

**Dissertations Forestales 321**

Fine root dynamics and below- and above-ground carbon  
inputs into soil in boreal forests

Yiyang Ding  
Department of Forest Sciences  
Faculty of Agriculture and Forestry  
University of Helsinki

Academic dissertation

To be presented, with the permission of the Faculty of Agriculture and Forestry of the University of Helsinki, for public examination in Forest Sciences building, Viikki, Lecture Hall B3 (Latokartanonkaari 7, Helsinki) on November 12<sup>th</sup> 2021, at 13 o'clock

*Title of dissertation:* Fine root dynamics and below- and above-ground carbon inputs into soil in boreal forests

*Author:* Yiyang Ding

*Dissertationes Forestales* 321

<https://doi.org/10.14214/df.321>

Use licence CC BY-NC-ND 4.0 (<https://creativecommons.org/licenses/by-nc-nd/4.0/>)

*Thesis Supervisor:*

Professor Dr. Heljä-Sisko Helmisaari

Department of Forest Sciences, University of Helsinki, Finland

*Pre-examiners:*

Docent Dr. Annamari Markkola

Department of Biology, University of Oulu, Finland

Professor Dr. Jiacun Gu

School of Forestry, Northeast Forestry University, Harbin, China

*Opponent:*

Professor Dr. Lars Vesterdal

Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark

ISSN 1795-7389 (online)

ISBN 978-951-651-732-5 (pdf)

ISSN 2323-9220 (print)

ISBN 978-951-651-733-2 (paperback)

*Printers:* Unigrafia, Helsinki 2021

*Cover photo:* Yiyang Ding

*Publishers:*

Finnish Society of Forest Science

Faculty of Agriculture and Forestry of the University of Helsinki

School of Forest Sciences of the University of Eastern Finland

*Editorial Office:*

Finnish Society of Forest Science

Viihkaari 6, FI-00790 Helsinki, Finland

<http://www.dissertationesforestales.fi>

**Ding Y. (2021)** Fine root dynamics and below- and above-ground carbon inputs into soil in boreal forests. *Dissertationes Forestales* 321. 52 p. <https://doi.org/10.14214/df.321>

## ABSTRACT

Below-ground carbon (C) allocation studies in boreal forests are scarce and have high levels of uncertainty in ecological and modelling studies. The uncertainty of fine root turnover and the heterogeneity of fine root distribution are the main barriers to quantifying the below-ground C allocation. Unravelling the below-ground C litter inputs of boreal forests, including fine roots and ectomycorrhizal (EcM) mycelia, could provide fundamental information for quantifying biogeochemical cycles. This thesis evaluated the below- and above-ground litter C inputs along a site type gradient of Scots pine (*Pinus sylvestris*) sites in southern Finland, and a distinct silver birch (*Betula pendula*) site in northern Finland. Furthermore, the Scots pine pioneer/fibrous root growth phenology was observed and compared with the modelled growth of the above-ground organs (predicted by the dynamic CASSIA model) in southern Finland in 2018, when there was an unusual summer drought. Fine root turnover was observed by minirhizotrons (MR) and the root growth phenology was observed by flat-bed scanners, both of which direct methods are known to provide reliable results in root research.

Based on the daily root growth monitoring experiments, we found that the timing of intensive root growth lagged behind the growth of above-ground organs (shoots, secondary xylem, buds, and needles). Interestingly, we found a clear root growth increase while the needle growth decreased, which may have been caused by a shift of non-structural carbohydrates (NSC) from above-ground to below-ground. The low temperature and summer droughts may have constrained the fibrous root growth, but not influenced the pioneer root growth, which indicates that pioneer roots could be more tolerant to severe climate variations.

Increasing nutrient availability could clearly increase the above-ground C allocation but not the below-ground allocation. Our study sites CT, VT, MT were named after Cajander's Finnish site type theory in the order of increasing nutrient availability. Our study found that the nutrient-poor site CT tends to have significantly higher fine root longevity and biomass than the relatively nutrient-rich sites VT and MT. Fine roots could allocate more biomass below the ground and survive longer in nutrient-poor conditions. The distal tips of tree roots reflect the forest foraging ability, as shown by the fact that EcM root tips per basal area and fine root biomass per basal area both increased gradually from nutrient-rich to nutrient-poor sites and from low to high latitudes. Overall, we found that below-ground litter accounts for 21-58% of total litter inputs in boreal forests. This finding indicates that the C allocation pattern could be a specific effect of species and latitudes. The Scots pine in the southern sites allocated up to one third of total litter inputs below the ground but the northern silver birch allocated over half of total litter inputs below the ground.

In conclusion, we suggest that the growth phenology and litter inputs of below- and above-ground organs should always be observed and quantified together. Understorey species contributed significantly to litter C inputs which should not be neglected in boreal forests.

Moreover, future studies should be focused on the shifting of below- and above-ground C allocation response to extreme climate and also on the need to include EcM mycelia and root exudates in the accounting of below-ground litter pools.

**Keywords:** fine root biomass, fine root longevity, litter inputs, C allocation, root growth phenology, abiotic constraints

## ACKNOWLEDGEMENTS

I appreciate that I have so many wonderful memories and studying experiences in Finland. After a short exchange programme which I attended in 2014, I was lucky to get another chance to continue my doctoral studies in the University of Helsinki at the end of 2015. I thank my supervisor Heljä-Sisko Helmisaari for her endless guidance and encouragement. You would always find time to teach me when I came across difficulties in my study. Your words always changed my mindset from impossible to possible. No matter how little progress I may have made, you always praised me and helped me to build my confidence. I also thank my second supervisor Jaana Leppälampi-Kujansuu who spent countless hours in teaching me image analysis and data analysis, thank you so much for the great company in the fieldwork and conferences. You taught me to be confident and that it was never too late to study. Thank you, Liisa Kulmala, Pauliina Schiestl-Aalto and Kira Ryhti (from our root research group) for contributing with your tremendous ideas, discussions and fruitful comments to the root phenology research, and a special thank you to Liisa for your endless encouragement. Moreover, I want to express my gratitude for funding support from Academy of Finland, Chinese Scholarship Council, Kone Foundation, Finnish Society of Forest Sciences, AGFOREE Doctoral programme, University of Helsinki. Without your support, I could not have finished my doctoral studies so smoothly in Finland.

Thank you, Michael Bailey for your carefully editing of the language. I would like to thank the pre-examiners Annamari Markkola and Jiacun Gu for taking your valuable time in reading my thesis and giving me constructive comments. I am also grateful to Lars Vesterdal for being my opponent. I would like to thank my other co-authors, Kari Minkkinen, Maija Salemaa, Naoki Makita, Liisa Ukonmaanaho, Pekka Nöjd, Peter Železnik and Päivi Merilä for their professional and supportive comments to my research. Thank you, Jussi Heinonsalo for being my follow-up group member and for giving me advice to my research. Thank you, Ivika Ostonen, Kristiina Karhu, Chunyang Li, Frank Berninger, Krista Peltoniemi, Tapani Repo, Hui Sun, Tongxin Hu, Changyi Lu and Yu Tang for your professional advices and discussion about fine root and mycorrhiza research. Thank you, Vasili, Qian, Jere, Chunzi and field assistants for your great help in the tedious fieldwork and lab work. Thank you, my officemates and people from our department for sharing the interesting experiences of life and work. I would like to express to my master's degree supervisor Zijun Mao and mentor Tao Sun: you inspired me to the way of forest sciences.

I want to thank my Taichi Master Wenlei and my yoga teachers Jessica and Yasmin for teaching me physical exercises and meditation. I would like to thank the best friends that I met in Finland, you gave me much faithful in convincing myself to finish my study: Han, Xiaohan, Xiaoxu, Yan, Zheliang, Zixuan and her parents. I express my thanks to the foodie/coffee group for their sharing of life experiences and delicious snacks during lunch breaks. Thank you Petri for your excellent concerts and for teaching me mushroom foraging. Thanks to my old friend Zaizhi and Lin for their great support. Thank you Pengyuan for letting me take care of your baby Corgi Toutou since 2019. Thank you, Toutou for teaching me how to be responsible and respectable to another living being.

Finally, I express my deepest gratitude to my family for their endless encouragement, love and support, especially thanks to my beloved Mom, Dad, my parents in law and my husband Shen!

Yiyang Ding, Helsinki, February, 2021

## LIST OF ORIGINAL ARTICLES

This thesis consists of an introductory review followed by three research articles, which are referred to in the review by their Roman numerals. The articles are reprinted with the permission of the publishers.

- I** **Ding, Y.**, Leppälammii-Kujansuu, J. & Helmisaari, H-S., 2019. Fine root longevity and below- and aboveground litter production in a boreal *Betula pendula* forest. For. Ecol. Manag. 431: 17–25.  
<https://doi.org/10.1016/j.foreco.2018.02.039>
- II** **Ding, Y.**, Schiestl-Aalto, P., Helmisaari, H-S., Makita, N., Ryhti, K. & Kulmala, L., 2019. Temperature and moisture dependence of daily growth of Scots pine (*Pinus sylvestris* L.) roots in southern Finland. Tree Physiol. 40: 272–283.  
<https://doi.org/10.1093/treephys/tpz131>
- III** **Ding, Y.**, Leppälammii-Kujansuu, J., Minkkinen, K., Kulmala, L., Salemaa, M., Schiestl-Aalto, P., Ukonmaanaho, L., Nöjd, P., Merilä, P. & Helmisaari, H-S., 2021. Distinct patterns of below- and aboveground growth phenology and litter carbon inputs along a boreal site type gradient. For. Ecol. Manag. in press.  
<https://doi.org/10.1016/j.foreco.2021.11908>

## **AUTHOR'S CONTRIBUTION**

Yiyang Ding (YD) was responsible for the summary of this thesis and she was the corresponding author in papers I, II and III. YD was responsible for most of laboratory work, image analysis, data analysis and interpreting the results. YD contributed to most of the fieldwork with great help from other co-authors and field assistants. YD planned the hypotheses and structured the articles with other co-authors. In papers II and III, Pauliina Schiestl-Aalto performed the CASSIA model to provide the growth pattern of aboveground organs. In paper III, Jaana Leppälampi-Kujansuu collected the EcM mycelia production samples and performed the ergosterol analyses; Jaana Leppälampi-Kujansuu and Naoki Makita performed the root morphology analyses.

**LIST OF TERMS AND ABBREVIATIONS**

MR	minirhizotron
AG	above-ground
ba	stand basal area
BG	below-ground
C	carbon
CT	Cladonia site type
D	diameter
DOC	dissolved organic carbon
EcM	ectomycorrhiza
FRL	fine root longevity
FRT	fine root turnover
HMT	Hylocomium–Myrtillus site type
KM	Kaplan-Meier survival analysis
RTD	root tissue density
SSA	specific surface area
SRL	specific root length
MT	Myrtillus site type
N	nitrogen
NSC	non-structural carbohydrate
VT	Vaccinium site type
WB	Weibull error distribution analysis

## Table of Contents

ACKNOWLEDGEMENTS.....	4
LIST OF ORIGINAL ARTICLES .....	5
AUTHOR'S CONTRIBUTION .....	5
LIST OF TERMS AND ABBREVIATIONS.....	7
1 INTRODUCTION.....	9
1.1 Background.....	9
1.2 Fine root morphology .....	10
1.3 Root growth phenology .....	11
1.4 Fine root biomass and turnover .....	12
1.5 Ectomycorrhizal mycelia production.....	15
1.6 Above- and below-ground C input to soil.....	15
2 OBJECTIVES AND HYPOTHESES.....	15
3 MATERIALS AND METHODS.....	16
3.1 Site description and stand inventory.....	16
3.2 Below-ground soil and root measurements.....	18
3.3 Above-ground understory composition and litter production .....	23
3.4 Statistical analyses .....	23
4 RESULTS AND DISCUSSION.....	24
4.1 Root morphology and chemical traits .....	24
4.2 Temperature and moisture effects of root growth timing and rate.....	26
4.3 Below- and above-ground biomass and litter C inputs between various site types, tree species and environmental conditions .....	28
5 CONCLUSIONS AND FUTURE PERSPECTIVES .....	37
References .....	39

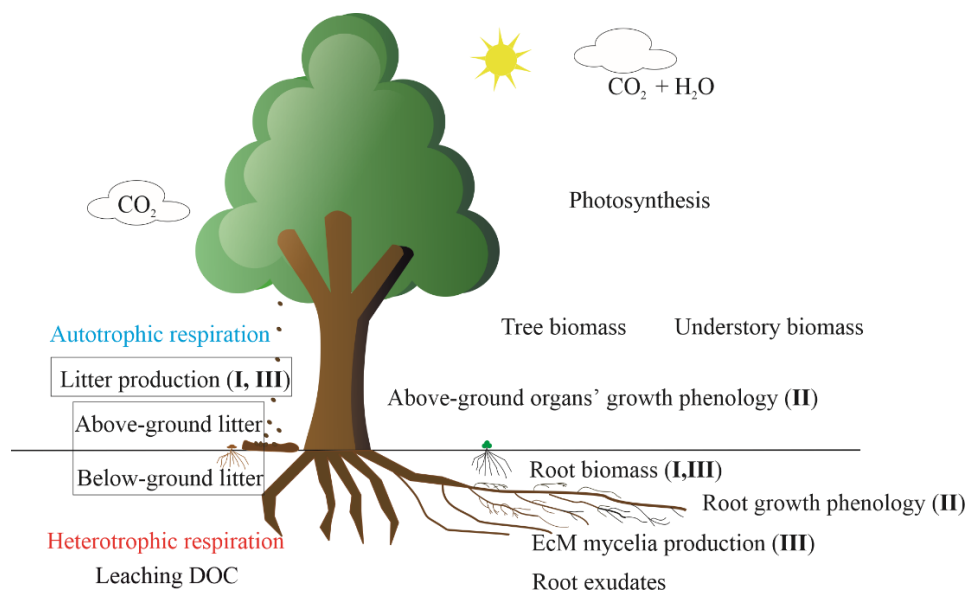
# 1 INTRODUCTION

## 1.1 Background

Roots have the main functions of plant anchorage and uptake and transport of nutrients and water for the needs of vegetation. Fine roots penetrate everywhere below-ground through the rotting litters and mineral particles, and even mycelia emerge from root distal tips to forage widely in the soil (Pregitzer 2002). Over half of the carbon (C) in boreal forests is stored in roots and root-associated symbionts (microorganisms), which also play key roles in long-term C sequestration in northern forests (Högberg et al. 2008, Clemmensen et al. 2013). According to previous studies, boreal forests were considered as important atmospheric C sinks, since the C output was far less than the C input (Jobbagy and Jackson 2000, Liski et al. 2003). Soil was commonly treated as a C source and vegetation as a C sink. The C stock in soils was ca. 5 Tg (1 Tg=10<sup>12</sup> g) C yr<sup>-1</sup> and that of trees was ca. 19 Tg C yr<sup>-1</sup> according to an inventory study of Nordic countries (Finland, Sweden and Norway) in the 1990s (Liski et al. 2002). However, with such a magnitude of stored C, the boreal biome was predicted to transit from a net C sink to a net C source gradually since the 1980s (Bradshaw and Warkentin 2015). Although there are uncertainties in the estimations of C fluxes, the rapid warming rate of boreal forests compared to the global average (Walsh 2014) could lead to an increase of C output from the soil.

In forest ecosystems, plants increase their above-ground biomass by C fixation from atmospheric CO<sub>2</sub> through photosynthesis (Fig. 1). The photosynthates are primarily utilized to build above-ground biomass by autotrophic respiration, and the extra carbohydrates are then transferred to below-ground via the phloem to build root systems and fungal mycelia in order to accomplish nutrient and water absorption. Meanwhile, through the processes of vegetation growth, senescence of foliage, and decomposition of litters, the C is released to the atmosphere by autotrophic and heterotrophic respiration (Fig. 1). The soil C stock is significantly affected by above- and below-ground litter C input and C output by respiration and leaching of dissolved organic carbon (DOC). The recalcitrant litter becomes organic matter which could persist in soil for decades or even hundreds of years (Fig. 1). The above-mentioned C circulation does not consider harvesting or other disturbances which might affect forests. The above-ground foliage litter has been shown to decompose significantly faster than below-ground fine roots (Freschet et al. 2013, Sun et al. 2018, Kvaschenko et al. 2019). Along the fertility gradient in boreal forests, root-derived inputs were convincingly more important than above-ground foliage inputs, thus having a primary importance in regulating soil organic matter accumulation (Kvaschenko et al. 2019). In order to understand the whole process chain of forest C and nutrient cycling, separate quantification of the above- and below-ground soil litter inputs is essential.

Constant renewal and shredding of fine roots are the major contributors to below-ground litter input (Lukac 2012). Fine root biomass (FRB) was reported to be higher in broad-leaved beech (*Fagus sylvatica* L.) forests, and lower in forests of conifers such as Norway spruce (*Picea abies* L. Karst.) and Scots pine (*Pinus sylvestris* L.), with significant differences in FRB between soil fertility classes of spruce and beech forests, but without any differences in pine stands (Finér et al. 2007). FRB response to soil fertility could be species-specific. In addition to fine roots, ectomycorrhizal (EcM) mycelia (Fig. 2), root exudates, soil microbes and soil fauna contribute less significantly to BG litter inputs. EcM mycelia and hyphae



**Figure 1** Simplified carbon flow in forest ecosystems. The Roman numbers in parentheses indicate the particular article of this thesis.

mantle biomass in boreal forests were predicted to represent similar amounts of biomass (between 700 to 900 kg ha<sup>-1</sup>) as fine roots at the same site (Wallander et al. 2001). The amount of C used for building vegetation tissues and mycelial biomass was relevant to net primary production (NPP), which is directly measured as plant biomass production, and to express the energy flux simply, as ‘g C m<sup>-2</sup> year<sup>-1</sup>’ (Lukac and Godbold 2011). According to limited above- and below-ground litter input studies, below-ground litter inputs account for 23-66% of total annual litter C inputs in European boreal forests (Kleja et al. 2008, Hansson et al. 2013b, 2013a, Leppälammı-Kujansuu et al. 2014a, Ding et al. 2019, 2021), and the below-ground C inputs, mainly by the dead mass of fine roots and mycorrhizal fungi, are the major contributors to stable soil organic C sequestration (Clemmensen et al. 2013, Ekblad et al. 2013, McCormack et al. 2015a, Adamczyk et al. 2019a). Above-ground litters were reported to decompose faster than fine root litters because the fine root litter was more recalcitrant than the above-ground foliage litter (Xia et al. 2015, Sun et al. 2018, Adamczyk et al. 2019b). Some tree species have higher soil C sequestration by stable form in the mineral soil, but it is unclear whether root litter input or macrofauna activity is the driven factor (Vesterdal et al. 2013). Unlike the above-ground production and turnover, which can be directly observed, the below-ground root turnover was poorly documented or had high variation due to methodological uncertainties (Majdi et al. 2005).

## 1.2 Fine root morphology

Roots showed high plasticity in response to environmental or chemical changes in soil (Ostonen et al. 2007b). Root diameter, specific root length (SRL, length per dry mass) and root tissue density (RTD, root dry mass to root volume ratio) were the main indicators to evaluate root functions adapted to soil conditions and site types. Root anatomical and morphological traits were strongly dependent on root functional (absorptive/transport)

classes (Guo et al. 2008). Absorptive roots, also called fibrous roots, exhibit primary development with the function of absorption of water and nutrients (Eissenstat and Achor 1999, Guo et al. 2008, McCormack et al. 2015a). Conversely, the higher-order roots with secondary development are transport roots or so-called pioneer roots, with no cortex or mycorrhiza colonization and mainly having the function of transporting nutrients and water (Eissenstat and Achor 1999, McCormack et al. 2015a). In boreal forests, because of the EcM colonization of first-order roots, some researchers define these roots as “distal root tips” or “EcM short roots” (Helmisaari et al. 2009, Leppälammil-Kujansuu et al. 2014a). Another study also concluded that among 23 studied tree species and their anatomical root traits in the first five orders, the first two orders of roots were absolute absorptive roots, the third-order roots could be either absorptive roots or transport roots depending on species, but fourth- and fifth-order roots were totally transport roots (Guo et al. 2008). Compared to transport roots, absorptive roots were lower in values of diameter, length, stele portion and turnover time, but higher in mycorrhiza colonization, N content and SRL (Guo et al. 2008, Zadworny and Eissenstat 2011, Zadworny et al. 2015). The absorptive roots were relatively affordable to build, with high SRL and primary development, but it was costly to maintain these roots with higher N content and root respiration (Eissenstat and Yanai 1997, Pregitzer et al. 1997, Pregitzer 2002). Consequently, absorptive roots have a faster turnover rate compared to transport roots.

Among all the morphology traits, SRL was the most used indicator to evaluate the nutrient availability of trees in forest ecosystems (Ostonen et al. 2007b). Higher values of SRL indicated thinner root diameter, higher root hydraulic conductivity and higher root length growth rate (Eissenstat and Achor 1999). Leaf economic spectrum (LES) has revealed significant patterns by linking the leaf traits to resource interception efficiency: the leaves with higher values in specific leaf area, leaf N content, photosynthetic capacity, respiration rate and shorter lifespan were separated to an acquisitive (opportunistic) module, and conversely, the leaves with opposite traits were grouped to a conservative module (Reich et al. 1992, Wright et al. 2004). In contrast to acquisition leaves, the conservative leaves require less water and a smaller nutrient supply, and generally have low respiration and photosynthesis rates but a long lifespan for resource exploration. Inspired by above-ground LES, fine roots were expected to have similar root economic spectrum (RES) traits such as SRL, N content, uptake capacity and longevity with nutrient availability. However, the results were inconsistent or contrasted between the different studies (McCormack et al. 2012, Weemstra et al. 2016, Kong et al. 2017, Ma et al. 2018).

### 1.3 Root growth phenology

The timing of root growth in terms of root phenology is affected by exogenous factors such as temperature and moisture, and by endogenous factors such as genetic variation, species and availability of carbohydrates (Abramoff and Finzi 2015). Generally, above-ground vegetation phenology shows seasonal variations in growth and senescence, which play critical roles in regulating ecosystem productivity and provide feedback to climate changes. Unlike the growth phenology of above-ground components, there is limited understanding of root growth phenology in the forest ecosystem (Steinaker and Wilson 2008), especially due to the poor temporal resolution of measurements (Menzel et al. 2006, Cleland et al. 2007) and the lack of direct measurement method. Root growth phenology has been studied by an indirect measure of root respiration (Du and Fang 2014), or by the direct minirhizotron (MR)

observation method (McCormack et al. 2014). Minirhizotrons have a rather limited observation area that cannot trace a single root growth for a long period, and previous studies often had rather long observation intervals of over two weeks. According to these uncertainties, several quantitative models assume that root growth phenology is synchronized with the above-ground shoots (Krinner et al. 2005, Thornton and Zimmermann 2007, Oleson et al. 2010). By contrast, empirical evidence showed that the growth phenology of roots was decoupled from the shoots in boreal, arctic and temperate biomes (Steinaker et al. 2010, Du and Fang 2014, Abramoff and Finzi 2015, McCormack et al. 2015b, Blume-Werry et al. 2016). A possible reason for the asynchronous growth phenomenon could be the spring-born roots, which used stored C instead of current photosynthates transferred from leaves (Gaudinski et al. 2009). Thus, the internal controls of C allocation, such as the distribution of photosynthates, hormonal signals and growth forms could lead to decoupling of growth patterns (Abramoff and Finzi 2015). However, other factors such as light availability, soil temperature and moisture need to be examined with further empirical data.

#### *Temperature*

Many studies have shown that temperature is the driving factor for root growth when soil moisture and nutrients are sufficient (Pregitzer et al. 2000, Steinaker et al. 2010, Du and Fang 2014, Abramoff and Finzi 2015). The control of environmental factors is extremely difficult in field conditions. Therefore, unexpected weather changes such as drought, flood, frost and variations in moisture and light availability could completely change the experimental results. A study conducted in a northern hardwood forest showed that monthly fine root production was strongly related to average monthly air temperature, rather than to moisture or nutrient availability, and that fine root production flushed during the warmest season of the year (Tierney et al. 2003). In boreal forests, air temperature increases faster than soil temperature in spring, and in autumn the soil is warm for a longer period, which leads to a 40% longer duration of root growth compared to leaves (Steinaker and Wilson 2008, Steinaker et al. 2010).

#### *Moisture (summer drought)*

Global warming is anticipated to induce a greater frequency of summer droughts in Europe, and especially in the boreal region the weather tends to become wetter in winter and drier in summer (Samaniego et al. 2018). The soil moisture deficits could have no significant effect on the lifespan of the fine roots with thick xylems but will shorten the lifespan of thin xylem species such as *Vaccinium* spp. (Valenzuela-Estrada et al. 2009). Several studies have found more root mortality or decrease in root lifespan during natural droughts in both coniferous and deciduous forests (Meier and Leuschner 2008). However, more detailed evidence showed that even in the same species, root types could react functionally differently if faced with severe drought. Compared to pioneer roots, absorptive roots of olive seedlings were more easily physiologically impaired by soil moisture deficit in greenhouse conditions (Polverigiani et al. 2011).

### **1.4 Fine root biomass and turnover**

In previous studies, fine root biomass (FRB) was evaluated in boreal forest ecosystems for different dominant species (Helmisaari et al. 2007, Ostonen et al. 2007a), stand ages (Vanninen and Mäkelä 1999), latitudes (Ostonen et al. 2007a, Zadworny et al. 2016) and different environmental conditions such as long-term artificial fertilization or temperature manipulation (Leppälammı-Kujansuu et al. 2013). It was frequently demonstrated that FRB

increases to adapt to low resource availability (e.g., cold soils, low nutrient availability). Along a latitude gradient (ranging from 51 to 70 °N) of a 2000 km study, Zadworny et al. (2016) found an increasing trend of absorptive (without secondary development) FRB proportion with increasing latitude. A similar observation showed that there were more FRB and EcM tips in northern latitudes compared to southern regions of Finland (Helmisaari et al. 2007, 2009). According to Leppälammii-Kujansuu et al. (2013), both fine root biomass and EcM tip numbers were higher in fertilized or warmed stands in an over 10-year experiment investigating temperature and fertility manipulation in northern Sweden. However, FRB alone cannot reflect the absorptive capacity and productivity of root systems in varying conditions. Several factors may have an impact on fine roots: variation in stand density, fine root definition by various diameter cutoffs, and root physiological characteristics could all significantly affect the amount of fine root biomass. For example, FRB per tree was positively correlated with stand basal area (Helmisaari et al. 2007), and basal area can be an accurate indicator to predict FRB in Scots pine forests (Vanninen and Mäkelä 1999). Moreover, in early days, fine roots were simply defined as roots <2 mm in D and roots >2mm in D as coarse roots (Finér et al. 2007). However, root morphology differed between species, and therefore, to distinguish roots precisely with various functions, root researchers started to separate roots with physiological functions such as absorptive and transport roots or by root orders (Guo et al. 2008, McCormack et al. 2015a). However, sorting by root orders or anatomically was tremendously time-consuming and therefore difficult to implement practically. Gradually, scientists found that the roots with diameter <1mm or <0.5mm generally have the acquisition function. Therefore, sorting fine roots by diameter cutoffs (e.g. <1 mm or <0.5 mm) is nowadays commonly used, even though a small portion of transport roots might be included.

Foliage longevity varies in conifer species, with solid evidence of 3.5-7 years (58-69°N) for pine needles and 6-15 years (46-63°N) for spruce needles in temperate and boreal forests. Needles were found to have a slower turnover rate in northern sites compared to southern locations (Reich et al. 2014). In Finland, *Pinus* spp. have been shown to have a shorter retention time than *Picea* spp. and needles in the more northern areas have longer longevity than in the south (Ukonmaanaho et al. 2008). Birch is a deciduous species and therefore birch leaves have a short retention time of one growing season. Unlike the above-ground leaf turnover that is easy to study, there are many uncertainties of below-ground root turnover due to limited numbers of studies and a variety of methodologies. Fine root turnover of boreal forests has been found to differ between species. Silver birch has a more efficient root foraging system, with thin and densely branched fine roots, compared to Scots pine (Curt and Prévosto 2003), indicating a faster turnover of deciduous fine roots than in the case of conifers. Empirical evidence in Nordic countries obtained by using the MR method showed that there was a similar fine root longevity in conifers but shorter fine root longevity in deciduous trees: 1.5-2 years in Norway spruce, 0.9-2.4 years in Scots pine, and 1 year in silver birch (Majdi 2001, Kleja et al. 2008, Leppälammii-Kujansuu et al. 2014b, 2014a, Repo et al. 2014, Ding et al. 2019). The fine root lifespans of Norway spruce, Scots pine and silver birch in south-west Sweden were reported as 3.1, 2.5 and 2.5 years, respectively (Hansson et al., 2013a), which is longer than in other Nordic studies. The authors conceded that the fine root lifespan might have been overestimated, since the death time was determined by root disappearance time, often after decomposition because of the poor MR image quality (Hansson et al. 2013b). Another uncertainty was that the above-mentioned fine root studies were mainly focused on Norway spruce forests but results on Scots pine and broad-leaved species were based on fewer studies.



**Figure 2** Ectomycorrhizal rhizomorphs and mycelia captured by a flat-bed scanner on 18.8.2017 at the SMEARII station (Scanner 2 of **study II**, image size 21 × 29.7 cm)

Among fine root physiological characteristics, fine root diameter is one of the most important indicator affecting fine root lifespan. Root diameter has an increasing effect on longevity, in terms of slower turnover rate of roots with increasing diameter (Matamala et al. 2003, Joslin et al. 2006). The root diameter effect on root lifespan may be due to the functional differences in roots, as pioneer/transport roots are generally thick in diameter with secondary development and have a long lifespan. Conversely, the fibrous/absorptive roots are thin in diameter without any secondary development and have rather short lifespans (McCormack et al. 2015a).

Fine root longevity was drastically inconsistent when measured by various methods, such as C isotope estimates or the newly-invented ‘growth ring’ method by counting annual growth rings of root anatomy in temperate and boreal regions and along the sub-arctic tree line (Solly et al. 2018). The C isotope method was reported to overestimate fine root age by only testing the C age, since the C building in the root tissue might not directly originate from recent C assimilation from the photosynthesis process (Solly et al. 2018). The same result of overestimating FRL by the isotope method was also reported in one review study (Strand et al. 2008). The reason for the inconsistency of FRL was reported by comparing MR with isotope dating ( $^{14}\text{C}$ ) methods, indicating that roots may use stored or recycled old C when building new root tissues (Helmisaari et al. 2015). Hitherto, the MR method is probably the more accurate method to detect fine root longevity, but still needs further empirical data from different sites and species.

### 1.5 Ectomycorrhizal mycelia production

In boreal biomes, massive EcM mycelia (Fig. 2) colonize coniferous fine roots and enhance their uptake of nutrients from soil. A mesh-bag method was developed to make it possible to accurately measure EcM mycelia in natural forests (Wallander et al. 2001). EcM mycelia production was estimated to range from 120 to 238 kg ha<sup>-1</sup> yr<sup>-1</sup>, but if the EcM rhizomorphs around the root mantle were included the total EcM fungal production was comparable to the production of fine roots (Wallander et al. 2001, Ekblad et al. 2016). Ekblad et al. (2013) claimed in a review paper on 140 forests that N availability (fertility) is possibly the most important factor affecting EcM mycelia production. Under artificially fertilized experimental conditions in natural forests, the production of EcM mycelia can in fact decrease after N fertilization (Nilsson and Wallander 2003, Wallander et al. 2011, Leppälammil-Kujansuu et al. 2013, Ekblad et al. 2016). Conversely, Clemmensen et al., (2006) concluded that the long-term fertilization could increase the abundance of EcM fungi in Arctic tundra. Other contributing factors may include the elevated atmospheric carbon dioxide concentration (Kasurinen et al. 2005). However, there were only few studies that focused on the EcM mycelia production over natural site type fertility gradients. Previous extensive studies on Norway spruce were concentrated in the southern boreal region (Ekblad et al. 2013).

### 1.6 Above- and below-ground C input to soil

In forests, litter is derived from different vegetation organs, such as branches, stems, leaves, cones, flowers, etc. Previous studies focused on the above-ground litter more than below-ground litter because it is easier to collect and quantify and sample. As a result, fine root litter inputs were often estimated by assumptions of above-ground litter inputs *in situ*. The fine root and mycelia litter inputs are the main contributors to soil stable C, and they contribute to stable soil C more efficiently than the above-ground litter (Sokol and Bradford 2019). Thus, fine root litter, as the major component of below-ground litter, is more recalcitrant in decomposition compared to above-ground leaf litter. As litter decomposes, C is released to the atmosphere from the forest C sink. Variations in forest soil fertility may cause differences in C allocations to above- and below-ground sinks. For example, Starr et al. (2005) stated that Scots pine above-ground litterfall production was increasing with soil fertility in Finnish boreal forests; The increase of soil nutrient availability could increase the below-ground litter input, as indicated by increasing the fine root turnover rate on a young loblolly pine plantation in a temperate climate zone (King et al. 2002); In several Swedish and Finnish Norway spruce forests, the ratio of AG/BG litter production was positively correlated with the organic layer C/N ratio, which indicated that in nutrient-poor sites the forest tends to increase the share of storage C to BG instead of AG (Leppälammil-Kujansuu et al. 2014a). However, there is insufficient published data about below-ground litter input dynamics of *Pinus* spp. in high latitudes.

## 2 OBJECTIVES AND HYPOTHESES

The main objectives of this thesis were firstly, to investigate internal and environmental control of root growth phenology and compare the timing of root growth with growth of the

above-ground organs *in situ*; secondly, to detect how dominating tree species fine root dynamics (e.g., morphological traits, biomass, turnover rate, litter C input) vary along a soil fertility gradient. The fine root biomass per basal area rather than fine root biomass as such could more accurately reflect the efficiency of resources uptake. To quantify the litter C input of the whole forest ecosystem, the above-ground litter C was also included.

Specifically, the objectives were (1) to investigate the temperature and moisture dependence of fine root growth phenology of a Scots pine forest in southern Finland, which experienced an extremely severe summer drought (**study II**); (2) to detect the fine root traits, fine root biomass, fine root turnover, above- and below-ground annual litter C input of trees and understory species of *Betula pendula* forests in northern Finland (**study I**), and of different site types of Scots pine forests in southern Finland (**study III**);

### Hypotheses

- (1) Root morphology and chemical traits (i.e., SRL, RTD, D, L, C% and N%) vary between site types (**study III**).
- (2) The root (pioneer, fibrous) growth rhythm is inconsistent with that of the above-ground organs (e.g. shoots), and summer drought is more likely to limit the growth of fibrous roots than that of pioneer roots (**study II**).
- (3) The FRB per tree level and the share of annual below-ground litter C input of total annual litter input are greater in environmentally constrained sites, which indicates a higher foraging ability (**studies I, III**).
- (4) Fine roots have a longer lifespan in less fertile or high latitude sites (**studies I, III**).
- (5) Below- and above-ground litter C inputs are related to site and soil properties (i.e. stand basal area, understory components, pH, organic layer thickness, latitude, C/N) in various site types (**studies, I, III**)

## 3 MATERIALS AND METHODS

### 3.1 Site description and stand inventory

#### *Kivalo*

Kivalo (**study I**), located in northern Finland (Fig. 3), represents typical boreal forests in the southern Lapland region. Site and soil characteristics are described in Table 1 and Table 2. The composition of understory species is *Vaccinium myrtillus* (42%), *Vaccinium vitisidaea* (2%), other dwarf shrubs (2%), grasses and herbs (23%) and 15% of the field layer is covered by mosses (Nieminen and Smolander 2006). Our study stand was a naturally regenerated single tree species stand of silver birch (*Betula pendula* Roth.). Along with the silver birch site, there were adjacent Norway spruce (*Picea abies* L. Karst) and Scots pine (*Pinus sylvestris* L.) sites belonging to the same site type *Hylocomium Myrtillus* according to Cajander (1949). The whole region was originally a homogeneous Norway spruce site, which was clear-cut in 1926 and three sites of each tree species were established. Three 25m×25m replicate study plots were established in each site. The fine root longevity and above- and below-ground C production data of an adjacent Norway spruce site have been published by Leppälammikujansuu *et al.*, (2014a). For more information on the site and soil characteristics, see Smolander & Kitunen (2002, 2011).

## Hyytiälä

**Studies II and III** were both conducted in Hyytiälä, southern Finland (Fig. 3). Site and soil characteristics are described in Table 1 and Table 2. **Study II** was only operated at SMEARII (Station for Measuring Forest Ecosystem Atmosphere Relations), also called MT in **study III**. **Study III** was operated at four sites called CTY, CT, VT, MT along an ecological site-type fertility gradient which was chosen near the SMEARII site (Station for Measuring Forest Ecosystem–Atmosphere Relations II). A.K. Cajander presented a concise site type theory for Finnish forests based on the main component of ground layer vegetation and soil fertility characteristics (Cajander 1926, 1949). According to the site-type theory (Cajander 1949), sites were named after the most common understory species: CT- *Calluna* type, VT- *Vaccinium vitis-idaea* type, MT- *Vaccinium myrtillus* type. CTY is a young stand adjacent to CT and unless otherwise mentioned, they share the same soil texture and background environmental information. The silt and clay content increases and sand content decreases from CT, VT to MT (Table 2), which reflects the fact that fertility is increasing from CT to MT. Three plots (30 m × 30 m) were established in each site. The mean annual air temperature sum was 3.5 °C, with a warmest monthly mean temperature of 16.0 °C in July and coldest monthly mean temperature of -7.7 °C in February. The average annual accumulative precipitation was 711 mm (data from 1980-2009, Pirinen *et al.*, (2012)). The temperature and moisture data for the site type gradient were downloaded from the AVAA database of the SMEARII site (<https://smear.avaa.csc.fi/>). CT, CTY, and VT were Scots pine monocultures, whereas MT was a mixture of dominating Scots pine with saplings of Norway spruce, silver birch and downy birch (*Betula pubescens*). The understory dwarf shrub species were limited in all sites; the most abundant species were *Vaccinium vitis-idaea*, *Vaccinium myrtillus*, *Calluna vulgaris*, *Empetrum spp.*, and forest mosses were abundant (i.e. *Pleurozium schreberi*, *Dicranum spp.*, *Ptilium crista-castrensi*). Lichens (*Cladonia spp.*) only appeared in the nutrient-poor sites CT, CTY and rarely in VT.



**Figure 3** Location of the study stands in southern and northern Finland. **Study I** was located in Kivalo (square dot), northern Finland; **studies II and III** were located in Hyytiälä (round dot), southern Finland.

**Table 1** Site characteristics.

Site	Kivalo	CTY	CT	VT	MT
Location	66°20'N, 26°40' E	61°50'N, 24°17'E	61°50'N, 24°17'E	61°52'N, 24°13'E	61°51'N, 24°17'E
Site type	Hylocomiu m–Myrtillus (HMT)	Cladonia (CT)	Cladonia (CT)	Vaccinium (VT)	Myrtillus (MT)
Dominant tree	Birch	Pine	Pine	Pine	Pine
Stem basal area (m <sup>2</sup> ha <sup>-1</sup> )	21.3	11.4 <sup>b</sup>	16.4	25.1	18.3
Stand age (years)	89	21	73	96	54
Mean DBH <sup>a</sup> (cm)	17.1	2.8	26.2	27.1	17.8
Mean height (m)	15.5	3.3	20.1	23.6	17.1
Stem density (no. ha <sup>-1</sup> )	1003	18433	407	422	684

<sup>a</sup>DBH abbreviated for diameter at breast height.

<sup>b</sup>CTY site was a young-age Scots pine site with a high density of seedlings; it was impossible to measure the stem basal area from the stand. Instead, we calculated its basal area from the mean DBH and stem density. Data was obtained from the year 2016 for sites CTY, CT, VT, MT.

**Table 2** Soil characteristics. Note: The general soil characteristics of the Kivalo site are reported in (Smolander and Kitunen 2002, 2011). The soil data for the Hyttiälä sites were measured in 2016. Asterisk indicates that the data was not measured.

Stand	Kivalo	CTY	CT	VT	MT
Soil type	Podzol	Ferric Podzol	Ferric Podzol	Ferric Podzol	Haplic Podzol
Soil moisture	*	dry	dry	dry	mesic
<i>Organic layer</i>					
Thickness (cm)	4.4	2.8	4	4.2	4.5
pH	4.3	3.4	3.8	3.4	3.5
N%	2	1.2	0.8	1.1	0.9
C/N	30	33.1	32.8	30.8	33
<i>Mineral soil</i>					
pH	*	5.0	4.6	4.5	4.4
N%	*	0.17	0.15	0.19	0.22
C/N	*	14.8	12.9	15.1	13.6
Stoniness (%)	25	21.1	21.1	13.1	46.5
Sand (%)	*	93.9	92.3	89.4	82.7
Silt and clay (%)	*	6.1	7.4	10.6	17.3

### 3.2 Below-ground soil and root measurements

#### *Soil and root sample preparation (Studies I, III)*

There were 60 soil-core samples sampled in August 1999 at Kivalo (**study I**) and 42 samples taken in Autumn 2013 at Hyytiälä by a cylindrical soil corer (D 40 mm) for measuring root biomass. Autumn sampling was reported to occur at the time of the maximum of fine root biomass at the end of the growing season (Makkonen and Helmisaari 1998, Ostonen et al. 2005). The samples were taken 2-5 m from MR tubes in **study I**. MR tubes in **study III** were placed in the excavated holes made by soil-core sampling. Three soil-core samples as well as MR tubes were located in each of the three subplots of CTY, CT, VT sites. Due to the shallower soil profile of MT, the soil sample numbers and MR tubes were increased to five at each subplot.

The soil samples in **studies I and III** went through similar steps of sample preparation and laboratory analysis. The soil samples were transported and stored at -18°C before laboratory analysis. Each soil core was divided into organic layer and 10 cm each of mineral soil layers. The deepest depth of the Kivalo (**study I**) soil sample was up to 34 cm, whereas in Hyytiälä the CTY, CT, VT, MT stands (**study II**) were up to 30 cm, 40 cm, 33 cm and 30 cm, respectively.

#### *Fine root biomass (Studies I, III)*

Each soil core sample was gently wet-sieved and roots were carefully selected with tweezers. A dissecting microscope was used to sort fine roots into species (tree/understory) and living status (alive/dead) according to root morphology, elasticity, thickness and toughness (Persson 1983, Vogt and Persson 1991, Vogt et al. 1993). The major identification characteristic of tree roots was that they have clusters of mycorrhizal short root tips (with typical dichotomous branching) at their distal parts (Fig. 4). The fine root diameter of trees is thicker than that of understory, but understory rhizome diameter could be much thicker than tree roots (Fig.4). Tree root colour varies between species, the suberized root colour of the conifers (e.g. pine, spruce) is brown or reddish, but broad-leaved tree species (birch, linden) usually have a brighter colour (my personal observations of birch from northern Finland and of linden from southern Finland). The living understory roots have the transparent colour of very fine roots, or totally white colour of thicker rhizomes (Fig. 4). However, colour was not a reliable standard to distinguish root living status, since distal roots colonized by EcM with darker colour could be alive. When we could not decide the living status of a root by its appearance, we scratched the root surface; the living root stele was bright and elastic whereas dead root stele was dark and with hollows. In addition, root samples were sorted into different diameter (D) classes of <1 mm, 1-2



**Figure 4** The morphological differences between tree and understory roots/rhizomes. The size of each minirhizotron image is 1.1 × 2 cm. The image was captured on August 25, 2004 from the Kivalo stand (**study I**).

mm, >2 mm. As most ephemeral roots were absorptive roots (Helmisaari et al. 2009), the roots under 1 mm in D were defined as fine roots in this study. When comparing FRB/ba in **study III**, 1-2 mm root biomass was also used. Ectomycorrhizal (EcM) short roots (root tips) were separated and estimated by counting 100%, 50% or 10% of total fine root biomass depending on the root tip density of each sample (**study I**).

The sorted root samples were oven dried at 70°C for over 48h and weighed. The stoniness of each subplot was measured and taken into consideration when calculating the dry mass of fine roots in the mineral soil layers by using the stoniness index (Viro 1952, Tamminen 1991). The FRB ( $\text{g m}^{-2}$ ) was calculated with equation (1):

$$F = \frac{m(1-\alpha)}{0.25\pi d^2} \quad (1)$$

where F is calculated fine root biomass, m is fine root weight,  $\alpha$  is stoniness index, d is soil core diameter.

### *Root morphology (Study III)*

First- and second- order roots certainly belong to absorptive roots, fourth-order root segments belong to transport roots, but the third-order roots could be either transport or absorptive roots (Guo et al. 2008). Therefore, we selected first-, second- and fourth-order root segments from several root branches with 18-30 root tips in each sample. Three samples were collected from each subplot. Root morphology traits were scanned and analysed by WinRHIZO™ Pro 2003b (Regent Instruments Inc., Quebec, Canada). After that, the root segments were dried in Petri dishes at 65°C for over 48 hours and weighed. Specific surface area (SSA), specific root length (SRL), and root tissue density (RTD) were described thoroughly in Ostonen *et al.*, (1999).

### *Fine root turnover and production (Studies I, III)*

The MR method (Bates 1937) was used to estimate fine root turnover (**studies I, III**) and for root length growth monitoring (**study II**). The MR method has for long been considered as the most reliable method to evaluate fine root production compared to soil core, ingrowth-core and N budget methods (Hendricks et al. 2006, Addo-Danso et al. 2016). Three transparent acrylic tubes were vertically installed in each subplot of CTY, CT and VT sites, but five tubes in each MT subplot since the high soil stoniness prohibited the deeper installation of tubes. The installation time was spring 2003 for Kivalo (**study I**) and autumn 2013 for the Hyytiälä stands (**study III**). A Bartz digital camera (BTC-2; Bartz Technology, Santa Barbara, USA) with a laptop system was used to collect MR images. At Kivalo (**study I**), 11 sessions of 2838 images were collected during the growing seasons of 2004-2006. At Hyytiälä (**study III**), 17 sessions of images were collected for stand MT during the growing seasons of 2014-2016, and 22 sessions for stands CTY, CT and VT during 2014-2017. Because VT was clear-cut in the spring of 2017, the turnover was calculated based on the first 17 sessions. The total numbers of images for CTY, CT, VT and MT (**study III**) were 4180, 5456, 4131 and 4284, respectively.

WinRHIZO Tron MF 2015a software (Regent Instruments Inc., Quebec, Canada) was used for the analysis of collected images (**studies I, II and III**), and root information such as diameter, length, depth, birth/death time, living status, etc. was recorded with this program. We sorted roots into tree (pine/birch) and understory roots as mentioned in the ‘fine root biomass’ section (see also Fig. 4). In tree roots, we then marked first order roots which later

became second order EcM short roots (Ostonen et al. 2013, Leppälammil-Kujansuu et al. 2014a) as ‘root tips’ because they mainly have an absorptive function, in contrast to long transport roots. The root tips generally live by clusters or at the distal end of the root segment (Helmisaari et al. 2009), with a typical dichotomous root branching system. We excluded roots of the first session since we could not know the real initiation time of these roots. Root living status was marked as ‘alive’, ‘dead’ and ‘gone’ (Hendrick and Pregitzer 1993). Roots were judged as ‘dead’ when the root diameter shrunk significantly and changed from straight to curly. However, we admit that it was possible to underestimate FRL of the roots which had a fake ‘dead’ appearance, as they could live for months until the actual death point. Conversely, Hansson et al. (2013b) only marked a root as ‘dead’ when the root decomposed, which might well have caused over-estimation of FRL. The roots that grew outside the images were eaten by soil fauna, grew back to the soil, or were covered by mycelia were all marked as ‘gone’. Living roots of the final session were treated as ‘right censored’ in our studies (**studies I, III**). The survival summary of different species, different stands, and other categories FRL were examined by Kaplan-Meier (KM) survival analysis (Kaplan and Meier 1958), and by Weibull error distribution analysis (Weibull 1951). All the statistical analyses and figures were produced by the R program. We used the ‘survival’ package (Therneau 2016), functions of ‘survfit’ and ‘survreg’ when processing the survival analyses. The ‘Survminer’ package was used to compare the FRL differences between stands (Kassambara et al. 2017).

#### *Ectomycorrhizal mycelia production (Study III)*

Fungal ingrowth nylon mesh bags (pore size of 90  $\mu\text{m}$ , 8 x 8 x 11 cm) filled with quartz-sand were used to determine the production of EcM mycelia. The fine mesh only allows fungal hyphae ingrowth and prevents roots from penetrating into the bags (Wallander 2000). Each bag was filled with 16.7 g acid-washed sand (0.2 mm in grain size).

Five in-growth mesh bags were placed at the interface between the organic layer and the mineral soil of each plot in May 2014. Three of these (the summer-bags) were collected and replaced with new mesh bags in September 2014. The rest of the bags (the winter-bags and the whole-year-bags) were collected in May 2015 and the experiment was repeated similarly to the 2014 protocol. The mesh bags were stored at  $-20^{\circ}\text{C}$  until analysed.

The mycelia production in the sand (5g wet weight, later corrected to dry weight) of each sample was further estimated by analysing the content of the fungal biomarker, ergosterol (erg), according to (Bååth 2001) and by using the conversion factor of  $3\mu\text{g ergosterol mg}^{-1}$  fungal biomass (Salmanowicz and Nylund 1988, Wallander et al. 2001). We analysed two to four replicates from each sample. One outlier containing 1.5 and 1.77 (2 repl.)  $\mu\text{g erg g}^{-1}$  of sand out of 85 samples analysed was removed from the dataset, due to its exceptionally high values.

#### *Below-ground litter production (studies I, III)*

Below-ground litter production includes fine root, mycelia, soil fauna and root exudation litter production. The measuring methods were limited in this study, and therefore we only considered fine root production (**study I**), or a combination of fine root and EcM mycelia production (**study III**). Below-ground root C input was estimated as 50% of fine root litter dry mass, and the indicator for EcM mycelia was 45% according to (Ekblad et al. 2013). KM survival analysis estimated median root longevity as FRL was used in **study I**, but FRL estimated by the WB method was used in **study III** to calculate the fine root production, due

to the fact that the understory roots did not reach 50% of death of the last session, which cannot be estimated by KM. Fine root turnover rate was broadly defined as the number of times of fine roots turnover in one year; it equals the inverse of fine root longevity. Fine root production was calculated by equation (2):

$$\text{Fine root production} = \text{Fine root biomass} \times \text{Fine root turnover rate} \quad (2)$$

### *Root length growth phenology monitoring (study II)*

Three flat-bed scanners with their protecting boxes were buried in the Hyytiälä SMEARII station (referred to as MT site in **study III**), named Scanners 1, 2 and 3. Scanner 2 was installed in May 2017 and the other scanners were installed in April 2018. The scanners were buried approximately 1 m away from a nearby mature Scots pine trunk, and they were all in an area of ca. 5 m in radius since they needed to share the same power supply and be connected to a PC in a nearby cottage. The long edge of the scanner box was buried parallel with the ground horizontal (see schematic diagram in **study II**, Fig S1). The root-free soil was carefully refilled to the space in front of the scanner screen in order to make sure that the soil layer was neither loose nor compact. Scanner images were collected on a daily basis during the growing season of 2018.

To monitor the daily root growth rate and daily active root numbers, WinRHIZO Tron software was used. The roots that appeared and later grew outside the screen were excluded at the final session. For this reason, the first root appearance of Scanner 2 on 7 May 2018 was recorded, but elongation was missing at this period. The root traits such as diameter, length and number were obtained from the last session of the images (31 Oct 2018, DOY 303).

The accumulated growth of the total root surface area accumulated from the three scanners was used to reflect the actual production of roots. The above-ground growth of organs (shoot xylem, secondary xylem, needle, bud) ( $\text{kg C day}^{-1}$ ) was estimated by a dynamic growth model ‘Carbon Allocation Sink Source Interaction’ CASSIA (Schiestl-Aalto et al. 2015) which was constructed and parameterized at the SMEARII site to simulate the accurate daily growth of above-ground organs according to environmental data. Finally, the relative growth rate of modelled above-ground organs was compared with the measured relative root growth in this study in order to detect the growth phenology of above- and below-ground organs.

Relative accumulated growth of organ of day  $i$ ,  $R_{i,j}$  ( $\in [0,1]$ ) was calculated as equation (3):

$$R_{i,j} = \frac{G_{i,j}}{G_{365,j}} \quad (3)$$

where  $G_{i,j}$  is the absolute growth accumulation on day  $i$  ( $\text{kg C}$ ) and  $G_{365,j}$  the total growth at the end of the year. Further, the relative growth rate of organ  $j$  on day  $i$  ( $dR_{i,j}$ ) is calculated as equation (4):

$$dR_{i,j} = R_{i,j} - R_{i-1,j} \quad (4)$$

### 3.3 Above-ground understory composition and litter production

The above-ground tree litter was collected with 12-20 funnel-shaped traps (with a collecting area of 0.5 m<sup>2</sup> of each trap) systematically distributed 0.6-1.5 m (varying between sites) above the ground in each stand except CT and CTY. The above-ground tree litter production in MT was originally published by Ilvesniemi *et al.*, (2009), and the tree litter was collected monthly during the years 1997-2008. The tree litter was collected twice a month during the snow-free season in Kivalo (Oct 1999-Oct 2002) and VT (May 2013- Nov 2016). The missing data of above-ground tree litterfall at the CT site was modelled according to multiple regression models (No.1 LF<sub>needle</sub> and No. 5 LF<sub>total</sub>) with the highest adjusted R<sup>2</sup>, and the models were parameterized by measured annual litterfall production and long-term climate data of Scots pine sites throughout the whole of Finland (Starr *et al.* 2005). The above-ground litter of both tree and understory in CTY were not collected because of the high density of tree seedlings. The sampled tree litter was either air-dried or 65°C oven dried over 48 hours and later sorted to needles, branches, cones, bark and others.

In our studies (**studies I, III**), the understory litter input was estimated by the understory vegetation biomass increase in one year. The Kivalo site annual understory above-ground litter production was measured in 2000 and published in Nieminen and Smolander (2006). At Hyytiälä, 9, 28 and 36 understory above-ground samples from CT, VT and MT were sampled systematically in late-August 2018, mid-July 2002 and in July 2015, respectively, by vegetation metal squares (300 × 300 mm). The understory litter was grouped into lichens, mosses, dwarf shrubs, herbs and others. At VT and MT, the understory annual biomass growth was estimated to 37%, 33%, 42% and 100% of measured total biomass for dwarf shrubs, grasses, mosses and herbs, respectively, according to different turnover rates of understory (Lehtonen *et al.* 2016). At CT, the vascular plants were separated into biomass of current year growth according to plant morphology changes in one growing season. An estimate of 20% of lichen biomass was used as the annual production based on the growth rate of *Cladonia* spp. (Helle *et al.* 1983). In addition, we used an estimate of 30% for mosses as the annual production (Merilä *et al.* 2014). All the understory samples were 60°C oven dried over 48 hours and weighed.

### 3.4 Statistical analyses

Significant differences between stands or different layers of soil profile (>2 groups) were determined by analysis of variance (ANOVA) or Kruskal-Wallis depending on how the data met the prerequisites of assumptions, all tests using a significance level of  $P < 0.05$ . The normality assumption was tested by the Shapiro-Wilk test and homogeneity was tested by Levene's test. If the data met both of the normality and homogeneity assumptions, ANOVA was used, followed by the Tukey HSD (honestly significant difference) test. If either of the assumptions did not meet the requirement, the Kruskal-Wallis test was used. To test two groups of data, e.g. comparing winter and summer production of EcM mycelia or two types of annual mycelia production (**study III**), the procedures were similar to when comparing three groups. If data met the requirements of both the normality and homogeneity tests, T test was performed. If not, Wilcoxon rank sum test was performed. Linear mixed-effect models (the tested models shown in **study II**) were built to test soil temperature, moisture, root types and spatial variability effects on root daily elongation rate. Analysis of variance (ANOVA) and Akaike information criterion (AIC) were used to screen the best model. When AIC values

were  $<2$  in several models, the model with fewer parameters was selected. Statistical analysis was performed using SPSS statistics 24 in **study I**, and statistical analysis and figures were produced in R programme in **studies II and III**.

## 4 RESULTS AND DISCUSSION

### 4.1 Root morphology and chemical traits

We observed distinct root morphology differences between transport and absorptive fine roots (**study II**: Table 1, Fig. 2; **study III**: Table S2). The transport roots were thicker, longer, and more robust than the fibrous roots. With an anatomical root morphology examination (**study III**) of the transport and absorptive roots *in situ*, we also concluded that the root diameter (D), root length (L), weight (W) per root segment and specific surface area (SSA) were significantly lower in absorptive roots than in transport roots (Table 3). By contrast, the values in root tissue density (RTD), specific root length (SRL), C%, and N% were significantly higher in absorptive roots than in transport roots (Table 3). When comparing only the morphology within the same root order, there were no significant differences between site types (**study III**: Table S2).

The transport roots with their high number of phloem layers are reported to have lower nutrient uptake capacity compared to absorptive roots (Zadworny et al. 2017). SRL is one of the most measured anatomical indices of root nutrient uptake efficiency: the thin and long roots with high SRL could be compared to thin leaves with high specific leaf area (SLA) for light interception, and roots with high SRL are assumed to have a corresponding strategy (Withington et al. 2006). We demonstrated that the root structure was composed of long-lived transport roots with low SRL, and short-lived absorptive roots with high SRL. The absorptive roots contributed to most of the length growth after the roots had anchored (**study II**). SRL decreased with increasing root diameter (Guo et al., 2008; Ostonen et al., 2007). We also showed that the first- and second-order roots had significantly ( $P < 0.05$ ) higher SRL than the fourth-order roots (Table 3). Obviously, the distal roots are more efficient in acquiring nutrients in the field.

*We hypothesized that there are variations in root morphology, such as SRL, between different site types, but the results did not show significant differences between the sites (study III, Table S2).* Comparable with our results, root morphology did not differ between sites of contrasting fertility *Quercus robur* (L.) in a study carried out in Poland (Zadworny et al. 2015). A previous study conducted in Finland found that SRL decreased with increasing site fertility of *Betula pendula* sites, whereas the SRL in coniferous sites did not change along the fertility gradient (Kallikowski et al. 2010). Makita et al. (2015) reported that a site with a higher nutrient status tends to have higher root N content and SRL, but lower RTD. Our results also indicated that the RTD of first order roots ranged between 519 and 567 kg m<sup>-3</sup> in the nutrient-poor sites CTY, CT and VT, and was 463 kg m<sup>-3</sup> in the relatively nutrient-rich site MT, but without statistical differences ( $P > 0.05$ ). However, we found inconsistencies in the root N% and SRL along the site fertility gradient (**study III**: Table S2). The reason for this could be that all the *Pinus* spp. forests in the boreal biome have rather poor soil fertility and the data was insufficient for detecting minor fine root morphological trait variations. Further investigations should examine the root morphological traits of individual species (i.e. *Pinus* spp.) of various latitudinal and fertility conditions. On the other hand, climatic variation

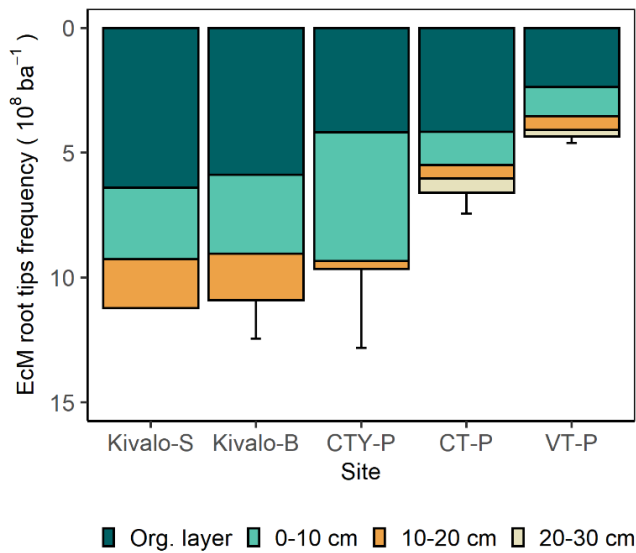
**Table 3** Absorptive (first and second orders) and transport (fourth order) root morphological and chemical traits. Values of samples (mean  $\pm$ SE) from Scots pine forests (N=4). Root average diameter (D), Root length of each root segment (L), Root weight of each root segment (W), Root tissue density (RTD), Specific root length (SRL), Specific surface area (SSA).

Order	First	Second	Fourth
D (mm)	0.21 <sup>b</sup> (0.01)	0.21 <sup>b</sup> (0.01)	0.44 <sup>a</sup> (0.02)
L (mm)	1.48 <sup>b</sup> (0.10)	1.69 <sup>ab</sup> (0.21)	1.73 <sup>a</sup> (0.08)
W (mg)	0.024 <sup>b</sup> (0.002)	0.027 <sup>b</sup> (0.002)	0.099 <sup>a</sup> (0.011)
RTD (kg m <sup>-3</sup> )	517 <sup>a</sup> (19)	509 <sup>a</sup> (22)	357 <sup>b</sup> (21)
SRL (m kg <sup>-1</sup> )	63.5 <sup>a</sup> (5.4)	74.5 <sup>a</sup> (11.8)	19.7 <sup>b</sup> (2.3)
SSA (m <sup>2</sup> kg <sup>-1</sup> )	95.6 <sup>b</sup> (13.6)	60.7 <sup>c</sup> (10.7)	415.0 <sup>a</sup> (68.6)
C (%)	46.5 <sup>a</sup> (1.1)	45.5 <sup>a</sup> (0.5)	45.9 <sup>a</sup> (0.3)
N (%)	1.27 <sup>a</sup> (0.06)	0.99 <sup>b</sup> (0.06)	0.71 <sup>c</sup> (0.03)
C:N	37.3 <sup>c</sup> (1.5)	47.4 <sup>b</sup> (2.2)	64.3 <sup>a</sup> (2.5)

may also make it more difficult to analyse site type variation.

Root morphological traits are not the only way to examine the root foraging ability on site. Counting EcM root tip numbers (so-called EcM short roots in other studies) per tree level could comprehensively increase our understanding of the site foraging ability of roots in boreal forests dominated by EcM trees (Ostonen *et al.*, 2007a; Helmisaari *et al.*, 2009a). There were 81-97% of Scots pine (97% in CTY, others ca. 80%) and 83% of silver birch EcM tips concentrated in the organic layer and the uppermost mineral soil layer (0-10 cm), which is in line with the results of Helmisaari *et al.* (2009), who showed that the conifers allocated over 80% of their EcM tips in the humus and upper soil layers. The EcM tips per basal area decreased from north to south, and from nutrient-poor to nutrient-rich sites (Fig. 5). The values in the adjacent Kivalo birch and spruce sites did not show any significant differences (Fig. 5), which is understandable as they both originated on similar soil belonging to the *Hylocomium Myrtilus* site type, and shared the same climate conditions.

*The results partly supported our third hypothesis in that fine roots in harsh conditions (limiting nutrient availability and environmental factors) branched more absorptive roots in order to maintain sufficient water and nutrient uptake.* Previous studies also supported our results that the EcM tip number per basal area for Norway spruce decreased from northern to southern Europe (Ostonen *et al.* 2011, Leppälammil-Kujansuu *et al.* 2014a), and Norway spruce EcM tip biomass/ba was 22% lower in the fertilized plots compared to the control plots (Leppälammil-Kujansuu *et al.* 2013). Ostonen *et al.* (2013) also indicated that the late-successional Norway spruce root plasticity index and morphological traits did not differ from those of the early-successional silver birch along a climate gradient with most of the study sites located in Finland and Estonia. When EcM tips were measured together (neither separate soil layers nor plots), the EcM tip frequency per mg for our Kivalo birch site was 9.2 pcs/mg, and that for the Kivalo spruce site was 6.9 pcs/mg (Leppälammil-Kujansuu *et al.* 2014a). Silver birch EcM root frequency per unit mass was previously reported as 2-2.5-fold higher than that of Norway spruce/Scots pine along a latitudinal gradient from northern Finland to southern Estonia (Ostonen *et al.* 2007a). The root density, genotype or species differences could lead to the differences in EcM root frequency per unit weight. This could be also explained by root foraging strategy (Ostonen *et al.* 2007a), as the silver birch roots have more

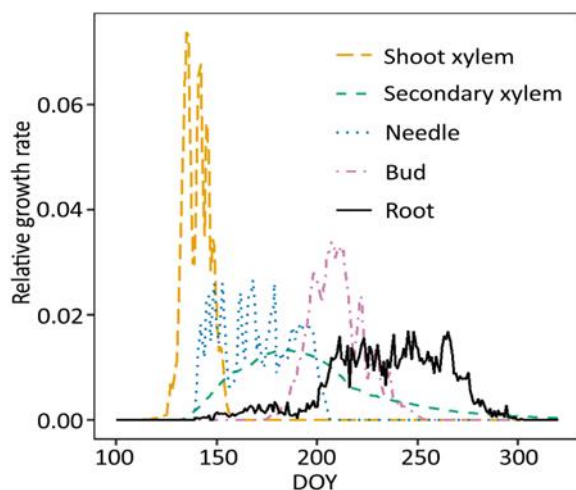


**Figure 5** Ectomycorrhizal root tip frequency per basal area. The capital letters -S, -B, and -P after the site names indicate dominating species of Norway spruce, silver birch and Scots pine, respectively. Error bars indicate standard errors at each site. The Kivalo-S data was originally published in Leppälammil-Kujansuu *et al.* (2014a). Kivalo-B (N=3); CTY-P (N=5); CT-P (N=7); VT-P (N=4); there were no significant differences between sites.

efficient foraging ability due to their higher root surface area per unit root weight than the Norway spruce on the same site and environmental conditions. If not considering the basal area/tree density of the site, the EcM frequency was similar for sites in the same latitude, 22.46-22.93 billion for the Kivalo site, 10.82-11.01 billion for the Hyttiälä site. When considering the per tree level, we concluded that in the VT site with higher density of trees, each tree had fewer EcM root tips which means less foraging ability per tree level compared to the CTY and CT sites. Unfortunately, the EcM root tip frequency on the MT site was not measured, but we assume that it could be even lower than on the VT site, since the fine root biomass per basal area was the lowest in MT (Fig. 8).

#### 4.2 Temperature and moisture effects of root growth timing and rate

The initiation time of roots in three scanners in 2018 varied between May 7 and July 19, and the cessation time varied from Oct 16 to Oct 26. The differences in the initiation and cessation times of roots were independent of different scanners, and there could have been roots that grew nearby the scanner but appeared at a later time on the screen. Nutrient availability, soil temperature and soil moisture could cause heterogeneity between scanners. In 2018 a summer drought occurred in Hyttiälä in August when the soil temperature was highest of the year and soil moisture was as low as  $0.10 \text{ m}^3 \text{ m}^{-3}$  (**study II**, Fig. 1). *This summer drought lasted ca. one month, causing fibrous roots to halt their growth at the beginning (two of three scanners were without fibrous root elongation during DOY 226-236), but pioneer root growth was not affected as drastically as the fibrous roots (study II, Fig. 3B; D), supporting our second hypothesis.* Pioneer roots accounted for 87% of the total traced root surface area.



**Figure 6** Relative growth rate of above- and below-ground organs at SMEARII in southern Finland. This figure was originally published in **study II**. The below-ground root relative growth was measured in this study, and the relative growth rate of above-ground organs was predicted by the CASSIA model (Schiestl-Aalto et al. 2015).

The relative below-ground root growth started and peaked later and lasted longer than the growth of the above-ground organs (Fig. 6). The mixed-effect models showed that root daily growth in all scanners was positively correlated with temperature, and pioneer roots grew significantly faster than fibrous roots, but soil moisture affected the scanners differently because of the spatial variability (**study II**, Table 2).

Temperature was reported as the most important abiotic factor affecting root production of woody species (Pregitzer et al. 2000, Iivonen et al. 2001, Abramoff and Finzi 2015, Schwieger et al. 2019). The increasing temperature induced soil litter decomposition and N mineralization and could promote root elongation and production (Pregitzer et al. 2000). When experiencing summer drought, the pioneer roots extend deeper and wider in the soil profile in an attempt to reach water. However, the pioneer roots themselves may have absorption ability only when they are young and unsubsized, but when they reach a wetter area, the absorptive roots initiate and help with the water absorption. In line with our results, several studies have reported that the root growth was either decreased or halted under summer drought conditions (Joslin et al. 2001). One study reported a remarkably lower FRB in a dry *Fagus sylvatica* forest than in five other beech forests without soil moisture deficiency in northwest Germany; the high mortality of fine roots when drought occurred could have caused this result (Leuschner et al. 2004). Polverigiani et al. (2011) reported that the fibrous roots faced physiological damage from drought, but pioneer roots with higher tissue density and suberin content had higher tolerance to drought than fibrous roots.

Root growth phenology is linked to the whole-plant growth phenology. Our study demonstrated that root growth has a time lag after the above-ground growth, and coincidentally we found that the root growth rate increased at the same time as the needle growth decreased. Although the CASSIA models predicted the relative growth rate of the above-ground organs in this study based on environmental factors, the predicted values were found to be close to the measured needle growth patterns. Unlike the obvious short peak period of the growth of the above-ground organs such as shoots, secondary xylem and buds, the peak time of the total

root production was not obvious, with a constantly high growth rate for over 2 months (Fig. 6). Our results showed that the offset between maximum shoot and root production was *ca.* 70 days. A review of the literature showed a similar result that the peak time of shoot growth was *ca.* 50 days earlier than that of roots in the boreal biome (Abramoff and Finzi 2015). Thus, the offset between the maximum of shoot and root production was significantly higher in conifers than in deciduous species (Abramoff and Finzi 2015). Similarly, Schwieger et al. (2019) reported that the synchrony of above- and below-ground growth varies in different ecosystems, and root phenology cannot be predicted from that of the above-ground growth phenology. The fact that the root growth of woody plants initiated, peaked and ceased inconsistently with the above-ground shoot growth was also reported in other studies (Steinaker and Wilson 2008, Steinaker et al. 2010, Du and Fang 2014, Blume-Werry et al. 2016, Kilpeläinen et al. 2019).

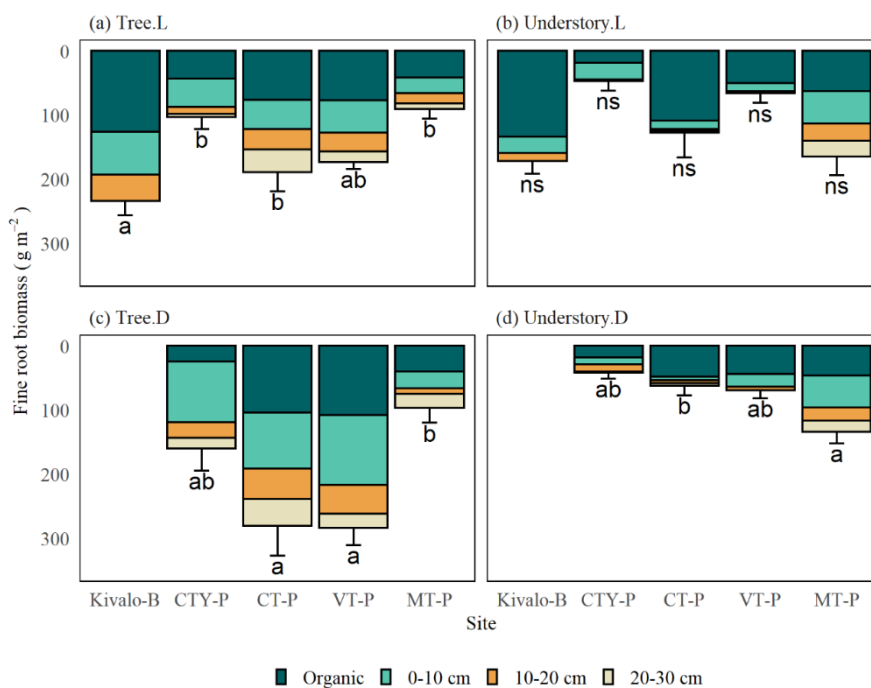
The time lag between the growth of the above-ground organs and the roots could be explained by exogenous and endogenous factors. Soil temperature directly affects the growth period of the roots, and forest soil temperature increases more slowly in the spring and also decreases more slowly in the autumn than air temperature because of the soil thermal effect. Therefore, the soil maintains a suitable temperature for root growth even after senescence of the above-ground organs (Blume-Werry et al. 2016). Furthermore, Landhäusser and Lieffers (2003) stated that the stored carbohydrates in twigs were used for leaf initiation, which was stimulated by warm air temperature. Root growth could be restricted in spring since the majority of new photosynthates are consumed by above-ground growth (Abramoff and Finzi 2015), which is then a strong carbohydrate and nutrient sink. Moreover, several specific hormones inside plants could regulate the root and shoot growth (Depuydt and Hardtke 2011, Leyser 2018), but the regulation mechanism of these hormones is not clear.

There is one undeniable shortcoming in our experiment: we did not have sufficient replications to detect the true root initiation time, as the three scanners showed time differences as long as two months. This is possibly due to the installation times that were different for the three scanners: scanners 1 and 3 were installed in the current year of measurements (2018), whereas scanner 2 was installed in the previous year before measurements (2017). Otherwise, growth patterns of the later growing seasons should be reliable. We will continue measuring the root phenology data in the coming years and examine it in future studies. Hitherto, the factors affecting the exact timing of production allocation of woody plants to below-ground organs are still unclear as only a few studies have been performed. More research is needed, as this topic is crucial to the understanding of ecosystem processes under varying environmental changes.

### **4.3 Below- and above-ground biomass and litter C inputs between various site types, tree species and environmental conditions**

#### *Fine root biomass and fine root turnover*

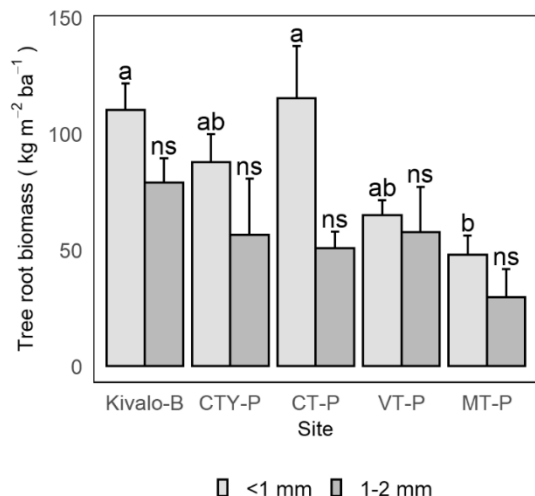
The fine root biomass (FRB) was highest in the Kivalo-birch site. The FRB of Scots pine dominated sites decreased from the nutrient-poor (CT) to the nutrient-rich site (MT). CTY was a young site on the CT site type that had the lowest FRB (Fig. 7a). The understory living root biomass did not differ statistically between all the sites, but the understory dead root mass increased from the nutrient-poor (CT) to the nutrient-rich site (MT), with a significantly ( $P < 0.05$ ) higher value in MT than CT site (Fig. 7d). In addition, the tree dead root masses of



**Figure 7** Living and dead fine root mass of tree and understory species. Error bars indicate the standard error (N=3) of each site mean value. The letters a and b indicate the significant differences ( $P < 0.05$ ) between sites, ns means not significant. L-Living, D-Dead. The amount of tree and understory dead root mass was extremely low in Kivalo-B, and therefore the data was excluded. The capital characters -P and -B at the site names indicate the site-dominating tree species of Scots pine or silver birch.

both nutrient-poorer sites CT and VT were significantly ( $P < 0.05$ ) higher than those of the nutrient-rich MT site (Fig. 7c). Comparing the FRB per stand basal area (FRB/ba), the values of the northern site (Kivalo-birch) and the nutrient-poor site (CT) were significantly higher than that of the nutrient-rich MT site (Fig. 8). If only the Scots pine sites are compared, the FRB/ba decreased gradually from the nutrient-poor site to the nutrient-rich site; even the young site with a high density of Scots pine saplings had a higher value than the relatively fertile sites VT and MT, although without statistically significant differences (Fig. 8). There were no significant differences in root biomass per stand basal area in the root diameter level of 1-2 mm (Fig. 8). The share of tree living FRB of total tree living and dead FRB was highest in the MT (48%), and somewhat lower in VT, CTY and CT (38-40%). The share of understory living FRB of total understory living and dead FRB was highest in CT (67%), followed by MT (55%), CTY (53%) and VT (49%). Understory was abundant in MT, where the share of understory living FRB of total tree and understory living FRB was 65%, whereas in Kivalo-birch, CT, CTY and VT it was 42%, 40%, 32% and 28%, respectively.

Understory roots were more superficially distributed (most in the organic and 0-10 cm mineral soil layers) than tree roots, but there was an exception that in the MT site, the understory roots penetrated as deep as the tree roots with a higher share (65%) of total living FRB (Fig. 7). It was probably due to a high stoniness of 47% in MT compared to other sites



**Figure 8** Root biomass per stand basal area by different root diameter (<1mm, 1-2 mm). Error bars indicate standard error (N=3). ba indicates stand basal area. The letters a, b indicate significant differences ( $P < 0.05$ ) between sites, ns means not significant. The capital characters after site names, -P or -B, indicate the site-dominating tree species of Scots pine or silver birch.

(13-25%; Table 2). Thus, the root competition was higher in the organic and upper mineral soil layers and understory tended to allocate more biomass to the deeper soil. The overall sharing of living to total (living + dead) FRB of understory in our southern Scots pine sites (49-67%) was higher than that of trees (38-48%), which is supported by the results of Helmisaari et al., (2007) indicating that understory roots are more persistent than those of trees in both northern and southern boreal coniferous forests.

Leppälammii-Kujansuu et al., (2014a) summarized that the percentage of FRB ( $D < 1$  mm) to FRB ( $D < 2$  mm) of Norway spruce ranged between 41 and 67% in a variety of studies conducted in Estonia, Finland, Sweden and Norway (Ostonen et al. 2005, Helmisaari et al. 2007, Børja et al. 2008, Leppälammii-Kujansuu et al. 2013). For a better comparison with our published FRB ( $D < 1$  mm) of tree species, we used 50% of FRB ( $D < 2$  mm) in publications which had different fine root diameters. Following from this, our results were comparable to tree FRB which was reported as 75-193 g m<sup>-2</sup> and to both tree and understory FRB that was 165-247 g m<sup>-2</sup> in Scots pine forests across a latitudinal gradient in Finland (Helmisaari et al. 2007). *Our results confirmed the third hypothesis that the FRB/ba was higher in harsh environmental conditions such as high latitudes or nutrient-poor sites.* FRB/ba for a 76-year-old Kivalo birch site (this study, 66°20' N) was 111.4 g m<sup>-2</sup> ba<sup>-1</sup> (Fig. 8). The FRB/ba was 33.4-43.1 g m<sup>-2</sup> on a chronosequence of 13-45 year old silver birch sites in Estonia (57°8'-58°4' N, (Varik et al. 2015)); and 60.1 g m<sup>-2</sup> on a 52-year-old silver birch site in SW Sweden (56°4' N; (Hansson et al. 2013b)). Comparing our study with the sites mentioned above, the FRB/ba of silver birch forests increased with increasing latitude from northern-temperate to northern-boreal climate zones. This indicates that silver birch forest in high latitudes could have more absorptive ability by having more fine roots at tree level. The EcM tip frequency per tree level decreased from north to south in boreal forests (Section 4.1), supporting this conclusion. Our finding was also consistent with that of Zadworny et al., (2016), who indicated that Scots pine forests at high latitudes have more foraging ability with a higher

**Table 4** Fine root median longevity (days) in different sites by Kaplan-Meier estimation (NA means that the data is skewed) and mean longevity  $\pm$  SE by Weibull error distribution regression model. The capital characters -P or -B at the site names indicate the site-dominating tree species of Scots pine or silver birch. Notes: The different letters a-c indicate significant differences ( $P < 0.05$ ) between Scots pine sites (Kivalo-B was excluded because of the different observation time), ns indicates not significant ( $P > 0.05$ ). The tips, long roots, organic layer, mineral soil all belong to tree roots

Sites	Kivalo-B	CTY-P	CT-P	VT-P	MT-P
<b>Kaplan-Meier</b>					
Tree	372	324 <sup>c</sup>	881 <sup>a</sup>	367 <sup>b</sup>	487 <sup>b</sup>
Understory	643	831 <sup>c</sup>	NA <sup>a</sup>	1088 <sup>c</sup>	NA <sup>b</sup>
<i>Tree roots</i>					
Tips	NA	318 <sup>c</sup>	867 <sup>a</sup>	326 <sup>c</sup>	417 <sup>b</sup>
Long roots	NA	480 <sup>b</sup>	927 <sup>a</sup>	942 <sup>a</sup>	965 <sup>a</sup>
Organic layer	349	517 <sup>ns</sup>	769 <sup>ns</sup>	324 <sup>ns</sup>	487 <sup>ns</sup>
Mineral soil	398	321 <sup>c</sup>	881 <sup>a</sup>	367 <sup>b</sup>	480 <sup>b</sup>
<b>Weibull</b>					
Tree	383 $\pm$ 12	340 $\pm$ 8	710 $\pm$ 51	494 $\pm$ 26	509 $\pm$ 21
Understory	493 $\pm$ 32	931 $\pm$ 39	1870 $\pm$ 296	724 $\pm$ 47	1032 $\pm$ 119
<i>Tree roots</i>					
Tips	NA	324 $\pm$ 7	598 $\pm$ 52	333 $\pm$ 18	436 $\pm$ 19
Long roots	NA	525 $\pm$ 36	865 $\pm$ 104	1147 $\pm$ 165	893 $\pm$ 105
Organic layer	340 $\pm$ 15	460 $\pm$ 35	576 $\pm$ 53	491 $\pm$ 54	614 $\pm$ 60
Mineral soil	439 $\pm$ 23	329 $\pm$ 8	962 $\pm$ 124	495 $\pm$ 30	482 $\pm$ 22

percentage of absorptive roots and thicker root cortex in order to adapt to nutrient limitation along a 2000-km latitudinal gradient of forest/common garden sites across Europe. Our results showed that FRB alone could hardly reflect the true absorption ability of the forest. Only by also considering the tree density, tree DBH and tree competition with understory species could a concise overview of the forest below-ground foraging efficiency be drawn.

The fine root longevity of tree species (WB 340-710 days) and understory (WB 493-1870 days) significantly differed in both northern deciduous forest and southern coniferous forests (**studies I and III**). We consider the fine root median lifespan as fine root longevity, but for a better comparison of our study with others, we use KM estimation of FRL in the following paragraphs. Silver birch FRL was 372 days in northern Finland (**study I**), and Scots pine mature tree FRL was 367-881 days in southern Finland along a site type gradient (**study III**). Norway spruce FRL was reported as 623-679 days from southern to northern Finland (Leppälammil-Kujansuu et al. 2014a), and 276-464 days under a frozen soil treatment in Eastern Finland (Repo et al. 2014). For the purpose of comparing the FRL of contrasting latitudes, we have different tree species from northern and southern Finland, which makes them difficult to compare. However, the FRLs of understory species are comparable from the northern and southern sites as they have similar understory species (*Vaccinium* spp.) and soil type (podzol). Our results indicated that understory fine roots lived longer in southern Finland Scots pine sites than in the northern Finland silver birch site (Table 4). *This result did not agree with the fourth hypothesis, but our data was limited and nutrient status is different in deciduous and coniferous forests.* The northern Finland Kivalo-birch site is HMT, with similar site fertility to MT.

*Our site type gradient CT, as the most nutrient-limited Scots pine site, has the longest FRL in both tree and understory species compared to the more fertile sites (VT and MT), which agreed with our fourth hypothesis, but there are no statistical differences of tree FRL between the more fertile sites VT and MT (Table 4).* Our fine root longevity was largely in agreement with other publications of *Pinus* spp. (248-753 days) and *Betula* spp. (84-308 days) which used the MR method (Withington et al. 2006, Pritchard et al. 2008, McCormack et al. 2014, Kou et al. 2016, Wang et al. 2016). Most of the reported studies have a relatively shorter FRL compared to ours, but they were all located in the temperate zone with different species. Hansson et al., (2013b) was the only publication we could find on Scots pine and silver birch species in European boreal forests using the MR method, reporting much longer longevity (Scots pine: 924-1150 days; silver birch: 917-1143 days) compared to ours. The difference may have been caused by the alive/dead criteria differences: Hansson et al., (2013b) determined a root to be dead when it had disappeared, which could be months longer than the actual root longevity. The criteria difference was due to the poor image quality and black roots which were colonized by certain mycorrhizal fungi.

The fine root longevity could be species-specific, but hitherto, the data of FRL measured by direct methods (i.e. MR, scanner, rhizobox) has been rather limited in European boreal forests, and scarcely reported for several tree species (especially *Pinus* spp. and *Betula* spp.) and for various site types. Nevertheless, several environmental factors that could affect the FRL, such as soil temperature, moisture and long-term N fertilization, were reported by root ecologists (Gill and Jackson 2000, Kitajima et al. 2010, Yuan and Chen 2010, Leppälammikujansuu et al. 2014a, 2014b, McCormack et al. 2014, 2015a, Kilpeläinen et al. 2019). However, we cannot simply assume that FRL was affected by a single factor, since there are several abiotic and biotic factors that affect FRL. For example, in **study II**, the absorptive roots suffered when summer drought occurred, but meanwhile the highest temperature in the year could hamper the fine root growth or shorten the FRL.

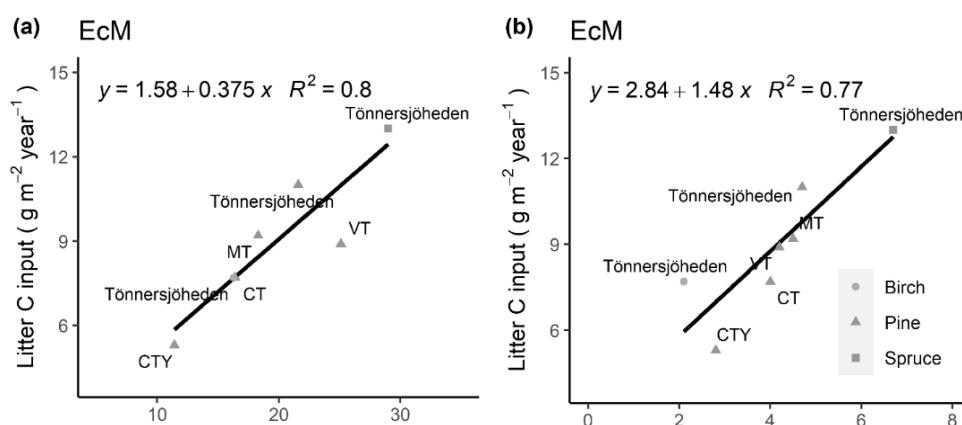
We found that the tree root tips FRL decreased from CT to MT and further to VT with statistical differences ( $P < 0.05$ ) between sites, but without significant differences in tree long roots, also called transport roots (Table 4). In agreement with our study, N fertilization was reported by Kou et al. (2018) to shorten the FRL of absorptive fine roots but not of transport fine roots in accordance with a cost-benefit tradeoff by different root types. However, nutrient addition experiments are not comparable to the natural fertility gradient when comparing the fine root lifespan.

We reported that the roots initiated late in the growing season have significantly longer FRL compared to those initiated in the early growing season (**study I**). This result was consistent with previous publications (Bai et al. 2008, Adams et al. 2013, Gu et al. 2017). The roots occurring late in the growing season have lower mortality during the following winter, which resulted in them having a relatively longer lifespan than the roots initiated early in the growing season (Gu et al. 2017). In **study II**, we observed clearly that the pioneer roots initiated late in the growing season have a node when they stopped growing before winter; they continued growing from the same root node in the following spring (personal observation). We assume that carbohydrates could be stored in the root node to support root growth when abiotic factors do not limit growth in the following spring. A similar phenomenon has been reported in above-ground shoots, in which stored carbohydrates were stimulated by warm air temperature to expand the leaves to fulfil photosynthesis in the early spring (Landhäusser and Lieffers 2003).

### *Ectomycorrhizal mycelia production*

Ectomycorrhizal (EcM) mycelia data combined in **study III** with the results of Hansson et al., (2013a) is positively correlated with stand basal area ( $R^2=0.8$ ,  $P=0.006$ , Fig. 9a) and organic layer thickness ( $R^2=0.77$ ,  $P=0.01$ , Fig. 9b). EcM-colonized root mantle and EcM mycelia was reported to have annually the same amount of fine root production in SW Sweden (Wallander et al. 2001). The great amount of EcM mycelia contributes to soil organic matter decomposition and increases N exploration efficiency (Clemmensen et al. 2021). The productivity of boreal forests is strictly limited by soil N availability and in Scandinavia the N deposition is rather low (Tamm 1991, Högberg et al. 1998). EcM mycelia enhance the nutrient acquisition of the trees (Smith and Read 2010), and over 97% of short roots of perennial trees in boreal forests are colonized by EcM fungi (Ostonen et al. 2013). Näsholm et al., (1998) reported that tree root-mycorrhiza associations could utilize organic N forms in conifers such as *Pinus sylvestris* and *Picea abies*. We found that the site with a thicker organic layer had more EcM mycelia. The organic layer was thicker in nutrient-rich sites (i.e. MT site in **study III**), with a high EcM mycelia biomass that will increase the site fertility by accelerating N mining. In that way, the nutrient-rich sites in boreal forests will be more fertile. In accordance with our findings, Salemaa et al., (2008) reported that the total N concentration of the organic layer was the key driver to boreal forest production. Moreover, nutrient-rich conditions have been shown to stimulate the fungal decomposition, which made the ecosystem even more fertile (Kyaschenko et al. 2017). Other studies have also reported that EcM production increased with increasing fertility (Ostonen and Löhmus 2003, Kalliokoski et al. 2010, Sterkenburg et al. 2015).

Our study also confirmed that with more microbial activities in the organic layer, the decomposition processes of relatively fertile sites (VT and MT) were faster than in the nutrient-poor site (CT), resulting in a lower organic layer pH (3.4-3.5) of VT and MT compared to CT (3.8). We reported that the EcM production increased gradually with site fertility, but without statistically significant differences ( $P>0.05$ , **study III**). Contrasting results have been presented of the relationships of EcM production and site fertility in previous publications from natural site-type fertility gradients and artificial N-addition



**Figure 9** Correlations of ectomycorrhizal mycelia litter C production with (a) stand basal area; (b) thickness of the organic layer; Note: The data of CTY, CT, VT, MT was from our study. The data of EcM litter from Tönnersjöheden, SW Sweden was originally published in (Hansson et al. 2013a), in which the EcM mycelia litter was predicted as 10% of fine root litter production and the C concentration of hyphae was assumed to be 45%, which is the same in our study.

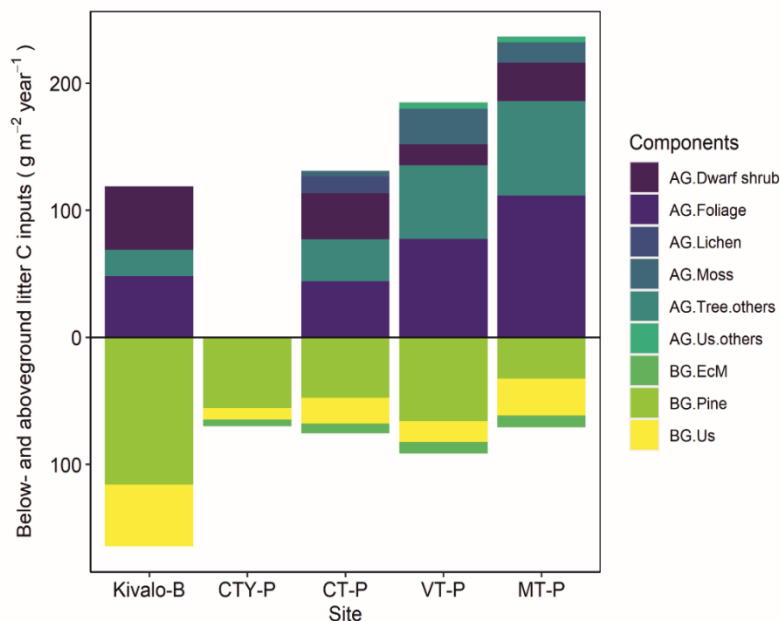
gradient experiments. Conversely, EcM production tended to decrease in N-fertilizer addition sites (Nilsson and Wallander 2003, Högberg et al. 2011), and the same result was also found in laboratory experiments (Wallander and Nylund 1992). N fertilizer addition experiments showed that the high C allocation to EcM fungi could increase the mycelia N retention, leading to a more severe N limitation in boreal forests (Näsholm et al. 2013). We assume that in non-N-fertilized Scots pine forests, EcM production could be positively related to the organic layer thickness (Fig. 9b). The abundance and continuous growth and turnover of EcM fungi will contribute to changing of the N-limited site towards a more fertile site. Our results together with the C allocation studies in northern forests (Kleja et al. 2008, Hansson et al. 2013b, 2013a, Leppälammii-Kujansuu et al. 2014b) show a strong positive correlation of total (above-ground +belowground) tree production with the organic layer thickness ( $R^2=0.53$ ,  $P=0.03$ ). This indicates that a more fertile site has a thicker organic layer than an infertile site. The nutrient-rich site in boreal Scots pine forests was reported to have a high amount of above-ground litter production (Starr et al. 2005), which induced a thick organic layer. A faster turnover rate of SOM in a nutrient-rich site was reported to be closely related to soil fungal decomposition (Mayer et al. 2021), confirming our assumption. Moreover, a defoliation experiment conducted in northern Finland reported that the defoliation increased the C limitation in colonized EcM mycelia by decreasing the EcM production and percentage of thick-mantled mycorrhizae of *Betula pubescens* seedlings (Markkola et al. 2004).

Furthermore, Soil temperature could be another constraint to EcM production. The nutrient-rich site MT with a thick humus layer could protect the microorganisms from suffering from summer drought, winter freeze or other extreme weather conditions. Our results of slightly higher temperature in winter and lower temperature in summer of VT and MT compared to CT demonstrated this (**study III**, Suppl. Fig. 2). In support of this, EcM production was found to be increased by long-term soil warming experiments (Leppälammii-Kujansuu et al. 2013). However, several other factors could also constrain the EcM production, such as limiting moisture (Kilpeläinen et al., 2017; Lehto and Zwiazek, 2011) or photosynthates (Högberg et al. 2008, 2010).

The EcM production values in this study did not include EcM mantle, but FRB included mantle which was tightly attached to fine roots. Hobbie and Colpaert, (2003) and Ostonen and Löhmus, (2003) reported that 12–28% of EcM root tissue biomass belongs to EcM mantle in conifers. The attached sand particles on roots could cause the overestimation of FRB, but usually with a low value of less than 6%, as reported by Helmisaari et al., (2007).

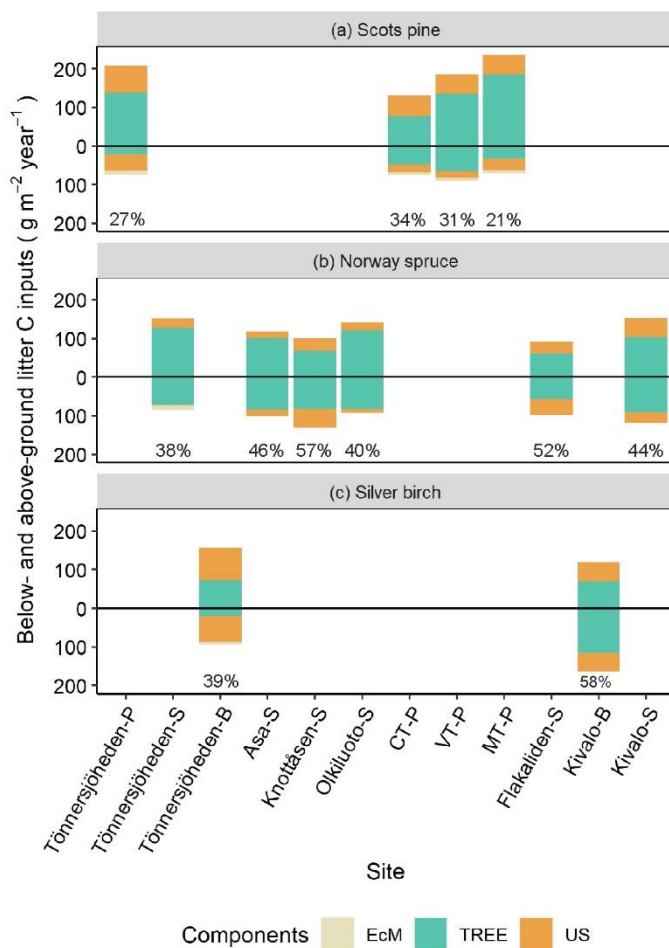
#### *Below- and above-ground litter C inputs*

Compared to the Northern site Kivalo, our southern sites (CTY, CT, VT, MT) have smaller below-ground litter inputs (Fig. 10). The dominant tree species in Kivalo is a broad-leaved tree species, silver birch, whereas trees on the other sites are needle-leaved Scots pine. The fine root litter C input at the Kivalo silver birch site was  $116 \text{ g C m}^{-2} \text{ year}^{-1}$ , which is comparable to the adjacent Norway spruce site with  $118 \text{ g C m}^{-2} \text{ year}^{-1}$  (Leppälammii-Kujansuu et al. 2014a), higher than in our southern sites. Similarly, a study conducted in Canadian boreal forests reported that in northern black spruce stands, net primary production of fine roots was four-fold higher than that of southern aspen stands (Steele et al. 1997). Furthermore, conifer (i.e. black spruce, jack pine) coarse and fine root NPP was ca. twofold higher than that of a deciduous stand (aspen) (Steele et al. 1997). Thus, different species among conifers appear to have differences in allocating C production to above- and below-ground, which could be indicated by the foliage: fine root ratio of production/biomass.



**Figure 10** Annual below- and above-ground litter C input ( $\text{g m}^{-2} \text{ year}^{-1}$ ) of trees and understory species. The capital characters -P or -B at the site names indicate the site-dominating tree species of Scots pine or silver birch. The CTY site has a high density of Scots pine saplings, thus the above-ground data was not measured. The capital characters at the site names, -P or -B, indicate the site-dominating tree species of Scots pine or silver birch.

We found that the foliage: fine root litter production ratio increased with the fertility gradient of Scots pine forests CT (0.9), VT (1.2), and MT (3.4), confirming our fifth hypothesis. However, this ratio was lowest in the Kivalo-birch site, because of the large amount of annually produced foliage. The least fertile site CT in our study has even more litter C production by fine roots than foliage. Our results demonstrated that the fertile site allocated less fixed C to below-ground and even transferred the extra C to form more EcM fungi than infertile sites (Fig. 10). In agreement with our results, Helmisaari et al., (2007) reported that the foliage to fine root biomass ratio was higher overall in Norway spruce (2.1-6.4) compared to Scots pine (0.8-2.2) across 16 stands throughout Finland. This reflected the fact that Norway spruce allocates relatively less assimilated C to fine roots compared to Scots pine. In boreal forests, Norway spruce grows on more fertile sites compared to Scots pine and thus the relative C allocation to fine roots increases from nutrient-rich to nutrient-poor sites (Helmisaari et al. 2007). We also found that the foliage: fine root ratio was related to forest site types, as the mesic site MT had the highest ratio of 3.4 and that for sub-xeric (VT) and xeric (CT) sites was in the range of 0.9-1.2. According to Hendricks et al., (2006), the foliage: fine root ratio was ca. twofold higher in a mesic stand (3.1) than in xeric (1.5) and hydric (1.4) stands of *Pinus palustris* forests. Fine root allocated more biomass below the ground and have a rather longer longevity which could be explained by (Bloom et al. 1985), stating that a plant is investing more to that organ, which is acquiring the limiting resource. For example, in this research the C allocation flow to the roots in case of the nutrient or water limitation.



**Figure 11** Annual below- and above-ground litter C input ( $\text{g m}^{-2} \text{ year}^{-1}$ ) of trees and understory species between sites from north to south. The capital characters at the site names, -P, -S or -B, indicate the site-dominating tree species of Scots pine, Norway spruce or silver birch, respectively. The site order from left to right is from low to high latitude ( $56^{\circ}40'$ - $66^{\circ}20'$  N). The numbers in the lower figure indicate the percentage of below-ground C of total litter C inputs.

To summarise our data in comparison with the most recently published literature which used the MR method to estimate FRT in European boreal forests (Kleja et al. 2008, Hansson et al. 2013b, 2013a, Leppälammil-Kujansuu et al. 2014b), we found that the below-ground litter C inputs to total litter C inputs in boreal forests were species-specific, with ranges of 21-34%, 36-52%, 38-58% for Scots pine, Norway spruce and silver birch, respectively (Fig. 11). In these studies, a range of 13-37% of total litter production was by understory species. Scots pine has more above-ground litter production but less below-ground litter production compared to Norway spruce and silver birch sites, which resulted in a lower below-ground to total above- and below-ground annual production ratio (Fig. 11). Steele et al., (1997) also confirmed that the ratio of fine root NPP to total (AG and BG) production was 27-69 %, comparable to our study, but that the ratios were greater in conifers than in deciduous forests. Maybe due to lack of sufficient data of silver birch forests or other deciduous tree species,

we did not find this pattern. Leppälampi-Kujansuu et al., (2014a) reported that the AG/BG litter inputs ratio of Norway spruce decreased significantly with increasing C/N ratio of the organic layer. C/N ratio could be one of the most important indices to describe nutrient availability in northern forests. For example, more fertile sites normally have lower C/N values. In that respect their study agreed with our results: the AG/BG litter inputs decreased with decreasing nutrient availability, which means that there was a shifting of C allocation from above-ground to below-ground in nutrient-poor areas.

## 5 CONCLUSIONS AND FUTURE PERSPECTIVES

Boreal forest soils contain a great amount of C storage in the organic layer and upper mineral soil. Continuous growth and turnover of fine roots and EcM fungi was the major contributor to below-ground C litter inputs. Unravelling the fine root dynamics has been a struggle for root researchers for decades. The limited quantification of fine root litter inputs into soil can lead to a great uncertainty in forest C cycling studies, especially in the case of forest C flux models. As technology has developed rapidly, root rhizoboxes, flat-bed scanners and minirhizotron methods now make it possible to partly observe the root growth, although not without root and soil disturbances. The root X-ray/MRI method could be harmless to roots or the soil profile, but impossible to conduct in natural forest ecosystems. Roots are tightly covered by soil particles and EcM fungi in boreal forests, which makes it even harder for researchers to observe fine root dynamics. These questions were recently frequently addressed in root studies: What is the timing of the root growth? How does root growth respond to abiotic and biotic constraints? What is the longevity of roots? How will climate change influence fine root dynamics and ultimately the below-ground C fluxes? Is below-ground biomass a C sink or a C source in the boreal biome?

In this study, we mainly detected the growth phenology of below-ground fine roots and EcM with that of the above-ground organs (i.e. shoot, secondary xylem, needle, bud; **study II**), fine root dynamics (**studies I, III**) and interactions of below- and above-ground C litter inputs across a Finnish site type gradient of Scots pine forests in southern Finland (**study III**) and one distinct silver birch site in northern Finland (**study I**). Our study is probably the first using flat-bed scanners with an automatic capture system to observe the root daily growth phenology response to abiotic constraints in boreal forests (**study II**). By comparing the measured pioneer and fibrous root relative growth rate and with the estimated relative growth of above-ground organs (the CASSIA dynamic model which was conducted and parameterized in the same site), a distinct increase of root growth was observed at the same time as the needle growth decreased. Although roots initiated at the same time as shoots, the intensive root growth was after the growth peaks of above-ground organs. Root growth rhythm varies between different root types (pioneer/fibrous), and on different scanners. Root growth was positively correlated with soil temperature, and pioneer roots grew faster than fibrous roots. The moisture dependence differences between scanners were largely due to the soil moisture heterogeneity in the natural forest site. A summer drought occurred in the summer of 2018, which caused a decrease in fibrous root growth but not in pioneer root growth. Moreover, the pioneer roots could initiate growth and also ceased growth at a 2 °C

lower temperature than the fibrous roots. These results indicated that the pioneer roots of Scots pine are more tolerant to abiotic constraints than the fibrous roots.

Fine root morphology did not differ among site types of Scots pine forests in southern Finland, but differed significantly by root types (i.e. transport roots, absorptive roots). It was interesting to note that the EcM short root (1st order roots) numbers per tree level were significantly higher in northern than in southern sites, regardless of the tree species (i.e. Norway spruce, silver birch). We also found that EcM root tip numbers reflected the root foraging ability, as both EcM root tip numbers/ba and FRB/ba decreased gradually from a nutrient-poor site to a nutrient-rich site along a site type gradient. The roots in a nutrient-poor site have more EcM root tips to exploit a broader area and seek more possibilities for absorbing nutrients and water. In our study, roots in a nutrient-poor site tended to live longer than roots in a nutrient-rich site, which also agrees with the root economic spectrum assumption that root systems with lower nutrient and water uptake tend to allocate more assimilated C to below-ground biomass and prolong root longevity in order to retain resources for longer. However, the concept of root economic spectrum is still debated, with contrasting blocks of evidence.

Our quantified litter C inputs of below-ground and above-ground litter with separating of trees and understory species could provide valuable data for boreal forest C-flux models. Our study showed that 21-58% of total litter inputs belong to below-ground litter (mostly to fine roots), and Scots pine species in southern Finland allocated 21-34% of total litter inputs into below-ground biomass, which is lower than that of the distinct silver birch site (58%) in northern Finland. However, the above- and below-ground C litter allocation of Scots pine and silver birch sites has seldom been reported in European boreal forests. Unlike above-ground litter decomposition, the below-ground fine root litter decomposition is another open question for root researchers. Fine root litters were reported as having 2-10-fold slower decomposition rates than foliage litters in boreal forests (Kyaschenko et al. 2019). Soil N is the main limiting factor to boreal forest productivity, and the limiting nutrient availability of soil constrains the understory growth, making the site suitable only for certain understory species. Based on the appearance and abundances of the tree and understory species on the ground, Finnish forests are classified by site types (Cajander 1926, 1949). We found that the ratio of below-ground: total litter inputs was decreased by increasing site fertility because of the increase in above-ground litter inputs with site fertility.

Our study showed that the sites in higher latitudes tended to have a higher proportion of below-ground litter inputs: total litter inputs, and that the below- and above-ground litter allocation patterns could be species-specific. *Pinus* spp. allocates more C to above-ground biomass than to below-ground biomass annually, but studies of sites dominated by *Pinus* spp. and *Betula* spp. are still scarce and plagued with many uncertainties.

This thesis demonstrated that the growth phenology and litter allocation/production of below- and above-ground organs are closely connected and should always be quantified together. Future studies could be more specific for one single species across various latitudes and could also consider the missing C fluxes of current studies (i.e. root exudation, root respiration) and the uncertainty of the EcM mycelia turnover rate. Finally, quantifying growth phenology and C allocation to below- and above-ground biomass by separating species (tree, understory) and site types of boreal forests has important implications for modelling forest ecosystem carbon and nutrient dynamics in changing climate.

## References

- Abramoff RZ, Finzi AC (2015) Are above- and below-ground phenology in sync? *New Phytol* 205: 1054–1061. <https://doi.org/10.1111/nph.13111>.
- Adamczyk B, Sietiö O-M, Straková P, Prommer J, Wild B, Hagner M, Pihlatie M, Fritze H, Richter A, Heinonsalo J (2019a) Plant roots increase both decomposition and stable organic matter formation in boreal forest soil. *Nat Commun* 10: 3982. <https://doi.org/10.1038/s41467-019-11993-1>.
- Adamczyk B, Sietiö O-M, Biasi C, Heinonsalo J (2019b) Interaction between tannins and fungal necromass stabilizes fungal residues in boreal forest soils. *New Phytol* 223: 16–21. <https://doi.org/10.1111/nph.15729>.
- Adams TS, McCormack ML, Eissenstat DM (2013) Foraging strategies in trees of different root morphology: The role of root lifespan. *Tree Physiol* 33:940–948. <https://doi.org/10.1093/treephys/tpt067>.
- Addo-Danso SD, Prescott CE, Smith AR (2016) Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A review. *For Ecol Manage* 359: 332–351. <https://doi.org/10.1016/j.foreco.2015.08.015>.
- Bååth E (2001) Estimation of fungal growth rates in soil using <sup>14</sup>C-acetate incorporation into ergosterol. *Soil Biol Biochem* 33: 2011–2018. [https://doi.org/10.1016/S0038-0717\(01\)00137-7](https://doi.org/10.1016/S0038-0717(01)00137-7).
- Bai WM, Wang ZW, Chen QS, Zhang WH, Li LH (2008) Spatial and temporal effects of nitrogen addition on root life span of *Leymus chinensis* in a typical steppe of Inner Mongolia. *Funct Ecol* 22: 583–591. <https://doi.org/10.1111/j.1365-2435.2008.01403.x>.
- Bates GH (1937) A device for the observation of root growth in the soil. *Nature* 139: 966–967. <https://doi.org/10.1038/139966b0>.
- Bloom AJ, Chapin SF, Mooney HA (1985) Resource limitation in plants-an economic analogy. *Annu Rev Ecol Syst* 16: 363–92. <https://doi.org/10.1146/annurev.es.16.110185.002051>.
- Blume-Werry G, Wilson SD, Kreyling J, Milbau A (2016) The hidden season: Growing season is 50% longer below than above ground along an arctic elevation gradient. *New Phytol* 209: 978–986. <https://doi.org/10.1111/nph.13655>.
- Børja I, De Wit HA, Steffenrem A, Majdi H (2008) Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in southeast Norway. *Tree Physiol* 28: 773–784. <https://doi.org/10.1093/treephys/28.5.773>.
- Bradshaw CJA, Warkentin IG (2015) Global estimates of boreal forest carbon stocks and flux. *Global Planet Change* 128: 24–30. <https://doi.org/10.1016/j.gloplacha.2015.02.004>.
- Cajander AK (1926) The theory of forest types. *Acta For Fenn* 29: 1–108. <https://doi.org/10.14214/aff.7193>.

Cajander AK (1949) Metsätyypit ja niiden merkitys. Forest types and their significance. Acta For Fenn 56: 1–79. <https://doi.org/10.14214/aff.7395>.

Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to global change. Trends Ecol Evol 22: 357–365. <https://doi.org/10.1016/j.tree.2007.04.003>.

Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle D, Lindahl BD (2013) Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339: 1615–1618. <https://doi.org/10.7551/mitpress/8876.003.0036>.

Clemmensen KE, Durling MB, Michelsen A, Hallin S, Finlay RD, Lindahl BD (2021) A tipping point in carbon storage when forest expands into tundra is related to mycorrhizal recycling of nitrogen. Ecol Lett 24: 1193–1204. <https://doi.org/10.1111/ele.13735>.

Clemmensen KE, Michelsen A, Jonasson S, Shaver GR (2006) Increased ectomycorrhizal fungal abundance after long-term fertilization and warming of two arctic tundra ecosystems. New Phytol 171: 391–404. <https://doi.org/10.1111/j.1469-8137.2006.01778.x>.

Curt T, Prévosto B (2003) Rooting strategy of naturally regenerated beech in Silver birch and Scots pine woodlands. Plant Soil 255: 265–279. <https://doi.org/10.1023/A:1026132021506>.

Depuydt S, Hardtke CS (2011) Hormone Signalling Crosstalk in Plant Growth Regulation. Current Biology 21: R365–R373. <https://doi.org/10.1016/j.cub.2011.03.013>.

Ding Y, Leppälammil-Kujansuu J, Helmisaari H-S (2019) Fine root longevity and below- and aboveground litter production in a boreal *Betula pendula* forest. For Ecol Manage 431: 17–25. <https://doi.org/10.1016/j.foreco.2018.02.039>.

Ding Y, Leppälammil-Kujansuu J, Salemaa M, Schiestl-aalto P, Kulmala L, Ukonmaanaho L, Nöjd P, Minkkinen K, Makita N, Zeleznik P, Merilä P, Helmisaari H-S (2021) Distinct patterns of below- and aboveground growth phenology and litter carbon inputs along a boreal site type gradient. For Ecol Manage 489: 119081. <https://doi.org/10.1016/j.foreco.2021.119081>.

Du E, Fang J (2014) Linking belowground and aboveground phenology in two boreal forests in Northeast China. Oecologia 176: 883–892. <https://doi.org/10.1007/s00442-014-3055-y>.

Eissenstat DM, Achor DS (1999) Anatomical characteristics of roots of citrus rootstocks that vary in specific root length. New Phytol 141: 309–321. <https://doi.org/10.1046/j.1469-8137.1999.00342.x>.

Eissenstat DM, Yanai RD (1997) The Ecology of Root Lifespan. In: Begon M, Fitter AH (eds) Advances in Ecological Research. Academic Press, London, pp 1–60. [https://doi.org/10.1016/S0065-2504\(08\)60005-7](https://doi.org/10.1016/S0065-2504(08)60005-7).

Ekblad A, Mikusinska A, Ågren GI, Menichetti L, Wallander H, Vilgalys R, Bahr A, Eriksson U (2016) Production and turnover of ectomycorrhizal extramatrical mycelial biomass and necromass under elevated CO<sub>2</sub> and nitrogen fertilization. New Phytol 211: 874–885. <https://doi.org/10.1111/nph.13961>.

Ekblad A, Wallander H, Godbold DL, Cruz C, Johnson D, Baldrian P, Björk RG, Epron D, Kieliszewska-Rokicka B, Kjeller R, Kraigher H, Matzner E, Neumann J, Plassard C (2013) The production and turnover of extramatrical mycelium of ectomycorrhizal fungi in forest soils: Role in carbon cycling. *Plant Soil* 366: 1–27. <https://doi.org/10.1007/s11104-013-1630-3>.

Finér L, Helmisaari H-S, Lohmus K, Majdi H, Brunner I, Børja I, Eldhuset TD, Godbold DL, Grebenc T, Konôpka B, Kraigher H, Möttönen M-R, Ohashi M, Oleksyn J, Ostonen I, Uri V, Vanguelova EI (2007) Variation in fine root biomass of three European tree species: Beech (*Fagus sylvatica* L.), Norway spruce (*Picea abies* L. Karst.), and Scots pine (*Pinus sylvestris* L.) *Plant Biosyst* 141: 394–405. <https://doi.org/10.1080/11263500701625897>.

Freschet GT, Cornwell WK, Wardle DA, Elumeeva TG, Liu W, Jackson BG, Onipchenko VG, Soudzilovskaia NA, Tao J, Cornelissen JHC (2013) Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J Ecol* 101: 943–952. <https://doi.org/10.1111/1365-2745.12092>.

Gaudinski JB, Torn MS, Riley WJ, Swanston C, Trumbore SE, Joslin JD, Majdi H, Dawson TE, Hanson PJ (2009) Use of stored carbon reserves in growth of temperate tree roots and leaf buds: analyses using radiocarbon measurements and modeling. *Glob Chang Biol* 15: 992–1014. <https://doi.org/10.1111/j.1365-2486.2008.01736.x>.

Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytol* 147: 13–31. <https://doi.org/10.1046/j.1469-8137.2000.00681.x>.

Gu J, Wang Y, Fahey TJ, Wang Z (2017) Effects of root diameter, branch order, soil depth and season of birth on fine root life span in five temperate tree species. *Eur J For Res* 136: 727–738. <https://doi.org/10.1007/s10342-017-1068-x>.

Guo DL, Xia M, Wei X, Chang W, Liu Y, Wang Z (2008) Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. *New Phytol* 180: 673–683. <https://doi.org/10.1111/j.1469-8137.2008.02573.x>.

Hansson K, Fröberg M, Helmisaari H-S, Kleja DB, Olsson BA, Olsson M, Persson T (2013a) Carbon and nitrogen pools and fluxes above and below ground in spruce, pine and birch stands in southern Sweden. *For Ecol Manage* 309: 28–35. <https://doi.org/10.1016/j.foreco.2013.05.029>.

Hansson K, Helmisaari H-S, Sah SP, Lange H (2013b) Fine root production and turnover of tree and understorey vegetation in Scots pine, silver birch and Norway spruce stands in SW Sweden. *For Ecol Manage* 309: 58–65. <https://doi.org/10.1016/j.foreco.2013.01.022>.

Helle T, Aspi J, Tarvainen L (1983) The growth rate of *Cladonia rangiferina* and *C. mitis* in relation to forest characteristics in Northeastern Finland. *Rangifer* 3: 2–5. <https://doi.org/10.7557/2.3.2.471>.

Helmisaari H-S, Derome J, Nöjd P, Kukkola M (2007) Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. *Tree Physiol* 27: 1493–1504. <https://doi.org/10.1093/treephys/27.10.1493>.

Helmisaari H-S, Ostonen I, Lohmus K, Derome J, Lindroos A-J, Merila P, Nojd P (2009) Ectomycorrhizal root tips in relation to site and stand characteristics in Norway spruce and Scots pine stands in boreal forests. *Tree Physiol* 29: 445–456. <https://doi.org/10.1093/treephys/tpn042>.

Helmisaari H-S, Leppälammil-Kujansuu J, Sah S, Bryant C, Kleja DB (2015) Old carbon in young fine roots in boreal forests. *Biogeochemistry* 125: 37–46. <https://doi.org/10.1007/s10533-015-0110-7>.

Hendrick RL, Pregitzer KS (1993) Patterns of fine root mortality in two sugar maple forests. *Nature* 361: 59–61. <https://doi.org/10.1038/361059a0>.

Hendricks JJ, Hendrick RL, Wilson CA, Mitchell RJ, Pecot SD, Guo DL (2006) Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. *J Ecol* 94: 40–57. <https://doi.org/10.1111/j.1365-2745.2005.01067.x>.

Hobbie EA, Colpaert JV (2003) Nitrogen availability and colonization by mycorrhizal fungi correlate with nitrogen isotope patterns in plants. *New Phytol* 157: 115–126. <https://doi.org/10.1046/j.1469-8137.2003.00657.x>.

Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm T, Högberg P (2010) Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytol* 187: 485–493. <https://doi.org/10.1111/j.1469-8137.2010.03274.x>.

Högberg P, Högberg MN, Göttlicher SG, Betson NR, Keel SG, Metcalfe DB, Campbell CD, Schindlbacher A, Hurry V, Lundmark T, Linder S, Näsholm T (2008) High temporal resolution tracing of photosynthate carbon from the tree canopy to forest soil microorganisms. *New Phytol* 177: 220–228. <https://doi.org/10.1111/j.1469-8137.2007.02238.x>.

Högberg P, Högbom L, Schinkel H (1998) Nitrogen-related root variables of trees along an N-deposition gradient in Europe. *Tree Physiol* 18: 823–828. <https://doi.org/10.1093/treephys/18.12.823>.

Högberg P, Johannisson C, Yarwood SA, Callesen I, Näsholm T, Myrold DD, Högberg MN (2011) Recovery of ectomycorrhiza after “nitrogen saturation” of a conifer forest. *New Phytol* 189: 515–525. <https://doi.org/10.1111/j.1469-8137.2010.03485.x>.

Iivonen S, Rikala R, Vapaavuori E (2001) Seasonal root growth of scots pine seedlings in relation to shoot phenology, carbohydrate status, and nutrient supply. *Can J For Res* 31: 1569–1578. <https://doi.org/10.1139/x01-094>.

Ilvesniemi H, Levula J, Ojansuu R, Kolari P, Kulmala L, Pumpanen J, Launiainen S, Vesala T, Nikinmaa E (2009) Long-term measurements of the carbon balance of a boreal Scots pine dominated forest ecosystem. *Boreal Environ Res* 14: 731–753.

Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10: 423–436. [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOS0\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOS0]2.0.CO;2).

Joslin JD, Gaudinski JB, Torn MS, Riley WJ, Hanson PJ (2006) Fine-root turnover patterns and their relationship to root diameter and soil depth in a <sup>14</sup>C-labeled hardwood forest. *New Phytol* 172: 523–535. <https://doi.org/10.1111/j.1469-8137.2006.01847.x>.

Joslin JD, Wolfe MH, Hanson PJ (2001) Factors controlling the timing of root elongation intensity in a mature upland oak stand. *Plant Soil* 228: 201–212. <https://doi.org/10.1023/A:1004866705021>.

Kalliokoski T, Pennanen T, Nygren P, Sievänen R, Helmisaari H-S (2010) Belowground interspecific competition in mixed boreal forests: fine root and ectomycorrhiza characteristics along stand developmental stage and soil fertility gradients. *Plant Soil* 330: 73–89. <https://doi.org/10.1007/s11104-009-0177-9>.

Kaplan EL, Meier P (1958) Nonparametric estimation from incomplete observations. *J Am Stat Assoc* 53: 457–481. <https://doi.org/10.1080/01621459.1958.10501452>.

Kassambara A, Kosinski M, Biecek P (2017) survminer: Drawing Survival Curves using “ggplot2”. R package version 0.3.1.

Kasurinen A, Keinänen MM, Kaipainen S, Nilsson LO, Vapaavuori E, Kontro MH, Holopainen T (2005) Below-ground responses of silver birch trees exposed to elevated CO<sub>2</sub> and O<sub>3</sub> levels during three growing seasons. *Glob Chang Biol* 11: 1167–1179. <https://doi.org/10.1111/j.1365-2486.2005.00970.x>.

Kilpeläinen J, Barbero-López A, Vestberg M, Heiskanen J, Lehto T (2017) Does severe soil drought have after-effects on arbuscular and ectomycorrhizal root colonisation and plant nutrition? *Plant Soil* 418: 377–386. <https://doi.org/10.1007/s11104-017-3308-8>.

Kilpeläinen J, Domisch T, Lehto T, Finér L, Aphalo PJ, Leinonen I, Ryyppö A, Repo T (2019) Root and shoot phenology and root longevity of Norway spruce saplings grown at different soil temperatures. *Can J For Res* 49: 1441–1452. <https://doi.org/10.1139/cjfr-2019-0190>.

King JS, Albaugh TJ, Allen HL, Buford M, Strain BR, Dougherty PM (2002) Below-ground carbon input to soil is controlled by nutrient availability and fine root dynamics in loblolly pine. *New Phytol* 154: 389–398. <https://doi.org/10.1046/j.1469-8137.2002.00393.x>.

Kitajima K, Anderson KE, Allen MF (2010) Effect of soil temperature and soil water content on fine root turnover rate in a California mixed conifer ecosystem. *J Geophys Res* 115: G04032. <https://doi.org/10.1029/2009JG001210>.

Kleja DB, Svensson M, Majdi H, Jansson P-E, Langvall O, Bergkvist B, Johansson M-B, Weslien P, Truusb L, Lindroth A, Ågren GI (2008) Pools and fluxes of carbon in three Norway spruce ecosystems along a climatic gradient in Sweden. *Biogeochemistry* 89: 7–25. <https://doi.org/10.1007/s10533-007-9136-9>.

Kong D, Wang J, Zeng H, Liu M, Miao Y, Wu H, Kardol P (2017) The nutrient absorption–transportation hypothesis: optimizing structural traits in absorptive roots. *New Phytol* 213: 1569–1572. <https://doi.org/10.1111/nph.14344>.

Kou L, Jiang L, Fu X, Dai X, Wang H, Li S (2018) Nitrogen deposition increases root production and turnover but slows root decomposition in *Pinus elliottii* plantations. *New Phytol* 218: 1450–1461. <https://doi.org/10.1111/nph.15066>.

Kou L, McCormack ML, Chen W, Guo D, Wang H, Gao W, Yang H, Li S (2016) Nitrogen ion form and spatio-temporal variation in root distribution mediate nitrogen effects on lifespan of ectomycorrhizal roots. *Plant Soil* 411: 261–273. <https://doi.org/10.1007/s11104-016-3018-7>.

Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC (2005) A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system. *Global Biogeochem Cycles* 19: 1–33. <https://doi.org/10.1029/2003GB002199>.

Kyaschenko J, Clemmensen KE, Karlton E, Lindahl BD (2017) Below-ground organic matter accumulation along a boreal forest fertility gradient relates to guild interaction within fungal communities. *Ecol Lett* 20: 1546–1555. <https://doi.org/10.1111/ele.12862>.

Kyaschenko J, Ovaskainen O, Ekblad A, Hagenbo A, Karlton E, Clemmensen KE, Lindahl BD (2019) Soil fertility in boreal forest relates to root-driven nitrogen retention and carbon sequestration in the mor layer. *New Phytol* 221: 1492–1502. <https://doi.org/10.1111/nph.15454>.

Landhäusser SM, Lieffers VJ (2003) Seasonal changes in carbohydrate reserves in mature northern *Populus tremuloides* clones. *Trees* 17: 471–476. <https://doi.org/10.1007/s00468-003-0263-1>.

Lehto T, Zwiazek JJ (2011) Ectomycorrhizas and water relations of trees: a review. *Mycorrhiza* 21: 71–90. <https://doi.org/10.1007/s00572-010-0348-9>.

Lehtonen A, Linkosalo T, Peltoniemi M, Sievänen R, Mäkipää R, Tamminen P, Salemaa M, Nieminen T, Āupek B, Heikkinen J, Komarov A (2016) Forest soil carbon stock estimates in a nationwide inventory: Evaluating performance of the ROMULv and Yasso07 models in Finland. *Geosci Model Dev* 9: 4169–4183. <https://doi.org/10.5194/gmd-9-4169-2016>.

Leppälammı-Kujansuu J, Aro L, Salemaa M, Hansson K, Kleja DB, Helmisaari H-S (2014a) Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. *For Ecol Manage* 326: 79–90. <https://doi.org/10.1016/j.foreco.2014.03.039>.

Leppälammı-Kujansuu J, Ostonen I, Strömngren M, Nilsson LO, Kleja DB, Sah SP, Helmisaari H-S (2013) Effects of long-term temperature and nutrient manipulation on Norway spruce fine roots and mycelia production. *Plant Soil* 366: 287–303. <https://doi.org/10.1007/s11104-012-1431-0>.

Leppälammı-Kujansuu J, Salemaa M, Kleja DB, Linder S, Helmisaari H-S (2014b) Fine root turnover and litter production of Norway spruce in a long-term temperature and nutrient manipulation experiment. *Plant Soil* 374: 73–88. <https://doi.org/10.1007/s11104-013-1853-3>.

- Leuschner C, Hertel D, Schmid I, Koch O, Muhs A, Hölscher D (2004) Stand fine root biomass and fine root morphology in old-growth beech forests as a function of precipitation and soil fertility. *Plant Soil* 258: 43–56. <https://doi.org/10.1023/B:PLSO.0000016508.20173.80>.
- Leysner O (2018) Auxin signaling. *Plant Physiol* 176: 465–479. <https://doi.org/10.1104/pp.17.00765>.
- Liski J, Nissinen A, Erhard M, Taskinen O (2003) Climatic effects on litter decomposition from arctic tundra to tropical rainforest. *Glob Chang Biol* 9: 575–584. <https://doi.org/10.1046/j.1365-2486.2003.00605.x>.
- Liski J, Perruchoud D, Karjalainen T (2002) Increasing carbon stocks in the forest soils of western Europe. *For Ecol Manage* 169: 159–175. [https://doi.org/10.1016/S0378-1127\(02\)00306-7](https://doi.org/10.1016/S0378-1127(02)00306-7).
- Lukac M (2012) Fine root turnover. In: Mancuso S (eds) *Measuring roots - An updated approach*. Springer, pp 363–373. [https://doi.org/10.1007/978-3-642-22067-8\\_18](https://doi.org/10.1007/978-3-642-22067-8_18).
- Lukac M, Godbold DL (2011) *Soil ecology in Northern forests*. Cambridge University Press, Cambridge, 238 pp. <https://doi.org/10.1017/CBO9780511976100>.
- Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat DM, McCormack ML, Hedin LO (2018) Evolutionary history resolves global organization of root functional traits. *Nature* 555: 94–97. <https://doi.org/10.1038/nature25783>.
- Majdi H (2001) Changes in fine root production and longevity in relation to water and nutrient availability in a Norway spruce stand in northern Sweden. *Tree Physiol* 21: 1057–1061. <https://doi.org/10.1093/treephys/21.14.1057>.
- Majdi H, Pregitzer K, Morén A-S, Nylund J-E, I. Ågren G (2005) Measuring Fine Root Turnover in Forest Ecosystems. *Plant Soil* 276: 1–8. <https://doi.org/10.1007/s11104-005-3104-8>.
- Makita N, Hirano Y, Sugimoto T, Tanikawa T, Ishii H (2015) Intraspecific variation in fine root respiration and morphology in response to in situ soil nitrogen fertility in a 100-year-old *Chamaecyparis obtusa* forest. *Oecologia* 179: 959–967. <https://doi.org/10.1007/s00442-015-3413-4>.
- Makkonen K, Helmisaari H-S (1998) Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. *For Ecol Manage* 102: 283–290. [https://doi.org/10.1016/S0378-1127\(97\)00169-2](https://doi.org/10.1016/S0378-1127(97)00169-2).
- Markkola A, Kuikka K, Rautio P, Härmä E, Roitto M, Tuomi J (2004) Defoliation increases carbon limitation in ectomycorrhizal symbiosis of *Betula pubescens*. *Oecologia* 140: 234–240. <https://doi.org/10.1007/s00442-004-1587-2>.
- Matamala R, Gonzalez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302: 1385–1387. <https://doi.org/10.1126/science.1089543>.

Mayer M, Rewald B, Matthews B, Sandén H, Rosinger C, Katzensteiner K, Tallian C, Berger T, Godbold D (2021) Soil fertility relates to fungal-mediated decomposition and organic-matter turnover in a temperate mountain forest. *New Phytol* 231: 777–790. <https://doi.org/10.1111/nph.17421>.

McCormack LM, Adams TS, Smithwick EAHH, Eissenstat DM, Luke McCormack M, Adams TS, Smithwick EAHH, Eissenstat DM (2012) Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol* 195: 823–831. <https://doi.org/10.1111/j.1469-8137.2012.04198.x>.

McCormack ML, Adams TS, Smithwick EAHH, Eissenstat DM, McCormack LM, Adams TS, Smithwick EAHH, Eissenstat DM, Luke McCormack M, Adams TS, Smithwick EAHH, Eissenstat DM (2014) Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95: 2224–2235. <https://doi.org/10.1890/13-1942.1>.

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari H-S, Hobbie EA, Iversen CM, Jackson RB, Leppälammii-Kujansuu J, Norby RJ, Phillips RP, Pregitzer KS, Pritchard SG, Rewald B, Zadworny M (2015a) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol* 207: 505–518. <https://doi.org/10.1111/nph.13363>.

McCormack ML, Gaines KP, Pastore M, Eissenstat DM (2015b) Early season root production in relation to leaf production among six diverse temperate tree species. *Plant Soil* 389: 121–129. <https://doi.org/10.1007/s11104-014-2347-7>.

Meier IC, Leuschner C (2008) Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Glob Chang Biol* 14: 2081–2095. <https://doi.org/10.1111/j.1365-2486.2008.01634.x>.

Menzel A, Sparks TH, Estrella N, Koch E, Aaasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella Y, Jatzak K, Måge F, Mestre A, Nordli Ø, Peñuelas J, Pirinen P, Remišová V, Scheffinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski FE, Zach S, Züst A (2006) European phenological response to climate change matches the warming pattern. *Glob Chang Biol* 12: 1969–1976. <https://doi.org/10.1111/j.1365-2486.2006.01193.x>.

Merilä P, Mustajärvi K, Helmisaari H-S, Hilli S, Lindroos AJ, Nieminen TM, Nöjd P, Rautio P, Salemaa M, Ukonmaanaho L (2014) Above- and below-ground N stocks in coniferous boreal forests in Finland: Implications for sustainability of more intensive biomass utilization. *For Ecol Manage* 311: 17–28. <https://doi.org/10.1016/j.foreco.2013.06.029>.

Näsholm T, Ekblad A, Nordin A, Giesler R, Högborg MN, Högborg P (1998) Boreal forest plants take up organic nitrogen. *Nature* 392: 914–916. <https://doi.org/10.1038/31921>.

Näsholm T, Högborg P, Franklin O, Metcalfe DB, Keel SG, Campbell C, Hurry V, Linder S, Högborg MN (2013) Are ectomycorrhizal fungi alleviating or aggravating nitrogen limitation of tree growth in boreal forests? *New Phytol* 198: 214–221. <https://doi.org/10.1111/nph.12139>.

Nieminen TM, Smolander A (2006) Forest under-storey vegetation and plant litter decomposition under three different dominant tree species. In: Rätty M, Bärlund I, Makkonen K, Kähkönen M, Esala M (eds) *Miten maamme makaa - Suomen maaperä ja sen tila IV Maaperätieteiden päivien laajennetut abstraktit*. Finnish soil science society and Uni. of Helsinki; Dept. Applied chemistry and microbial, Helsinki, pp 54–55

Nilsson LO, Wallander H (2003) Production of external mycelium by ectomycorrhizal fungi in a Norway spruce forest was reduced in response to nitrogen fertilization. *New Phytol* 158: 409–416. <https://doi.org/10.1046/j.1469-8137.2003.00728.x>.

Oleson KW, Lawrence DM, Gordon B, Flanner MG, Kluzek E, Peter J, Levis S, Swenson SC, Thornton E, Feddes J (2010) Technical description of version 4.0 of the Community Land Model (CLM) NCAR Technical Note NCAR/TN-478+STR, National Center for Atmospheric Research, Boulder, CO, pp 1–257.

Ostonen I, Helmisaari H-S, Borken W, Tedersoo L, Kukumägi M, Bahram M, Lindroos A-J, Nöjd P, Uri V, Merilä P, Asi E, Löhmus K (2011) Fine root foraging strategies in Norway spruce forests across a European climate gradient. *Glob Chang Biol* 17: 3620–3632. <https://doi.org/10.1111/j.1365-2486.2011.02501.x>.

Ostonen I, Löhmus K (2003) Proportion of fungal mantle, cortex and stele of ectomycorrhizas in *Picea abies* (L.) Karst. in different soils and site conditions. *Plant Soil* 257: 435–442. <https://doi.org/10.1023/A:1027305906159>.

Ostonen I, Lohmus K, Helmisaari H-S, Truu J, Meel S (2007a) Fine root morphological adaptations in Scots pine, Norway spruce and silver birch along a latitudinal gradient in boreal forests. *Tree Physiol* 27: 1627–1634. <https://doi.org/10.1093/treephys/27.11.1627>.

Ostonen I, Löhmus K, Lasn R (1999) The role of soil conditions in fine root ecomorphology in Norway spruce (*Picea abies* (L.) Karst.) *Plant Soil* 208: 283–292. <https://doi.org/10.1023/A:1027305906159>.

Ostonen I, Löhmus K, Pajuste K (2005) Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. *For Ecol Manage* 212: 264–277. <https://doi.org/DOI:10.1016/j.foreco.2005.03.064>.

Ostonen I, Püttsepp Ü, Biel C, Alberton O, Bakker MR, Löhmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A, Vanguelova E, Weih M, Brunner I (2007b) Specific root length as an indicator of environmental change. *Plant Biosyst* 141: 426–442. <https://doi.org/10.1080/11263500701626069>.

Ostonen I, Rosenvald K, Helmisaari H-S, Godbold D, Parts K, Uri V, Löhmus K (2013) Morphological plasticity of ectomycorrhizal short roots in *Betula* sp and *Picea abies* forests across climate and forest succession gradients: Its role in changing environments. *Front Plant Sci* 4: 1–10. <https://doi.org/10.3389/fpls.2013.00335>.

Persson H (1983) The distribution and productivity of fine roots in boreal forests. *Plant Soil* 71: 87–101. <https://doi.org/10.1007/BF02182644>.

Pirinen P, Simola H, Aalto J, Kaukoranta JP, Karlsson P, Ruuhela R (2012) Climatological statistics of Finland 1981–2010. Finnish Meteorological Institute Reports 1: 1–96.

Polverigiani S, McCormack ML, Mueller CW, Eissenstat DM (2011) Growth and physiology of olive pioneer and fibrous roots exposed to soil moisture deficits. *Tree Physiol* 31: 1228–1237. <https://doi.org/10.1093/treephys/tp110>.

Pregitzer KS (2002) Fine roots of trees – a new perspective. *New Phytol* 154: 267–270. [https://doi.org/10.1046/j.1469-8137.2002.00413\\_1.x](https://doi.org/10.1046/j.1469-8137.2002.00413_1.x).

Pregitzer KS, King JS, Burton AJ, Brown SE (2000) Responses of tree fine roots to temperature. *New Phytol* 147: 105–115. <https://doi.org/10.1046/j.1469-8137.2000.00689.x>.

Pregitzer KS, Kubiske ME, Yu C, Hendrick RL (1997) Relationships among root branch order, carbon, and nitrogen in four temperate species. *Oecologia* 111: 302–308. <https://doi.org/10.1007/s004420050239>.

Pritchard SG, Strand AE, McCormack LM, Davis MA, Oren R (2008) Mycorrhizal and rhizomorph dynamics in a loblolly pine forest during 5 years of free-air-CO<sub>2</sub>-enrichment. *Glob Chang Biol* 14: 1252–1264. <https://doi.org/10.1111/j.1365-2486.2008.01567.x>.

Reich PB, Rich RL, Lu X, Wang YP, Oleksyn J (2014) Biogeographic variation in evergreen conifer needle longevity and impacts on boreal forest carbon cycle projections. *P Natl Acad Sci USA* 111: 13703–13708. <https://doi.org/10.1073/pnas.1216054110>.

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecol Monogr* 62: 365–392. <https://doi.org/10.2307/2937116>.

Repo T, Sirkiä S, Heinonen J, Lavigné A, Roitto M, Koljonen E, Sutinen S, Finér L (2014) Effects of frozen soil on growth and longevity of fine roots of Norway spruce. *For Ecol Manage* 313: 112–122. <https://doi.org/10.1016/j.foreco.2013.11.002>.

Salemaa M, Derome J, Nöjd P (2008) Response of boreal forest vegetation to the fertility status of the organic layer along a climatic gradient. *Boreal Environ Res* 13: 48–66.

Salmanowicz B, Nylund J-E (1988) High performance liquid chromatography determination of ergosterol as a measure of ectomycorrhiza infection in Scots pine. *Eur J Forest Pathol* 18: 291–298. <https://doi.org/10.1111/j.1439-0329.1988.tb00216.x>.

Samaniego L, Thober S, Kumar R, Wanders N, Rakovec O, Pan M, Zink M, Sheffield J, Wood EF, Marx A (2018) Anthropogenic warming exacerbates European soil moisture droughts. *Nat Clim Chang* 8: 421–426. <https://doi.org/10.1038/s41558-018-0138-5>.

Schiestl-Aalto P, Kulmala L, Mäkinen H, Nikinmaa E, Mäkelä A (2015) CASSIA - a dynamic model for predicting intra-annual sink demand and interannual growth variation in Scots pine. *New Phytol* 206: 647–659. <https://doi.org/10.1111/nph.13275>.

Schwieger S, Blume-Werry G, Peters B, Smiljanić M, Kreyling J (2019) Patterns and drivers in spring and autumn phenology differ above- and belowground in four ecosystems under the

same macroclimatic conditions. *Plant Soil* 445: 217–229. <https://doi.org/10.1007/s11104-019-04300-w>.

Smith SE, Read DJ (2010) *Mycorrhizal symbiosis*. Academic Press, 769 pp.

Smolander A, Kitunen V (2002) Soil microbial activities and characteristics of dissolved organic C and N in relation to tree species. *Soil Biol Biochem* 34: 651–660. [https://doi.org/10.1016/S0038-0717\(01\)00227-9](https://doi.org/10.1016/S0038-0717(01)00227-9).

Smolander A, Kitunen V (2011) Comparison of tree species effects on microbial C and N transformations and dissolved organic matter properties in the organic layer of boreal forests. *Appl Soil Ecol* 49: 224–233. <https://doi.org/10.1016/j.apsoil.2011.05.002>.

Sokol NW, Bradford MA (2019) Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nat Geosci* 12: 46–53. <https://doi.org/10.1038/s41561-018-0258-6>.

Solly EF, Brunner I, Helmisaari H-S, Herzog C, Leppälampi-Kujansuu J, Schöning I, Schrupf M, Schweingruber FH, Trumbore SE, Hagedorn F (2018) Unravelling the age of fine roots of temperate and boreal forests. *Nat Commun* 9: 1–8. <https://doi.org/10.1038/s41467-018-05460-6>.

Starr M, Saarsalmi A, Hokkanen T, Merilä P, Helmisaari H-S (2005) Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. *For Ecol Manage* 205: 215–225. <https://doi.org/10.1016/j.foreco.2004.10.047>.

Steele SJ, Gower ST, Vogel JG, Norman JM (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiol* 17: 577–587. <https://doi.org/10.1093/treephys/17.8-9.577>.

Steinaker DF, Wilson SD (2008) Phenology of fine roots and leaves in forest and grassland. *J Ecol* 96: 1222–1229. <https://doi.org/10.1111/j.1365-2745.2008.01439.x>.

Steinaker DF, Wilson SD, Peltzer DA (2010) Asynchronicity in root and shoot phenology in grasses and woody plants. *Glob Chang Biol* 16: 2241–2251. <https://doi.org/10.1111/j.1365-2486.2009.02065.x>.

Sterkenburg E, Bahr A, Brandström Durling M, Clemmensen KE, Lindahl BD (2015) Changes in fungal communities along a boreal forest soil fertility gradient. *New Phytol* 207: 1145–1158. <https://doi.org/10.1111/nph.13426>.

Strand AE, Pritchard SG, McCormack LM, Davis MA, Oren R (2008) Irreconcilable differences: Fine-root life spans and soil carbon persistence. *Science* 319: 456–458. <https://doi.org/10.1126/science.1151382>.

Sun T, Hobbie SE, Berg B, Zhang H, Wang Q, Wang Z, Hättenschwiler S (2018) Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. *P Natl Acad Sci USA* 115: 10392–10397. <https://doi.org/10.1073/pnas.1716595115>.

Tamm CO (1991) Nitrogen in terrestrial ecosystems. Questions of productivity, vegetational changes, and ecosystem stability. *Ecol Stud* 81: 115 p. Springer, Berlin. <https://doi.org/10.1007/978-3-642-75168-4>.

Tamminen P (1991) Kangasmaan ravinnetunnusten ilmaiseminen ja viljavuuden alueellinen vaihtelu Eelä-Suomessa. Expression of soil nutrient status and regional variation in soil fertility of forested sites in southern Finland. *Folia For* 777: 1-40. [In Finnish with English summary]. <http://urn.fi/URN:ISBN:951-40-1170-8>.

Therneau TM (2016) A Package for Survival Analysis in S. version 2.38. 2015. Reference Source.

Thornton PE, Zimmermann NE (2007) An improved canopy integration scheme for a land surface model with prognostic canopy structure. *J Clim* 20: 3902–3923. <https://doi.org/10.1175/JCLI4222.1>.

Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT, Yavitt JB (2003) Environmental control of fine root dynamics in a northern hardwood forest. *Glob Chang Biol* 9: 670–679. <https://doi.org/10.1046/j.1365-2486.2003.00622.x>.

Ukonmaanaho L, Merilä P, Nöjd P, Nieminen TM (2008) Litterfall production and nutrient return to the forest floor in Scots pine and Norway spruce stands in Finland. *Boreal Environ Res* 13: 67–91.

Valenzuela-Estrada LR, Richards JH, Diaz A, Eissensat DM (2009) Patterns of nocturnal rehydration in root tissues of *vaccinium corymbosum* L. under severe drought conditions. *J Exp Bot* 60: 1241–1247. <https://doi.org/10.1093/jxb/ern367>.

Vanninen P, Mäkelä A (1999) Fine root biomass of Scots pine stands differing in age and soil fertility in southern Finland. *Tree Physiol* 19: 823–830. <https://doi.org/10.1093/treephys/19.12.823>.

Varik M, Kukumägi M, Aosaar J, Becker H, Ostonen I, Lõhmus K, Uri V (2015) Carbon budgets in fertile silver birch (*Betula pendula* Roth) chronosequence stands. *Ecol Eng* 77: 284–296. <https://doi.org/10.1016/j.ecoleng.2015.01.041>.

Vesterdal L, Clarke N, Sigurdsson BD, Gundersen P (2013). Do tree species influence soil carbon stocks in temperate and boreal forests? *For Ecol Manage* 309: 4–18. <https://doi.org/10.1016/j.foreco.2013.01.017>.

Viro PJ (1952) Kivisyyden määrittämisestä. Summary: On the determination of stoniness. *Inst For Fenn* 40: 23. <http://urn.fi/URN:NBN:fi-metla-201207171072>.

Vogt KA, Persson H (1991) Measuring growth and development of roots. In: Lassoie JP, Hinckley TM (eds) *Techniques and approaches in forest tree ecophysiology*. CRC Press, Boca Raton, pp 477–501.

Vogt KA, Publicover DA, Bloomfield J, Perez JM, Vogt DJ, Silver WL (1993) Belowground responses as indicators of environmental change. *Environ Exp Bot* 33: 189–205. [https://doi.org/10.1016/0098-8472\(93\)90065-N](https://doi.org/10.1016/0098-8472(93)90065-N).

- Wallander H (2000) Uptake of P from apatite by *Pinus sylvestris* seedlings colonised by different ectomycorrhizal fungi. *Plant Soil* 218: 249–256. <https://doi.org/10.1023/A:1014936217105>.
- Wallander H, Ekblad A, Bergh J (2011) Growth and carbon sequestration by ectomycorrhizal fungi in intensively fertilized Norway spruce forests. *For Ecol Manage* 262: 999–1007. <https://doi.org/10.1016/j.foreco.2011.05.035>.
- Wallander H, Nilsson LO, Hagerberg D, Bååth E (2001) Estimation of the biomass and seasonal growth of external mycelium of ectomycorrhizal fungi in the field. *New Phytol* 151: 753–760. <https://doi.org/10.1046/j.0028-646x.2001.00199.x>.
- Wallander H, Nylund J-E (1992) Effects of excess nitrogen and phosphorus starvation on the extramatrical mycelium of ectomycorrhizas of *Pinus sylvestris* L. *New Phytol* 120: 495–503. <https://doi.org/10.1111/j.1469-8137.1992.tb01798.x>.
- Walsh JE (2014) Intensified warming of the Arctic: Causes and impacts on middle latitudes. *Global Planet Change* 117: 52–63. <https://doi.org/10.1016/j.gloplacha.2014.03.003>.
- Wang X, Fujita S, Nakaji T, Watanabe M, Satoh F, Koike T (2016) Fine root turnover of Japanese white birch (*Betula platyphylla* var. *japonica*) grown under elevated CO<sub>2</sub> in northern Japan. *Trees* 30: 363–374. <https://doi.org/10.1007/s00468-015-1282-4>.
- Weemstra M, Mommer L, Visser EJW, van Ruijven J, Kuyper TW, Mohren GMJ, Sterck FJ (2016) Towards a multidimensional root trait framework: a tree root review. *New Phytol* 211: 1159–1169. <https://doi.org/10.1111/nph.14003>.
- Weibull W (1951) A statistical distribution function of wide applicability. *J Appl Mech* 103: 293–297. <https://doi.org/10.1115/1.4010337>.
- Withington JM, Reich PB, Oleksyn J, Eissenstat DM (2006) Comparisons of structure and life span in roots and leaves among temperate trees. *Ecol Monogr* 76: 381–397. [https://doi.org/10.1890/0012-9615\(2006\)076\[0381:COALS\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2006)076[0381:COALS]2.0.CO;2).
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. *Nature* 428: 821–827. <https://doi.org/10.1038/nature02403>.
- Xia M, Talhelm AF, Pregitzer KS (2015) Fine roots are the dominant source of recalcitrant plant litter in sugar maple-dominated northern hardwood forests. *New Phytol* 208: 715–726. <https://doi.org/10.1111/nph.13494>.
- Yuan ZY, Chen HYH (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. *CRC Crit Rev Plant Sci* 29: 204–221. <https://doi.org/10.1080/07352689.2010.483579>.

Zadworny M, Eissenstat DM (2011) Contrasting the morphology, anatomy and fungal colonization of new pioneer and fibrous roots. *New Phytol* 190: 213–221. <https://doi.org/10.1111/j.1469-8137.2010.03598.x>.

Zadworny M, McCormack ML, Mucha J, Reich PB, Oleksyn J (2016) Scots pine fine roots adjust along a 2000-km latitudinal climatic gradient. *New Phytol* 212: 389–399. <https://doi.org/10.1111/nph.14048>.

Zadworny M, McCormack ML, Rawlik K, Jagodziński AM (2015) Seasonal variation in chemistry, but not morphology, in roots of *Quercus robur* growing in different soil types. *Tree Physiol* 35: 644–652. <https://doi.org/10.1093/treephys/tpv018>.

Zadworny M, McCormack ML, Żytkowiak R, Karolewski P, Mucha J, Oleksyn J (2017) Patterns of structural and defense investments in fine roots of Scots pine (*Pinus sylvestris* L.) across a strong temperature and latitudinal gradient in Europe. *Glob Chang Biol* 23: 1218–1231. <https://doi.org/10.1111/gcb.13514>.