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Author(s): Wei He, Päivi Mäkiranta, Petra Straková, Paavo Ojanen, Timo Penttilä, Rabbil Bhuiyan, Kari Minkkinen & Raija Laiho

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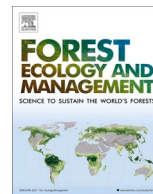
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Fine-root production in boreal peatland forests: Effects of stand and environmental factors

Wei He^{a,b}, Päivi Mäkiranta^b, Petra Straková^{b,c}, Paavo Ojanen^{a,b}, Timo Penttilä^b, Rabbil Bhuiyan^{a,b}, Kari Minkkinen^a, Raija Laiho^{b,*}

^a Department of Forest Sciences, University of Helsinki, Helsinki, Finland

^b Natural Resources Institute Finland (LUKE), Helsinki, Finland

^c Department of Ecosystem Biology, Faculty of Science, University of South Bohemia, České Budějovice, Czechia

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ABSTRACT

Fine roots are an important component of ecosystem carbon (C) cycling in boreal forests and peatlands. We aimed to estimate fine-root production (FRP) for a range of peatland forests, examine the patterns in, and develop models for estimating, the relationships between FRP and tree stand characteristics as well as environmental conditions.

Fine-root production of 28 drained boreal peatland forest sites in Finland, representing different site types and soil water-table conditions, was measured using the ingrowth-core method. Total FRP and FRP of conifers decreased from south to north but long-term mean annual temperature sum and precipitation alone did not significantly explain this trend. Tree stand basal area predicted FRP better than any other stand variable alone, explaining 16 % of the variation in stand-level total FRP. Basal areas of pine and spruce correlated positively with the FRP of conifers. Total FRP varied considerably among the site types and, with the exception of the most fertile site type, decreased with decreasing fertility. A model that included stand basal area and site type accounted for 47% of the variation in stand-level total FRP. Total FRP was generally higher with a deeper water-table level (WT). Together, WT and basal area explained 25 % of the variation in stand-level total FRP. Most FRP occurred in the top 20-cm layer comprising 76–95% of total FRP. The most fertile site type showed lower FRP in deeper layers than the other site types. These results can be used for estimation of FRP with forest inventory data.

1. Introduction

Peatland ecosystems are the carbon (C) hotspots of our planet, covering only 3 % of the global land surface but storing over 30 % of the global soil C pool in their peat deposits (Page et al., 2011; Xu et al., 2018; UNEP 2022). A critical component of the C cycle in boreal forests and peatlands is fine-root production (FRP), which may be equal to or larger than aboveground production (Persson, 1983; Gower et al., 2001; Korrensalo et al., 2018; Mäkiranta et al., 2018). Fine roots may represent a small part of the total forest biomass, but they play a vital role in nutrient and water absorption and are key contributors to soil C due to their fast turnover (Laiho et al., 2003; Clemmensen et al. 2013; Pandey et al., 2023). A small change in FRP can thus affect the ecosystem C sink. Fine-root production may be more sensitive to environmental and biotic changes and respond more strongly to disturbances than fine-root biomass (FRB) (Yuan and Chen, 2012). In addition, FRP may respond

differently from FRB to gradients in environmental conditions (Lampela et al., 2023). Generally, however, estimates of root-mediated C fluxes in peatlands are still scarce, even though there is indication that they may play an important role in the C budget (Murphy and Moore, 2010), also following climate and/or land use change, e.g., to forestry (Ojanen et al., 2014, Bhuiyan et al., 2023).

A considerable proportion of peatlands has been drained for forestry, particularly in the European part of the boreal zone. In Finland, peatlands (undrained and drained) make up 35 % (9.1 million ha) of the forest land area, of which around 4.9 million ha are drained peatland forests (Kulju et al., 2023). Drawdown of the soil water-table level (WT) can significantly alter vascular plant productivity and species composition (Weltzin et al., 2000; Laiho et al., 2003). These changes may have considerable impacts on ecosystem C and nutrient cycling through changes in C and nutrient inputs to soils by aboveground litter, as well as root production and turnover (Laiho, 2006). Our understanding of the

* Corresponding author.

E-mail address: raija.laiho@luke.fi (R. Laiho).

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response of peatlands to environmental change is based primarily on aboveground plant dynamics (e.g., Laine et al., 1995; Sarkkola et al., 2005; Straková et al., 2010; McPartland et al., 2020), and far less is known about the belowground component (e.g., Finér and Laine, 1998; Bhuiyan et al., 2017; Malhotra et al., 2020).

This gap in our knowledge concerning the belowground world largely stems from methodological holdbacks. Separating fine roots from soil and distinguishing between live and dead roots as well as the species identification of fine roots are arduous; especially so when it comes to peat soils that solely consist of plant remains, including roots, at various stages of decay (Sjörs, 1991). If the relationships between FRP and more easily measurable variables could be identified, it would make an important contribution to C modeling and reporting.

Fine-root production in boreal forest ecosystems has been found to correlate with climatic variables, such as latitude, temperature, and precipitation (Vogt et al., 1995; Gill and Jackson, 2000; Yuan and Chen, 2010; Finér et al., 2011). Moreover, soil properties such as soil nutrient regime can also affect FRP (Nadelhoffer 2000; Yuan and Chen, 2012), and these effects on FRP may be specific to stand type or species. Due to the lack of information concerning peatlands, it is still common to generalize patterns observed in mineral soil forests in ecosystem and earth models. Since the major constraints for ecosystem functioning - temperature, moisture, and nutrient regimes - as well as the physical, chemical, and biological properties of peat soils fundamentally differ from those of mineral soils (Westman and Laiho, 2003; Päivänen and Hånell, 2012), the patterns of FRP likely differ as well.

Boreal forest ecosystems in northern regions have a cold climate that likely restricts the availability of nitrogen (N) and thus fine root growth (Nadelhoffer, 2000; Rasse, 2002). In contrast to mineral soils, peat soils have a higher nitrogen (N) content but less mineral nutrients (Westman and Laiho, 2003; Päivänen and Hånell, 2012). Therefore, especially at the most N-rich sites, the availability of N should be favourable, but higher FRP may be required to explore for mineral nutrients such as phosphorus (P) or potassium (K) that are often scarce in peat soils (Westman and Laiho, 2003). The limited observations in peatlands available so far suggest that total FRP is greater in more nutrient-rich sites (Laiho et al., 2014; Bhuiyan et al., 2017). However, the FRP patterns of individual species may differ from the pattern in total FRP. For example, Scots pine may produce fewer fine roots in peatland forests when the soil nutrient regime is better (Finér and Laine, 1998, 2000; Bhuiyan et al., 2017). In peatlands, even when drained, we also need to consider the WT, which largely determines the soil volume where aerobic processes can take place, and is thus a major factor controlling ecosystem structure and function in these sites (Murphy et al., 2009; Murphy and Moore, 2010; Peltoniemi et al., 2021).

Stand variables such as tree species, plant functional types (PFTs) making up the ground vegetation, FRB, and stand basal area also affect FRP (Tingey et al., 2005; Hendricks et al., 2006; Finér et al., 2011; Yuan and Chen, 2010). In peatlands, different species or PFTs may have different rooting patterns and rooting depths (Ruseckas, 2000; Bhuiyan et al., 2017; Proctor and He, 2019). Fine-root production correlates positively with FRB in boreal forests (Li et al., 2003; Chen et al., 2004). Based on a compilation of tree FRB (diameter < 2 mm) data from 95 Finnish forest stands, Lehtonen et al. (2016) developed models for estimating FRB of boreal forests and found that stand basal area was a better predictor of FRB than any other stand variable alone. However, it is still unclear whether this predictor can be utilized to estimate FRP.

In this study, we examined FRP and its depth distribution at 28 study sites to fill the knowledge gap in the root production of drained boreal peatland forests. We used an ingrowth core method that has been modified (Laiho et al., 2014) to minimize disturbance to the soil and roots, and determined FRP by PFT using Fourier Transform Infrared (FTIR) spectroscopy method developed by Straková et al. (2020). Since determination of FRP is laborious and costly, and FRP may be related to aboveground plant characteristics (Murphy et al., 2009, 2010) we sought for patterns in, and developed models for estimating, the

relationships between FRP and aboveground stand parameters plus environmental and climatic conditions. Our hypotheses were that (1) FRP increases with increased mean annual temperature sum and precipitation; (2) nutrient-rich sites show higher FRP; (3) sites with deeper WT have higher FRP; (4) basal area is the major determinant of FRP; (5) FRP of various species and PFTs show different depth distributions.

2. Materials and methods

2.1. Study sites

The 28 forestry-drained peatland forest sites used in this study (Table 1) were a subset of the sites used by Ojanen et al. (2010, 2013) to quantify soil greenhouse gas emissions. We selected sites with a peat layer of at least 40 cm. The sites were situated between 60 and 67°N, covering a wide range of variation in climatic conditions, site types and stand characteristics. Site types of these drained peatland forests ranged from the most fertile to the nutrient poorest (e.g., Westman and Laiho, 2003; Fig. 8): Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). Both *Vaccinium* types were divided into two classes according to pre-drainage site type and characteristics: class II sites were sparsely treed or totally treeless before drainage, while class I sites were forested. Class II sites have on average more nitrogen (N) but less potassium (K) in the surface peat than class I sites. Based on peat N content, we rank the class II sites higher in the fertility gradient than their type I counterparts (Table 1). All stands included both trees that were on the site before drainage and those that appeared following drainage. These two classes are not always easily separated due to different growth dynamics, which makes estimating stand age challenging, even misleading. That is why we do not include stand age as a parameter, as the values would not be comparable among our sites.

Long-term temperature and rainfall data for the study sites for the period 1983–2015 were obtained from a database with a 10 km × 10 km grid of daily weather data from the Finnish Meteorological Institute (FMI). The mean annual temperature sum (sum of daily mean temperatures exceeding 5 °C in degree days (dd)) varied between 1032 and 1424 dd. The mean annual precipitation varied between 506 and 617 mm.

Stand, soil, and WT data (Tables 1, 2) were the same as used by Ojanen et al. (2010, 2013) and Lehtonen et al. (2016). The stand basal area varied from 4.7 to 39.1 m²/ha (average 19.1 m²/ha). The growing stock stem volume varied from 15.9 to 300.9 m³/ha (average 125.3 m³/ha). The C: N (carbon: nitrogen) ratios for the topmost 20 cm peat layer varied from 19.6 to 43.8 (average 28.1). The mean WT of the sites varied

Table 1

Mean characteristics of the study sites by site type ± standard error. Soil bulk density (BD; g cm⁻³), calcium, phosphorus, and potassium concentrations (Ca, P, K; mg kg⁻¹), and C:N ratios are for the 0–20 cm peat layer. Soil water-table level (WT; cm) was measured over May–October. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). n = number of study sites.

Site types	n	BD	C:N	Ca	P	K	WT
HrT	4	0.093 ± 0.003	23 ± 0.18	6719 ± 2762	1166 ± 132	504 ± 29	28 ± 2.5
MT(II)	5	0.130 ± 0.005	28 ± 0.22	3023 ± 887	895 ± 160	432 ± 114	50 ± 3.3
MT(I)	3	0.157 ± 0.001	31 ± 1.92	4527 ± 147	943 ± 318	479 ± 41	46 ± 0.2
VT(II)	7	0.125 ± 0.001	25 ± 0.44	2908 ± 734	823 ± 125	334 ± 36	30 ± 2.1
VT(I)	3	0.100 ± 0.005	32 ± 0.56	1746 ± 105	1051 ± 201	567 ± 72	24 ± 1.5
DsT	5	0.064 ± 0.001	40 ± 0.39	2345 ± 162	526 ± 37	491 ± 55	25 ± 1.4

Table 2

Mean stand basal area (m^2/ha) and stand stem volume (m^3/ha) of the study sites by site type \pm standard error. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT).

Site types	Stand basal area				Stand stem volume			
	Deciduous	Spruce	Pine	Total	Deciduous	Spruce	Pine	Total
HrT	21.0 \pm 1.2	7.4 \pm 0.7	0.6 \pm 0.2	29.0 \pm 1.6	163.0 \pm 11.8	48.8 \pm 5.5	3.5 \pm 1.0	215.4 \pm 15.3
MT(II)	12.5 \pm 1.0	5.9 \pm 0.9	7.3 \pm 0.6	25.7 \pm 1.4	93.2 \pm 7.7	32.8 \pm 4.6	59.4 \pm 6.4	185.4 \pm 11.1
MT(I)	4.1 \pm 0.2	17 \pm 0.5	0	21.1 \pm 0.5	24.6 \pm 1.4	121.5 \pm 8.6	0	146.1 \pm 8.8
VT(II)	4.7 \pm 0.4	0.6 \pm 0.1	11.7 \pm 0.8	16.9 \pm 1.0	25.3 \pm 2.4	1.7 \pm 0.3	68.4 \pm 5.1	95.5 \pm 6.7
VT(I)	2.1 \pm 0.5	0	11.7 \pm 1.0	13.8 \pm 1.5	13.7 \pm 3.7	0	75.7 \pm 8.4	89.4 \pm 11.6
DsT	0	0	11.0 \pm 1.0	11.0 \pm 1.0	0	0	54.1 \pm 6.5	54.1 \pm 6.4

between 7 and 70 cm below soil surface during the snow-free period.

2.2. Ingrowth cores

We applied the ingrowth core method according to the recently developed methodological guidelines for peat soils (Laiho et al., 2014; Bhuiyan et al., 2017, 2023). The novel type of corer-installer reduces disturbance during installation by pushing the holes for the cores in the peat instead of cutting and removing the peat. The diameter of the ingrowth cores was kept small to reduce the volume of ‘unnatural’ root-free substrate introduced in the soil.

The cores were made of polyester fabric with a mesh size of about 1 mm \times 1 mm. Four peat substrates were chosen to mimic the soil quality of the study sites (Table 3): deep-horizon sedge (*Carex*) peat – to avoid abundant presence of live sedge roots – was used for the MT II and VT II sites, swamp peat consisting mostly of *Sphagnum* and tree remains for the MT I and HrT sites, and *Sphagnum* peat for the VT I and DsT sites. *Carex-Sphagnum* peat was used for one VT II site. The initial diameter of the filled core was 3.2 cm; however, post-incubation diameter was used in the calculations as the pressure of the surrounding soil was expected to modify the core diameters soon after the installation. The effective length was planned to be 50 cm with an additional tail that remained unfilled and above ground, to facilitate locating the cores after incubation. The first test sets of similar cores have been analyzed earlier (Laiho

Table 3

Calcium (Ca), phosphorus (P) and potassium (K) concentrations in the three peat types used in the ingrowth cores, $\text{mg kg}^{-1} \pm$ standard deviation, after incubation. Depth indicates the 10-cm segments into which the cores were divided. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT).

Site type	Depth (cm)	Peat type	Ca	K	P
HrT, MT (I)	0–10	<i>Sphagnum</i> and tree remains	2965 \pm 424	279 \pm 96	295 \pm 11
	10–20		2825 \pm 1219	184 \pm 88	260 \pm 2
	20–30		3643 \pm 2190	182 \pm 63	260 \pm 17
	30–40		4337 \pm 2250	126 \pm 42	254 \pm 11
MT(II), VT(II)	0–10	<i>Carex</i>	2810 \pm 1059	234 \pm 62	862 \pm 173
	10–20		2357 \pm 1082	163 \pm 42	822 \pm 159
	20–30		2422 \pm 1140	155 \pm 45	827 \pm 157
	30–40		2461 \pm 1428	134 \pm 19	830 \pm 146
VT(I), DsT	0–10	<i>Sphagnum</i>	2584 \pm 1360	399 \pm 187	436 \pm 117
	10–20		1822 \pm 453	257 \pm 107	390 \pm 96
	20–30		1790 \pm 335	178 \pm 77	358 \pm 84
	30–40		1928 \pm 454	151 \pm 66	360 \pm 82

et al., 2014; Bhuiyan et al., 2017). The results showed faster colonization by tree and shrub roots than in traditional ingrowth cores (Finér and Laine, 2000; Murphy et al., 2009), and indicated that 2-year incubation is long enough for estimating fine-root production (Bhuiyan et al., 2017).

The ingrowth cores were installed between October 15th and November 27th, 2013, and recovered after two years in late November 2015. In all, 15 ingrowth cores were installed at each site. During recovery of the cores, a long sharp knife was employed to carefully cut around the cores to separate any aboveground plant components attached to or growing through the cores, and to cut the root systems, especially rhizomes and any hard lateral expansion, to avoid risk of pulling out roots from the cores. The soil surface level was marked in the cores at recovery. In some sites, all cores were not found at the time of recovery, and some had been pulled out from the soil by some curious animals. The number of cores per site thus finally ranged from 7 to 13. After recovery, the cores were wrapped in plastic foil and stored frozen (-20°C) until further processing.

In the laboratory, the cores were removed from the freezer and defrosted overnight in a refrigerator. The defrosted cores were cut into five 10-cm segments. The top and bottom diameter of each segment was measured from two perpendicular directions. All above-ground biomass that was still attached to the cores was removed. Any roots found outward of a core segment were cut off along the fabric surface. Then, the roots inside the core were gently separated from the peat and washed clean with water. Estimation of living and dead roots was based on colour, elasticity and toughness (Makkonen and Helmsaari, 1999; Tufekcioglu et al., 1998; Bhuiyan et al., 2017). The roots were oven-dried to constant mass at 30°C and weighed.

Fine-root production was estimated by transforming the total mass of the fine roots (including living and dead roots) extracted from the ingrowth cores to represent $\text{g m}^{-2} \text{year}^{-1}$ using the post-incubation core diameter and dividing the value by the incubation time (2 years) (Bhuiyan et al., 2017; Yuan and Chen 2012).

2.3. Fourier Transform Infrared spectroscopy

To prepare the samples, dried roots from each segment were powdered using an oscillating ball-mill. Subsequently, FTIR spectra of the powdered samples were acquired using a Bruker VERTEX 70 FTIR spectrometer (Bruker Optics, Germany) equipped with a horizontal diamond ATR sampling accessory. The powdered samples were directly placed on the diamond crystal with a diameter of 1.8 mm. To ensure uniform distribution and contact between the sample and crystal, a MIRacle high-pressure digital clamp was utilized. Each spectrum consisted of 65 averaged absorbance measurements within the range of 4000 to 650 cm^{-1} , with a resolution of 2 cm^{-1} . The measured data was collected using OPUS software.

2.4. Statistical analyses

2.4.1. Effect of climatic, environmental and stand variables on fine-root production

The effects of climatic, stand, and environmental variables such as mean annual precipitation (P), temperature sum (Tsum), latitude (L), tree stand stem volume (V), tree stand basal area (G) and stand basal area of tree species including Scots pine (GP), Norway spruce (GS) and deciduous trees (GD), site type (ST), C:N ratio of topmost 20 cm peat layer (CN), grouping of sites to nutrient rich (HrT, both MTs) and nutrient poor (VTs, DsT) (SG) as an alternative to specific site types, and average soil water-table level (WT) on FRP were tested with linear mixed-effect models using the 'lme4' package (Bates et al., 2015) in R (R Core Team; R version 3.5.3; RStudio version 1.2.1335).

We started by fitting a model with no predictors, a 'null model':

$$\text{FRP} = a + c_{\text{site}} + \varepsilon \quad (1)$$

where a is a fixed effect intercept, c_{site} is the random effect factor of the site, accounting for correlation between observations within each site, and ε is sampling error. Next, we fitted the models using each of the variables in turn as a single dependent variable. The models are presented in Table 4, where b_i is the fixed effect parameter of variable i .

Different combinations of predictors were then tested by adding them one-by-one into a model version having intercept and the single variable that had the best predictive power, tree stand basal area. This test included predictors with a significant effect on FRP based on models 2–11 (Table 4), where $b_{G \times ST}$ is a fixed effect parameter related to site-type specific parameter for stand basal area. P values and R^2 values were achieved from package 'lmerTest' (Kuznetsova et al., 2017). We used analysis of variance (ANOVA) and Akaike Information Criterion (AIC) to select the best model. As the FRP on HrT sites was surprisingly low (see Results and Discussion), we further ran a second set of models excluding the HrT sites from the data (Table 5).

2.4.2. Depth distribution of fine-root production

The vertical distribution of FRP was modeled using the asymptotic equation proposed by Gale and Grigal (1987) and Jackson et al. (1996) for root biomass depth distribution. The equation

$$Y = 1 - \beta^d \quad (2)$$

models the cumulative root fraction (Y) as a function of soil depth (d , cm) with β as the depth distribution parameter. The β values were calculated individually for each ingrowth core using SYSTAT software. Higher β values indicate a greater proportion of roots at deeper soil depths, while lower values indicate a shallower distribution of roots (Jackson et al., 1996). We then applied the linear mixed models for β values using the 'lme4' package in R, as described above for FRP, to analyze the response of the root depth distribution (in terms of coefficient β) to the climatic and stand variables.

2.4.3. Plant functional type contributions derived from Fourier Transform Infrared spectra

The FTIR data underwent preprocessing steps including Savitzky-Golay smoothing (second polynomial order, 11 smoothing points), baseline correction, mean normalization, and second derivative transformation (Savitzky-Golay derivative, second polynomial order, 15 smoothing points). The FTIR calibration models for the main plant functional types (PFTs) of northern peatlands (Straková et al., 2020) were used to predict the mass proportions of roots of the main PFTs: (1) graminoids; (2) forbs; (3) ferns; (4) shrubs and birch (*Betula pubescens*); (5) conifers, in the root samples manually separated from the ingrowth cores. The forb *Rubus chamaemorus* was included in shrubs, as its fine roots do not differ from shrub roots chemically (Straková et al., 2020).

During the calibration and validation of the models, any predicted values of the dependent variable that were less than 0 % were set to 0 %,

while values predicted to be greater than 100 % were set to 100 %. Data analyses were performed using the Unscrambler 10.3 (Camo Process AS; Oslo, Norway) package. The effects of environmental and stand variables on FTIR-derived FRP by plant functional types were tested similarly to the total FRP with linear mixed-effect models using the 'lme4' package in R.

3. Results

3.1. Total fine-root production

Individual core FRP values ranged from 5 to 800 g m⁻² y⁻¹ with a mean of 118 g m⁻² y⁻¹. Individual site FRP values ranged from 30 to 473 with a mean of 120 g m⁻² y⁻¹. FRP varied considerably among the site types (Fig. 1), being at its lowest, 48 ± 7 g m⁻² yr⁻¹, in the HrT sites, and at its highest, 234 ± 27 g m⁻² yr⁻¹, in the MT II sites. Excluding the HrT sites, FRP decreased with decreasing fertility of the site type. The very low FRP in the most fertile HrT sites was an unexpected result and we cannot fully rule out a bias (see Discussion). Because of that, we are showing model results both with and without HrT data (Table 4 versus Table 5).

Mean annual precipitation had a non-significant relation to FRP (model 2 in Table 4 and 5), as did mean annual temperature sum (model 3 in Table 4 and 5). Latitude correlated negatively with FRP as expected (model 4 in Table 4 and 5, $p = 0.025$ and 0.029 , respectively), indicating that FRP decreases from south to north along the studied geographic range.

Tree stand stem volume (model 5 in Table 4 and 5, $p = 0.053$ and < 0.001 , respectively) and basal area (model 6 in Table 4 and 5, $p = 0.006$ and < 0.001 , respectively) correlated positively with FRP. At the stand level, tree stand stem volume alone explained 8 % of the variation in FRP (Fig. 2a), while tree stand basal area explained 16 % (Fig. 2c). When we excluded the most fertile sites (HrT), tree stand stem volume alone explained 24 % of the variation in FRP (Fig. 2b), and the tree stand basal area explained 34 % (Fig. 2d), and mean FRP was 130 g m⁻² y⁻¹. Tree stand basal area was the best individual predictor for FRP (Tables 4 and 5). When the basal area was divided into three groups (pine, spruce and deciduous trees), the linear relationship between FRP and stand basal area was significant for pine ($p < 0.05$). Fitness of the group-level model (model 7) was not as good as that of total basal area (model 6) based on both AIC and ANOVA comparisons (Table 6). When we excluded the most fertile sites (HrT), the outcome was reversed (Table 6).

The C:N ratio of the topmost 20 cm peat had a non-significant relation to FRP at the stand level (model 9 in Tables 4 and 5). When we excluded the most fertile sites (HrT), FRP was significantly higher in nutrient-rich than in nutrient-poor sites (model 10 in Table 5, $p = 0.010$). The depth of the WT correlated positively with FRP (Fig. 3, model 11 in Table 4 and 5, $p < 0.001$).

We observed that site type (model 12 in Table 4 and 5, $p < 0.001$ and $= 0.029$, respectively) was significant when added into model with tree stand basal area. Site type and basal area together were the best predictors for FRP, explaining 47 % of the variation in stand-level FRP (Fig. 4). Also, WT (model 13 in Table 4, $p = 0.007$) was significant when added into model with basal area. Together, WT and basal area explained 25 % of the variation in stand-level FRP. When we incorporated WT into the model with site type and basal area (model 14), we discovered that the model was not improved (Table 6). Similarly, inclusion of factors such as latitude (model 15) did not enhance the model (Table 6).

3.2. Fine-root production by plant functional types

Woody species (shrubs and trees) accounted for most of the FRP, on average 83 % of the total FRP in HrT, 94 % in MT II, 90 % in VT I, 81 % in VT II, and 72 % in DsT (Fig. 5). The remaining FRP was accounted for by herbaceous species (graminoids, forbs, and ferns). Fine-root production

Table 4

Models for predicting fine-root production (FRP; $\text{g m}^{-2} \text{ year}^{-1}$) and β value using the full data set (including HrT sites), with parameter estimates (a , b_i), Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and P values (P). Parameter a is the fixed effect intercept, b_i is the fixed effect parameter of variable i (mean annual precipitation (P ; mm year^{-1}), temperature sum (Tsum; dd), latitude (L ; $^{\circ}$), tree stand stem volume (V ; m^3/ha), tree stand basal area (G ; m^2/ha), stand basal area of tree species including (pine (GP; m^2/ha), spruce (GS; m^2/ha) and deciduous trees (GD; m^2/ha), site type (ST), C:N ratio of topmost 20 cm peat layer (CN), grouping of sites to nutrient rich or poor (SG), and soil water-table level (WT; cm)). Models 1, 16 and 19 are the null model. Bolded values indicate statistical significance at $p < 0.05$.

Model	Formula	a	b_i	AIC	BIC	P
1	$\text{FRP} = a + c_{\text{site}} + \varepsilon$	120.15	–	3164.1	3174.8	–
2	$\text{FRP} = a + b_P P + c_{\text{site}} + \varepsilon$	88.25	0.56	3165.6	3180.0	0.913
3	$\text{FRP} = a + b_{\text{Tsum}} \text{Tsum} + c_{\text{site}} + \varepsilon$	–128.47	0.21	3162.8	3177.2	0.070
4	$\text{FRP} = a + b_L L + c_{\text{site}} + \varepsilon$	1.45×10^3	-1.89×10^{-4}	3161.0	3175.4	0.025
5	$\text{FRP} = a + b_V V + c_{\text{site}} + \varepsilon$	72.45	0.38	3162.3	3176.7	0.053
6	$\text{FRP} = a + b_G G + c_{\text{site}} + \varepsilon$	36.16	4.43	3158.4	3172.8	0.006
7	$\text{FRP} = a + b_{\text{GP}} \text{GP} + b_{\text{GS}} \text{GS} + b_{\text{GD}} \text{GD} + c_{\text{site}} + \varepsilon$	28.62	$b_{\text{GP}} = 5.44$ $b_{\text{GS}} = 5.75$ $b_{\text{GD}} = 3.65$	3161.9	3183.5	0.044
8	$\text{FRP} = a + b_{\text{ST}} \text{ST} + c_{\text{site}} + \varepsilon$	86.17	$b_{\text{HrT}} = -38.45$ $b_{\text{MT(II)}} = 155.36$ $b_{\text{MT(I)}} = 36.42$ $b_{\text{VT(II)}} = 31.80$ $b_{\text{VT(I)}} = -1.66$ $b_{\text{DsT}} = 0$	3157.7	3186.5	0.011
9	$\text{FRP} = a + b_{\text{CN}} \text{CN} + c_{\text{site}} + \varepsilon$	140.37	–0.71	3165.4	3179.8	0.765
10	$\text{FRP} = a + b_{\text{SG}} \text{SG} + c_{\text{site}} + \varepsilon$	99.76	47.65	3164.2	3178.6	0.956
11	$\text{FRP} = a + b_{\text{WT}} \text{WT} + c_{\text{site}} + \varepsilon$	12.94	3.22	3152.6	3167.0	<0.001
12	$\text{FRP} = a + b_{\text{G} \times \text{ST}} \text{G} + c_{\text{site}} + \varepsilon$	30.04	$b_{\text{G} \times \text{HrT}} = 0.65$ $b_{\text{G} \times \text{MT(II)}} = 8.70$ $b_{\text{G} \times \text{MT(I)}} = 4.22$ $b_{\text{G} \times \text{VT(II)}} = 4.74$ $b_{\text{G} \times \text{VT(I)}} = 4.44$ $b_{\text{G} \times \text{DsT}} = 4.81$	3138.7	3171.0	<0.001
13	$\text{FRP} = a + b_G G + b_{\text{WT}} \text{WT} + c_{\text{site}} + \varepsilon$	–4.37	$b_G = 2.04$ $b_{\text{WT}} = 2.60$	3153.0	3171.0	0.007
14	$\text{FRP} = a + b_{\text{G} \times \text{ST}} \text{G} + b_{\text{WT}} \text{WT} + c_{\text{site}} + \varepsilon$	18.19	$b_{\text{G} \times \text{HrT}} = 0.31$ $b_{\text{G} \times \text{MT(II)}} = 7.70$ $b_{\text{G} \times \text{MT(I)}} = 3.23$ $b_{\text{G} \times \text{VT(II)}} = 4.18$ $b_{\text{G} \times \text{VT(I)}} = 3.98$ $b_{\text{G} \times \text{DsT}} = 4.40$ $b_{\text{WT}} = 0.72$	3139.7	3175.7	0.410
15	$\text{FRP} = a + b_{\text{G} \times \text{ST}} \text{G} + b_L L + c_{\text{site}} + \varepsilon$	5.392×10^2	$b_{\text{G} \times \text{HrT}} = -1.490 \times 10^{-1}$ $b_{\text{G} \times \text{MT(II)}} = 7.773$ $b_{\text{G} \times \text{MT(I)}} = 2.694$ $b_{\text{G} \times \text{VT(II)}} = 3.401$ $b_{\text{G} \times \text{VT(I)}} = 3.307$ $b_{\text{G} \times \text{DsT}} = 2.895$ $b_L = -6.941 \times 10^{-5}$	3139.8	3175.7	<0.001
16	FRP of conifers = $a + c_{\text{site}} + \varepsilon$	41.540	–	924.8	932.3	–
17	FRP of conifers = $a + b_L L + c_{\text{site}} + \varepsilon$	6.998×10^2	-9.341×10^{-5}	922.7	932.7	0.044
18	FRP of conifers = $a + b_{\text{BP}} \text{GP} + b_{\text{BS}} \text{GS} + c_{\text{site}} + \varepsilon$	1.384	$b_{\text{GP}} = 2.331$ $b_{\text{GS}} = 5.443$	917.4	929.9	0.003
19	$\beta \text{ value} = a + c_{\text{site}} + \varepsilon$	0.89	–	–686.9	–676.3	–
20	$\beta \text{ value} = a + b_P P + c_{\text{site}} + \varepsilon$	0.88	8.74×10^{-6}	–684.9	–670.7	0.970
21	$\beta \text{ value} = a + b_{\text{T}} \text{T} + c_{\text{site}} + \varepsilon$	0.95	-4.86×10^{-5}	–685.6	–671.3	0.429
22	$\beta \text{ value} = a + b_L L + c_{\text{site}} + \varepsilon$	0.85	5.92×10^{-9}	–685.0	–670.7	0.841
23	$\beta \text{ value} = a + b_V V + c_{\text{site}} + \varepsilon$	0.91	-1.52×10^{-4}	–687.7	–673.5	0.098
24	$\beta \text{ value} = a + b_G G + c_{\text{site}} + \varepsilon$	0.92	-1.21×10^{-3}	–687.5	–673.3	0.114
25	$\beta \text{ value} = a + b_{\text{GP}} \text{GP} + b_{\text{GS}} \text{GS} + b_{\text{GD}} \text{GD} + c_{\text{S,i}} + \varepsilon$	0.90	$b_{\text{GP}} = 2.13 \times 10^{-4}$ $b_{\text{GS}} = -1.50 \times 10^{-3}$ $b_{\text{GD}} = -1.15 \times 10^{-3}$	–685.6	–664.3	0.197
26	$\beta \text{ value} = a + b_{\text{ST}} \text{ST} + c_{\text{site}} + \varepsilon$	0.91	$b_{\text{HrT}} = -0.095$ $b_{\text{MT(II)}} = -0.004$ $b_{\text{MT(I)}} = -0.047$ $b_{\text{VT(II)}} = -0.056$ $b_{\text{VT(I)}} = -0.178$ $b_{\text{DsT}} = 0$	–701.4	–672.9	<0.001
27	$\beta \text{ value} = a + b_{\text{CN}} \text{CN} + c_{\text{site}} + \varepsilon$	0.83	2.22×10^{-3}	–689.7	–675.4	0.030
28	$\beta \text{ value} = a + b_{\text{NN}} \text{NN} + c_{\text{site}} + \varepsilon$	0.91	-2.94×10^{-2}	–688.6	–674.4	0.056
29	$\beta \text{ value} = a + b_{\text{WT}} \text{WT} + c_{\text{site}} + \varepsilon$	0.88	0.16×10^{-4}	–685.1	–670.9	0.712
30	$\beta \text{ value} = a + b_{\text{CN} \times \text{ST}} \text{CN} + c_{\text{site}} + \varepsilon$	0.85	$b_{\text{CN} \times \text{HrT}} = -1.68 \times 10^{-3}$ $b_{\text{CN} \times \text{MT(II)}} = -2.45 \times 10^{-3}$ $b_{\text{CN} \times \text{MT(I)}} = -5.07 \times 10^{-4}$ $b_{\text{CN} \times \text{VT(II)}} = -1.74 \times 10^{-3}$ $b_{\text{CN} \times \text{VT(I)}} = -1.23 \times 10^{-3}$ $b_{\text{CN} \times \text{DsT}} = -1.45 \times 10^{-3}$	–699.0	–666.9	<0.001

Table 5

Models for predicting fine-root production (FRP) and β value using data without the HrT sites, with parameter estimates (a , b_i), Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC) and P values (P). Parameter a is the fixed effect intercept, b_i is the fixed effect parameter of variable i (mean annual precipitation (P ; mm year⁻¹), temperature sum (Tsum; dd), latitude (L ; °), tree stand stem volume (V ; m³/ha), tree stand basal area (G ; m²/ha), stand basal area of tree species including (pine (GP; m²/ha), spruce (GS; m²/ha) and deciduous trees (GD; m²/ha), site type (ST), C:N ratio of topmost 20 cm peat layer (CN), grouping of sites to nutrient rich or poor (SG), and soil water-table level (WT; cm)). Models 1, 16 and 19 are the null model. Bolded values indicate statistical significance at $p < 0.05$.

Model	Formula	a	b_i	AIC	BIC	P
1	FRP = $a + c_{site} + \varepsilon$	132.22	–	2731.9	2742.2	–
2	FRP = $a + b_P P + c_{site} + \varepsilon$	101.89	0.05	2733.9	2747.7	0.928
3	FRP = $a + b_{Tsum} Tsum + c_{site} + \varepsilon$	–152.42	0.24	2731.1	2744.9	0.098
4	FRP = $a + b_L L + c_{site} + \varepsilon$	1.58×10^3	-2.06×10^{-4}	2728.9	2742.7	0.029
5	FRP = $a + b_V V + c_{site} + \varepsilon$	47.48	0.77	2722.6	2736.4	<0.001
6	FRP = $a + b_G G + c_{site} + \varepsilon$	0.89	1.77×10^{-5}	2715.0	2728.7	<0.001
7	FRP = $a + b_{GP} GP + b_{GS} GS + b_{GD} GD + c_{site} + \varepsilon$	35.92	$b_{GP} = 2.57$ $b_{GS} = 4.24$ $b_{GD} = 11.76$	2708.1	2728.8	<0.001
8	FRP = $a + b_{ST} ST + c_{site} + \varepsilon$	123.56	$b_{MT(II)} = 117.99$ $b_{MT(I)} = 0$ $b_{VT(II)} = -5.58$ $b_{VT(I)} = -39.06$ $b_{DSt} = -37.39$	2728.4	2752.5	0.021
9	FRP = $a + b_{CN} CN + c_{site} + \varepsilon$	224.24	–3.08	2732.6	2746.3	0.248
10	FRP = $a + b_{SG} SG + c_{site} + \varepsilon$	99.74	99.64	2727.3	2741.1	0.010
11	FRP = $a + b_{WT} WT + c_{site} + \varepsilon$	20.56	3.27	2722.0	2735.8	<0.001
12	FRP = $a + b_{G \times ST} G + c_{site} + \varepsilon$	30.55	$b_{G \times MT(II)} = 8.68$ $b_{G \times MT(I)} = 4.20$ $b_{G \times VT(II)} = 4.72$ $b_{G \times VT(I)} = 4.41$ $b_{G \times DSt} = 4.78$ $b_G = 5.71$ $b_{WT} = 1.37$	2712.2	2739.7	<0.001
13	FRP = $a + b_G G + b_{WT} WT + c_{site} + \varepsilon$	–14.10	$b_{G \times MT(II)} = 7.83$ $b_{G \times MT(I)} = 3.35$ $b_{G \times VT(II)} = 4.26$ $b_{G \times VT(I)} = 4.05$ $b_{G \times DSt} = 4.48$ $b_{WT} = 0.65$	2714.7	2731.9	0.132
14	FRP = $a + b_{G \times ST} G + b_{WT} WT + c_{site} + \varepsilon$	19.00	$b_{G \times MT(II)} = 7.813$ $b_{G \times MT(I)} = 2.752$ $b_{G \times VT(II)} = 3.456$ $b_{G \times VT(I)} = 3.545$ $b_{G \times DSt} = 2.972$ $b_L = -6.711 \times 10^{-5}$	2713.6	2744.6	0.442
15	FRP = $a + b_{G \times ST} G + b_L L + c_{site} + \varepsilon$	5.221×10^2	$b_{G \times MT(II)} = 7.813$ $b_{G \times MT(I)} = 2.752$ $b_{G \times VT(II)} = 3.456$ $b_{G \times VT(I)} = 3.545$ $b_{G \times DSt} = 2.972$ $b_L = -6.711 \times 10^{-5}$	2713.6	2744.5	<0.001
16	FRP of conifers = $a + c_{site} + \varepsilon$	45.45	–	830.1	837.3	–
17	FRP of conifers = $a + b_L L + c_{site} + \varepsilon$	8.525×10^2	-1.145×10^{-4}	827.12	836.64	0.025
18	FRP of conifers = $a + b_{GP} GP + b_{GS} GS + c_{site} + \varepsilon$	11.110	$b_{GP} = 1.675$ $b_{GS} = 6.077$	819.97	831.88	<0.001
19	β value = $a + c_{site} + \varepsilon$	0.90	–	–662.7	–652.3	–
20	β value = $a + b_P P + c_{site} + \varepsilon$	0.86	6.74×10^{-5}	–660.8	–647.1	0.726
21	β value = $a + b_T T + c_{site} + \varepsilon$	0.99	-7.18×10^{-5}	–663.1	–649.3	0.122
22	β value = $a + b_L L + c_{site} + \varepsilon$	0.80	1.46×10^{-8}	–661.0	–647.3	0.564
23	β value = $a + b_V V + c_{site} + \varepsilon$	0.91	-9.36×10^{-5}	–662.0	–648.3	0.249
24	β value = $a + b_G G + c_{site} + \varepsilon$	0.91	7.36×10^{-4}	–662.0	–648.2	0.255
25	β value = $a + b_{GP} GP + b_{GS} GS + b_{GD} GD + c_{S,i} + \varepsilon$	0.92	$b_{GP} = -1.45 \times 10^{-3}$ $b_{GS} = -2.82 \times 10^{-3}$ $b_{GD} = 1.14 \times 10^{-3}$	–663.8	–643.3	0.068
26	β value = $a + b_{ST} ST + c_{site} + \varepsilon$	0.87	$b_{MT(II)} = 5.15 \times 10^{-2}$ $b_{MT(I)} = 0$ $b_{VT(II)} = 3.11 \times 10^{-2}$ $b_{VT(I)} = 2.94 \times 10^{-2}$ $b_{DSt} = 4.69 \times 10^{-2}$	–662.1	–638.1	0.117
27	β value = $a + b_{CN} CN + c_{site} + \varepsilon$	33.40	0.78	–661.3	–647.6	0.437
28	β value = $a + b_N N + c_{site} + \varepsilon$	0.90	-3.14×10^{-3}	–660.7	–647.0	0.819
29	β value = $a + b_{WT} WT + c_{site} + \varepsilon$	0.91	-2.12×10^{-4}	–661.0	–647.4	0.535

of ferns was minor at all sites, on average, 2 %. Fine-root production of graminoids was highest in the DsT sites, 17 %, whereas FRP of forbs was highest in the HrT sites, 10 %. Separation of FRP by depth and plant functional type indicated that shrubs and trees distributed the majority of their FRP in the top 20 cm of the soil profile whereas herbs distributed the majority of their root production from 30 to 50 cm below the soil surface (Fig. 6).

Few correlations were found between PFT-level FRP and the climatic

and stand variables. Latitude correlated negatively with FRP of conifers (model 17 in Table 4 and 5, $p = 0.042$ and 0.025 , respectively), indicating FRP of conifers decreases from south to north. No such trend existed in FRP of shrubs and birch. Pine and spruce basal areas correlated positively with the FRP of conifers (model 18 in Table 4 and 5, $p = 0.003$ and < 0.001 , respectively).

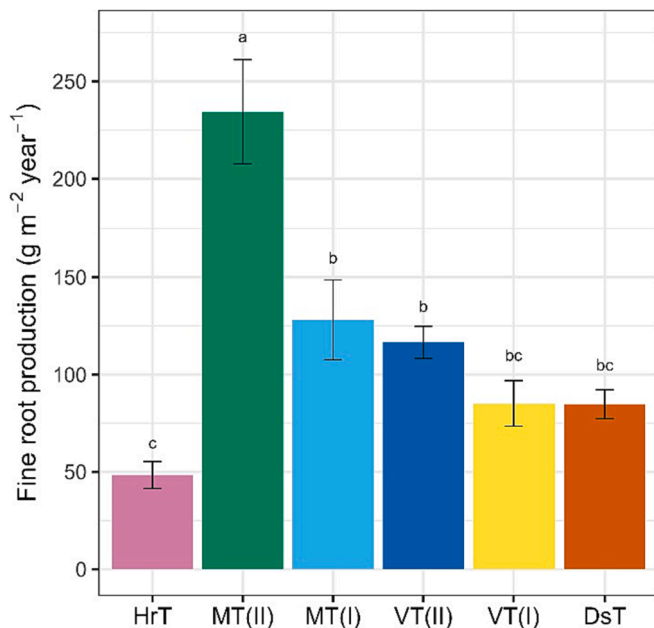


Fig. 1. Mean fine-root production, $\text{g m}^{-2} \text{yr}^{-1} \pm$ standard error, by site type: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). Site types are here ordered based on their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

3.3. Depth distribution of total fine-root production

Overall, most (76–95 %) of the FRP took place in the uppermost 20 cm of the peat profile (Table 7). The asymptotic depth distribution model (Equation 2) fitted well to the data (Fig. 7). The climatic variables did not have significant relationships with the β value (Table 4, $p > 0.05$). Of the stand variables only site type (Model 26 in Table 4, $p < 0.001$) and the C:N ratio of topmost 20 cm peat layer (Model 27 in Table 4, $p = 0.03$) had significant relationships with β value. The most fertile HrT sites showed smaller proportion of FRP in deeper layers than the other sites, while the depth distribution of FRP in the nutrient poorest DsT sites was deeper than the other sites (Fig. 7). Correspondingly, β value correlated positively with the C:N ratio of topmost 20 cm peat layer (Fig. 8) indicating that roots are produced proportionally deeper with decreasing fertility. Site type and soil C:N ratio together explained 20 % of the variation in the β value (Figs. 8, $R^2_m = 0.201$). Water-table level had a non-significant effect on the β value (Model 29 in Table 4). When we excluded the HrT sites, neither climatic nor stand variables had a significant effect on the β value (Table 5).

4. Discussion

4.1. Fine-root production in peatland forests

To our knowledge, this is the first comprehensive survey of fine-root production (FRP) in boreal peatland forests, covering a wide north–south range as well as different tree stand structures, and soil nutrient and water-level regimes. We found a strong correlation between basal area and total FRP at the stand level. Stand basal area alone explained 16 % of the variation in FRP. Finér et al. (2011) examined the relationships between environmental and stand variables and FRP in forests at the stand or tree level. They discovered that stand basal area explained 28 % and FRB as much as 53 % of the variation in the FRP for trees at the tree level. Less variation in FRP could be explained at the stand level. Lehtonen et al. (2016) used data from 95 forest stands (both mineral-soil and peatland forests) to develop models for estimating FRB

(diameter < 2 mm) of boreal forests, and found that stand basal area predicted also FRB better than any other stand variable alone. As trees grow in diameter and add to their basal area, they require more resources to support their growth and maintenance, and this is often achieved by increasing the allocation of resources to the root system. However, the strength of this relationship can vary depending on site-specific factors such as soil nutrient and hydrological regimes, as well as tree species composition. The relationship between stand basal area and FRP at the MT (I) sites was not consistent with the other site types, but this is probably just due to the small variation in the basal area not facilitating reliable estimation of the relationship for this site type. Adding site type, a general descriptor of site nutrient regime, to the stand basal area model increased the coefficient of determination to 47 %.

The soil nutrient regime thus clearly influences FRP; however, the directions of the responses have varied among studies in different ecosystems. Recent FRP studies from stands on mineral soils have shown total FRP (pine and understorey) to decrease with increasing site fertility (Ding et al., 2021). For peatlands, total FRP has previously been observed to be higher in more nutrient-rich and floristically diverse sites than in nutrient-poor sites (Finér and Laine, 2000; Bhuiyan et al., 2017). In contrast, a recent study by Lampela et al. (2023) reported that FRP was generally higher in the nutrient-poor, pine-dominated sites than the nutrient-rich, spruce-dominated sites. These contrasting findings highlight the complexity of FRP dynamics and suggest that factors such as tree species composition and their associated nutrient requirements may influence root productivity. Our extensive data yet generally indicates decreasing FRP with decreasing site fertility, apart from HrT.

Unexpectedly, we observed the lowest FRP for the most fertile site type, HrT. Apart from that, production decreased with decreasing site type fertility. We have two potential explanations. First, we observed that the peat used in the cores of the HrT sites contained clearly less phosphorus (P) than the ambient soils of the sites (Tables 1 and 2). Thus, the lowest FRP observed for the most fertile HrT sites may simply mean that roots avoided the cores in these sites, where P is often a growth-limiting nutrient (Päivänen and Hånell, 2012). Second, the HrT sites were relatively wet (Fig. 3), which can both limit the availability of oxygen to plant roots retarding FRP, but also increase nutrient availability with the inflowing water leading to less need for FRP. Verifying the critical mechanism would require a specific further study.

In addition to the soil nutrient regime, the growth of tree roots on drained peatlands may be limited intermittently due to a lack of oxygen, and several studies have shown a positive correlation between the depth of the soil water-table level (WT) and FRP (Liefers and Rothwell, 1987; Finér and Laine, 1998; Murphy et al., 2009; Murphy and Moore, 2010). When WT is deeper, air-filled pore volume of the rooting zone is greater, which promotes root growth (Boggie, 1972). Also in our study sites, total FRP was generally higher with a deeper WT, possibly as a result of a greater volume of aerated soil. However, stand basal area and WT depth generally have a positive correlation, due to both better site conditions for tree growth when the WT is deeper and the biological drainage through evapotranspiration increasing with increasing stand basal area (Sarkkola et al., 2005). This hampers determination of the primary factor leading to higher FRP with deeper WT.

Our results indicated that FRP in peatland forests decreases with increasing latitude but does not correlate with either mean annual temperature sum or precipitation. It is possible that latitude, as a measure of geographical location, encompasses a range of environmental conditions that are not captured by mean annual temperature or precipitation alone. Stand characteristics were also earlier found to explain a greater proportion of the variation in FRP than environmental factors (Finér et al., 2011). So, also the possible effect of climate, as well as WT depth, seems to be largely explained by stand characteristics.

In comparison to earlier studies in drained peatland forests, our total FRP estimates fluctuated within a wider range. Finér and Laine (1998, 2000) reported annual FRP (88 to 239 $\text{g m}^{-2} \text{yr}^{-1}$, diameter < 2 mm) for

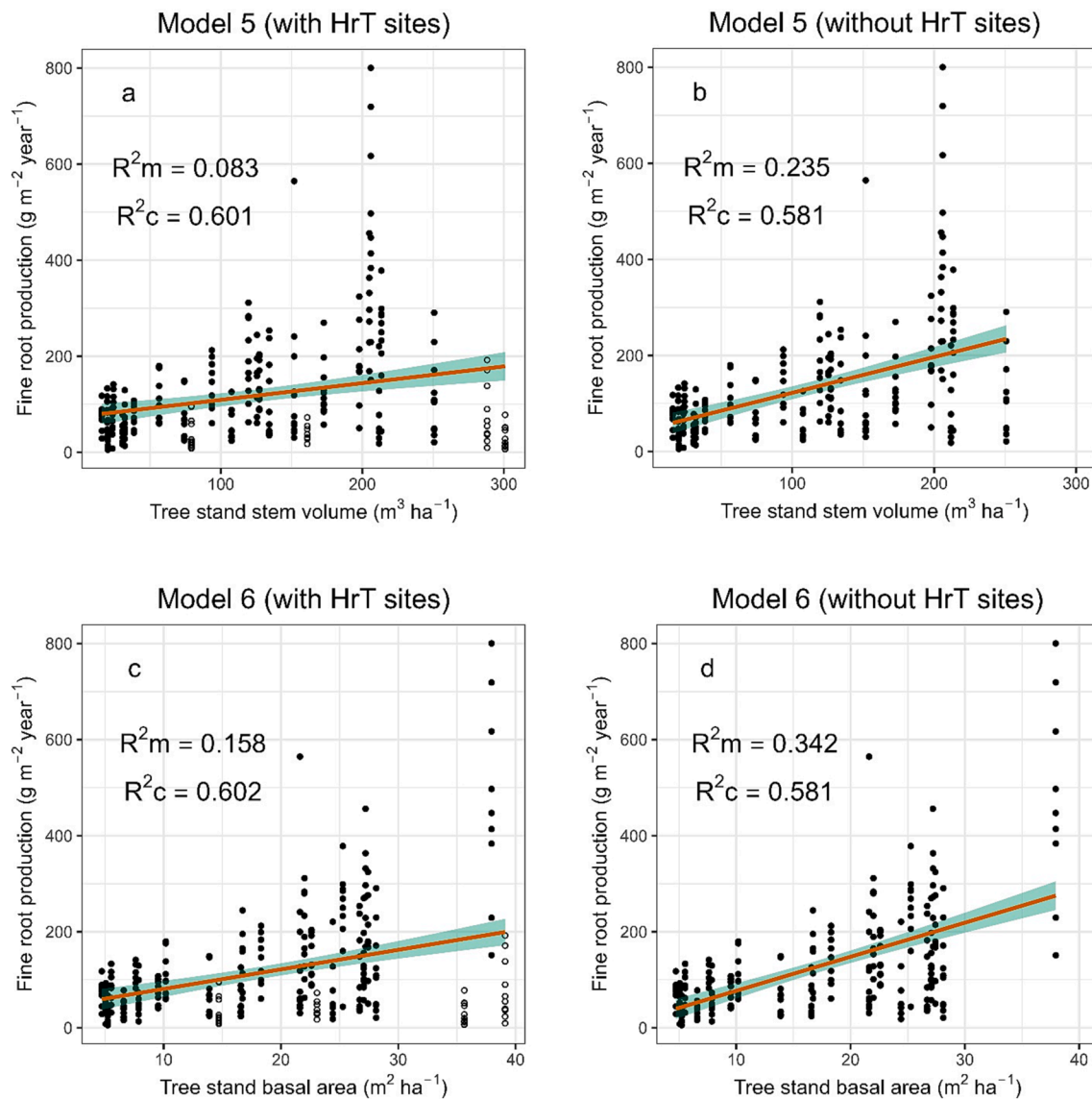


Fig. 2. Relationship between tree stand stem volume and fine-root production (a, with HrT sites; b, without HrT sites), and tree stand basal area and fine-root production (c, with HrT sites; d, without HrT sites). Open circles represent HrT Sites. Solid line depicts the fitted linear regression lines,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

Table 6
Comparisons of the linear mixed models. * Probability of the lower order model is better than that of the latter model, P indicates P values in ANOVA comparison; Δ AIC indicates difference of AIC values.

Compared models	Δ AIC	P
with HrT sites		
Model 6 and 7	−3.5	0.804
Model 6 and 12	19.7	1.671×10^{-5} *
Model 6 and 13	5.4	6.596×10^{-3} *
Model 12 and 14	−1	0.319
Model 12 and 15	−1.1	0.343
without HrT sites		
Model 6 and 7	6.9	4.384×10^{-3} *
Model 6 and 12	2.8	2.87×10^{-2} *
Model 6 and 13	0.3	0.132
Model 12 and 14	−0.4	0.443
Model 12 and 15	−1.4	0.439

three drained peatland forests using sequential coring and ingrowth cores over a 3-year period. The DsT sites from that study yielded FRP ($88 \text{ g m}^{-2} \text{ yr}^{-1}$) similar to ours ($85 \text{ g m}^{-2} \text{ yr}^{-1}$). Bhuiyan et al. (2017) reported a production of 244, and 561 g m^{-2} for fine roots derived from ingrowth cores installed for 2 years in a DsT site, and a MT (II) site, respectively. Other estimates were based on 1-year production data, e.g., $118 \text{ g m}^{-2} \text{ yr}^{-1}$ for a DsT (Laiho et al., 2014), $216 \text{ g m}^{-2} \text{ yr}^{-1}$ for a MT (II) (Laiho et al., 2014) similar to our 2-year mean ($234 \text{ g m}^{-2} \text{ yr}^{-1}$), and $78 \text{ g m}^{-2} \text{ yr}^{-1}$ for a DsT site (Murphy et al., 2009). These differences may result from our study covering a higher number and wider geographic range of sites, as well as different tree stand structures and development stages.

4.2. Fine-root production by plant functional type

Visually distinguishing between the roots of different tree species and plant functional types can be difficult and occasionally arbitrary, especially when multiple tree roots grow in the same layer and resemble one another in terms of form and color. As a result, misidentification of

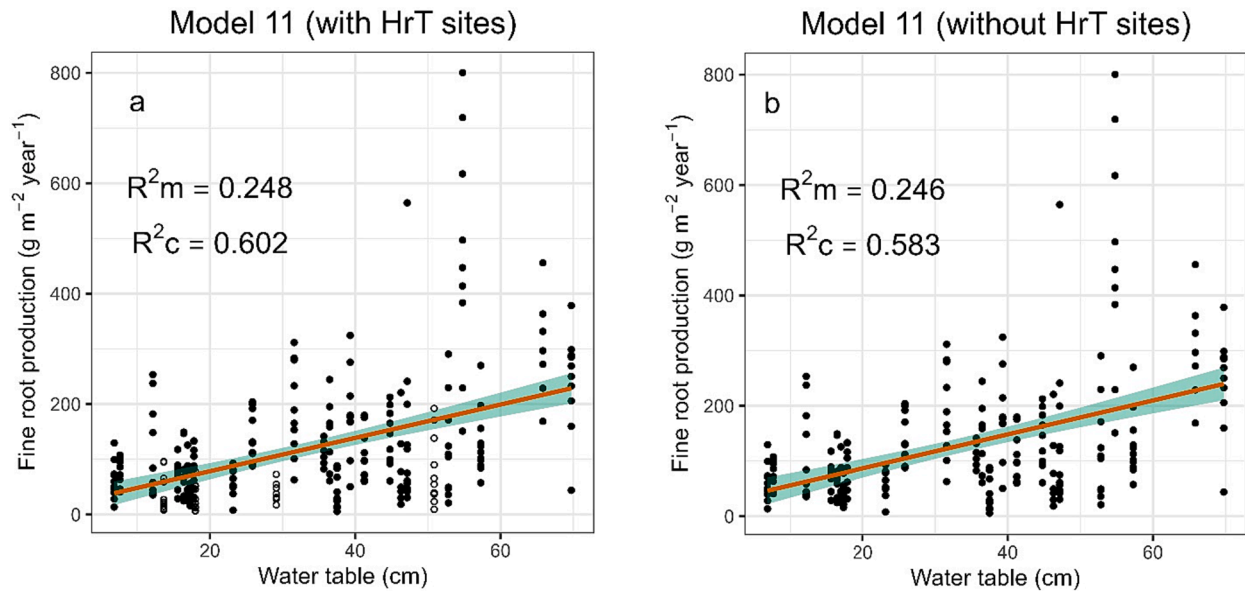


Fig. 3. Relationship between soil water-table level and total fine-root production (a, with HrT sites; b, without HrT sites). Open circles represent HrT Sites. Solid line depicts the fitted linear regression lines, with their 95 % confidence intervals indicated by the shaded areas. R^2m describes the proportion of variance explained by fixed effects. R^2c represents the proportion of variance explained by both fixed and random effects.

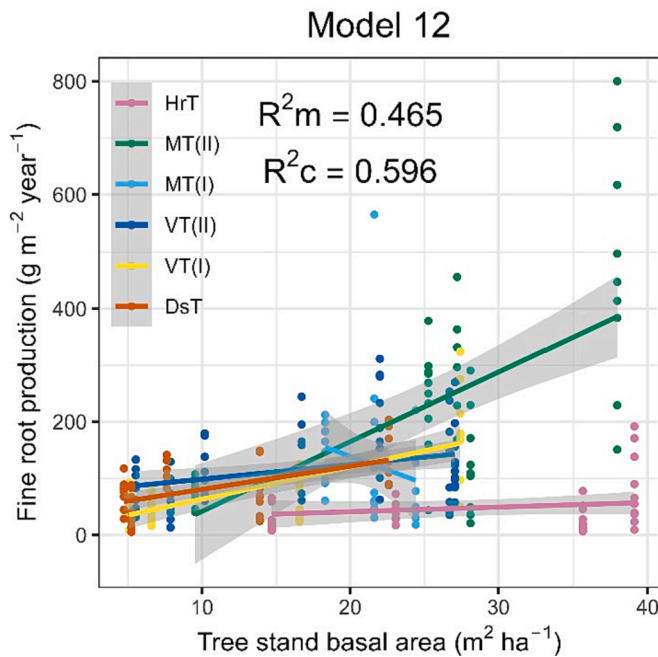


Fig. 4. Relationship between tree stand basal area and fine-root production for the different site types separately. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). R^2m describes the proportion of variance explained by fixed effects. R^2c represents the proportion of variance explained by both fixed and random effects. Solid lines depict the fitted linear regression lines, with their 95 % confidence intervals indicated by the shaded areas.

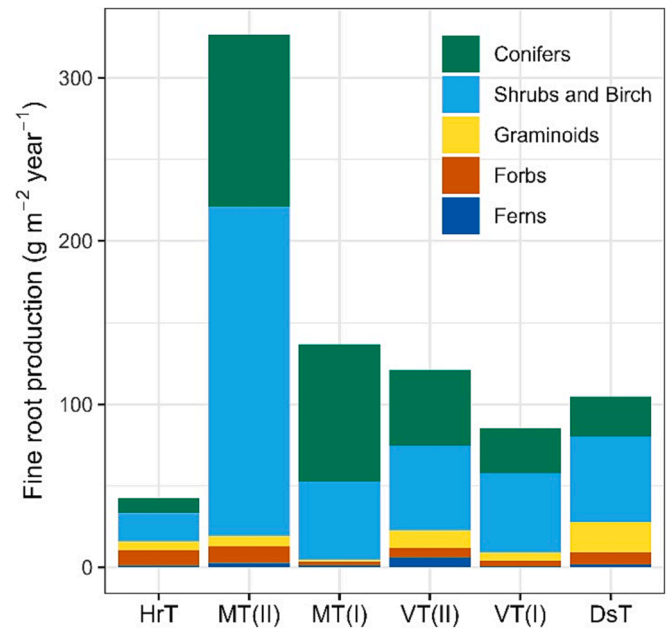


Fig. 5. Arithmetic means of FTIR-derived fine-root production by plant functional type in different site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT).

extent replaced by trees and shrubs at drained sites (Lampela et al., 2023). Our results, quite logically, indicated that shrubs and trees account for most of the FRP in peatland forests.

4.3. Vertical distribution of fine-root production

Most of the total FRP occurred in the top 0–20-cm of the peat soil and declined significantly at subsequent depths, which is in accordance with previous observations (Ruseckas, 2000; Murphy and Moore, 2010; Bhuiyan et al., 2017; Lampela et al., 2023). The majority of the FRP from shrubs and trees was similarly distributed in the top 20 cm of the soil

roots may occur. Our study is the first to quantify the FRP and its depth distribution by different tree species and plant functional types in peatland forests using FTIR spectroscopy. In peatlands where the carbon cycle is dominated by fluxes mediated by vascular PFTs: sedges, shrubs, and/or trees (Sjörs, 1991; Saarinen, 1996; Laiho et al., 2003; Jauhiainen et al., 2005; Bubier et al., 2006), such analysis provides a further insight into ecosystem structure and function. Herbaceous PFTs are to a large

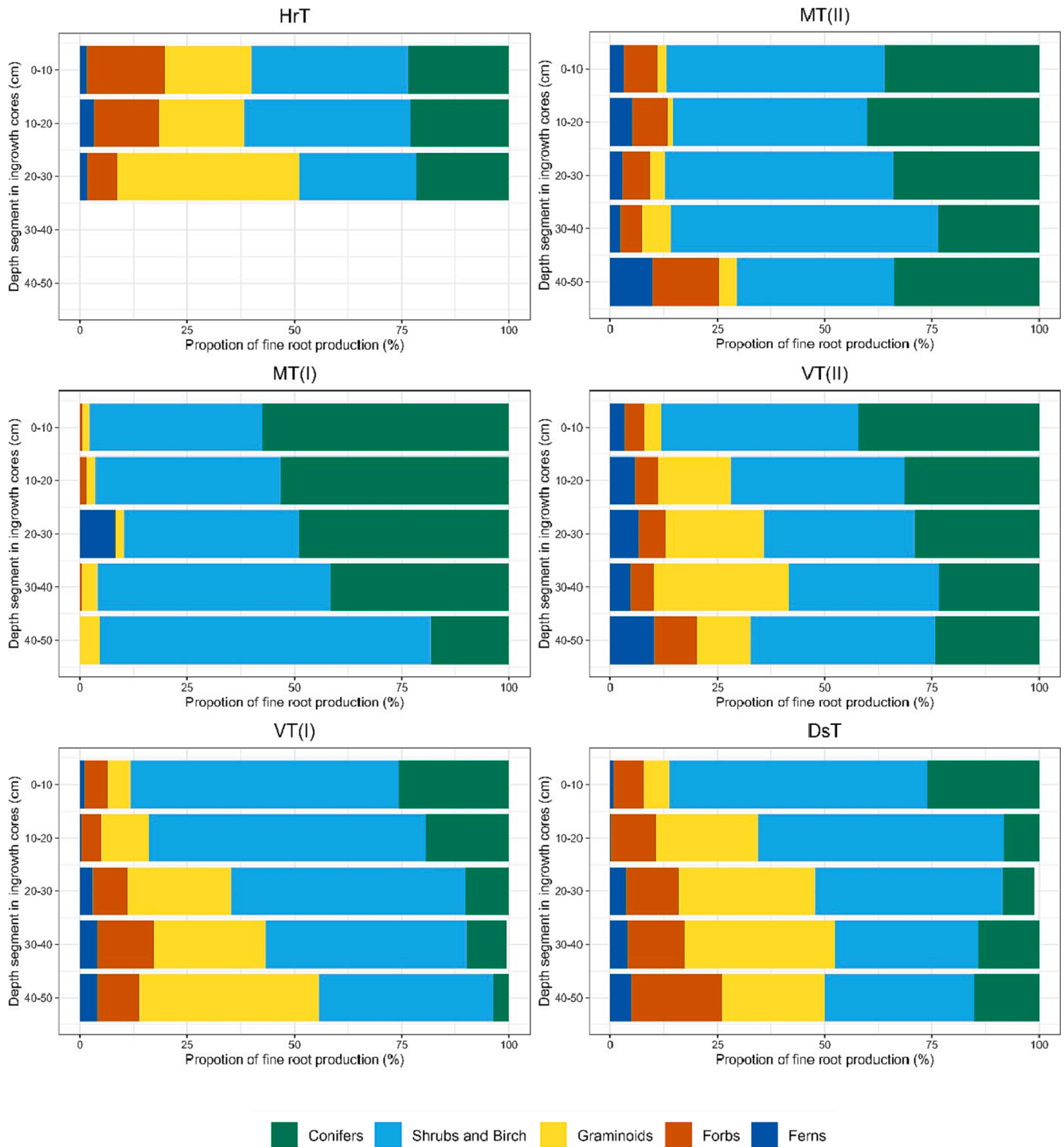


Fig. 6. The proportions of FTIR-derived fine-root production by plant functional types in different depths in different site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). In HrT, no fine-root production was observed below 30 cm.

profile, whereas herbs distributed most of their root production from 30 to 50 cm below the soil surface. For woody trees and shrubs that do not form aerenchymous roots, the extent of the oxic soil layer above the WT logically plays a critical role in determining the distribution of fine roots (Schenk and Jackson, 2002; Murphy and Moore, 2010). Better nutrient availability in the upper soil layers may also play a role (Jobbágy and Jackson, 2000; Murphy and Moore, 2010). Many graminoids, on the other hand, have aerenchymous roots and may produce substantial root biomass even under waterlogged conditions and deep into the anoxic

soil layers (Bernard et al., 1988; Saarinen, 1996; Proctor and He, 2019).

Somewhat surprisingly, our results suggested that WT has no effect on the depth distribution of FRP in peatland forests. Similarly, Heikurainen (1955) and Paavilainen (1966) reported that the average depth of the root systems increases only little when forested peatlands are drained, even though the WT drops deeper. Yet, it seems that at the nutrient-poor sites (VT II and I, DsT), a higher proportion of FRP occurring at depth may be needed to scavenge enough mineral nutrients. Although shrubs and trees are shallow-rooted, they still produce a

Table 7

Mean fine-root production, $\text{g/m}^{-2}(-)\text{yr}^{-1} \pm$ standard error, by depth and site type. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT).

Depth (cm)	HrT	MT(II)	MT(I)	VT (II)	VT(I)	DsT
0 to 10	38.8 \pm 5.7	132.7 \pm 18.3	88.6 \pm 12.3	69.2 \pm 6.8	55.2 \pm 9.0	49.0 \pm 5.0
10 to 20	7.7 \pm 1.7	48.4 \pm 7.8	26.9 \pm 11.4	24.4 \pm 3.0	18.7 \pm 3.7	14.8 \pm 1.8
20 to 30	2.1 \pm 0.8	28.5 \pm 3.4	6.9 \pm 1.5	13.1 \pm 1.6	6.8 \pm 1.4	9.4 \pm 1.2
30 to 40	0.4 \pm 0.3	18.3 \pm 3.5	5.8 \pm 1.4	7.8 \pm 1.1	3.7 \pm 0.6	8.4 \pm 1.2
40 to 50	0.2 \pm 0.1	10.2 \pm 3.5	2.7 \pm 2.3	5.0 \pm 1.1	1.4 \pm 0.4	4.0 \pm 0.8

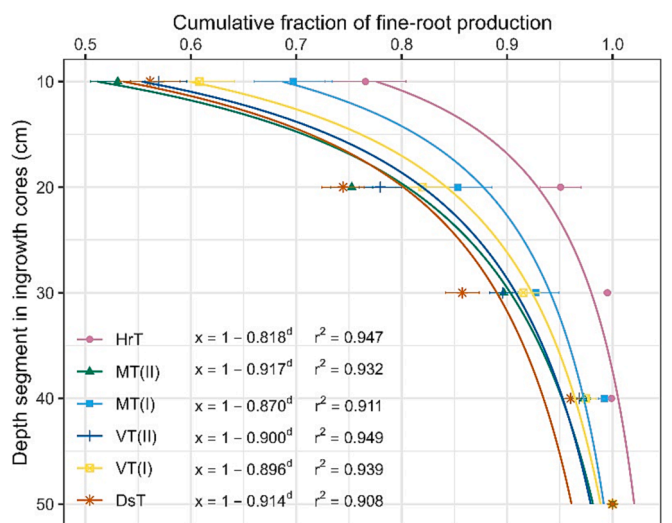


Fig. 7. Mean cumulative fraction of fine-root production for different site types. Error bars are standard error of the mean. The lines represent the asymptotic regressions to the data using the equation $x = 1 - \beta^{-d}$, where β describes the relative proportion of root located at depth.

considerable amount of fine-root biomass (also Finér and Laine, 2000; Iversen et al., 2018).

5. Conclusions

This study presents a set of models that can be used with forest inventory data to quantify FRP in boreal peatland forests. Stand basal area, site type, and WT were the variables best predicting FRP in our drained peatland forests. Even though the FRP models were based on a large dataset representing well the variation in basal area, fertility and climatic conditions of boreal drained peatland forests, half of the variation in FRP remained unexplained. More detailed reporting of stand and environmental characteristics in forthcoming studies could increase the predictive power of FRP models and improve our understanding of the C cycle in boreal peatland forests. To avoid biased results in further studies, the ingrowth cores should preferably be filled with peat from the study sites or alternatively, the main nutrient contents of the standard peats should be extensively compared with the peat of the study sites in advance, even though both options increase the amount of labor involved.

Author contributions

Raija Laiho designed the research with contributions from Päivi

Model 27

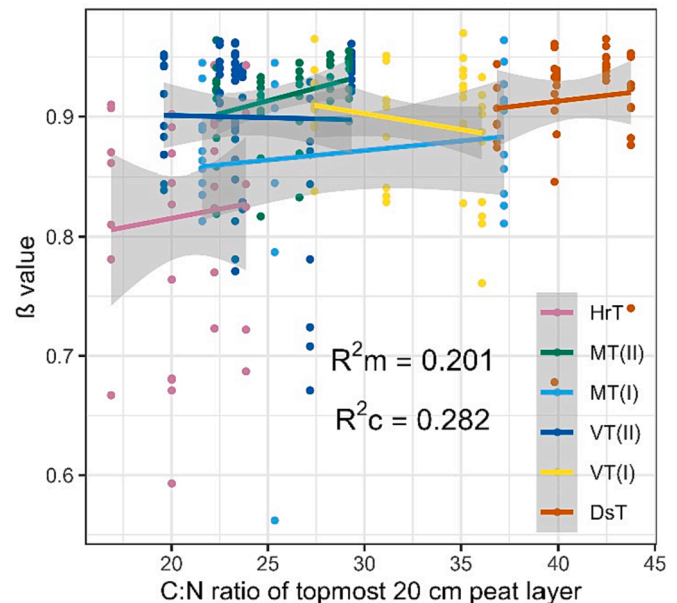


Fig. 8. Relationship between β values (ingrowth-core level) and the C:N ratio of the topmost 20 cm peat (*in situ*) for the different site types. Site types: Herb-rich type (HrT), *Vaccinium myrtillus* types II and I (MT II and I), *Vaccinium vitis-idaea* types II and I (VT II and I), and Dwarf shrub type (DsT). R^2c represents the proportion of variance explained by both fixed and random effects. Solid lines depict the fitted linear regression lines, with their 95 % confidence intervals indicated by the shaded areas. R^2m describes the proportion of variance explained by fixed effects.

Mäkiranta, Paavo Ojanen, Timo Penttilä and Kari Minkkinen. Wei He performed Fourier Transform Infrared (FTIR) spectroscopy analyses under supervision of Petra Straková. Data analyses were done by Wei He. Wei He led the writing under supervision of Raija Laiho, Päivi Mäkiranta and Paavo Ojanen. All authors participated in material preparation, data collection and analysis, commented on the manuscript, and approved the submitted version.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are available at Zenodo, <https://doi.org/10.5281/zenodo.8182401>

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