Scandinavian Journal of Forest Research

ISSN: 0282-7581 (Print) 1651-1891 (Online) Journal homepage: www.tandfonline.com/journals/sfor20

Foliar and coarse root biomass in three forestry-drained boreal peatlands dominated by Downy birch (Betula pubescens Ehrh.)

Md Rezaul Karim, Katja T. Rinne-Garmston & Sakari Sarkkola

To cite this article: Md Rezaul Karim, Katja T. Rinne-Garmston & Sakari Sarkkola (21 Jan 2026): Foliar and coarse root biomass in three forestry-drained boreal peatlands dominated by Downy birch (Betula pubescens Ehrh.), Scandinavian Journal of Forest Research, DOI: 10.1080/02827581.2026.2618219

To link to this article: https://doi.org/10.1080/02827581.2026.2618219

SCANDINAVIAN JOURNAL OF FOREST RESEARCH
https://doi.org/10.1080/02827581.2026.2618219

Taylor & Francis
Taylor & Francis Group

Foliar and coarse root biomass in three forestry-drained boreal peatlands dominated by Downy birch (Betula pubescens Ehrh.)

Md Rezaul Karim, Katja T. Rinne-Garmston and Sakari Sarkkola

Natural Resources Institute Finland (Luke), Helsinki, Finland

ABSTRACT

Stand biomass in boreal forests has gained recognition for its crucial role in carbon cycling. While stand biomass is influenced by multiple factors, including stand age, tree species, and site fertility, stand age is often considered the most important factor. Most research has focused on conifer stands, with limited attention to foliage biomass and belowground biomass in peatland sites dominated by deciduous tree species. This study examined foliage and coarse root biomass allocation in three downy birch (Betula pubescens Ehrh.) stands on drained peatland sites in Central Finland. The stands represented three developmental classes: young (10 years), middle-aged (50 years), and mature (80 years). Results showed that foliage biomass ranged from 0.7 t ha^{-1} to 6.6 t ha^{-11}, peaking in the middle-aged stand compared to the young and mature stands. Additionally, coarse root biomass in the 0–50 cm peat layer totaled 0.45 t ha^{-1}, 2.50 t ha^{-1}, and 1.10 t ha^{-1} for the young, middle-aged, and mature stands, respectively, with 77% occurring in the top 20 cm layer. These findings enhance our understanding of biomass allocation patterns, particularly foliage biomass, over time and their impact on litter inputs into the soil.

ARTICLE HISTORY
Received 14 August 2025
Accepted 10 January 2026

KEYWORDS
Above-ground biomass; coarse root biomass; forest peatland; stand age; tree diameter

Introduction

Forests have the potential to positively impact climate change by reducing atmospheric carbon dioxide (CO_2) and sequestering C over the short- or mid-term (Beedlow et al. 2004). They act as carbon sinks in terrestrial biomes, comprising about 80% of the global aboveground biomass (AGB) (Ometto et al. 2014). However, due to increasing demands for forest resources, the forest ecosystem is changing rapidly (Perea-Moreno et al. 2019). Therefore, the tree AGB plays a crucial role in estimating and monitoring forest carbon stocks (Dulamsuren et al. 2019). Further, tree AGB estimations allow us to understand the interaction between forest growth and biomass productivity (Chave et al. 2005). Research has shown that tree AGB yield is affected by factors such as stand age, tree species, and site fertility, with stand age being considered the most important factor (Jagodziński et al. 2018; Schepaschenko et al. 2018).

Foliage (leaves) biomass, in terms of quantity, is not the most important biomass pool in a forest ecosystem. Nevertheless, due to its short lifespan, it has great potential to contribute to carbon dynamics in addition to photosynthesis and respiratory functions. On the other hand, the woody parts of the tree, such as stems, branches, and bark, store carbon for a longer period, as they remain active throughout the tree's life, thus contributing to forests' long-term carbon storage (Thornley and Cannell 2000). The relationship between stand age and leaf biomass is complicated and the stand structure, such as stand age, stand density, canopy depth, and tree size influence light level and light intensity, and therefore leaf biomass. For instance, Starr et al. (2005) reported a weak negative correlation between stand age (35 to over 200 years) and foliage biomass production in Scot's pine (*Pinus sylvestris* L.) stands in Finland. Yet counterintuitively a small set of studies suggested foliage biomass could increase with the increment of stand age (Vanninen et al. 1996; Hu et al. 2020).

In forest ecosystems, roots are important contributors to net primary production and play a crucial role in carbon cycling (Prescott et al. 2016). Fine and coarse root fractions are distinguished based on their diameter and exhibit different morphological and functional characteristics, decomposition dynamics, and resource availability responses (Litton et al. 2007). Based on a widely accepted definition, 2 mm diameter is considered the limit between the coarse roots and fine roots (Vogt

CONTACT Md Rezaul Karim ext.rezaul.karim@luke.fi Natural Resources Institute Finland (Luke), Latokartanonkaari 9, Helsinki 00790, Finland

et al. 1995). While fine roots (<2 mm) play a crucial role in resource acquisition and contribute to soil carbon and nitrogen input through rapid turnover, coarse roots (>2 mm) are perennial, support fine root networks, transport water and nutrients, store carbohydrates, and provide physical support for aboveground biomass (Landsberg and Sands 2011), accounting for up to 80% of belowground biomass (Butnor et al. 2003) and 10–20% of net primary productivity (NPP) (Maier et al. 2004). Further, coarse roots contribute to long-lived wood biomass formation (Mobley et al. 2013), which persists for decades following senescence (Johnsen et al. 2001; Ludovici et al. 2002; Anderson et al. 2018) and is vital for forests ecosystem carbon storage over the long-term (Walker et al. 2019).

Birches are an abundant deciduous tree genus in Northern Europe, the Baltic Sea region, and Northwestern Russia (Niemistö et al. 2008). For example, downy birch (Betula pubescens Ehrh.) and silver birch (Betula pendula Roth.) make up a significant proportion of the total volume of growing stocks in the region, with 16% in Finland, 11–16% in other Nordic countries, and 17–28% in the Baltic countries (Korhonen et al. 2007; Hynynen et al. 2010). According to the Finnish National Forest Inventory (NFI11), the total area of birch-dominated stands on drained peatlands is ca 600 000 ha (Korhonen et al. 2007). Further, downy birch is a primary succession tree on drained peatland sites in Finland and plays a significant role in the pulp and paper industry, as well as contributing to forest biodiversity. Despite being an important tree species in boreal forest ecosystems, the succession and biomass allocation of downy birch is not well understood (Lehtonen et al. 2004; Wirth et al. 2004).

Our aim of this study was to estimate the foliage and coarse root biomass (CRB) at different stages of the succession of downy birch stands on drained forested peatlands in Central Finland during three successive years (2019–2021). The stand succession was categorized into three distinct developmental stages: young stand (stand age approximately 10 years), middle-aged stand (app. 50 years), and mature stand (app.80 years). We hypothesize that foliage biomass peaks in middle-aged stands due to optimal light availability and stand density, while coarse root biomass increases with stand age due to greater nutrient accumulation and structural support requirements, reflecting successional changes in downy birch-dominated drained peatlands.

Materials and methods

Study sites

Three naturally established downy birch-dominated stands, growing on forestry-drained peatland sites located in Juupajoki, Central Finland (N 61°50′36.542″, E 24°17′37.010″), were included in the study to investigate the effect of stand age (Table 1). The area belongs to the southern boreal forest zone (Ahti et al. 1968). The mean ages of the trees within the stands were 10, 50, and 80 years, representing a chronology of young, middle-aged, and mature stands, respectively (Table 1). According to Hynynen et al. (2010), the maximum rotation length of downy birch is 70–80 years due to biological ageing, with decreased growth and an increased risk of rot. Thus, in our study, the 80-year-old birch stand is considered mature.

The Nälkärasinsuo site (young stand) is part of a regeneration experiment established in winter 2007 on a spruce-dominated peatland that had been clear-cut in 2006. Following harvesting, a dense cover of naturally regenerated downy birch (Betula pubescens Ehrh.) emerged. The seedlings were selectively thinned in 2016 to maintain a dense birch canopy, and no further silvicultural treatments have been applied since. The site was originally drained in the 1930s and is currently classified as a herb-rich drained peatland forest (Rhtkg, Vasander and Laine 2008, Table 1).

The Rajasuo site (middle-aged stand) has been monitored since 1961 as a permanent sample plot

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[a]	Rhtkg (herb-rich type)	Mtkg II (Vaccinium myrtillus- type)	Rhtkg (herb-rich type)
Stand age (years)	10	50	80
Study area (ha)	0.06	0.01	0.06
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
Mean DBH (cm)	4.5 ± 0.2	8.9 ± 0.2	12.9 ± 0.5
Mean H (m)	4.6 ± 0.1	11.4 ± 0.8	16.7 ± 0.7
N, trees (ha^{-1})	2767	4600	2883

[a] Vasander and Laine (2008). DBH: diameter at breast height; H: tree height; N: stand density; H_{dom}: stand dominant height. For DBH and H, the standard error is presented.

representing a spruce–birch mixed stand that naturally regenerated on a previously drained spruce peatland. According to the Finnish classification system for drained peatland forests (Vasander and Laine 2008), the site is classified as a Vaccinium myrtillus (Mtkg II) type (Table 1). The area was initially drained in 1950, and pre-commercial thinning of the seedling stand was conducted in the mid-1970s; no further silvicultural treatments have been applied.

The Loukaskorpi site (mature stand) represents the development of a two-storied, unmanaged stand on a drained peatland, consisting of a dense downy birch overstorey and a Norway spruce (Picea abies) understorey. The stand naturally regenerated after clear-cutting in the early 1930s. A light thinning of the birch overstorey was conducted in 1958, and no further management has been applied. The site was originally drained in 1909, with supplementary ditching in the 1920s and 1964, and is classified as a drained herb-rich peatland forest (Rhtkg, Vasander and Laine 2008, Table 1).

The mean drainage depth (ditch depth) at the sites ranged between 0.3–0.8 m, and the ditch embankment heights were approximately 0.2–0.5 m. At the time of the study, peat depths at the sites varied between 0.7 and 1.2 m (Table 1). In early summer 2021, soil samples were collected from the study sites at depths of 0–10, 10–20, 20–30, 30–40, and 40–50 cm. A total of fifteen samples were collected, with five samples taken from each site. Bulk density was determined by drying the peat samples of known volume at 105 °C overnight (Blake and Hartge 1986).

In 2019, rectangular sample plots ranging in size from 100 to 600 m^2 – depending on the density of the stands – were established at all studied sites (Table 1). Plot size was adjusted so that each plot contained a representative number of trees and reflected the structural variability within each stand. The plot centers were in visually homogeneous areas of the stands, avoiding edges, ditches, and other irregular features to minimize boundary effects. Within each plot, measurement locations for soil cores and litter traps were selected systematically along transects crossing the plot diagonally to ensure spatial representativeness of the samples. Standard tree characteristics, including tree species, diameter at breast height (1.3 m, DBH), and height (H), were measured for all trees using a diameter tape and a hypsometer (Vertex III and Transponder T3, Haglöf Sweden AB). In autumn 2020, soil temperature data loggers (iButton, model 1921G, Dallas Semiconductor Corp.) were installed at depths of 5 cm and 30 cm at each site to monitor soil temperatures, which were automatically recorded at 3-hour intervals. Additionally, water table data loggers (Odyssey® capacitance water logger, Dataflow Systems Limited © 2022) were installed at a depth of 2 m to track water levels, which were recorded every 30 minutes from October 2020 to October 2022.

Litterfall

To determine foliage biomass, we measured annual litterfall for three years (2019–2021). Litterfall was collected using seven plastic tube traps per site (Laasasenaho 1982), which were on the ground at a height and diameter of 52 cm and 47.5 cm, respectively (Figure 1). Traps were equipped with polyester textile bags, and six evenly spaced drainage holes (0.5 cm) were drilled at the bottom to drain water and reduce moisture-driven decomposition. Twelve rectangular traps (0.5 m^2, four traps per site) on the ground were used to collect herbaceous litterfall and were constructed of net mesh (1 × 1 cm^2).

Traps were collected twice per month during the most productive period of the growing season (June–August) and left in place over autumn and winter (September–February), with accumulated litter collected in late spring (May) to produce annual litterfall estimates. This approach follows common practice in cold-climate studies because decomposition during the frozen winter period is typically very slow, and most mass loss over the non-growing season is attributable to leaching rather than microbial breakdown (Bokhorst et al. 2013; Blok et al. 2016; Venn and Thomas 2021). To minimize decomposition and moisture-driven mass loss during winter, we used textile collection bags and drainage holes in the buckets to prevent prolonged waterlogging and reduce anaerobic decomposition; the trap design also limits macrofaunal access. We note, however, that some winter leaching or minor winter decomposition may occur under certain conditions (e.g., variable snow

Figure 1. Foliage biomass collectors installed in a drained peatland forest for litterfall measurement.

insulation or freeze–thaw events), and we include this as a caveat in the discussion.

The litter samples were sorted into leaves, needles, branches, and other parts (seeds, bark, buds, etc.) and weighed for fresh mass. The samples were then dried at 105°C for 24 hours, after which we measured the dry mass (ME-T, Mettler Toledo group, Switzerland). Oven-dry foliage (leaves) biomass for the growing season (December–January) was calculated as t ha^{-1} yr^{-1}. The foliage sample analyses were carried out at the Natural Resources Institute Finland (Luke).

Belowground biomass

Coarse root

The CRB was measured using the soil coring technique as described by Varik et al. (2013), in October 2020. In all studied stands, ten soil cores (depth to 50 cm) were obtained using a cylindrical corer with a diameter of 46 mm. Sampling locations were selected systematically within each stand to represent the average site conditions, avoiding tree bases, drainage ditches, and visibly disturbed areas. To capture the variability across different depths, the soil cores were divided into five (Varik et al. 2013) layers (0–10; 10–20; 20–30; 30–40, and 40–50 cm) and subsequently placed in polyethylene bags. The samples were then transported to the laboratory and immediately stored at -18 °C until analysis.

The roots were thoroughly washed to remove any attached soil and sorted into four categories based on their diameter ranges: $d < 2$ mm, 2 mm $\leq d < 5$ mm, 5 mm $\leq d < 10$ mm, and $\geq$ 10 mm. At all sites, coarse roots were combined without distinction by tree species or understory functional groups; they were treated as total roots. The roots were dried at 60 °C for 24 hours and weighed to 1-mg precision (ME-T, Mettler Toledo group, Switzerland). A drying temperature of 60 °C was used for roots to prevent thermal degradation and loss of volatile compounds, while a higher temperature (105 °C) was used for litter to ensure complete removal of moisture. The CRB per square meter was calculated by summing up the average values of coarse root mass for the successive soil layers from the soil cores. However, the fine root fraction ($d < 2$ mm) was not included in this calculation due to significant losses (65–75%) reported in previous studies (Uri et al. 2002).

Statistical analysis

We used repeated measures analysis of variance to evaluate the differences in CRB in the soil depth in all three stands. Stand age was to be a between-subjects (grouping) factor, and depth (layer within a core) was the within-subjects (repeated) factor. For foliage biomass and coarse root biomass, post hoc tests were conducted to identify pairwise differences among age groups. Specifically, Least Significant Difference (LSD) tests were applied to foliage biomass (Table A2), while Tukey HSD, LSD, and Bonferroni tests were applied to coarse root biomass (Table A3). Different post hoc tests were used to verify the robustness and consistency of the results across multiple comparison methods with varying levels of stringency. The LSD test was selected for foliage biomass because it provides higher sensitivity when the number of groups is limited, while multiple tests were applied for coarse root biomass to confirm that the significant differences among age groups were consistent regardless of the correction method. The results were highly similar across tests, supporting the reliability of the observed differences. All statistical tests were evaluated at significance levels of $\alpha = 0.05$ and $\alpha = 0.001$, depending on the strength of the observed differences. All analyses were carried out using IBM SPSS Statistics 25 and R software (v3.6.0) (R Core Team 2013).

Results

Foliage biomass dynamics across stand ages

The biomass of dry foliage (leaves) from litter fall ranged from 0.7 to 6.6 t ha^{-1} and total biomass from 1.5 to 13.3 t ha^{-1} (Figure 2). The effect of stand age on dry foliage biomass was statistically significant, indicating that there is likely a relationship between the age of a stand and the amount of dry foliage biomass it produces (ANOVA, $p < 0.05$). The middle-aged stand showed a statistically significant difference, while the young and mature stands did not differ significantly from each other in the LSD Post Hoc test (Table A2).

The middle-aged stand appeared to peak in foliage biomass more than the other stands during the studied years (Figure 2). In 2020, DB-50 reached its peak with a mean dry foliage biomass of 6.6 ± SE 1.3 t ha^{-1}, corresponding to a total of 13.3 t ha^{-1}. In 2021, the mean biomass was 4.7 ± 0.5 t ha^{-1} (total 9.5 t ha^{-1}), and in 2019 it was 2.7 ± 0.7 t ha^{-1} (total 5.4 t ha^{-1}). The mature stand (DB-80) ranked second, with mean biomass values of 5.0 ± 0.4 t ha^{-1} in 2020 (total 10.0 t ha^{-1}), 3.5 ± 0.2 t ha^{-1} in 2021 (total 7.0 t ha^{-1}), and 2.1 ± 0.2 t ha^{-1} in 2019 (total 4.2 t ha^{-1}). The young stand (DB-10) consistently showed the lowest foliage biomass, with mean values of 0.7 ± 0.5 t ha^{-1} in 2019 (total 1.5 t ha^{-1}), 1.5 ± 1.0 t ha^{-1} in 2020 (total 3.0 t ha^{-1}), and 1.1 ± 0.2 t ha^{-1} in 2021 (total 2.2 t ha^{-1}). Across all years, the results clearly indicate that foliage biomass increases with stand age, with the middle-aged and mature stands

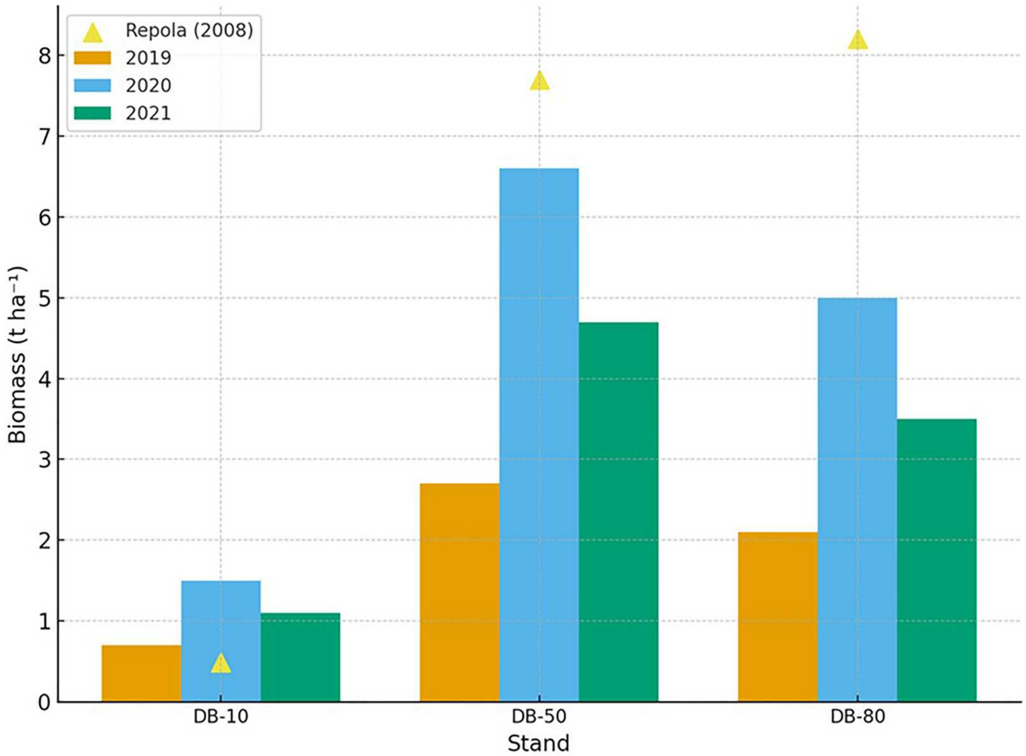

Figure 2. Mean dry foliage biomass (t ha^{-1}) measured from litter fall across three Downy birch stand age classes (DB-10, DB-50, DB-80) and three measurement years (2019, 2020, 2021) in drained peatlands. Mean foliage biomass estimated by the biomass equation of Repola (2008) for downy birch is shown as triangle markers for comparison. DB-10: Young stand; DB-50: Middle-age stand; DB-80: Mature stand. Bars represent the standard error of means (SE). Results of the post-hoc tests are provided in Appendix Table A2.

supporting substantially higher foliage production compared to the young stand.

The foliage biomass results were compared with estimates derived from the allometric equations by Repola (2008) (Figure 2), which revealed both underestimations and overestimations that varied by stand age and year. For the young stand (DB-10), the Repola (2008) equation estimated 0.49 t ha^{-1}, which was lower than the measured biomass in all years (0.7, 1.5 and 1.1 t ha^{-1} in 2019, 2020 and 2021, respectively). For the middle-aged stand (DB-50), the predicted biomass of 7.7 t ha^{-1} exceeded the measured values in 2019, 2020 and 2021 (2.7, 6.6 and 4.7 t ha^{-1}, respectively). Similarly, the mature stand (DB-80) was overestimated by the equation (8.2 t ha^{-1}), compared with measured biomass of 2.1, 5.0 and 3.5 t ha^{-1} in 2019, 2020 and 2021, respectively.

DB-80: Mature stand. Bars represent the standard error of means (SE). Results of the post-hoc tests are provided in Table A2.

Distribution and allocation of coarse root biomass

Coarse root biomass of downy birch stands in the 0–50 cm peat layer totaled 0.45 t ha^{-1}, 2.50 t ha^{-1}, and 1.10 t ha^{-1} in the young, middle-aged, and mature stands, respectively (Table 2). All three stands showed

Table 2. Coarse root biomass (t ha^{-1}) with standard deviation (SD), standard error (SE), minima and maxima by depth in the drained forests. N = 10 for each site.

	DB-10 (Rhtkg)				DB-50 (Mtkg II)				DB-80 (Rhtkg)			
Depth, cm	Mean	SD	SE	Min–Max	Mean	SD	SE	Min–Max	Mean	SD	SE	Min–Max
0–10	0.25^{a}	0.14	0.04	0.0–0.55	0.90^{c}	0.42	0.13	0.0–1.50	0.30^{b}	0.19	0.06	0.0–0.60
10–20	0.10^{a}	0.09	0.03	0.0–0.34	0.80^{c}	0.43	0.13	0.0–1.55	0.21^{b}	0.14	0.04	0.0–0.46
20–30	0.06^{a}	0.03	0.01	0.0–0.10	0.40^{b}	0.34	0.11	0.0–1.25	0.45^{b}	0.23	0.07	0.0–0.78
30–40	0.04^{a}	0.03	0.01	0.0–0.10	0.30^{b}	0.30	0.09	0.0–1.10	0.05^{a}	0.05	0.01	0.0–0.17
40–50	0.0^{a}	0.0	0.0	0.0–0.0	0.10^{b}	0.15	0.04	0.0–0.46	0.09^{b}	0.08	0.02	0.0–0.28
Total 0–50	0.45^{a}	0.30	0.09	0.0–1.09	2.50^{c}	1.65	0.52	0.0–5.86	1.10^{b}	0.71	0.22	0.0–2.29

Notes: DB-10: Young stand; DB-50: Middle-age stand; DB-80: Mature stand. Rhtkg = herb-rich type; Mtkg = Vaccinium myrtillus-type (Vasander and Laine 2008). Letters indicate post-hoc results means sharing the same letter are not significantly different, different letters show significant differences at $p < 0.05$.

Table 3. Repeated measures analysis of Variance on the effects of stand age (young, middle-aged, and mature) on coarse root biomass (g m^{-2}). Data are from cores and were divided into five 10-cm layers per core (within-factor Depth).

Effect	df	MS	F	*P*
	Between subject			
Stand age	2	11024	27	<0.001
Error	147	415		
	Within subject			
Depth	1	43344	94	<0.001
Depth × Stand age	2	11024	24	<0.001
Error	147	459		

statistically significant differences in CRB allocation by depth (Table 3, Figure 3).

The largest share of the coarse root biomass (55%) was in the upper 10 cm soil layer (Figure 3). Most of the CRB was allocated within the upper 0–30 cm layer, showing a consistent depth-wise distribution pattern across all sites (Figure 3). Depth and stand age were statistically significant, indicating differing CRB depth profiles for the stands (Table 3, Figure 3, $p < 0.001$). On the other hand, the largest diameter ($d \geq 10$ mm) accounted for 68% of the total coarse root biomass (data not shown). The corresponding shares of the root fractions $5 \leq d < 10$ mm and $2 \leq d < 5$ mm were similar (17% and 15%, respectively).

The results of ANOVA showed that the stand age effect on coarse root biomass was significant ($p < 0.05$); the effect of the depth of the soil layer was also statistically significant ($p < 0.001$). Further, according to multiple comparisons of the mean, all three stands showed significant differences in coarse root biomass (LSD test; $p < 0.05$; Table A3).

Seasonal variation in soil temperature and water table levels

The seasonal (May–November) soil temperature and water table levels were measured across young (DB-10), middle-aged (DB-50), and mature (DB-80) downy birch stands in 2021 and 2022 (Figures 4 and 5, Table A1). These data are presented as background information to describe site-specific growing conditions during the study years, providing context for interpreting stand-level biomass results. Soil temperature (at 5 cm depth) showed significant variation across the years and stands, with higher values recorded in 2022. Temperatures ranged from 9.96 ± 5.95°C to 15.74 ± 5.98°C (Figure 4). Soil water table levels also varied, with the mature stand (DB-80) showing the highest levels, particularly in 2022 (73.53 ± 12.32 cm). Middle-aged and young stands had lower water table levels, highlighting stand-specific and temporal variation in both temperature and hydrological conditions (Figure 5, Table A1).

Discussion

Variability in foliage biomass across stand ages

In this study, our objective was to estimate the foliage and coarse root biomass at different stages of succession in downy birch stands on drained forested peatlands. We observed that foliage biomass in the middle-aged stand was significantly higher than in the young and mature stands. Additionally, our study revealed that the biomass equation by Repola (2008) overestimated

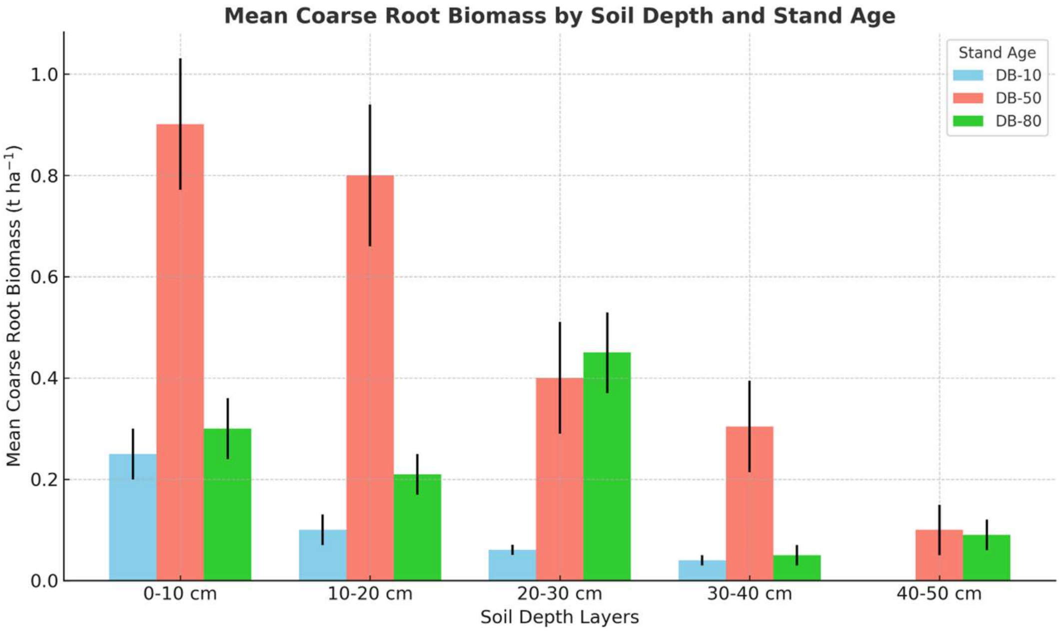

Figure 3. Mean coarse root biomass (t ha^{-1}) in the drained peatland forests. Error bars are standard error of means. Layer 1: 0–10 cm depth from moss surface; layer 2: 10–20 cm; layer 3: 20–30 cm; layer 4: 30–40 cm; layer 5: 40–50 cm.

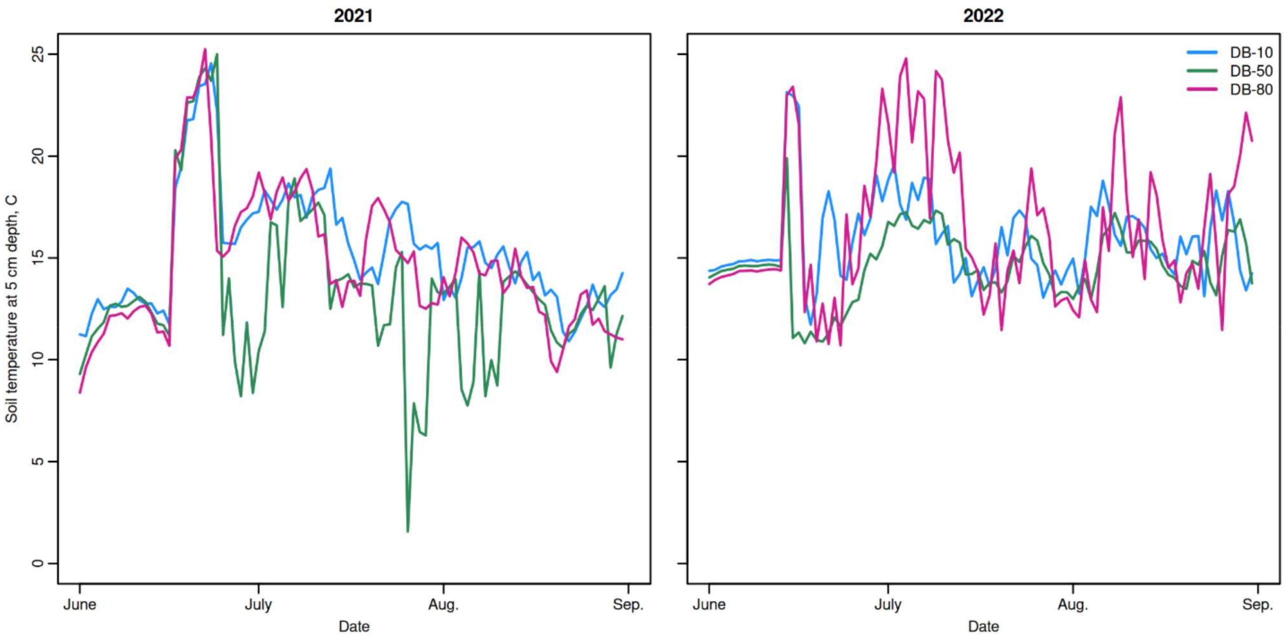

Figure 4. Daily mean soil temperature (°C) at 5 cm depth in DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand) sites (June–September in 2021 and 2022).

the foliage biomass in both the middle-aged and mature stands. This deviation may be attributed to factors such as inter-tree competition, stand structure, stand density, the self-thinning process, and tree relative growth rate, all of which can influence the number of branches and biomass of downy birch trees (Mäkelä and Vanninen 1998). Litter fall in a forest ecosystem provides important insights into the dynamics of nutrient cycling and serves as a primary link between producers and decomposers (Ukonmaanaho et al. 2008). However, estimating the amount of branch and foliage biomass at the level of individual trees within a stand can be difficult because trees exhibit a high degree of variability in their size, shape, and foliage density (Zianis et al. 2005; Teobaldelli et al. 2009). This variability can make it challenging to accurately estimate the amount of biomass present in branches and leaves, as different trees within the same stand may have vastly different amounts of these

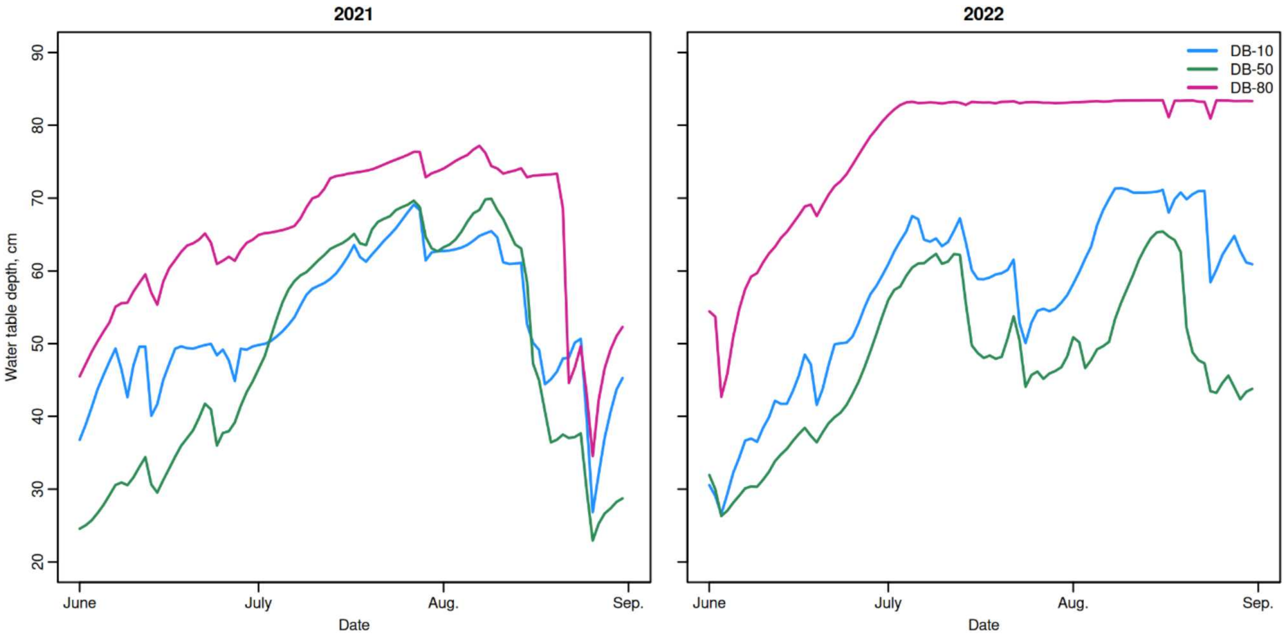

Figure 5. Daily mean water level (cm) at DB-10 (Young stand), DB-50 (Middle-aged stand), and DB-80 (Mature stand) sites (June–September in 2021 and 2022).

materials. Therefore, accurately measuring stand-level branch and foliage biomass requires careful consideration of this variability, as well as the use of appropriate sampling and measurement techniques to ensure accurate and representative estimates (Wojtan et al. 2011; Castedo-Dorado et al. 2012). Further, estimating foliage biomass in matured stands can be difficult because the applicability of biomass equations is often limited to smaller trees, as the variance and potential error increase with stand age (Lehtonen 2005). This result could have important implications for forestry management and conservation efforts, as it suggests that the age of a forest stand can play a significant role in determining its productivity and ecological function. Further research may be needed to explore the specific mechanisms underlying this relationship and to identify strategies for optimizing foliage biomass production in different stand ages.

Stand density is an essential factor that affects tree growth and crown structure by altering the growing space available for individual trees (Lochhead and Comeau 2012; Farooq et al. 2021). In the present study, dry foliage biomass was of the same magnitude in the young and mature stands but notably higher in the middle-aged stand, which can be attributed to its higher stand density, as stand density influences total AGB (Table 1) (Uri et al. 2012). The stem numbers in all the stands indicate that stand density remains high in our unmanaged middle-aged and mature stands due to self-thinning and closed canopy formation. This suggests that in pristine downy birch stands, foliage biomass tends to develop early during succession (Table 1). According to Uri et al. (2012) and Rytter and Rytter (2016), both foliage biomass and leaf area typically increase during the early development stages of deciduous stands until reaching an optimal level and stabilizing, which in fast-growing species like silver birch and grey alder generally occurs between the ages of 5 and 10 years. The proportion of senescent leaves' biomass is closely related to the amount of aboveground litter fall, which can vary between species and years (Ukonmaanaho et al. 2008). For instance, a smaller litter fall biomass may indicate longer foliage retention within the canopy. The consistency of foliage biomass results across successive years in this study suggests that the measured values reflect actual leaf mass rather than being anomalous. It should be noted that our litterfall traps remained in place over the autumn and winter months (September–February) and were collected in late spring (May) to produce annual estimates. While microbial decomposition during the frozen period is generally very slow in boreal conditions, some minor mass loss due to leaching or freeze–thaw events may occur (Bokhorst et al. 2013; Blok et al. 2016; Venn and Thomas 2021), and this potential limitation is acknowledged in the interpretation of foliage biomass estimates.

Belowground biomass allocation and coarse root dynamics

Belowground biomass allocation is a vital aspect of forest productivity, with forests investing 20–65% of their net primary productivity into root and mycorrhizal growth (Landsberg and Sands 2011). However, empirical data on the coarse root biomass of downy birch remain limited. Our results showed that coarse root biomass was highest in the middle-aged stand, likely reflecting the higher nutrient availability at this successional stage. The majority (77%) of coarse roots were located in the upper 20 cm of the soil profile, consistent with patterns of nutrient availability and favorable physical and chemical soil conditions near the surface (Uri et al. 2007). This concentration of roots in the topsoil is typical of forest ecosystems, where nutrient cycling, microbial activity, and oxygen levels are highest, promoting efficient nutrient and water uptake. In contrast, deeper soil horizons – particularly in drained peatlands – are often more compacted, acidic, and anaerobic, with lower nutrient availability, leading to significantly reduced root biomass in these layers (Cairns et al. 1997). This vertical distribution is a clear reflection of tree adaptation to maximize resource acquisition and efficiency under site-specific conditions.

It is important to note that our estimates (0.45–2.50 t ha^{-1}) reflect only the sampled 0–50 cm peat layer and therefore exclude deeper and lateral coarse roots, as well as stumps. For comparison, applying Repola's (2008) allometric functions to the mature stand would yield approximately 39 t ha^{-1} of coarse roots (>1 cm), highlighting that our values represent a partial fraction of the total coarse root system. This difference reflects methodological differences between soil coring and tree-level allometric approaches, with the former capturing only the sampled fraction of the root system.

Trees growing in nutrient-rich environments tend to allocate more biomass to root systems in the upper profile to exploit readily available nutrients and maintain growth (Vanninen et al. 1996). Our results align with this ecological strategy, showing the highest coarse root biomass in the middle-aged stand, likely due to a combination of favorable nutrient availability, optimal stand density, and active belowground growth during that successional stage (Litton et al. 2007). This peak in root development reflects both ontogenetic changes and environmental drivers. Understanding such root distribution patterns is crucial for improving carbon budget assessments and for developing management strategies that support soil health and forest resilience in drained peatland ecosystems.

Understanding belowground biomass distribution is critical for predicting forest responses to environmental changes, such as elevated atmospheric CO_2 levels (Walker et al. 2019). The distribution of coarse roots and their significant allocation to nutrient-rich horizons highlight the need for further research into belowground biomass dynamics across forest successional stages. These insights contribute to a more comprehensive understanding of carbon allocation and nutrient cycling in drained peatland ecosystems.

We acknowledge several limitations of this study. Our analyses were based on only three downy birch stands, each representing a different successional stage, without true replication of stand age classes. Thus, the stands form a chronosequence, where age serves as an indicator of successional stage rather than a directly comparable variable. Differences in drainage history, peat properties, and stand density may also have influenced biomass patterns. Therefore, the findings should be interpreted as site-specific case studies rather than generalized patterns across all drained birch-dominated peatlands. In particular, the middle-aged stand differed from the young and mature stands in both stand density and site type, which may have contributed to the observed differences in foliage biomass in addition to stand age (Table 1). More broadly, the observed differences in foliage and coarse root biomass may reflect not only stand age but also site history, past management interventions, and local environmental conditions. While our results provide novel insights into biomass allocation in drained birch stands, confirmation and broader generalization will require future studies with a larger number of replicated stands across diverse site conditions.

Generative Artificial Intelligence (AI)

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

Acknowledgments

We would like to express gratitude to all laboratory staff at Hyytiälä forestry station in central Finland. Also, many thanks go to Jacqelin De Faveri for the language revisions.

Author contribution statement

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

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

This research was funded by “Marjatta and Eino Kolli foundation”, and “Niemi foundation”, (decision number: 20180001). Katja Rinne-Garmston acknowledges funding from the European Research Council (755865).

References

Ahti T, Hämet-Ahti L, Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. Ann Bot Fenn. 5(3):169–211.

Anderson PH, Johnsen KH, Butnor JR, Gonzalez-Benecke CA, Samuelson LJ. 2018. Predicting longleaf pine coarse root decomposition in the southeastern US. Forest Ecol Manage. 425:1–8. https://doi.org/10.1016/j.foreco.2018.05.024

Beedlow PA, Tingey DT, Phillips DL, Hogsett WE, Olszyk DM. 2004. Rising atmospheric CO_2 and carbon sequestration in forests. Front Ecol Environ. 2(6):315–322.

Blake GR, Hartge KH. 1986. Bulk density. Methods of soil analysis: part 1. Phys Mineral Meth. 5:363–375.

Blok D, Elberling B, Michelsen A. 2016. Initial stages of tundra shrub litter decomposition may be accelerated by deeper winter snow but slowed down by spring warming. Ecosystems. 19(1):155–169. https://doi.org/10.1007/s10021-015-9924-3

Bokhorst S, Metcalfe DB, Wardle DA. 2013. Reduction in snow depth negatively affects decomposers but impact on decomposition rates is substrate dependent. Soil Biol Biochem. 62:157–164. https://doi.org/10.1016/j.soilbio.2013.03.016

Butnor JR, Johnsen KH, Oren RAM, Katul GG. 2003. Reduction of forest floor respiration by fertilization on both carbon dioxide-enriched and reference 17-year-old loblolly pine stands. Glob Change Biol. 9(6):849–861. https://doi.org/10.1046/j.1365-2486.2003.00630.x

Cairns MA, Brown S, Helmer EH, Baumgardner GA. 1997. Root biomass allocation in the world’s upland forests. Oecologia. 111:1–11. https://doi.org/10.1007/s004420050201

Castedo-Dorado F, Gómez-García E, Diéguez-Aranda U, Barrio-Anta M, Crecente-Campo F. 2012. Aboveground stand-level biomass estimation: a comparison of two methods for major forest species in northwest Spain. Ann Forest Sci. 69:735–746. https://doi.org/10.1007/s13595-012-0191-6

Chave J et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia. 145:87–99. https://doi.org/10.1007/s00442-005-0100-x

Dulamsuren C, Klinge M, Bat-Enerel B, Ariunbaatar T, Tuya D. 2019. Effects of forest fragmentation on organic carbon pool densities in the Mongolian forest-steppe. Forest Ecol Manage. 433:780–788. https://doi.org/10.1016/j.foreco.2018.10.054

Farooq TH et al. 2021. Annual growth progression, nutrient transformation, and carbon storage in tissues of Cunninghamia lanceolata monoculture in relation to soil quality indicators influenced by intraspecific competition intensity. J Soil Sci Plant Nutr. 21(4):3146–3158. https://doi.org/10.1007/s42729-021-00595-w

Hu M, Lehtonen A, Minunno F, Mäkelä A. 2020. Age effect on tree structure and biomass allocation in Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* [L.] Karst.). Ann Forest Sci. 77(3):1–15. https://doi.org/10.1007/s13595-020-00988-4

Hynynen J et al. 2010. Silviculture of birch (Betula pendula Roth and Betula pubescens Ehrh.) in Northern Europe. Forestry. 83(1):103–119. https://doi.org/10.1093/forestry/cpp035

Jagodziński AM, Dyderski MK, Gęsikiewicz K, Horodecki P. 2018. Tree-and stand-level biomass estimation in a Larix decidua Mill. Chronosequence. Forests. 9(10):587. https://doi.org/10.3390/f9100587

Johnsen KH et al. 2001. Meeting global policy commitments: carbon sequestration and southern pine forests. J Forestry. 99(4):14–21. https://doi.org/10.1093/jof/99.4.14

Korhonen KT, Ihalainen A, Heikkinen J, Henttonen H, Pitkänen J. 2007. Suomen metsävarat metsäkeskuksittain 2004–2006 ja metsävarojen kehitys 1996–2006. Metsätieteen aikakauskirja. 2B:149–213.

Laasasenaho J. 1982. Taper curve and volume functions for pine, spruce and birch. Commun Inst Forestalis Fenniae. 108:1–74.

Landsberg JJ, Sands P. 2011. Physiological ecology of forest production: principles processes and models. Tree Physiology. 31(6):680–681. https://doi.org/10.1093/treephys/tpr062

Lehtonen A. 2005. Estimating foliage biomass in Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*) plots. Tree Physiol. 25(7):803–811. https://doi.org/10.1093/treephys/25.7.803

Lehtonen A, Mäkipää R, Heikkinen J, Sievänen R, Liski J. 2004. Biomass expansion factors (BEFs) for Scots pine, Norway spruce and birch according to stand age for boreal forests. Forest Ecol Manage. 188(1–3):211–224. https://doi.org/10.1016/j.foreco.2003.07.008

Litton CM, Raich JW, Ryan MG. 2007. Carbon allocation in forest ecosystems. Glob Change Biol. 13(10):2089–2109. https://doi.org/10.1111/j.1365-2486.2007.01420.x

Lochhead KD, Comeau PG. 2012. Relationships between forest structure, understorey light and regeneration in complex Douglas-fir dominated stands in south-eastern British Columbia. Forest Ecol Manage. 284:12–22. https://doi.org/10.1016/j.foreco.2012.07.029

Ludovici KH, Zarnoch SJ, Richter DD. 2002. Modeling in-situ pine root decomposition using data from a 60-year chronosequence. Can J Forest Res. 32(9):1675–1684. https://doi.org/10.1139/x02-073

Maier CA, Albaugh TJ, Allen L, Dougherty H, M P. 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Glob Change Biol. 10(8):1335–1350. https://doi.org/10.1111/j.1529-8817.2003.00809.x

Mäkelä A, Vanninen P. 1998. Impacts of size and competition on tree form and distribution of aboveground biomass in Scots pine. Can J Forest Res. 28(2):216–227. https://doi.org/10.1139/x97-199

Mobley ML, Richter DD, Heine PR. 2013. Accumulation and decay of woody detritus in a humid subtropical secondary pine forest. Can J Forest Res. 43(2):109–118. https://doi.org/10.1139/cjfr-2012-0222

Niemistö P, Viherä-Aarnio A, Velling P, Heräjärvi H, Verkasalo E. 2008. Koivun kasvatus ja käyttö. Metla and Metsäkustannus Karisto Oy, Hämeenlinna, Finland (1–254) [in Finnish].

Ometto JP et al. 2014. Amazon forest biomass density maps: tackling the uncertainty in carbon emission estimates. Clim Change. 124:545–560. https://doi.org/10.1007/s10584-014-1058-7

Perea-Moreno MA, Samerón-Manzano E, Perea-Moreno AJ. 2019. Biomass as renewable energy: worldwide research trends. Sustainability. 11(3):863. https://doi.org/10.3390/su11030863

Prescott C, Godbold DL, Helmisaari HS, Addo-Danso SD. 2016. Introduction to Forests, roots and soil carbon. Forest Ecol Manage. 359:321. https://doi.org/10.1016/j.foreco.2015.11.013

R Core Team. 2013. R: A language and environment for statistical computing.

Repola J. 2008. Biomass equations for birch in Finland. Silva Fenn. 42(4):605–624. https://doi.org/10.14214/sf.236

Rytter L, Rytter RM. 2016. Growth and carbon capture of grey alder (Alnus incana (L.) Moench.) under north European conditions–estimates based on reported research. Forest Ecol Manage. 373:56–65. https://doi.org/10.1016/j.foreco.2016.04.034

Schepaschenko D et al. 2018. Improved estimates of biomass expansion factors for Russian forests. Forests. 9(6):312. https://doi.org/10.3390/f9060312

Starr M, Saarsalmi A, Hokkanen T, Merilä P, Helmisaari HS. 2005. Models of litterfall production for Scots pine (*Pinus sylvestris* L.) in Finland using stand, site and climate factors. Forest Ecol Manage. 205(1-3):215–225. https://doi.org/10.1016/j.foreco.2004.10.047

Teobaldelli M, Somogyi Z, Migliavacca M, Usoltsev VA. 2009. Generalized functions of biomass expansion factors for conifers and broadleaved by stand age, growing stock and site index. Forest Ecol Manage. 257(3):1004–1013. https://doi.org/10.1016/j.foreco.2008.11.002

Thornley JHM, Cannell MGR. 2000. Managing forests for wood yield and carbon storage: a theoretical study. Tree Physiol. 20(7):477–484. https://doi.org/10.1093/treephys/20.7.477

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

Uri V et al. 2007. Biomass production, foliar and root characteristics and nutrient accumulation in young silver birch (Betula pendula Roth.) stand growing on abandoned agricultural land. Eur J Forest Res. 126:495–506. https://doi.org/10.1007/s10342-007-0171-9

Uri V et al. 2012. Biomass production and carbon sequestration in a fertile silver birch (Betula pendula Roth) forest chronosequence. Forest Ecol Manage. 267:117–126. https://doi.org/10.1016/j.foreco.2011.11.033

Uri V, Tullus H, Lõhmus K. 2002. Biomass production and nutrient accumulation in short-rotation grey alder (*Alnus incana* (L.) Moench) plantation on abandoned agricultural land. Forest Ecol Manage. 161(1-3):169–179. https://doi.org/10.1016/S0378-1127(01)00478-9

Vanninen P, Ylitalo H, Sievänen R, Mäkelä A. 1996. Effects of age and site quality on the distribution of biomass in Scots pine (*Pinus sylvestris* L.). Trees. 10:231–238.

Varik M, Aosaar J, Ostonen I, Lõhmus K, Uri V. 2013. Carbon and nitrogen accumulation in belowground tree biomass in a chronosequence of silver birch stands. Forest Ecol Manage. 302:62–70. https://doi.org/10.1016/j.foreco.2013.03.033

Vasander H, Laine J. 2008. Site type classification on drained peatlands. In: Riitta K., Leila K., Sakari S., editor. Finland-Fenland: research and sustainable utilisation of mires and peat. Finnish Peatland Society; p 146–151.

Venn SE, Thomas HJ. 2021. Snowmelt timing affects short-term decomposition rates in an alpine snowbed. Ecosphere. 12(3):e03393. https://doi.org/10.1002/ecs2.3393

Vogt KA et al. 1995. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil. 187:159–219. https://doi.org/10.1007/BF00017088

Walker AP et al. 2019. Decadal biomass increment in early secondary succession woody ecosystems is increased by CO_2 enrichment. Nat Commun. 10:454. https://doi.org/10.1038/s41467-019-08348-1

Wirth C, Schumacher J, Schulze ED. 2004. Generic biomass functions for Norway spruce in Central Europe—a meta-analysis approach toward prediction and uncertainty estimation. Tree Physiol. 24(2):121–139. https://doi.org/10.1093/treephys/24.2.121

Wojtan R et al. 2011. Trees and their components biomass expansion factors for Scots pine (*Pinus sylvestris* L.) of western Poland. Sylwan. 155(4):236–243.

Zianis D, Muukkonen P, Mäkipää R, Mencuccini M. 2005. Biomass and stem volume equations for tree species in Europe. Silva Fennica Monogr. 4:63. https://doi.org/10.14214/sf.sfm4

Appendix

Table A1. Seasonal (May–November) soil temperature (at 5 cm, °C), soil ground water table level (WL, cm), (mean ± standard deviation) across the sites and year.

Variables	DB-10 (Young stand)		DB-50 (Middle-aged stand)		DB-80 (Mature stand)	
Year	2021	2022	2021	2022	2021	2022
Soil temperature (°C)	10.38 ± 5.71	15.74 ± 5.98	10.48 ± 5.66	14.90 ± 5.94	9.96 ± 5.95	14.97 ± 6.76
Soil water level (cm)	53.22 ± 13.56	52.51 ± 13.76	42.72 ± 16.01	40.83 ± 10.52	61.05 ± 11.95	73.53 ± 12.32

Table A2. Least significant difference–LSD Post Hoc test statistics of measured foliage.

					95 % confidence interval	
	(I) Age group	(J) Age groups	Mean difference (I-J)	Sig.	Lower band	Upper band
LSD	10	50	−0.068*	**0.001**	−0.106	−0.030
		80	−0.008	0.675	−0.046	0.030
	50	10	0.068*	**0.001**	0.030	0.106
		80	0.060*	**0.003**	0.022	0.098
	80	10	0.008	0.675	−0.030	0.046
		50	−0.060*	**0.003**	−0.098	−0.022

Notes: Dependent Variable: Measured foliage (t ha^{-1}); *The mean difference is significant at the 0.05 level. The *p* values in bold were statistically significant at an alpha level of 0.05.

Table A3. Least significant difference–Tukey HSD, LSD, and Bonferroni Post Hoc test statistics of coarse root biomass.

					95% Confidence Interval	
	(I) Age group	(J) Age groups	Mean difference (I-J)	Sig.	Lower bound	Upper bound
Tukey HSD	10	50	−41.08*	**<.001**	−55.06	−27.10
		80	−12.98	.075	−26.96	1.00
	50	10	41.08*	**<.001**	27.10	55.06
		80	28.10*	**<.001**	14.12	42.08
	80	10	12.98	.075	−1.00	26.96
		50	−28.10*	**<.001**	−42.08	−14.12
LSD	10	50	−41.08*	**<.001**	−52.75	−29.41
		80	−12.98*	.029	−24.65	−1.31
	50	10	41.08*	<.001	29.41	52.75
		80	28.10*	**<.001**	16.43	39.77
	80	10	12.98*	.029	1.31	24.65
		50	−28.10*	**<.001**	−39.77	−16.43
Bonferroni	10	50	−41.08*	**<.001**	−55.38	−26.78
		80	−12.98	.088	−27.28	1.32
	50	10	41.08*	**<.001**	26.78	55.38
		80	28.10*	**<.001**	13.80	42.40
	80	10	12.98	.088	−1.32	27.28
		50	−28.10*	**<.001**	−42.40	−13.80

Notes: Dependent Variable: Coarse root biomass (g m^{-2}); *The mean difference is significant at the 0.05 level.
The *p* values in bold were statistically significant at an alpha level of 0.05.