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The hidden carbon fluxes — unearthing root-related processes in boreal peatland forests

Wei He

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

Academic dissertation

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Thesis Supervisors:
Senior Scientist Dr. Päivi Mäkiranta
Natural Resources Institute Finland (Luke), Finland

Professor Dr. Raija Laiho
Natural Resources Institute Finland (Luke), Finland

University Researcher Dr. Paavo Ojanen
Department of Forest Sciences, University of Helsinki, Finland

Pre-examiners:
Dr. Avni Malhotra
Pacific Northwest National Laboratory, USA

Assistant Professor Dr. Brian Tobin
University College Dublin, Ireland

Opponent:
Professor Dr. Ivika Ostonen
Department of Geography, Institute of Ecology and Earth Sciences, University of Tartu, Tartu, Estonia

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ABSTRACT

Fine-root production (FRP) and decomposition are critical processes influencing element cycling and carbon (C) balance in boreal peatlands. The aim of this thesis was to estimate FRP across various peatland forests, examine the patterns in, and develop statistical models for estimating, the relationships between FRP and stand and site characteristics, as well as climate variables (**I**); and to quantify fine-root decomposition rates in various types of drained peatland forests and compare them with corresponding rates in mineral-soil forests (**II**).

FRP was measured using ingrowth cores, covering the 0−50 cm peat profile across 28 drained peatland forest sites in Finland (**I**). Total site-level FRP values ranged from 30 to 473 g m^{-2} $year^{-1}$ of dry mass, with an average of 120 g m^{-2} $year^{-1}$, with 76–95% occurring in the 0−20 cm soil layers. Total FRP showed significant variation across different site types and generally declined with decreasing fertility, except for the most fertile site type. Additionally, total FRP tended to be higher in sites with a deeper water table (WT). Stand basal area was the best predictor of total FRP, explaining 16% of the variation at the stand-level. A model incorporating stand basal area and site type explained 47% of the variation in total FRP.

Fine-root decomposition was studied using litterbags containing roots from three dominant tree species (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*) and one fern species (*Dryopteris carthusiana*), covering the 0−30 cm soil profile in six drained peatland and four mineral-soil forest sites in Finland (**II**). Fine-root decomposition showed significant variation with soil type and nutrient regime. On nutrient-poor sites, the decomposition of fine roots was slower in peat soils compared to corresponding mineral-soil sites, while the opposite was observed in nutrient-rich sites. Consequently, fine-root decomposition was fastest in nutrient-rich peat soils. Sampling depth and root diameter also influenced decomposition rates, with slower rates in deeper soil layers and for larger diameter roots. Among the tree species, *P. abies* had the slowest decomposition rate.

In conclusion, FRP varied significantly across site types, with higher production observed in deeper WT sites and nutrient-rich conditions, while stand basal area emerged as a key predictor. Fine-root decomposition was influenced by soil type and nutrient regime, root diameter, and sampling depth, with faster decomposition in nutrient-rich peat soils and slower rates in deeper layers and for larger roots. These findings provide valuable insights into the interactions between fine-root dynamics and site-specific characteristics, contributing to a better understanding of C cycling in drained peatland forests.

Keywords: fine-root production (FRP); fine-root decomposition; drained peatland forests; ingrowth-cores; litterbag

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Thank you - Kiitos - 谢谢！
Helsinki, Ferbury 2025, Wei He

LIST OF ORIGINAL ARTICLES

The thesis is based on the following articles which are referred to in the text by Roman numerals. The articles are reprinted with the permission of the publisher.

I. **He W**, Makirantä P, Straková P, Ojanen P, Penttilä T, Bhuiyan R, Minkkinen K, Laiho R (2023) Fine-root production in boreal peatland forests: Effects of stand and environmental factors. Forest Ecology and Management 550, article id 121503. https://doi.org/10.1016/j.foreco.2023.121503

II. **He W**, Mäkiranta P, Ojanen P, Korrensalo A, Laiho R (2025) Dynamics of fine-root decomposition and its response to site nutrient regimes in boreal draine. Forest Ecology and Management 582, article id 122564. https://doi.org/10.1016/j.foreco.2025.122564

Other articles during the doctoral period that are not included in this thesis:

- **He W,** Yuan Y, Zhang Z, Xiao J, Liu Q, Laiho R, Yin H (2021) Effect of N addition on root exudation and associated microbial N transformation under Sibiraea angustata in an alpine shrubland. Plant and Soil 460: 469−481. https://doi.org/10.1007/s11104-020-04753-4
- Lampela M, Minkkinen K, Straková P, Bhuiyan R, **He W,** Mäkiranta P, Ojanen P, Penttilä T, Laiho R (2023) Responses of fine-root biomass and production to drying depend on wetness and site nutrient regime in boreal forested peatland. Frontiers in Forests and Global Change 6, article id 1190893. https://doi.org/10.3389/ffgc.2023.1190893

AUTHOR’S CONTRIBUTION

Wei He (WH) was responsible for the summary of this thesis, the discussion of its results and conclusions, and served as the first author for papers **I**, **II**. WH participated in lab work and data collection, and conducted data analysis, visualization and interpretation of the results. WH developed the hypotheses and structured the articles in collaboration with co-authors. In Paper **I**, WH performed Fourier Transform Infrared (FTIR) spectroscopy analyses under the supervision of Petra Straková. In Paper **II**, Aino Korrensalo conducted the nonlinear mixed-effects model (NLMIXED) analysis.

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1 INTRODUCTION

1.1 Background

Peatland ecosystems are the carbon (C) hotspots of our planet, encompassing approximately 3% of the land surface but containing approximately 33% of all soil C (Page et al. 2011; Xu et al. 2018). The C pool in peat is the result of a relatively small imbalance between production and decay. In northern peatlands, high water-table (WT) level, which creates anoxic conditions, accompanied with low soil temperatures are considered the major causes for the imbalance. This has resulted in peatlands functioning as a C sink from the atmosphere (Gorham 1991; Schulze and Freibauer 2005). Based on a review of different methods in the literature, the best estimate for C stored in northern peatlands is 500 ± 100 gigatons of C (GT C) (Yu 2012). The C sequestration capacity of peat soils is altered by climate and land-use change, e.g. forestry and shaped by the site and environmental characteristics of peatland ecosystems.

A significant portion of peatlands, especially in the boreal regions of Europe, has been drained for forestry purposes. In Finland, peatlands (both pristine and drained) account for 35% (9.1 million ha) of the forest land area, with approximately 4.9 million ha consisting of drained peatland forests (Kulju et al., 2023). Lowering of WT accelerates forest succession in peatland sites, gradually shifting biomass and nutrient cycles from ground vegetation dominance to tree dominance in two decades (Laiho et al. 2003). Simultaneously, the quantity and quality of both above- and below-ground litter, along with the location (depth distribution) of below-ground litter, differ significantly after WT drawdown compared to those in pristine conditions (Laiho et al. 2003; Murphy et al. 2009b; Straková et al. 2010). In pristine peatlands, *Sphagnum* mosses, sedges and shrubs are the major litter sources. After drainage, the tree stand, especially its foliage and fine roots, becomes the major litter source (Laiho et al. 2003).

Fine roots, typically defined as roots less than 2 mm in diameter, contribute significantly to the annual NPP of vascular plants in peatlands, accounting for an estimated 25% to 75% of annual NPP (Reader and Stewart 1972; Backeus 1990; Weltzin et al. 2000; Wang et al. 2003; Bond-Lamberty et al. 2004; Wieder 2006). In boreal sedge fens, approximately 90% of the plant biomass is allocated to below-ground plant parts (Sjörs 1991; Saarinen 1996, 1998). Due to the high belowground allocation of plant material, decomposition of fine roots contributes greatly to C and nutrient turnover in the soil. Logically, lowered WT with the consequent increase in oxygen availability in the surface soil may be assumed to result in accelerated decomposition. However, the production and decomposition of fine roots remain poorly understood compared to aboveground processes, leading to significant uncertainties in determining whether these drained peatland forests are sinks or sources of C to the atmosphere (Ojanen et al. 2014).

The gap in our knowledge largely stems from methodological holdbacks. Measuring fine-root production (FRP) and decomposition often requires disturbing the system to some extent, which can influence the outcome (Milchunas 2009), and is very time-consuming. While fine root dynamics in mineral-soil forests are increasingly well understood (Hansson et al. 2013; Herzog et al. 2014; Leppälammi-Kujansuu et al. 2014; McCormack et al. 2014; Smith et al. 2014), the major constraints for ecosystem functioning (e.g., temperature, moisture, and

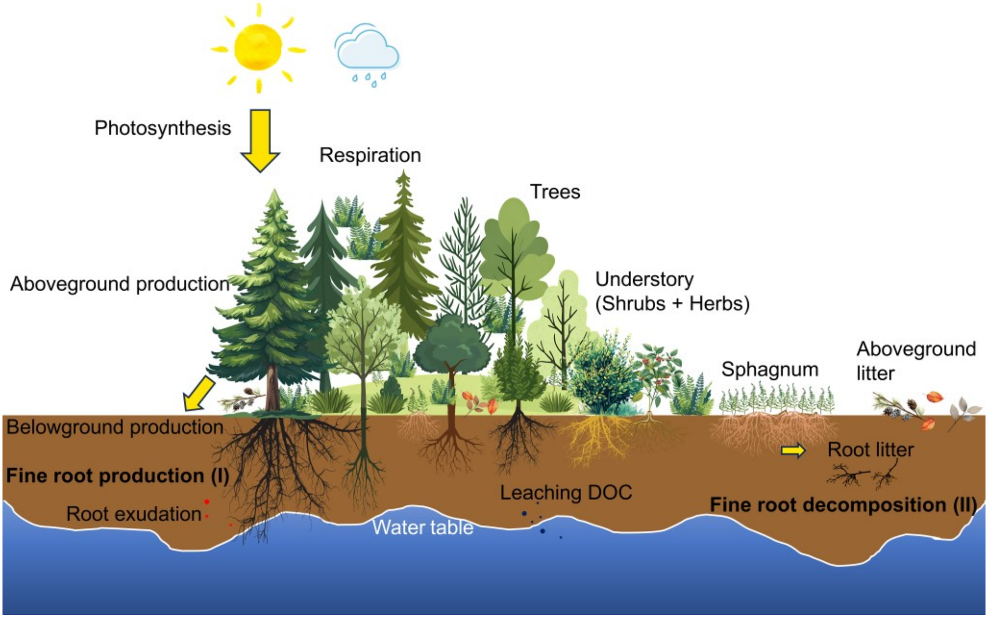

Figure 1. Simplified carbon (C) flow in peatland forests. The Roman numerals in parentheses indicate the specific topics of the two main studies comprising this thesis.

nutrient availability), as well as the soil physical, chemical and biological properties fundamentally differ between peat and mineral soils (Westman and Laiho 2003; Päivänen and Hånell 2012), so the patterns of C allocation belowground are likely to differ as well. This study aims to examine the production and decomposition of fine roots in boreal peatland forests (**Figure 1**), focusing on how these C fluxes depend on site and environmental characteristics.

1.2 Fine-root production (FRP)

1.2.1 Factors controlling FRP

The production of fine roots in forest ecosystems is influenced by stand and site characteristic, as well as climatic variables, such as plant species, root biomass, latitude, mean annual air temperature, and precipitation (Yuan and Chen 2010; Finér et al. 2011b, a). Generally, higher annual air temperatures and precipitation promote FRP, and these two climatic variables are closely correlated with each other and with latitude (Yuan and Chen 2010; Finér et al. 2011b). However, the relationships between FRP and latitude, temperature, and precipitation explain less than 45% of the observed variation in FRP, as these relationships are strongly affected by data grouping, such as by tree species or stand age (Yuan and Chen 2010; Finér et al. 2011b, a).

Stand characteristics have been found to account for more variation in FRP than environmental variables (Finér et al. 2011b). There is a strong positive relationship between

FRP and fine-root biomass (FRB) in boreal and cold temperate forests (Li et al. 2003; Chen et al. 2004). FRB has been shown to be strongly and positively correlated with stand characteristics, mainly with stand basal area (Helmisaari et al. 2007; Finér et al. 2011a; Lehtonen et al. 2016).

Moreover, soil properties such as soil nutrient regime can also affect FRP (Nadelhoffer 2000; Yuan and Chen 2010, 2012), and these effects on FRP may be specific to stand type or tree species. Different tree species or plant functional types (PFTs) in peatlands may exhibit varying rooting patterns and depths, which reflect their adaptation to specific site conditions (Ruseckas 2000; Bhuiyan et al. 2017).

1.2.2 FRP in drained peatland forests

Due to the lack of information concerning peatland forests, it is still common to generalize patterns observed in mineral-soil forests in ecosystem and earth models (Yuan and Chen 2010; Lehtonen et al. 2016). Since the major constraints for ecosystem functioning—temperature, moisture, and nutrient regimes—along with the physical, chemical, and biological properties of peat soils, differ fundamentally from those of mineral soils (Westman and Laiho 2003; Päivänen and Hånell 2012), the patterns of FRP are also likely to differ.

Boreal forest ecosystems in northern regions have a cold climate that likely restricts the availability of nitrogen (N) and thus fine root growth (Nadelhoffer 2000; Rasse 2002). In contrast to mineral soils, peat soils have a higher N content but less mineral nutrients (Westman and Laiho 2003; Päivänen and Hånell 2012). Therefore, especially at the most N-rich sites, the availability of N should be favourable, but higher FRP may be required to explore for mineral nutrients such as phosphorus (P) or potassium (K) that are often scarce in peat soils (Westman and Laiho 2003). The limited observations in peatland forests available so far suggest that total FRP is greater in more nutrient-rich sites (Finér and Laine 1998; Bhuiyan et al. 2017). But the FRP patterns of individual species may differ from the pattern in total FRP. For example, Scots pine may produce fewer fine roots in peatland forests when the soil nutrient regime is better (Finér and Laine 1998; Finér and Laine 2000; Bhuiyan et al. 2017). In peatlands, even when drained, we also need to consider the WT, which largely determines the soil volume where aerobic processes can take place, and is thus a major factor controlling ecosystem structure and function in these sites (Murphy et al. 2009a; Peltoniemi et al. 2009; Murphy and Moore 2010). A meta-analysis of seven studies (65 observations) showed that warming (0–9.0°C) and WT drawdown (4.0–62.5 cm) significantly increased FRB in boreal peatlands, with PFTs being a stronger predictor of FRB than treatment magnitude (Bucher et al. 2023).

In peatlands, different species or PFTs may have different rooting patterns and rooting depths (Ruseckas 2000; Bhuiyan et al. 2017; Proctor and He 2019). FRB was the most significant factor explaining the variation in FRP, and more so at the tree level than at the stand level, explaining 53% of the variation in FRP for trees at the tree level in forest ecosystems (Finér et al. 2011b). Based on a compilation of tree FRB (diameter < 2 mm) data from 95 Finnish forest stands, Lehtonen et al. (2016) developed models for estimating FRB of mineral-soil and drained peatland forests and found that basal area of forest stand was a better predictor of FRB than any other stand variable alone. However, it is still unclear whether stand characteristics, such as basal area of forest stand can be utilized to estimate FRP in peatland forests.

1.2.3 How to measure FRP?

Sequential soil coring, ingrowth core and minirhizotron are major methods for measuring the FRP, but no one method is ideal for all ecosystems or study purposes (Milchunas 2009, 2012). Sequential soil coring is simple and effectively captures spatial and temporal heterogeneity in FRB distribution over large scales (Makkonen and Helmisaari 1999). FRP can be calculated from sequential soil coring data using various approaches, including summing changes in living and dead root biomasses and accounting for decomposition (Finér and Laine 1998). However, obtaining accurate results requires a large number of core samples, and the extensive processing time makes this method costly and impractical for highly replicated experiments (Addo-Danso et al. 2016). Minirhizotrons, in which clear plastic tubes are inserted into the ground at an angle and then photographed along the top of the tube at a known distance (Milchunas 2012), are widely regarded as the most effective method for estimating root lifespan and turnover (Johnson et al. 2001). However, they require time-intensive image analysis, additional data to calculate area-based production estimates, and are impractical for use in large-scale inventories. Ingrowth core method involves installing mesh cores filled with root-free soil to holes cored in the ground, recovering them after a set period, and separating and weighing the roots that have grown in and represent production during the incubation period. This method is the most commonly used due to the relatively low costs of the equipment required, and the results can be readily interpreted. However, it may introduce biases in absolute root production estimates, though it is generally reliable for relative comparisons (Milchunas 2009, 2012).

All methods for estimating FRP require the separation of fine roots from the soil and are subject to biases in that procedure (Milchunas 2012). Separating fine roots from soil and distinguishing between live and dead roots as well as the species identification of fine roots are arduous; especially so when it comes to peat soils that solely consist of plant remains, including roots, at various stages of decay (Sjörs 1991). And fine roots from different tree species and plant functional type species co-occur in the same layer and exhibit similarities in shape and color, making visual identification unreliable. Infrared spectroscopy has been shown to be an effective method for identifying species composition within simple root mixtures (Roumet et al. 2006; Lei and Bauhus 2010; Straková et al. 2020). If the relationships between FRP and more easily measurable stand and site variables could be identified, it would make an important contribution to improve soil C stock change estimation in GHG inventories and for future predictions.

1.3 Fine-root decomposition

1.3.1 Below ground decomposition and controlling factors

The decomposition of plant tissues in terrestrial ecosystems regulates the transfer of C and nutrients to the soil and is a major source of CO_2 to the atmosphere. Although most previous decomposition studies have focused on above-ground litter, isotopic analyses and assessments of root and shoot biomarkers suggest root-derived C is retained more efficiently in soils and microorganisms than are C inputs from above-ground litter (Kramer et al. 2010; Mendez-Millan et al. 2010). Unlike above-ground litter (e.g. foliage and stems), which decomposes on or close to the soil surface, root decomposition products are more effectively incorporated into soil aggregates and more readily adsorbed onto mineral surfaces (Rasse et al. 2005; Sanaullah et al. 2011). Consequently, below-ground litter, comprising dead roots, is a major source of soil organic matter, the largest terrestrial pool of C (Schmidt et al. 2011).

Litter decomposition is driven by abiotic and biotic factors, including climate, litter quality and soil organisms (Krishna and Mohan 2017; Ge et al. 2023). Models of above-ground litter decay generally suggest that climate is the primary predictor of decomposition rates, with litter quality playing a secondary but important role (Aerts 1997; Gholz et al. 2000; Trofymow et al. 2002). Because climate is considered a primary controller of the activity of decomposers, few studies have assumed that soil decomposers are direct factors influencing decomposition rates at the regional scale (Bradford et al. 2016). However, the decomposition of roots does not always follow the same patterns as above-ground litter (Silver and Miya 2001; Hobbie et al. 2010), largely due to differences in the chemical composition of both litter types (Kögel-Knabner 2002), and because above-ground litter experiences different environmental conditions compared to belowground litter (Hobbie et al. 2010). Previous studies comparing root and leaf chemical features showed that roots have higher concentrations of lignin, and the lower lignin content in leaves is frequently cited as the main factor for their rapid decomposition (Fujimaki et al. 2008).

1.3.2. Fine-root decomposition in drained peatland forests

While most fine roots are found relatively close to the soil surface in both boreal peatland and mineral-soil forests (Yuan and Chen 2010; He et al. 2023; Lampela et al. 2023), they may extend down to about 60 cm (Schenk and Jackson 2002). The temperature and moisture conditions may differ markedly in the depth range where root decomposition takes place, likely regulating the decomposition rate. In the 0–10 cm soil layers, roots decompose more quickly due to favorable conditions for microbial activity, including higher temperatures, greater nutrient availability, and increased oxygen levels. These factors enhance microbial breakdown of organic material, resulting in faster root decay near the surface. In contrast, deeper soil layers (below 10 cm) experience slower decomposition, possibly due to limited oxygen and nutrient availability, which are thought to be essential for microbial degradation (Silver and Miya 2001). Studies in both peatlands (Jackson et al. 2009; Steinweg et al. 2018) and mineral-soil forests (Herold et al. 2014; Han et al. 2019) have shown that microbial biomass and extracellular enzyme activity, both critical for decomposition, decrease with increasing soil depth.

Peat soils have a distinct nutrient regime compared to mineral soils, with significantly higher N content but lower levels of mineral nutrients (Westman and Laiho 2003). While the higher N concentration in peat soils may promote faster decomposition because of higher microbial activities, the better aeration of the drier mineral soils may promote effective decomposition due to higher oxygen availability (Abdul Rahman et al. 2021). However, to our knowledge, only three studies on fine-root decomposition have been conducted in drained peatlands (Domisch et al. 2000; Laiho et al. 2004; Bhuiyan et al. 2023). Moreover, fine-root decomposition rates have not been compared between peatland and mineral-soil forests and overall, such comparisons are scarce but indicating that foliar litter decomposes more slowly in peatland compared to mineral-soil forests (Moore et al. 2005; Moore et al. 2008). In peatland ecosystems, even drained ones, the WT largely determines the soil volume where aerobic processes, such as FRP and decomposition, can occur. Decomposition rates may decrease down the soil profile when approaching anoxic conditions, but in some studies it has been suggested that the decomposition rate may be at its highest close to the WT, especially in relatively dry peatlands (Laiho 2006). On the other hand, lack of moisture may not as likely restrain decomposition in peatlands as in the surface layers of the drier mineral-soil forests, even though such a pattern has been recognized also for drained peatland forests (Lieffers 1988; Laiho et al. 2004).

In oxic soil layers, the rate of organic matter decomposition is largely determined by litter quality, including its chemical composition and physical structure (Straková et al. 2012). Litter quality in turn is dependent on the plant species or plant functional type (Straková et al. 2010; Smith et al. 2014). In global scale, the decomposition rate of graminoid species is the fastest, followed by that of broadleaf tree roots and then conifer tree roots (Silver and Miya 2001). Root diameter also changes the physical and chemical properties of litter that regulate the decomposition process (Usman et al. 2000; Zhang and Wang 2015). Among tree roots, the distal small-diameter lateral branches comprising first- and second-order roots (Pregitzer et al. 2002; Guo 2008) lack secondary (wood) development (Guo 2008). Moreover, first- and second-order roots have higher N concentrations (Pregitzer et al. 2002; Guo et al. 2004) and shorter life spans (Guo et al. 2008a; Guo et al. 2008b) than higher order roots. Therefore, finer (lower order) roots are expected to decompose more rapidly than coarser (higher order) woody roots (reviewed in (Hishi 2007)).

1.3.3. How to measure fine-root decomposition?

The litterbag method involves incubating litter in mesh bags and measuring its mass over a certain period to estimate decomposition rates. Although the reliability of litterbags has been questioned because the process of their preparation requires the separation of fine roots from soil and rhizosphere communities, as well as the washing and drying of live fine roots before field incubation (Dornbush et al. 2002; Beidler and Pritchard 2017), the method is simple, cost-effective, applicable to all forest types, and capable of assessing decomposition rates for individual species (Li et al. 2022). Consequently, litterbags have become the most commonly used method for estimating litter decomposition rates in forest ecosystems (Prescott 2005; Harmon et al. 2009; See et al. 2019). The intact core method has been considered an enhanced alternative to the litterbag method (Dornbush et al. 2002). This approach assesses fine-root decomposition rates by sampling cores from field soils, which are enclosed in plastic sleeves, installed in situ, and periodically resampled. However, due to the stringent requirements for soil homogeneity and the substantial labour demands, the intact core method is rarely applied (Sun et al. 2013).

Most of litterbag studies have been of short duration. A survey of the duration of exposure of litterbag studies in temperate, boreal and subarctic ecosystems showed that most (69%) were of 1 to 2 years in duration, 84% were 3 or fewer years, and only 5% were exposed for more than 5 years (Moore et al. 2017). There are few studies on fine-root decomposition in boreal peatlands (Domisch et al. 2000; Richert et al. 2000; Thormann et al. 2001; Laiho et al. 2004; Bérubé and Rochefort 2018; Bhuiyan et al. 2023), and all of them have used the litterbag method over an incubation period of 1 to 2 years. These short durations, however, may not adequately reflect the long-term decomposition process, especially in colder soils where decomposition progresses more slowly. This raises concerns about the extent to which short-term incubations represent long-term litter decomposition.

Litter mass loss rates are frequently estimated using single-exponential decay curves (Olson 1963), which enables the prediction of long-term decay rates from short-term studies. However, long-term experiments have shown that the rate of decomposition may decelerate in the later stages, deviating from what can be effectively captured by a single-exponential decay curve (Berg et al. 2001; Trofymow et al. 2002; Moore et al. 2005). Harmon *et al.* (2009)

showed that after 10 years of decomposition, the double-exponential and asymptotic models had superior statistical and biological accuracy compared to a single-exponential model for both leaf and fine root litter. In a 23-year experiment on above-ground litter (e.g. leaves, shoots, stems) conducted in an English peat bog (Latter et al. 1997), an asymptotic model was found to provide the best fit. Therefore, determining the most appropriate model for describing fine-root decomposition dynamics in boreal peatland forests, where decomposition processes can persist for decades, remains a critical research question.

2 OBJECTIVES AND HYPOTHESES

My study focuses on determining the two largest fine root-mediated C fluxes in peatland forest ecosystems; root production (**I**) and root decomposition (**II**). While FRP patterns have been studied in mineral-soil forests, comprehensive estimates across a range of drained peatland forests remain limited, hindering the development of robust predictive models. Similarly, the decomposition rates of fine roots in drained peatland forests have not been systematically compared with those in mineral-soil forests. There is no clear evidence of whether soil type (peatland or mineral-soil forests) is significant in controlling decomposition rates. These knowledge gaps limit our ability to assess the C cycling and ecosystem functioning of these ecosystems.

The main objective of study **I** was to estimate FRP for drained peatland forests, examine the patterns in, and develop models for estimating, the relationships between FRP and stand characteristics as well as environmental conditions. The main objective of study **II** was to estimate the rates and controls of fine-root decomposition in drained peatland forests, and compare them to decomposition rates and their controls in forests on mineral soils.

The following hypotheses were stated:

*Fine-root production in drained peatland forests (**I**):*

1) FRP increases with increased mean annual temperature sum and precipitation;
2) Nutrient-rich sites have higher FRP than nutrient-poor sites;
3) Sites with deeper WT support higher FRP;
4) Stand basal area is the strongest predictor of FRP in peatland forests;
5) FRP of various species and PFTs show different depth distributions.

*Fine-root decomposition in drained-peatland and mineral-soil forests (**II**):*

1) Fine-root decomposition rate decreases from nutrient-rich to nutrient-poor sites;
2) Fine-root decomposition rate is slower in drained peatland forests than in adjacent mineral-soil forests;
3) Fine-root decomposition rate decreases with increasing depth from soil surface;
4) Fine roots of deciduous species decompose faster than coniferous species.

3 MATERIALS AND METHODS

A brief overview of the materials and methodology used in this study is provided below. For more comprehensive details, please refer to the studies **I** and **II**.

3.1 Study sites

Fine-root production

Study **I** included 28 sites on forestry-drained peatlands located between 60° and 67°N (**Figure 2**) and were a subset of the sites used by Ojanen et al. (2010, 2013) to quantify soil greenhouse gas emissions. We used the site type classification by Laine (1989; see Vasander and Laine, 2008) from the most fertile *Herb-rich* type (HrT) via *Vaccinium myrtillus* types II and I (MT II and I) and *Vaccinium vitis-idaea* types II and I (VT II and I) to the poor *Dwarf shrub* type (DsT).These sites covered a range of climatic conditions, with mean annual air temperature sum (sum of daily mean temperatures exceeding 5 °C) between 1032 and 1424 degree days (dd) and annual precipitation between 506 and 617 mm.

Fine-root decomposition

Study **II** included four drained peatland forest sites located at the Lakkasuo peatland complex (**Figure 2**, 61°47′ N, 24°18′ E), representing the nutrient and productivity gradient (*Herb-rich* type (HrT-P; most nutrient-rich of the sites), *Vaccinium myrtillus* type I (MT I), *Vaccinium vitis-idaea* type II (VT II) and *Dwarf-shrub* type (DsT; most nutrient-poor of the sites). For comparison, their counterparts in mineral-soil forests around the Lakkasuo area were selected: Herb-rich type (HrT-M), *Vaccinium myrtillus* type (MT-M; mesic forest), *Vaccinium vitis-idaea* type (VT-M; sub-xeric forest), and *Calluna* type (DsT-M; xeric forest) according to the forest site-type classification system developed in Finland (Pohjanmies et al. 2021).

Two other drained peatland forests were also included: Kalevansuo (**Figure 2**, 60°38′ N, 24°21′ E), a nutrient-poor *Dwarf-shrub* type (DsT), and Lettosuo (**Figure 2,** 60°39′ N, 23°57′ E), a more nutrient-rich *Vaccinium myrtillus* type II (MT II).

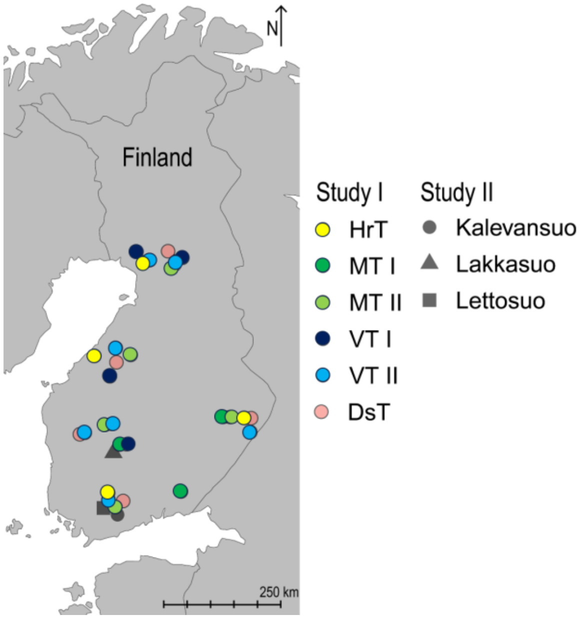

Figure 2. Location of the study sites in Finland. **Study I** included 28 forestry-drained peatland sites: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). **Study II** was carried out in Lakkasuo area, Kalevansuo and Lettosuo, Southern Finland.

3.2 Ingrowth cores

FRP (**I**) was studied using the ingrowth core method (**Figure 3**) following guidelines by Laiho et al. (2014) and Bhuiyan et al. (2017). The cores were made of polyester fabric with a 1 mm × 1 mm mesh, with an initial diameter of 4.2 cm, though post-incubation diameters were used in calculations due to soil pressure effects. The 1 x 1 mm mesh size was chosen to balance two key considerations: (1) retaining the homogenized peat within the cores and (2) allowing for the ingrowth and radial growth of roots. While the target was to capture roots below 2 mm in diameter, the flexible mesh material enabled roots to grow through it, as demonstrated in sedge fens where rhizomes thicker than 2 mm were observed growing through the cores (Bhuiyan et al. 2023). Each core had an effective length of 50 cm with a visible tail above ground for easy recovery.

The ingrowth cores were installed between October 15 and November 27, 2013, and recovered two years later in November 2015. While 15 cores were placed at each site, some cores were not found at the time of recovery, resulting in the recovery of between 7 and 13 cores per site. After collection, the cores were frozen at −20 °C until processing.

In the laboratory, the cores were defrosted overnight, cut into five 10-cm segments, and their diameters were measured. Any root parts extending beyond the core were cut off, and the roots inside were separated from soil, cleaned, and identified as living or dead based on color, elasticity, and toughness (Bhuiyan et al. 2017). Cleaned roots were then dried at 30 °C and weighed.

FRP was calculated as grams per square meter per year (g m^{-2} $year^{-1}$) based on root dry mass and post-incubation core diameter, divided by the 2-year incubation period.

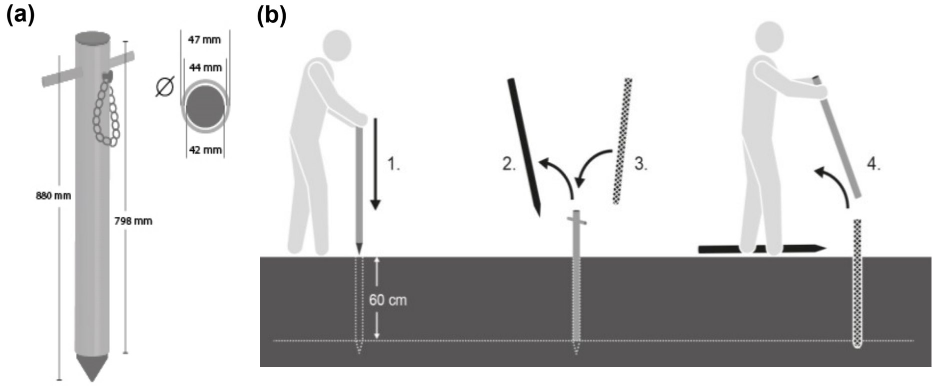

Figure 3. (a) The corer-installer. Inner tube in darker grey, outer tube in lighter grey, lock in black. (b) Installation of ingrowth cores using the corer-installer. The inner, closed and sharp-end tube pushes the hole to the ground (1); i.e., no soil volume is removed. When the desired depth has been reached, the lock linking the two tubes is released, and the inner tube pulled out (2). The hollow outer tube then allows us to drop the ingrowth core into the hole (3). The diameter of the cores is chosen so that the core falls freely but when the tube is pulled out, the soil closes in tightly around the core (4). The outer tube has an outer diameter of 4.7 cm, and an inner diameter of 4.2 cm. To ensure that the cores fall freely, we set the theoretical core diameter to 3.18 cm (perimeter 10 cm), when preparing the cores. When the tube is pulled out, the displaced soil closes in around the core. From Laiho et al. (2014).

3.3 Fourier Transform Infrared (FTIR)

We determined FRP by plant functional types using Fourier Transform Infrared (FTIR) spectroscopy (**I**) following Straková et al. (2020). Dried roots from each segment were powdered with an oscillating ball-mill, and FTIR spectra were obtained using a Bruker VERTEX 70 FTIR spectrometer (Bruker Optics, Germany) equipped with a horizontal diamond ATR sampling accessory. The powdered samples were directly placed on the diamond crystal with a diameter of 1.8 mm. To ensure uniform distribution and contact between the sample and crystal, a MIRacle high-pressure digital clamp was utilized. Each spectrum comprised 65 averaged absorbance measurements between 4000 and 650 cm^{-1}, with a resolution of 2 cm^{-1}. Data were collected using OPUS software.

3.4 Litterbag preparation and installation

For the litterbags, we used polyester fabric with a 1 mm × 1 mm mesh, allowing small mesofauna typical of the sites (Silvan et al. 2000) to enter the bag. Fine root (<2 mm) litterbags representing the tree species Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and Downy birch (*Betula pubescens*), covering the 0–30 cm depth from soil surface in three 10-cm segments, were installed in autumn 2015 at Lakkasuo for recovery after 1, 2, 4, and 5 years.

At the Kalevansuo site, root litterbags were installed in 2008, covering the 0–30 cm soil profile, containing fine roots (<2 mm) and small roots (2–10 mm) of *P. sylvestris*. These were recovered after 1, 2, 3, and 4 years.

At the Lettosuo site, litterbags were installed in 2009 and 2010, covering the 0–20 cm soil profile, and recovered after 1, 3, and 5 years. They represented fine roots and small roots of *P. sylvestris*, as well as fine roots of *P. abies*, *B. pubescens* and *D. carthusiana*.

After recovery, litterbags were transported to the laboratory, where the contents were cleaned to remove ingrown materials (**Figure 4**). The roots were dried to a constant mass and weighed with 0.001 g precision.

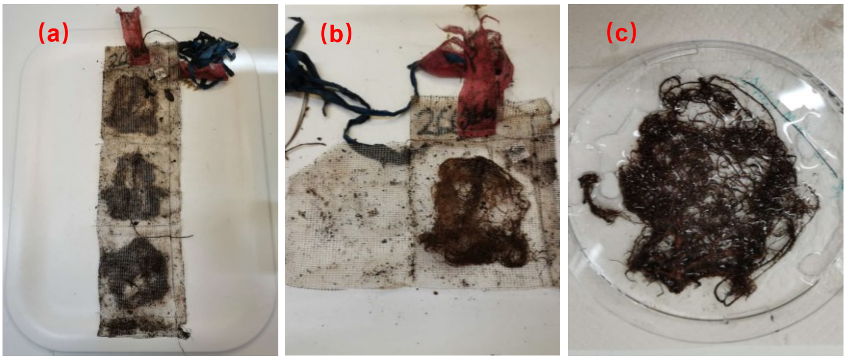

Figure 4. The sequential stages of root litterbag recovery and preparation for mass analysis. The first stage (a) involves the recovery of the entire litterbag from the 0−30 cm soil profile. The second stage (b) divides the entire litter-bag into three 10-segments. The third stage (c) shows the cleaned remaining root litter from the litter bag segment (0−10 cm).

3.5 Statistical analyses

Effect of climatic, environmental and stand variables on FRP

The effects of climatic variables and stand characteristics on FRP were tested using linear mixed-effect models with the ‘lme4’ package (Bates et al., 2015) in R software (**I**). Climatic variables included mean annual precipitation (P) and temperature sum (Tsum) from 1983−2015, and latitude (L), while stand characteristics included stem volume (V), total tree basal area (G), and species-specific basal areas for Scots pine (GP), Norway spruce (GS), and deciduous trees (GD). Additional variables tested were site type (ST), the C:N ratio of the top 20 cm of peat (CN), nutrient regimes (rich: HrT, MTs; poor: VTs, DsT) (SG), and WT.

First, a ‘null model’ with no predictors was fitted:

$$FRP = a + c_{site} + \varepsilon \tag{1}$$

where a is the fixed-effect intercept, c_{site} is site-specific random intercept, and ε is within-site variation. Each climatic, environmental and stand variables was then modeled individually, with results shown in Table 4 (from models 2–11 in **I**), where b_i represents the fixed-effect parameter for each variable.

Different combinations of predictors were then tested by adding them one-by-one into a model version having intercept and the single variable that had the best predictive power, G. This test included predictors (L, ST, WT) with a significant effect on FRP based on models 2–11 (Table 4 in **I**). P-values and R^2 values were calculated using the “lmerTest” package, and model selection was based on ANOVA and Akaike Information Criterion (AIC). As the FRP on HrT sites was surprisingly low (see Results and Discussion), a second set of models was run to exclude the HrT sites from the data (Table 5 in **I**).

Depth distribution of FRP

The vertical distribution of FRP was modeled using the asymptotic equation:

$$X = 1 - \beta^{d} \tag{2}$$

where X represents the cumulative root fraction at a given soil layer (d, cm), and β is the depth distribution parameter (Gale and Grigal 1987). The β values, calculated individually for each ingrowth core using SYSTAT software, indicate the depth distribution: higher β values suggest a greater proportion of roots at deeper layer, while lower values suggest a shallower root distribution (Jackson et al. 1996). Then, linear mixed-effect models with the ‘lme4’ package in R software were applied to analyze β values, as described earlier for FRP, to assess how root depth distribution (in terms of β) responds to climatic and stand variables (**I**).

FTIR-derived plant functional type contributions to FRP

The FTIR data were preprocessed with Savitzky-Golay smoothing, baseline correction, mean normalization, and second derivative transformation (Esbensen et al. 2002; Straková et al. 2020). The FTIR calibration models for the main plant functional types (PFTs) of northern peatlands (open and forestry-drained peatland sites) (Straková et al. 2020) were used to predict root mass proportions of five PFTs: graminoids, forbs, ferns, shrubs and birch (*B. pubescens*), and conifers. Then, the linear mixed-effect models with the ‘lme4’ package in R software were used to test how environmental and stand variables affect FTIR-derived FRP by plant functional types (**I**).

Fine-root decomposition

I assessed how well the proportion of initial mass remaining over time fit three decomposition models using nonlinear modeling (Wieder and Lang 1982; Harmon et al. 2009):

a single-exponential model, $X(t)/X0 = \mathrm{e}^{-kt}$ (3)

a double-exponential model, $X(t)/X0 = A\mathrm{e}^{-k1t} + (1 - A)\mathrm{e}^{-k2t}$ (4)

an asymptotic model, $X(t)/X0 = A + (1 - A)\mathrm{e}^{-kat}$ (5)

where $X(t)$ is the litter mass at time t, and $X0$ is the initial mass. In the single-exponential model, k represents the decomposition rate. The double-exponential model separates decomposition into two fractions: A (slow-decomposing, rate $k1$) and $(1 - A)$ (fast-decomposing, rate $k2$). The asymptotic model includes a non-decomposing fraction (A) and a decomposing fraction with rate ka.

The best-fitting model was identified using Akaike's information criterion for small samples (AICc; (Burnham et al. 2011). The double-exponential model fit mass loss data relatively well and seemed biologically most realistic (Fig. 1 and Table 3 in **II**). Therefore, I used the double-exponential model parameters (A, $k1$, $k2$) to describe fine-root decomposition dynamics in Study **II**. Subsequently, a nonlinear mixed-effects model (NLMIXED) was employed to assess the influence of species, soil depth, root diameter, soil type (peat or mineral soil), nutrient regime (rich or poor), and their interactions on the double-exponential model parameters. All analyses were conducted in R software.

Simulation of fine-root contribution to soil organic matter accumulation in drained peatland forests

To estimate soil organic matter (SOM) accumulation from fine roots, a simple simulation was conducted using FRP and decomposition data. The standing fine-root biomass was assumed to remain constant throughout the simulation period. Consequently, fine-root litter input was considered to be equal to FRP. The simulation covered a five-year period and the 0−30 cm soil layer, as this aligns with the temporal and vertical range of the available decomposition data (Study **II**). The inputs were expected to decompose at the measured rates, with the remaining masses summed over five years. Annual litter input estimates (L) were based on the mean values of FRP in different soil layers of drained peatland forests from different site types in Study **I** (**Table 1**). Annual mass loss data (D) for each year was calculated by Equation 4 from Study **II** (**Table 1**). Total organic matter accumulation ($OMaccu$) from litter input (L) and decomposition (D) over the five-year period was estimated using the following equation (Bhuiyan et al. 2023):

$$OMaccu = L\sum_{i=1}^{5}\left(\prod_{j=1}^{i}(1 - D_j)\right) \quad (6)$$

Table 1. The annual fine root litter input (*L*, g m^{-2} $year^{-1}$) and annual mass loss ratio for years 1 to 5 (*D1 to D5*) for different site types and soil depths.

Site type	Soil depth	*L* (g m^{-2} $year^{-1}$)	*D1*	*D2*	*D3*	*D4*	*D5*
MT	0−10 cm	110.65±15.3	0.48	0.50	0.53	0.55	0.57
MT	10−20 cm	37.65±9.6	0.42	0.51	0.57	0.61	0.64
MT	20−30 cm	17.7±2.45	0.36	0.40	0.43	0.46	0.48
VT	0−10 cm	62.2±7.9	0.46	0.54	0.58	0.61	0.63
VT	10−20 cm	21.55±3.35	0.37	0.45	0.49	0.52	0.54
VT	20−30 cm	9.95±1.6	0.47	0.47	0.48	0.48	0.49
DsT	0−10 cm	49±5.1	0.48	0.51	0.53	0.55	0.57
DsT	10−20 cm	14.8±1.8	0.32	0.34	0.37	0.40	0.42
DsT	20−30 cm	9.4±1.2	0.48	0.49	0.50	0.51	0.53

where L is the annual litter input (g m^{-2} $year^{-1}$), which is equal to FRP, and D_i is the annual mass loss ratio (ratio of mass lost during year i to mass in the beginning of year i) during each year *i*, with *i* representing each year from 1 to 5.

4 RESULTS AND DISCUSSION

4.1. Fine-root production (FRP)

4.1.1. Mean annual precipitation and temperature sum had no significant effect on total FRP

Mean annual precipitation (Model 2 in Tables 4 and 5 in **I**) and temperature sum (Model 2 in Tables 4 and 5, **I**) showed no significant relationship with total FRP. Latitude correlated negatively with total FRP as expected (model 4 in Table 4 and 5 in **I**, $p = 0.025$ and 0.029, respectively), indicating that total FRP decreases from south to north along the studied geographic range. It is possible that latitude, as a measure of geographical location, encompasses a range of environmental conditions that are not captured by mean annual temperature or precipitation alone.

4.1.2 Total FRP decreased with decreasing fertility

Total FRP varied considerably among the site types (**Figure 5**), being at its lowest, 48 ± 7 g m^{-2} $year^{-1}$, in the HrT sites, and at its highest, 234 ± 27 g m^{-2} $year^{-1}$, in the MT II sites.

Excluding the HrT sites, FRP decreased with decreasing fertility of the site type. The very low total FRP in the most fertile HrT sites was an unexpected result. We have two potential explanations. First, we observed that the peat used in the cores of the HrT sites contained clearly less phosphorus (P) than the ambient soils of the sites (Tables 1 and 2 in **I**). Thus, the lowest FRP observed for the most fertile HrT sites may simply mean that roots avoided the

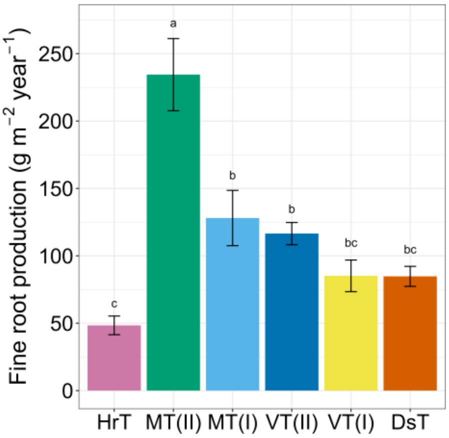

Figure 5. Mean fine-root production, g m^{-2} yr^{-1} ± standard error, by site type: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). Site types are here ordered based on their surface peat N content, decreasing from HrT to DsT (Westman and Laiho 2003). Different letters denote statistically significant differences between site types.

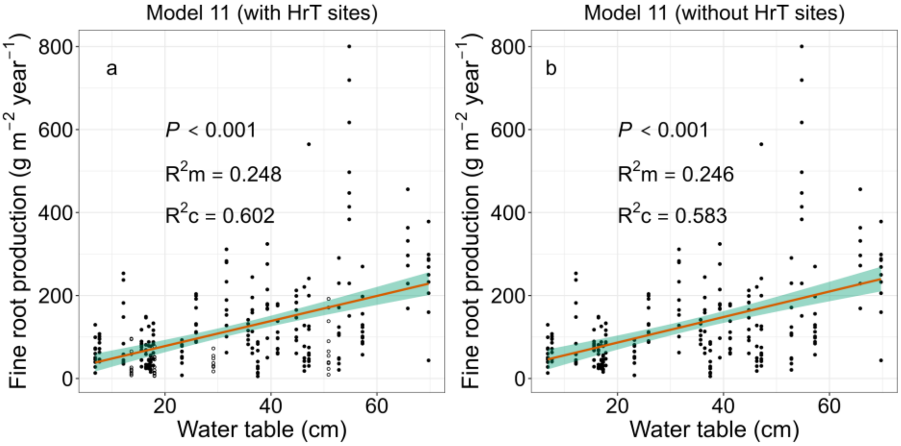

Figure 6. Relationship between soil water-table level and total fine-root production (a, with HrT sites; b, without HrT sites). Open circles represent HrT Sites. Solid line depicts the fitted linear regression lines, with their 95% confidence intervals indicated by the shaded areas. R^2m describes the proportion of variance explained by fixed effects. R^2c represents the proportion of variance explained by both fixed and random effects.

cores in these sites, where P is often a growth limiting nutrient (Päivänen and Hånell 2012). To avoid biased results in further studies, the ingrowth cores should preferably be filled with peat from the study sites or alternatively, peat from the study sites or alternatively, the main nutrient contents of the standard peats should be extensively compared with the peat of the study sites in advance, even though both options increase the amount of labour involved. Second, the HrT sites were relatively wet, (Fig. 3 in **I**), which can both limit the availability of oxygen to plant roots retarding FRP but also increase nutrient availability with the inflowing water leading to less need for FRP. Verifying the critical mechanism would require a specific further study.

Because of unexpected lowest FRP for the most fertile site type (HrT), we are showing model results both with and without HrT data (Table 4 versus Table 5 in **I**). The C:N ratio of the topmost 20 cm peat had a non-significant relation to total FRP at the stand level (model 9 in Tables 4 and 5 in **I**). When we excluded the most fertile sites (HrT), total FRP was significantly higher in nutrient-rich than in nutrient-poor sites (model 10 in Table 5 in **I**, $p = 0.010$). Recent FRP studies from stands on mineral-soil forests have shown total FRP (pine and understorey) to decrease with increasing site fertility (Ding et al. 2021). For peatlands, total FRP has previously been observed to be higher in more nutrient-rich and floristically diverse sites than in nutrient-poor sites (Finér and Laine 2000; Bhuiyan et al. 2017). In contrast, a recent study by Lampela et al. (2023) reported that total FRP was generally higher in the nutrient-poor, pine-dominated sites than the nutrient-rich, spruce-dominates sites. These contrasting findings highlight the complexity of FRP dynamics and suggest that factors such as tree species composition and their associated nutrient requirements may influence root productivity.

4.1.3 Total FRP was higher with deeper water table level (WT)

WT also played a significant role in determining total FRP (model 11 in table 4 and 5 in **I**, $p < 0.001$), with deeper WT generally linked to higher total FRP (**Figure 6**). In addition to the soil nutrient regime, the growth of tree roots on drained peatlands may be limited intermittently due to a lack of oxygen, and several studies have shown a positive correlation between WT and total FRP (Finér and Laine 1998; Murphy et al. 2009a; Murphy and Moore 2010). When WT is deeper, air-filled pore volume of the rooting zone is greater, which promotes root growth (Boggie 1972). Also in our study sites, total FRP was generally higher with a deeper WT, possibly as a result of a greater volume of aerated soil. However, stand basal area and WT depth generally have a positive correlation, due to both better site conditions for tree growth when the WT is deeper and the biological drainage through evapotranspiration increasing with increasing stand basal area (Sarkkola et al. 2005).This hampers determination of the primary factor leading to higher total FRP with deeper WT.

4.1.4 FRP increased with increasing stand basal area and stem volume

Stand characteristics were also earlier found to explain a greater proportion of the variation in FRP than environmental factors (Finér et al. 2011b). So, also the possible effect of climate, as well as WT, seems to be largely explained by stand characteristics. The basal area of a stand of trees is the sum of the cross-sectional surface areas of each live tree, measured at 1.37 m above ground (DBH), and reported on a per unit area basis (Bettinger et al. 2017). Stand stem volume (model 5 in Table 4 and 5 in **I**, $p = 0.053$ and < 0.001, respectively) and basal area (model 6 in Table 4 and 5 in **I**, $p = 0.006$ and < 0.001, respectively) correlated positively with FRP. At the stand level, stem volume alone explained 8% of the variation in FRP (**Figure 7**a), while stand basal area explained 16% (**Figure 7**c).

When we excluded the most fertile sites (HrT), stand stem volume alone explained 24% of the variation in FRP (**Figure 7**b), and the stand basal area explained 34% (**Figure 7**d), and mean FRP was 130 g m^{-2} $year^{-1}$. Stand basal area was the best individual predictor for FRP (Tables 4 and 5 in **I**). Finér et al. (2011b) examined the relationships between environmental and stand variables and FRP in forests at the stand or tree level. They discovered that basal area explained 28% and FRB as much as 53% of the variation in the FRP for trees at the tree level. Less variation in FRP could be explained at the stand level. Lehtonen et al. (2016) used

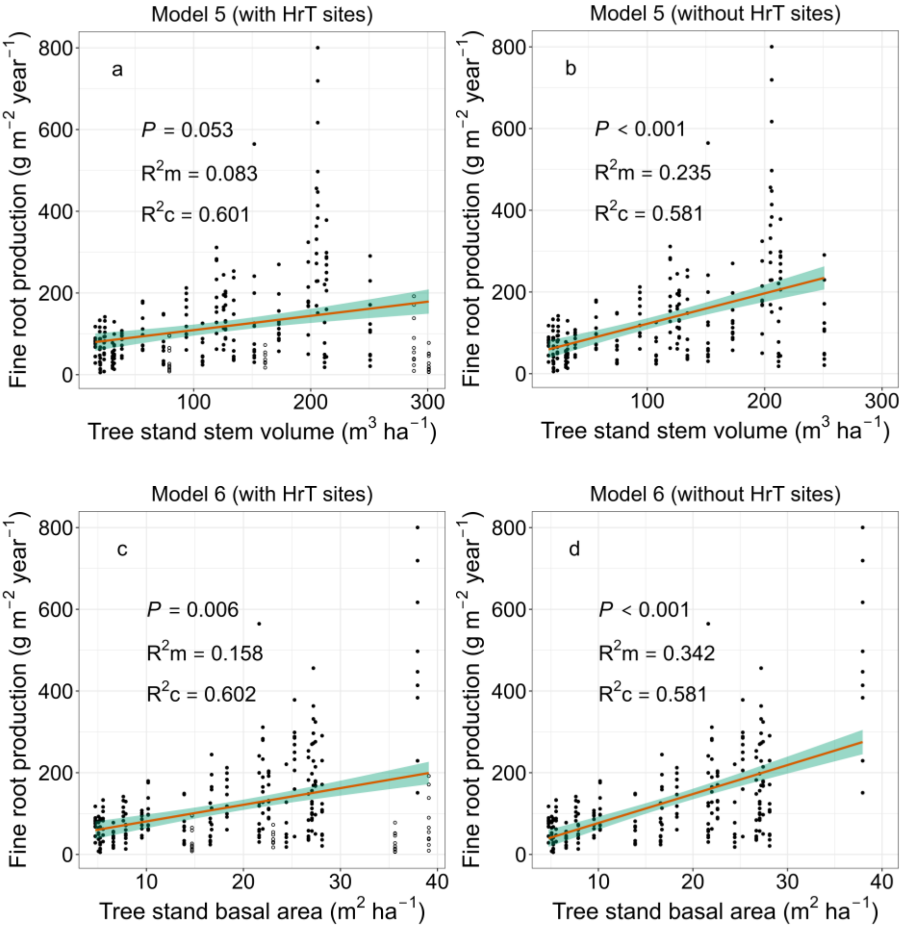

Figure 7. Relationship between stand stem volume and fine-root production (a, with HrT sites; b, without HrT sites), and stand basal area and fine-root production (c, with HrT sites; d, without HrT sites). Open circles represent HrT sites. Solid line depicts the fitted linear regression lines, with their 95% confidence intervals indicated by the shaded areas. R^2m describes the proportion of variance explained by fixed effects. R^2c represents the proportion of variance explained by both fixed and random effects.

data from 95 forest stands (both mineral-soil and peatland forests) to develop models for estimating FRB (diameter < 2 mm) of boreal forests and found that stand basal area predicted also FRB better than any other stand variable alone. As trees grow in diameter and add to their basal area, they require more resources to support their growth and maintenance (Forrester 2019), and this is often achieved by increasing the allocation of resources to the root system. However, the strength of this relationship can vary depending on site specific factors such as soil nutrient and hydrological regimes, as well as tree species composition (Finér et al. 2011b; Lehtonen et al. 2016). The relationship between stand basal area and FRP at the MT (I) sites was not consistent with the other site types, but this is probably just due to the small variation in the basal area not facilitating reliable estimation of the relationship for this site type.

We observed that site type, a general descriptor of site nutrient regime, was significant when added into models with stand basal area (model 12 in Table 4 and 5 in **I**, $p < 0.001$ and $= 0.029$, respectively). Site type and basal area together were the best predictors for FRP, explaining 47% of the variation in stand-level FRP (**Figure 8**). The relationship between stand basal area and FRP at the MT (I) sites was not consistent with the other site types, but this is probably just due to the small variation in the basal area not facilitating reliable estimation of the relationship for this site type. Also, WT (model 13 in Table 4 in **I**, $p = 0.007$) was significant when added into the model with basal area. When we incorporated WT into the model with site type and basal area (model 14 in **I**), we found that the model was not improved (Table 6 in **I**). More detailed reporting of stand and environmental characteristics in forthcoming studies could increase the predictive power of FRP models and improve our understanding of the C cycle in boreal peatland forests.

4.1.5 Fine-root production by plant functional type

This study is the first to use FTIR spectroscopy to quantify FRP and its depth distribution across different tree species and plant functional types in boreal drained peatland forests (**I**; also Lampela *et al.* 2023). FRP in drained peatland forests was primarily driven by woody species (shrubs and trees), which contributed 72% to 94% of the total FRP across various site types (Fig. 5 in **I**). The remaining FRP was contributed by herbaceous species, including graminoids, forbs, and ferns (Fig. 5 in **I**). This illustrates how herbaceous species are largely replaced by trees and shrubs following drainage (Lampela et al. 2023).

The majority of FRP from woody species was concentrated within the upper 20 cm of the peat profile, while FRP of herbaceous plants, particularly that of graminoids, reached down to 50 cm below the soil surface (Fig. 6 in **I**). This pattern suggests that trees and shrubs, which rely on well-aerated soils, confine their root growth to shallower layers where oxygen availability is higher (Murphy and Moore 2010). Graminoids, which often have aerenchymatous roots, are better adapted to exploiting deeper, less aerated layers (Proctor and He 2019).

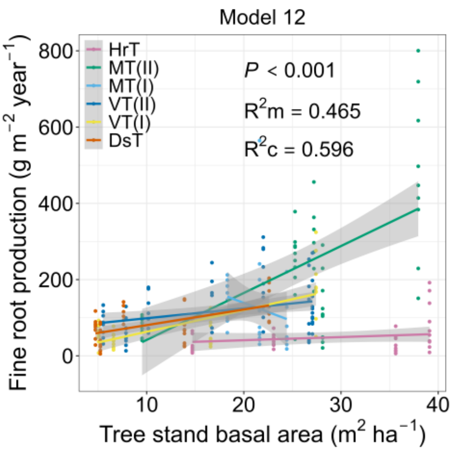

Figure 8. Relationship between tree stand basal area and fine-root production for the different site types separately. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). R^2m describes the proportion of variance explained by fixed effects. R^2c represents the proportion of variance explained by both fixed and random effects. Solid lines depict the fitted linear regression lines, with their 95% confidence intervals indicated by the shaded areas.

4.1.6 Total FRP decreases from soil surface to deeper layers

The majority of FRP in drained peatland forests was concentrated in the upper soil layers, with 76–95% of total FRP occurring within the top 20 cm of the soil profile (Table 7 in **I**). The decline in FRP with increasing depth is consistent with the findings of previous studies (Ruseckas 2000; Murphy and Moore 2010; Bhuiyan et al. 2017; Lampela et al. 2023). The β value was employed to describe the depth distribution of FRP. Higher β values indicate a greater proportion of roots at deeper soil depths, while lower values indicate a shallower distribution of roots. Our findings indicate that neither climatic variables, such as mean annual air temperature and precipitation, nor WT exert a significant influence on the vertical distribution of total FRP (β value). This finding aligns with the earlier studies, which reported that when peatlands are drained, the mean depth of the root system increases only marginally, even if the WT drops deeper (Heikurainen 1955; Paavilainen 1966).

The depth distribution of FRP varied by site type, with more fertile sites, such as herb-rich sites (HrT), showing a lower proportion of FRP in deeper soil layers (lowest β value) compared to nutrient-poor sites like dwarf shrub sites (DsT) (**Figure 9**).

A positive correlation was observed between β values and C:N ratio of the topmost 20 cm of peat (Model 27 in Table 4 in **I**), suggesting that roots in nutrient-poor sites tend to grow deeper in search of available mineral nutrients (Jackson et al. 1996). The combination of site type and soil C:N ratio was found to account for 20% of the variation in β values (Fig. 8 in **I**), thereby further suggesting that soil nutrient regime plays a crucial role in determining root depth distribution.

4.2. Fine-root decomposition

4.2.1 Fine-root decomposition rate was slower in drained peatland forests than in mineral-soil forests

Study **II** is the first to compare fine-root decomposition between drained peatland forests and mineral-soil forests. The results showed that the decomposition rate (*k1*) of the slow-decomposing pool was significantly lower in peat soils compared to mineral soils (Table 6 in **II**), leading to greater fine-root mass remaining in drained peatland forests by the end of the study (after 5 years). Although waterlogged, anaerobic conditions are common in undrained peatlands, the litterbags in Study **II** were placed in the 0−30 cm soil layer, mostly above the average monthly WT, which was 20–32 cm below the surface (Table 1 in **II**). Therefore, the WT may not be the primary factor behind the differences in decomposition rates between drained peatlands and mineral-soil forests, suggesting the need to consider factors such as litter quality and soil properties.

In mineral soils, nutrient-rich sites (HrT-M, MT-M) showed lower *k1* values compared to nutrient-poor sites (VT-M, DsT-M) (Table 6 in **II**), leading to greater fine-root mass remaining in the nutrient-rich sites by the end of the study (**Figure 10**). This finding may be explained by the suppressive effect of rich N on lignin-degrading enzymes in these ecosystems, which slows the decomposition of lignin-rich fine roots that are characteristic of temperate and boreal forests (Rasse et al. 2005; Xia et al. 2015). In contrast, fine-root decomposition was faster in nutrient-rich peatland sites (HrT, MT) compared to nutrient-poor sites (VT, DsT) (**Figure 10**). Compared to mineral soils, peat soils usually contain more N but less mineral nutrients such as P and K (Westman and Laiho 2003). A previous study in

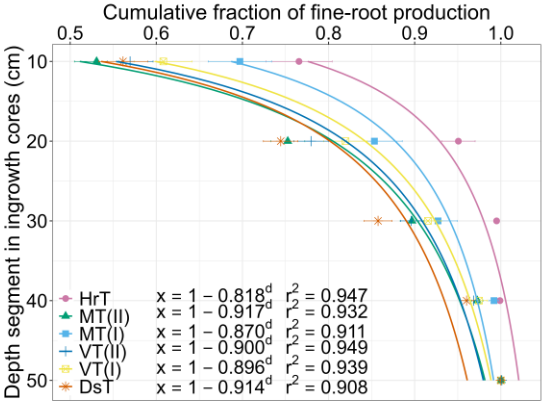

Figure 9. Mean cumulative fraction of fine-root production for different site types. Error bars are standard error of the mean. Site types: Herb-rich type (HrT, n=4), *Vaccinium myrtillus* types II (MT II, n=5) and I (MT I, n=3), *Vaccinium vitis-idaea* types II (VT II, n=7) and I (VT I, n=3), and Dwarf shrub type (DsT, n=5). The lines represent the asymptotic regressions to the data using the equation $x=1–ß^d$, where ß describes the relative proportion of root located at depth.

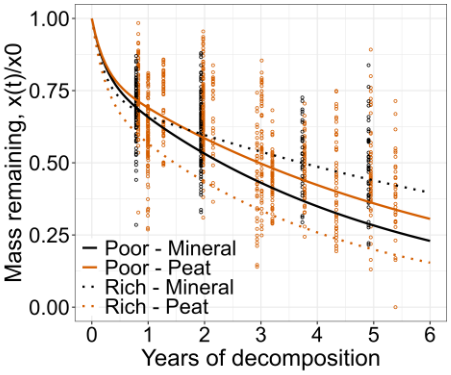

Figure 10. Comparative decomposition patterns of fine roots across different soil types (peat soils and mineral soils) and nutrient regime conditions (nutrient-rich and nutrient-poor). The lines represent the double-exponential model-predicted decomposition patterns.

two temperate fens found that low nutrient status and pH reduce microbial activity, leading to slower decomposition rates (Scheffer and Aerts 2000). In our study, pH showed little variation among sites, but WT differed (Table 2 in **II**). The deeper WT observed in nutrient-rich sites (HrT, MT) suggests more favorable oxygenation conditions. This is likely to have provided a more favorable environment for decomposition.

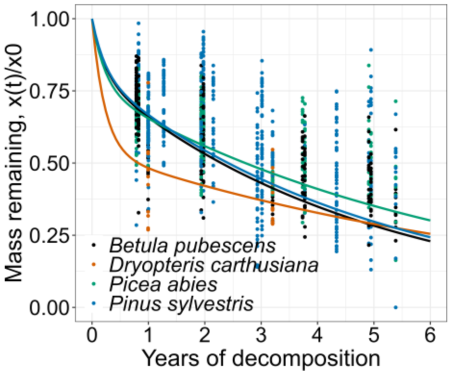

Figure 11. Decomposition patterns of fine roots in *Pinus sylvestris* (blue), *Picea abies* (green), *Betula pubescens* (black), and *Dryopteris carthusiana* (red). The lines are the double-exponential model-predicted decomposition patterns.

4.2.2 Fine roots of deciduous species decompose faster than those of coniferous species

Species-specific traits play a crucial role in determining the rate and extent of fine-root decomposition in boreal drained peatland and mineral-soil forests (**II**). In our study, we compared two evergreen coniferous tree species (*P. abies and P. sylvestris*) and a broadleaf deciduous tree species (*B. pubescens*), which are the three dominant tree species in peatland forests in the region. The fine roots of *B. pubescens* decomposed more rapidly than those of *P. abies* (**Figure 11**), as evidenced by significant differences in the proportion (*A*) and decomposition rate (*k1*) of the slow-decomposing pool (Table 6 in **II**). Silver and Miya (2001) analysed 176 root decomposition datasets from diverse geographical locations and found that fine roots (0−2 mm) of conifers had the lowest levels of calcium and N, the highest C:N and lignin:N ratios, and decomposed at the slowest rates compared to broadleaf trees. In contrast, fine-root decomposition of another conifer, *P. sylvestris*, was not statistically different from that of *B. pubescens* (Table 6 in **II**). Similarly, Lin et al. (2011) reported that for fine-root decomposition, there was no significant difference between conifers and broadleaf trees in mid-subtropical China. These results suggest that the decomposition rates of conifer species are not always lower than those of broadleaf species, challenging the traditional view based solely on botanical classification.

Additionally, we found that the fern *D. carthusiana* had the lowest proportion of material in the slow pool (A) compared to the tree species, while the mass loss rate of its slow decomposition pool (k1) was similar to that of *Betula pubescens*. It suggests that *D. carthusiana* undergoes an initial decomposition that is faster than the woody tree species, followed by a stabilizing phase.

4.2.3 Fine roots decompose faster than small roots

Root diameter also significantly influenced decomposition rates. I compared the decomposition of two root size classes: fine roots (<2 mm) and small roots (2–10 mm) in *P. sylvestris* (**Figure 12**). The results are consistent with previous research on other pine species, showing that fine roots decompose more quickly than small roots (Usman et al. 2000;

Ludovici and Kress 2006; Mao et al. 2011). Globally, when the roots were divided into three sizes (<2 mm, 2–5 mm and >5 mm) or two classes (fine roots <2 mm vs. small roots >2 mm), fine roots decompose significantly faster (Silver and Miya 2001; Zhang and Wang 2015).

FTIR analysis by Straková et al. (2020) indicates that fine roots (0–2 mm) had higher levels of polyphenolics (lignin) and aliphatic compounds (wax, lipids), while small roots (2–10 mm) contained higher polysaccharide concentrations. High lignin concentrations in fine roots typically slow down decomposition (Luo et al. 2017). Helmisaari (1991) found a decrease in nutrient concentrations (N, P, K, and Mg) in *P. sylvestris* roots with increasing root diameter in eastern Finland. Hence, as root diameter increases, cellulose and alpha-cellulose contents also rise, while lignin content and nutrient concentrations decline (Thomas et al. 2014; Zhang et al. 2014), resulting in slower decomposition rates (Jing et al. 2019).

4.2.4 Fine-root decomposition rate decreases with increasing depth from the soil surface

Sampling depth had a significant impact on the decomposition of fine roots both in boreal drained peatland and mineral-soil forests (**II**). A negative correlation between sampling depth and decomposition rate (*k1*) of the slow-decomposing pool was observed in our study **II** (**Figure 12**). The results showed that fine-root decomposition was fastest in the 0−10 cm soil layer and slowed down with increasing soil depth. Similar decline in fine-root decomposition at deeper soil layers was also observed in previous studies conducted in boreal peatland forests (Laiho et al. 2004; Straková et al. 2012) and temperate mineral-soil forests (Sariyildiz 2015; Sun et al. 2016). Generally, increasing soil depth reduces soil microbial activity, substrate availability, and alters soil moisture and temperature. Studies in both peatlands (Jackson et al. 2009; Steinweg et al. 2018) and mineral-soil forests (Herold et al. 2014; Han et al. 2019) have shown decreases in microbial biomass and the activity of extracellular microbial enzymes involved in decomposition with increasing soil depth.

Specific factors like WT position and oxygen availability may uniquely influence peatland sites. In the drained peatland sites of study **II**, the mean growing season WT was about 20–32 cm below the surface (Table 1 in **II**), and litterbags were incubated at depths of 0–10 cm, 10–20 cm, and 20–30 cm. In the summer, the aerobic limit may be approximately 5−30 cm closer to the peatland surface than to the WT (Lähde 1969), therefore anaerobic or reducing conditions may impede fine-root decomposition even in the drained sites, particularly in the greater incubation depths (Laiho et al. 2004).

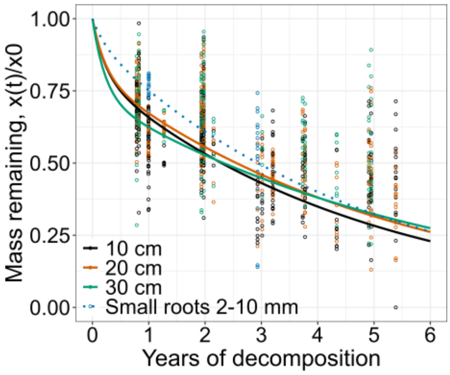

Figure 12. Decomposition patterns of fine roots (<2 mm) across different soil depths as marked by their lower boundaries, and small roots (2−10 mm). The black lines indicate the decomposition patterns of fine roots in the 0−10 cm soil layer, the red lines correspond to the 10−20 cm layer, and the green lines to the 20−30 cm layer. The blue dotted line represents the decomposition patterns of small roots. The lines are the double-exponential model-predicted decomposition patterns.

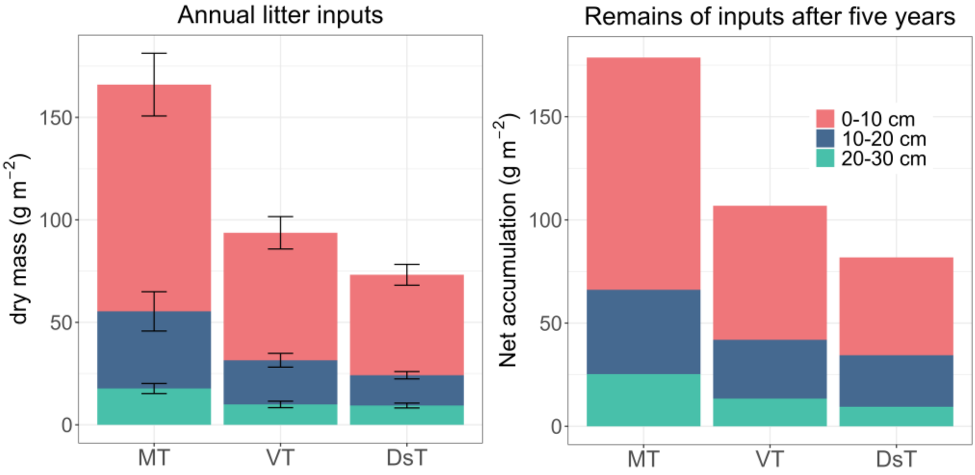

Figure 13. Annual litter inputs (**I**) vs. remains of the inputs after five years. Site types in the drained peatland forests from the most fertile to the nutrient poorest: *Vaccinium myrtillus* type (MT), *Vaccinium vitis-idaea* type (VT) and *Dwarf-shrub* type (DsT).

4.3 Fine-root contribution to C inputs and soil organic matter accumulation in drained peatland forests

The annual litter inputs varied significantly across the different site types, ranging from 73.2 to 166 g m^{-2} of dry mass (**Figure 13**). Based on the assumption that the C content in root biomass was 48% for broadleave-dominated stands and 51% for conifer-dominated stand (Lamlom and Savidge 2003; Bārdule et al. 2021; Bardule et al. 2023), the estimated annual C input with fine-root litter in our drained peatland forest in Finland ranged from 0.36 to 0.82 t C ha^{-1} $year^{-1}$. These values are comparable to those observed in drained or naturally wet hemiboreal forest stands in Latvia, where C input with fine root litter ranged from 0.28 ± 0.06 to 0.68 ± 0.14 t C ha^{-1} $year^{-1}$ (Lazdiņš et al. 2024). While well-drained peatlands in Estonia showed higher annual C input from fine-root litter, ranging from 0.9 to 1.5 t C ha^{-1} $year^{-1}$ (Uri et al. 2017), though this may be attributed to better drainage conditions supporting larger FRP.

The estimated potential for soil organic matter (SOM) accumulation from fine roots in our study is a reflection of the combined effects of FRP and decomposition rates in drained peatland forests. While the results of this simplistic evaluation should be interpreted with caution, they provide insight into the contribution of fine roots to SOM accumulation in drained peatland forests. Despite variation in estimated annual fine-root litter inputs, a clear pattern emerged: after five years, a significant portion of the inputs had decomposed, leaving 81.8–178.7 g m^{-2} remaining (**Figure 13**). Although fine root decomposition rates were high at the nutrient-rich site (MT), inputs of fine root litter were also high, resulting in a greater net accumulation in nutrient-rich sites than in nutrient-poor sites. It could be inferred that environmental conditions favourable for root production also favour root abscission and decomposition. This suggests that more productive and nutrient-rich sites can retain at least in short term more SOM from fine roots than less productive and nutrient-poor sites, even with higher decomposition rates, thereby showing greater potential for C sequestration.

4.4 Implications for ecosystem C cycling

Fine roots provide a direct input of organic matter to soil, and their turnover is a major component of the C cycle. A small change in FRP can thus affect the ecosystem C sink. In peatlands, land-use practices often involve artificial drainage, and a substantial proportion of these ecosystems, particularly in the European boreal zone, has been drained for forestry purposes. Furthermore, climate warming is projected to enhance evapotranspiration (Helbig et al. 2020) and lead to lowered WT in peatlands. The increase in total FRP in lower WT environments (**I**) represents a significant increase in C flux to peat soil. As a result of this labile C addition, the decomposition of old SOM may either increase (positive priming) or decrease (negative priming) (Kuzyakov 2010). Gavazov et al. (2018) and Yan et al. (2022) studied root-induced priming on pristine peatlands, showing a positive priming effect on peat decomposition. On the contrary, Linkosalmi et al. (2023) found that in forestry-drained peatlands, microbial communities preferentially utilize fresh C inputs from vegetation over older C in the short term, resulting in suppressed peat decomposition. This effect is particularly pronounced in nutrient-poor peat soils, where the presence of fresh C inputs exerts a stronger influence on decomposition dynamics.

Also plant functional group shifts due to WT lowering have important implications for ecosystem C cycling as different life strategies can create inherent differences in the partitioning of C, as well as in the decomposition of different plant parts. Following drainage, the tree layer typically dominates biomass composition (Laiho et al. 2003). In drained peatland forests (Study **I**), trees and shrubs account for the largest proportion of total FRP, contributing nearly 80%. However, the precision of our Fourier Transform Infrared (FTIR) spectroscopy analysis was insufficient to distinguish between tree species. Future research should focus on examining the response of FRP across different tree species to changes in WT driven by global warming or drainage practices. Additionally, certain herbaceous species, particularly graminoids, allocate a larger proportion of their root production to deeper soil layers compared to trees (**I**). This pattern is likely driven by their aerenchymatous roots, which enable them to access less-aerated soil layers (Proctor and He 2019), thereby contributing plant-derived C to the soil organic matter pool at greater depths. In contrast, boreal trees and shrubs primarily confine their root growth to shallower layers where oxygen availability is higher.

The shift in functional groups influencing fine root production (FRP) also has implications for the decomposability of root tissues. Study **II** revealed that the fine roots of fern species (*D. carthusiana)* initially decompose more rapidly than those of tree species (*P. sylvestris*, *P. abies*, *B. pubescens*). This finding aligns with broader patterns observed in other studies, which demonstrate that herbaceous roots tend to decompose faster than woody roots due to their lower lignin content, higher nutrient concentrations, and more favorable C:N ratios (Silver and Miya 2001; Cornwell et al. 2008; Sun et al. 2018; See et al. 2019). Future studies should consider the root systems of other herbs, such as graminoids and forbs, in peatlands for comparison with trees and shrubs. Several studies have demonstrated that drainage triggers a shift in vegetation structure, with shrubs being the first to benefit from lowered WT (Laine et al. 1995; Laiho et al. 2003). Over time, trees often become dominant, leading to the gradual replacement of mire species by forest species (Laine et al. 1995; Vasander et al. 2018). These changes are most evident in initially wet, nutrient-rich sites, while nutrient-poor sites experience smaller shifts (Laine et al. 1995). I hypothesize that drainage increases the proportion of roots produced by more decomposition-resistant functional groups, such as trees and shrubs, thereby contributing a greater amount of root-derived C to the SOM pool following drainage. This highlights the complex interplay between plant functional group composition, WT conditions, and decomposition processes in shaping SOM dynamics.

5 CONCLUSIONS

In this study (**I**), a set of models was developed to estimate the FRP by using stand and environmental variables. Stand basal area predicted FRP better than any other stand variable alone, explaining 16% of the variation in stand-level total FRP. Total FRP varied considerably among the site types and, with the exception of the most fertile site type, decreased with decreasing fertility. A model that included stand basal area and site type accounted for 47% of the variation in stand-level total FRP. Total FRP was generally higher with a deeper WT. Together, WT and basal area explained 25% of the variation in stand-level total FRP. These results can be used with forest inventory data to improve the quantification of FRP in peatland forests.

The decomposition process (**II**) in peatlands was fastest in nutrient-rich peat soils compared to poorer soils, while in mineral-soil forests the trend was the opposite, emphasizing different relationships between nutrient regime and the decomposer communities. Soil depth emerged as another influential factor, with deeper layers exhibiting slower decomposition rates compared to surface layers across both peatland and mineral-soil forests. Additionally, root diameter exerted an impact on decomposition dynamics, with smaller-diameter roots decomposing at a faster rate than larger-diameter roots. Among the dominant tree species (*P. sylvestris*, *P. abies*, *B. pubescens*), fine roots of *P. abies* decomposed the slowest.

Overall, the results highlight the multifaceted nature of fine-root production and decomposition in boreal forests, which is influenced by species composition, site characteristics, and environmental factors. The results of this study can be used in modelling peatland ecosystem structure and function, and their responses to changes in, e.g. water level and nutrient regime. A major practical use for the information is developing more reliable belowground forest C budgets to support greenhouse gas inventories in peatlands under climate or land use change.

LISTS OF REFERENCES

Abdul Rahman NSN, Abdul Hamid NW, Nadarajah K (2021) Effects of Abiotic Stress on Soil Microbiome. International Journal of Molecular Sciences 22(16), article id 9036. https://doi.org/10.3390/ijms22169036

Addo-Danso SD, Prescott CE, Smith AR (2016) Methods for estimating root biomass and production in forest and woodland ecosystem carbon studies: A review. Forest Ecology and Management 359: 332−351. https://doi.org/10.1016/j.foreco.2015.08.015

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos: 439−449. https://doi.org/10.2307/3546886

Backeus I (1990) Production and depth distribution of fine roots in a boreal open bog. Annales Botanici Fennici 27: 261−265. https://doi.org/https://www.jstor.org/stable/23725366

Bārdule A, Petaja G, Butlers A, Purviņa D, Lazdiņš A (2021) Estimation of litter input in hemi−boreal forests with drained organic soils for improvement of GHG inventories. BALTIC FORESTRY 27(2), article id 534. https://doi.org/10.46490/bf534

Bardule A, Polmanis K, Krumšteds L, Bardulis A, Lazdinš A (2023) Fine root morphological traits and production in coniferous- and deciduous-tree forests with drained and naturally wet nutrient-rich organic soils in hemiboreal Latvia. iForest - Biogeosciences and Forestry 16: 165−173. https://doi.org/10.3832/ifor4186-016

Beidler KV, Pritchard SG (2017) Maintaining connectivity: understanding the role of root order and mycelial networks in fine root decomposition of woody plants. Plant and Soil 420: 19−36. https://doi.org/10.1007/s11104-017-3393-8

Berg B, McClaugherty C, Santo AVD, Johnson D (2001) Humus buildup in boreal forests: effects of litter fall and its N concentration. Canadian Journal of Forest Research 31: 988−998. https://doi.org/10.1139/x01-031

Bérubé V, Rochefort L (2018) Production and decomposition rates of different fen species as targets for restoration. Ecological Indicators 91: 105−115. https://doi.org/10.1016/j.ecolind.2018.03.069

Bettinger P, Boston K, Siry J, Grebner D (2017) Valuing and characterizing forest conditions. In: Bettinger P, Boston K, Siry J, Grebner D (eds) Forest Management and Planning, 2nd ed. Academic Press, New York, pp 21–64. https://doi.org/10.1016/B978-0-12-809476-1.00002-3

Bhuiyan R, Mäkiranta P, Straková P, Fritze H, Minkkinen K, Penttilä T, Rajala T, Tuittila ES, Laiho R (2023) Fine-root biomass production and its contribution to organic matter accumulation in sedge fens under changing climate. Science of the Total Environment 858, article id 159683. https://doi.org/10.1016/j.scitotenv.2022.159683

Bhuiyan R, Minkkinen K, Helmisaari HS, Ojanen P, Penttilä T, Laiho R (2017) Estimating fine-root production by tree species and understorey functional groups in two contrasting peatland forests. Plant and Soil 412: 299−316. https://doi.org/10.1007/s11104-016-3070-3

Boggie R (1972) Effect of water-table height on root development of Pinus contorta on deep peat in Scotland. Oikos: 304−312. https://doi.org/10.2307/3543168

Bond-Lamberty B, Wang C, Gower ST (2004) Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Global Change Biology 10: 473−487. https://doi.org/10.1111/j.1529-8817.2003.0742.x

Bradford MA, Berg B, Maynard DS, Wieder WR, Wood SA (2016) FUTURE DIRECTIONS: Understanding the dominant controls on litter decomposition. Journal of Ecology 104: 229−238. https://doi.org/10.1111/1365-2745.12507

Bucher M, Ofiti NOE, Malhotra A (2023) Plant functional types and microtopography mediate climate change responses of fine roots in forested boreal peatlands. Frontiers in Forests and Global Change 6, article id 1170252. https://doi.org/10.3389/ffgc.2023.1170252

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65: 23−35. https://doi.org/10.1007/s00265-010-1029-6

Chen W, Zhang Q, Cihlar J, Bauhus J, Price DT (2004) Estimating fine-root biomass and production of boreal and cool temperate forests using aboveground measurements: A new approach. Plant and Soil 265: 31−46. https://doi.org/10.1007/s11104-005-8503-3

Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Pérez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, Van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Díaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV, Westoby M (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11: 1065−1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x

Ding Y, Leppälammi-Kujansuu J, Salemaa M, Schiestl-Aalto P, Kulmala L, Ukonmaanaho L, Nöjd P, Minkkinen K, Makita N, Železnik 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. Forest Ecology and Management 489, artcile id 119081. https://doi.org/10.1016/j.foreco.2021.119081

Domisch T, Finér L, Laiho R, Karsisto M, Laine J (2000) Decomposition of Scots pine litter and the fate of released carbon in pristine and drained pine mires. Soil Biology & Biochemistry 32: 1571−1580. https://doi.org/10.1016/s0038-0717(00)00070-5

Dornbush ME, Isenhart TM, Raich JW (2002) Quantifying fine-root decomposition: An alternative to buried litterbags. Ecology 83: 2985−2990. https://doi.org/10.1890/0012-9658(2002)083[2985:QFRDAA]2.0.CO;2

Esbensen KH, Guyot D, Westad F, Houmoller LP (2002). Multivariate data analysis: in practice: an introduction to multivariate data analysis and experimental design 5th edition. CAMO Sosftware, Woodbridge

Finér L, Laine J (1998) Root dynamics at drained peatland sites of different fertility in southern Finland. Plant and Soil 201: 27−36. https://doi.org/10.1023/a:1004373822354

Finér L, Laine J (2000) The ingrowth bag method in measuring root production on peatland sites. Scandinavian Journal of Forest Research 15: 75−80. https://doi.org/10.1080/02827580050160493

Finér L, Ohashi M, Noguchi K, Hirano Y (2011a) Factors causing variation in fine root biomass in forest ecosystems. Forest Ecology and Management 261: 265−277. https://doi.org/10.1016/j.foreco.2010.10.016

Finér L, Ohashi M, Noguchi K, Hirano Y (2011b) Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. Forest Ecology and Management 262: 2008−2023. https://doi.org/10.1016/j.foreco.2011.08.042

Forrester DI (2019) Linking forest growth with stand structure: Tree size inequality, tree growth or resource partitioning and the asymmetry of competition. Forest Ecology and Management 447: 139−157. https://doi.org/10.1016/j.foreco.2019.05.053

Fujimaki R, Takeda H, Wiwatiwitaya D (2008) Fine root decomposition in tropical dry evergreen and dry deciduous forests in Thailand. Journal of Forest Research 13: 338−346. https://doi.org/10.1007/s10310-008-0087-3

Gale MR, Grigal DF (1987) Vertical root distributions of northern tree species in relation to successional status. Canadian Journal of Forest Research 17: 829−834. https://doi.org/10.1139/x87-131

Gavazov K, Albrecht R, Buttler A, Dorrepaal E, Garnett MH, Gogo S, Hagedorn F, Mills RTE, Robroek BJM, Bragazza L (2018) Vascular plant-mediated controls on atmospheric carbon assimilation and peat carbon decomposition under climate change. Global Change Biology 24: 3911−3921. https://doi.org/10.1111/gcb.14140

Ge L, Chen C, Li T, Bu Z-J, Wang M (2023) Contrasting effects of nitrogen and phosphorus additions on fine root production and morphological traits of different plant functional types in an ombrotrophic peatland. Plant and Soil 490: 451−467. https://doi.org/10.1007/s11104-023-06087-3

Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. Global Change Biology 6: 751−765. https://doi.org/10.1046/j.1365-2486.2000.00349.x

Gorham E (1991) Northern Peatlands: Role in the Carbon Cycle and Probable Responses to Climatic Warming. Ecological Applications 1: 182−195. https://doi.org/10.2307/1941811

Guo D (2008) Branch order as a predictor of root uptake capacity and mycorrhizal colonization in 23 Chinese temperate tree species. New Phytol 180: 673−683. https://doi.org/10.1111/j.1469-8137.2008.02573.x

Guo D, Li H, Mitchell RJ, Han W, Hendricks JJ, Fahey TJ, Hendrick RL (2008a) Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. New Phytologist 177: 443−456. https://doi.org/10.1111/j.1469-8137.2007.02242.x

Guo D, Mitchell RJ, Withington JM, Fan PP, Hendricks JJ (2008b) Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. Journal of Ecology 96: 737−745. https://doi.org/10.1111/j.1365-2745.2008.01385.x

Guo DL, Mitchell RJ, Hendricks JJ (2004) Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140: 450−457. https://doi.org/0.1007/s00442-004-1596-1

Han SH, Kim S, Chang H, Kim H-J, Khamzina A, Son Y (2019) Soil depth- and root diameter-related variations affect root decomposition in temperate pine and oak forests. Journal of Plant Ecology 12: 871−881. https://doi.org/10.1093/jpe/rtz023

Hansson K, Fröberg M, Helmisaari H-S, Kleja DB, Olsson BA, Olsson M, Persson T (2013) Carbon and nitrogen pools and fluxes above and below ground in spruce, pine and birch stands in southern Sweden. Forest Ecology and Management 309: 28−35. https://doi.org/10.1016/j.foreco.2013.05.029

Harmon ME, Silver WL, Fasth B, Chen H, Burke IC, Parton WJ, Hart SC, Currie WS (2009) Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Global Change Biology 15: 1320−1338. https://doi.org/10.1111/j.1365-2486.2008.01837.x

He W, Makirantä P, Straková P, Ojanen P, Penttilä T, Bhuiyan R, Minkkinen K, Laiho R (2023) Fine-root production in boreal peatland forests: Effects of stand and environmental factors. Forest Ecology and Management 550, article id 121503. https://doi.org/10.1016/j.foreco.2023.121503

Heikurainen L (1955) Structure of Scots pine root systems in a pine swamp and effect of draining on the structure. Silva Fennica 65, article id 7466. https://doi.org/10.14214/aff.7466

Helbig M, Waddington JM, Alekseychik P, Amiro BD, Aurela M, Barr AG, Black TA, Blanken PD, Carey SK, Chen J, Chi J, Desai AR, Dunn A, Euskirchen ES, Flanagan LB, Forbrich I, Friborg T, Grelle A, Harder S, Heliasz M, Humphreys ER, Ikawa H, Isabelle P-E, Iwata H, Jassal R, Korkiakoski M, Kurbatova J, Kutzbach L, Lindroth A, Löfvenius MO, Lohila A, Mammarella I, Marsh P, Maximov T, Melton JR, Moore PA, Nadeau DF, Nicholls EM, Nilsson MB, Ohta T, Peichl M, Petrone RM, Petrov R, Prokushkin A, Quinton WL, Reed DE, Roulet NT, Runkle BRK, Sonnentag O, Strachan IB, Taillardat P, Tuittila E-S, Tuovinen J-P, Turner J, Ueyama M, Varlagin A, Wilmking M, Wofsy SC, Zyrianov V (2020) Increasing contribution of peatlands to boreal evapotranspiration in a warming climate. Nature Climate Change 10: 555−560. https://doi.org/10.1038/s41558-020-0763-7

Helmisaari HS (1991) Variation in nutrient concentrations of *Pinus sylvestris* roots. In: McMichael BL, Persson H (eds) Plant Roots and Their Environment. Elsevier, Amsterdam, pp 204–212. https://doi.org/10.1016/B978-0-444-89104-4.50031-1

Helmisaari HS, Derome J, Nojd P, Kukkola M (2007) Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiology 27: 1493−1504. https://doi.org/10.1093/treephys/27.10.1493

Herold N, Schöning I, Berner D, Haslwimmer H, Kandeler E, Michalzik B, Schrumpf M (2014) Vertical gradients of potential enzyme activities in soil profiles of European beech, Norway spruce and Scots pine dominated forest sites. Pedobiologia 57: 181−189. https://doi.org/10.1016/j.pedobi.2014.03.003

Herzog C, Steffen J, Graf Pannatier E, Hajdas I, Brunner I (2014) Nine Years of Irrigation Cause Vegetation and Fine Root Shifts in a Water-Limited Pine Forest. Plos One 9(5), article id e96321. https://doi.org/10.1371/journal.pone.0096321

Hishi T (2007) Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. Journal of Forest Research 12: 126−133. https://doi.org/10.1007/s10310-006-0260-5

Hobbie SE, Oleksyn J, Eissenstat DM, Reich PB (2010) Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. Oecologia 162: 505−513. https://doi.org/10.1007/s00442-009-1479-6

Jackson CR, Liew KC, Yule CM (2009) Structural and Functional Changes with Depth in Microbial Communities in a Tropical Malaysian Peat Swamp Forest. Microbial Ecology 57: 402−412. https://doi.org/10.1007/s00248-008-9409-4

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108: 389−411. https://doi.org/10.1007/bf00333714

Jing H, Zhang P, Li J, Yao X, Liu G, Wang G (2019) Effect of nitrogen addition on the decomposition and release of compounds from fine roots with different diameters: the importance of initial substrate chemistry. Plant and Soil 438: 281−296. https://doi.org/10.1007/s11104-019-04017-w

Johnson MG, Tingey DT, Phillips DL, Storm MJ (2001) Advancing fine root research with minirhizotrons. Environmental and Experimental Botany 45: 263−289. https://doi.org/10.1016/s0098-8472(01)00077-6

Kögel-Knabner I (2002) The macromolecular organic composition of plant and microbial residues as inputs to soil organic matter. Soil Biology and Biochemistry 34: 139−162. https://doi.org/10.1016/s0038-0717(01)00158-4

Kramer C, Trumbore S, Fröberg M, Cisneros Dozal LM, Zhang D, Xu X, Santos GM, Hanson PJ (2010) Recent (<4 year old) leaf litter is not a major source of microbial carbon in a temperate forest mineral soil. Soil Biology and Biochemistry 42: 1028−1037. https://doi.org/10.1016/j.soilbio.2010.02.021

Krishna M, Mohan M (2017) Litter decomposition in forest ecosystems: a review. Energy, Ecology and Environment 2: 236−249. https://doi.org/10.1007/s40974-017-0064-9

Kuzyakov Y (2010) Priming effects: Interactions between living and dead organic matter. Soil Biology and Biochemistry 42: 1363−1371. https://doi.org/10.1016/j.soilbio.2010.04.003

Lähde E (1969) Biological activity in some natural and drained peat soils with special reference to oxidation-reduction conditions. Acta Forestalia Fennica 69.

Laiho R (2006) Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. Soil Biology and Biochemistry 38: 2011−2024. https://doi.org/https://doi.org/10.1016/j.soilbio.2006.02.017

Laiho R, Laine J, Trettin CC, Finér L (2004) Scots pine litter decomposition along drainage succession and soil nutrient gradients in peatland forests, and the effects of inter-annual weather variation. Soil Biology & Biochemistry 36: 1095−1109. https://doi.org/10.1016/j.soilbio.2004.02.020

Laiho R, Vasander H, Penttilä T, Laine J (2003) Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. Global Biogeochemical Cycles 17(2), article id 1053. https://doi.org/10.1029/2002gb002015

Laine J, Vasander H, Laiho R (1995) Long-Term Effects of Water Level Drawdown on the Vegetation of Drained Pine Mires in Southern Finland. The Journal of Applied Ecology 32: 785−802. https://doi.org/10.2307/2404818

Lamlom SH, Savidge RA (2003) A reassessment of carbon content in wood: variation within and between 41 North American species. Biomass and Bioenergy 25: 381−388. https://doi.org/10.1016/s0961-9534(03)00033-3

Lampela M, Minkkinen K, Straková P, Bhuiyan R, He W, Mäkiranta P, Ojanen P, Penttilä T, Laiho R (2023) Responses of fine-root biomass and production to drying depend on wetness and site nutrient regime in boreal forested peatland. Frontiers in Forests and Global Change 6, article id 1190893. https://doi.org/10.3389/ffgc.2023.1190893

Latter PM, Howson G, Howard DM, Scott WA (1997) Long-term study of litter decomposition on a Pennine peat bog: which regression?. Oecologia 113: 94−103. https://doi.org/10.1007/s004420050357

Lazdiņš A, Petaja G, Bārdule A, Polmanis K, Kalēja S, Maliarenko O, Melnik N (2024) Fine Roots in Hemiboreal Forest Stands and Clearcut Areas with Nutrient-Rich Organic Soils in Latvia: Morphological Traits, Production and Carbon Input. Forests 15(9), article id 1500. https://doi.org/10.3390/f15091500

Lehtonen A, Palviainen M, Ojanen P, Kalliokoski T, Nöjd P, Kukkola M, Penttilä T, Mäkipää R, Leppälammi-Kujansuu J, Helmisaari HS (2016) Modelling fine root biomass of boreal tree stands using site and stand variables. Forest Ecology and Management 359: 361−369. https://doi.org/10.1016/j.foreco.2015.06.023

Lei P, Bauhus J (2010) Use of near-infrared reflectance spectroscopy to predict species composition in tree fine-root mixtures. Plant and Soil 333: 93−103. https://doi.org/10.1007/s11104-010-0325-2

Leppälammi-Kujansuu J, Aro L, Salemaa M, Hansson K, Kleja DB, Helmisaari H-S (2014) Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. Forest Ecology and Management 326: 79−90. https://doi.org/10.1016/j.foreco.2014.03.039

Li X, Zheng X, Zhou Q, McNulty S, King JS (2022) Measurements of fine root decomposition rate: Method matters. Soil Biology and Biochemistry 164, article id 108482. https://doi.org/10.1016/j.soilbio.2021.108482

Li Z, Kurz WA, Apps MJ, Beukema SJ (2003) Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Canadian Journal of Forest Research 33: 126−136. https://doi.org/10.1139/x02-165

Lieffers VJ (1988) SPHAGNUM AND CELLULOSE DECOMPOSITION IN DRAINED AND NATURAL AREAS OF AN ALBERTA PEATLAND. Canadian Journal of Soil Science 68: 755−761. https://doi.org/10.4141/cjss88-073

Lin C, Yang Y, Guo J, Chen G, Xie J (2011) Fine root decomposition of evergreen broadleaved and coniferous tree species in mid-subtropical China: dynamics of dry mass, nutrient and organic fractions. Plant and Soil 338: 311−327. https://doi.org/10.1007/s11104-010-0547-3

Linkosalmi M, Lohila A, Biasi C (2023) Stronger negative priming effect and lower basal respiration rates in nutrient-poor as compared to nutrient-rich forestry-drained peatland. Rapid Communications in Mass Spectrometry 37, article id 9540. https://doi.org/10.1002/rcm.9540

Ludovici KH, Kress LW (2006) Decomposition and nutrient release from fresh and dried pine roots under two fertilizer regimes. Canadian Journal of Forest Research 36: 105−111. https://doi.org/10.1139/x05-227

Luo D, Cheng R, Shi Z, Wang W (2017) Decomposition of Leaves and Fine Roots in Three Subtropical Plantations in China Affected by Litter Substrate Quality and Soil Microbial Community. Forests 8, article id 412. https://doi.org/10.3390/f8110412

Makkonen K, Helmisaari H-S (1999) Assessing fine-root biomass and production in a Scots pine stand–comparison of soil core and root ingrowth core methods. Plant and Soil 210: 43−50. https://doi.org/10.1023/A:1004629212604

Mao R, Zeng D-H, Li L-J (2011) Fresh root decomposition pattern of two contrasting tree species from temperate agroforestry systems: effects of root diameter and nitrogen enrichment of soil. Plant and Soil 347: 115−123. https://doi.org/10.1007/s11104-011-0830-y

McCormack ML, Adams TS, Smithwick EAH, 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

Mendez-Millan M, Dignac MF, Rumpel C, Rasse DP, Derenne S (2010) Molecular dynamics of shoot vs. root biomarkers in an agricultural soil estimated by natural abundance ^{13}C labelling. Soil Biology and Biochemistry 42: 169−177. https://doi.org/10.1016/j.soilbio.2009.10.010

Milchunas DG (2009) Estimating Root Production: Comparison of 11 Methods in Shortgrass Steppe and Review of Biases. Ecosystems 12: 1381−1402. https://doi.org/10.1007/s10021-009-9295-8

Milchunas DG (2012) Biases and errors associated with different root production methods and their effects on field estimates of belowground net primary production. In: Mancuso S (ed) Measuring Roots: An Updated Approach. Springer Berlin Heidelberg, pp 303–339. https://doi.org/10.1007/978-3-642-22067-8_16

Moore TR, Trofymow JA, Prescott CE, Titus BD (2017) Can short-term litter-bag measurements predict long-term decomposition in northern forests? Plant and Soil 416: 419−426. https://doi.org/10.1007/s11104-017-3228-7

Moore TR, Trofymow JA, Siltanen M, Kozak LM (2008) Litter decomposition and nitrogen and phosphorus dynamics in peatlands and uplands over 12 years in central Canada. Oecologia 157: 317−325. https://doi.org/10.1007/s00442-008-1076-0

Moore TR, Trofymow JA, Siltanen M, Prescott C, Group CW (2005) Patterns of decomposition and carbon, nitrogen, and phosphorus dynamics of litter in upland forest and peatland sites in central Canada. Canadian Journal of Forest Research 35: 133−142. https://doi.org/10.1139/x04-149

Murphy M, Laiho R, Moore TR (2009a) Effects of Water Table Drawdown on Root Production and Aboveground Biomass in a Boreal Bog. Ecosystems 12: 1268−1282. https://doi.org/10.1007/s10021-009-9283-z

Murphy MT, McKinley A, Moore TR (2009b) Variations in above- and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland. Botany 87: 845−853. https://doi.org/10.1139/b09-052

Murphy MT, Moore TR (2010) Linking root production to aboveground plant characteristics and water table in a temperate bog. Plant and Soil 336: 219−231. https://doi.org/10.1007/s11104-010-0468-1

Nadelhoffer KJ (2000) The potential effects of nitrogen deposition on fine-root production in forest ecosystems. New Phytologist 147: 131−139. https://doi.org/10.1046/j.1469-8137.2000.00677.x

Ojanen P, Lehtonen A, Heikkinen J, Penttilä T, Minkkinen K (2014) Soil CO_2 balance and its uncertainty in forestry-drained peatlands in Finland. Forest Ecology and Management 325: 60−73. https://doi.org/10.1016/j.foreco.2014.03.049

Ojanen P, Minkkinen K, Alm J, Penttilä T (2010) Soil–atmosphere CO_2, CH_4 and N_2O fluxes in boreal forestry-drained peatlands. Forest Ecology and Management 260: 411−421. https://doi.org/10.1016/j.foreco.2010.04.036

Ojanen P, Minkkinen K, Penttilä T (2013) The current greenhouse gas impact of forestry-drained boreal peatlands. Forest Ecology and Management 289: 201−208. https://doi.org/10.1016/j.foreco.2012.10.008

Olson JS (1963) Energy Storage and the Balance of Producers and Decomposers in Ecological Systems. Ecology 44: 322−331. https://doi.org/10.2307/1932179

Paavilainen E (1966) On the effect of drainage on root systems of Scots Pine on peat soils. Communicationes Instituti Forestalis Fenniae 61: 100−110. [in Finnish]

Page SE, Rieley JO, Banks CJ (2011) Global and regional importance of the tropical peatland carbon pool. Global Change Biology 17: 798−818. https://doi.org/https://doi.org/10.1111/j.1365-2486.2010.02279.x

Päivänen J, Hånell B (2012). Peatland ecology and forestry–a sound approach. Helsingin yliopiston metsätieteiden laitos, Helsinki

Peltoniemi K, Fritze H, Laiho R (2009) Response of fungal and actinobacterial communities to water-level drawdown in boreal peatland sites. Soil Biology and Biochemistry 41: 1902−1914. https://doi.org/10.1016/j.soilbio.2009.06.018

Pohjanmies T, Genikova N, Hotanen JP, Ilvesniemi H, Kryshen A, Moshnikov S, Oksanen J, Salemaa M, Tikhonova E, Tonteri T, Merilä P (2021) Site types revisited: Comparison of traditional Russian and Finnish classification systems for European boreal forests. Applied Vegetation Science 24, article id 12525. https://doi.org/10.1111/avsc.12525

Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002) Fine root architecture of nine North American trees. Ecological Monographs 72: 293−309. https://doi.org/10.1890/0012-9615(2002)072[0293:FRAONN]2.0.CO;2

Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220: 66−74. https://doi.org/10.1016/j.foreco.2005.08.005

Proctor C, He Y (2019) Quantifying wetland plant vertical root distribution for estimating the Interface with the anoxic zone. Plant and Soil 440: 381−398. https://doi.org/10.1007/s11104-019-04079-w

Rasse DP (2002) Nitrogen deposition and atmospheric CO_2 interactions on fine root dynamics in temperate forests: a theoretical model analysis. Global Change Biology 8: 486−503. https://doi.org/10.1046/j.1365-2486.2002.00481.x

Rasse DP, Rumpel C, Dignac M-F (2005) Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. Plant and Soil 269: 341−356. https://doi.org/10.1007/s11104-004-0907-y

Reader RJ, Stewart JM (1972) The Relationship Between Net Primary Production and Accumulation for a Peatland in Southeastern Manitoba. Ecology 53: 1024−1037. https://doi.org/10.2307/1935415

Richert M, Dietrich O, Koppisch D, Roth S (2000) The Influence of Rewetting on Vegetation Development and Decomposition in a Degraded Fen. Restoration Ecology 8: 186−195. https://doi.org/10.1046/j.1526-100x.2000.80026.x

Roumet C, Picon-Cochard C, Dawson LA, Joffre R, Mayes R, Blanchard A, Brewer MJ (2006) Quantifying species composition in root mixtures using two methods: near-infrared reflectance spectroscopy and plant wax markers. New Phytologist 170: 631−638. https://doi.org/10.1111/j.1469-8137.2006.01698.x

Ruseckas J (2000) Root abundance of pine, spruce, birch and black Alder in the peat soils. Balt For 6: 10−15.

Saarinen T (1996) Biomass and production of two vascular plants in a boreal mesotrophic fen. Canadian Journal of Botany 74: 934−938. https://doi.org/10.1139/b96-116

Saarinen T (1998) Demography of Carex rostrata in a boreal mesotrophic fen: shoot dynamics and biomass development. Annales Botanici Fennici 35: 203−209.

Sanaullah M, Chabbi A, Leifeld J, Bardoux G, Billou D, Rumpel C (2011) Decomposition and stabilization of root litter in top- and subsoil horizons: what is the difference? Plant and Soil 338: 127−141. https://doi.org/10.1007/s11104-010-0554-4

Sariyildiz T (2015) Effects of tree species and topography on fine and small root decomposition rates of three common tree species (Alnus glutinosa, Picea orientalis and Pinus sylvestris) in Turkey. Forest Ecology and Management 335: 71−86. https://doi.org/10.1016/j.foreco.2014.09.030

Sarkkola S, Hökkä H, Laiho R, Päivänen J, Penttilä T (2005) Stand structural dynamics on drained peatlands dominated by Scots pine. Forest Ecology and Management 206: 135−152. https://doi.org/10.1016/j.foreco.2004.10.064

Scheffer RA, Aerts R (2000) Root decomposition and soil nutrient and carbon cycling in two temperate fen ecosystems. Oikos 91: 541−549. https://doi.org/10.1034/j.1600-0706.2000.910316.x

Schenk HJ, Jackson RB (2002) THE GLOBAL BIOGEOGRAPHY OF ROOTS. Ecological Monographs 72: 311−328. https://doi.org/https://doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2

Schmidt MWI, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DAC, Nannipieri P, Rasse DP, Weiner S, Trumbore SE (2011) Persistence of soil organic matter as an ecosystem property. Nature 478: 49−56. https://doi.org/10.1038/nature10386

Schulze ED, Freibauer A (2005) Carbon unlocked from soils. Nature 437: 205−206. https://doi.org/10.1038/437205a

See CR, Luke Mccormack M, Hobbie SE, Flores-Moreno H, Silver WL, Kennedy PG (2019) Global patterns in fine root decomposition: climate, chemistry, mycorrhizal association and woodiness. Ecology Letters 22: 946−953. https://doi.org/10.1111/ele.13248

Silvan N, Laiho R, Vasander H (2000) Changes in mesofauna abundance in peat soils drained for forestry. Forest Ecology and Management 133: 127−133. https://doi.org/10.1016/s0378-1127(99)00303-5

Silver WL, Miya RK (2001) Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129: 407−419. https://doi.org/10.1007/s004420100740

Sjörs H (1991) Phyto-and necromass above and below ground in a fen. Ecography 14: 208−218. https://doi.org/10.1111/j.1600-0587.1991.tb00654.x

Smith SW, Woodin SJ, Pakeman RJ, Johnson D, Van Der Wal R (2014) Root traits predict decomposition across a landscape-scale grazing experiment. New Phytologist 203: 851−862. https://doi.org/10.1111/nph.12845

Steinweg JM, Kostka JE, Hanson PJ, Schadt CW (2018) Temperature sensitivity of extracellular enzymes differs with peat depth but not with season in an ombrotrophic bog. Soil Biology and Biochemistry 125: 244−250. https://doi.org/10.1016/j.soilbio.2018.07.001

Straková P, Anttila J, Spetz P, Kitunen V, Tapanila T, Laiho R (2010) Litter quality and its response to water level drawdown in boreal peatlands at plant species and community level. Plant and Soil 335: 501−520. https://doi.org/10.1007/s11104-010-0447-6

Straková P, Larmola T, Andrés J, Ilola N, Launiainen P, Edwards K, Minkkinen K, Laiho R (2020) Quantification of Plant Root Species Composition in Peatlands Using FTIR Spectroscopy. Frontiers in Plant Science 11, article id 597. https://doi.org/10.3389/fpls.2020.00597

Straková P, Penttilä T, Laine J, Laiho R (2012) Disentangling direct and indirect effects of water table drawdown on above- and belowground plant litter decomposition: consequences for accumulation of organic matter in boreal peatlands. Global Change Biology 18: 322−335. https://doi.org/10.1111/j.1365-2486.2011.02503.x

Sun T, Dong L, Wang Z, Lü X, Mao Z (2016) Effects of long-term nitrogen deposition on fine root decomposition and its extracellular enzyme activities in temperate forests. Soil Biology and Biochemistry 93: 50−59. https://doi.org/10.1016/j.soilbio.2015.10.023

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. Proceedings of the National Academy of Sciences 115: 10392−10397. https://doi.org/10.1073/pnas.1716595115

Sun T, Mao Z, Dong L, Hou L, Song Y, Wang X (2013) Further evidence for slow decomposition of very fine roots using two methods: litterbags and intact cores. Plant and Soil 366: 633−646. https://doi.org/10.1007/s11104-012-1457-3

Thomas FM, Molitor F, Werner W (2014) Lignin and cellulose concentrations in roots of Douglas fir and European beech of different diameter classes and soil depths. Trees 28: 309−315. https://doi.org/10.1007/s00468-013-0937-2

Thormann MN, Bayley SE, Currah RS (2001) Comparison of decomposition of belowground and aboveground plant litters in peatlands of boreal Alberta, Canada. Canadian Journal of Botany-Revue Canadienne De Botanique 79: 9−22. https://doi.org/10.1139/b00-138

Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camiré C, Duschene L, Kozak L, Kranabetter M, Visser S (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Canadian Journal of Forest Research 32: 789−804. https://doi.org/10.1139/x01-117

Uri V, Kukumägi M, Aosaar J, Varik M, Becker H, Morozov G, Karoles K (2017) Ecosystems carbon budgets of differently aged downy birch stands growing on well-drained peatlands. Forest Ecology and Management 399: 82−93. https://doi.org/10.1016/j.foreco.2017.05.023

Usman S, Singh SP, Rawat YS, Bargali SS (2000) Fine root decomposition and nitrogen mineralisation patterns in Quercus leucotrichophora and Pinus roxburghii forests in central Himalaya. Forest Ecology and Management 131: 191−199. https://doi.org/10.1016/s0378-1127(99)00213-3

Vasander H, Laiho R, Laine J (2018). Changes in Species Diversity in Peatlands Drained for Forestry. Routledge, pp. 109−119. https://doi.org/10.1201/9780203745380-9

Wang C, Bond-Lamberty B, Gower ST (2003) Carbon distribution of a well-and poorly-drained black spruce fire chronosequence. Global Change Biology 9: 1066−1079. https://doi.org/10.1046/j.1365-2486.2003.00645.x

Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81: 3464−3478. https://doi.org/10.2307/177507

Westman CJ, Laiho R (2003) Nutrient dynamics of drained peatland forests. Biogeochemistry 63: 269−298. https://doi.org/10.1023/a:1023348806857

Wieder RK (2006) Primary production in boreal peatlands. In: Wieder RK, Vitt DH (eds) Boreal Peatland Ecosystems. Springer, Berlin, pp 145–164. https://doi.org/10.1007/978-3-540-31913-9_8

Wieder RK, Lang GE (1982) A Critique of the Analytical Methods Used in Examining Decomposition Data Obtained From Litter Bags. Ecology 63(6): 1636−1642. https://doi.org/10.2307/1940104

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 Phytologist 208: 715−726. https://doi.org/10.1111/nph.13494

Xu J, Morris PJ, Liu J, Holden J (2018) PEATMAP: Refining estimates of global peatland distribution based on a meta-analysis. CATENA 160: 134−140. https://doi.org/10.1016/j.catena.2017.09.010

Yan W, Wang Y, Ju P, Huang X, Chen H (2022) Water level regulates the rhizosphere priming effect on SOM decomposition of peatland soil. Rhizosphere 21, article id 100455. https://doi.org/10.1016/j.rhisph.2021.100455

Yu ZC (2012) Northern peatland carbon stocks and dynamics: a review. Biogeosciences 9: 4071−4085. https://doi.org/10.5194/bg-9-4071-2012

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. Critical Reviews in Plant Sciences 29: 204−221. https://doi.org/10.1080/07352689.2010.483579

Yuan ZY, Chen HYH (2012) Fine root dynamics with stand development in the boreal forest. Functional Ecology 26: 991−998. https://doi.org/10.1111/j.1365-2435.2012.02007.x

Zhang C-B, Chen L-H, Jiang J (2014) Why fine tree roots are stronger than thicker roots: The role of cellulose and lignin in relation to slope stability. Geomorphology 206: 196−202. https://doi.org/10.1016/j.geomorph.2013.09.024

Zhang X, Wang W (2015) The decomposition of fine and coarse roots: their global patterns and controlling factors. Scientific Reports 5, article id 9940. https://doi.org/10.1038/srep09940