually with reduced rates of nutrient uptake and respiration (Van Rees & Comerford, 1990; Comas et al., 2000). The rate of colour changes can be initiated or even magnified by changes in the environment.

Previous studies have shown that increased soil temperature or water deficiency increases the browning rate of roots (Rogers, 1939; Bartsch, 1987). The browning of fine roots can also be attributed to accelerated lignin and suberin deposition in root tissues in response to changes in soil moisture to restrict water loss from the roots (Cruz et al., 1992; Polverigiani et al., 2011). To assess the developmental stage of fine roots, colourisation can also be considered (McCrary & Comerford, 1998). A study that classified first- and second-order fine roots into white and brown roots found that white terminal roots were thicker and had lower root tissue density than brown fine roots (Rewald et al., 2014), indicating the possibility of classifying roots based on their colour.

In addition to acquiring and storing carbon (C), plant roots exude primary and secondary metabolites into the soil, which influences rhizosphere microbial communities and nutrient availability (Jones et al., 2004; Haichar et al., 2014). Up to 20% of photosynthesised carbon can be either actively or passively exuded into soil (Whipps, 1990; Pinton et al., 2001; Marschner, 2012). Environmental changes, especially stressful conditions, such as drought or soil warming, have been shown to increase the exudation rate in various species' roots (Yin et al., 2013; Preece et al., 2018). Root exudation supports the activity of rhizosphere microbial communities that are carbon-limited; in turn, the availability of phosphorus, nitrogen and other mineral nutrients in soil is enhanced (Meier et al., 2017; Canarini et al., 2019). Microbial activity is highest near root tips (Herron et al., 2013), while mycorrhizal absorptive roots and fast-growing pioneer roots are expected to exude carbon compounds at the highest rate. At the same time, the dominant nitrogen form in the soil may affect the activity of microbial communities in the rhizosphere, as well as the carbon exudation rate. From a methodological point of view, C exudation is measured mainly on fine root segments, considering diameter classes, but not the share of absorptive, transport and especially pioneer roots separately (Phillips et al., 2008; Meier et al., 2020).

Fine root respiration accounts for a significant proportion of total soil respiration, 45–60%, on average (Hanson et al., 2000; Kukumägi et al., 2017). Root respiration is highest in absorptive roots (Trocha et al., 2017); however, the respiration of functionally different roots has rarely been measured. Changes in the soil environment influence the root respiration rate; for example, drought decreases, but soil warming increases the root respiration rate (Zogg et al., 1996; Burton et al., 1998; Pumpanen et al., 2012). The effect of elevated air humidity on fine root respiration is, however, still unknown.

## 1.4. Studied tree species

Three early successional light-demanding tree species, *Populus × wettsteinii*, *Betula pendula*, *Pinus sylvestris* and two late successional shade-tolerant species, *Picea abies* and *Tilia cordata*, were investigated. Hybrid aspen (*Populus × wettsteinii* Hämet-Ahti) is a fast-growing deciduous tree species favoured in short-rotation plantations in northern Europe (Tullus et al., 2012a). Poplars in general demand high nutrient levels and require adequate soil moisture throughout the growing season (Stanturf & van Oosten, 2014). Hybrid and trembling aspen are capable of using both inorganic N forms as a nitrogen source but seem to prefer ammonium rather than nitrate (Choi et al., 2005). Silver birch (*Betula pendula* Roth.) is a pioneer species that is widely distributed throughout Europe (Beck et al., 2016). *Betula pendula* grows best in moderately fertile and well-drained soils (Hynynen et al., 2010; Beck et al., 2016). Scots pine (*Pinus sylvestris* L.) is the most common tree species in Estonia and one of the most widely distributed coniferous species in the northern hemisphere because of its wide ecological amplitude (Hytteborn et al., 2005). *Pinus sylvestris* tolerates drought and usually grows on nutrient-poor sandy soils, where it is not outcompeted by other species (Mátyás et al., 2004). Norway spruce (*Picea abies* (L.) H. Karst.) is the second most common conifer species in Estonia (Estonian Environmental Agency, 2022). *Picea abies* prefers wetter sites and acidic soil and is quite vulnerable to changing topsoil moisture conditions because of its shallow root system (Farjon, 2010). The small-leaved linden (*Tilia cordata* Mill.) is the only natural linden species growing in Estonia, with the most northern growth area in southern Finland. With climate warming, the distribution area of small-leaved linden has been predicted to expand even further north (Hemery et al., 2010; Eaton et al., 2016). *Tilia cordata* grows on nutrient-rich, moderately moist, neutral or alkaline soils (Radoglou et al., 2009).

## 1.5. Aims of this thesis

The objective of this study was to analyse the ecophysiological adaptation mechanisms of five hemiboreal tree species on two soil nitrogen sources at different air humidity treatments. The aboveground measurements included tree biomass allocation, photosynthesis, transpiration rate and the leaf nutrient concentrations. The focus of this thesis was on the belowground acclimation of tree saplings. Fine root biomass, growth dynamics, morphology, functional distribution, phenology and fine root carbon fluxes, such as exudation and respiration in changing environmental conditions, were analysed. The aim was to advance time- and resource-consuming root research by introducing smart technologies and deep learning techniques.

The specific aims were to elucidate the effects of elevated relative air humidity and different soil nitrogen sources on:

- 1) Tree water flux and related nutrient uptake (**I, II, IV**);
- 2) Tree growth and biomass allocation, including the functional distribution of absorptive, pioneer and transport roots (**II, IV**);
- 3) Fine root morphology, C exudation and respiration and whether these depend on trees successional status and phylogenetic relatedness (**II, IV**);
- 4) Fine root seasonal growth dynamics. To understand the changes in root phenology, the formation of young white fine roots and root browning were analysed separately (**III**).

The main hypotheses were as follows:

- 1) Elevated air humidity decreases transpiration and water mass-flow-related nitrogen uptake in trees (**I, II, IV**).
- 2) Elevated air humidity increases fine root C exudation and respiration at the expense of carbon allocation to biomass. The carbon allocated to fine root C exudation is influenced by leaf photosynthetic capacity and fine root functional distribution (**II, IV**).
- 3) Elevated air humidity and the preferred soil N source increase fine root growth and change root phenology (the share of young white roots and senescing brown roots) over time (**III**).
- 4) The ecophysiological acclimation mechanisms to environmental change are inherent in the successional status of the studied tree species (**IV**).

## 2. MATERIAL AND METHODS

### 2.1. Experimental setup

Four separate experiments with comparable treatments were conducted on five tree species, including 20 one-year-old micropropagated *Populus × wettsteinii*, 20 two-year-old *Betula pendula*, 32 five-year-old *Pinus sylvestris*, 24 three-year-old *Picea abies* and 12 four-year-old *Tilia cordata* saplings. Trees were grown for four months in two double-sided Percival AR-95 HIL (Percival Scientific Inc., USA) growth chambers at a constant temperature ( $\sim 21.6$  °C) and light intensity ( $\sim 400\text{--}800$   $\mu\text{mol m}^{-2} \text{s}^{-1}$  at the top of the saplings). The  $[\text{CO}_2]$  in chambers was measured irregularly and it varied between 400–600 ppm. The lengths of night and day in the chambers were 8 h and 16 h, respectively, for all tree species. Each sample tree was planted in a 10-litre pot filled with sphagnum peat, containing  $\sim 900$  g oven-dried peat mass. The growing medium in the pots also contained 500 g granite gravel ( $\varnothing$  2–6 mm) and 130 g milled limestone. Half of the trees of each species were fertilised with nitrate as the main nitrogen source (each pot contained 1.12 g  $\text{NO}_3^-$ -N, 0.1 g  $\text{NH}_4^+$ -N) and the other half of the trees were fertilised with ammonium as the main nitrogen source (each pot contained 1.10 g  $\text{NH}_4^+$ -N, 0.1 g  $\text{NO}_3^-$ -N). The other mineral elements added to the growth substrate per pot were 0.33 g P ( $\text{P}_2\text{O}_5$ ), 1.24 g K ( $\text{K}_2\text{O}$ ), 0.27 g Ca ( $\text{CaO}$ ), 0.27 g Mg ( $\text{MgO}$ ,  $\text{MgOSO}_3$ ) and 0.56 g S ( $\text{SO}_3$ ,  $\text{MgOSO}_3$ ). To provide microelements, the saplings were fertilised with a 2 mL Agrimix-Micro Profi (INTERMAG, Poland) fertiliser. The pH of the growth substrate was 6.0–6.4. The air humidity treatments were as follows: moderate (mRH), where the chamber RH values were set at 80% and 65% during night and day, respectively, and elevated (eRH), where the chamber RH values were set at 80% during both night and day. To compensate for water loss due to transpiration, every plant was weighed and watered every morning to restore the soil water reserve and maintain the upper limit of the soil water content at 60% of the field capacity. To exclude evaporation from the soil, the soil surface of the pots was covered with aluminium foil. From the pot weight and leaf/needle area data, the whole tree transpiration rate ( $E$ ,  $\text{g m}^{-2}\text{h}^{-1}$ ) was calculated on the 8<sup>th</sup>–9<sup>th</sup> week of the experiments, when the leaf area of the trees was highest.

### 2.2. Tree water flux, leaf/shoot gas exchange and nutrient concentration measurements

The hydraulic conductance of whole shoots ( $K_s$ ) and their parts, leaves and stems, was determined with a high-pressure flow metre (HPFM; Dynamax, USA) applied in a quasi-steady-state mode and using deionised water at the end of the experiment. The hydraulic conductance of the root system ( $K_r$ ) was measured in situ by

applying the HPFM in transient mode. All aboveground hydraulic conductance measurements and root hydraulic conductance are expressed per unit leaf area. Whole-plant hydraulic conductance ( $K_{\text{plant}}$ ) was calculated as follows:

$$K_{\text{plant}} = \frac{1}{1/K_s + 1/K_r}$$

The net photosynthesis rate ( $P_{\text{net}}$ ,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) of the deciduous species was measured in three fully developed sample leaves per tree using a portable gas analyser CIRAS-2 (PP-systems, Amesbury, MA, USA). In *P. × wettsteinii* and *T. cordata*, the sample leaves were randomly selected from the upper canopy position. In *B. pendula*, the third, fifth and seventh leaves from the top of the upper canopy branch were measured. The  $P_{\text{net}}$  of *P. sylvestris* of one previous and two current year shoots (each bearing ~60 needles) was measured inside a growth chamber with CIRAS-2 provided with a conifer cuvette. Similarly, the  $P_{\text{net}}$  of *P. abies* was measured in two current-year shoots. In *P. × wettsteinii* and *B. pendula*, 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 *T. cordata* and *P. abies*, daytime gas exchange was measured at a PAR of  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ , using the external light unit of the cuvette. In *P. sylvestris*, 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 of  $\sim 400 \mu\text{mol m}^{-2} \text{s}^{-1}$ . All gas exchange measurements were conducted at a constant temperature ( $22 \text{ }^\circ\text{C}$ ), external  $\text{CO}_2$  concentration ( $\sim 400 \text{ ppm}$ ) and the ambient RH was  $\leq 70\%$  inside the cuvette to avoid water vapour condensation in the measuring unit.

The total leaf area at the end of the experiment was measured with an area metre LI-3100C (LICOR Biosciences, USA). In conifers, the projected area of a subsample of 100 needles from previous and current years was measured. The biomass (stem/branches, leaves/needles) was dried 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, dry mass and total needle dry mass. The nitrogen, phosphorous and potassium concentrations of leaves and needles were determined using a Kjeltac Auto 1030 Analyser (FOSS Tecator AB, Höganäs, Sweden).

### 2.3. Fine root carbon exudation and respiration measurements

Root carbon exudates were collected from one lateral fine root segment ( $\sim 10 \text{ cm}$  long) per sapling following the culture-based cuvette method (Phillips et al., 2008) at the end of the experiments. Intact fine root segments of all tree species contained absorptive and transport roots, as well as pioneer root tips. Each sapling was taken out of its pot with the soil ball, which was tightly covered with plastic

film to avoid drying and a root segment was chosen and carefully cleaned of soil particles. Since the saplings of Norway spruce were tightly packed into the transparent pots and removing the soil ball would have damaged the roots, we conducted exudation measurements on one side of the pot, digging carefully deeper from the top of the soil until the root segment was found. Each root sample was placed into a sterile plastic 30 mL syringe tube filled with ~20 mL of sterile glass beads ( $\emptyset$  0.5–1.25 mm) to imitate mechanical support and soil porosity. The syringe tube was sealed with a rubber septum covered with parafilm, with a wedge cut for the root to maintain contact with the plant and the tube was filled with C-free nutrient solution (0.5 mM  $\text{NH}_4\text{NO}_3$ , 0.1 mM  $\text{KH}_2\text{PO}_4$ , 0.2 mM  $\text{K}_2\text{SO}_4$ , 0.2 mM  $\text{MgSO}_4$  and 0.3 mM  $\text{CaCl}_2$ ). After 24 h of stabilisation in the syringe, the roots were flushed three times with clean carbon-free solution to remove the organic C exuded during the stabilisation period and incubated for the next 24 h with fresh C-free solution. Exudate-containing samples were collected in 40 mL glass vials with silicone caps and stored at 4 °C until determination of total organic carbon (TOC,  $\text{mg C l}^{-1}$ ) by a Vario TOC analyser (Elementar GmbH, Germany). All samples were analysed within 24 h after collection. TOC was multiplied by the quantity of the solution and exudation was calculated by dividing the carbon content by the surface area ( $\text{Ex}_{\text{C\_area}}$ ,  $\mu\text{gC cm}^{-2}\text{day}^{-1}$ ) and the dry mass of fine root segments ( $\text{Ex}_{\text{C\_mass}}$ ,  $\mu\text{gC g}^{-1}\text{day}^{-1}$ ).

At the end of the exudation measurements and before the fractionation of saplings, similar root segments were collected for fine root respiration measurements. The respiration of fine roots ( $\text{CO}_2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) was measured with a CIRAS-2 equipped with a conifer cuvette. The fine root sample was rinsed to remove soil particles and immediately placed into the conifer cuvette. The respiration values were recorded after ~5 min when the readings had stabilised. The measurements were carried out at a constant cuvette temperature (22 °C), external  $\text{CO}_2$  concentration (~400 ppm) and high RH (~90%) inside the cuvette to avoid root sample drying during respiration measurements. The fine root surface area was measured with WinRHIZO™ Pro (Regent Instruments Inc., 2003) to calculate fine root respiration per unit fine root area ( $R_{\text{root\_area}}$ ,  $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$ ) and dry weight was used to calculate the per unit fine root dry weight ( $R_{\text{root\_mass}}$ ,  $\mu\text{mol CO}_2 \text{g}^{-1} \text{s}^{-1}$ ).

All fine root samples were cleaned from glass beads and soil particles, and the following characteristics were measured with WinRHIZO™ Pro (Regent Instruments Inc., 2003): sample root length (cm), surface and projection area ( $\text{cm}^2$ ), average root diameter (AD, mm) and number of root tips. Different parameters were calculated, including the specific root area ( $\text{SRA}=\text{surface area/mass}$ ,  $\text{m}^2 \text{kg}^{-1}$ ), specific root length ( $\text{SRL}=\text{length/mass}$ ,  $\text{m g}^{-1}$ ), root tissue density ( $\text{RTD}=\text{mass/volume}$ ,  $\text{kg m}^{-3}$ ), and branching intensity ( $\text{BI}=\text{tips/mass}$ ,  $\text{mg}^{-1}$ ) (Ostonen et al., 1999). The dry weight (g) of all samples was measured after drying at 65 °C for 48 h. Nine fine root samples in hybrid aspen, 10 in silver birch, 32 samples in Scots pine, 24 in Norway spruce and 12 in small-leaved linden were divided into absorptive, pioneer and transport roots (Supplementary Fig. 1; II). The length (L, cm) and surface area (SA,  $\text{cm}^2$ ) of every subsample were measured separately

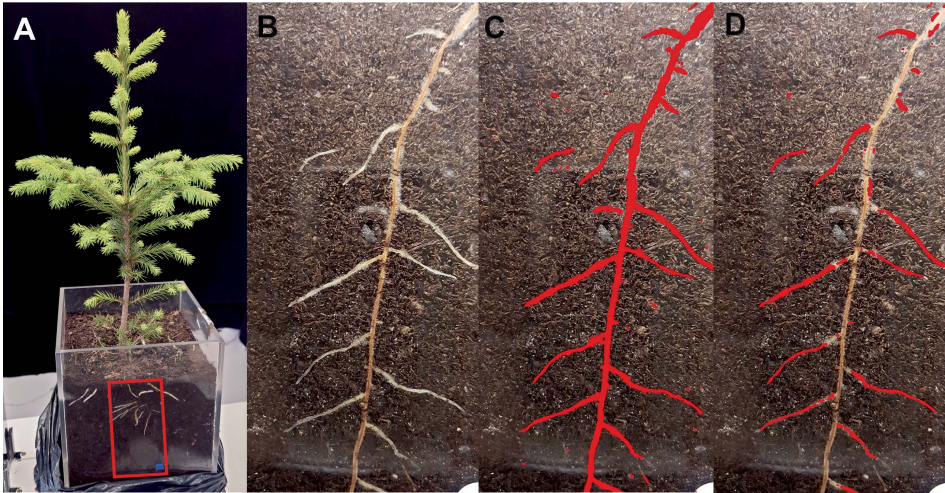


with WinRhizo, and after drying at 65°C for 48 h, the dry weight (DW, g) was measured. Subsequently, the absorptive, pioneer and transport root proportion (%) of total fine root sample area (SA), length (L) and dry weight (DW) were calculated.

## 2.4. Imaging and analysis of *Picea abies* roots

To follow the growth dynamic, photos of the fine roots of *Picea abies* were taken (Fig 1AB). The transparent pot with a sapling was lifted out of the chamber once a week, resulting in six imaging sessions (Fig. 1; III). The first imaging session was on the 22nd day after planting. Photos were taken with two different personal mobile phones from each of the four sides of the boxes, with 572 images in total. To maintain a fixed distance between the plants and the phone, a stand was built from a cardboard box. We imaged all four sides of each pot. Two perpendicular rulers with mm accuracy were glued onto the same region of the pot while imaging. Photos were later cut to the same width and length and resized to 1300×2700 pixels using IrfanView 4.56 (Irfan Skiljan, Wiener Neustadt, Austria).

Image analysis was performed with RootPainter (Smith et al., 2022), a deep learning programme, to train a model to segment roots and measure the total and young (white) root projection area (PA). The training dataset consisted of image tiles of the original photos. Roots were marked red and background green using the RootPainter client graphical user interface. Via the training process, the programme created a model for recognising roots, which was then corrected accordingly. In each subsequent image tile, a blue area is presented, which is the root area suggested by the RootPainter model. The annotation procedure is as follows: marking an area red teaches the programme to include this as a root, and marking an area green teaches the programme the errors that should be excluded in creating the model. The first model ( $M1_{total}$ ) was trained to recognise all roots and exclude soil, and the second model ( $M2_{white}$ ) was taught to exclude roots with light to dark brown colour and to detect only white roots, root tips and root hairs (Fig. 1CD). Root browning is an indicator of the beginning of root senescence (Wells & Eissenstat, 2003). Thus, we considered white roots to be young and brown roots to be older. Young white roots are mainly pioneer roots, which are usually longer and have a sharp root tip compared to short absorptive roots with a more rounded root tip (Löhmus et al., 1986). The models were taught until all different parts of the images were represented, such as reflection from the camera, water droplets as condensation, fungal hyphae, or other non-soil or non-root-related errors. Based on the segmentation, the programme calculates the projection area of roots in pixels, which is then converted to cm<sup>2</sup> according to the photo size.



**Figure 1.** Root imaging set up, red window represents the imaged area (A), an example image (B), Model 1 ( $M1_{total}$ ) identified all roots (C), Model 2 ( $M2_{white}$ ) identified only young white root tips, root hairs (D).

## 2.5. Data analysis

Statistical analysis was conducted in STATISTICA 7.1 (StatSoft Inc., USA), and figures were constructed in SigmaPlot Version 12.5 (Systat Software, Inc., USA), RStudio Version 1.3.1093 (RStudio, PBC, MA, USA) or Microsoft Excel 2019 version 1808. A factorial analysis of variance (ANOVA) test was used to determine the effects of nitrogen source on leaf, stem, root and whole tree hydraulic conductance on 12 *B. pendula* trees. The effect between air humidity treatments on total, aboveground, belowground, leaves, fine roots and the proportions of fine roots (absorptive, pioneer, transport roots) of each tree species was calculated with one-way ANOVA (type III). A Kruskal–Wallis multiple comparison analysis was used for the C exudation analysis between the air humidity treatments of each tree species. There were two exudation measurements for each *Picea abies* sapling ( $N = 48$ ) but one analysis per tree for morphology ( $N = 24$ ). The Tukey HSD test was used to determine the effects of air humidity on fine root respiration, morphological traits and physiological measurements (net photosynthesis and transpiration rate) within and between tree species, between successional groups and between deciduous and conifer groups. Nitrogen treatment did not affect the trees' biomass, fine root C exudation, respiration or morphological traits of the studied species, and the data of both N treatments were pooled together. The correlation between fine root C exudation and respiration of tree species, successional groups and phylogenetically related tree groups was conducted with Spearman correlation. The correlation between fine root traits and fine root proportions was conducted with Pearson correlation (Spearman correlation was used for the mass proportion of absorptive roots in *P. sylvestris*). The coefficient

of variation ( $cv = 100 \times (SD/mean)$ ) was checked for absorptive, pioneer and transport root length proportions for all tree species (Ostonen et al., 2007). The leaf nutrient percentages (nitrogen, phosphorous, potassium) between humidity or N source treatments were analysed with a non-parametric Kruskal–Wallis multiple comparison test.

In each imaging session, the effect of either humidity or soil N source on *Picea abies* fine root projection area was analysed with factorial ANOVA (type III). The proportion (%) of white roots' PA of total root PA ( $M2_{white}/M1_{total} \times 100$ ) was calculated separately for each treatment. The brown root proportion was calculated by subtracting the white root proportion from 100%. Each of the relative growth peaks of either the white or brown root projection area was different from the previous imaging session.

Redundancy analysis (RDA, Ter Braak & Šmilauer, 2002) was used to explain the variation between fine root morphological traits (AD, SRA, SRL, RTD, BI), including fine root carbon exudation rates (per root area (SA) and per dry weight (DW)) by following datasets 1) plant physiological variables and 2) proportions of functionally different roots within fine roots as explanatory variables. The plant physiological variables were net photosynthesis rate, transpiration rate, leaf N, P, K concentration, fine root respiration rate (per root surface area and per dry weight), leaf biomass, and fine root biomass. The functional distribution indicating variables were absorptive, pioneer and transport (L%, SA%, DW%) proportions within the fine root sample. To assess the effect of each explanatory dataset for each tree species, partial canonical analysis (forward selection) was performed at  $P < 0.05$  level, whereas soil N source and the proportion of pioneer roots with a significance level of  $P < 0.01$  (one-tailed test) (Legendre & Legendre, 2012). The significance of the RDA results was tested with a permutation test (Monte Carlo test (999);  $P < 0.01$ ).

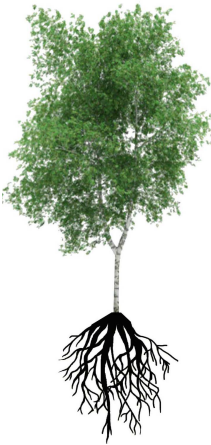
### 3. RESULTS

#### 3.1. Effects of air humidity and soil N sources

##### 3.1.1. Water fluxes

The average transpiration rate (E) of *P. × wettsteinii*, *B. pendula* and *T. cordata* was  $29 \pm 2$ ,  $26 \pm 1$  and  $17 \pm 1$  g m<sup>-2</sup> h<sup>-1</sup>, respectively (Fig. 6D). The average E of *P. sylvestris* and *P. abies* were  $33 \pm 1$  and  $21 \pm 2$  g m<sup>-2</sup> h<sup>-1</sup>, respectively. Elevated air humidity decreases the transpiration rate in all studied species ( $P < 0.05$ ), except for *T. cordata*, with an insignificant but similar trend. Only in *B. pendula* was the transpiration rate affected by the soil nitrogen source, where E was higher in nitrate-fertilised trees than in ammonium-fertilised trees (I, II).

In the case of *B. pendula*, whole-plant hydraulic conductance was higher in nitrate-fertilised trees compared to ammonium-fertilised trees (Fig. 2). In detail, the root system hydraulic conductance was also higher in NO<sub>3</sub><sup>-</sup> treatment compared to NH<sub>4</sub><sup>+</sup> treatment, but the difference between the treatments was not statistically significant in the leaves or stems.



	NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>
→ Whole tree hydraulic conductance (g m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	0.101±0.006 a	0.082±0.003 b
→ Leaf hydraulic conductance (g m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	0.32±0.023 a	0.268±0.016 a
→ Stem hydraulic conductance (g m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	0.26±0.021 a	0.22±0.018 a
→ Root hydraulic conductance (g m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup> )	0.35±0.024 a	0.272±0.013 b

**Figure 2.** The average ± standard error of whole tree, leaf, stem and root hydraulic conductance of *Betula pendula* saplings in nitrate (NO<sub>3</sub><sup>-</sup>) or ammonium (NH<sub>4</sub><sup>+</sup>) treatment. Small letters indicate a significant difference in each measured hydraulic conductance value between soil nitrogen treatments ( $P < 0.05$ ).

### 3.1.2. Tree biomass and belowground biomass fractions

The highest aboveground (AG), belowground (BG) and total biomass was found in *T. cordata*, followed by *P. sylvestris*, *P. × wettsteinii*, *B. pendula* and *P. abies* (Table 1). Only in *P. sylvestris* did the total biomass (also AG and BG biomass separately) increase significantly at eRH ( $P < 0.05$ ). The AG biomass of *T. cordata* increased significantly at eRH ( $P < 0.05$ ). The highest AB/BG biomass ratio was found in *P. abies*, whereas the lowest was found in *T. cordata*. The AB/BG biomass ratio was significantly higher in the eRH treatment compared to the mRH treatment in *P. × wettsteinii* and *T. cordata* ( $P < 0.05$ ). The fine root biomass of *P. sylvestris* increased at eRH, whereas *P. abies* showed a decrease in fine root biomass at eRH compared to mRH. This was mainly caused by the amount of transport roots within the fine roots, which increased in *P. sylvestris* and decreased in *P. abies* at eRH ( $P < 0.05$ ).

**Table 1.** The average  $\pm$  standard error of total, aboveground (AG), belowground (BG), leaf, fine root and partitioning of fine root (absorptive, pioneer, transport root) biomass of *Populus*  $\times$  *wetsteinii*, *Betula pendula*, *Pinus sylvestris*, *Picea abies* and *Tilia cordata* at moderate (mRH) or elevated (eRH) relative air humidity treatment. Lowercase letters indicate the significant difference of biomass between moderate (mRH) and elevated (eRH) air humidity ( $P < 0.05$ ); insignificant differences are not marked.

Biomass (g)	<i>Populus</i> $\times$ <i>wetsteinii</i>		<i>Betula pendula</i>		<i>Pinus sylvestris</i>		<i>Picea abies</i>		<i>Tilia cordata</i>	
	mRH	eRH	mRH	eRH	mRH	eRH	mRH	eRH	mRH	eRH
Total	112 $\pm$ 7	100 $\pm$ 7	98 $\pm$ 6	93 $\pm$ 6	108 $\pm$ 6 b	126 $\pm$ 5 a	79 $\pm$ 6	74 $\pm$ 6	137 $\pm$ 20	183 $\pm$ 15
AG	86 $\pm$ 5	81 $\pm$ 5	76 $\pm$ 5	74 $\pm$ 5	86 $\pm$ 5 b	100 $\pm$ 3 a	65 $\pm$ 5	62 $\pm$ 5	85 $\pm$ 13 b	127 $\pm$ 11 a
BG	26 $\pm$ 2	19 $\pm$ 2	22 $\pm$ 1	20 $\pm$ 2	22 $\pm$ 6 b	26 $\pm$ 1 a	14 $\pm$ 1	12 $\pm$ 1	52 $\pm$ 7	55 $\pm$ 5
Leaf	31 $\pm$ 2	32 $\pm$ 2	24 $\pm$ 1	25 $\pm$ 1	42 $\pm$ 3	49 $\pm$ 3	23 $\pm$ 2	22 $\pm$ 2	19 $\pm$ 3	27 $\pm$ 3
Fine root	9 $\pm$ 0.7	7 $\pm$ 0.7	8 $\pm$ 0.8	7 $\pm$ 0.5	8 $\pm$ 0.7 b	11 $\pm$ 0.8 a	7 $\pm$ 0.7 a	5 $\pm$ 0.3 b	18 $\pm$ 3	15 $\pm$ 1
Absorptive root	0.7 $\pm$ 0.1	2.2 $\pm$ 0.7	1.1 $\pm$ 0.1	1.5 $\pm$ 0.2	1 $\pm$ 0.3	0.5 $\pm$ 0.06	0.4 $\pm$ 0.09	0.4 $\pm$ 0.08	2.1 $\pm$ 0.6	1.6 $\pm$ 0.2
Pioneer root	3.5 $\pm$ 0.08	1.6 $\pm$ 0.4	1.2 $\pm$ 0.4	0.8 $\pm$ 0.5	1 $\pm$ 0.1	1.3 $\pm$ 0.2	0.6 $\pm$ 0.09	0.4 $\pm$ 0.09	0.1 $\pm$ 0.03	0.1 $\pm$ 0.05
Transport root	5.2 $\pm$ 0.2	3.3 $\pm$ 1	6.9 $\pm$ 2.2	4.9 $\pm$ 0.5	6.3 $\pm$ 0.5 b	9.2 $\pm$ 0.7 a	5.7 $\pm$ 0.6 a	4 $\pm$ 0.3 b	15.5 $\pm$ 2.3	12.8 $\pm$ 1.3

### 3.1.3. Leaf chemistry

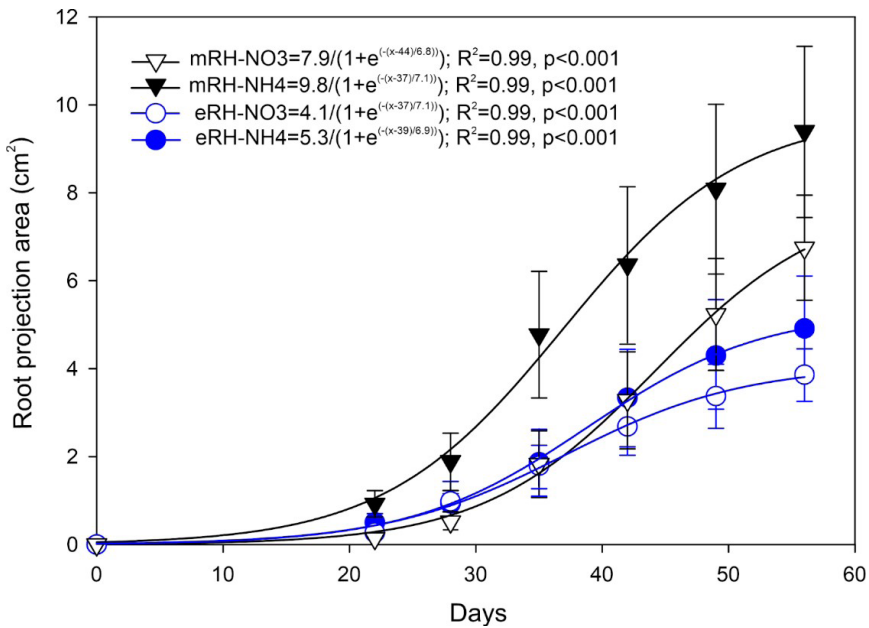
In *B. pendula*, the foliar N concentration was lower at eRH than at mRH (Table 2), and the difference was driven by nitrate-fed trees (I, II). The P% of *B. pendula* leaves was higher in  $\text{NH}_4^+$ -fertilised soil. Needle K% was higher in the *P. sylvestris* saplings grown in mRH than in eRH. The foliar N and P percentages in *P. abies* needles were higher in ammonium-fertilised soil compared to nitrogen-fertilised soil, irrespective of air humidity treatment. The leaves of *T. cordata* had higher P% and K% when grown in eRH conditions compared to mRH. *Tilia cordata* trees grown in nitrate had a higher N% compared to nitrate-fertilised trees.

**Table 2.** The average  $\pm$  standard error of leaf nitrogen (N), phosphorus (P), and potassium (K) content (%) of *Populus  $\times$  wettsteinii*, *Betula pendula*, *Pinus sylvestris*, *Picea abies* and *Tilia cordata*. Significant differences in humidity (RH) and soil nitrogen (N) sources were determined with the Kruskal–Wallis non-parametric test.

		<i>Populus <math>\times</math> wettsteinii</i>	<i>Betula pendula</i>	<i>Pinus sylvestris</i>	<i>Picea abies</i>	<i>Tilia cordata</i>
N%	Mean $\pm$ SE	2.65 $\pm$ 0.08	3.74 $\pm$ 0.05	1.6 $\pm$ 0.02	1.56 $\pm$ 0.04	3 $\pm$ 0.1
	RH	ns	< 0.05	ns	ns	ns
	N source	ns	ns	ns	< 0.005	< 0.05
P%	Mean $\pm$ SE	0.23 $\pm$ 0.007	0.27 $\pm$ 0.02	0.15 $\pm$ 0.003	0.13 $\pm$ 0.003	0.22 $\pm$ 0.01
	RH	ns	ns	ns	ns	< 0.05
	N source	ns	< 0.05	ns	< 0.05	ns
K%	Mean $\pm$ SE	1.46 $\pm$ 0.05	1.2 $\pm$ 0.03	0.53 $\pm$ 0.02	0.51 $\pm$ 0.01	1.14 $\pm$ 0.14
	RH	ns	ns	< 0.05	ns	< 0.05

### 3.1.4. Fine root growth dynamics

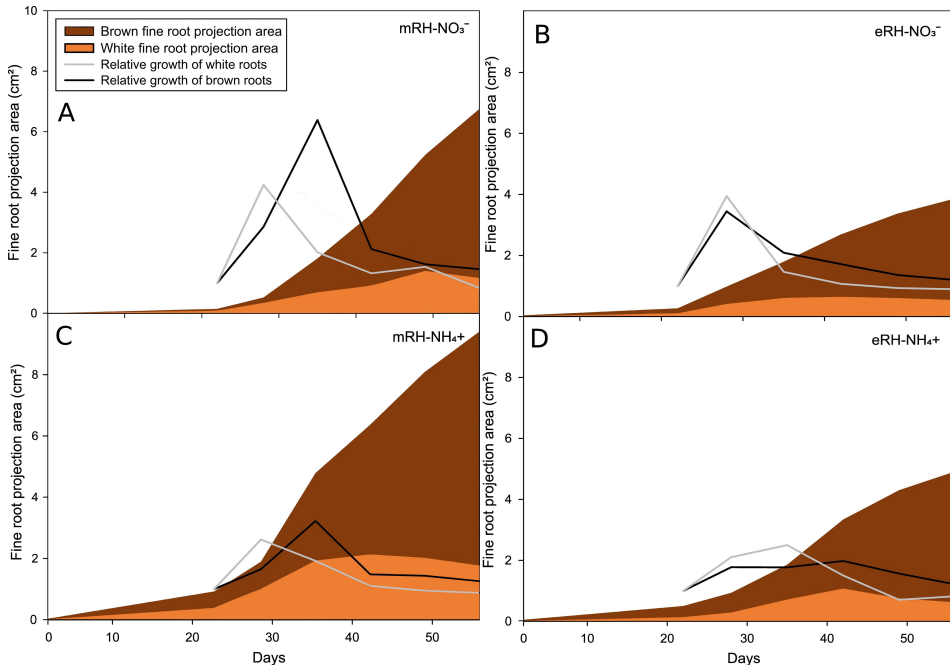
Fine root growth dynamics analysis of *Picea abies* showed that the fine root projection area (PA) followed a sigmoidal growth curve in all treatments (Fig. 3). Trees grown at moderate air humidity and in ammonium-fertilised soil had the highest fine root projection area. Fine root growth was affected by the nitrogen source in the soil; the PA was higher in  $\text{NH}_4^+$  treatments compared to  $\text{NO}_3^-$ -fertilised trees. The last imaging session showed a clear difference between air humidity treatments, indicating that, at the end of the experiment, the elevated air humidity significantly decreased the fine root PA.



**Figure 3.** Sigmoidal growth of the fine root projection area of *Picea abies* saplings. Whiskers indicate the standard error of root projection area per treatment ( $n = 6$ ) at each sampling time of 56 days.

The total fine root growth was analysed according to colour proportions, white and brown fine root area. The white root area peaked 28 to 35 days after planting, whereas root browning was already visible on the first imaging session (22nd day after planting) (Fig. 4). At moderate RH, the relative growth of white and brown roots reached a peak on the 28<sup>th</sup> and 35<sup>th</sup> day, respectively, showing a clear delay in brown root peak (III). At eRH, the peaks of the white and brown roots were reached in the same period, but the peaks coincided and stabilised earlier than at mRH.





**Figure 4.** The fine root projection area of model  $M1_{total}$  (brown area) and  $M2_{white}$  (orange area) at treatments moderate air humidity and nitrate –  $mRH-NO_3^-$  (A); moderate air humidity and ammonium –  $mRH-NH_4^+$  (B), elevated air humidity and nitrate –  $eRH-NO_3^-$  (C), and elevated air humidity and ammonium –  $eRH-NH_4^+$  (D) as a soil nitrogen source over time. Grey and black lines indicate the relative weekly growth rate of white young and older brown roots, respectively.

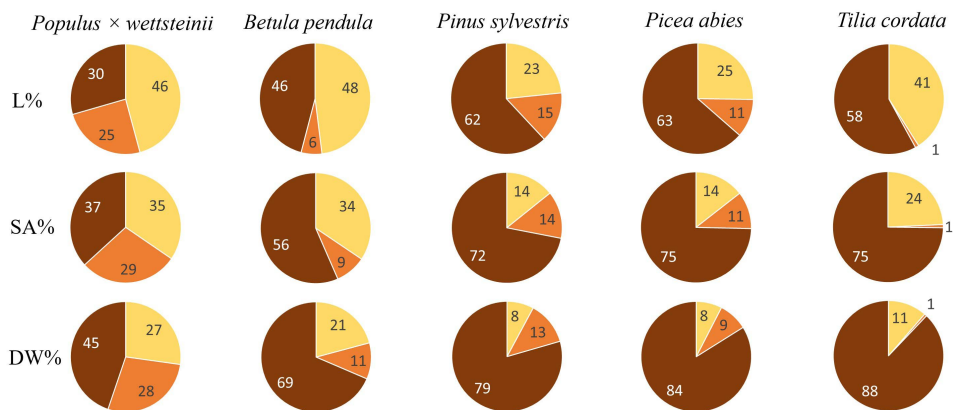
### 3.1.5. Fine root morphology and fine root proportioning

Fine root morphology differed between the early and late successional species (Table 2, IV). SRA, SRL and BI were significantly higher, while AD and RTD were significantly lower in early successional species compared to late successional species. Fine root morphology also differed between the deciduous and coniferous species (Table 2, IV). Average SRL, SRA, BI, RTD and BI were all higher in deciduous species compared to coniferous tree species. The average diameter of fine roots was higher in coniferous than in deciduous tree species. The increase in air humidity caused contrasting changes in the fine root morphology of different tree species. The average SRA in *P. sylvestris* decreased significantly because of the thicker roots at eRH, while RTD was not affected by RH treatment (Table 3). In *P. abies*, the RTD was significantly lower at eRH than at mRH. The increase in SRA at eRH compared to mRH in *B. pendula* was driven by the significantly decreased RTD (Table 3).

**Table 3.** The average and standard error of fine root morphological traits (AD—average diameter, mm; SRA—specific root area, m<sup>2</sup> kg<sup>-1</sup>; SRL—specific root length, m g<sup>-1</sup>; RTD—root tissue density, kg m<sup>-3</sup>; BI—branching intensity, mg<sup>-1</sup>), fine root carbon exudation per mass (EXC<sub>mass</sub>, mg C g<sup>-1</sup> day<sup>-1</sup>), fine root respiration (R<sub>root,mass</sub>, μmol CO<sub>2</sub> g<sup>-1</sup> s<sup>-1</sup>) at moderate (mRH) and elevated relative air humidity (eRH) treatments for *Populus × wettsteinii*, *Betula pendula*, *Pinus sylvestris*, *Picea abies* and *Tilia cordata*. Lowercase letters indicate trait significance when comparing the humidity treatment of each tree species (P < 0.05); insignificant differences are not marked.

Traits	<i>Populus × wettsteinii</i>		<i>Betula pendula</i>		<i>Pinus sylvestris</i>		<i>Picea abies</i>		<i>Tilia cordata</i>	
	mRH	eRH	mRH	eRH	mRH	eRH	mRH	eRH	mRH	eRH
AD	0.3±0.04	0.3±0.06	0.2±0.02	0.2±0.02	0.5±0.03 b	0.6±0.02 a	0.6±0.04	0.6±0.03	0.3±0.05	0.3±0.02
SRA	77±9	92±11	121±7 b	170±14 a	66±5 a	52±3 b	36±3	44±3	61±7	68±7
SRL	102±28	133±39	198±22	274±39	50±7 a	31±2 b	21±3	26±3	70±14	77±11
RTD	199±21	184±31	168±14 a	118±9 b	138±3	144±6	195±10 a	168±7 b	227±13	213±15
BI	37±10	56±22	72±9	82±14	20±3 a	12±1 b	10±2	12±2	44±9	46±8
EXC <sub>mass</sub>	1.4±0.7	2.7±1.3	1.8±0.6	3.3±0.8	4.1±0.9 a	2.0±0.4 b	0.4±0.06	0.7±0.1	1.7±1.0	0.4±0.07
R <sub>root,mass</sub>	0.031±0.002	0.029±0.002	0.24±0.02	0.19±0.02	0.09±0.005	0.085±0.004	0.15±0.04	0.1±0.02	0.08±0.006	0.09±0.01

The variation in absorptive root L% was highest in *P. abies* and the variation of transport root L% was highest in *P. × wettsteinii* (cv were approximately 53% and 40%, respectively). The lowest  $L_{\text{absorp}}$  and  $L_{\text{transp}}$  was observed in *B. pendula* (cv ~10%). The pioneer root L% varied most in *T. cordata* fine roots and least in *P. sylvestris*. In *P. abies*, the SA% proportions of absorptive and pioneer roots at the end of the experiment were 14% and 11% of the total root surface area, respectively (Fig. 5). From the *P. abies* fine root photos analysed, the white young roots were about 13–19%, which consisted of absorptive roots but mainly pioneer roots (III). Higher humidity decreased the absorptive and transport root proportions in *P. sylvestris* (II). Early successional species had a significantly higher share of pioneer roots (L%, SA%) and fewer transport roots (SA%) compared to the studied late successional species (IV). The amount of absorptive roots was similar in both successional groups. Deciduous species had significantly more absorptive roots (L%, SA%) (IV). Coniferous species had a higher proportion of pioneer and transport roots (L%, SA%).



**Figure 5.** Pie chart showing the proportion per length (L%), surface area (SA%), dry weight (DW%) of absorptive (yellow), pioneer (orange) and transport (brown) roots within fine root.

The share of absorptive roots was negatively correlated with the average diameter of fine roots and positively correlated with SRA, SRL and BI (Table 4). Pioneer root L% were positively correlated with AD and negatively correlated with SRL in *P. sylvestris* and *T. cordata*. The DW% of the transport root was negatively correlated with SRA, SRL and BI for all species (except *P. × wettsteinii*).

**Table 4.** The correlation between the fine root proportions (%) of absorptive (absorb), pioneer and transport (transp) roots per length (L), surface area (SA) or dry weight (DW) and fine root morphological traits (AD—average diameter, mm; SRA—specific root area, m<sup>2</sup> kg<sup>-1</sup>; SRL—specific root length, m g<sup>-1</sup>; RTD—root tissue density, kg m<sup>-3</sup>; BI—branching intensity, mg<sup>-1</sup>). Significant correlations are marked in bold (Pearson correlation, P < 0.05).

<i>Populus× wettsteinii</i>	L <sub>absorb</sub>	L <sub>pioneer</sub>	L <sub>transp</sub>	SA <sub>absorb</sub>	SA <sub>pioneer</sub>	SA <sub>transp</sub>	DW <sub>absorb</sub>	DW <sub>pioneer</sub>	DW <sub>transp</sub>
AD	<b>-0,84</b>	0,50	<b>0,85</b>	-0,40	0,11	0,32	0,00	-0,14	0,12
SRA	0,46	-0,29	-0,54	0,48	-0,22	-0,43	0,36	-0,02	-0,38
SRL	<b>0,75</b>	-0,55	<b>-0,67</b>	0,59	-0,33	-0,42	0,33	-0,06	-0,32
RTD	0,54	-0,42	-0,36	0,10	-0,13	0,08	-0,22	-0,03	0,27
BI	<b>0,77</b>	-0,63	-0,62	0,64	-0,41	-0,42	0,40	-0,16	-0,31
<i>Betula pendula</i>									
AD	0,12	-0,05	-0,09	-0,13	0,00	0,24	-0,45	0,11	0,41
SRA	-0,03	0,37	-0,38	0,14	0,33	<b>-0,66</b>	0,51	0,25	<b>-0,82</b>
SRL	-0,03	0,26	-0,27	0,18	0,20	-0,58	0,57	0,11	<b>-0,75</b>
RTD	-0,09	-0,33	0,49	0,02	-0,35	0,42	-0,07	-0,40	0,45
BI	0,11	0,18	-0,39	0,23	0,11	-0,54	0,61	0,03	<b>-0,70</b>
<i>Pinus sylvestris</i>									
AD	-0,25	<b>0,45</b>	-0,06	<b>-0,52</b>	<b>0,49</b>	0,16	<b>-0,52*</b>	<b>0,50</b>	0,16
SRA	<b>0,39</b>	<b>-0,45</b>	-0,08	<b>0,64</b>	<b>-0,44</b>	-0,31	<b>0,52*</b>	<b>-0,41</b>	<b>-0,36</b>
SRL	<b>0,47</b>	<b>-0,50</b>	-0,14	<b>0,71</b>	<b>-0,48</b>	-0,35	<b>0,51*</b>	<b>-0,43</b>	<b>-0,39</b>
RTD	-0,08	0,02	0,05	-0,18	-0,01	0,18	<b>-0,20*</b>	-0,03	0,27
BI	<b>0,56</b>	<b>-0,51</b>	-0,25	<b>0,78</b>	<b>-0,47</b>	<b>-0,43</b>	<b>0,70*</b>	<b>-0,41</b>	<b>-0,49</b>
<i>Picea abies</i>									
AD	<b>-0,58</b>	0,32	0,41	<b>-0,60</b>	0,16	<b>0,43</b>	<b>-0,70</b>	-0,07	<b>0,55</b>
SRA	0,14	0,22	-0,28	0,21	0,29	-0,35	0,40	<b>0,43</b>	<b>-0,59</b>
SRL	0,37	-0,02	-0,37	<b>0,45</b>	0,09	<b>-0,45</b>	<b>0,66</b>	0,31	<b>-0,69</b>
RTD	0,41	-0,41	-0,19	0,38	-0,32	-0,15	0,27	-0,26	-0,01
BI	<b>0,79</b>	-0,27	<b>-0,66</b>	<b>0,83</b>	-0,10	<b>-0,67</b>	<b>0,90</b>	0,07	<b>-0,70</b>
<i>Tilia cordata</i>									
AD	-0,53	<b>0,86</b>	0,50	<b>-0,64</b>	<b>0,70</b>	<b>0,61</b>	<b>-0,76</b>	0,28	<b>0,73</b>
SRA	0,41	-0,51	-0,39	0,46	-0,34	-0,44	<b>0,64</b>	0,09	<b>-0,65</b>
SRL	0,39	<b>-0,58</b>	-0,36	0,48	-0,41	-0,47	<b>0,69</b>	0,03	<b>-0,70</b>
RTD	-0,03	-0,24	0,02	0,10	-0,31	-0,09	0,06	-0,40	-0,01
BI	<b>0,59</b>	<b>-0,67</b>	-0,57	<b>0,73</b>	-0,50	<b>-0,72</b>	<b>0,88</b>	0,00	<b>-0,89</b>

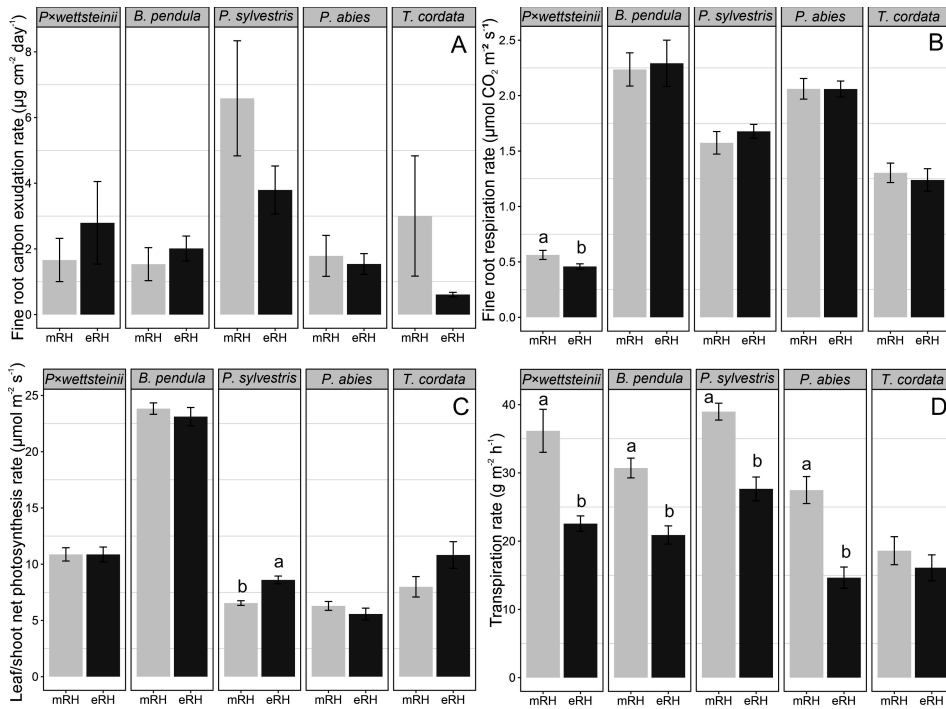
\* Spearman correlation ( $P < 0.05$ ).

### 3.1.6. Tree C fluxes: leaf photosynthesis, fine root C exudation and respiration

Leaf net photosynthesis ( $P_{\text{net}}$ ) was on average  $10.9 \pm 0.4$ ,  $23.5 \pm 0.5$  and  $9.4 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$  in *P. \times wettsteinii*, *B. pendula* and *T. cordata*, respectively (Fig. 6C). The shoot average  $P_{\text{net}}$  of *P. sylvestris* and *P. abies* was  $7.6 \pm 0.3$  and  $5.9 \pm 0.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ , respectively. Net photosynthesis was higher at eRH compared to mRH in *P. sylvestris* ( $P < 0.05$ ).

The C exudation per root DW was on average  $2.0 \pm 0.6$ ,  $2.4 \pm 0.4$  and  $1.05 \pm 0.5 \text{ mg C g}^{-1} \text{ day}^{-1}$  for *P. \times wettsteinii*, *B. pendula* and *T. cordata*, respectively (Table 3). The average  $\text{Ex}_{\text{C\_mass}}$  was  $3.0 \pm 0.4$  and  $0.8 \pm 0.2 \text{ mg C g}^{-1} \text{ day}^{-1}$  for *P. sylvestris* and *P. abies*, respectively. *Pinus sylvestris* had the highest fine root C exudation rate per DW of all tree species and decreased at eRH compared to mRH (Table 3).  $\text{Ex}_{\text{C\_area}}$  was higher in *T. cordata* at mRH compared to eRH but remained insignificant (Fig. 6A). *Populus \times wettsteinii* and *B. pendula* showed an increase in the fine root exudation rate at eRH, but the increase remained insignificant (Fig. 5A).

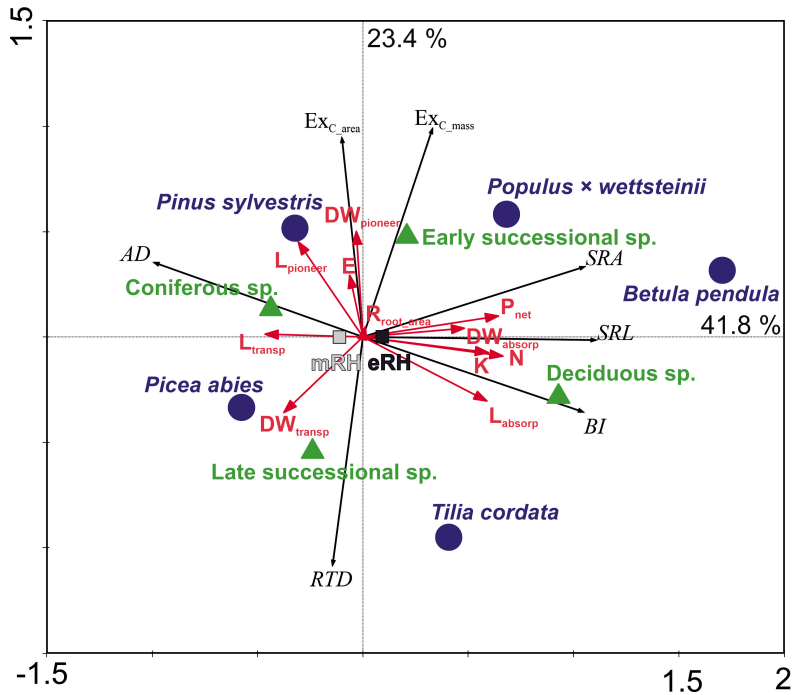
The fine root respiration rates per root DW for *P. \times wettsteinii*, *B. pendula* and *T. cordata* were  $0.03 \pm 0.001$ ,  $0.2 \pm 0.01$  and  $0.08 \pm 0.005 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ , respectively (Table 3). The  $R_{\text{root\_mass}}$  for *P. sylvestris* and *P. abies* was  $0.9 \pm 0.03$  and  $0.08 \pm 0.004 \mu\text{mol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$ , respectively. The highest fine root respiration rate was  $2.3 \pm 0.1 \mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ , on average, in *B. pendula* (Fig. 6B). In *P. \times wettsteinii*, the fine root respiration per fine root surface area decreased significantly under eRH compared to mRH ( $P < 0.05$ ). Fine root respiration correlated positively with fine root C exudation rate only within early successional and within coniferous tree groupings ( $\rho = 0.24$  and  $0.58$ , respectively,  $P < 0.05$ ).



**Figure 6.** 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); leaf/shoot net photosynthesis rate (C); transpiration rate (D) of *Populus × wettsteinii*, *Betula pendula*, *Pinus sylvestris*, *Picea abies* and *Tilia cordata*. The lowercase letters show the significant difference within a tree species between moderate (mRH) and elevated (eRH) humidity treatments ( $P < 0.05$ ).

### 3.2. Successional status vs phylogenetic relatedness

According to the redundancy analysis based on fine root traits, the investigated tree species can be divided into the following groups: deciduous and coniferous species separated along the first axis that described about 42% of the fine root morphological variation and early and late successional tree species grouped along the second axis that described about 23% of the variation (Fig. 7). The first axis was positively correlated with SRA, SRL and BI, which increased towards *P. × wettsteinii* and *B. pendula* and was related to higher photosynthesis rate, leaf N and P content, and increasing proportion of absorptive roots of total fine roots. The average fine root diameter increased towards coniferous species and was related to a higher proportion of transport roots within fine roots. The second axis correlated negatively with fine root RTD and positively with C exudation rate, which increased towards early successional species and was related to transpiration rate and a higher proportion of pioneer roots within fine roots. The higher share of transport roots correlated with the increase in fine root RTD towards late successional species.



**Figure 7.** The ordination biplot based on redundancy analysis of the fine root morphological traits and carbon exudation rates in relation to the proportion (L—length, SA—surface area, DW—dry weight, %) of the absorptive (absorp), pioneer (pioneer) and transport (transp) roots of the fine root sample,  $R_{\text{root\_area}}$ —fine root respiration per sample mass ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ),  $P_{\text{net}}$ —net photosynthesis rate ( $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ),  $E$ —transpiration rate ( $\text{g m}^{-2} \text{ h}^{-1}$ ), leaf nitrogen percentage (N), leaf potassium percentage (K) (red arrows) and tree species (blue circles). The green triangles show the trees grouped into early or late successional species or into deciduous or coniferous species. The relative eigenvalues of axes 1 and 2 are 41.8% and 23.4%, respectively. In total, the model described 71.4% of the variation in fine root traits (999 Monte Carlo permutation test,  $P = 0.001$ ). Abbreviations for dependent variables: AD—mean fine root diameter (mm), SRA—specific root area ( $\text{m}^2 \text{ kg}^{-1}$ ); SRL—specific root length ( $\text{m g}^{-1}$ ); RTD—root tissue density ( $\text{kg m}^{-3}$ ); and BI—branching intensity ( $\text{mg}^{-1}$ ),  $\text{ExC}_{\text{area}}$ —fine root carbon exudation per root area ( $\mu\text{g C cm}^{-2} \text{ day}^{-1}$ ),  $\text{ExC}_{\text{mass}}$ —fine root carbon exudation per root DW ( $\text{mg C g}^{-1} \text{ day}^{-1}$ ). mRH—moderate relative air humidity, and eRH—elevated relative air humidity.

### 3.3. Novel tools for measuring fine root growth dynamics

The combination of smartphone images and the recently published software RootPainter as an image analysis tool (Smith et al., 2022) gave reliable results in our pilot study of fine root dynamics in *Picea abies* manipulation experiments. The fine root PA from the manually annotated root images correlated with the fine root projection area analysed with RootPainter ( $R_2 = 0.989$ ;  $P < 0.05$ , Fig. 9, III). The relationship between fine root projection area measured with RootPainter was positively correlated with total fine root biomass measured at the end of the experiment ( $R^2 = 0.71$ ,  $P < 0.05$ ). However, irrespective of treatment, the fine root biomass increased at a higher rate than the fine root area (Fig. 5, III). RootPainter underestimated the root PA when the fine root projection area was more than  $4 \text{ cm}^2$  (III). We analysed errors, such as false positives, which were pixels predicted as roots that were annotated as background, and false negatives, which were pixels of background that were annotated as roots. The percentage of errors was, on average, 1% of all pixels and did not differ between treatments (III). The false positives increased over time but remained marginal in terms of the total fine root area. The error correlated positively with the brown root area, indicating that errors increased with more roots, especially more brown roots on images.

Comparing the models  $M1_{\text{total}}$  and  $M2_{\text{white}}$ ,  $M2_{\text{white}}$  was more specific, as it was trained to recognise white and small root tips (III). Therefore,  $M2_{\text{white}}$  misidentified small white reflections and white elements in soil as young white roots more frequently than in the model  $M1_{\text{total}}$ . In some cases, the programme detected more roots in  $M2_{\text{white}}$  than in  $M1_{\text{total}}$ , although  $M2_{\text{white}}$  should be a part of  $M1_{\text{total}}$ . This problem occurred only for images taken during the first two imaging sessions of the experiment, while  $\sim 25\%$  of the images resulted in higher root PA in  $M2_{\text{white}}$  compared to the fine root projection area estimated by  $M1_{\text{total}}$  (III). However, the median root projection area that was incorrectly identified was relatively marginal ( $0.01\text{--}0.05 \text{ cm}^2$ ).



## 4. DISCUSSION

Plants are affected by climate change in different ways. The most attention-receiving climate change scenarios consider the effects of increasing CO<sub>2</sub> in the atmosphere and a rise in air temperature (Lee et al., 2021). Often, plants' photosynthesis rate increases at elevated [CO<sub>2</sub>] or with climate warming, which triggers changes in plant physiological mechanisms to acclimate according to the new growth condition (Kirschbaum, 2011; Reich et al., 2018). In addition, climate change models for Northern Europe predict higher air temperatures, increased precipitation (Jaagus et al., 2017; Jaagus & Mändla, 2018; Kjellström et al., 2018) and periodically higher relative air humidity. High RH remains inside forest canopies due to the evaporation of intercepted water (Von Arx et al., 2012), leading to physiological changes and acclimation processes in different tree species (Sellin et al., 2017). Exploring the response of the above- and belowground C and water fluxes of trees to environmental change is critical for improving our understanding of plant acclimation mechanisms.

### 4.1. Water flux and nutrient uptake in changing environments

Previous studies of the effects of the predicted rise in relative air humidity have shown decreased transpiration rates in various tree species (Sellin et al., 2017; Fanourakis et al., 2020), which was also observed in our experiments (Fig. 6D). However, in some conditions, increased leaf conductance to water vapour could enhance the transpiration rate at a high RH (Kupper et al., 2017). Although, in our study, leaf conductance increased in *P. × wettsteinii* and *P. sylvestris*, the transpiration rate remained significantly lower in eRH than in mRH (II).

The decrease in transpiration flux can reduce the transport of nutrients from roots to leaves and slow down the mass flow of water, which carries mobile mineral nutrients in soil towards the rhizosphere (Cramer et al., 2009). The foliar N concentration of *B. pendula* was lower at eRH compared to mRH but depended on the soil nitrogen source (II). Changes in plant hydraulic conductance, specifically root hydraulic conductance, have been observed at different soil N sources (Faustino et al., 2015). Inorganic nitrogen ions, such as NO<sub>3</sub><sup>-</sup> and NH<sub>4</sub><sup>+</sup>, affect the expression and regulation of water channels, aquaporins, which determine water transport capacity through roots (Gao et al., 2018). *Betula pendula* seedlings grown in NO<sub>3</sub><sup>-</sup>-fertilised soil showed increased root system hydraulic conductance (I), which can potentially compensate for the diminished nutrient transport via water mass flow. Although both *E* and hydraulic conductance were higher in nitrate-fertilised soil (I), the N concentration in the leaves remained lower at eRH. These findings are concurrent with a previous study in silver birch, where elevated RH led to a decline in foliar N concentration (Sellin et al., 2013). *Tilia cordata*, however, had higher P and K in leaves at eRH but did not show a

significant decrease in the transpiration rate. *Betula pendula* had a higher root-specific area at eRH, showing a higher water absorption area per root mass.

Higher N availability in soil generally stimulates plant growth, although the species' preference for specific nitrogen ion uptake depends on environmental conditions (Lambers et al., 2008). Plant species often prefer one nitrogen form over the other according to the available N in the soil in a specific habitat (Cui & Song, 2007). Some studies suggest that late successional species, especially conifers, prefer to grow in ammonium-dominated soil compared to deciduous and pioneer species, which prefer nitrate uptake (Cui & Song, 2007; Britto & Kronzucker, 2013). However, many plant species can utilise various organic and inorganic N forms (Marshcner, 2012). For example, Pinaceae species usually grow in acidic soils where nitrification is low, which makes  $\text{NH}_4^+$  the preferred source of N (Andrews & Raven, 2022). Plants growing in neutral or alkaline soils prefer  $\text{NO}_3^-$ , whereas plants in more acidic soils prefer  $\text{NH}_4^+$  uptake (Gigon & Rorison, 1972). For example, *Pinus radiata* and *Picea glauca* usually have greater growth and higher N uptake in ammonium-fertilised soil than in nitrate-fertilised soil (McFee & Stone, 1968). In the current study, the soil was close to neutral, with a pH of 6.0–6.4, and needle N and P concentrations were higher in *P. abies* trees growing on  $\text{NH}_4^+$ -fertilised soil compared to nitrate-fertilised soil (Table 2). However, soil N sources can also affect the uptake of P or K (Marshcner, 2012). Studies on crop species have shown that P uptake is higher in  $\text{NH}_4^+$ -fertilised soil, whereas K uptake is higher when the dominant N form in the soil is  $\text{NO}_3^-$  (Hoffmann et al., 1994; Zhang et al., 2010). In my work, *B. pendula* and *P. abies* had higher P concentrations in leaves/needles in  $\text{NH}_4^+$ -fertilised compared to  $\text{NO}_3^-$ -fertilised trees (Table 2).

The preference for the nitrogen form does not always affect plant growth. In this study, the N source in the soil did not affect the biomass allocation of any studied tree species. A study with *B. pendula* showed that tree biomass was similar in  $\text{NO}_3^-$  and  $\text{NH}_4^+$ -fertilised soils (Esmeijer-Liu et al., 2009). In addition, mature conifer trees assimilated both  $\text{NH}_4^+$  and  $\text{NO}_3^-$  even at low nitrate concentrations (Zhou et al., 2021). However, the growth dynamics of the *P. abies* fine root area showed significantly higher young white root growth at the beginning of the experiment, whereas the root area growth was greater at  $\text{NH}_4^+$  treatment (III). However, the nitrogen effect was insignificant during the following measurements until the end of the experiment (III).

## 4.2. Tree growth and acclimation to a changing environment

Environmental changes affect photosynthesis rate and plant growth. Our studies showed an increase in the net photosynthesis rate in *P. sylvestris* at higher air humidity, which was related to significantly higher aboveground and belowground biomass (Fig. 6C, Table 1). The relationships between photosynthesis rate

and growth vary greatly among tree species with different growth strategies (Lambers et al., 2008). Photosynthesis is generally enhanced at higher temperatures and [CO<sub>2</sub>], but only in the short term; in the long term, the photosynthesis rate may decrease to the initial level because of limited N (or other nutrients') availability (Nakano et al., 1997; Makino & Mae, 1999; Way & Oren, 2010; Kirchbaum, 2011). Nevertheless, there is limited information about the effects of increasing air humidity on biochemical processes, such as photosynthesis, growth, fine root carbon exudation and respiration. Previous studies have shown that increased relative air humidity decreased the photosynthetic capacity in *B. pendula* (Sellin et al., 2013); however, the net photosynthesis rate and tree height growth in hybrid aspen were not affected by air humidity (Niglas et al., 2014). We did not determine a clear effect of air humidity on the photosynthesis rate or biomass in either *B. pendula* or in *P. × wettsteinii*. The difference between our growth chamber experiment and the measurements in situ probably comes from environmental fluctuations or concomitant effects (Tullus et al., 2012b; Sellin et al., 2017).

About 30–60% of photosynthetically fixed carbon is translocated to the roots for their growth; however, half is released by root respiration and one-third by fine root exudates (Pinton et al., 2001; Högberg et al., 2002; Nguyen, 2003). Tree species-specific differences in relation to both soil nutrient availability and environmental change can interactively affect root-related C-cycles in forest soil.

In the experiments carried out in the frame of this work, the improved growth of saplings indicated that, photosynthetically, a higher rate of fixed carbon was allocated into increasing total or aboveground biomass under elevated air humidity rather than into root exudates (II, IV). Fine root biomass increased in response to higher humidity only in *P. sylvestris* and decreased in *P. abies* (II; IV). None of the deciduous tree species showed any significant change in root biomass or in total belowground biomass. Plant roots release a wide range of exudates; these metabolites provide necessary carbon compounds to rhizosphere microbial communities (Canarini et al., 2019). In return, the microbial activity mediates nutrient availability, whereas the activity of both roots and soil microbiome changes the chemical or physical properties of the soil (Walker et al., 2003; Nardi et al., 2000). When an environmental factor suppresses the plant growth then photosynthetically captured carbon is rather used for growth of plant roots, stored or exuded as the surplus carbon (Prescott et al., 2020). At the species level, the rates of fine root carbon exudation decreased in *P. sylvestris*, and fine root respiration decreased only in *P. × wettsteinii* at higher humidity. Fine root C exudation rates per root DW varied on average from 1.05–3 mg g<sup>-1</sup> day<sup>-1</sup>, which is somewhat lower than the average measured rates in temperate forests 0.2–7.2 (Brzostek et al., 2013; Yin et al., 2014; Tückmantel et al., 2017; Brunn et al., 2022). However, in the current study, the fine root carbon exudation rates were higher among early successional tree species, whereas exudation was significantly correlated with root respiration per DW (IV). This fits with studies showing that early successional species generally have higher photosynthesis rates and leaf nutrient content than late successional species (Raaimakers et al.,

1995; Reich et al., 1998; Nogueira et al., 2004; Ziegler et al., 2020). Moreover, early successional tree species emerge first after disturbances and cope well with high light intensity or harsh soil conditions, whereas late successional species are rather shade tolerant, prefer more fertile soils and start to dominate at the later phase of the stand (Bazzaz, 1979). Thus, our findings support fine root exudation as being related to the growth strategies of tree species (IV).

Fine root carbon exudation usually correlates well with fine root respiration (Sun et al., 2017; Ataka et al., 2020; Sun et al., 2021). We did not find a significant correlation between fine root C exudation and respiration at the species level; however, there was a correlation between C exudation and respiration within early successional grouping. Across all studied tree species, the root respiration rate was one of the factors explaining the variation in fine root morphology and exudation (Fig. 7). In situ studies have shown that fine roots of deciduous trees usually respire more intensively than coniferous tree species (Han & Zhu, 2020). However, this contradicts our results obtained in growth chamber conditions. Instead, the fine root respiration of coniferous tree species was significantly higher, irrespective of air humidity manipulation.

Sun et al. (2021) suggested that the exudation rate is one of the competitive traits in fine roots. Since most fine root C exudation measuring studies use fine root segments without considering the functionally different fine root groups, we analysed the effect of the proportions of absorptive, pioneer and transport roots on both the fine root C exudation rate and fine root morphological traits. The fine root exudation rate and fine root morphological traits strongly depended on the proportion of absorptive, pioneer and transport roots in the fine root sample (II, IV). Our results agree with indirect indications from the literature. Tückmantel et al. (2017) measured higher C exudation from topsoil compared to subsoil fine roots with different morphologies at different soil depths. Root segments in topsoil had a greater proportion of absorptive root tips compared to subsoil roots, where pioneer root tips dominated, which still had a considerable amount of root exudates. In our study, a higher fine root C exudation was related to a higher length and mass (root DW) proportion of pioneer roots (Fig. 7). Sun et al. (2021) described higher root C exudation close to the apexes of the root, and root respiration has been shown to be highest in most active functional groups, such as absorptive roots (Trocha et al., 2017).

However, both the fine root functional architecture and the response to environmental change were species-specific (II, IV). The investigated environmental changes affected the fine root proportions. *Pinus sylvestris* had a significantly higher share of absorptive root tips (SA%) at mRH and pioneer and transport roots at eRH; furthermore, trees grown in nitrate-fertilised soil had a higher proportion of pioneer roots (II). Plants have also been shown to increase their fine root exudation rate in stressful conditions, for example, in drought, decreased nutrient availability and elevated atmospheric CO<sub>2</sub> concentrations (Phillips et al., 2011; Preece et al., 2018; Meier et al., 2020). However, there is a need for more detailed analyses because our results underline the functional distribution of fine

roots in changing environments as an important acclimation mechanism determining the C exudation rate.

In the current study, the high photosynthesis rate and leaf nutrient content of saplings were related to high fine root SRA/SRL and a greater proportion of absorptive roots within fine roots (IV), indicating more efficient nutrient uptake. Specific root area and length are considered competitive root traits because plants increase root contact with soil and explore greater volumes of soil (Ostonen et al., 1999; Sun et al., 2021). SRA depends inversely on the variation in average diameter and root tissue density, and the higher variability of RTD might drive the variation in SRA (Ostonen et al., 2007). Root tissue density is related to dry mass content and the lifespan of roots; however, this trait is considered to reflect root functioning (Ostonen et al., 2013; Freschet et al., 2021). RTD has been shown to relate significantly to root C exudation in ectomycorrhizal tree species (Akatsuki & Makita, 2020). We also found a negative correlation between fine root carbon exudation and RTD, whereas the lower RTD coincided with a higher proportion of pioneer roots within fine roots (Fig. 7). Both pioneer and absorptive roots anatomically have a primary structure and lower dry mass content compared to woody transport roots with secondary growth (Zadworny & Eissenstat, 2011; Bagniewska-Zadworna et al., 2012; Bagniewska-Zadworna et al., 2014). In our study, the pioneer root proportion (L%) varied most in *T. cordata* compared to other species (Fig. 5). The small proportion of pioneer roots in *T. cordata* may come from shorter pioneer root tips that lignify quickly and become transport roots. Goebel et al. (2011) compared the first two orders of fine roots of *T. cordata* and *P. sylvestris* and found less lignin content in the fine roots of *P. sylvestris*. The acclimation to different environmental conditions has rarely been investigated separately for absorptive and pioneer root tips. Pioneer roots have shown less sensitivity to soil moisture deficits and low temperatures compared to absorptive roots (Polverigiani et al., 2011; Ding et al., 2020). Only absorptive roots showed increase at eRH in deciduous species (IV), whereas the pioneer roots only in *P. sylvestris* showed changes under higher humidity (II). Pioneer roots are a way for plants to build up new structures of roots further away from, for example, dry patches and are therefore beneficial in stressful conditions (Zadworny & Eissenstat, 2011).

We expected fine root morphological traits to represent root features related to their form and to reflect their uptake, exudation and respiration capacities. However, fine root morphology was influenced by tree species, phylogenetic relatedness and successional status. Fine root morphology differed significantly between the studied deciduous and coniferous tree species (IV). Fine roots in deciduous species showed higher SRA, SRL and branching intensity compared to coniferous species (IV). BI has been shown to be correlated with SRL and to indicate root plasticity (Liese et al., 2017). Species with a higher BI have a higher ability of fine roots to proliferate into resource-rich patches (Kong et al., 2014). The variation in root diameter and SRL is affected by evolutionary history, in which evolutionarily older taxa have thicker roots on average (Ma et al., 2018). Coniferous tree species have thicker roots and lower SRA (IV), which is

explained by the higher need for carbohydrates and mineral nutrients for growth per root area than deciduous trees (Bauhus & Messier, 1999; Meier et al., 2020). Fine roots of deciduous tree species were more responsive to changes in relative air humidity with increased SRA and absorptive root proportions at eRH (IV). Previous studies have shown longer and thinner roots with higher SRA in higher humidity conditions, which is expected to be related to facilitated nutrient acquisition (Parts et al., 2013; Rosenvald et al., 2014).

For the first time, the effect of higher air humidity on the fine root growth dynamics of *P. abies* was followed continuously throughout the experiment using a novel approach and by combining smartphone images and the deep-learning programme RootPainter (III). Fine root growth was lower at a higher humidity, but more importantly, a shift in root development was detected. Under mRH conditions that simulated normal diurnal air humidity variation, the first fine root growth peak was the formation of young roots (white in colour) between the 28 and 35 days after planting, followed by ageing of these roots (peak of brown roots). At higher humidity, both white and brown root peaks were lower and overlapped (III). Based on this, we hypothesised that increased air humidity has a direct effect on root-associated microbial communities because of earlier root senescence (Herron et al., 2013), which might cause a decrease in C exudation. Rewald et al. (2014) estimated significantly lower root respiration and higher RTD for brown roots compared to white roots. Interestingly, high white root respiration did not differ between tree species, but brown root respiration was significantly different between *Carpinus betulus* and *Quercus robur*. The effect of changing environmental factors on root phenology and growth dynamics has rarely been studied, although recent innovations in technology will advance the understanding of the role of root dynamics in the rhizosphere carbon cycle.

### **4.3. Future implications for measuring fine root growth dynamics**

Experiments in growth chambers are an important approach to understanding the changes in tree morphology or physiology without any other non-determined disturbances in situ, such as extreme weather conditions or biotic stress. Along with aboveground changes, belowground changes are more difficult to measure during experiments, as many sampling techniques are destructive. There is ongoing rapid development of novel technologies for root research. Quite time- and cost-effective methods for measuring fine root growth dynamics and related root traits are all image-based techniques, particularly with regard to current developments of machine-learning based programmes. For example, the machine-learning programme RootPainter has been recently recognised as one of the most effective tools for image analysis (Bauer et al., 2022).

The method of imaging fine root growth with smartphones and using RootPainter to assess growth dynamics was convenient and accurate (III). The magnitude of errors remained minimal at 1% of the total pixels, on average. We agree that erroneously adding pixels to the width or end of the root should not cause any significant difference in the total measurements (Smith et al., 2022). The false positives, the background pixels that were identified as roots, increased over time due to the similarities between soil particles and root browning. The second model, segmentation of only white root tips, mistook light reflections and white-coloured elements in soil as white roots. Therefore, it was important to teach the programme to exclude as much noise on the training images as possible, such as reflections, condensation and fungi on our images. While training the models, the evaluation of the transitional zone from white to brown in fine roots is subjective. Automated segmentation provides reductions in both intra-observer and inter-observer variation in measurements. In the current work, we did not measure root hairs separately from roots or include fungal hyphae; however, RootPainter can be taught with pixel accuracy. The more specific model is created, the higher is the importance of elements increasing noise in images, for example light reflections in case of segmenting only white roots. Most fine root tips, especially in forest soils, are colonised by ectomycorrhizal fungi that can be with different colour (Agerer, 1997). Ectomycorrhizal colonisation was detected, but not measured in this study.

## 5. CONCLUSION

This overall objective of this thesis was to demonstrate the above- and below-ground physiological changes of three early (*Populus × wettsteinii*, *Betula pendula*, *Pinus sylvestris*) and two late successional tree species (*Picea abies*, *Tilia cordata*) in response to elevated relative air humidity and different soil N sources. The focus of the study was on the morphological and physiological acclimation of fine roots and their carbon fluxes, such as C exudation and respiration, which are likely to be significantly affected by changing soil conditions in interaction with climate change. In addition, we introduced a time- and resource-effective method for measuring fine root growth dynamics in growth chamber conditions, enabling us to understand changes in root development and senescence in response to changing environments.

Increased relative air humidity affects plants' nutrient uptake and depends on the prevailing nitrogen source in the soil. Higher air humidity slowed down the transpiration rate in all studied tree species, potentially decreasing mass flow and facilitating nutrient uptake. However, the tree water flux depended on the particular nitrogen source in *B. pendula*, in which root hydraulic conductance increased in  $\text{NO}_3^-$ -fertilised soil (I). The leaf [N] of *B. pendula* saplings grown on  $\text{NH}_4^+$ -fertilised soil was not affected by tree water flux, but the leaf [N] in  $\text{NO}_3^-$ -fertilised soil was considerably lower at eRH (II). In response to higher air humidity, the fine roots increased the specific area to increase water and nutrient absorption capability. Irrespective of humidity treatment, *P. abies* had higher needle N and P concentrations growing in  $\text{NH}_4^+$ -fertilised soil. This finding supports earlier studies that suggested *P. abies*' preference for ammonium as a soil N source (McFee and Stone, 1968; Andrews & Raven, 2022).

The effect of elevated air humidity on tree biomass formation and allocation was species-specific and was not affected by the dominating nitrogen form in the soil. *Pinus sylvestris* trees grown under increased humidity had higher above- and belowground biomass, while in *T. cordata*, only the aboveground biomass increased significantly at eRH. The increased photosynthesis rate at eRH supported the increase in aboveground biomass in *P. sylvestris*. The fine root growth dynamics of *Picea abies* were affected by  $\text{NH}_4^+$  only at the beginning of the experiment, whereas the fine root projection area increased levelled off after the middle of the experiment (III). Deciduous species had, on average, a higher proportion of absorptive root area (31%) compared to coniferous species (14%). Higher air humidity significantly increased the proportion of absorptive roots in deciduous tree species. However, one of the coniferous species, *P. sylvestris*, showed a decreased proportion of absorptive roots at eRH compared to mRH (II).

The higher air humidity did not increase the fine root carbon exudation and respiration in the studied tree species. On the contrary, the fine root C exudation in *P. sylvestris* and fine root respiration in *P. × wettsteinii* decreased at eRH, compared to mRH. Moreover, we did not find any significant relationship between fine root C exudation and the leaf net photosynthesis rate ( $P_{\text{net}}$ ) (II).



However, a higher  $P_{\text{net}}$  was related to a greater fine root SRA/SRL and absorptive root proportion (IV). The higher proportion of pioneer roots in the fine root sample was related to a greater carbon exudation rate, highlighting the importance of fine root functional distribution in estimating C fluxes in the rhizosphere. We did not find a relationship between exudation rate and tree biomass either, except in *P. sylvestris*, in which increased  $P_{\text{net}}$  in eRH was not associated with greater C exudation but with increased biomass (IV). The fine root morphology changed in response to increased air humidity, although the change was species specific and depended significantly on the proportion of absorptive, pioneer and transport roots. The fine root morphological difference was greatest between the deciduous and coniferous trees. However, the successional status of the tree species was related to the fine root carbon exudation rate. C exudation was higher in early successional tree species and correlated negatively with functional root traits, such as RTD. Thus, the tree species and their phylogenetic and successional status determine the ecophysiological acclimatisation mechanism to environmental change.

Air humidity changed the fine root development. At moderate RH, the relative growth of brown (pigmented) *P. abies* roots followed the relative growth of young white roots. However, the relative growth of brown and white roots coincided with the growth of trees under eRH. Our results confirm that a constantly higher RH alters the dynamics of root senescence, as reflected by the share of white and brown fine roots of Norway spruce saplings.

Methodologically, the combination of smartphone cameras and the machine-learning programme RootPainter for estimating the root growth dynamics of *Picea abies* proved to be an efficient and accurate method. Errors where the root was misidentified as part of the soil or *vice versa* were marginal. Some aspects of annotating pictures must be considered, such as including images with fungal structures, reflections or artificial elements in the training images, because colour elements similar to roots might overestimate the investigated root area.

This thesis demonstrates different species' acclimation capacities to changes in the environment, both soil nutrient availability and air humidity changes. The novelty of this work is in understanding the contribution of functionally different fine root proportions to fine root carbon exudation rates. In future studies, the potential carbon exudation by pioneer root tips to total fine root carbon exudation must be considered, because fine root functional proportions vary between species and between functional groups, such as successional or phylogenetically related tree groups. Moreover, fine root area imaging with smartphones and analysis with machine-learning software yielded reliable results and is a suggested method for future plant growth manipulation experiments.

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## SUMMARY IN ESTONIAN

### **Keskkonnamuutuste mõju hemiboreaalsete puuliikide ökofüsioloogiale – maa-alused kohanemismehhanismid**

21. sajandi lõpuks prognoositakse Põhja-Euroopas kuni 4 °C temperatuuri tõusu ja 5–20% sademete hulga suurenemist (Jaagus ja Mändla, 2018, Kjellström jt., 2018). Sadmete hulga suurenemisega kaasneb ka õhuniiskuse suurenemine puistus, mille tagajärjel transpiratsiooni (vee auramine taime lehe pinnalt) põhjustav jõud väheneb (Von Arx jt., 2012). Tänapäevaks on mitmed uurimused analüüsinud mõningate puuliikide kohanemist suhtelise õhuniiskuse suurenedes. Ühelt poolt võib õhuniiskuse suurenemine parandada kasvu suurema veepotentsiaali tõttu ning vähendada õhulõhedest tingitud fotosünteesi limitatsiooni (Lendzion ja Leuschner, 2009; Fanourakis jt., 2020). Teisalt, kõrge õhuniiskus võib vähendada taime transpiratsiooni, mille tõttu veevoog taimes kahaneb ning sellega koos väheneb ka mullas vee massivooga liikuvate toitainete kandumine juurte suunas (Cramer jt., 2009). Varasemad uuringud viitavad, et õhuniiskuse muutus mõjutab kiirekasvuliste lehtpuude peenjuurte morfoloogiat, mis on üheks kohanemismehhanismiks, kui toitainete kättesaadavus on vähenenud. Juured muudavad oma kuju ja vormi nii, et nende imav pind mullas suureneks, näiteks suureneb juuretippude arv, samuti võivad juured olla peenemad ja pikemad (Rosenthal jt., 2014, Parts jt., 2013).

Taimede juured eritavad fotosünteesi käigus omastatud süsinikühendeid mulda eritistena, milleks on enamasti primaarsed metaboliidid, nagu suhkrud, orgaanilised happed või aminohapped, aga ka sekundaarsed metaboliidid (kõrgmolekulaarsed ühendid) (Canarini jt., 2019). Osa süsinikust väljub juure hingamisega CO<sub>2</sub>-na, seejuures moodustab juure hingamine märkimisväärse osa mullahingamisest ning mõjutab seeläbi kogu süsinikuringet (Hanson jt., 2000, Kukumägi et al., 2017). Erinevate keskkonnamuutustega kohanemiseks suudab taime juureeritiste koostise muutumise abil mõjutada juurte lähiümbrust ehk risosfääri. Juureeritised eritatakse mulda kas passiivselt või aktiivselt (Whipps, 1990). Aktiivselt väljutatud juureeritisi võib taime kasutada toitainete kättesaadavuse muutmiseks mullas. Juurest mulda liikuvad süsinikühendid on toiduks mulla mikroobidele, aga mõjutavad nii mikroobikoosluste struktuuri, metaboolset aktiivsust ja mitmekesisust kui ka konkureeriva taime kasvu või isegi mulla keemilisi või füüsikalisi omadusi (Jones jt., 2004; Haichar jt., 2014). Erinevad keskkonnatingimused, nagu põud, toitainete puudus mullas või süsihappegaasi tõus atmosfääris mõjutavad eritiste kogust ning koostist (Preece jt., 2018; Meier jt., 2020; Phillips jt., 2011). Üks töö eesmärke oli välja selgitada, kas õhuniiskuse suurenemine põhjustab taimedele stressi, mis suurendab või vähendab süsinikühendite voogu mulda ning mõjutab seeläbi mulla süsinikuringet.

Puude juurestikus eritatakse jämedaid puitunud juuri, mis ankurdavad taime mulda ning alla 2 mm läbimõduga peenjuuri. Viimased on juurestiku kõige dünaamilisem osa, mis vastutab puu vee- ja mineraalsete toitainetega varustamise eest (Bauhus ja Messier, 1999; Tufekcioglu jt., 1999; Lucash jt., 2005; Freschet jt.,

2021). Peenjuured, jagatakse omakorda funktsionaalseteks gruppideks nagu imijuured, kasvajuured (pioneerjuured) ja juhtejuured (transportjuured) (Kubikova, 1967; Wells ja Eissenstat, 2003; McCormack jt., 2015). Imi- ja kasvajuured on primaarse ehitusega, ehkki kasvajuured lähevad basaalses osas üle sekundaar-kasvule ning muutuvad juhtejuurteks (Sutton ja Tinus, 1983; Bagniewska-Zadworna jt., 2012). Kasvajuured on kiirekasvulised, suurema läbimõõduga ja hõivavad kiiresti kasvades uut mullaruumala (Freschet jt., 2021). Imijuured on tavaliselt alla 0.5 mm läbimõõduga, rohkesti hargnenud ning pigem lühiealised (Ostonen jt., 2013). Meie metsapuude imijuured on enamasti ektomükoriisises sümbioosis seentega ning seeneliik mõjutab oluliselt imijuurte morfoloogiat (Ostonen jt., 2017). Imijuured moodustuvad kasvajuurte basaalsele osale ning nende funktsioon on vee- ja toitainete omastamine (Wells ja Eissenstat, 2003). Juhtejuured, mis on sekundaarse ehitusega puitunud peenjuured, transpordivad toitaineid juuretippudest jämejuurtesse ja kust need liiguvad edasi taime maa-pealsetesse osadesse. Kuna imijuured on lühiealised, siis nende morfoloogilised, füsioloogilised ja keemilised tunnused muutuvad, kui keskkond muutub ning tagavad taimejuurte kohanemise ning talitlemise uutes oludes. Seega saame imi- ning laiemalt ka peenjuurte morfoloogilisi ja füsioloogilisi parameetreid käsitleda keskkonnamuutuste indikaatoritena (Ostonen jt., 2007). Levinuimad juureparameetrid on eripind (SRA,  $\text{m}^2 \text{kg}^{-1}$ ) ja eripikkus (SRL,  $\text{m g}^{-1}$ ), mis väljendavad juure pinda ja pikkust tema massiühiku kohta, peegeldades seeläbi kaudselt vee- ja toitainete omastamise efektiivsust (Freschet jt., 2021). Olulised tunnused on ka juurte keskmine diameeter (AD, mm) ning juurte kudede tihedus (RTD,  $\text{kg m}^{-3}$ ), viimane peegeldab kaudselt nende talituslikku tõhusust, sest väikese kuivmassi ning suure ruumalaga juurteil on potentsiaalselt parem vee ja toitainete läbilaskvus (Freschet jt., 2021). Kuigi enamasti mõõdetakse funktsionaalselt erinevaid juuri eraldi, siis juurte hingamist ning eksudatsioonimäära mõõdetakse tehnilistel põhjustel peenjuurteil.

Peenjuurte kasvu ja tunnuste mõõtmine on keerukas, sest juurte mullast välja pesemine on aja- ja ressursimahukas ning lõhub taime kasvukeskkonna. Tänapäevaks on arendatud mitmesuguseid tehnoloogiaid, mis võimaldavad juurte kasvu mullas näha ja mõõta. Üks enamlevinud meetoditest on minirisotronide meetod, kui mulda sisestatud läbipaistvate torude ja neisse sobiva kaameraga jälgitakse juurte kasvu (Rewald ja Ephrath, 2003). Selle meetodi miinuseks on suur hulk pilte, mille töötlemine on endiselt väga ajamahukas. Tänapäevased masinõppemeetodid pakuvad uusi võimalusi õpetada masinal piltidelt juuri ära tundma ning nende pikkust ja pindala mõõtma (Smith jt., 2022). Esimesed läbimurdelised lahendused võimaldavad juurepiltide töötlemise täielikku automatiseerimist (Bauer jt., 2022).

Töös uuritud puuliigid kasvavad põhja laiuskraadidel, mis eristuvad ka suktsessiooni ja fülogeneesi poolest (leht- ja okaspuud). Varasuktsessionilised liigid on kiirekasvulised ning kasvavad tihtipeale esimestena peale häiringut, kui hilissuktsessionilised liigid on aeglasema kasvuga, taluvad varju ning pigem on teise rinde puuliigid (Bazzaz, 1979). Uuritavateks lehtpuudeks olid valitud kaks varajast ning üks hilissuktsessioniline liik vastavalt hübriidhaab (*Populus* ×

*wettsteinii* Hämet-Ahti), arukask (*Betula pendula* Roth.) ja harilik pärn (*Tilia cordata* Mill.). Okaspuudest vara- ja hilissuktsessioonilised vastavalt harilik mänd (*Pinus sylvestris* L.) ja harilik kuusk (*Picea abies* (L.) H. Karst.).

Doktoritöö eesmärk oli analüüsida viie hemiboreaalsetes metsades laialt levinud puuliigi ökofüsioloogilisi kohanemismehhanisme kõrgema suhtelise õhuniiskuse tingimustes muldadel, kus peamiseks lämmastikuallikaks oli kas ammoonium või nitraat. Maapealsed mõõtmised hõlmasid puude biomassi jaotust, fotosünteesi ja transpiratsiooni intensiivsust ning viie puuliigi lehtede toitainete kontsentratsioone. Töös keskenduti noorte 1–5 aastaste puude maaaluse osa kohanemisele. Analüüsisin peenjuure biomassi ja kasvudünaamikat, morfoloogiat, funktsionaalset jaotumist, fenoloogiat ja peenjuure süsinikuvooge, nagu eksudatsioon ja hingamine muutuvates keskkonnatingimustes. Samuti kasutasin esmakordselt nutikaid tehnoloogiaid ja süvaõppe tehnikaid, mis vähendavad drastiliselt aega ja ressursse, mida muidu oleks juureuringuteks vaja.

Konkreetsed eesmärgid olid selgitada kõrge suhtelise õhuniiskuse ja erinevate mulla lämmastikuallikate mõju:

- 1) puude veevoogudele ja sellega potentsiaalselt seotud toitainete omastamisele (I, II, IV);
- 2) puude kasvudünaamikale ja biomassi jaotusele, sealhulgas imi-, kasvu- ja juhtejuurte funktsionaalsele jaotusele (II, IV);
- 3) peenjuurte morfoloogiale, süsiniku eritusele ja hingamisele ning analüüsida tunnuseid suktsessiooniliste ja fülogeneetiliste gruppide vahel (II, IV);
- 4) peenjuure sesoonsele kasvudünaamikale (III).

Peamised hüpoteesid olid:

- 1) Kõrgenenud õhuniiskus vähendab puude transpiratsioonivoogu ja puude vee massivooluga seotud lämmastiku omastamist (I, II, IV);
- 2) kõrgenenud õhuniiskus suurendab peenjuure süsiniku eritumist ja hingamist süsiniku biomassi suunamise arvelt. Peenjuurest erituvat süsinikuvoogu mõjutavad lehtede fotosünteesivõime ja peenjuure arhitektuur st. funktsionaalselt erinevate imi-, kasvu- ja juhtejuurte proportsionaalne jaotus (II, IV).
- 3) kõrgenenud õhuniiskus ja mulla domineeriv lämmastiku vorm mõjutavad peenjuurte kasvudünaamikat ning arengut; juurte moodustumis- ja vananemiskiirus muutuvad (III) ning
- 4) ökofüsioloogilised kohanemismehhanismid keskkonnamuutustega sõltuvad uuritud puuliikide suktsessioonilisest ja/või fülogeneetilisest staatusest (IV).

Peenjuurte eritiste kogumiseks kasutati kambrimeetodit (Phillips jt., 2008), mille puhul mullast puhastatud peenjuure tipmine segment koos imi-, kasvu- ja juhtejuurtega sisestati süsinikuvaba toitelahusega täidetud kambrisse nii, et juurt ei lõigatud taime küljest ära. Kamber täideti süsinikuvaba toitelahusega. Peale stabilisatsiooni koguti ööpäevaks installeeritud süsinikuvaba toitainelahu ning määrati sinna kogunenud orgaanilise süsiniku sisaldus. Kogu lahusesse eraldunud süsinik oli pärit taimelt, isegi kui see oli vahepeal omastatud juurepinnal elavate

mikroobide poolt. Seejärel lõigati analüüsitav juur taime küljest ära ning mõõdeti morfoloogilised parameetrid eraldi imi-, kasvu- ja juhtejuurtel ning hinnati nende proportsiaalne pikkus, pind ja mass peenjuure segmendi kohta. Töö raames viidi läbi neli eksperimenti kontrollitud tingimustega kasvukambrites. Noored (1–5 aastased) puud kasvasid eraldi 10 L plastpottides – neist harilik kuusk istutati läbipaistvatesse pleksiklaasist pottidesse, mis võimaldas kasvavaid juuri nädalase sammuga pildistada. Kasvukambrites olid päeva ning öö pikkused vastavalt 8 ja 16 h, õhutemperatuur ~21.6 °C ja kambrite valgusintensiivsus võra ülemises positsioonis 400–800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . Puud kasvasid erinevail õhuniiskuse tingimustes: 1) mõõdukal õhuniiskusel (mRH), kus päevane ja öine õhuniiskus oli vastavalt 65% või 80% küllastavast õhuniiskusest ning 2) kõrgel õhuniiskusel (eRH), kus nii päevane kui öine õhuniiskus oli 80% küllastavast. Mõlema õhuniiskuse töötuluse puhul kasvasid iga puuliigi puhul pooled puud nitraatlämmastikuga ning pooled puud ammoniumlämmastikuga väetatud turvasmullal.

Üks kulutõhus meetod on pildistada kasvukambri läbipaistvates pottides kasvavate puude juuri nutitelefoni abil. Tänapäeval on võimalik analüüsida pilte masinõppemeetodil, mis on üks arenevatest tehisintellekti suundadest. Antud töös kasutati programmi RootPainter, mis õpetati eristama juuri mullast ning noori valgeid juuri vanematest pruuniks värvunud juurtest. Pruun värvus iseloomustab osaliselt või täielikult sekundaarset kasvu ning juure vananemise algust (Wells ja Eissenstat, 2003). Samal ajal võib juur siiski olla veel aktiivne ning isegi vähemal määral toitaineid omastada (van Rees ja Comerford, 1990; Comas jt., 2000). Pruunistumise intensiivistumine juurtel võib olla ajendatud ka keskkonna muutustest tingituna näiteks mullaniiskuse vähenemisest või kõrgemast mullatemperatuurist (Rogers, 1939; Bartsch, 1987). Seni pole teada, kuidas keskkonnategurid nagu mulla anorgaanilise lämmastiku vormid või suurenenud õhuniiskus mõjutavad juurte vananemisprotsesse ja seeläbi nende värvuse muutust. Kuna juurte fenoloogia ja vananemisega seotud protsessid on määrava tähtsusega mulla aineringses, siis on aja- ja kulutõhusate meetodite kasutamine väga oluliseks eelduseks selle uurimissuuna edasisel arendamisel.

Kõrgem õhuniiskus vähendas transpiratsiooni määra kõigil uuritud puuliikidel, mida on ka täheldatud varasemates töödes (Sellin jt., 2017; Fanourakis jt., 2020). Transpiratsioonivoo vähenemine võib taimedel pärssida toitainete kättesaadavust, kuna aeglustub vee massivool mullas, mis kannab toitaineid juure suunas (Cramer jt., 2009). Üheks mehhanismiks veevoogude taimesisel regulatsioonil on juure hüdraulilise juhtivuse muutmine, mis sõltub osaliselt mulla anorgaanilise lämmastiku vormide (nitraat, ammonium) mõjust rakumembraanides paiknevatele veekanalitele ehk akvaporiinidele (Faustino jt., 2015; Gao jt., 2018). Uuringus oli nitraadiga väetatud arukaskede juurestiku hüdrauliline juhtivus ja transpiratsioon kõrgem kui ammoniumiga väetatud puudel (I, II). Selles lämmastiku töötuluses põhjustas transpiratsioonivoo vähenemine kõrgel õhuniiskusel ka lehestiku lämmastiku sisalduse vähenemist, mis viitab nitraatioonide vähenenud liikumisele mullas. Lisaks suurenes arukaskedel kõrgel õhuniiskusel ka peenjuurte eripind, mis viitab vee ja toitainete omastamise tõhustamisele.

Erinevad liigid eelistavad sõltuvalt kättesaadavusest üht või teist lämmastikvormi mullas (olles sageli võimelised efektiivselt omastama ka erinevaid lämmastiku vorme), mille omastamine sõltub ka keskkonnatingimustest (Lambers jt., 2008; Cui ja Song, 2005; Marshcner, 2012). Erinevate uuringute kohaselt eelistavad varajase suktsessiooniga liigid ning peamiselt okaspuud lämmastiku omastamist ammooniumina (Cui ja Song, 2005; Britto ja Kronzucker, 2013). Kuused ning männid kasvavad pigem happelisema reaktsiooniga mullal, kus nitrifikatsioon on madal ning lihtsam on omastada lämmastikku ammooniumina (Andrews ja Ravel, 2022). Domineeriv lämmastiku vorm mullas võib mõjutada ka teiste toitainete omastamist, näiteks fosfor või kaalium (Hoffmann jt., 1994; Zhang jt., 2010). Minu töös oli kõrgem fosfori sisaldus ammooniumiga väetatud arukase lehtedes ja kuuse okastes võrreldes puudega, mis kasvasid nitraadiga väetatud mullas. Siiski ei tarvitse konkreetse lämmastikuvormi kasutamine tingida muutusi taime kasvus. Näiteks uuringud arukasega ei tuvastanud biomasside erinevusi nitraadi ja ammooniumiga väetatud puudel (Esmeijer-Liu jt., 2009; Zhou jt., 2021). Puude biomassi muutus ei sõltunud ka selles töös mulla lämmastiku vormist. Ammooniumiga väetatud mullal kasvanud kuuskedel juurte pind küll suurenes, kuid ainult katse alguses, hiljem mõju kadus.

Keskkonnamuutused mõjutavad taime fotosünteesi ja kasvu. Töös leidsin, et kõrgemal õhuniiskusel kasvanud mändide fotosüntees suurenes ning suurenes ka nii maapealne kui -alune biomass. Fotosünteesi ja kasvu vaheline seos erineb liigiti, kuna taimedel on erinevad kasvustrateegiad (Lambers jt., 2008). Õhuniiskusega manipuleeritud välikatses leiti, et kõrgema õhuniiskuse tingimustel kasvanud arukaskede fotosüntees väheneb (Sellin jt., 2013). Samas katses aga ei muutunud kõrgemal õhuniiskusel kasvanud hübriidhaabade kasv ega fotosüntees (Niglas jt., 2014). Käesolevas töös suurema õhuniiskuse käes kasvanud arukase ega hübriidhaava puhul ei olnud seost fotosünteesi ja puu kasvu vahel. Muutus võib olla liigispetsiifiline, kuid välikatses võisid fotosünteesi efektiivsust mõjutada erinevad keskkonnatingimused, mille mõju on kasvukambri katsetes minimeeritud (Tullus jt., 2012; Sellin jt., 2017).

Fotosünteesi käigus omastatud süsinikku kasutatakse biomassi kasvuks, kusjuures kuni 60% seotud süsinikust võidakse suunata juurte kasvuks, eritistesse või kasutatakse hingamiseks (Pinton jt., 2001; Högberg jt., 2003; Nguyen, 2003). Katsete käigus selgus, et kõrgemal õhuniiskusel kasvanud mändide peenjuurte biomass oli suurem, kuusel seevastu väiksem ning lehtpuudel õhuniiskus puude kogu biomassi ja selle suhtelist jaotust pigem ei mõjutanud (II, IV). Ka juurte kaudu mulda eritatava süsiniku hulka suures plaanis õhuniiskus ei mõjutanud; küll aga vähenesid männi juureeritiste voog ja hübriidhaava juurte hingamine. Juureeritiste hulk varieerus katses üle kõikide liikide 1,05–3 mg süsinikku grammi peenjuure (g) kohta ööpäevas, mis on mõnevõrra madalam looduslikes tingimustes parasvöötme metsades mõõdetust 0,2–7,2 mg g<sup>-1</sup> päev<sup>-1</sup> (Brzostek jt., 2013; Yin jt., 2014; Tückmantel jt., 2017; Brunn jt., 2022). Varasuktsessiooniga puuliigid eritasid juurte kaudu keskmiselt rohkem süsinikku, mis seostub varem kirjeldatud varasuktsessiooniga liikide kõrgema fotosünteesi määraga ja toitainete sisaldusega lehtedes (Raaimakers jt., 1995; Reich jt., 1998; Nogueira jt.,



2004; Ziegler jt., 2020). Seega võib oletada, et puu suktsessiooni staatusel on mõju peenjuurte eritatavake süsiniku kogusele (IV).

Süsinikühendite voogu juurest mulda mõjutab peenjuurte funktsionaalne koostis ehk mõõdetava peenjuure segmendi imi-, kasvu- või juhtejuurte osakaalust. Selgus, et kasvujuurte suur osakaal seostus oluliselt suurema juureeritiste vooga (II, IV), mida on kaudselt ka varem leidnud Tückmantel jt (2017), kes leidsid erinevusi peenjuurte morfoloogias ja juureeritiste koguses mulla erinevates kihtides. Seega saab minu töö tulemusena väita, et juureeritiste voogude hindamisel on väga oluline arvestada peenjuurte funktsionaalset jaotust hindamaks süsinikvooge risosfääris korrektselt. Varase suktsessiooniga liikide süsinikeritiste ja juurehingamise määrad korreleerusid positiivselt, mis viitab kõrgemale peenjuure aktiivsusele. Me ei leidnud liigisisest positiivset seost juureeritiste ja hingamise voogude vahel, mida on varasemalt täheldatud (Ataka jt., 2020; Sun jt., 2021). Küll aga seletas peenjuure hingamisaktiivsus ka peenjuure morfoloogia ja süsinikeritiste varieerumist. Varasemalt on leitud, et lehtpuud hingavad aktiivsemalt kui okaspuud (Han ja Zhu, 2020; Reich jt., 1998). Minu tulemused viitasid vastupidisele, okaspuude juurehingamine oli intensiivsem kui lehtpuude juurtel (IV). See võib tuleneda väli- ja laborikatsete, aga ka noorte puude arengulistest eripäradest.

Peenjuurte morfoloogilisi parameetreid kasutatakse sageli keskkonnamuutuste indikaatoritena, neist levinumad on eripind ja -pikkus ning hargnevus, talitulislikku efektiivsust väljendab kaudselt juurte kudede tihedus (Ostonen jt, 1999; 2013; 2017; Freschet jt. 2021). Minu töö tulemused näitasid, et kõrgem fotosünteesi määr ja toitainete sisaldus lehtedes seostusid suurema peenjuurte eripinna ja -pikkusega, aga ka suurema imijuurte osakaaluga. Kõrgema eripinna ja -pikkusega juurte toitainete omastamist hinnatakse tõhusamaks, sest selliste juurte kontaktpind mullaga on suurem (Ostonen jt., 1999; Sun jt., 2021). Juureeritiste hulk suurenes, kui keskmine juurte kudede tihedus oli väiksem, mis viitab suuremale noorte juurte või imi- ja kasvujuurte osakaalule (IV) ning suuremale metaboolsele aktiivsusele. Suurema juurte kudede tiheduse korral oli ka väiksem kasvujuurte osakaal hinnatud peenjuurte segmentidel. Imi-, ja kasvujuured ongi ehituslikult primaarse kasvuga ning väiksema RTD-ga kui puitunud juhtejuured (Zadworny ja Eissenstat, 2011; Bagniewska-Zadworna jt., 2012; Bagniewska-Zadworna jt., 2014).

Keskkonnamuutused võivad oluliselt mõjutada juurte kuju, suurust ning teisi tunnuseid või juurte kaudu eritatava orgaanilise süsiniku hulka mulda. Samas on peenjuure funktsionaalselt erinevate juurte proportsionaalne jaotus liigispetsiifiline ning varieerub nii vara-hilissuktsessiooni puu gruppide kui ka leht-okaspuude vahel. Lehtpuudel on suhteliselt rohkem imijuuri ning vähem juhtejuuri kui okaspuudel. Hariliku männi ja kuuse kasvujuurte osakaal peenjuurtest oli väga sarnane, ligikaudu 11–15%. Pärnal oli kasvujuuri seevastu keskmiselt vaid 1% kogu peenjuurtest. Pärna kasvujuured võivad olla lühemad ning kiiresti üle minna juhtejuurteks. Juurte morfoloogia erines peale liikide ka selliste funktsionaalsete rühmade nagu vara- ja hilissuktsessiooniga või fülogeneetiliselt erinevate leht- ja okaspuude vahel. Okaspuude peenjuured on enamasti jämedamad ja

suurema tihedusega võrreldes lehtpuudega (Eissenstat ja Yanai 1997; Meier jt., 2020). Kõrgel õhuniiskusel kasvanud lehtpuude peenjuurte eripind suurenes ning seda on näidatud ka varasemates töodes (Rosensvald jt., 2013; Parts jt., 2014).

Hariliku kuuse kasvudünaamikat analüüsiti mobiiltelefoniga tehtud piltidelt. Kõrgemas õhuniiskuses kasvanud kuuskede keskmiselt väiksem peenjuurte projetsioonipindala langes kokku biomassihinnangutega katse lõpus. Hoopis uudsed tulemused saadi juurte suhtelise kasvu ja arengu hindamisel. Noorte ja valgete peenjuurte suurim suhteline kasvukiirus oli kontroll-õhuniiskusel 28–35 päeval peale taimede istutamist ning sellele järgnes pigmenteerunud (pruunistunud) juurte suurim suhteline kasvukiirus. Ent kõrgeenenud õhuniiskusel olid suurimad kasvukiirused esiteks madalamad ja langesid lisaks ka kokku. Seega mõjutas õhuniiskuse suurenemine oluliselt peenjuurte kasvu ja arengut ning põhjustas noorte valgete juurte kiiremat pigmenteerumist (vananemist). Need uudsed tulemused aitavad mõista võimalikke muutusi mulla juurtega seotud süsinikuringes, sest juurte vananemisel muutuvad ka juurtega seotud mikroobikooslused (Herron jt 2013).

Senised juurte uurimise meetodeid on olnud külaltki aja- ning ressursimahukad. Viimastel aastatel on plahvatuslikult kasvanud masinõppe ja pildi-analüüsi tehnoloogiate areng, mis muudab andmete kogumise taimede maa-aluse kasvudünaamika kohta kiiremaks ja lihtsamaks. Töös analüüsisin mobiiltelefoniga tehtud juurepiltide masinõppel põhineva programmi RootPainter'ga (Smith jt., 2022). Hindamiseks mõõtmiste täpsust, hinnati juurte kasvu piltidel ka manuaalselt. Selgus, et programmi (RootPainter) tulemused vastasid peaaegu täielikult inimese mõõdetule (III). Keskmise suhteline viga jäi alla 3%. Selgus küll, et kui juurte projektsioonipind on suurem kui 4 cm<sup>2</sup> hakkab RootPainter juurte pindala alahindama. Vead, kus programm arvas, et mullaosake on juur, olid ühtlaselt väikesed kõikide eksperimendi jooksul tehtud piltidel. Vead, kus programm märgib juure mullaks, kasvasid ajas, mis tõenäoliselt tulenes juurte pigmenteerumisest.

Kuna tegemist on piksel-põhise programmiga, genereerisime ka teise mudeli, mis õppis ära tundma ainult valgeid juuretippe. Vigadena lisandusid valguspeegeldused või muu väga hele mullaosake. Õpetamise käigus on oluline programmile võimalikult palju võõrelemente õpetada ehk taustaks märkida, et programm suudaks neid mudeli väljatöötamisel välistada. Kasutatud innovatiivne nutikas kombinatsioon mobiiltelefonidega tehtud piltidest ja masinõppe mudelist oli kiire, tõhus ning usaldusväärne.

Doktoritöös hinnati esmakordselt viie enamlevinud puuliigi peenjuurtest lähtuvat orgaanilise süsiniku voogu, mis eritistena mulda jõuab. Seejuures hinnati muutusi juureeritiste voos kui puud kasvasid kõrgemas suhtelises õhuniiskuses. Hinnati peenjuurte hulka kuuluvate funktsionaalselt erinevate imi-, kasvu- ja juhtejuurte proportsionaalse osakaalu rolli eritatava orgaanilise süsiniku kogusele ning juurte morfoloogilistele parameetritele, mida sageli kasutatakse keskkonnamuutuste indikaatorina. Selgunud kasvujuurte osakaalu ja orgaanilise süsinikuvoo positiivne seos viitab vajadusele teha mõõtmisi talituslikult erinevatel juurtel eraldi ning hinnata nende osakaalu peenjuurestikus. Puuliikide suksessioon ja

fülogeentiline kuuluvus võib olla seoses juureeritiste koguhulgaga. Uute nutikate tehnoloogiate arendamine avab võimalusi hinnata juurte kasvudünaamikat kiiresti ning kulutõhusamalt ning mis veel olulisem, selguvad täiesti uued keskkonnatingimuste otsesed mõjud juurte kasvudünaamikale, mis omakorda potentsiaalselt mõjutavad nii elurikkust mullas kui ka selle aineriinget. Mobiiltelefonidega juurte kasvu pildistada on lihtne ning masinõppe meetodid võimaldavad spetsiifiliste uurimisküsimuste lahendamiseks välja töötada mudeleid, mis annavad usaldusväärse tulemuse. Uudse lähenemise ja nutika tehnoloogia abil tuvasime, et tulevikus üha suurenev õhuniiskus kiirendab peenjuure vananemist.

## **ACKNOWLEDGEMENTS**

First of all, I would like to thank my two supervisors, Ivika Ostonen and Priit Kupper. Thank you for guiding and supporting me during my studies. Thank you for your patience and encouragements. I am also grateful for including me in additional interesting measurement campaigns and supporting me in scientific conferences and meetings.

I would like to thank all the co-authors who were part of writing the articles. Thank you for your patience and understanding.

I acknowledge all colleagues, who gave valuable comments, advice, revision or helped out with the experiments.

Finally, I would like to thank my family and friends for being there for me.

This study was funded by the Estonian Research Council grants (IUT34-9; PUT1350; PRG916; PRG1434), the European Regional Development Fund (Center of Excellence EcolChange).

## **PUBLICATIONS**

## CURRICULUM VITAE

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### Education

2018– University of Tartu, PhD, Botany and Ecology, specializing in plant ecology and ecophysiology  
2016 Erasmus+ aftergraduate practices in Antwerp, Belgium  
2014 Erasmuse+ exchange student, Prague, Czech Republic  
2014–2016 University of Tartu, MSc in environmental technology, specializing in ecosystem technologies  
2011–2014 University of Tartu, BSc in environmental technology  
2010–2011 University of Tartu, undergraduate studies in mathematics

### Professional career

2022– University of Tartu, Institute of Ecology and Earth Sciences, ecology specialist

### Main fields of research:

Measuring early and late successional tree fine root acclimation mechanism in response to environmental change. Measurements include fine root morphology, partitioning, carbon exudation, and respiration. In addition, analyzing the fine root growth dynamics with smart technologies.

### A list of publications and patents:

Kupper, P.; Rohula-Okunev, G.; Sell, M.; Kangur, O.; Sellin, A. (2020). Effects of air humidity and soil nitrogen source on diurnal water flux in hybrid aspen and silver birch. In: T. Hölttä, Y. Salmon (Ed.). *Acta Horticulturae* (153–160) DOI: 10.17660/ActaHortic.2020.1300.20  
Sell, Marili; Ostonen, Ivika; Rohula-Okunev, Gristin; Rusalepp, Linda; Reza-pour, Azadeh; Kupper, Priit. (2022) 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): 557–569. <https://doi.org/10.1093/treephys/tpab118>  
Sell M, Smith AG, Burdun I, Rohula-Okunev G, Kupper P, Ostonen I. (2022) Assessing the fine root growth dynamics of Norway spruce manipulated by air humidity and soil nitrogen with deep learning segmentation of smartphone images. *Plant and Soil* <https://doi.org/10.1007/s11104-022-05565-4>

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### **Other administrative and professional activities**

- 2016, The 9th Scandinavian Plant Physiology Society PhD Student Conference, Oslo, Norway, poster „The effects of soil moisture and air humidity on the growth of Silver birch“
- 2017, 7th international symposium on physiological processes in roots of woody plants, Tartu, Estonia, poster „The effects of air humidity on root acclimation and nutrient acquisition“
- 2018, 10th Scandinavian Plant Physiology Society PhD Student Conference, Kopenhagen, Taani, plakatettekanne „Root carbon exudation and respiration at different nitrogen sources and air humidity“
- 2019, Rhizosphere 5 Conference, Saskatoon, Canada. University of Saskatchewan, presentation „Fine root carbon exudation and morphology effects in different nitrogen sources and air humidity treatments“
- 2021, EGU General Assembly, online poster presentation „Carbon allocation in early successional tree species at elevated air humidity and different soil nitrogen sources“
- 2021, CAR-ES conference, Hallormsstaður, Iceland, presentation „Fine root C exudation and respiration of early- and late successional tree species in future climate“
- 2022, EGU General Assembly, Austria, Vienna, presentation “Application of deep learning segmentation techniques in smartphone images to assess growth of fine roots of spruce seedlings manipulated by air humidity and soil nitrogen source”
- 2022, 8th International Symposium on Physiological Processes in Roots of Woody Plants (WoodyRoot8), State College; USA, presentation “Do environmental changes affect the fine root morphology and carbon exudation rates in early and late successional tree species?”
- 2022, New Phytologist next generation scientist 2022, Tartu, Estonia, poster “Using mobile phones and teaching AI to measure root growth dynamics”

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2016 Erasmuse välispraktika Antwerpenis, Belgias  
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Lisainformatsioon: bakalaureuse lõputöö teema „Raskmetallide fütoakumulatsioon ja taimede kasutamine saastunud keskkonna puhastamiseks“; magistri lõputöö teema „Mulla- ja õhuniiskuse mõju arukase kasvule“; välispraktika Belgias Antwerpenis, raskmetallide ja linnasaaste kogunemine erinevatesse linna puit- ja põdsastaimedesse.

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Sell M, Smith AG, Burdun I, Rohula-Okunev G, Kupper P, Ostonen I. (2022). Assessing the fine root growth dynamics of Norway spruce manipulated by air humidity and soil nitrogen with deep learning segmentation of smartphone images. *Plant and Soil* <https://doi.org/10.1007/s11104-022-05565-4>

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**Konverentsiettekanded:**

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- 2017, 7th international symposium on physiological processes in roots of woody plants, Tartu, Eesti, plakatettekane „The effects of air humidity on root acclimation and nutrient acquisition“
- 2018, 10th Scandinavian Plant Physiology Society PhD Student Conference, Kopenhaagen, Taani, plakatettekane „Root carbon exudation and respiration at different nitrogen sources and air humidity“
- 2019, Rhizosphere 5 Conference, Saskatoon, Kanada. University of Saskatchewan, suuline ettekanne „Fine root carbon exudation and morphology effects in different nitrogen sources and air humidity treatments“
- 2021, EGU General Assembly, online lühiettekanne „Carbon allocation in early successional tree species at elevated air humidity and different soil nitrogen sources“
- 2021, CAR-ES conference, Hallormsstaður, Island, suuline ettekanne „Fine root C exudation and respiration of early- and late successional tree species in future climate“
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