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Estimating fine-root production in three forestry-drained boreal peatlands dominated by Downy birch (*Betula pubescens* Ehrh.)

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ABSTRACT

Fine roots of trees significantly contribute to the carbon cycle within boreal forest ecosystems. Despite their importance, fine root production (FRP) remains one of the least understood processes, particularly in deciduous forests. This study estimated fine-root biomass (FRB) and FRP in downy birch (*Betula pubescens* Ehrh.) dominated stands on drained peatland sites in Central Finland. The stands were classified into three stages: young (10 years), middle-aged (50 years), and mature (80 years). In 2021, the middle-aged stand had the highest total FRB at 751.5 g m^{-2}, followed by the mature stand (329.5 g m^{-2}) and young stand (136.8 g m^{-2}). In 2022, all stands showed increased total FRB, with middle-aged stand reaching 889.5 g m^{-2}. The FRP in the middle-aged stand (445 g m^{-2} y^{-1}) was more than double that of the mature aged stand (228 g m^{-2} y^{-1}) and four times larger than in the young stand (107 g m^{-2} y^{-1}). Soil depth significantly affected FRP, with minimal root activity beyond the second soil layer. Over 90% of total FRP occurred in the top 20 cm soil layer, declining drastically tow.

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Deciduous tree; ingrowth core; soil depth; soil bulk density; stand age

Introduction

Peatlands are highly effective at storing carbon (C), with peat accumulation being a key natural process for transferring carbon from the atmosphere into long-term organic deposits (Page et al. 2011; Yu 2012). Despite the diversity of habitats within peatlands, they share a common feature: the presence of organic soil, known as peat (Histosols). In the boreal region, peatlands exhibit a wide range of conditions from the extremely nutrient-poor environments of *Sphagnum*-dominated bogs to the nutrient-rich conditions of eutrophic fens. They also range from the very wet flark fens to peatland forests, where the water table (WT) can drop to 30 cm or more below the soil surface, especially during the growing season (Laine et al. 2004; Maanavilja et al. 2014). Forested peatlands, which are frequently found in relatively dry, either naturally or artificially drained, peatland environments (Beaulne et al. 2021), have roots as a significant component of biomass, and their production plays a critical role in carbon flux dynamics from the soil (Mäkiranta et al. 2018; Schwieger et al. 2021). However, there remains still a notable lack of data on root biomass and production within these ecosystems (Iversen et al. 2018).

Fine roots (<2 mm in diameter) are essential components of belowground ecosystems, playing a pivotal role in carbon (C) fluxes across diverse ecosystems. Globally, FRP can contribute up to 76% of the annual net primary production (NPP) within forest ecosystems (Gower et al. 1996; Jackson et al. 1997). In boreal forests, FRP accounts for up to 73% of the total root production and 32% of the total forest production (Marschner and Rengel 2007). Furthermore, fine roots contribute to long-term C accumulation by promoting peat formation (Laiho et al. 2003). However, despite their significant role in the carbon dynamics of peatlands – critical hotspots for carbon storage – our understanding of fine-root-mediated carbon fluxes within these ecosystems remains limited (Bhuiyan et al. 2023). This knowledge gap persists even though land-use such as forestry will likely substantially impact these fluxes (Ojanen et al. 2014). Accurately estimating C fluxes in peatlands affected by such land use is crucial for creating reliable C budgets, which are essential for greenhouse gas inventories (Ojanen et al. 2014).

Ecosystem models, such as SUSI-simulator (Laurén et al. 2021), require accurate biomass data. However, outdated root distribution estimates undermine their reliability. Enhancing fine root production data improves model accuracy, thereby supporting peatland management and climate change mitigation measures.

Stand age is an important factor affecting ecosystem processes such as NPP, carbon storage, sequestration, and nutrient cycling (Wardle et al. 2004). As forest stands progress through developmental stages, NPP typically follows a pattern of increasing, peaking, and then declining (Binkley et al. 2002). During the decline phase, there is usually a transition from highly productive pioneer species to less productive late-successional species, accompanied by changes in nutrient availability. Specifically, on mineral soils reductions in soil nitrogen (N) and increased phosphorus (P) limitations

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are common in older stands, leading to greater investment in belowground structures (Wardle et al. 2004; Bond-Lamberty et al. 2006). Conversely, the N and P stores in a 0–50 cm peat layer increased with increasing drainage age on peatlands (Laiho and Laine 1994). This was primarily due to the subsidence of the mire surface following drainage, which led to compaction, increased peat bulk density, and brought deeper peat layers into the observed layer (Laiho and Laine 1994). Additionally, intensive mineralization enhanced nitrogen availability, further contributing to increased production in drained organic soils. Previous research on fine root biomass and production has often yielded conflicting results. For example, in five downy birch stands (aged 12–78 years) on fertile, well-drained Histosols in eastern Estonia, FRB remained stable across stand ages, averaging ∼1.5 t ha^{-1}, whereas in the oldest stand (1.95 t ha^{-1}), no clear relationship between FRB or FRP and stand age was observed (Uri et al. 2017). In Scots pine (*Pinus sylvestris* L.) stands on mineral soils in eastern Finland, fine root production (FRP) increases with stand age. Higher FRP has been observed in 35-year-old stands (77.5 Mg ha^{-1} yr^{-1}) compared to 15-year-old stands (16.5 Mg ha^{-1} yr^{-1}), with further increases in 100-year-old stands (86 Mg ha^{-1} yr^{-1}) (Makkonen and Helmisaari 2001). Since the present study focuses on organic soils (herb-rich and *Vaccinium myrtillus* types) in drained peatland forests, direct comparisons should account for differences in soil type and site conditions.

Downy birch (*Betula pubescens* Ehrh.) plays an important ecological and economic role in northern Europe. In Finland, peatlands account for 12% of Finland's total growing stock volume of Downy birch (Niemistö and Korhonen 2008). Downy birch stands play an important role in forestry, particularly in the pulp and paper industry. According to data from the Finnish National Forest Inventory (NFI11, measured in 2009–2013) indicate that birch-dominated stands on drained peatlands cover approximately 572,000 hectares. However, even though there are several studies concerning the FRP in coniferous-dominated stands in Finland, the understanding of deciduous-dominated stands on organic soils is scanty (Laiho et al. 2014; Bhuiyan et al. 2017; Lampela et al. 2023).

This study aims to estimate FRB and FRP in downy birch-dominated stands at different stages of succession on drained forested peatlands in Central Finland over two successive years. Our study seeks to address the current knowledge gap in fine root dynamics in downy birch-dominated ecosystems and provide insights into how stand age affects FRP in peatland sites. We hypothesized that mature downy birch stands on drained peatlands would exhibit higher FRP compared to younger stands, due to enhanced nutrient availability and greater allocation of resources to belowground biomass in older stands.

Materials and methods

Study sites

This study was carried out at three forestry-drained peatland sites located close to each other in Juupajoki, Central Finland (N 61° 50′ 36.542″, E 24° 17′ 37.010″, 180 m above sea level). The study locations were selected from a network of permanent sample plots connected to long-term research areas managed by the Hyytiälä Forestry Field Station. The average tree ages in these stands were 10, 50, and 80 years, representing young, middle-aged, and mature stands, respectively (Table 1). According to Hynynen et al. (2010), the optimal rotation period for downy birch is 70–80 years, as biological aging results in diminished growth and an increased risk of decay. Consequently, an 80-year-old birch stand in our study is classified as mature. The Nälkärasinsuo site, occupied by a 10-year-old young stand, was initially drained for forestry in 1936, with the tree stand regenerated through clearcutting in 2006. The Rajasuo site, with a 50-year-old middle-aged stand, was drained in 1950 and managed with a light thinning in the 1970s The Loukaskorpi site, featuring an 80-year-old mature stand, was initially drained in 1909. The drainage network was complemented in the 1920s and underwent ditch network maintenance treatment in year 1964. The current tree stands are predominantly downy birch (88%), with Norway spruce (*Picea abies*) present as an understory species at varying densities. The management history and successional development of the tree stands are well documented by long-term monitoring. According to the Finnish classification system for drained peatland forests (Vasander and Laine 2008), these sites are categorized as nutrient-rich Herb-rich (Rhtkg II) or *Vaccinium myrtillus* (Mtkg II) types (Table 1). In this classification, the suffix "II" indicates sites that were originally treeless or sparsely treed mires before drainage operations. At the time of the study, peat depths in the area ranged from 71 cm to 120 cm (Table 1). In early summer 2021, soil samples were collected from the sites at depths of 0–10, 10–20, 20–30, 30–40, and 40–50 cm. Five samples were taken from each site, making a total of fifteen samples for analysis. Bulk density was determined by drying the peat samples of known volume at 105 °C overnight (Blake and Hartge 1986). Bulk density is measured to compare the compaction and structure between the ingrowth core soil and the surrounding soil, providing insight into potential differences in soil physical properties.

Table 1. General description of the study sites (mean ± standard deviation).

	DB-10 (Young stand)	DB-50 (Middle-aged stand)	DB-80 (Mature stand)
Coordinates (WGS84)	61° 50′ 55.65″ N 24° 19′ 14.52″ E	61° 51′ 13.75″ N 24° 17′ 14.83″ E	61° 53′ 10.70″ N 24° 24′ 07.34″ E
Site type[1]	Rhtkg (herb-rich type)	Mtkg II (*Vaccinium myrtillus*- type)	Rhtkg (herb-rich type)
Stand age (years)	10	50	80
Peat depth (n = 30), cm	85.2 ± 3.2	74.6 ± 2.5	115.1 ± 3.5
Bulk density (n = 15) (g cm^{-3})	0.13 ± 0.04	0.12 ± 0.03	0.16 ± 0.02
Drainage year	1936	1950	1909
Stand density, trees (ha^{-1})	2767	4600	2883
Mean height (m)	4.6 ± 0.1	11.4 ± 0.8	16.7 ± 0.7
Stand dominant height (m)	6.18	22.55	24.01

(1) Vasander and Laine 2008.

Table 2. Carbon and nutrient content of the soil (peat) at the sites (0–20 cm depth). The values are derived from volumetric sampling, with each sample consisting of five systematically collected subsamples from each site. Data from Päivänen and Sarkkola (2016).

Nutrient content (kg ha^{-1})	DB-10 (Young stand)	DB-50 (Middle-aged stand)	DB-80 (Mature stand)
N	4880	5350	5929
P	323	546	376
K	107	80	139
C	131327	128750	154516

Soil temperature data loggers (iButton, model 1921G, Dallas Semiconductor Corp.) were installed at each site in autumn 2020 at a depth of 5 cm to monitor the soil temperatures. Soil temperatures were recorded automatically at 3-h intervals. Water table data loggers (Odyssey® capacitance water logger, Dataflow Systems Limited © 2022) were installed at each site in autumn 2020 to a depth of 2 m to monitor the water levels. Water-levels were logged every 30 minutes from October 2020 to October 2022 (Table 2).

Ingrowth core preparation and installation

The preparation and installation of ingrowth cores followed the methodology described by Laiho et al. (2014). The cores were made from polyester fabric with a mesh size of approximately 1 mm × 1 mm, and the initial diameter of the filled core was 3.4 cm. The cores were sown to have a perimeter of 10 cm and, resulting in a theoretical diameter of 3.18 cm. The core had an effective length of 50 cm, with an extra unfilled tail left above ground level to help locate the cores after the incubation period. The cores were filled with deep-horizon *Sphagnum* peat, collected from the studied stands, to ensure that the substrate contained no fresh live root material, thereby minimizing any potential effects of pre-existing roots on root ingrowth. The bare peat used in the cores was chosen to mimic the soil quality of the sites, being obtained from deeper soil horizons at the study locations. This approach ensured that the physical and chemical properties of the peat closely resembled those of the surrounding soil, minimizing variations in bulk density, decomposition stage, and nutrient availability that could affect root ingrowth. Additionally, using site-specific peat prevented the introduction of fresh live roots, ensuring that root production measured within the cores was attributed solely to new ingrowth. The bulk density of peat in all sites was measured and the filling was planned to mimic that in 10-cm sections.

At the drained peatland forest sites, 20 ingrowth cores were installed at each site, arranged in two different transects with 10 cores in each transect. The cores were installed using a two-piece corer-installer, as described by Laiho et al. (2014), which is designed to minimize disturbance to the surrounding soil compared to traditional coring methods. In all sites, the cores were installed in late October 2020. The first set cores were recovered after the first growing season in November 2021, with 10 cores per site collected for analysis, while the remaining cores were left in place to monitor long-term term root growth patterns and were alter recovered in November 2022. During removal of the cores, a long sharp knife was used to carefully cut around the cores to detach any aboveground plant parts attached to or growing through the cores, preventing roots from being pulled out of the cores. After removal, the cores were cut into five segments according to the 10-cm interval marks made during preparation. They were then wrapped in plastic foil, labeled with their incubation location, and frozen at −20 °C until further analysis.

The diameters of the peat-filled cores were not precisely measured because even the fresh *Sphagnum* peat was drier than that typically found under field conditions. It was anticipated that the cores would expand slightly after installation. Therefore, the accurate diameter was measured after their recovery. However, it was clear that the diameters of the peat-filled cores were smaller than the theoretical 3.18 cm (Laiho et al. 2014).

Separation of fine roots

In the laboratory, the ingrowth cores were taken from the freezer and placed in a refrigerator overnight to defrost. To avoid decomposition after defrosting, only one or two cores were thawed at a time (Appendix: Figure A1). The cores were cleaned of any adhering above-ground biomass, which was removed. Each core was cut into 10 cm segments, resulting in five segments down to the 40–50 cm depth. The diameters of the peat core segments were measured by taking two perpendicular measurements at both the top and bottom of each segment. All roots extending outside the core segments were trimmed and removed, while those within the cores were carefully picked. Root viability (living or dead) was estimated based on color and friability by gently pulling them with tweezers. At all sites, fine roots were pooled together without distinguishing between tree species or understory functional groups and were treated as total fine root components.

Roots were categorized into three diameter classes: ≤ 1 mm, 1–3 mm, and 3–5 mm, as these were the most utilized diameter classes (Finér et al. 2011). The roots were oven-dried to constant mass at 30 °C, then weighed with a precision of 1 mg. Similarly, the peat material from each core was collected and oven-dried at 30 °C and then weighed. The values were converted to per m^2 using the surface area of the cores. To calculate the annual FRP (g m^{-2} year^{-1}) for each core, we divided the dry mass by two (years; incubation time) and by the surface area of the cores (Bhuiyan et al. 2017).

Statistical analysis

We used repeated measures analysis of variance to evaluate the differences in FRP in the soil depth in all three stands. Stand age was to be a within-subjects (repeated) factor, and depth (layer within a core) was the between-subjects (grouping) factor. The differences in root biomass and biomass production between sites, layers, and years were tested with the analysis of variance. All these analyses were done, using the IBM SPSS Statistics 25 and R software (v3.6.0) (R Core Team 2019).

Results

Fine root biomass and soil bulk density

The total FRB varied significantly with stand age, soil depth, and year across all sites (Tables 3 and 4). In 2021, the middle-aged stand (DB-50) exhibited the highest total biomass at 751.5 g m^{-2}, with the majority concentrated in the 0–10 cm layer (558.2 g m^{-2}). In contrast, the mature stand (DB-80) and young stand (DB-10) had lower total root biomasses of 329.5 g m^{-2} and 136.8 g m^{-2}, respectively. By 2022, biomass increased across all stands, with the middle-aged stand reaching 889.5 g m^{-2}, the mature stand 455.8 g m^{-2}, and the young stand 214.9 g m^{-2}. Across both years, the highest fine root biomass consistently occurred in the 0–10 cm soil layer with progressively lower values in deeper layers.

To evaluate the comparability of soil conditions across the study sites, we analyzed the carbon and nutrient (N, P, K) content of the peat in the 0–20 cm layer (Table 2). The total soil carbon content was relatively consistent across the sites, with only slight variations between stand ages. Similarly, nitrogen (N), phosphorus (P), and potassium (K) concentrations showed comparable ranges among the study sites (Table 2), indicating no substantial differences in nutrient availability.

Data from cores, segmented into five 10-cm layers per core (within-factor Depth), revealed significant differences both between and within subjects. Between subjects, the analysis identified a notable effect of depth (Table 4, F (4, 95) = 156.824, $p < 0.01$), indicating variations in fine root biomass across different soil depths. Within subjects, significant effects were observed for stand age (F (2, 190) = 47.039, $p < 0.01$) and the interaction between stand age and depth (Table 4, F (8, 190) = 25.053, $p < 0.01$), further emphasizing how both factors influence biomass distribution (Table 4).

The bulk density of the peat within the cores closely matched that of the surrounding peat soil in the drained bog (t (29) = −5.52, $p < 0.001$, Figure 1, Appendix: Table A1). Both datasets showed a clear trend of increasing bulk density with advancing stand age. For the young stand, the bulk density inside the cores was 0.102 ± 0.02 g/cm^3, while in the soil it was slightly higher at 0.13 ± 0.04 g/cm^3. Similarly, the middle-aged stand had a bulk density of 0.100 ± 0.02 g/cm^3 inside the cores and 0.12 ± 0.03 g/cm^3 in the soil, reflecting a consistent pattern across both measures. In the mature stand, although the bulk density inside the cores (0.108 ± 0.03 g/cm^3) and in the soil (0.16 ± 0.02 g/cm^3) differed, both values were the highest among the stands (Figure 1).

Table 4. Repeated measures Analysis of Variance on the effects of stand age (young, middle-aged, and mature) on fine root biomass production (g m^{-2} y^{-1}) in our three study sites on drained peatlands. Data are from cores and were divided into five 10-cm layers per core (within-factor Depth).

Effect	*df*	*MS*	*F*	*P*
Between subject				
Depth	4	4.878	156.824	< 0.01
Error	95	0.031		
Within subject				
Stand age	2	1.460	47.039	< 0.01
Stand age × Depth	8	0.777	25.053	< 0.01
Error	190	0.031		

Fine root production

The FRP varied significantly across the stands (DB-10, DB-50, and DB-80) and soil depths ($p< =0.002$) for both study years 2021 and 2022 ($p < 0.001$) (Table A2 and A3). The FRP peaked in the top layer (0–10 cm) for all stands, with DB-50 showing the highest value at 326 g/m^2. A significant decline in FRP was observed with increasing soil depth ($p < 0.01$), with minimal root activity detected below the second layer (deeper than 20 cm) (Table 4). Comparisons between stands revealed that DB-50 had the highest overall FRP, followed by DB-80, while DB-10 had the lowest (Figure 2).

Soil temperature and water table level

The mean soil temperature of DB-10, DB-50 and DB-80 stands was 13.6, 13.4 and 13.1°C, respectively, in 2021, and 13.5, 12.6 and 11.8°C, respectively, in 2022 (Figure 3). The WT level below the surface during the growing seasons (May – August) for DB-10, DB-50 and DB-80 stands was 48, 43 and 60 cm, respectively, in 2021, and 50, 43, 70 cm, respectively, in 2022 (Figure 3). In 2021, water levels increased steadily from May, peaking in mid-July with a maximum reading around July 24 (DB-10: 65.83 cm, DB-50: 68.32 cm, DB-80: 75.28 cm), followed by a gradual decline in August. Similarly, in 2022, WT showed a comparable trend with rising levels from May, peaking around mid-July, but with slightly higher maximum readings. The peak for 2022 occurred around July 22 (DB-10: 70.45 cm, DB-50: 72.85 cm, DB-80: 78.65 cm).

Table 3. Fine root biomass (g m^{-2}) with standard error (SE), minima and maxima by depth in ingrowth cores recovered after first (2021) and second (2022) incubation years in drained forests. *N* = 20 for each site.

Years		DB-10 (Young stand)			DB-50 (Middle-aged stand)			DB-80 (Mature stand)		
	Depth, cm	Mean	SE	Min–Max	Mean	SE	Min–Max	Mean	SE	Min–Max
2021	0–10	113.3	12.0	0.0–324.0	558.2	54.3	0.0–888.0	317.2	40.1	0.0–841.0
	10–20	12.7	7.8	0.0–116.6	177.7	28.9	0.0–357.2	7.8	3.5	0.0–81.0
	20–30	5.7	5.9	0.0–169.6	14.2	5.8	0.0–88.9	2.4	1.1	0.0–16.8
	30–40	3.7	1.5	0.0–25.0	1.2	1.4	0.0–46.2	1.8	0.7	0.0–14.4
	40–50	1.4	0.7	0.0–16.0	0.2	0.1	0.0–2.6	0.25	0.2	0.0–4.4
	Total 0–50	136.8	27.8	0.0–650.6	751.5	90.4	0.0–1383.0	329.5	45.6	0.0–957.7
2022	0–10	193.5	20.6	0.0–361.0	652.0	44.2	0.0–961.0	441.7	61.1	0.0–1156.0
	10–20	11.6	3.1	0.0–64.0	188.9	29.8	0.0–412.1	8.6	6.6	0.0–118.8
	20–30	5.2	2.4	0.0–60.8	47.5	17.1	0.0–400.4	2.6	1.4	0.0–36.0
	30–40	3.2	1.2	0.0–25.0	0.9	0.6	0.0–14.4	2.6	1.1	0.0–25.0
	40–50	1.4	0.6	0.0–16.0	0.2	0.1	0.0–1.4	0.3	0.1	0.0–3.6
	Total 0–50	214.9	27.9	0.0–526.8	889.5	91.8	0.0–1789.4	455.8	70.3	0.0–1339.4

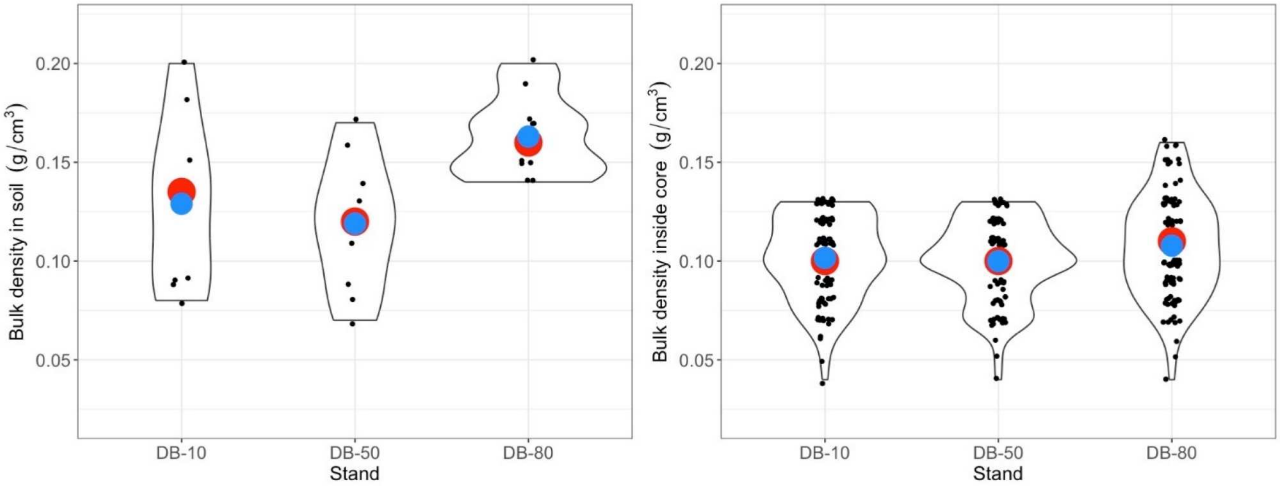

Figure 1. Bulk density (g cm $^{-3}$) of the soil and inside the soil core for DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand) sites. The red dot shows the median, and the blue dot is the mean value. Black dots indicate individual measurements. The lines on both sides of the dots show the range of estimated densities.

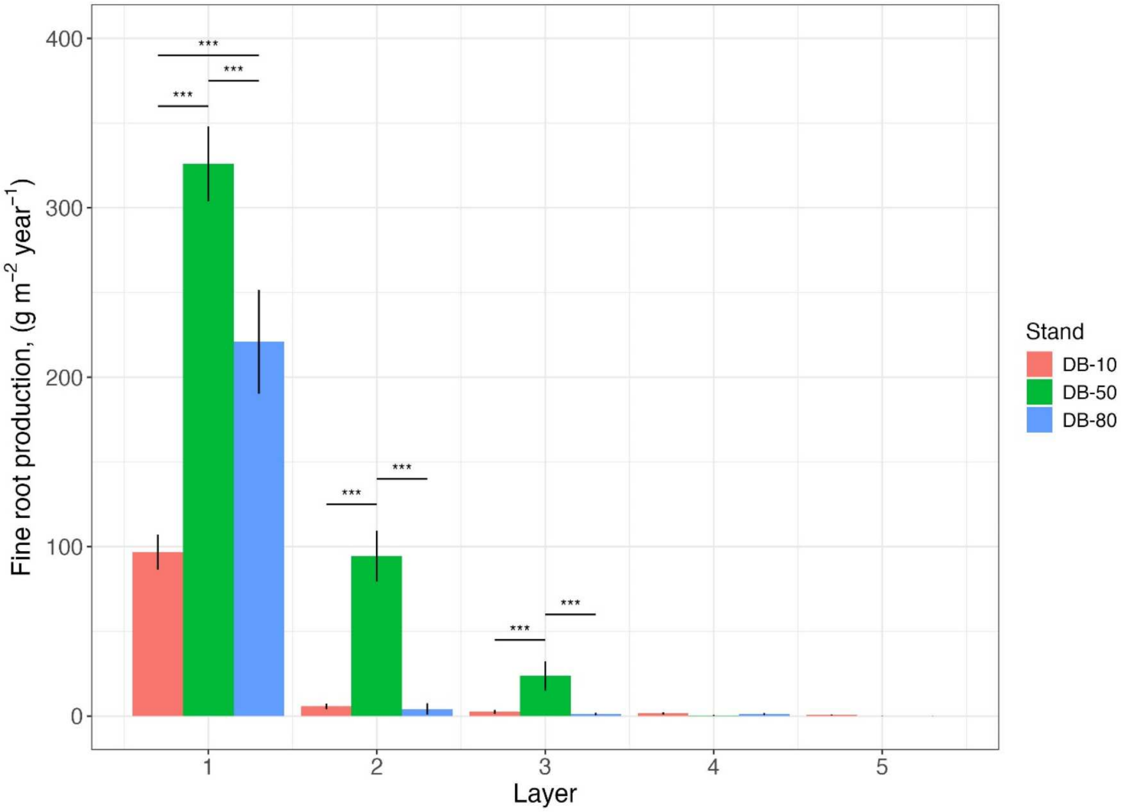

Figure 2. Mean fine root production in three study sites (DB-10, DB-50, and DB-80) on drained peatland forests. Error bars show standard errors of the mean. Layer 1: 0–10 cm depth from moss surface; layer 2: 10–20 cm; layer 3: 20–30 cm; layer 4: 30–40 cm; layer 5: 40–50 cm. Asterisks indicate statistical significance: ***$p <$ 0.001 (Results of the paired t-tests presented in the Tables A2 and A3 in the appendix).

Discussion

Fine root biomass and soil bulk density

The bulk density of peat within the cores closely matched the surrounding soil, ensuring that root ingrowth conditions were representative of the drained forest environment. While Steingrobe et al. (2000) noted that lower-than-ambient soil density does not hinder root ingrowth, higher-than-ambient density can restrict it, potentially leading to underestimation of root production. However, despite differences in site types, the carbon and nutrient content of the peat (0–20 cm) remained relatively similar across stands (Table 2), with total soil carbon ranging from 128750 to 154516 kg ha^{-1} and moderate variation in nitrogen, phosphorus, and potassium levels. This consistency suggests that differences in FRB are primarily driven by stand age rather than major soil fertility disparities. To further minimize potential biases in root production

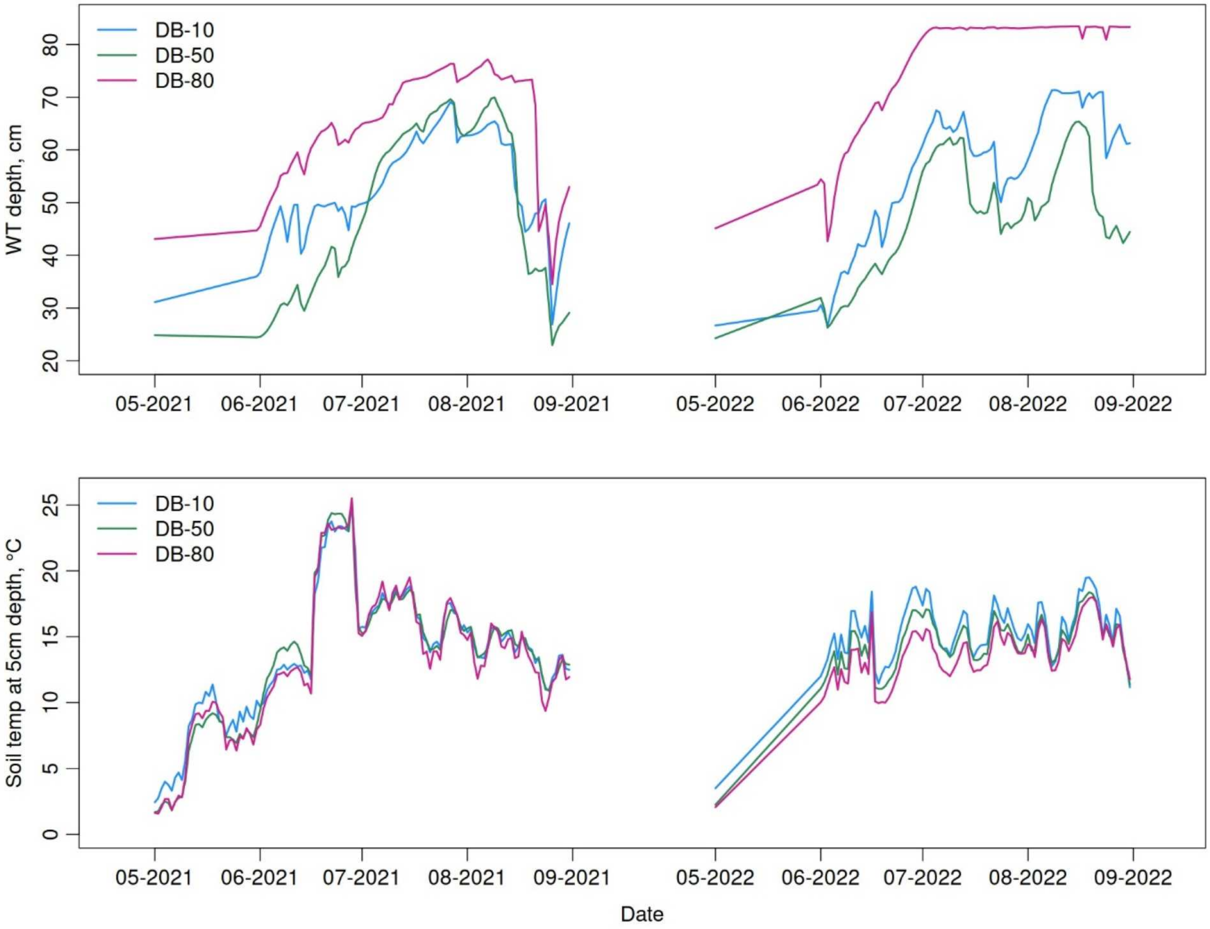

Figure 3. Soil temperature (°C) at 5 cm depth and water table (cm) from the surface for DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand) sites for the year 2021–2022 (May-August).

estimates, we recommend using fresh peat when filling ingrowth cores to better replicate the natural soil conditions.

We recognize the limitations of using ingrowth cores to measure belowground production, especially after just one year. The disturbance caused during core installation and the differences between soil conditions inside and outside the cores – such as the initial absence of roots in the cores and variations in peat substrate characteristics – can result in both overestimations and underestimations of production rates (Laiho et al. 2014). In our study, these limitations are particularly relevant as the variability in peatland conditions may further influence the accuracy of FRP estimates obtained using this method. While this method is particularly effective for estimating the growth of roots less than 2 mm in diameter over one year, it tends to underestimate the production of larger roots (>2 mm) (Finér and Laine 2000). Therefore, we interpret our FRP values as an estimate of potential fine root growth, assuming that the observed variations between sites provide a reliable indication of differences in actual FRP (Vogt et al. 1998; Finér and Laine 2000).

Figure A1. The recovered ingrowth core bag filled with deep horizon *Sphagnum* peat after defrosting from the refrigerator. The measuring tape shows the length of the core bag.

Estimating the true value of FRP involves inherent uncertainties due to methodological limitations and natural variability (Milchunas 2009). Despite these challenges, our findings offer valuable insights into fine root dynamics in drained peatland ecosystems and provide a useful approximation of root production under varying stand conditions.

Fine-root production in peatland forests

Our FRP estimates of 0.1–326 g m^{-2} yr^{-1} were clearly higher than those obtained earlier with the previous studies from forestry-drained peatlands. For instance, Lampela et al. (2023) reported mean FRP values ranging from 30.7 g m^{-2} yr^{-1} in an herb-rich hardwood-spruce swamp drained forest to 119.9 g m^{-2} yr^{-1} over a two-year ingrowth core incubation period in a tall-sedge pine fen drained forest in southern Finland. While their estimates fall within the lower to mid-range of our results, our maximum FRP values are substantially higher, likely due to the presence of nutrient-rich peat and less severe drainage impacts at our study sites in drained forest peatlands. Our sites predominantly feature downy birch, a fast-growing species that promotes greater root biomass, while Lampela et al. (2023) focused on the partly drained Lakkasuo raised bog, which may have more limited nutrient availability and less favorable moisture conditions. Additionally, our sites benefit from enhanced microbial activity and specific forest management practices, such as selective logging and controlled drainage, which optimize conditions for fine root growth, thereby contributing to the observed differences in FRP (Xu et al. 2021; Duchesneau et al. 2024).

Finér and Laine (2000) found mean FRP for Scots pine roots less than 2 mm in diameter ranging from 60 to 225 g m^{-2} yr^{-1} over three years using ingrowth cores in southern Finland, which aligns well with the higher end of our FRP range. Similarly, Finér and Laine (1998) reported comparable or lower FRP estimates in bog forests using the sequential coring method, suggesting that our study captured a wider variation in root production, potentially due to differences in site conditions or methodological approaches. Murphy et al. (2009) estimated mean FRP at 62 g m^{-2} yr^{-1} for Scots pine on drained nutrient-poor boreal bog forests in central Finland from a 1-year incubation period ingrowth core biomass data, and Murphy and Moore (2010) reported 108 g m^{-2} yr^{-1} for pristine but naturally dry bog forests dominated by Woody, ericaceous shrubs and sporadically grey birch (*Betula populifolia*) obtained from a1-year biomass data in Southern Canada – both falling within the mid-range of our findings. The concentration of total FRP in the top 0–20 cm of the peat soil at both sites, accounting for more than 90% of total FRP, is consistent with previous studies on FRB and FRP in peatland forests (Ruseckas 2000; Murphy and Moore 2010).

The variability in our FRP values reflects the complexity of peatland ecosystems and highlights the influence of stand development stage and local environmental factors on root dynamics. While drainage history may play a role in shaping fine root traits, our study design does not allow for direct assessment of its effects, as we lack untreated control sites or sites with varying drainage regimes. Several factors may have contributed to the higher FRP observed in the drained peatland forest sites. In general, above-ground biomass and production are higher in nutrient-rich drained peatland sites compared to nutrient-poor drained peatlands and undrained peatlands. These nutrient-rich sites also tend to have deeper water table levels, resulting in more oxygenated peat, which favors the growth of trees and other vascular plants. The higher nutrient availability at our study sites likely contributed to the elevated FRP observed, consistent with the general hypothesis that nutrient-rich conditions favor more extensive root systems. However, it is important to note that our findings focus on specific site conditions – namely, drained peatlands with varying ages of downy birch stands – so direct comparisons with other sites, such as those with pine or spruce dominance, may not be fully applicable. While other studies, like Lampela et al. (2023), have observed higher FRP in nutrient-poor, pine-dominated sites, this discrepancy underscores the complexity of FRP dynamics and suggests that factors like tree species composition and nutrient requirements can significantly influence root productivity in different environments.

Given that this study examined only three sites from the wide diversity of drained peatland forests, further research encompassing a broader range of conditions is necessary to better understand the main factors influencing FRP and the associated carbon fluxes it mediates in peatland ecosystems. Our study revealed that FRP was highest in the middle-aged stand (DB-50) compared to the young (DB-10) and matured stands (DB-80). The FRP-to-FRB ratio, indicating root turnover, was higher in the DB-50 stand, ranging from 0.4–1.7, while it ranged from 0.4–0.9 in DB-10 and 0.5–0.6 in DB-80 (results not shown). Fine root turnover, which reflects the rate at which fine root litter is added to the soil, plays a crucial role in belowground carbon cycling and nutrient dynamics. Estimating carbon flux mediated by fine roots requires precise measurements of both FRB and FRP. Our results reveal significant vertical and horizontal variations in root biomass across the study sites, underscoring the importance of accurately characterizing root distribution to improve predictions of carbon cycling and inform land management strategies in drained peatlands.

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Author contributions

Conceptualization, Formal analysis: M.R.K and J.A; investigation: M.R.K and S.S; data curation, writing – review and editing: M.R.K, J.A, K.R.G, and S.S; writing – original draft preparation: M.R.K and J.A.

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Generative Artificial Intelligence (AI)

The ChatGpt 4 (basic version) was utilized for language improvement, according to the Taylor & Francis AI Policy.

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Appendix

Table A1. paired two sample t-test for means of soil bulk density (g cm^{-3}) and core soil bulk density (g cm^{-3}, N = 30).

	Core bulk density, g cm^{-3}	Soil bulk density, g cm^{-3}
Mean	0.103933333	0.137
Variance	0.000360892	0.001359655
Observations	30	30
Pearson Correlation	0.459972473	
Hypothesized Mean Difference	0	
df	29	
t Stat	−5.521003251	
P(T<=t) one-tail	0.000003	
t Critical one-tail	1.699127027	
P(T<=t) two-tail	0.000006	
t Critical two-tail	2.045229642	

Table A2. Analysis of Variance (ANOVA) for Fine Root Production (FRP) and soil layer depth for the year 2021.

Source of Variation	Sum of Squares (SS)	Degrees of Freedom (df)	Mean Square (MS)	F-Value	*P*-Value	F-Crit
Between Groups	120453.13	1	120453.13	10.04	0.002	4.007
Within Groups	695719.46	58	11995.16			
Total	816172.60	59				

Table A3. Analysis of Variance (ANOVA) for Fine Root Production (FRP) for the year 2022.

Source of Variation	Sum of Squares (SS)	Degrees of Freedom (df)	Mean Square (MS)	F-Value	*P*-Value	F-Crit
Between Groups	55809166.54	1	55809166.54	4652.99	<0.0001	4.007
Within Groups	695666.96	58	11994.26			
Total	56504833.50	59				