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Ingrowth core method in determining fine-root biomass production in boreal peatlands

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Academic dissertation

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ABSTRACT

Fine roots constitute a major pathway of carbon input to soils in many ecosystems, including boreal peatlands. However, accurate quantification of fine-root biomass production (FRBP) remains challenging, with substantial uncertainties arising from methodological limitations and limited understanding of root dynamics across peatland types and along hydrological and climatic gradients. This thesis aims to derive robust annual FRBP estimates in boreal peatlands using ingrowth core method and to refine its protocols.

Field experiments were conducted in drained bog and fen forests, and in undrained southern and northern sedge fens along environmental gradients. A modified ingrowth core method with small-diameter cores and a novel corer-installer was applied to minimize disturbance. FRBP was estimated using three methods—ingrowth-dividing (ID), ingrowth-subtracting with negative values adjusted to zero (IS-I) and ingrowth-subtracting without adjustment (IS-II)—under two biomass calculations: total root biomass ($FRBP_{TotalRB}$) and decomposition-corrected biomass ($FRBP_{DecCorr}$). Peat and inorganic substrates (glass or plastic) were tested to facilitate root separation from cores in sedge fens, and infrared spectroscopy (IRS) was evaluated for estimating FRBP directly from unseparated cores.

Across sites and methods, one-year incubations generally produced lower $FRBP_{TotalRB}$ estimates (71−215 g m^{-2} yr^{-1}) than two- and three-year incubations (93−913 g m^{-2} yr^{-1}), reflecting early root colonization. $FRBP_{TotalRB}$ estimates tended to plateau after approximately two years, indicating that a two-year incubation period is sufficient to capture root colonization and production dynamics. Decomposition correction improved $FRBP_{DecCorr}$ estimates mainly in sedge fens with high mortality rates. The ID method combined with the $FRBP_{TotalRB}$ approach, and a two-year incubation yielded the most robust estimates. Peat-filled cores produced higher FRBP than inorganic substrates, although crushed glass performed comparably under wet conditions. IRS models yielded high coefficient of determination (0.72–0.83) and low prediction error (5–8 %).

Overall, this thesis provides a practical and scalable framework for quantifying FRBP, improving assessment of peatland carbon dynamics.

Keywords: experimental warming, ingrowth core incubation period, infrared spectroscopy, organic matter accumulation, water-level drawdown

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LIST OF ORIGINAL ARTICLES

The thesis is based on the following research articles which are referred to in the text by Roman numerals I–IV. Articles I. II and III are reprinted with the kind permission of the publishers or with rights retained as author. Article IV is a submitted version of the manuscript.

I. Laiho, R., Bhuiyan, R., Straková, P., Mäkiranta, P., Badorek, T., Penttilä, T. (2014) Modified ingrowth core method plus infrared calibration models for estimating fine root production in peatlands. Plant Soil 385, 311–327. https://doi.org/10.1007/s11104-014-2225-3.

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

III. Bhuiyan, R., Mäkiranta, P., Straková, P., Fritze, H., Minkkinen, K., Penttilä, T., Rajala, T., Tuittila, E.S., 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, 159683. https://doi.org/10.1016/j.scitotenv.2022.159683.

IV. Bhuiyan, R., Mäkiranta, P., Straková, P., Fritze, H., Tuittila, E.S., Laiho, R. How to estimate annual fine-root biomass production in boreal sedge fens from ingrowth-core data? Manuscript submitted to Mires and Peat.

AUTHOR'S CONTRIBUTION

Md. Rabbil Bhuiyan is fully responsible for the summary of this doctoral thesis. He was the first author in articles II, III and IV, and was the second author in article I.

I In article I, Md. Rabbil Bhuiyan contributed to the processing of the ingrowth cores, preparing the fine-root biomass data for drained bog and fen forests, preparing the infrared spectroscopic data for calibration models and contributed to reviewing and revising the manuscript. Raija Laiho was the lead author and was responsible for methodology, data collection and data analysis. Petra Straková designed and supervised the infrared spectral analyses, contributing the final calibration models and related results.

II In article II, Md. Rabbil Bhuiyan contributed to investigation and methodology, processed the cores, identified the roots, analyzed the data, interpreted the results, and wrote the original draft.

III In article III, Md. Rabbil Bhuiyan contributed to investigation and methodology, analyzed the data, interpreted the results, and wrote the original draft.

IV In article IV, Md. Rabbil Bhuiyan originated, planned and conceptualized the study, designed the methodology, conducted analysis, interpreted the results, wrote the original draft and was the lead and corresponding author.

LIST OF TERMS AND ABBREVIATIONS

FRB	fine-root biomass
FRBP	fine-root biomass production
$FRBP_{TotalRB}$	fine-root biomass production based on total root biomass (living + dead) accumulated in cores
$FRBP_{DecCorr}$	fine-root biomass production adjusted for the mass lost from dead root decomposition
NPP	net primary production
IG	ingrowth core
IRS	infrared spectroscopy
ID	ingrowth-dividing
WL	water level
IS	ingrowth-subtracting
IS-I	ingrowth-subtracting method with negative biomass differences adjusted to zero
IS-II	ingrowth-subtracting method retaining negative biomass differences without adjustment
WLD	water level drawdown
OTC	open top chamber
OM	organic matter
PFT	plant functional type

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1 INTRODUCTION

1.1 Background

Peatlands are carbon-rich ecosystems where organic matter accumulates as peat due to slow decomposition facilitated by waterlogged, anoxic conditions. The peat deposits in these ecosystems are estimated to store 545−1055 gigatons (Pg) of carbon (Gorham 1991; Yu 2012; Nichols and Pettet 2019), representing roughly one-third of the world's soil carbon pool (IPCC 1996c; Turunen et al. 2002; Tarnocai 2006; Tarnocai et al. 2009). This unique carbon accumulation potential—derived largely from the partially decomposed plant materials such as roots, rhizomes, *Sphagnum* mosses, and microbial and faunal litter—makes peatlands key players in global carbon cycling and climate feedback (Gorham 1991; Yu 2012).

While *Sphagnum* mosses are often regarded as the principal drivers of peat accumulation, vascular plant roots also play a major role in certain peatland types—particularly sedge-dominated fens—where belowground input from roots can equal or even exceed those from mosses (e.g. Schwieger et al. 2021). Fine roots—typically defined as those with a diameter of ≤ 2mm (Gill and Jackson 2000; Hendricks et al. 2006; Finér et al. 2007; Yuan and Chen 2010; Osawa and Aizawa 2012; Li et al. 2013)—play a critical role in belowground carbon dynamics in terrestrial ecosystems. Fine roots have both direct and indirect impacts on soil carbon cycling. Directly, they increase soil carbon with biomass production and turnover as the roots grow and die. Indirectly, they release root exudates and when decomposing they stimulate microbial activity and enhance transformation of organic matter into soil organic matter (SOM) pools. Together, these pathways make fine roots a major source of labile (easily decomposable) carbon in the soil (Ruess et al. 2003; Read et al. 2004; Kalyn and Rees 2006; Addo-Danso et al. 2016; Wang et al. 2020a). Globally, fine-root biomass production (FBRP) accounts for approximately 22−33% of total annual net primary production (NPP) in most terrestrial ecosystems (Jackson et al. 1997; McCormack et al. 2015). In boreal peatlands, this proportion may be even higher—ranging from 25−90% depending on peatland types (Backéus 1990; Saarinen 1996, 1998; Weltzin et al. 2000; Wieder 2006; Clemmensen et al. 2013; Mäkiranta et al. 2018; Kyaschenko et al. 2019). Quantifying of FRBP is essential for understanding ecosystem function, and for improving carbon-cycle models. This is particularly critical in boreal peatlands, where root dynamics are closely linked to land-use driven hydrological changes and climate variability.

In future the climate change may result in stronger warming in the northern regions (boreal and sub-arctic zones) where peatlands are widespread (Bintanja et al. 2011; Kjellström et al. 2018; IPCC 2021). Higher temperature and altered hydrology may substantially affect the function of these ecosystems. Observed and projected changes in ecosystem function include increased root growth and turnover (Weltzin et al. 2003; Sullivan et al. 2008; Murphy et al. 2009; Iversen et al. 2015; Mäkiranta et al. 2018), enhanced decomposition of organic matter including roots (Straková et al. 2012), vegetation shifts from herbaceous to shrub and tree species (Berg et al. 2009; Kokkonen et al. 2019) and deeper carbon input allocation through roots (Murphy et al. 2009a; Keuper et al. 2012; Proctor and He 2019).

However, the effect of these changes remains uncertain, as it depends on many interacting factors including vegetation composition, hydrology, site-specific conditions (e.g. nutrient status), and the balance between biomass production and decomposition. While many studies have focused on aboveground responses to climate change, research on FRBP under changing environmental conditions remains limited largely because of methodological challenges of measuring fine roots in-situ. Most existing studies are short-term or conducted in controlled environments like mesocosms (Weltzin et al. 2000, 2001; Bridgham et al. 2008), which may not reflect long-term field dynamics. Since ecosystems may take time to adjust to warming treatments—generally requiring over a year for measurable changes (Updegraff et al. 2001; Wiedermann et al. 2007)—long-term, in-situ studies are essential for advancing the understanding of belowground responses, particularly FRBP in peatland ecosystems under a changing climate.

1.2 Evaluating methods for estimating FRBP

Over the past several decades, numerous experimental approaches have been adopted to estimate FRBP in different ecosystems. The experiments include direct and often destructive sampling methods such as ingrowth cores (Finér et al. 1997; Ostonen et al. 2005), sequential coring (Makkonen and Helmisaari 1999; Ostonen et al. 2005), direct but non-destructive methods like minirhizotrons (Hendrick and Pregitzer 1993; Majdi and Őhrvik 2004), root scanners (Dannoura et al. 2008), indirect methods such as radiocarbon (^{13}C, ^{14}C) method (Gaudinski et al. 2001; Majdi et al. 2005), N budget method (Aber et al. 1985; Nadelhoffer et al. 1985), C budget method (Raich and Nadelhoffer 1989). FRBP has been estimated also by using empirical models (Kurz et al. 1996). A comprehensive overview of these methods can be found in the reviews by Vogt et al. (1998), Smit et al. (2000) and Addo-Danso et al. (2016).

Among all methods, sequential soil coring, ingrowth core and minirhizotron are the three most commonly used methods for measuring FRBP in natural ecosystems. All these methods have both advantages and disadvantages (Santantonio and Grace 1987; Vogt et al. 1998; Majdi et al. 2005; Hendricks et al. 2006; Milchunas 2012). Several studies have attempted to synthesize and compare existing methods for FRBP, but inconsistencies in FRBP estimates persist, with no consensus on the best approach of estimating FRBP (e.g. Addo-Danso et al. 2016; Freschet et al. 2020). Consequently, method selection often depends on multiple factors including cost, labor intensity, time constraints, site-specific limitations (e.g. peat versus mineral soils), the root size (fine versus coarse roots), research objectives (e.g. carbon fluxes, carbon pool versus productivity relationships), and even researcher preference (Vogt et al. 1998; Smit et al. 2000; Levillain et al. 2011; Makita et al. 2011; Freschet et al. 2020). These considerations often outweigh methodological refinements, such as minimizing method-specific uncertainty or improving efficiency through reduced labor and processing time.

Sequential soil coring, a traditional method for estimating FRBP from temporal changes in fine-root biomass, may lead to both under- and over-estimation (Lauenroth 2000; Milchunas and Lauenroth 2001; Milchunas 2009, 2012), as the method relies on the unrealistic assumption that root production and mortality do not occur simultaneously (Hertel & Leuschner 2002, Milchunas 2012). The method is also both labor- and time-intensive as it requires many cores to produce good estimates, limiting its use for large-scale inventories. Minirhizotrons enable continuous observation of fine root growth and death (e.g. Johnson et

al. 2001; Andersson and Majdi 2005; Iversen et al. 2012, 2018), but its application is restricted by equipment cost, laborious image processing despite automation advances (Hendrick and Pregitzer 1996; Godbold et al. 2007; Rewald et al. 2020) and potential installation artifacts such as root severing that alter water, temperature, and rooting environment at the tube-soil interface (Johnson et al. 2001; Withington et al. 2003). The method further requires conversion factors and additional spatial data to obtain area-based FRBP estimates. These challenges make it impractical for large-scale applications.

Ingrowth core (IG) method is the most widely adopted method to estimate FRBP (Oliveria et al. 2000; Milchunas 2009, 2012; Arndal et al. 2018; He et al. 2023; Lampela et al. 2023; Karim et al. 2025) due to its cost-effectiveness, simple field implementation, and straightforward interpretation. The method involves inserting mesh cores filled with root-free soil into pre-drilled holes, allowing new roots to be produced inside the cores during an incubation period. The harvested roots provide a direct measure of new root biomass production, making IG particularly suitable for large-scale peatland inventories, where alternative methods are impractical. Despite these advantages, the IG method is not without limitations (reviewed in Vogt et al. 1998; Majdi et al. 2005; Hendricks et al. 2006; Li et al. 2013; Milchunas 2012). Underestimations can occur due to soil disturbance during installation or the use of substrates poorer in growth resources than the surrounding soils (Steele et al. 1997; Vogt et al. 1998; Lukac and Godbold 2001; Ostonen et al. 2005; Hendricks et al. 2006; Milchunas 2009, 2012). Overestimation may result when the inserted substrate offers more favorable rooting conditions than the ambient soil, or when root proliferation is stimulated by severing existing roots (Vogt et al. 1998; Fahey et al. 1999; Lauenroth 2000; Oliveira et al. 2000; Steingrobe et al. 2000).

While all methods of estimating FRBP have some sorts of limitations and biases—and no method provides a definitive absolute value—the IG method was chosen for this study, because at the time of planning (and arguably still today), it was the only method that could be used in larger-scale FRBP inventories in peatlands. A key focus of this study was to evaluate how incubation length and calculation approaches within the IG method influence potential biases related to root colonization, spatial heterogeneity and root decomposition.

1.3 Enhancing the ingrowth core method for peatland conditions

1.3.1 Methodological modifications

Several modifications to the ingrowth core (IG) method have been proposed to address its limitations, under various names, such as the mesh screen (Fahey and Hughes 1994), root inclusion net (Lukac and Godbold 2010) or net/mesh method (Godbold et al. 2003; Montagnoli et al. 2007; Hirano et al. 2009; Jentschke et al. 2001). However, these approaches still involve cutting existing roots for instance, inserting slits to place the mesh—which may artificially stimulate root growth (Hirano et al. 2009). While some level of disturbance is unavoidable when studying FRBP, structural modifications to the core design can help minimize artifacts. Studies have shown that reducing core diameter and increasing incubation time can reduce installation effects and improve root colonization (Lukac and Godbold 2001; Hertel and Leuschner 2002; Li et al. 2013). Also important is the choice of substrate, as cores filled with materials poorer or richer in nutrients than the surrounding soil may lead to under- or over-estimation of production (Steingrobe et al. 2000).

In practice, it is not possible to create a root-free substrate completely identical to undisturbed soil. As a result, researchers must choose among different substrate materials to fill the ingrowth cores. In mineral soils, soil extracted from study sites is often reused after root removal, sometimes even maintaining the original sequence of soil horizons during packing cores. However, in peatlands this approach may be less feasible because root separation is challenging in peat composed of plant remains at various stages of decay (Sjörs 1991). This difficulty is particularly pronounced in sedge peat, which consists largely of fine root remains, making it especially hard to distinguish living roots from decomposing material. As an alternative, commercially available, non-fertilized horticultural peat has often been used as a standard substrate. In minerotrophic peatlands, particularly those with sedge dominance, plants often receive nutrients from the in-flowing water (Anderson et al. 1996; Saarinen 1996). In these systems, root colonization may be less dependent on organic substrate quality and more influenced by external nutrient supply than in ombrotrophic bogs. In this context, an inert inorganic substrate e.g. crushed glass or plastic granule could potentially be used as the substrate in ingrowth cores. These materials offer several advantages: they are chemically stable, non-degradable, reusable, and facilitate rapid and clear separation of newly produced roots from the substrate. However, it needs to be tested whether root production patterns in inert inorganic substrates match those observed in peat.

Another important yet often overlooked consideration in applying the IG method is sampling depth. Many studies focus predominantly on the upper soil layers, particularly the top 0–20 cm, where fine root density is typically highest (Jackson et al. 1996; Finér and Laine 2000; Yuan and Chen 2010; Finér et al. 2011). The limited attention to the deeper layer may lead to significant underestimation of total FRBP in ecosystems where deeper rooting occurs. Particularly, in sedge-dominated fens, sedge fine roots may extend well beyond 1 m (Saarinen 1996, 1998). Moreover, climate- or land-use-driven water-level drawdown may promote deeper rooting as plants seek more favorable moisture and nutrient conditions (Iversen et al. 2012; Murphy et al. 2009). Reaching reliable estimates therefore require sampling to a depth sufficient for capturing the full depth distribution of roots in the particular sites rather than assuming roots are concentrated near the surface (Bledsoe et al. 1999; Oliveira et al. 2000). While deep sampling may be physically difficult in stony soils (Park et al. 2007), it is relatively easy in peat soil.

1.3.2 Approaches for calculating FRBP from ingrowth core data

Several methods exist for calculating FRBP, most of which were originally developed for sequential soil coring that involves repeated sampling at regular intervals—typically monthly—over an extended period (e.g. Finér and Laine 1998). Common calculation methods include the Maximum-Minimum method (McClaugherty et al. 1982), Decision Matrix method (Fairley and Alexander 1985), and Compartment Flow method (Santantonio and Grace 1987), all of which rely on temporal changes in living and/or dead root biomass. In contrast, the IG method does not require repeated sampling within the same year, making it a practical option for estimating annual FRBP and can potentially be developed for reducing labor and time requirements. Nevertheless, in tropical systems, shorter incubation periods or multiple measurements per year have been applied when using IG method (Katayama 2019). For one-year incubation period with IG method, FRBP is generally calculated from the total biomass accumulated in the core during that period (Vogt et al. 1998; Brassard et al. 2011). Yet, a one-year incubation period primarily captures the production of new roots colonizing the cores, reflecting the regenerative potential of the root

system after disturbance rather than actual FRBP in undisturbed conditions (Cudlín and Chmelíková 1999; Finér and Laine 2000). With longer incubation periods, the roots within the cores in principle tend to develop more mature and natural structures, including branching and radial growth. This raises an important question: how should annual and steady-state FRBP be estimated from multi-year ingrowth-core data? Annual FRBP estimation becomes more complex over multi-year periods because fine roots grow and die continuously during the growing season. For incubation periods of 2−4 years, determining an appropriate incubation duration for a standardized FRBP estimate is critical. In the literature, the annual production from multi-year ingrowth biomass data has been calculated using several approaches: (i) the differential approach (tracking changes in biomass over time, similar to the Decision Matrix), (ii) the dividing approach (dividing the total biomass by the number of incubation years; e.g. Yuan and Chen 2012), and (iii) the mean biomass approach (mean biomass of ingrowth cores; e.g. Hendricks et al. 2006).

Among available approaches, the Decision Matrix method—also known as the balancing transfer method—is the most widely used, but it relies on several assumptions. These include considering only statistically significant biomass changes (e.g. Stober et al. 2000), setting negative biomass changes to zero (Osawa and Aizawa 2012; Yuan and Chen 2013; Van Do et al. 2016), or discarding them entirely from estimates (Fairley and Alexander, 1985; Finér and Laine 1998). While living root biomass in the soil (or soil core) can decrease between two sampling occasions, root growth itself cannot be negative. However, in practice negative biomass changes may occur because of high spatial variability in FRBP estimates. Excluding these negative values or converting them to zero introduces bias and therefore, they should be retained in the dataset to ensure accurate estimates.

Several refinements have been proposed, including: the Compartment Flow model, which integrates biomass, mortality, and decay coefficients (Santantonio and Grace 1987); the Dynamic Flow model, which accounts for declining decay rates (Li and Lang 2015); the Continuous Inflow method, which uses root litter bags to estimate decay rates (Osawa and Aizawa 2012); the Balance Hybrid model, which combines soil coring and minirhizotrons (Li et al. 2020a); and the Simplified Decision Matrix, which applies logical loops to improve estimates (Yuan and Chen 2013). Despite these advances, no method fully resolves uncertainties because none simultaneously capture all components of root dynamics—growth, death, and decay. Negative biomass changes, while ecologically meaningful (Sala et al. 1988), are inconsistently treated across studies, limiting comparability. Though increasing the number of replicates and shortening sampling intervals—typically monthly—can minimize errors associated with negative production estimates, but this approach is primarily suited to sequential coring. In contrast, for the ingrowth core method such adjustments may not be feasible—especially in slow-growing ecosystems such as boreal peatlands, where sampling intervals typically span a year. Therefore, developing alternative approaches for calculating FRBP with ingrowth-core data is essential to reduce the risk of potential biases introduced by these underlying assumptions.

1.3.3 Improving FRBP estimation by integrating IG methods

To enhance the accuracy of FRBP estimates, combining multiple methods is increasingly recommended. For example, soil coring combined with minirhizotrons (Hendrick and Pregitzer 1993; Hendricks et al. 2006; Addo-Danso et al. 2016; Li et al. 2020a), or ingrowth cores combined with minirhizotrons or scanners (Van Do et al. 2016) provide a more comprehensive view of root dynamics. Infrared spectroscopy (IRS) characterizes root

samples based on molecular signatures (i.e. presence, character or abundance) of chemical bonds in the 4000–400 cm^{-1} wavenumber range (reviewed by Rewald and Meinen 2013). When combined with a calibration dataset with known root composition and corresponding infrared (IR) spectra, it can predict mass proportion of roots in the unseparated cores (peat + root) based solely on their IR spectra. IRS has been successfully applied to identify and quantify species composition in root mixtures of forest tree species (Lei and Bauhus 2010; Domisch et al. 2015; Tong et al, 2016; Finér et al. 2017) and to differentiate living roots from dead roots in forage species (Roumet et al. 2006; Picon-Cochard et al. 2009). Recently, this method has been applied in peatlands to identify and quantify plant root species composition, demonstrating its potential for estimating the chemical composition of root material (Straková et al. 2020). If root and peat chemical bond compositions differ from each other sufficiently, it might be possible to use IRS to analyze the proportion of roots in peat directly without manual separation, which would be a great time-saving innovation. While no single technique suffices across the ecosystems, combining ingrowth cores with imaging or spectroscopic approaches may represent a promising direction for advancing root research in peatlands.

2 AIMS OF THE STUDY

The starting point for this research was the ingrowth core method as presented in Paper **I**. The overall aim of this study was to improve the methodological protocol of ingrowth core method to obtain 'best estimates' of fine-root biomass production (FBRP) in different kinds of boreal peatlands (**Figure 1**). The 'best estimate' here is defined to be as **robust** and **resource efficient** estimates. A robust estimate has minimal inter-annual (temporal) variation under the assumption that the actual *in situ* FRBP does not vary greatly from year to year and inexplicably during the study period. A resource efficient estimate has the shortest incubation period possible, thereby saving time and cost.

The study comprises three peer-reviewed articles and one manuscript addressing the following specific aims:

1. To quantify fine-root biomass production (FRBP) estimates in different kinds of peatland types dominated by both arboreal (trees and shrubs) and herbaceous (sedges and forbs) plant communities (**II**, **III**).
2. To determine annual FRBP estimates, by quantifying the appropriate ingrowth core incubation period and developing an approach for calculating robust FRBP estimates from multi-year ingrowth core biomass data in boreal peatlands (**II, IV**).
3. To investigate whether inert inorganic materials (e.g. crushed glass or plastic granule), can replace peat as core substrate in FRBP estimation, thereby facilitating fast separation of roots from the cores (**I**).
4. To test whether an IRS-based calibration model can predict FRBP directly from unseparated ingrowth core samples, reducing the need for manual separation of roots (**I**).
5. To assess to which depth the ingrowth cores should extend to for accurate total FRBP estimates in different peatland types (**II**, **III**).
6. To evaluate the effects of experimental warming and water-level drawdown (WLD) on FRBP in sedge-dominated fens (**III**).

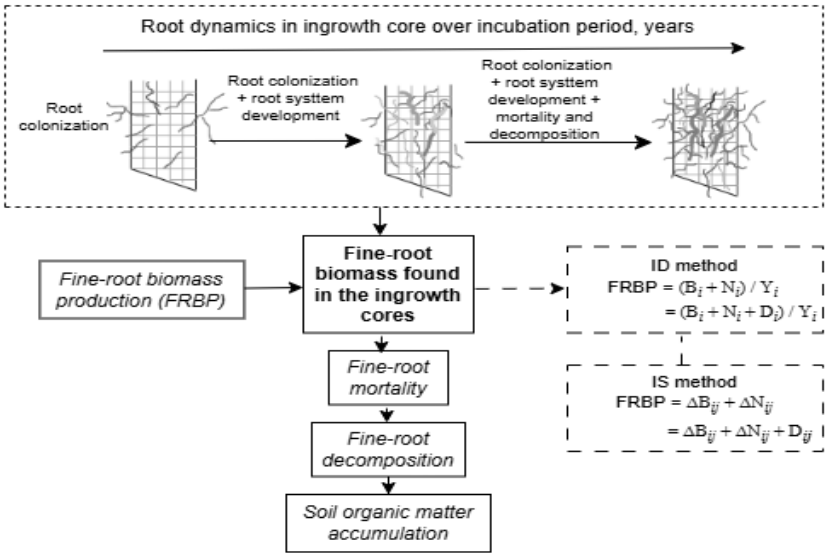


Figure 1 Schematic compartment model illustrating the fine-root biomass pools (**bold**) and fluxes (*italics*) examined in this thesis using the ingrowth core method in boreal peatland ecosystems. The upper dashed panel outlines the conceptual sequence of root colonization, root system development, mortality and decomposition within ingrowth cores over one- to three-year incubation periods (from left to right). Fine-root biomass production (FRBP) was calculated using ingrowth-dividing (ID) and ingrowth-subtracting (IS) methods as shown on the right. B_i and N_i denote living fine-root biomass and dead fine-root mass at the end of incubation period *i*, respectively. ΔB_{ij} and ΔN_{ij} represent changes in living fine-root biomass and dead fine-root mass at the end of incubation periods *i* and *j* (*j* > *i*), respectively. D_i denotes the mass of dead roots decomposed by the end of incubation period *i*, and D_{ij} the decomposed mass at the end of incubation periods *i* and *j*. Y denotes the incubation period length (years).

3 MATERIALS AND METHODS

3.1 Study sites

The research was conducted in four peatland sites in Finland, including two drained peatland forests and two minerotrophic sedge fens. The selected sites represent a range of hydrological and vegetative conditions found in boreal and sub-arctic peatlands. A brief description of each site is provided below; some basic site characteristics are presented in **Table 1**.

Drained peatland forests

The drained bog forest site (**I**, **II**) was located at Kalevansuo in Loppi, southern Finland (60°39'N, 24°22'E). The site was originally an ombrotrophic bog dominated by dwarf-shrubs

and Scots pine (*Pinus sylvestris* L.). It was classified as a dwarf-shrub pine bog before drainage, and as dwarf-shrub type I drained peatland forest at the time of this study (Laine and Vasander 1996; Laine et al. 2018). The site was drained for forestry in 1971 using open ditches approximately 1 m deep and spaced 40 m apart. Phosphorus-potassium (PK) fertilization was carried out soon after the drainage. Hereafter, the site is referred to as a 'drained bog forest'. During this study the site was characterized by a Scots pine dominated stand with scattered downy birch (*Betula pubescens* Roth) and Norway spruce (*Picea abies* (L.) H. Karst.) (Lohila et al. 2011). The ground vegetation comprised typical forest and mire dwarf shrubs (e.g. *Vaccinium myrtillus* L., *V. vitis-idaea* L., *V. uliginosum* L., *Ledum palustre* L.), with *Eriophorum vaginatum* L. and *Rubus chamaemorus* L. species. The bottom layer (moss layer) was dominated by *Pleurozium schreberi* Mitt., *Dicranum polysetum* Sw., *Sphagnum angustifolium* Russow, and *S. russowii* Warnst.

The drained fen forest site (**I**, **II**) was located at Lettosuo in Tammela, southern Finland (60°39'N, 23°57'E), approximately 22 km west of Kalevansuo. It was originally (before drainage) classified as herb-rich tall sedge birch-pine fen (Laine and Vasander 1996; Laine et al. 2018). The site was drained in 1969 with open ditches spaced 40 m apart followed by PK fertilization. By the time of this study, the site had transitioned to a *Vaccinium myrtillus* type II drained peatland forest (Laine and Vasander 1996; Laine et al. 2018). Hereafter, the site is referred to as 'drained fen forest'. The stand was dominated by Scots pine, with co-dominant downy birch and Norway spruce forming a vigorous understorey. The understorey was diverse but less dense than in drained bog forest, featuring several herb species such as *Dryopteris carthusiana* Vill. and *Trientalis europaea* L., in addition to species common to the drained bog forest.

Sedge fens

The southern sedge fen site (**I**, **III**, **IV**) was located at Lakkasuo in Orivesi, southern Finland (61°48' N 24°19' E) and hence referred to as the 'southern fen'. The site was a wet minerotrophic sedge fen, dominated by several sedges such as *Carex lasiocarpa* Ehrh., *C. chordorrhiza* L.f. and *C. limosa* L., Additionally, some dwarf shrubs such as *Andromeda polifolia* L., *Betula nana* L., and *Vaccinium oxycoccos* L., as well as a few forbs like *Menyanthes trifoliata* L. were present. The moss layer consisted mainly of *Sphagnum papillosum* Lindb. and *S. flexuosum* Dozy & Molk, with smaller patches of *S. fallax* H. Klinggr., *S. subfulvum* Sjörs and *S. subnitens* Russow & Warnst.

The northern sedge fen site (**III**, **IV**) was located at Lompolojänkkä in Kittilä, northern Finland (68°N, 24°12'E) and hence referred to as the 'northern fen'. Like the southern fen, the northern fen featured a wet, minerotrophic sedge fen dominated by sedges, especially *Carex rostrata* Stokes, and dwarf shrubs such as *Andromeda polifolia* L. and *Vaccinium oxycoccos* L., with *V. oxycoccos* L. being more abundant than in the southern fen. However, the northern fen lies in high-latitude and represents the climatic conditions characteristic of the sub-arctic zone (cold winters, short cool summers), making it important contrast to the southern site within the boreal zone. The herbs in that site included *Menyanthes trifoliata* L. and *Comarum palustre* L. as well as *Equisetum fluviatile* L. The moss layer was patchier than at the southern fen and dominated by *Sphagnum fallax, S. riparium* Angstr., *S. flexuosum*, and *S. jensenii* H. Lindb.

In both sedge fens, a split-plot experimental design was applied to evaluate the effects of warming and water-level drawdown (WLD) on FRBP as well as on root litter decomposition.

Table 1 Basic characteristics of the study sites. Soil bulk density (BD, g cm^{-3}), element concentrations (mg g^{-1}) and C:N ratio are average for 0−20 cm layer in drained bog and fen forests. The corresponding values for sedge fens are average of 5−25 cm layer (obtained from Peltoniemi et al. 2015) except the BD and N values that are measured in this study prior to the start of experiment. In sedge fens, Wet is the ambient control plot, Dry is the water-level drawdown plot and OTC (Open Top Chamber) is the warming plot. The plant cover is projection in % measured after the experimental period in drained peatland forests and those in sedge fens are obtained from Mäkiranta et al. (2018). The stand basal area in the forested sites which is sum of tree stem areas measured at 1.3 m (m^2 ha^{-1}) separately for Scots pine (*Pinus sylvestris* L.), downy birch (*Betula pubescens* Ehrh.) and Norway spruce (*Picea abies* L.). WT represents the mean water-table level in cm below the surface during the growing seasons (May−October/November).

Site	Types	BD	Ca	Fe	Mg	N	P	K	C:N	Plant cover (%)				Stand basal area (m^2 ha^{-1})			WT (cm)
										Sedge	Forb	Shrub	Moss	Pine	Birch	Spruce	
Kalevansuo	Drained bog forest	0.093				14	0.56	0.31	36.0		< 1	30	95	17.6	0.7	< 0.1	38.4
Lettosuo	Drained fen forest	0.162				23	0.79	0.23	24.5		10	5	50	17.4	6.1	4.5	52.4
Lakkasuo	Wet-OTC sedge fen		4.62	10.31	0.50		0.88	0.34	19.2	18	18	8	88				
Lakkasuo (slightly drained)	Wet sedge fen	0.072	5.27	12.74	0.55	24	0.73	0.42	22.0	15	14	8	98				7.0
	Dry-OTC sedge fen		5.11	10.65	0.51		0.89	0.29	19.4	15	4	26	65				
	Dry sedge fen	0.087	5.12	10.47	0.57	25	0.88	0.42	18.7	12	5	17	81				14.2
Lompolojänkkä	Wet-OTC sedge fen		6.13	5.08	1.23		0.86	0.50	29.7	37	8	11	67				
Lompolojänkkä (slightly drained)	Wet sedge fen		5.23	5.25	1.05	17	0.99	0.86	28.0	23	4	11	60				7.5
	Dry-OTC sedge fen		6.22	3.97	0.97		0.87	0.26	24.8	15	0	26	79				
	Dry sedge fen		6.07	4.95	0.93	20	0.89	0.29	25.8	10	0	23	78				8.8

The design involved two distinct water-level (WL) regimes: a wet regime, where the natural (ambient) water level was maintained, and a dry regime (WLD), where the water level was artificially lowered. WLD had been implemented by digging shallow ditches (25–30 cm deep) around the plots during May−June 2008. Warming was achieved using passive heating through hexagonal open-top chambers (OTCs) (Marion et al. 1997; Hollister and Webber 2000). The OTCs were constructed from clear plastic sheets, 60 cm tall and each side panel was 76 cm long at the bottom (maximum diagonal distance of 131 cm). The panels were inclined at 60° angle to improve the transmittance of solar radiation and help trap heat and were placed on 10 cm tall supports to allow ventilation of the air space and minimize disturbance to the soil surface. During the growing seasons (May−October), OTCs increased daily air temperature 1.4° and 2° C on an average within the subplot at 15 cm above the peat surface in the northern and southern fen, respectively. Within each WL regime, three pairs of subplots were established. In each pair, one subplot was kept at ambient temperature (control), while the other was exposed to OTC-based warming. Temperatures were monitored using automatic data loggers (Maxim iButtons), which record data every two hours from the air (15 cm above the *Sphagnum* moss surface) and from the soil at depths of 5 cm and 15 cm. Water-level fluctuations in both wet and dry plots were tracked using water table loggers (Intech WT-HR data logger).

3.2 Modifications to the ingrowth core method

The modification of the ingrowth core method was developed based on its previous application within the same research framework (Murphy et al. 2009). Since ingrowth cores provide an initially root-free and therefore unnatural growth environment within the peat, the method assumes that any disturbance from installation and differences between the core substrate and natural peat have negligible effects on FRBP estimates. However, in practice core installation often causes significant disturbances, such as cutting through and removing portions of the existing root systems (Nakahata and Osawa 2017), which may introduce uncertainties in the biomass production estimates (Milchunas 2009). Furthermore, traditional corer designs are usually cumbersome and time-consuming as the procedure requires pre-digging holes by extracting long soil cores before placing and filling the mesh bags (Oliveria et al. 2000; Hirano et al. 2009). These limitations make the traditional corer less practical for extensive studies that require large number of samples.

In this study, a novel two-piece corer-installer was designed for installing small-diameter ingrowth cores, with the primary aim of minimizing disturbance to existing root systems. A smaller-diameter core may have a reduced volume of root-free, competition-free substrate, which likely exerts less influence on root growth dynamics and shortens delays in core colonization (Hertel and Leuschner 2002; Li et al. 2013). A diameter of 3.2 cm corer was used in this study, considerably smaller than the larger diameter (≥ 8 mm) commonly employed in previous studies (Murphy et al. 2009; Lukac and Godbold 2010). The corer consists of an inner and outer tube (**Figure 2**). The inner tube features a closed, sharp end that pushes through the peat rather than cutting it, thereby preserving the integrity of surrounding roots and soil. Since peat predominantly consists of organic matter (Price and Schlotzhauer 1999) and both peat and root systems exhibit flexibility—adapting to fluctuations in water and gas content (Päivänen 1973; Price 2003; Kellner et al. 2005; Waddington et al. 2010; Kettridge et al. 2013)—this structural adjustment allows the creation of small-diameter holes without causing major damage to existing roots. Ideally, the cores

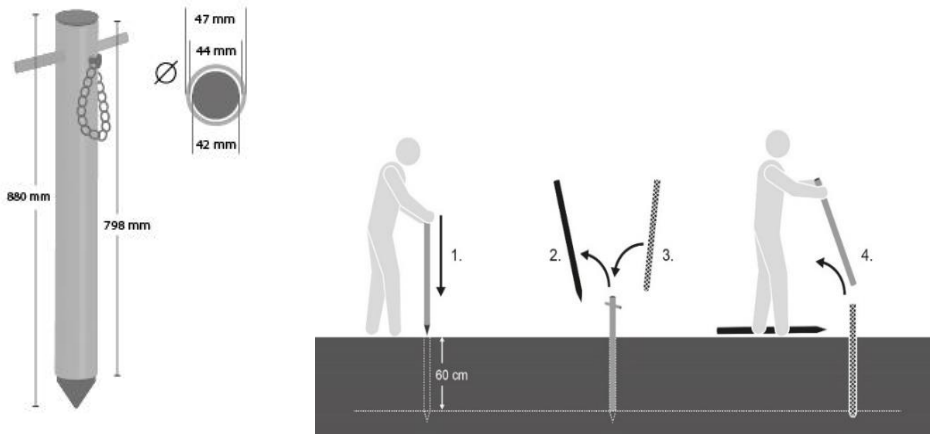


Figure 2 Corer-installer design and application (**I**). The inner tube (darker gray) and outer tube (lighter gray) are linked by a lock (black). The inner tube featured with a closed and sharp end, pushes into the ground to create the hole (1), minimizing disturbance by pushing rather than cutting through the soil. The flexibility and low density of peat soil facilitate this process. Upon reaching the desired depth (here 60 cm), the lock is released, and the inner tube is pulled out (2). The hollow outer tube remains in place, allowing the pre-filled core to drop into the hole (3). The diameter of the cores (32 mm) is chosen so that the core falls freely, but when the outer tube is pulled out (4), the displaced soil closes in tightly around the core. The corer-installer (left) was prepared by Anne Siika, and the core installation sequence (right) was prepared by Jouni Hyvärinen.

are installed in late autumn, after root growth has ceased for the year, allowing them to settle in the soil before root growth resumes in the following spring.

During installation, once the desired depth is reached, the lock connecting the inner and outer tubes is released, and the inner tube is removed. This leaves the hollow outer tube in place, which allows the pre-filled ingrowth-core to be inserted directly into the hole (as illustrated stepwise in **Figure 2**). The outer tube has an inner diameter of 44 mm (4.4 cm), while the inner tube is slightly smaller at 42 mm (4.2 cm). The ingrowth-cores themselves were designed with a diameter of 32 mm (3.2 cm) to fit freely within the space. Previous studies have shown that smaller core sizes significantly reduce disturbance to roots and their surrounding environment (Lukac and Godbold 2001). The displaced peat naturally closes around the core due to its organic and flexible nature. These peat properties are advantageous, and the cores can be pushed into the peat with limited disruption —unlike in ecosystems with dry mineral soils, where cores may become locked in place and tear during retrieval. In cases where the peat surface was dry, the soil around the core was gently compressed to ensure proper closure of core.

3.3 Laboratory and field work

3.3.1 Ingrowth core preparation and installation

The ingrowth cores were constructed using flexible polyester mesh fabric with an approximate mesh size of 1 mm x 1 mm. The effective lengths of the cores were 50 cm for drained peatland forests (**I**, **II**) and 60 cm for sedge fens (**III**, **IV**). Each core included an additional short unfilled section (2–3 cm) extending aboveground to facilitate location after incubation, as well as at the lower end (**Figure 2**). These sections were not planned to be included in the effective length of the core. The top of each core was tightly sealed with a rubber band above the substrate surface. Cores were filled with four substrate types: two peat types and two types of inorganic materials. The inorganic substrates were used in the sedge fen only (**I**). Peat substrates were selected to closely resemble the soil quality of the recipient sites and were free of living roots. To ensure consistency and practicality, peat substrates were chosen based on homogeneity, availability, and cost-effectiveness. *Sphagnum* and *Carex* peats were used, as most of the peat in the boreal zone originate predominantly from these genera, often mixed with other constituents. For the drained bog forest, which was dominated by *Sphagnum* moss derived peat, non-fertilized horticultural *Sphagnum* peat was used. For the drained fen forest and sedge fens, characterized by *Carex* dominated peat, sedge peat harvested for energy use was selected. The sedge peat was sourced from deep horizons to exclude the presence of fresh root remains. The inorganic substrates consisted of crushed glass (average particle diameter of 0.8 cm), and polyethylene granules (diameter of 0.3 mm), commonly used in the plastic industry. These inorganic materials were chosen based on their ease of root separation, accessibility and affordability.

The ingrowth cores were installed for one-, two- and three-year incubation periods during late autumn. At each of the two forested peatland sites (**I, II**), a total of sixty cores were installed, 20 for each incubation period. In the drained bog forest, cores were installed in October 2009, whereas in the drained fen forest, installation was delayed until early May 2010, just before the growing season as early soil frost prevented installation during preceding autumn. The cores recovered in November 2010, 2011, and 2012, respectively. In the sedge fens (**III, IV**), the split-plot experimental design was followed (as described earlier in site description). Within each water-level treatment (wet and dry), two replicate cores were installed in each subplot in October 2010. This resulted in 36 cores per water-level regime (12 for each of the incubation periods) and 72 cores in total across both regimes and sites. Of these, half were subjected to ambient conditions (no temperature manipulation), while the remaining half received artificial warming using open-top chambers (OTC). The cores recovered in October 2011, 2012, and 2013 respectively.

3.3.2 Post-recovery root processing

Upon field recovery, the ingrowth cores were transported to the laboratory and stored in freezer until further processing. To prevent decomposition following thawing, only one to two ingrowth cores were defrosted overnight at a time. The effective length of each core was determined by excluding the uppermost and lowermost 2–3 cm sections, which were typically irregular and not fully circular. Each core was then cut into 10-cm segments and any roots found outward of core segment were trimmed along the exterior surface to isolate only those that had grown inside the cores. The actual diameter of each core was also measured at the time of retrieval rather than assuming the initial theoretical diameter of 3.18 cm, to account for potential expansion of the cores due to dry condition of the fresh peat substrate compared to field peat.

In drained bog and fen forests, all roots found inside the cores were sorted by living and dead roots as well as by tree species and understory functional group. Dead roots were

identified based on a combination of visual and tactile characteristics, such as color, elasticity, toughness, and the appearance of phloem tissue (Table 3, in article **II**). In sedge fens, root materials were not separated by living and dead roots due to practical limitations. Instead, all roots—including living and dead roots, as well as occasional rhizomes—were collected and gently washed with water to remove any adhering soil particles. Cleaned roots were oven-dried at 30 °C to a constant mass and weighed. Fine-root biomass (FRB) was calculated as the biomass of dry roots divided by the actual surface area of the peat core when recovered.

3.3.3 Litterbag installation

To estimate the sedge root mass loss over a two-year incubation period, the litterbag method (Straková et al. 2012) was applied in the sedge fens (**III**) following the split-plot experimental design described earlier for the FRBP study. The *Carex* root litter was collected from whole sedge plant grown in containers, air-dried at 20 °C, and placed into litterbags with a known initial dry mass. Six litterbags were installed within the 0−30 cm soil profile at each WL treatment plot (wet and dry) during September−October 2009. In total, twelve litterbags per site were installed annually across both WL regimes. Within each regime, three litterbags were installed under ambient conditions and three under OTC warming treatment. Litterbags were retrieved annually over a two-year incubation period. After each retrieval, the litterbags were transported to the laboratory, where root materials were gently cleaned to remove adhering soil and any newly ingrown roots. The root contents were then air-dried at room temperature and weighed to determine the remaining dry mass. Further details on litter preparation and installation procedures are provided in Article **III**.

To estimate the accumulation of organic matter in the soil and to evaluate the relative contribution of sedge fine-root litter versus above-ground plant litter, a simple short-term simulation was conducted using production and decomposition values. The simulation assumed that standing biomass of each plant component remained constant over the two-year simulation period, meaning that annual biomass production was equal to litter input. Annual fine-root inputs were represented by the FRBP 'best estimate', while above-ground production values for sedges and mosses were obtained from Mäkiranta et al. (2018). Each litter component was then allowed to decompose at the measured rates.

Total organic matter accumulation (OM_{accu}) was calculated based on litter input (L) and decomposition (D) as shown in Equation 1:

$$OM_{accu} = ((L - L \times D_1) - (L - L \times D_1) \times D_2) + (L - L \times D_1) \quad (1)$$

where L is the annual litter input (g m^{-2} yr^{-1}), equal to biomass production, and D_1 and D_2 are the mass loss rates (%) after the first and second year of incubation, respectively.

3.4 Procedures for calculating FRBP with ingrowth core data

Fine-root biomass (FRB) measured in ingrowth cores after incubation was used to calculate annual fine-root biomass production (FRBP). FRBP was expressed as annual values in g m^{-2} yr^{-1}, enabling direct comparison across different ingrowth-core incubation periods (**II**, **IV**). Two primary methods were used to calculate FRBP: ingrowth-dividing (ID) method and ingrowth-subtracting (IS) methods, with two variations of the latter such as IS (I)—where

negative biomass changes were adjusted to zero and IS (II)—where negative biomass changes were retained without adjustment. These approaches account for both living and dead roots, as well as root decomposition over time.

3.4.1 Total root biomass vs decomposition-corrected approaches

Both the ID and IS methods included two calculation approaches for estimating FRBP. In the first approach, FRBP was calculated directly from the total root biomass (living + dead) accumulated in the cores during the incubation period and is hereafter referred to as the total root biomass ($FRBP_{TotalRB}$) method. This approach does not account for mass loss due to decomposition of roots that died during incubation period. However, root mortality and decomposition often occur simultaneously during fine root growth (Osawa and Aizawa 2012). In the second approach, FRBP was adjusted for the mass lost from dead root decomposition during the incubation period. This approach is hence referred to as the decomposition-corrected ($FRBP_{DecCorr}$) method. It tests whether accounting for mortality and decomposition significantly alters FRBP estimates compared to the $FRBP_{TotalRB}$ method.

In drained bog and fen forests, dead roots were separated and measured from the ingrowth cores, whereas in sedge fens, dead root mass could not be separated due to practical limitations. For these sites, dead root mass was estimated from total root biomass using an annual root mortality rate of 80%, based on empirical estimates for sedge-dominated peatlands (Bernard and Gorham 1978; Bernard and Fiala 1986). To obtain decomposition-corrected FRBP estimates, an annual decomposition rate of 30%—based on the mass remaining after one year of fine-root decomposition obtained from Strakova et al. (2012)—was applied to the drained bog and fen forest sites. In the sedge fens, decomposition rates of *Carex rostrata* roots were derived from litterbag experiments conducted at the same sites (**III**). Mean decomposition rates from one- and two-year litterbag incubations across WL and temperature regimes (Fig. 7 in **III**; with no significant treatment differences) were applied to calculate $FRBP_{DecCorr}$ estimates for the two- and three-year ingrowth-core incubation periods. For the one-year ingrowth core incubation period, decomposition adjustment was not applied, assuming that new roots primarily colonize root-free space and rarely die during this initial phase.

3.4.2 Ingrowth-subtracting method

The ingrowth-subtracting (IS) method calculates FRBP based on the changes in root biomass between consecutive incubation periods and conceptually similar to the 'Decision matrix' approach used in earlier studies (Fairley and Alexander 1985; Osawa and Aizawa 2012). Using the total root biomass approach, FRBP estimates between incubation periods *i* and *j*, denoted as $FRBP_{IS,(i,j),TotalRB}$, was calculated as the sum of change in living fine-root biomass ($\Delta B_{ij,}$ g m^{-2}) and the change in dead root mass or necromass ($\Delta N_{ij,}$ g m^{-2}), as shown in Equation 2:

$$FRBP_{IS,(i,j),TotalRB} = \Delta B_{ij} + \Delta N_{ij} \quad (2)$$

The changes in living root biomass and dead root mass were defined as:

$$\Delta B_{ij} = B_j - B_i \quad (3)$$

$$\Delta N_{ij} = N_j \neg N_i \quad (4)$$

where B_i and B_j represent living fine-root biomass, and N_i and N_j are the dead root mass at the end of incubation periods *i* and *j*, respectively (*j* > *i*).

The decomposition-corrected FRBP estimate, denoted as $FRBP_{IS,(i,j),DecCorr}$, was obtained by adding the estimated mass of dead roots lost through decomposition (D_{ij}) to the total biomass estimate as expressed in Equation 5:

$$FRBP_{IS,(i,j),DecCorr} = \Delta B_{ij} + \Delta N_{ij} + D_{ij} \quad (5)$$

where D_{ij} (g m^{-2}) is the decomposed dead fine root mass occurring between the end of incubation periods *i* and *j* and calculated as in Equation 6:

$$D_{ij} = N_{ij} \times d_{ij} \quad (6)$$

where d_{ij} is the decomposition rate of dead root mass at the end of incubation periods *i* and *j*. The values of d_{ij} were determined using the litter bag method and calculated according to Equation 7:

$$d_{ij} = (\text{initial mass} - \text{remaining mass})/(\text{initial mass}) \quad (7)$$

Both the total root biomass and the decomposition-corrected approaches were applied within two variants of the IS method: IS (I), in which negative biomass changes were set to zero, and IS (II), in which negative values were retains in the calculation.

3.4.3 Ingrowth-dividing method

The ingrowth-dividing (ID) method calculates FRBP by dividing the accumulated root biomass in ingrowth core by the length of the incubation period. Annual FRBP based on the total root biomass approach and the ID method, denoted as $FRBP_{ID,(i),TotalRB}$, was calculated by dividing the sum of living root (B_i) and dead root (N_i) masses that accumulated in the core during the incubation period *i* by the duration of that incubation period (Y_i, years), where *i* represents the number of incubation period (1–3 years), as expressed in Equation 8:

$$FRBP_{ID,(i),TotalRB} = (B_i + N_i) \ / \ Y_i, \text{ where } i \geq 1 \quad (8)$$

To obtain the decomposition-corrected FRBP estimates, denoted as $FRBP_{ID,(i),DecCorr}$, the estimated mass of dead fine roots lost through decomposition during incubation period *i* (D_i, g m^{-2}; calculated as in Equation 6) was added to the sum of living fine root ($B_{i,}$ g m^{-2}), dead root ($N_{i,}$ g m^{-2}) masses, which was then divided by the corresponding length of incubation period, Y_i, as shown in Equation 9:

$$FRBP_{ID,(i),DecCorr} = (B_i + N_i + D_i) \ / \ Y_i \quad (9)$$

3.5 Infrared spectroscopy based FRBP estimation without root separation

To build the Infrared Spectroscopy (IRS) calibration models for estimating the mass proportion of roots within ingrowth cores, ten ingrowth cores were selected from both the drained bog and fen forests (**I**). After the manual separation of roots from the cores, the root samples were air-dried and then pulverized into a fine, homogeneous powder using an oscillating ball-mill MM400 (Retsch, Germany). The root-free peat substrate (0–10 cm layer) from each core was pulverized similarly.

Ten peat-root mixtures simulating the original root/peat composition within the ingrowth cores were then prepared for each site. These mixtures matched the root-to-peat mass ratios as determined from the manual separation process. Additionally, ten artificial peat-root mixtures were created for each site, by mixing roots into the peat in concentrations ranging from 0 to 5%, with increments of 0.5%. The 5% upper limit was chosen because root mass generally constituted 5% or less of the total bulk mass in the samples, making this range representative of typical field conditions. In total, 40 mixture samples were thus generated to establish the calibration dataset for the IRS models.

The spectral data for the calibration models were obtained using a Vertex FTIR (Fourier Transform InfraRed) Spectrometer (Bruker Optics, Germany), equipped with a Pike MIRacle ATR (Attenuated Total Reflectance) crystal detector. Using this setup, infrared spectra were directly measured from each root and peat-root mixture sample. The spectra were recorded within the mid-infrared range of 4000–650 cm^{-1} at a resolution of 4 cm^{-1}, as these preliminary analyses showed that this range provided optimal information with minimal noise.

3.6 Data analyses

Differences in FRB between bog and fen forests were assessed using Repeated Measures Analysis of Variance (ANOVA) (**II**), whereas differences between southern and northern sedge fens were analyzed using mixed-effect linear regression models (**III**).

To identify the 'best estimate' of FRBP, variations of FRBP across incubation periods were examined using the Kruskal-Wallis test (a non-parametric one-way ANOVA), followed by post hoc pairwise comparisons, with statistical significance set at $p < 0.05$ (**II**, **IV**). The same procedure was applied to evaluate differences among FRBP calculation methods. A non-parametric approach was selected because the data did not meet the assumptions of normality and homogeneity of variances. Normality was tested with the Shapiro-Wilk test, and homogeneity using Bartlett test.

Differences in substrate performance (**I**) were analyzed using Repeated Measures Analysis of Variance (ANOVA), with substrate treated as the between-subjects (grouping) factor, and root sampling depth as the within-subjects (repeated) factor. IRS calibration models (**I**) were developed using multivariate partial least squares (PLS) regression, where spectral absorbance served as the independent variable and the percentage of in-grown roots relative to total ingrowth core mass (peat plus roots) as the dependent variable. Spectral data were preprocessed using the Savitzky-Golay first derivative to correct baseline shifts and amplitude variation. The dataset was partitioned into 75% for calibration and 25% for validation by systematically removing every fourth sample. Model performance was evaluated using the coefficient of determination (R^2) and root mean square error (RMSE). RMSE was calculated for both calibration (model fit to training data) and prediction

(performance on new data), with values expressed as the percentage of in-grown roots in the total core mass.

Repeated measures analysis of variance (ANOVA) was used to assess FRBP depth distribution patterns in bog and fen forests, while one way ANOVA was applied to assess FRBP depth distribution in sedge fens.

The vertical distribution of sedge roots was also modeled using the asymptotic equation proposed by Gale and Grigal (1987) and Jackson et al. (1996):

$$\gamma = 1 - \beta^d \quad (10)$$

where γ represents the cumulative root fraction from the surface to depth d (cm), and β is the estimated distribution parameter. The β values indicate root depth distribution and range from 0.1 to 1, where higher β values suggest a greater proportion of roots at deeper layer and lower values suggest a shallower root distribution. β was calculated individually for each ingrowth core using SYSTAT software. Then, liner mixed-effect regression models were applied, to analyze the response of depth distribution (in terms of β) to warming and WLD treatments. Linear mixed-effect models were also applied to assess the effects of warming and WLD treatments on total FRBP and root mass loss (Equation 1 in **III**). Fixed effects included drying, warming, site, incubation period, depth distribution (β) and interactions, while subplot (sample plot) was treated as random effect. Model performance was evaluated using the intra-class correlation coefficient (ICC; Table S1 a-e in **III**), along with residuals and random-effects analyses.

The analyses were conducted in R (**II**, **III**, **IV**), IBM SPSS Statistics 22 (**II**), and SYSTAT11 (**I**). Spectral preprocessing and calibration modeling (**I**) were performed in Unscrambler (CAMO, Norway).

4 RESULTS AND DISCUSSION

4.1 Total FRBP estimations across different peatlands

Total fine-root biomass (FRB) quantified from ingrowth cores after an incubation period of 1−3 years, was significantly higher in the fen forest (215−1473 g m^{-2}) than in the bog forest (118−624 g m^{-2}), with variation across incubation periods (Tables 4 and 5 in **II**, $p < 0.001$). Similarly, FRB was greater in the southern fen (118–698 g m^{-2}) than in the northern fen (39–491 g m^{-2}), depending on incubation period and treatment (Table S2a in **III**, $p = 0.001$).

Differences of FRB between forest sites may result from several factors, such as nutrient availability, above-ground biomass and drainage conditions, which were more favorable in the drained fen forest (**I**, **II**). Previous studies have shown that FRB tends to be higher in nutrient-rich than in nutrient-poor sites (Finer and Laine 2000; He et al. 2023), although the opposite pattern has also occasionally been observed in peatlands (Lampela et al. 2023) as well as in mineral soils (Ding et al. 2021), highlighting the complexity of FRB dynamics. In sedge fens (**III, IV**), FRB differences may be attributed to plant community composition—particularly greater forb cover in the southern fen (Mäkiranta et al. 2018)—as well as latitude (temperature regime) and moisture conditions (wetness). A general decline in FRB with increasing latitude has been observed in boreal peatland forests (He et al. 2023) and the

northern fen exhibited a much wetter regime, with an average WLD of 7 cm in the southern fen and 3 cm in the northern fen (Mäkiranta et al. 2018; Peltoniemi et al. 2015).

4.2 Protocol for the 'best estimate' of FRBP

4.2.1 Determining how long to incubate the core?

Across all sites and methods under the simple total root biomass approach, the one-year incubation period consistently resulted in lower $FRBP_{TotalRB}$ estimates than the two-year incubation period—except in the northern sedge fen. At the northern fen, $FRBP_{TotalRB}$ estimates for the one-year incubation were lower than for the three-year incubation. This systematic underestimation during the one-year incubation period likely reflects the early stages of root colonization when ingrowth cores receive primarily new explorative roots (Finér and Laine 2000; Hertel and Leuschner 2002). At this stage, root branching, secondary development and the growth of older, thicker fine roots have not yet fully contributed to the accumulated biomass, resulting in lower FRBP. Compared with the two-year incubation period, $FRBP_{TotalRB}$ estimates declined during the three-year incubation; however, this decrease was not statistically significant for any site or method, with the exception of northern sedge fen (**Figure 3**), particularly in the wet plot (Fig. 1 in **IV**). These results indicate that FRBP inside the ingrowth core levels off after approximately two years of incubation. Thus, a two-year incubation period is long enough to capture well the main phases of root colonization and production. Extending the incubation period beyond two years is unlikely to substantially improve FRBP estimates, although a three-year incubation period may theoretically allow the development of a more mature root system inside the cores that better reflects natural conditions.

In the northern sedge fen—particularly in the wet plot (**IV**)—$FRBP_{TotalRB}$ estimates were similar between the one- and two-year incubation periods with all methods, suggesting that one-year incubation period may be the most time-efficient option in that specific environment. This efficiency in sedge fens is largely due to the rapid colonization of ingrowth cores by sedge roots (Finér and Laine 2000). However, from an ecological point of view, a one-year incubation period may provide conservative estimates, as it primarily involves only the exploration of new roots into the cores and may not capture other production components associated with more mature root systems, such as root branching and radial growth. Longer incubation may also better capture root production at deeper layers, as observed in study **III**, although sedge roots generally persist for only 1–2 years (Gill and Jackson 2000, Sullivan et al. 2007). Notably, $FRBP_{TotalRB}$ values were highest after three-year incubation period in the northern sedge fen, potentially reflecting either delayed root colonization or slower root dynamics in this colder environment, where root lifespans are typically longer (Gill and Jackson 2000, Nadelhoffer 2000). However, this increase in root production may result from random variation rather than a true biological response, since root biomass at this site was extremely low. Overall, a two-year incubation period is generally sufficient for sedge fens similar to the arboreal-dominated peatlands, as it avoids potential initial underestimation and captures full production dynamics while saving time and resources. Nevertheless, site-specific factors such as temperature and hydrology should be taken into account when determining the length of incubation period.

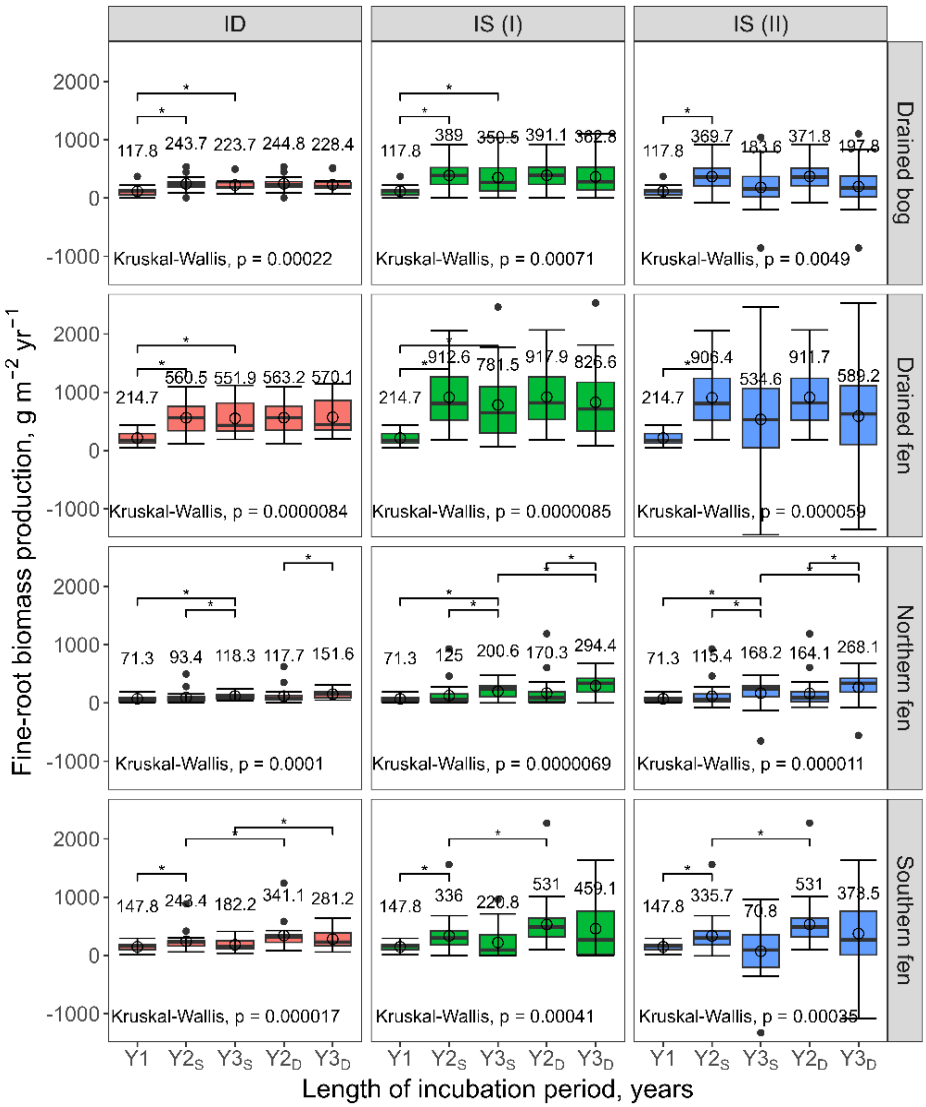


Figure 3 Fine-root biomass production (FRBP) estimates across one-, two- and three-year incubation periods (denoted as Y1, Y2, and Y3 respectively) in different boreal peatland types, calculated using three methods: ingrowth-dividing (ID), ingrowth-subtracting (IS-I) with negative biomass differences adjusted to zero, and ingrowth-subtracting (IS-II) accounting for negative biomass differences in the estimates. The suffix 'S' denotes the simple total root biomass (living + dead) method and 'D' denotes the decomposition-corrected method accounting for estimated mortality and decomposition of dead roots. Box-whisker plots show median, 25- and 75- percentiles and extremes (black dot). Open circles within the boxes are the mean values, which are also displayed with numbers on top of each box. Asterisks indicate significant differences between incubation periods determined using Kruskal-Wallis pairwise test at a significance level of $p < 0.05$.

4.2.2 Accounting for root decomposition in core incubation

At the drained bog and fen sites, incorporating root decomposition during incubation period did not significantly affect $FRBP_{DecCorr}$ estimates compared to those obtained without accounting for root decomposition ($FRBP_{TotalRB}$), regardless of the calculation method. This outcome is attributed to the relatively low root mortality rates observed at these sites (Table 5 in **II**), and the slow decomposition rates reported by Strakova et al. (2012).

In contrast, at the southern sedge fen, where root mortality was higher, accounting for root decomposition significantly increased $FRBP_{DecCorr}$ estimates during the two-year incubation period across all methods. This finding aligns with previous studies showing that excluding root mortality and decomposition can lead to underestimation of FRBP (Osawa and Aizawa 2012; Li et al, 2012; Katayama et al. 2019). However, this effect diminished over the three-year incubation period, except when using the ID method, suggesting that root inputs and losses may reach equilibrium by the end of two-year incubation. At the northern sedge fen, decomposition adjustments had no effect on FRBP estimates during the two-year incubation period, despite applying a higher mortality rate. This may be partially explained by the relatively slow decomposition rates (32–35%) observed at that site (Fig. 7 in **III**). However, the decomposition effects became evident during the three-year incubation period, particularly for the IS methods, indicating potential sensitivity to method choice and temporal variability in root dynamics. This underscores a key limitation of IS approach, as FRB differences between consecutive incubation periods often show high variability, including both large increases in some years and large decreases in others.

Theoretically, the most accurate FRBP estimates are obtained when all three root components—live, dead and decomposed—are considered, as roots may simultaneously grow, die and decompose during multi-year ingrowth core incubations. However, incorporating decomposition adds methodological complexity, especially for IS methods (Table 1 in **IV**) and increases labour and costs. Given that the differences between decomposition-corrected ($FRBP_{DecCorr}$) and total root biomass ($FRBP_{TotalRB}$), estimates are not consistently statistically significant, the simpler total root biomass ($FRBP_{TotalRB}$) approach may be sufficient in certain contexts, particularly where decomposition rates are low. Combining this method with a two-year incubation period may represent a practical and efficient option for large-scale FRBP inventories. Accordingly in the subsequent analyses, the simpler total root biomass ($FRBP_{TotalRB}$) approach has been focused.

4.2.3 Preferred FRBP calculation method – ID or IS?

Across sites, FRBP estimates obtained using the IS methods ($FRBP_{IS,(i,j),TotalRB}$) were generally higher than those from the ID method ($FRBP_{ID,(i),TotalRB}$), although the differences were not statistically significant (data not shown), indicating the applicability of both approaches. The ID method typically produced lower estimates because it includes first-year values in the calculation, which are known underestimates since root requires time to colonize the new space within the cores (e.g. Finér and Laine 2000; Hertel and Leuschner 2002). In contrast, IS methods exclude these underestimated first-year values by calculating differences between the consecutive incubation years rather than averaging across the years, as in the ID method.

The ID method ($FRBP_{ID,(i),TotalRB}$) produced relatively consistent $FRBP_{ID,(i),TotalRB}$ values for the two- and three-year incubation periods at all the sites (**Figure 3**). In contrast, IS methods showed greater fluctuations of $FRBP_{IS,(i,j),TotalRB}$ estimates between incubation

periods, though these differences were not statistically significant. Across sites, the IS methods yielded overall maximum values during the two-year incubation period and minimum values during the three-year period, i.e. 370 and 184 g m^{-2} yr^{-1} in drained bog, 906 and 535 g m^{-2} yr^{-1} in drained fen, 336 and 70 g m^{-2} yr^{-1} in southern fen respectively. The northern fen was an exception, showing increased production potential during the three-year incubation period, likely reflecting site-specific root dynamics. The higher FRBP estimates for two-year incubation period by the IS method likely result from the exclusion of underestimated first-year data, whereas the FRBP estimates for three-year incubation more closely approximated those obtained with the ID method. Overall, the smaller variability in ID estimates across incubation periods suggests that they provide more robust results.

The $FRBP_{IS,(i,j),TotalRB}$ methods also exhibited greater random variations in the FRBP estimates than $FRBP_{ID,(i),TotalRB}$ method. This is due to the use of separate set of ingrowth cores for each incubation period, introducing spatial heterogeneity in FRBP. The IS methods calculate differences between independent core sets, which can sometimes result in negative biomass changes due to random variation. Theoretically, negative production (biomass changes) in ecology cannot exist and can rather be interpreted as mortality. But we can't confirm whether the negative increment in biomass is net mortality, as we did not measure the temporal development in the same core. Including negative biomass differences in the calculation, as in IS(II) method, can bias FRBP estimates by lowering the average values. Conversely, setting negative values to zero, as in IS (I) method, may introduce a net positive bias, resulting in higher average FRBP estimates (Sala et al. 1988). In contrast, the $FRBP_{ID,(i),TotalRB}$ method offers more stable estimates by avoiding negative biomass changes, i.e. method-specific random errors, altogether, though it may underestimate due to the first-year colonization lag. Based on these observations, the ID method ($FRBP_{ID,(i),TotalRB}$) when coupled with a two-year incubation period, may be considered as the most robust and efficient ('best estimate') protocol for estimating annual FRBP. This approach minimizes method-specific random errors and reduces labor and cost. While decomposition correction can enhance accuracy of FRBP estimates, its inclusion is site-specific and time dependent. In particular, peatland ecosystems characterized by rapid root turnover and decay would benefit from incorporating decomposition into FRBP calculations to achieve more accurate estimates.

Several studies recommend using multiple methods at the same sites to validate FRBP estimates (e.g. Ostonen et al. 2005; Hendricks et al. 2006; Gaul et al. 2009). Although this study did not apply additional methods simultaneously to validate the FRBP estimates, results from sequential coring by Finér and Laine (1998) at the southern sedge fen support our findings, yielding comparable FRBP estimates. For the drained bog and fen forests, no independent FRBP estimates were available for direct comparison. However, when comparing fine-root biomass (FRB) in the 0−20 cm soil layer, our estimates were consistent with independent soil coring results reported by Ojanen et al. (2013) for the drained bog forest (Table 9 in **II**). This suggests that our FRBP estimate for the drained bog forest is likely realistic. In contrast, for the drained fen forest, Ojanen et al. (2013) reported higher FRB values than those in our study (Table 9 in **II**), likely due to the inclusion of larger roots (2−50 mm diameter). Overall, the 'best estimate' of annual FRBP of this study ($FRBP_{ID,(i),TotalRB}$) falls well within the range reported in previous studies at peatland ecosystems (**Table 2**).

Table 2 Annual fine-root biomass production (FRBP) estimates derived using the ingrowth core method in boreal peatlands and comparable wetland ecosystems, calculated with different estimation approaches.

Forest type	Country	Core diameter (cm)	Incubation depth (cm)	Incubation period (year)	Calculation approaches	FRBP (g m^{-2} yr^{-1})	Reference
Drained bog forest	Finland	3.2	50	3	best estimate ID method	244	This study
Drained fen forest	Finland	3.2	50	3	best estimate ID method	561	This study
Northern sedge fen	Finland	3.2	60	3	best estimate ID method	93	This study
Southern sedge fen	Finland	3.2	60	3	best estimate ID method	243	This study
Drained bog forest	Finland	8	50–60	1	Total ingrown root	62–78	Murphy et al. 2009
Drained bog peatland	Finland	4.4	20	3	Subtracting method	7–119	Finer and Laine 2000
Drained fen peatland	Finland	4.4	20	3	Subtracting method	29–218	Finer and Laine 2000
Pristine sedge peatland	Finland	4.4	45	3	Subtracting method	141–226	Finer and Laine 2000
Drained bog forest (DsT site)	Finland	3.2	50	2	Dividing method	85	He et al. 2023
Drained fen forest (MT–II site),	Finland	3.2	50	2	Dividing method	234	He et al. 2023
Forested peatland sites	Finland	3.2	50	2	Dividing method	31–120	Lampela et al. 2023
Sedge tundra	Greenland	4.9	25	1	Total ingrown root	90	Sullivan et al. 2007
Sedge-dominated tundra	USA	3.2	15	< 1	Total ingrown root	198–364	Fisk et al. 1998

4.3 Ingrowth core substrate comparisons

FRBP estimates were consistently higher in cores filled with peat than in those filled with inorganic substrates (**Figure 4**, Tables 4 and 5 in **I**). A significant interaction between substrate type and depth was detected, indicating that root depth distribution differed among substrate types. In peat-filled cores, roots were highly concentrated in the uppermost 0−10 cm layer and declined sharply beyond 10 cm depth, reflecting natural root distribution patterns commonly observed in sedge-dominated peatlands (Saarinen 1996, 1998). In contrast, roots in inorganic substrates were more evenly spread with depths and particularly showed low root density in deeper layers. This variation highlights the influence of substrate composition on belowground root biomass allocation.

For total root production in the 0–50 cm layer, both drying and substrate types significantly affected FRBP (not shown). In the wet sedge fen site, total FRBP was comparable between peat and glass, whereas plastic yielded significantly lower values than peat. In the slightly drained sedge site, glass and plastic produced similar total root production, and consistently lower estimates than peat. These patterns suggest that in wet sedge fens, crushed glass may serve as a viable alternative substrate for ingrowth cores, if the only goal is to estimate total root production. However, inorganic substrates generally attracted fewer roots near the surface—likely due to differences in porosity, pore-size distribution, and water-holding capacity. Despite this, they offer a practical advantage: facilitating the easy separation of very fine roots from the substrate, which is otherwise challenging in peat (Sjörs 1991; Finér and Laine 2000). However, if depth distribution of root production is of particular interest, crushed glass may be less suitable. Its large, irregular pores, when water-filled, could alter root distribution patterns, especially in nutrient-rich, water-fed peatlands where roots uptake nutrients from water. Plastic granules performed poorly overall; their lower chemical inertness compared to glass may lead to the release of compounds that inhibit root growth, possibly explaining the suppressed FRBP values observed.

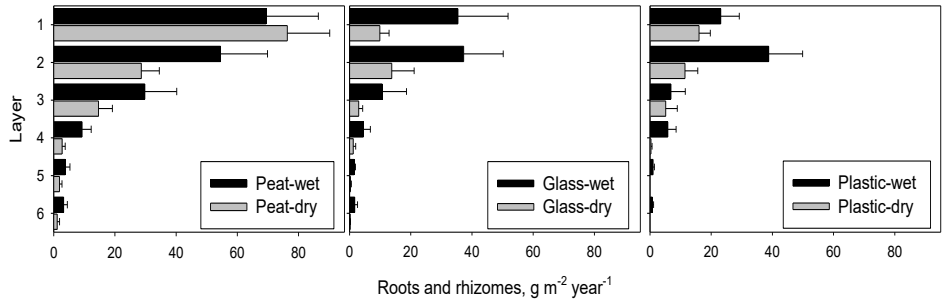


Figure 4 Fine-root biomass production in the wet and slightly drained site conditions in the sedge fen, measured with ingrowth cores filled with: a: peat; b: crushed glass, c: plastic granules. Layer 1: 0–10 cm depth from moss surface; layer 2: 10–20 cm; layer 3: 20–30 cm; layer 4: 30–40 cm; layer 5: 40–50 cm; layer 6: 50–60 cm.

Overall, the choice of substrate type not only affects total root production but also influences vertical root distribution patterns. Peat substrate best preserves the natural rooting environment of sedge fens, whereas inorganic substrates may alter the rooting behavior. However, an important consideration should be given while using commercial peat: the peat should as closely as resemble the recipient site, as studies have demonstrated that nutrient mismatches between core substrates and surrounding soils can significantly affect FRBP (Steingrobe et al. 2000).

4.4 Infrared spectroscopy as an alternative to manual root separation

The infrared spectroscopy (IRS) method proved to be a promising tool for estimating FRBP directly from unseparated ingrowth cores, providing a faster alternative to manual root separation. Site-specific calibration models showed the best predictive performance, with RMSE values of 5.2% for drained bog and 6.7% for drained fen, compared with ≤8.2% in a combined-site model (**Figure 5**). The accuracy of these models was comparable to results obtained in other studies evaluating the mass proportions of plant roots of different species or functional groups (Lei and Bauhus 2010; Tong et al. 2016; Straková et al. 2020; Straková et al. unpublished data).

The lower accuracy of the combined-site model is likely due to the differences in peat substrates between sites. *Sphagnum*-dominated peat in bogs and *Carex*-dominated peat in fens have distinct chemical compositions (Bohlin et al. 1989; Fig. 9 in **I**). Suh chemical variation among species and substrates has been highlighted previously (Straková et al. 2010), underscoring the need for site-specific calibration for reliable root biomass estimation. Nevertheless, even small amounts of site-specific peat appear sufficient for robust calibration at the plant functional type (PFT) level (Straková et al. unpublished data), indicating that only a minor sampling effort needed.

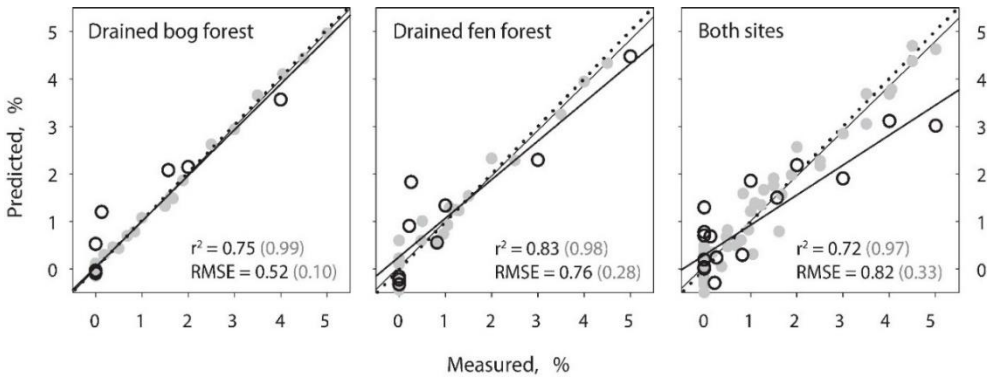


Figure 5 Relationship between the actual mass proportion of roots in the ingrowth cores and the proportion predicted by infrared reflectance spectroscopy (IRS) using partial least squares regression (PLS) calibration. The dotted line represents the 1:1 line. Altogether forty test samples (20 from each site) were used, of those ¾ for calibration (grey circles) and ¼ for validation of model (open circles). The coefficient of variation (r^2) and root mean square error (RMSE) of prediction are shown in black numbers and those for calibration in grey numbers.

When site-specific peat is unavailable, general calibration using *Sphagnum* or *Carex* peat can be effective, as boreal peats are typically dominated by these genera. For example, non-fertilized horticultural *Sphagnum* peat has been successfully applied in bog studies across Finland, the UK, and Canada (Straková et al. unpublished data). While species within these genera may exhibit some chemical differences, their substrates are relatively homogenous than those of other plant groups (Straková et al. 2010).

Although this study tested IRS calibration on a limited dataset from two Finnish sites, subsequent research has demonstrated its broader applicability. Straková et al. (2020) showed that FTIR (Fourier Transform InfraRed) calibration models developed from samples of Finnish site can be successfully applied to quantify the roots of PFT across sites in Canada, Czechia, Sweden, and the UK. Building on these findings, Straková et al. (unpublished data) applied FTIR models to estimate total and PFT-specific root proportions in unseparated ingrowth cores and simulated samples and found that these models could be effectively applied across distant peatland sites such as those in Sweden, the UK, and Canada. These findings highlight the potential of IRS for root studies across diverse geographic and ecological contexts.

4.5 Root distribution pattern by depth

Fine-root biomass production (FRBP) declined significantly with depth across drained bog and fen sites (**Figure 6**, Table 6 in **II**) and in sedge fens (**Figure 6**, significance results not shown). In bog and fen forests, 82% and 76% of total production, respectively, occurred within the upper 0−20 cm soil layer, which aligns with previous findings in boreal peatlands (Murphy and Moore 2010; He et al. 2023; Lampela et al. 2023; Karim et al. 2025).

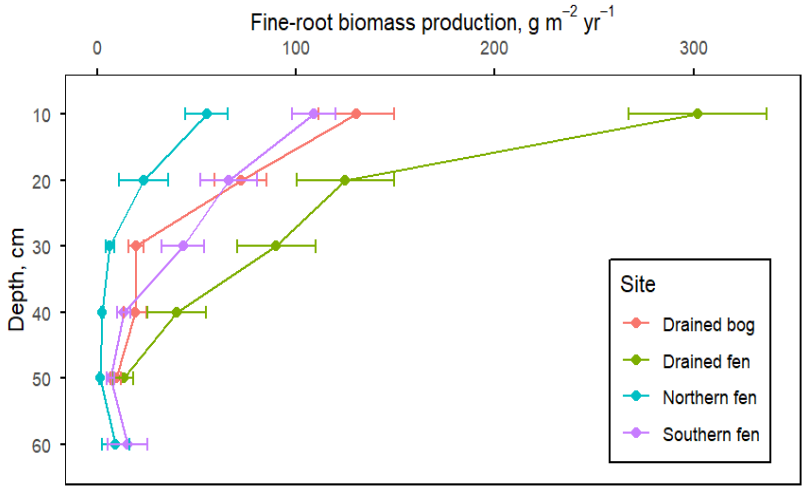


Figure 6 Vertical distribution of fine-root biomass production (FRBP, g m^{-2} yr^{-1}) based on ingrowth-dividing and two-year incubation period estimates ('best estimate') in different peatland types. The bar indicates the standard error of the mean.

In sedge fens—particularly in the southern site—root distribution extended deeper, with 69% of FRBP in the upper 20 cm and the remaining 31% occurring in the 30−60 cm layer. The estimated β parameter values further supported this pattern, showing higher values (0.91−0.94) for southern fen compared to the northern fen (0.81−0.93), indicating greater deep-root allocation at the southern fen (Fig. 4 in **III**).

At the species level in forested sites, Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and shrubs concentrated root production near the surface in both drained bog and fen forests (Fig. 3 in **II**), while downy birch (*Betula pubescens*) showed this pattern only in fen forest. Birch roots were scarce in bog forest and did not exhibit a similar distribution. Herbaceous species in drained bog and fen forests produced most roots between 20−50 cm, indicating a deeper rooting strategy. These findings emphasize the importance of tailoring ingrowth core sampling depth to peatland vegetation types. For reliable FRBP estimates, sampling should preferably extend to 50−60 cm in sedge dominated peatlands, whereas 20 cm may suffice for bog and fen forests.

4.6 FRBP under changing climate

4.6.1 Effects of warming and water-level drawdown on FRBP

Water-level drawdown (WLD) significantly increased FRBP, as indicated by higher FRB accumulated in ingrowth cores during the incubation period. This effect was more pronounced at the northern fen, where FRBP was systematically higher in the dry plot, as supported by a significant site x WLD interaction (**Figure 7**, Table S2a in **III**). This suggests that drier conditions may enhance root growth in sedge-dominated fens. This outcome likely results from improved soil aeration as the water table drops, creating more favorable conditions for root respiration and growth. These findings are consistent with Strack et al. (2006), who observed enhanced root growth under water table drawdown in fen peatlands. However, contrasting results are reported in other fen ecosystems (Weltzin et al. 2000; Sullivan et al. 2008) and forested peatlands (Malhotra et al. 2020), where drying reduced root production, likely due to moisture stress. It is worth noting that Strack et al. (2006) employed more extensive water table drawdown (10–20 cm), compared to the moderate 5–10 cm drawdown in this study. Nevertheless, the results of this study indicate that even moderate long-term water table reductions can drive substantial shifts in vegetation dynamics in sedge fens, in line with earlier findings from boreal peatland ecosystems (Laiho et al. 2003; Kokkonen et al. 2019).

In contrast, warming did not significantly alter FRBP (based on FRB measurement; **Figure 7**, Table S2a in **III,** $p = 0.096$), consistent with previous findings for sedge roots (Ma et al. 2022) and other ecosystem components at these sites, such as sedge leaves (Mäkiranta et al. 2018) and CO_2 exchange (Laine et al. 2019). One possible explanation for the lack of FRBP response to warming is the modest increase in peat soil temperature (average 1.7° C), likely buffered by groundwater inflow and the low thermal conductivity of peat soil. Although other peatland studies have shown that even small increases (<1° C) in air temperature can affect soil temperature (Sullivan et al. 2008; Chivers et al. 2009; Dorrepaal et al. 2009; Delarue et al. 2015). Additionally, the large diurnal temperature fluctuations at our sites (up to 25° C; Mäkiranta et al. 2018) may have masked the effect of a small 1.7 °C increase on FRBP. While warming effects were not statistically significant, the marginal trend ($p = 0.096$) suggests that longer-term experiments may reveal stronger responses.

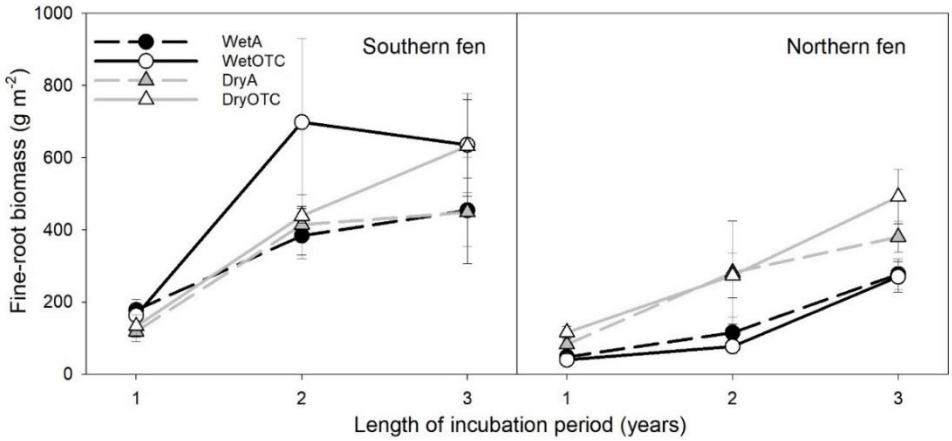


Figure 7 Mean fine-root biomass recovered from ingrowth cores incubated for 1–3 years under Wet-Ambient (WetA), Wet-Warmed (WetOTC), Dry-Ambient (DryA), and Dry-Warmed (DryOTC) treatments. The ingrowth cores extended down to 60 cm depth from the peatland surface. All incubations started in 2010. Error bars show the standard error of mean.

Indeed, warming effects became apparent in the northern fen only after three years of incubation, indicating that sedge root systems may require extended time to adjust to new thermal regimes. A long-term experimental period—spanning a decade or more—may be necessary for sedge vegetation to fully respond to warming, particularly under scenarios where peatlands remain wet or experience more drastic environmental changes (Wiedermann et al. 2007).

Although warming did not affect total FRBP, it altered vertical root distribution as indicated by β values. Warming significantly increased β, indicating greater allocation of root production to deeper peat layers (Fig. 4 in **III**). In contrast, WLD (drying) had no significant effect on vertical root distribution, consistent with the findings by Lampela et al. (2023), despite stronger drying in the northern fen. These results point to warming as a key driver of deeper sedge root allocation, potentially reflecting adaptive strategies. Supporting this interpretation, Mäkiranta et al. (2018) reported species-specific responses in northern fen, with forbs and shrubs increasing deep root production under drying, while sedges concentrated root production nearer the surface.

4.6.2 Effects of warming and water-level drawdown on root decomposition

The sedge root mass remaining after one-year incubation ranged from 48–51% in the southern fen and 65–70% in the northern fen. During the two-year incubation, additional mass loss was more pronounced in the southern fen, with remaining root mass declining to 28–36%, but was minimal in the northern fen, with 60–69% still remaining (Fig. 7 in **III**). These findings indicate slower decomposition under cooler northern conditions. Over the two-year incubation period, neither warming nor WLD had a significant effect on sedge root decomposition rates (Table S2c in **III**). This outcome contrasts with earlier research demonstrating that drying can accelerate decomposition by improving soil aeration (Trettin

et al. 1995; Thormann et al. 1999; Straková et al. 2012). A plausible explanation is that the modest increases in soil temperature observed in these fen ecosystems may have been insufficient to trigger substantial changes in root decay dynamics. Furthermore, even after drying the water-level (WL) in these very wet ecosystems remained relatively high as compared to any terrestrial systems, likely constraining oxygen availability and limiting decomposition responses.

4.6.3 Contribution of fine roots to organic matter accumulation under changing climate

In the southern fen, the estimated net accumulation of organic matter (OM) over two-year period was 603, 393, 280 and 283 g m^{-2} yr^{-1} for the Wet-Ambient, Wet-Warmed, Dry-Ambient and Dry-Warmed treatment plots respectively, indicating reduction of OM accumulation under drying and combination of drying and warming conditions. The corresponding values in the northern fen were 279, 230, 299 and 330 g m^{-2} yr^{-1} respectively (Fig. 8 in **III**), showing relatively minor variation among treatments. These differences of OM accumulation between the sites, or treatment plots are interpreted as indicative rather than statistically confirmed, as significance testing was not possible. This limitation arose because input and mass loss data could not be individually matched; ingrowth cores and litterbags were placed in different spots within the subplots to minimize disturbance during recovery. Nevertheless, when compared with independent CO_2 exchange measurements from the same site (Laine et al. 2019), the patterns observed here are consistent. At the southern fen, net CO_2 uptake decreased under drying, and this reduction was amplified by warming—mirroring the decline in OM accumulation reported in this study. This suggests that even small, statistically non-significant changes in FRBP may have important implications for ecosystem carbon dynamics. At the northern fen, the net CO_2 uptake remained stable (Laine et al. 2019), while this study observed only minor variation of OM accumulation among treatments. The relatively stable OM accumulation at northern fen may be attributed to the sustained or increased fine-root production.

Treatment effect, especially drying, led to some shifts in vegetation composition in both fens, marked by an increased contribution of sedge roots and a concurrent decline in sedge leaves or moss. For instance, in the southern fen, sedge root proportion increased from 20% under ambient conditions to 44% in the Dry-Warmed condition, while moss litter decreased sharply from 62% to 14% in the same treatment. Similarly, in the northern fen, sedge root proportion increased from 28% (ambient) to 45% (Dry-Warmed), while sedge leaves decreased from 57% (ambient) to 35% in the dry-ambient condition (Fig. 8 in **III**). These shifts are consistent with previous studies showing that drying reduces moss cover and forb abundance in fen ecosystems (Riutta et al. 2007; Chivers et al. 2009, Weltzin et al. 2000), indicating that climate-induced drying will likely alter fen vegetation composition. Laine et al. (2019) emphasized that even slight changes in water table depth can have profound ecological effects. While northern fen still seems to be going strong following the treatment effects, the already drier southern fen appears particularly vulnerable to future changes—especially if subject to several consecutive dry years—potentially leading to drastic ecosystem shifts.

5 CONCLUSIONS

This study advances the estimation of fine-root biomass production (FRBP) in boreal peatlands by introducing a modified ingrowth core method. The streamlined design of the core installer enables easy installation while minimizing disturbances to existing roots.

The results show that the simpler total root biomass and ID calculation method ($FRBP_{ID,(i),TotalRB}$) combined with a two-year incubation period offers a robust and practical approach for estimating FRBP in peatlands. This protocol reduces potential method-specific errors, avoids the complications associated with longer incubation periods, and is well suited for large-scale field applications. Accounting for root mortality and decomposition increases FRBP estimates—especially where root mortality rates are high. When reliable mortality data are available from literature, applying such corrections requires little additional analytical effort. Otherwise, the simpler total root biomass ($FRBP_{,TotalRB}$) method remains a practical and efficient alternative in estimating FRBP, reducing time and resource requirements. Future work aimed at quantifying site-specific root mortality rates would refine the estimates and improve peatland carbon budget models.

Peat proved to be the most reliable substrate for ingrowth cores in sedge fens, consistently yielding higher FRBP estimates than inorganic alternatives. Crushed glass may be considered in wet sedge fens when ease of root separation is prioritized, provided its limitations are acknowledged.

Infrared spectroscopy (IRS) demonstrated strong potential as a rapid, non-destructive method for estimating FRBP without manual root separation. While site-specific IRS calibration yielded the highest accuracy, generalized calibrations based on *Sphagnum*- or *Carex*-dominated peats also performed well. These generalized models offer a plausible alternative when site-specific calibration samples are unavailable, reducing the need for labor-intensive root sorting. Further development and validation of generalized IRS models within the research group have continued to expand their applicability across global peatland types and support future application of IRS-based FRBP estimation in diverse peatland ecosystems.

FRBP was strongly concentrated on surface peat layers in the bog and fen forests but extended deeper into peat profile in sedge fens, particularly at the southern site. Different species groups showed distinct rooting strategies, with trees and shrubs shallow-rooted, and herbs rooting deeper. Experimental warming promoted deeper root allocation in sedge fens, while WLD had little effect on rooting depth. However, WLD (drying) substantially increased total FRBP, particularly at the northern sedge fen. These results suggest that shift in water-table regimes may influence peatland carbon cycling more rapidly than mere temperature increases.

Overall, this study provides a comprehensive framework for utilizing the ingrowth core method to estimate FRBP in boreal peatlands. The combined use of the total root biomass-based ID calculation method ($FRBP_{ID,(i),TotalRB}$) with a two-year incubation period and IRS offer a robust, time- and cost-efficient tool for large-scale assessment of FRBP in these ecosystems.

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