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Dynamics of fine-root decomposition and its response to site nutrient regimes in boreal drained-peatland and mineral-soil forests

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ABSTRACT

Fine roots may contribute significantly to soil organic matter pool in forest ecosystems; however, their decomposition is often overlooked in studies on litter decomposition and carbon (C) and nutrient cycling. To address this gap, we conducted a five-year litterbag experiment encompassing three representative tree species (*Pinus sylvestris*, *Picea abies*, *Betula pubescens*), and one fern species (*Dryopteris carthusiana*) across various boreal peatland forest types, comparing them with corresponding rates in upland forests on mineral soils. Litterbags were recovered annually, and mass remaining was first characterized by three different model types with varying complexity. Based on this preliminary screening, we chose for the final analyses a double-exponential model, which examined parameters A, i.e. the proportion of material in the slow-decomposing pool, k_1, the mass loss rate of the slow-decomposing pool, and k_2, the rate of mass loss in the fast-decomposing pool. Fine-root decomposition exhibited significant variation with soil type and nutrient regime. In mineral soil, lower k_1 values indicated slower decomposition in more nutrient-rich sites. Conversely, in peat soil, higher k_1 values indicated faster decomposition in more nutrient-rich sites. Soil depth and root diameter emerged as influential factors, with deeper layers and larger diameter roots exhibiting slower decomposition rates. Species-specific effects were also significant, with *D. carthusiana* exhibiting the lowest A value, indicating faster initial decomposition compared to tree species. Among the tree species, differences in A value were minor, with variation observed primarily in k_1 value, where *P. abies* had the lowest rate. No significant effects on k_2 value were observed. These findings underscore the complex interplay between species characteristics, soil type, site nutrient regimes, and root morphology in determining fine-root decomposition dynamics in boreal forests. Importantly, our results show that soil type must be considered when modeling decomposition dynamics.

1. Introduction

One of the main mechanisms influencing nutrient and carbon (C) cycling in terrestrial ecosystems is the decomposition of plant litter (Berg and McClaugherty, 2003; Krishna and Mohan, 2017). In pristine peatlands, decomposition is slower than the production, and thus these ecosystems are accumulating organic matter. High soil water-table levels (WT) and the consequent anoxia are considered the major causes for the imbalance (Laiho, 2006). This imbalance has resulted that peatlands are a significant sink of C from the atmosphere, and the greatest terrestrial C pool (Gorham, 1991). Some peatlands are naturally forested, and the amount of peatland forests has been further increased by drainage for forestry that facilitates increased tree growth in sites that were suboptimally wet for trees (Heikurainen, 1964; Macdonald and Yin, 1999; Socha, 2012; Beaulne et al., 2021). In peatland forests, whether drained or undrained, several ecosystem properties differ from those in open, non-forested peatlands, including vegetation composition (Tuittila et al., 2007; Talbot et al., 2010; Laine et al., 2021), litter inputs, litter quality and decomposability (Laiho, 2006; Straková et al., 2010, 2012). One significant difference in ecosystem structure is the prevalence of tree roots (Lampela et al., 2023) and their contribution to below-ground processes.

Fine roots (diameter less than 2 mm) may account for 33–75 % of annual net primary production in forest ecosystems (Grier et al., 1981; Santantonio and Grace, 1987; Vogt, 1991; Jackson et al., 1997), while more recent estimates, however, place this range between 13 % and 27 % (McCormack et al., 2015). The rapid turnover of fine roots in forests (ca. 56 % annually) brings a high labile litter input to soil (Gill

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and Jackson, 2000). In boreal forests, fine roots are one of the largest sources of litter input to the soil (Clemmensen et al., 2013; Leppälammi-Kujansuu et al., 2014; Ojanen et al., 2014). The decomposition of these litters significantly contributes to the flux of C to the atmosphere (Girkin et al., 2018; Hermans et al., 2022). However, decomposition of fine roots is much less studied for all types of peatlands than that of leaf litter (Latter et al., 1997; Moore et al., 2007, 2008; Straková et al., 2012), and still especially so for drained peatland forests that are an important group of forest ecosystems in northern Europe, e.g., Finland. Where fine roots have been considered (Laiho et al., 2004; Straková et al., 2012), the time period covered has remained too short to capture the decomposition dynamics apart from the first two years.

Unlike above-ground litter (e.g. foliage and stems), which decomposes on or close to the soil surface, the decomposition location of roots depends on their distribution in the soil. While most fine roots are found relatively close to the soil surface in both boreal peatland and mineral-soil forests (Yuan and Chen, 2010; He et al., 2023; Lampela et al., 2023), they may extend down to about 60 cm (Schenk and Jackson, 2002). The temperature and moisture conditions may differ markedly in the depth range where root decomposition takes place, likely regulating the decomposition rate. These depth-related gradients are often (e.g., Gill and Burke, 2002; Sariyildiz, 2015; Hicks Pries et al., 2018; Han et al., 2019) but not always (e.g., Solly et al., 2015; Bhuiyan et al., 2023) reflected as decreasing decomposition rates with increasing depth. In addition to the depth-related factors, local site conditions, including nutrient regime, litter and soil chemistry, as well as decomposer community, also affect litter decomposition (Chapin et al., 2011). Low nutrient status may result in lower microbial activity, and consequently lower decomposition rates (Scheffer and Aerts, 2000; Kyaschenko et al., 2019).

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

In oxic soil layers, the rate of organic matter decomposition is largely determined by litter quality, including its chemical composition and physical structure (Straková et al., 2012). Litter quality in turn is dependent on the plant species or plant functional type (Straková et al., 2010; Smith et al., 2014). In global scale, the decomposition rate of graminoid species is the fastest, followed by that of broadleaf tree roots and then conifer tree roots (Silver and Miya, 2001). Root order and diameter also describe the physical and chemical properties of litter that regulate the decomposition process (Usman et al., 2000; Zhang and Wang, 2015). Among tree roots, small-diameter roots generally decompose faster than large-diameter roots (Han et al., 2019; Liu et al., 2019) because they contain more nutrients and less structural carbohydrates (Silver and Miya, 2001; Ludovici and Kress, 2006). The distal small-diameter lateral branches comprising first- and second-order roots (Pregitzer et al., 2002; Guo et al., 2008c) lack secondary (wood) development (Guo et al., 2008c). Moreover, first- and second-order roots have higher N concentrations (Pregitzer et al., 2002; Guo et al., 2004) and shorter life spans (Guo et al., 2008a, 2008b) than higher order roots. Therefore, finer (lower order) roots are expected to decompose more rapidly than coarser (higher order) woody roots (reviewed in Hishi, 2007).

Litter mass loss rates are frequently estimated using single-exponential decay curves (Olson, 1963), which enable the prediction of long-term decay rates from short-term studies. However, long-term experiments have shown that the rate of decomposition may decelerate in the later stages, deviating from what can be effectively captured by a single-exponential decay curve (Berg et al., 2001; Trofymow et al., 2002; Moore et al., 2005). Harmon et al. (2009) showed that after 10 years of decomposition, the double-exponential and asymptotic models had superior statistical and biological accuracy compared to a single-exponential model for both leaf and fine root litter. In a 23-year experiment on aboveground litter (e.g. leaves, shoots, stems) conducted in an English peat bog (Latter et al., 1997), an asymptotic model was found to provide the best fit. Therefore, determining the most appropriate model for describing fine-root decomposition dynamics in boreal peatland forests, where decomposition processes can persist for decades, remains a critical research question.

In this study, we assessed the fine-root decomposition rates of three representative tree species: Scots pine (*Pinus sylvestris*), Downy birch (*Betula pubescens*) and Norway spruce (*Picea abies*), and one fern species (*Dryopteris carthusiana*) in different boreal peatland forest types and compared them with the corresponding rates in upland forests on mineral soils. Our study involved root litterbag experiments over a five-year period at most, collecting data at three soil depths. The overall aim of this study was to improve our understanding of the complex dynamics of fine-root decomposition in boreal peatland forests and to identify the influence of substrate and environmental factors on decomposition rates. We hypothesized that fine-root decomposition rates 1) are slower in peatlands than in nearby forests on mineral soils; 2) decrease with soil depth; and 3) are faster for fine roots (diameter <2 mm) compared to small roots (diameter 2–10 mm). We also hypothesized that double-exponential and asymptotic models would provide a more accurate description of fine-root decomposition dynamics than single-exponential models.

2. Materials and methods

2.1. Study sites

The study was conducted in six drained peatland forest sites and four mineral-soil forest sites. Four of the drained peatland forests (described in Lampela et al., 2023) as well as the mineral-soil forests (Merilä et al., 2014; Ding et al., 2021) were located at or adjacent to the Lakkasuo peatland complex. The two other drained peatland forests were Kalevansuo (Minkkinen et al., 2018) and Lettosuo (Bhuiyan et al., 2017). All sites were located in southern Finland, and they covered the fertility and productivity gradient of southern boreal forests as distinguished by site types defined based on understorey vegetation composition.

Lakkasuo (61°47′ N, 24°18′ E) is a partially drained eccentric boreal raised bog complex characterized by a vast lagg area and diverse site types. The region experiences an annual precipitation of 710 mm, with about one-third of it falling as snow. The average annual temperature sum (with a threshold value of 5 °C) is 1160 degree days. The average temperatures for January and July are −8.9 °C and 15.3 °C, respectively (Finnish Meteorological Institute, Juupajoki weather station 1961–1990). For this study, we chose four forestry-drained sites at Lakkasuo or the Hanhisuo basin next to it: Herb-rich type (HrT-P; most nutrient-rich of the sites; drained 1928), *Vaccinium myrtillus* type (MT-P; drained 1965), *Vaccinium vitis-idaea* type (VT-P; drained 1961) and Dwarf-shrub type (DsT-P; most nutrient-poor of the sites; drained 1961), according to the drained peatland forest site-type classification used in

Finland (Vasander and Laine, 2008). For comparison, their counterparts in mineral-soil forests around the Lakkasuo area were selected: Herb-rich type (HrT-M), *Vaccinium myrtillus* type (MT-M; mesic forest), *Vaccinium vitis-idaea* type (VT-M; sub-xeric forest), and *Calluna* type (DsT-M; xeric forest) according to the forest site-type classification system developed in Finland (Pohjanmies et al., 2021). For soil and stand characteristics see Table S1 and Table S2.

Kalevansuo (60°38′ N, 24°21′ E) was a Dwarf-shrub type peatland forest (DsT-P), drained in 1971. The long-term annual mean precipitation in the region has been 722 mm, with an annual mean air temperature of 5 °C (Kasimir et al., 2021). The tree stand was mainly composed of *P. sylvestris* with a scattered understorey of *B. pubescens* and *P. abies*. The forest floor vegetation was mainly made up of dwarf shrubs such as *Betula nana*, *Empetrum nigrum*, *Ledum palustre*, *V. myrtillus*, *Vaccinium. uliginosum*, and *V. vitis-idea*, as well as some cottongrass (*Eriophorum vaginatum*) and cloudberry (*Rubus chamaemorus*).

Lettosuo (60°39′ N, 23°57′ E) is located approximately 22 km west of Kalevansuo and shares similar long-term annual mean precipitation and air temperature conditions. The site, drained in 1969, was classified as *V. myrtillus* type (MT-P). The stand consisted mainly of *P. sylvestris*, with some co-dominant *B. pubescens* and *P. abies* forming a vigorous understorey. Notably, Lettosuo exhibited a more diverse forest floor vegetation compared to Kalevansuo, featuring additional species such as certain *Carex* species and herbs such as *D. carthusiana* and *Trientalis europaea*.

In the following analyses, the site types HrT-P, MT-P in peatlands and HrT-M, MT-M in mineral-soil forests were grouped as “nutrient rich”, and the site types VT-P, DsT-P in peatlands and VT-M, DsT-M in mineral-soil forests “nutrient poor”, similarly to, e.g., Ojanen et al. (2014). This is because the number of replicates was not high enough to facilitate more detailed site-type level analysis.

2.2. *Litterbag preparation and installation*

We applied the litterbag method (e.g., Straková et al., 2012) to analyze the mass loss of fine roots. For preparing the litterbags, we used polyester fabric with a mesh size of approximately 1 mm × 1 mm. This mesh size enables small mesofauna, typical of the sites (Silvan et al., 2000), to enter the bags. Three tree species (*B. pubescens, P. abies, P. sylvestris*) were selected as they were the primary biomass production components in the sites. Litterbags with different tree species roots were distributed to the sites based on their tree stand composition. Full sets were installed for the dominant tree species of each site, while tree species found as admixture were represented to the extent made possible by the amount of homogeneous root materials available.

For the Lakkasuo area sites, we used fine roots (<2 mm), harvested from tree seedlings cultivated in the nursery, which were washed and air-dried at room temperature until reaching a constant weight. The weights of fine roots for each individual litterbag were as follows: 0.211 −1.644 g for *B. pubescens*, 0.285 −2.429 g for *P. abies*, and 0.120 −1.129 g for *P. sylvestris*. The variation in fine roots weight among litterbags was due to our choosing to maintain their intact form by not cutting or mixing them. The litterbags were divided into three 10-cm segments that covered the 0 −30 cm soil profile. They were installed in the autumn of 2015 and recovered after 1, 2, 4, and 5 years. For each soil depth and species, 3 −7 litterbags were recovered each time.

In Kalevansuo, litterbags covering the 0–30 cm peat profile as three 10-cm segments were installed in 2008 for recovery after 1, 2, 3, 4 years. Roots from mature *P. sylvestris* trees from a seed orchard were washed and air-dried at room temperature to constant weight and sorted into two diameter classes: fine roots and small roots (2–10 mm). For each separate litterbag, 1.364–2.871 g fine roots and 2.722–5.586 g small roots were weighed. For each soil depth and root size, 10 litterbags were recovered each time.

In Lettosuo, litterbags covering the 0−20 cm peat profile as two 10 cm segments were installed in 2009 and 2010 for recovery after 1, 3, 5 years. Fine roots from nursery-grown seedlings of *B. pubescens*, *P. abies* and *P. sylvestris*, as well as fine and small roots of *P. sylvestris* from the same mature trees as for Kalevansuo, were used. Fine roots of *D. carthusiana* were further locally harvested, as they were common in this site and no earlier information was available about their decomposition rate. All roots were washed and air-dried at room temperature until a constant weight was achieved. The weights of roots for each individual litterbag were as follows: 0.502–0.673 g for *B. pubescens*, 0.692–0.809 g for *P. abies*, 0.409–1.88 g for *P. sylvestris* fine roots, 3.938−4.897 g for *P. sylvestris* small roots, and 0.460–0.540 g for *D. carthusiana*. For each soil depth, species, and root size, 5−10 litterbags were recovered each time.

After each recovery, litterbags were transported to a laboratory where the content was cleaned by gently removing all additional (ingrowth) materials, to determine the remaining root mass. The roots were dried at 60 ℃ to a constant mass and weighed with a 0.001 g precision.

We acknowledge that the litterbag method along with the use of living roots as substrate involves weaknesses, such as substrate quality and altered effects of living roots and mycorrhizal fungi, that may affect the results (e.g., Li et al., 2022). However, it has been widely used and generally considered the best available method for generating large data sets (Zhang and Wang, 2015) that are used in modelling (Bona et al., 2018).

2.3. *Statistical analyses*

Data analyses were conducted using R software (R Core Team; R version 3.5.3; RStudio version 1.2.1335). We examined how well the data representing the proportion of initial mass remaining over time fit simple mathematical models by comparing three types of decomposition models using nonlinear modeling (Wieder and Lang, 1982; Harmon et al., 2009):

a single-exponential model, $X(t)/X0 = \exp(-kt)$;

a double-exponential model, $X(t)/X0 = A \exp(-k_1 t) + (1 - A) \exp(-k_2 t)$;

an asymptotic model, $X(t)/X0 = A + (1 - A) \exp(-k_a t)$.

In all models, $X(t)$ is litter mass at time t, $X0$ is initial litter mass, $X(t)/X0$ is the proportion of initial mass remaining at time t. In the single-exponential model, k is the decomposition rate loss (Olson, 1963). In the double-exponential decomposition model, k_1 is the decomposition rate of the more slowly decomposing fraction of the initial mass (A) and k_2 is the decomposition rate of the more rapidly decomposing fraction of the remaining mass ($1 - A$). Finally, in the asymptotic model, A is the fraction of initial mass that decomposes at a rate of zero (i.e., the asymptotic mass remaining) and k_a is the decomposition rate of the remaining mass ($1 - A$; i.e., the more rapidly decomposing fraction).

We used Akaike’s information criteria modified for small sample sizes (AIC; (Burnham et al., 2011) to select the best decomposition model. The model with the lowest AIC value is considered the best fit and most aligned with the true model. After selecting which decomposition models to use, we employed a nonlinear mixed-effects model (NLMIXED) to determine the effect of species, soil depth, root diameter, soil type (peat, mineral soil), site nutrient regimes (nutrient-rich, nutrient-poor) and their interactions on the parameters of the best fit model.

3. Results

3.1. *Decomposition models*

When assessing model performance by pooling time points from each site, we found that asymptotic models provided the best fit for the mass loss data (lowest AIC in Table 1) but tended to overestimate mass loss in the early stages of decomposition while underestimating it in later years (Fig. 1). In contrast, double-exponential models appeared to be

Table 1
Summary of results of three exponential decomposition models.

	Model	df	AIC	Test	*P*
Single exponential model	1	4	−1301.292		
Double exponential model	2	5	−1560.903	1 vs 2	**< 0.0001**
Asymptotic model	3	9	−1621.713	2 vs 3	**< 0.0001**

AIC indicates is Akaike's information criteria. Test indicates compared models. *P* indicates p values in ANOVA comparison.

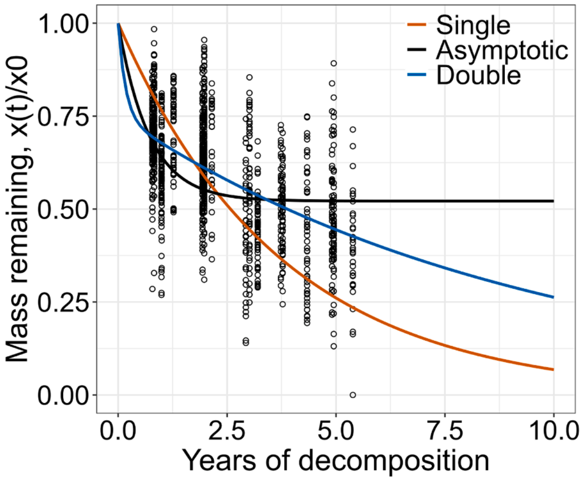

Fig. 1. Decomposition patterns of fine roots across all sites, species, and soil depths in a 10-year timescale. Red line is the single-exponential model, black line is the asymptotic model, blue line is the double-exponential model.

biologically the most realistic (Fig. 1) and provided a relatively good fit to the mass loss data, as shown by the AIC comparison (Table 1). Single-exponential models had the highest AIC values (Table 1), predicting disproportionately low mass loss initially and excessively high levels in later years (Fig. 1).

We further compared the fit of the three competing models to individual fine-root decomposition curves (Figs. 2 and 3). AIC comparison showed that the double-exponential model best described the pattern of litter mass loss in 38 % of the individual decomposition curves (153 out of 405 cases), while the single-exponential model and the asymptotic model met these criteria in 30 % (129 cases) and 31 % (123 cases) of instances, respectively. In mineral-soil forests (120 cases), 63 % of the individual decomposition curves could be best characterized by double-exponential model, compared to 17 % for the asymptotic model. In peatlands (135 cases), the single- and double-exponential model best fit 40 % and 36 % of cases, respectively, while the asymptotic model described only 24 %. Therefore, the double-exponential model appeared to better capture the dynamics of fine-root decay over time, exhibiting a more balanced prediction throughout the study period.

3.2. Effects of species and root size, soil type and nutrient regime, depth

We describe the decomposition dynamics using the double-exponential model parameters (A, k_1, k_2) (Tables 2 and 3). The proportion (A) and decomposition rate (k_1) of the slow-decomposing pool were affected differently by species and root size, and soil type. However, no significant effects on the decomposition rate (k_2) of the fast-decomposing pool were observed.

Species had a significant effect on A and k_1 values. For *P. abies*, both the proportion (A Table 4, $p = 0.036$) and the decomposition rate (k_1 Table 4, $p < 0.001$) of the slow-decomposing pool were lower than those of *B. pubescens* and *P. sylvestris*, which exhibited a similar pattern on both parameters with no statistically significant differences (Fig. 4). From the root biomass of the fern *D. carthusiana*, it was observed that it had the lowest A values (Table 4, $p = 0.000$), indicating that a larger proportion of the material was fast decomposing ($1 - A$) compared to that of the tree species. However, no statistically significant differences were observed in decomposition rates, with k_1 values similar to those of *B. pubescens* (Table 4).

Soil type (peat and mineral soils) and nutrient regime (rich and poor) significantly influenced both A and k_1 values. The decomposition rate (k_1) of the slow-decomposing pool was generally significantly slower in peat than in mineral soils (Table 4, $p = 0.001$; Fig. S1). In nutrient-rich sites (HrT, MT), decomposition proceeded more rapidly initially compared to poor sites (VT, DsT) (Fig. 5). This trend was also reflected in the proportion (A) of the slow-decomposing pool, which was significantly smaller at nutrient-rich sites than at nutrient-poor sites (Table 4, $p < 0.001$). On nutrient-poor sites, the decomposition rate ($k1$) of the slow-decomposing pool was slower in peat soils compared to corresponding mineral soil sites (Table 4, $p < 0.001$), while the opposite was observed in nutrient-rich sites. Consequently, decomposition was fastest in nutrient-rich peat soils (Fig. 5).

Soil depth had a significant effect on the decomposition dynamics of fine roots (Fig. 6). A negative correlation between soil depth and k_1 (Table 4, $p = 0.000$) indicated a slower rate of mass loss from the slow decomposing pool in deeper soil layers. There was no significant interaction between soil type and depth, nor between soil nutrient regime and depth, affecting fine-root decomposition rates.

Root diameter significantly influenced the composition of the decomposing material. Small roots (2 −10 mm) showed a higher proportion of material allocated to the slow-decomposing pool (A) (Fig. 6 and Table 4, $p < 0.001$), compared to fine roots (<2 mm). This indicated that larger roots tended to retain a greater proportion of their mass in the slow decomposing pool, thereby slowing the overall decomposition rates.

4. Discussion

4.1. Model selection

Double-exponential and asymptotic models offered superior statistical accuracy compared to single-exponential models in delineating fine-root decomposition dynamics within boreal peatland forests, as well as adjacent upland forests. This aligns with a previous 23-year litter-bag study on aboveground litter (leaves, stem, shoot) decomposition in an undrained peatland (Latter et al., 1997). In boreal peatlands, single-exponential models generally provided a poor fit across above- and below-ground litter (a total of 39 litter types) also in an earlier two-year study carried out in different locations at Lakkasuo (Straková et al., 2012). Trofymow et al. (2002) observed that while the single-exponential model generally fit well across most sites and below-ground litter types during a six-year exposure at 18 mineral-soil forest sites across Canada, it exhibited the least accuracy for cold sites with low-quality materials. Single-exponential models, which assume a constant decomposition rate, tend to underestimate the remaining mass in the later stages of decomposition (Manzoni et al., 2012; Xia et al., 2018), as observed in our study. Multi-pool models, such as double-exponential models (Xia et al., 2018) or asymptotic models (Hobbie et al., 2010; Sun et al., 2016), have been shown to outperform single-exponential models in fitting fine-root decomposition data in temperate forests. In a 10-year litter-bag study encompassing leaf and fine root litter across various forest ecosystems ranging from tropical to temperate to boreal zones, as well as a few grasslands and wetlands sites, Harmon et al. (2009) compared several models and found that the double-exponential and asymptotic model statistically and biologically fit more combinations of litter type and site than the single-exponential model. Our study extends this study by focusing specifically on boreal peatlands and adjacent upland forests on mineral soil, addressing a gap in previous research. By doing so, we emphasize the importance of model selection in accurately capturing decomposition dynamics across

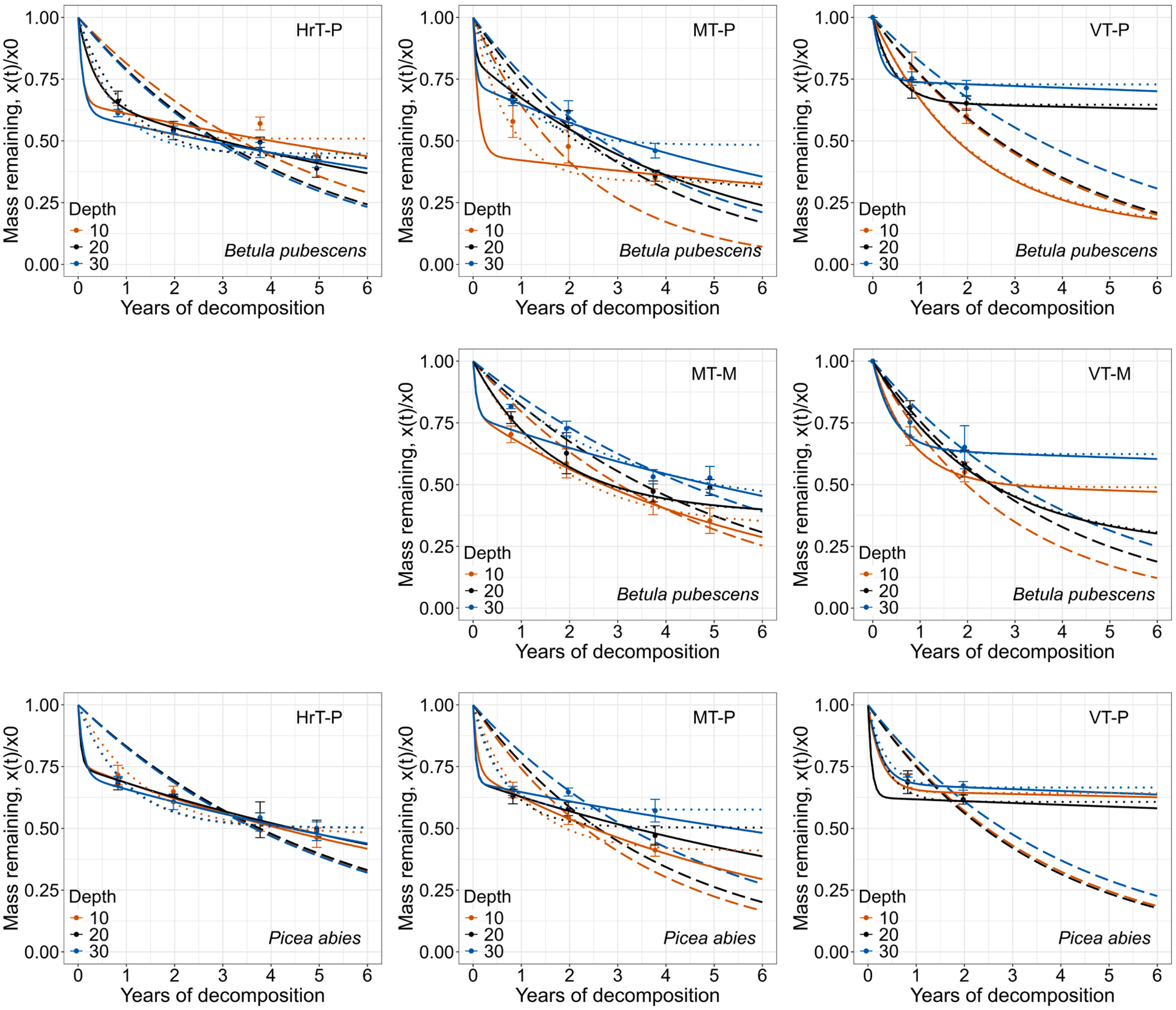

Fig. 2. Fine-root decomposition patterns of *Betula pubescens*, *Picea abies*, and *Pinus sylvestris* at various depths in peatland and mineral-soil forests in the Lakkasuo area. Site types in the peatland sites from the most fertile to the nutrient poorest: Herb-rich type (HrT-P), *Vaccinium myrtillus* type (MT-P), *Vaccinium vitis-idaea* type (VT-P), and Dwarf-shrub type (DsT-P), as well as their counterparts in mineral-soil forests: Herb-rich type (HrT-M), *Vaccinium myrtillus* type (MT-M), *Vaccinium vitis-idaea* type (VT-M), and Dwarf-shrub type (DsT-M). Each data point represents the mean with standard error. The dashed lines represent the predicted decomposition patterns of the single-exponential model, the solid lines represent the predicted decomposition patterns of the double-exponential model, and the dotted lines represent the predicted decomposition patterns of the asymptotic model. Red lines represent the 0 −10 cm soil layer, black lines represent the 10 −20 cm soil layer, and blue lines represent the 20 −30 cm soil layer.

different ecosystems. It was possible to describe the decomposition dynamics with one model when soil type was included as a factor.

The multi-pool models suggest that decomposition begins with the rapid breakdown of easily decomposable compounds like sugars, starch, and simple phenolics, along with cellulose and hemicellulose, often leading to about 40 % mass loss (Coûteaux et al., 1995; Heim and Frey, 2004). Further, soluble carbohydrates leach out quickly and are utilized by soil bacteria, accelerating decomposition (Ahmed et al., 2022). Following this initial phase, the decomposition slows as it involves more resistant polymers like lignocellulose, condensed tannins, and cutin, which account for the remaining 40–100 % mass loss, leading to a convex curve of remaining mass over time (Berg, 2000; Berg and McClaugherty, 2003). While our study found a strong fit for the asymptotic model based on the five-year litterbag incubation period, this model tended to overestimate mass loss during the early stages of decomposition and underestimate it in later years. The double-exponential model parameters (A, k_1, k_2), which account for both rapid (k_2) and slow (k_1) decomposition rates of different chemical fractions, offer a biologically realistic depiction of fine-root decomposition (Berg and McClaugherty, 2003).

4.2. *Effects of species and root size*

Fine-root decomposition is a complex ecological process influenced by climate factors, root substrate quality, soil properties and microorganisms (Saha et al., 2023). In general, root substrate quality in forest ecosystems is largely dependent on tree species and root size (Makita et al., 2015; Sariyildiz, 2015). Botanical criteria, such as the distinction between conifer and broadleaf trees, are sometimes used to predict decomposition rates based on the quality of roots. Silver and Miya

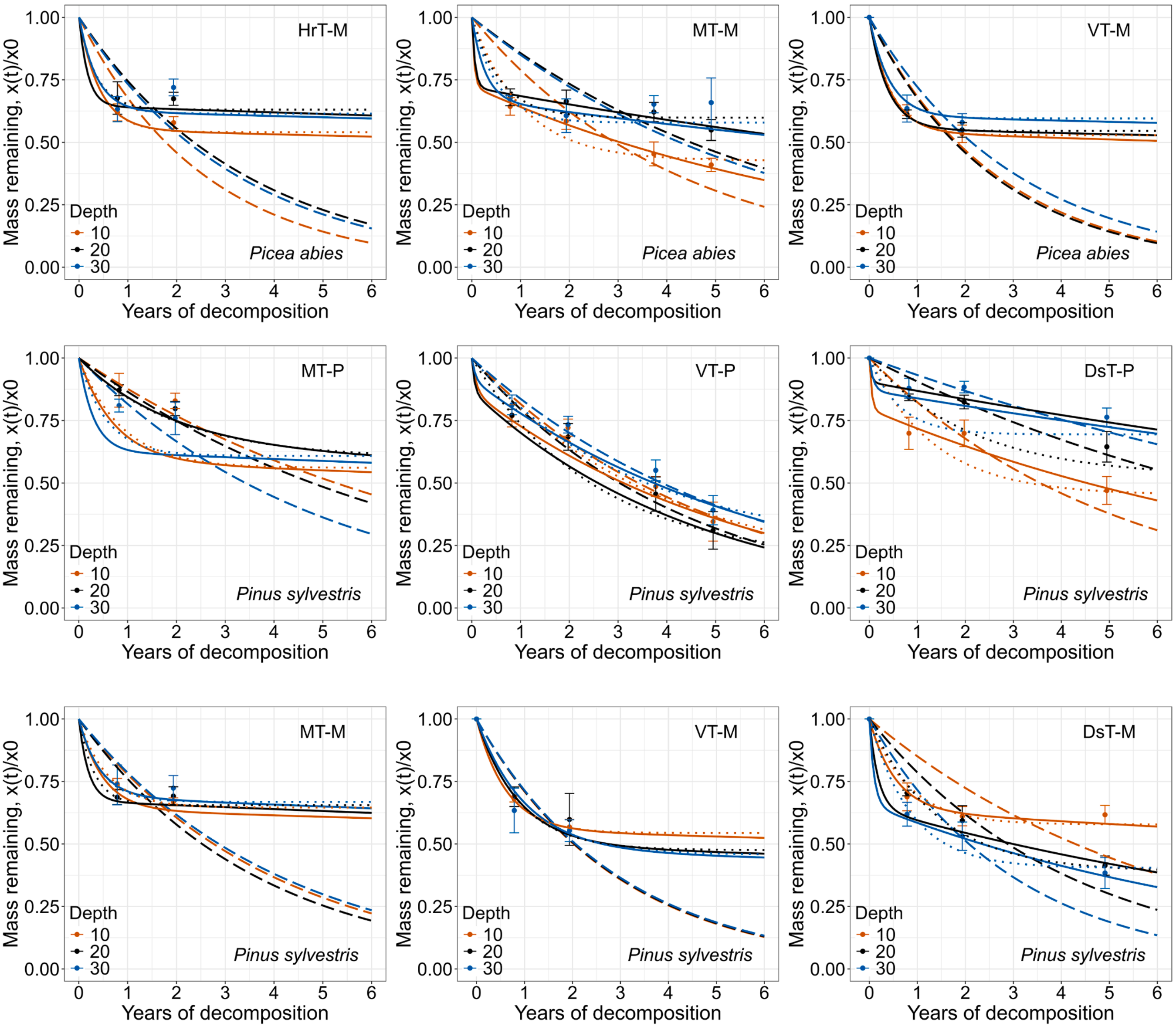

Fig. 2. (*continued*).

(2001) analysed 176 root decomposition datasets from diverse geographical locations and found that fine roots (0−2 mm) of conifers had the lowest levels of calcium and N, the highest C:N and lignin:N ratios, and decomposed at the slowest rates compared to broadleaf trees. In our study, fine roots (0–2 mm) of the broadleaf *B. pubescens* tended to decay faster than those of the conifer *P. abies*, as reflected by significant differences in the proportion (*A*) and decomposition rate of the slow-decomposing pool (k_1). Contrary to that, the proportion and decomposition rate of the slow-decomposing pool for another conifer, *P. sylvestris*, were nearly indistinguishable from those of *B. pubescens*. Similarly, Lin et al. (2011) reported that for fine-root decomposition, there was no significant difference between conifers and broadleaf trees in mid-subtropical China. Additionally, in the alpine forests of the eastern Tibetan Plateau in China, Zhuang et al. (2018) reported the root litter of a broadleaf tree (*B. albosinensis*) tended to decay faster than those of two coniferous trees (*A. faxoniana and P. asperata*) for coarser roots (2–5 mm and 5–10 mm), with no significant difference observed for fine roots (<2 mm). Together, these results suggest that the decomposition rates of conifer species are not always lower than those of broadleaf species, challenging the traditional notion based on botanical criteria alone. Instead, other traits should be used to group the litters in models.

In northern peatlands, for woody species including shrubs, *B. pubescens*, *P. abies*, and *P. sylvestris*, the within-species variation in root chemistry related to diameter was generally higher than the differences between species, as evaluated by Fourier transform infrared spectroscopy (FTIR) (Straková et al., 2020). Our results showed that fine roots of *P. sylvestris* tended to decay faster than small roots, which is consistent with our hypothesis. Similar results have been observed in other pine species such as *P. roxburghii, P. taeda* and *P. tabulaeformis* (Usman et al., 2000; Ludovici and Kress, 2006; Mao et al., 2011). Globally, when the roots were divided into three sizes (<2 mm, 2–5 mm and >5 mm) or two classes (fine roots <2 mm vs. small roots >2 mm), fine roots decomposed significantly faster (Silver and Miya, 2001; Zhang and Wang, 2015).

The FTIR analysis by Straková et al. (2020) indicates that fine roots (0–2 mm) have higher levels of polyphenolics (lignin) and aliphatic compounds (wax, lipids), while small roots (2–10 mm) contain higher polysaccharide concentrations (Straková et al., 2020). High lignin concentrations in fine roots typically slow down decomposition (Luo et al.,

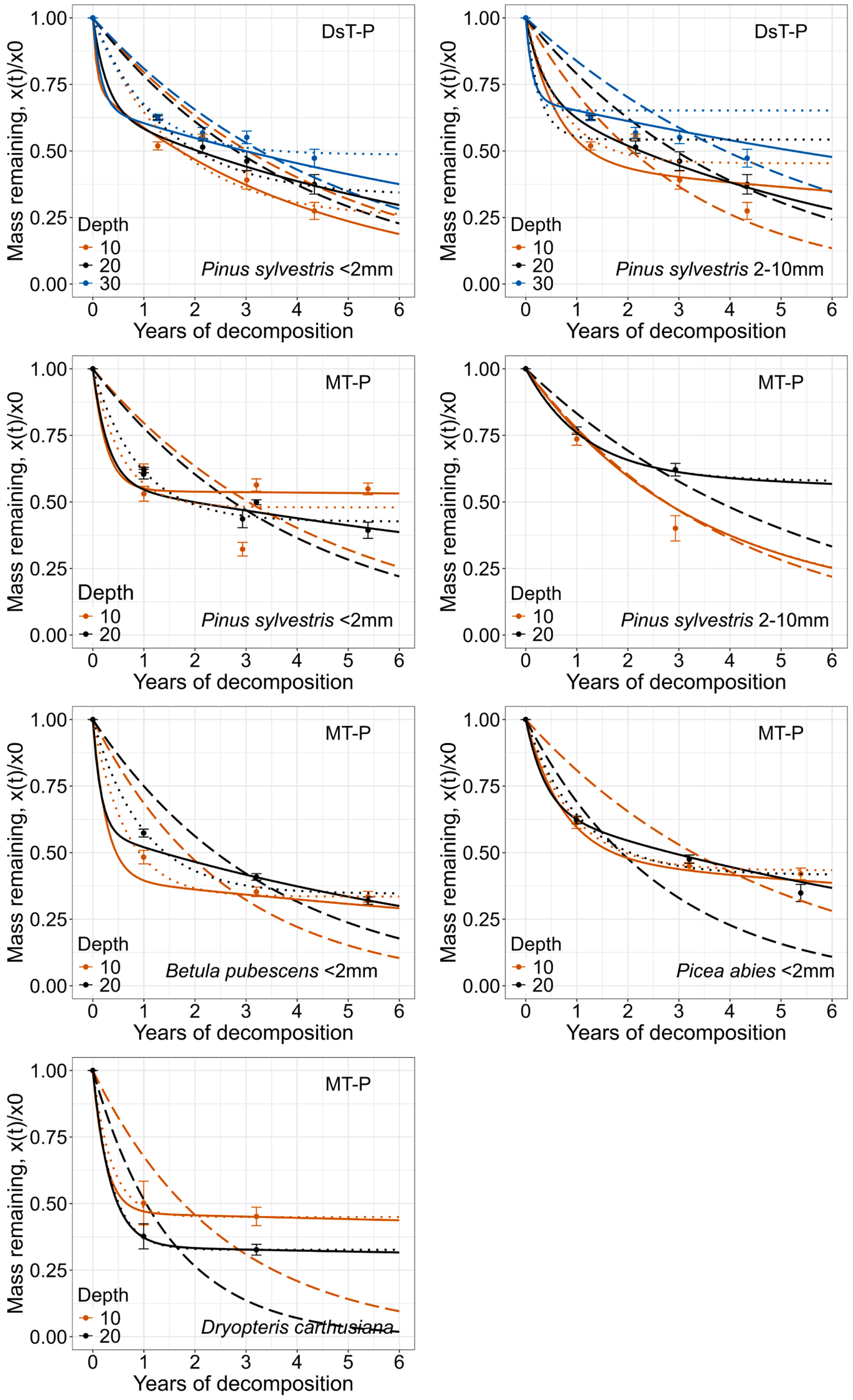

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Fig. 3. Fine-root decomposition patterns of *Pinus sylvestris*, *Picea abies*, *Betula pubescens*, and *Dryopteris carthusiana* at various depths in Lettosuo (*Vaccinium myrtillus* type, MT-P), and Kalevansuo (Dwarf-shrub type, DsT-P) peatlands. *P. sylvestris* roots are categorized into two classes: < 2 mm and 2 −10 mm, while roots of other tree species are < 2 mm. Each data point represents the mean with standard error. Dashed lines depict the predicted decomposition patterns of the single-exponential model, solid lines represent the double-exponential model, and dotted lines depict the asymptotic model. Red lines represent the 0 −10 cm soil layer, black lines represent the 10 −20 cm soil layer, and blue lines represent the 20 −30 cm soil layer.

Table 2
Fine-root decomposition rates (k_1, k_2, year^{-1}) and slow pool proportions (A) obtained by fitting a double-exponential decay model for each site type, species, root size class, and soil depth in the peatland forests.

Location	Site type	Species	Diameter (mm)	Depth (cm)	Double exponential model: $X(t)/X0 = A\exp(-k_1t) + (1-A)\exp(-k_2t)$		
					A ± SE	k_1 ± SE	k_2 ± SE
Lakkasuo (61°47'N, 24°18'E)	HrT-P	*Betula pubescens*	< 2	0 −10	0.626 ± 0.073	0.054 ± 0.047	12.175 ± 9.558
				10 −20	0.676 ± 0.166	0.097 ± 0.076	9.150 ± 9.107
				20 −30	0.607 ± 0.094	0.074 ± 0.042	10.231 ± 10.319
		Picea abies	< 2	0 −10	0.771 ± 0.048	0.102 ± 0.032	10.153 ± 7.772
				10 −20	0.670 ± 0.150	0.057 ± 0.061	12.061 ± 9.231
				20 −30	0.695 ± 0.100	0.069 ± 0.051	10.006 ± 10.688
	MT-P	*Betula pubescens*	< 2	0 −10	0.433 ± 0.171	0.044 ± 0.062	8.380 ± 10.257
				10 −20	0.438 ± 0.383	0.098 ± 0.081	6.100 ± 10.291
				20 −30	0.715 ± 0.106	0.105 ± 0.058	12.113 ± 9.045
		Pinus sylvestris	< 2	0 −10	0.596 ± 0.353	0.005 ± 0.006	6.538 ± 12.183
				10 −20	0.394 ± 0.386	0.013 ± 0.010	0.660 ± 0.656
				20 −30	0.607 ± 0.344	0.004 ± 0.005	4.859 ± 6.355
		Picea abies	< 2	0 −10	0.623 ± 0.185	0.107 ± 0.076	9.134 ± 9.374
				10 −20	0.691 ± 0.119	0.099 ± 0.077	13.959 ± 10.331
				20 −30	0.704 ± 0.072	0.057 ± 0.067	18.625 ± 8.679
	VT-P	*Betula pubescens*	< 2	0 −10	0.222 ± 0.230	0.011 ± 0.000	0.532 ± 0.480
				10 −20	0.635 ± 0.073	0.006 ± 0.006	6.007 ± 8.080
				20 −30	0.729 ± 0.042	0.007 ± 0.007	11.858 ± 9.651
		Pinus sylvestris	< 2	0 −10	0.303 ± 0.418	0.057 ± 0.075	4.776 ± 9.583
				10 −20	0.167 ± 0.292	0.025 ± 0.027	0.563 ± 0.716
				20 −30	0.204 ± 0.323	0.022 ± 0.028	4.213 ± 8.955
		Picea abies	< 2	0 −10	0.645 ± 0.040	0.008 ± 0.008	10.330 ± 11.382
				10 −20	0.631 ± 0.053	0.020 ± 0.021	7.274 ± 10.992
				20 −30	0.673 ± 0.027	0.007 ± 0.005	6.410 ± 9.357
	DsT-P	*Pinus sylvestris*	< 2	0 −10	0.543 ± 0.319	0.049 ± 0.040	8.058 ± 10.377
				10 −20	0.714 ± 0.400	0.042 ± 0.033	10.602 ± 8.948
				20 −30	0.532 ± 0.489	0.023 ± 0.022	7.578 ± 9.267
Kalevansuo(60°39'N, 24°22'E)	DsT-P	*Pinus sylvestris*	< 2	0 −10	0.657 ± 0.237	0.181 ± 0.109	12.293 ± 4.566
				10 −20	0.480 ± 0.281	0.065 ± 0.087	3.479 ± 5.011
				20 −30	0.562 ± 0.221	0.048 ± 0.056	6.495 ± 6.964
			2–10	0 −10	0.138 ± 0.312	0.020 ± 0.028	1.536 ± 4.255
				10 −20	0.322 ± 0.424	0.021 ± 0.024	1.935 ± 3.426
				20 −30	0.552 ± 0.389	0.025 ± 0.026	5.286 ± 6.033
Lettosuo (60°39'N, 23°57'E)	MT-P	*Betula pubescens*	< 2	0 −10	0.433 ± 0.124	0.050 ± 0.067	7.148 ± 8.487
				10 −20	0.523 ± 0.137	0.084 ± 0.059	8.762 ± 8.779
		Pinus sylvestris	< 2	0 −10	0.479 ± 0.045	$3.001 \times 10^{-4} \pm 0.001$	1.956 ± 0.806
				10 −20	0.558 ± 0.143	0.059 ± 0.063	6.498 ± 7.937
			2–10	0 −10	0.149 ± 0.227	$0.011 \pm 1.988 \times 10^{-4}$	0.475 ± 0.241
				10 −20	0.551 ± 0.213	0.010 ± 0.004	1.035 ± 0.640
		Picea abies	< 2	0 −10	0.527 ± 0.088	0.032 ± 0.057	5.131 ± 7.484
				10 −20	0.626 ± 0.126	0.091 ± 0.088	10.786 ± 9.728
		Dryopteris carthusiana		0 −10	0.359 ± 0.148	0.005 ± 0.006	11.771 ± 10.143
				10 −20	0.320 ± 0.030	0.007 ± 0.006	25.434 ± 42.505

Herb-rich type (HrT-P), *Vaccinium myrtillus* type (MT-P), V*accinium vitis-idaea* type (VT-P), and Dwarf shrub type (DsT-P).

2017). High-quality root litters, characterized by higher nutrient contents and lower stoichiometric ratios, generally decay faster than poorer-quality root litters (Makita et al., 2015). Helmisaari (1991) found a decrease in nutrient concentrations (N, phosphorus (P), potassium (K), and Magnesium (Mg) in *P. sylvestris* roots with increasing root diameter. Hence, with increasing root diameter, the cellulose content and alpha-cellulose content increase, and the lignin content and nutrient concentration decrease (Thomas et al., 2014; Zhang et al., 2014), leading to slower decomposition rates (Jing et al., 2019).

Additionally, we found that the fern *D. carthusiana* had lower proportion of material in the slow pool (A) compared to the tree species, while its mass loss rate of the slow decomposition pool ($k1$) was similar to that of *Betula pubescens*. It suggests that *D. carthusiana* undergoes an initial decomposition that is faster than tree species, followed by a stabilizing phase. These results highlight differences in decomposition dynamics between ferns and tree species. However, further research is necessary to clarify the underlying mechanisms.

4.3. Effects of soil type and nutrient regime

Our results showed that root decomposition occurred at a slower rate in peatlands than in adjacent mineral-soil forests, aligning with our hypothesis and previous findings on foliar litters and wood blocks (Moore et al., 2008). Although the WT may be a primary control on these differences, other factors such as nutrient regime are also important. Our results suggest that in nutrient-rich sites, a smaller proportion of fine root material is in the slowly decomposing pool (A) compared to nutrient-poor sites. However, interesting patterns emerged when considering the interaction between soil type and nutrient regime in the rate of mass loss (k_1) from slowly decomposing pools.

Table 3

Fine-root decomposition rates (k_1, k_2, year^{-1}) and slow pool proportions (A) obtained by fitting a double-exponential decay model for each site type, species, root size class, and soil depth in the mineral-soil forests.

Location	Site type	Species	Diameter (mm)	Depth (cm)	Double exponential model: $X(t)/X0 = A\ \exp(-k_1t) + (1-A)\ \exp(-k_2t)$		
					A ± SE	k_1 ± SE	k_2 ± SE
Lakkasuo (61°47'N, 24°18'E)	HrT-M	*Picea abies*	< 2	0 −10	0.534 ± 0.054	0.007 ± 0.006	5.776 ± 8.372
				10 −20	0.522 ± 0.296	0.005 ± 0.007	18.155 ± 17.278
				20 −30	0.637 ± 0.081	0.002 ± 0.005	17.120 ± 9.633
	MT-M	*Betula pubescens*	< 2	0 −10	0.646 ± 0.197	0.120 ± 0.097	8.440 ± 10.071
				10 −20	0.462 ± 0.182	0.017 ± 0.034	0.819 ± 0.431
				20 −30	0.582 ± 0.358	0.050 ± 0.064	3.794 ± 6.749
		Pinus sylvestris	< 2	0 −10	0.638 ± 0.095	0.009 ± 0.005	2.044 ± 0.981
				10 −20	0.649 ± 0.041	0.006 ± 0.008	6.679 ± 8.637
				20 −30	0.632 ± 0.135	0.005 ± 0.007	5.789 ± 9.367
		Picea abies	< 2	0 −10	0.602 ± 0.177	0.073 ± 0.062	14.405 ± 12.309
				10 −20	0.708 ± 0.076	0.045 ± 0.019	14.098 ± 10.240
				20 −30	0.643 ± 0.088	0.006 ± 0.014	10.451 ± 11.139
	VT-M	*Betula pubescens*	< 2	0 −10	0.456 ± 0.189	0.009 ± 0.005	7.000 ± 13.583
				10 −20	0.345 ± 0.336	0.011 ± 0.001	0.740 ± 0.523
				20 −30	0.573 ± 0.332	0.005 ± 0.005	6.052 ± 9.077
		Pinus sylvestris	< 2	0 −10	0.556 ± 0.066	0.010 ± 0.002	1.653 ± 0.354
				10 −20	0.494 ± 0.310	0.010 ± 0.006	6.267 ± 10.690
				20 −30	0.403 ± 0.261	0.008 ± 0.007	5.864 ± 10.169
		Picea abies	< 2	0 −10	0.531 ± 0.126	0.011 ± 0.001	2.466 ± 0.954
				10 −20	0.557 ± 0.044	0.011 ± 0.001	2.712 ± 0.615
				20 −30	0.598 ± 0.049	0.009 ± 0.007	8.877 ± 9.342
	DsT-M	*Pinus sylvestris*	< 2	0 −10	0.644 ± 0.100	0.015 ± 0.024	9.534 ± 10.741
				10 −20	0.674 ± 0.160	0.097 ± 0.058	6.090 ± 9.632
				20 −30	0.532 ± 0.489	0.023 ± 0.022	7.578 ± 9.267

Herb-rich type (HrT-M), *Vaccinium myrtillus* type (MT-M), *Vaccinium vitis-idaea* type (VT-M), and Dwarf shrub type (DsT-M).

Table 4

Summary of nonlinear mixed-effects model results for double-exponential model parameters (A, k_1, k_2).

	Estimate ± SE	*P*-value
k_1.(Intercept)	0.210 ± 0.024	**0.000**
k_1.species *Dryopteris carthusiana*	−0.085 ± 0.062	0.170
k_1.species *Picea abies*	−0.056 ± 0.016	**0.001**
k_1.species *Pinus sylvestris*	−0.009 ± 0.017	0.610
k_1.soiltype peat	−0.048 ± 0.014	**0.001**
k_1.nutrient regime rich	−0.108 ± 0.023	**0.000**
k_1.depth 10 −20 cm	−0.022 ± 0.005	**0.000**
k_1.depth 20 −30 cm	−0.047 ± 0.005	**0.000**
k_1.soiltype peat: nutrient regime rich	0.097 ± 0.017	**0.000**
k_2	4.436 ± 2.613	0.090
A.(Intercept)	0.809 ± 0.031	**0.000**
A.nutrient regime rich	−0.078 ± 0.023	**0.001**
A.species *Dryopteris carthusiana*	−0.268 ± 0.058	**0.000**
A.species *Picea abies*	−0.049 ± 0.023	**0.036**
A.species *Pinus sylvestris*	0.004 ± 0.025	0.870
A.root size 2 −10 mm	0.117 ± 0.018	**0.000**

In the summary, the intercept is *Betula pubescens*, poor mineral soil, depth 0 −10 cm, and root size below 2 mm. Everything else is compared against that. $P < 0.05$ indicated in bold.

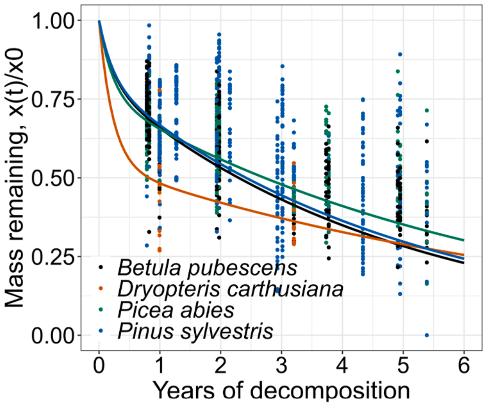

Fig. 4. Comparative decomposition patterns of fine roots of *Pinus sylvestris* (blue), *Picea abies* (green), *Betula pubescens* (black), and *Dryopteris carthusiana* (red). The lines are the double-exponential model-predicted decomposition patterns.

Contrary to our expectations, in mineral soils, nutrient-rich sites exhibited lower k_1 values compared to nutrient-poor sites, resulting in greater fine-root mass remaining in the more fertile sites at the end of the study (Fig. 5). This finding may potentially be explained by the inhibitory effect of added N on lignin-degrading enzymes in these ecosystems, which slows the decomposition of lignin-rich fine roots typical of temperate and boreal forests (Rasse et al., 2005; Xia et al., 2015). In mineral-soil forests, N is considered the growth-limiting nutrient. Deforest et al. (2004) and Edwards et al. (2011) observed that the activity of lignin-degrading enzymes is reduced when N is added to soil, leading to slower decomposition rates. For instance, Xia et al. (2018) reported that N additions inhibited the later stages of fine-root decomposition at four sugar maple dominated northern hardwood forests following a three-year litter-bag study, which was consistent with observed decreases in lignin-degrading enzyme activities with N additions at these sites. However, this explanation remains tentative. A comparison between robust site nutrient regime classes, such as ours, has to our knowledge not been done before. Such a grouping may be a useful way to handle the variation in site characteristics, and we recommend testing it in future studies involving sites with varying nutrient status.

Peat soils generally contain more N but fewer mineral nutrients like P or K compared to mineral soils (Westman and Laiho, 2003). In peat soils, we observed higher decomposition rate of the slow-decomposing pool (k_1) for fine roots in nutrient-rich sites (HrT-P, MT-P) compared to nutrient-poor sites (VT-P, DsT-P), which is consistent with our expectations. At nutrient-rich sites, N and P are more readily available compared with nutrient-poor sites, which enhances microbial activities and thus instigates greater mass loss (Straková et al., 2011). Similarly, Scheffer and Aerts (2000) reported that a low nutrient status and a low pH resulted in lower microbial activity, and consequently lower

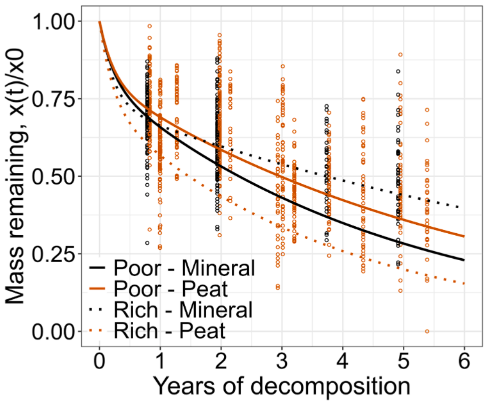

Fig. 5. Comparative decomposition patterns of fine roots across different soil types (peat soils and mineral soils) and nutrient regime conditions (nutrient-rich and nutrient-poor). The lines represent the double-exponential model-predicted decomposition patterns.

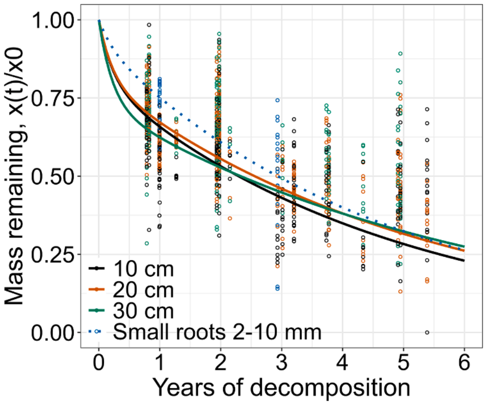

Fig. 6. Comparative decomposition patterns of fine roots (<2 mm) across different soil depths as marked by their lower boundaries, and small roots (2 −10 mm). The black lines indicate the decomposition patterns of fine roots in the 0 −10 cm soil layer, the red lines correspond to the 10 −20 cm layer, and the green lines to the 20 −30 cm layer. The blue dotted line represents the decomposition patterns of small roots. The lines are the double-exponential model-predicted decomposition patterns.

decomposition rates in two temperature fen ecosystems. While there was little difference in pH between our sites, WT levels varied. Nutrient-rich sites, with deeper WT (Table S1) and more oxic conditions, possibly facilitated increased decomposition through several mechanisms.

4.4. *Effects of soil depth*

As hypothesized, our findings showed that the mass loss rate of the slow-decomposition pool (k_1) peaked in the topsoil (0 −10 cm) and decreased in deeper soil depths, both in peatland and mineral-soil forests. Similar decline in fine-root decomposition at deeper soil layers was also observed in previous studies conducted in boreal peatland forests (Laiho et al., 2004; Straková et al., 2012) and temperate mineral-soil forests (Sariyildiz, 2015; Sun et al., 2016). Similarly, fine-root biomass and production decline from the topmost 0–10 cm layer toward deeper layers in both peatland and mineral-soil forests (Ding et al., 2021; He et al., 2023; Lampela et al., 2023), suggesting that soil environmental conditions favorable for fine-root biomass and production also facilitate faster fine-root decomposition. Generally, increasing soil depth reduces soil microbial activity, substrate availability, and alters soil moisture and temperature. Studies in both peatlands (Jackson et al., 2009; Steinweg et al., 2018) and mineral-soil forests (Herold et al., 2014; Han et al., 2019) have shown decreases in microbial biomass and the activity of extracellular microbial enzymes involved in decomposition with increasing soil depth.

Specific factors like WT position and oxygen availability may uniquely influence peatland sites. In our boreal drained peatland sites, the WT during the growing seasons was about 20–30 cm below the surface. Our root litter was incubated at depths of 0 −10 cm, 10 −20 cm, and 20 −30 cm below the surface. In the summer, the aerobic limit may be approximately 5 −30 cm closer to the peatland surface than to the WT (Lähde, 1969), therefore anaerobic or reducing conditions may impede fine-root decomposition even in the drained sites, particularly in the greater incubation depths. Previous research has shown that mass loss from fine-root (diameter <2 mm) litter is more rapid in the 0 −10 cm layer than in the 10 −20 cm layer in peatland forests (Laiho et al., 2004). Our results align with the conclusion of Straková et al. (2012), based on cellulose decomposition, that the best environmental conditions for decomposition in peatlands are generally in moss patches and soil 0–10 cm layer.

4.5. *Implications for forest management*

Linked with data on fine-root biomass, production, and longevity (Lehtonen et al., 2016; He et al., 2023; Lampela et al., 2023; Minkkinen et al., 2024) the results of this study can be used to support forest carbon management. Even though decomposition rates are very basic ecological parameters, they had so far not been rigorously evaluated for fine roots in drained peatland forests. Lack of data on root-related C fluxes leads to significant uncertainties in determining whether forest soils are sinks or sources of C to the atmosphere (Ojanen et al., 2014). This is especially critical for drained peatland forests that are soil C hotspots and range from strong sources to moderate sinks of atmospheric C (Jauhiainen et al., 2023). Our decomposition models are the final tool needed to facilitate evaluating how management-induced changes in tree stand basal area and species composition, which determine the quantity and quality of fine-root litter inputs to soil, affect the amount of SOM deriving from fine roots in different forest site types. Comparing different options helps optimizing C sequestration and minimizing C losses. For instance, the slow decomposition rates of *P. abies* fine roots suggest that promoting this species may enhance long-term soil C storage, in such site types where this nutrient-demanding species can be grown. Decomposition models are further needed for model-based Tier 3 methods in greenhouse gas inventories.

5. Conclusions

Our study provides insight into the complex dynamics of fine-root decomposition in boreal forests growing on different soil types. The model selection process revealed that the double-exponential model provides a statistically and biologically superior fit compared to both the single-exponential and asymptotic models for characterizing fine-root decomposition. This model's ability to capture both the rapid initial mass loss and the subsequent slower rates highlights the importance of understanding the temporal dynamics of decomposition. Accurately modelling these phases allows us to better predict where and how mass loss might converge over time, underscoring the value of studies that can capture these critical decomposition stages.

Species composition was found to be a crucial factor affecting fine-root decomposition rates. The fern *D. carthusiana* showed a distinct decomposition pattern, with rapid initial decay followed by stabilization. Although the tree species studied had similar proportions of material allocated to the slow decomposition pool (A), differences were observed in the mass loss rate (k_1) of the slow-decomposition pool, with *P. abies* exhibiting the slowest decomposition. Moreover, the dynamics of fine-root decomposition were significantly influenced by soil type and nutrient regime. The decomposition process in peatlands was fastest in nutrient-rich peat soils, while in mineral-soil sites it was the opposite, emphasizing different relationships between nutrient availability and soil characteristics. Soil depth emerged as another influential factor, with deeper layers exhibiting slower decomposition rates compared to surface layers across both peatland and mineral-soil forests. Additionally, root diameter exerted an impact on decomposition dynamics, with smaller-diameter roots decomposing at a faster rate than larger-diameter roots.

Overall, our results highlight the multifaceted nature of fine-root decomposition in boreal forests, which is influenced by species composition, site characteristics, and environmental factors. The results may be used in modelling peatland ecosystem structure and function, and to support forest C management and model-based greenhouse gas inventories.

CRediT authorship contribution statement

Mäkiranta Päivi: Writing – review & editing, Supervision, Resources, Methodology, Data curation. **Ojanen Paavo:** Writing – review & editing, Supervision, Methodology. **Korrensalo Aino:** Supervision, Methodology, Formal analysis. **Laiho Raija:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **He Wei:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation.

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.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122564.

Data availability

Data are openly available at Zenodo, https://doi.org/10.5281/zenodo.13353797

References

Abdul Rahman, N.S.N., Abdul Hamid, N.W., Nadarajah, K., 2021. Effects of abiotic stress on soil microbiome. Int. J. Mol. Sci. 22, 9036. https://doi.org/10.3390/ijms22169036.

Ahmed, M., Aslam, M.A., Fayyaz Ul, H., Hayat, R., Nasim, W., Akmal, M., Mubeen, M., Hussain, S., Ahmad, S., 2022. Nutrient Dynamics and the Role of Modeling. Springer International Publishing, pp. 297–316. https://doi.org/10.1007/978-3-030-79408-8_19.

Beaulne, J., Garneau, M., Magnan, G., Boucher, É ., 2021. Peat deposits store more carbon than trees in forested peatlands of the boreal biome. Sci. Rep. 11. https://doi.org/10.1038/s41598-021-82004-x.

Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manag. 133, 13–22. https://doi.org/10.1016/s0378-1127(99)00294-7.

Berg, B., McClaugherty, C., 2003. Decomposition of fine root and woody litter. Springer Berlin Heidelberg, pp. 173–189. https://doi.org/10.1007/978-3-662-05349-2_9.

Berg, B., McClaugherty, C., Santo, A.V.D., Johnson, D., 2001. Humus buildup in boreal forests: effects of litter fall and its N concentration. Can. J. For. Res. 31, 988–998. https://doi.org/10.1139/x01-031.

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

Bhuiyan, R., Mäkiranta, P., Straková, P., Fritze, H., Minkkinen, K., Penttilä, T., Rajala, T., Tuittila, E.S., Laiho, R., 2023. Fine-root biomass production and its contribution to organic matter accumulation in sedge fens under changing climate. Sci. Total Environ. 858. https://doi.org/10.1016/j.scitotenv.2022.159683.

Bona, K.A., Hilger, A., Burgess, M., Wozney, N., Shaw, C., 2018. A peatland productivity and decomposition parameter database, 2406 Ecology 99, 2406. https://doi.org/10.1002/ecy.2462.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6.

Chapin, F.S., Matson, P.A., Vitousek, P.M., 2011. Decomposition and Ecosystem Carbon Budgets. Springer New York, pp. 183–228. https://doi.org/10.1007/978-1-4419-9504-9_7.

Clemmensen, K.E., Bahr, A., Ovaskainen, O., Dahlberg, A., Ekblad, A., Wallander, H., Stenlid, J., Finlay, R.D., Wardle, D.A., Lindahl, B.D., 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. Science 339, 1615–1618. https://doi.org/10.1126/science.1231923.

Coûteaux, M.-M., Bottner, P., Berg, B., 1995. Litter decomposition, climate and liter quality. Trends Ecol. Evol. 10, 63–66. https://doi.org/10.1016/s0169-5347(00)88978-8.

Deforest, J.L., Zak, D.R., Pregitzer, K.S., Burton, A.J., 2004. Atmospheric nitrate deposition, microbial community composition, and enzyme activity in northern hardwood forests. Soil Sci. Soc. Am. J. 68, 132–138. https://doi.org/10.2136/sssaj2004.1320.

Ding, Y., Leppälammi-Kujansuu, J., Salemaa, M., Schiestl-Aalto, P., Kulmala, L., Ukonmaanaho, L., Nöjd, P., Minkkinen, K., Makita, N., Železnik, P., Merilä, P., Helmisaari, H.-S., 2021. Distinct patterns of below- and aboveground growth phenology and litter carbon inputs along a boreal site type gradient. For. Ecol. Manag. 489, 119081. https://doi.org/10.1016/j.foreco.2021.119081.

Edwards, I.P., Zak, D.R., Kellner, H., Eisenlord, S.D., Pregitzer, K.S., 2011. Simulated atmospheric N deposition alters fungal community composition and suppresses ligninolytic gene expression in a northern hardwood forest. Plos One 6, e20421. https://doi.org/10.1371/journal.pone.0020421.

Gill, R.A., Burke, I.C., 2002. Influence of soil depth on the decomposition of Bouteloua gracilis roots in the shortgrass steppe. Plant Soil 241, 233–242. https://doi.org/10.1023/a:1016146805542.

Gill, R.A., Jackson, R.B., 2000. Global patterns of root turnover for terrestrial ecosystems. N. Phytol. 147, 13–31. https://doi.org/10.1046/j.1469-8137.2000.00681.x.

Girkin, N.T., Turner, B.L., Ostle, N., Sjögersten, S., 2018. Root-derived CO2 flux from a tropical peatland. Wetl. Ecol. Manag. 26, 985–991. https://doi.org/10.1007/s11273-018-9617-8.

Gorham, E., 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. Ecol. Appl. 1, 182–195. https://doi.org/10.2307/1941811.

Grier, C.C., Vogt, K.A., Keyes, M.R., Edmonds, R.L., 1981. Biomass distribution and above- and below-ground production in young and mature Abiesamabilis zone ecosystems of the Washington Cascades. Can. J. For. Res. 11, 155–167. https://doi.org/10.1139/x81-021.

Guo, D., Li, H., Mitchell, R.J., Han, W., Hendricks, J.J., Fahey, T.J., Hendrick, R.L., 2008a. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. N. Phytol. 177, 443–456. https://doi.org/10.1111/j.1469-8137.2007.02242.x.

Guo, D., Xia, M., Wei, X., Chang, W., Liu, Y., Wang, Z., 2008c. Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. N. Phytol. 180, 673–683. https://doi.org/10.1111/j.1469-8137.2008.02573.x.

Guo, D., Mitchell, R.J., Withington, J.M., Fan, P.P., Hendricks, J.J., 2008b. Endogenous and exogenous controls of root life span, mortality and nitrogen flux in a longleaf pine forest: root branch order predominates. J. Ecol. 96, 737–745. https://doi.org/10.1111/j.1365-2745.2008.01385.x.

Guo, D.L., Mitchell, R.J., Hendricks, J.J., 2004. Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140, 450–457 https://doi.org/0.1007/s00442-004-1596-1.

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

Harmon, M.E., Silver, W.L., Fasth, B., Chen, H., Burke, I.C., Parton, W.J., Hart, S.C., Currie, W.S., 2009. Long-term patterns of mass loss during the decomposition of leaf and fine root litter: an intersite comparison. Glob. Change Biol. 15, 1320–1338. https://doi.org/10.1111/j.1365-2486.2008.01837.x.

He, W., Mäkiranta, P., Straková, P., Ojanen, P., Penttilä, T., Bhuiyan, R., Minkkinen, K., Laiho, R., 2023. Fine-root production in boreal peatland forests: effects of stand and environmental factors. For. Ecol. Manag. 550. https://doi.org/10.1016/j.foreco.2023.121503.

Heikurainen, L., 1964. Improvement of Forest Growth on Poorly Drained Peat Soils. Elsevier, pp. 39–113. https://doi.org/10.1016/b978-1-4831-9975-7.50007-7.

Heim, A., Frey, B., 2004. Early stage litter decomposition rates for swiss forests. Biogeochemistry 70, 299–313. https://doi.org/10.1007/s10533-003-0844-5.

Helmisaari, H.S., 1991. Variation in Nutrient Concentrations of Pinus sylvestris Roots. Elsevier, pp. 204–212. https://doi.org/10.1016/b978-0-444-89104-4.50031-1.

Hermans, R., McKenzie, R., Andersen, R., Teh, Y.A., Cowie, N., Subke, J.-A., 2022. Net soil carbon balance in afforested peatlands and separating autotrophic and heterotrophic soil CO2 effluxes. Biogeosciences 19, 313–327. https://doi.org/10.5194/bg-19-313-2022.

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

Hicks Pries, C.E., Sulman, B.N., West, C., O'Neill, C., Poppleton, E., Porras, R.C., Castanha, C., Zhu, B., Wiedemeier, D.B., Torn, M.S., 2018. Root litter decomposition slows with soil depth. Soil Biol. Biochem. 125, 103–114. https://doi.org/10.1016/j.soilbio.2018.07.002.

Hishi, T., 2007. Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. J. For. Res. 12, 126–133.

Hobbie, S.E., Oleksyn, J., Eissenstat, D.M., Reich, P.B., 2010. Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. Oecologia 162, 505–513. https://doi.org/10.1007/s00442-009-1479-6.

Jackson, C.R., Liew, K.C., Yule, C.M., 2009. Structural and functional changes with depth in microbial communities in a tropical Malaysian peat swamp forest. Microb. Ecol. 57, 402–412. https://doi.org/10.1007/s00248-008-9409-4.

Jackson, R.B., Mooney, H.A., Schulze, E.D., 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proc. Natl. Acad. Sci. 94, 7362–7366. https://doi.org/10.1073/pnas.94.14.7362.

Jauhiainen, J., Heikkinen, J., Clarke, N., He, H., Dalsgaard, L., Minkkinen, K., Ojanen, P., Vesterdal, L., Alm, J., Butlers, A., Callesen, I., Jordan, S., Lohila, A., Mander, Ü., Óskarsson, H., Sigurdsson, B.D., Søgaard, G., Soosaar, K., Kasimir, Å., Bjarnadottir, B., Lazdins, A., Laiho, R., 2023. Reviews and syntheses: greenhouse gas emissions from drained organic forest soils – synthesizing data for site-specific emission factors for boreal and cool temperate regions. Biogeosciences 20, 4819–4839. https://doi.org/10.5194/bg-20-4819-2023.

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

Kasimir, Å., He, H., Jansson, P.E., Lohila, A., Minkkinen, K., 2021. Mosses are important for soil carbon sequestration in forested Peatlands. Front. Environ. Sci. 9. https://doi.org/10.3389/fenvs.2021.680430.

Krishna, M.P., Mohan, M., 2017. Litter decomposition in forest ecosystems: a review. Energy, Ecol. Environ. 2, 236–249. https://doi.org/10.1007/s40974-017-0064-9.

Kyaschenko, J., Ovaskainen, O., Ekblad, A., Hagenbo, A., Karltun, E., Karina, Lindahl, B. D., 2019. Soil fertility in boreal forest relates to root-driven nitrogen retention and carbon sequestration in the mor layer. N. Phytol. 221, 1492–1502. https://doi.org/10.1111/nph.15454.

Lähde, E., 1969. Biological activity in some natural and drained peat soils with special reference to oxidation-reduction conditions. Acta For. Fenn. 69.

Laiho, R., 2006. Decomposition in peatlands: Reconciling seemingly contrasting results on the impacts of lowered water levels. Soil Biol. Biochem. 38, 2011–2024. https://doi.org/10.1016/j.soilbio.2006.02.017.

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

Laine, A.M., Korrensalo, A., Kokkonen, N.A.K., Tuittila, E.S., 2021. Impact of long-term water level drawdown on functional plant trait composition of northern peatlands. Funct. Ecol. 35, 2342–2357. https://doi.org/10.1111/1365-2435.13883.

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

Latter, P.M., Howson, G., Howard, D.M., Scott, W.A., 1997. Long-term study of litter decomposition on a Pennine peat bog: which regression? Oecologia 113, 94–103. https://doi.org/10.1007/s004420050357.

Lehtonen, A., Palviainen, M., Ojanen, P., Kalliokoski, T., Nöjd, P., Kukkola, M., Penttilä, T., Mäkipää, R., Leppälammi-Kujansuu, J., Helmisaari, H.S., 2016. Modelling fine root biomass of boreal tree stands using site and stand variables. For. Ecol. Manag. 359, 361–369. https://doi.org/10.1016/j.foreco.2015.06.023.

Leppälammi-Kujansuu, J., Aro, L., Salemaa, M., Hansson, K., Kleja, D.B., Helmisaari, H.-S., 2014. Fine root longevity and carbon input into soil from below- and aboveground litter in climatically contrasting forests. For. Ecol. Manag. 326, 79–90. https://doi.org/10.1016/j.foreco.2014.03.039.

Li, X., Zheng, X., Zhou, Q., McNulty, S., King, J.S., 2022. Measurements of fine root decomposition rate: Method matters. Soil Biol. Biochem. 164, 108482. https://doi.org/10.1016/j.soilbio.2021.108482.

Lieffers, V.J., 1988. Sphagnum and cellulose decomposition in drained and natural areas of an alberta Peatland. Can. J. Soil Sci. 68, 755–761. https://doi.org/10.4141/cjss88-073.

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

Liu, Q., Zhuang, L., Yin, R., Ni, X., You, C., Yue, K., Tan, B., Liu, Y., Zhang, L., Xu, Z., 2019. Root diameter controls the accumulation of humic substances in decomposing root litter. Geoderma 348, 68–75. https://doi.org/10.1016/j.geoderma.2019.04.016.

Ludovici, K.H., Kress, L.W., 2006. Decomposition and nutrient release from fresh and dried pine roots under two fertilizer regimes. Can. J. For. Res. 36, 105–111. https://doi.org/10.1139/x05-227.

Luo, D., Cheng, R., Shi, Z., Wang, W., 2017. Decomposition of leaves and fine roots in three subtropical plantations in China affected by litter substrate quality and soil microbial community. Forests 8, 412. https://doi.org/10.3390/f8110412.

Macdonald, S.E., Yin, F., 1999. Factors influencing size inequality in peatland black spruce and tamarack: evidence from post-drainage release growth. J. Ecol. 87, 404–412. https://doi.org/10.1046/j.1365-2745.1999.00370.x.

Makita, N., Kawamura, A., Osawa, A., 2015. Size-dependent morphological and chemical property of fine root litter decomposition. Plant Soil 393, 283–295. https://doi.org/10.1007/s11104-015-2491-8.

Manzoni, S., Piñeiro, G., Jackson, R.B., Jobbágy, E.G., Kim, J.H., Porporato, A., 2012. Analytical models of soil and litter decomposition: solutions for mass loss and time-dependent decay rates. Soil Biol. Biochem. 50, 66–76. https://doi.org/10.1016/j.soilbio.2012.02.029.

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

McCormack, M.L., Dickie, I.A., Eissenstat, D.M., Fahey, T.J., Fernandez, C.W., Guo, D., Helmisaari, H.S., Hobbie, E.A., Iversen, C.M., Jackson, R.B., Leppälammi-Kujansuu, J., Norby, R.J., Phillips, R.P., Pregitzer, K.S., Pritchard, S.G., Rewald, B., Zadworny, M., 2015. Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. N. Phytol. 207, 505–518. https://doi.org/10.1111/nph.13363.

Merilä, P., Mustajärvi, K., Helmisaari, H.-S., Hilli, S., Lindroos, A.-J., Nieminen, T.M., Nöjd, P., Rautio, P., Salemaa, M., Ukonmaanaho, L., 2014. Above- and below-ground N stocks in coniferous boreal forests in Finland: Implications for sustainability of more intensive biomass utilization. For. Ecol. Manag. 311, 17–28. https://doi.org/10.1016/j.foreco.2013.06.029.

Minkkinen, K., Ojanen, P., Penttilä, T., Aurela, M., Laurila, T., Tuovinen, J.-P., Lohila, A., 2018. Persistent carbon sink at a boreal drained bog forest. Biogeosciences 15, 3603–3624. https://doi.org/10.5194/bg-15-3603-2018.

Minkkinen, K., Laiho, R., Salomäki, J., 2024. Fine root longevity and biomass production in boreal peatlands. Copernic. GmbH. https://doi.org/10.5194/egusphere-egu24-10218.

Moore, T.R., Trofymow, J.A., Siltanen, M., Prescott, C., Group, C.W., 2005. Patterns of decomposition and carbon, nitrogen, and phosphorus dynamics of litter in upland forest and peatland sites in central Canada. Can. J. For. Res. 35, 133–142. https://doi.org/10.1139/x04-149.

Moore, T.R., Bubier, J.L., Bledzki, L., 2007. Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. Ecosystems 10, 949–963. https://doi.org/10.1007/s10021-007-9064-5.

Moore, T.R., Trofymow, J.A., Siltanen, M., Kozak, L.M., 2008. Litter decomposition and nitrogen and phosphorus dynamics in peatlands and uplands over 12 years in central Canada. Oecologia 157, 317–325. https://doi.org/10.1007/s00442-008-1076-0.

Ojanen, P., Lehtonen, A., Heikkinen, J., Penttilä, T., Minkkinen, K., 2014. Soil CO2 balance and its uncertainty in forestry-drained peatlands in Finland. For. Ecol. Manag. 325, 60–73. https://doi.org/10.1016/j.foreco.2014.03.049.

Olson, J.S., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44, 322–331. https://doi.org/10.2307/1932179.

Pohjanmies, T., Genikova, N., Hotanen, J.P., Ilvesniemi, H., Kryshen, A., Moshnikov, S., Oksanen, J., Salemaa, M., Tikhonova, E., Tonteri, T., Merilä, P., 2021. Site types revisited: comparison of traditional russian and finnish classification systems for European boreal forests. Appl. Veg. Sci. 24. https://doi.org/10.1111/avsc.12525.

Pregitzer, K.S., DeForest, J.L., Burton, A.J., Allen, M.F., Ruess, R.W., Hendrick, R.L., 2002. Fine root architecture of nine North American trees. Ecol. Monogr. 72, 293–309.

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

Saha, S., Huang, L., Khoso, M.A., Wu, H., Han, D., Ma, X., Poudel, T.R., Li, B., Zhu, M., Lan, Q., Sakib, N., Wei, R., Islam, M.Z., Zhang, P., Shen, H., 2023. Fine root decomposition in forest ecosystems: an ecological perspective. Front. Plant Sci. 14. https://doi.org/10.3389/fpls.2023.1277510.

Santantonio, D., Grace, J.C., 1987. Estimating fine-root production and turnover from biomass and decomposition data: a compartment–flow model. Can. J. For. Res. 17, 900–908. https://doi.org/10.1139/x87-141.

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

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

Schenk, H.J., Jackson, R.B., 2002. The global biogeography of roots. Ecol. Monogr. 72, 311–328. https://doi.org/10.1890/0012-9615(2002)072[0311:TGBOR]2.0.CO;2.

Silvan, N., Laiho, R., Vasander, H., 2000. Changes in mesofauna abundance in peat soils drained for forestry. For. Ecol. Manag. 133, 127–133. https://doi.org/10.1016/s0378-1127(99)00303-5.

Silver, W.L., Miya, R.K., 2001. Global patterns in root decomposition: comparisons of climate and litter quality effects. Oecologia 129, 407–419. https://doi.org/10.1007/s004420100740.

Smith, S.W., Woodin, S.J., Pakeman, R.J., Johnson, D., Van Der Wal, R., 2014. Root traits predict decomposition across a landscape-scale grazing experiment. N. Phytol. 203, 851–862. https://doi.org/10.1111/nph.12845.

Socha, J., 2012. Long-term effect of wetland drainage on the productivity of Scots pine stands in Poland. For. Ecol. Manag. 274, 172–180. https://doi.org/10.1016/j.foreco.2012.02.032.

Solly, E.F., Schöning, I., Herold, N., Trumbore, S.E., Schrumpf, M., 2015. No depth-dependence of fine root litter decomposition in temperate beech forest soils. Plant Soil 393, 273–282. https://doi.org/10.1007/s11104-015-2492-7.

Steinweg, J.M., Kostka, J.E., Hanson, P.J., Schadt, C.W., 2018. Temperature sensitivity of extracellular enzymes differs with peat depth but not with season in an ombrotrophic bog. Soil Biol. Biochem. 125, 244–250. https://doi.org/10.1016/j.soilbio.2018.07.001.

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

Straková, P., Niemi, R.M., Freeman, C., Peltoniemi, K., Toberman, H., Heiskanen, I., Fritze, H., Laiho, R., 2011. Litter type affects the activity of aerobic decomposers in a boreal peatland more than site nutrient and water table regimes. Biogeosciences 8, 2741–2755. https://doi.org/10.5194/bg-8-2741-2011.

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

Straková, P., Larmola, T., Andrés, J., Ilola, N., Launiainen, P., Edwards, K., Minkkinen, K., Laiho, R., 2020. Quantification of plant root species composition in peatlands using FTIR spectroscopy. Front. Plant Sci. 11. https://doi.org/10.3389/fpls.2020.00597.

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

Talbot, J., Richard, P.J.H., Roulet, N.T., Booth, R.K., 2010. Assessing long-term hydrological and ecological responses to drainage in a raised bog using paleoecology and a hydrosequence. J. Veg. Sci. 21, 143–156. https://doi.org/10.1111/j.1654-1103.2009.01128.x.

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

Trofymow, J.A., Moore, T.R., Titus, B., Prescott, C., Morrison, I., Siltanen, M., Smith, S., Fyles, J., Wein, R., Camiré, C., Duschene, L., Kozak, L., Kranabetter, M., Visser, S., 2002. Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. Can. J. For. Res. 32, 789–804. https://doi.org/10.1139/x01-117.

Tuittila, E.S., Väliranta, M., Laine, J., Korhola, A., 2007. Quantifying patterns and controls of mire vegetation succession in a southern boreal bog in Finland using partial ordinations. J. Veg. Sci. 18, 891–902. https://doi.org/10.1111/j.1654-1103.2007.tb02605.x.

Usman, S., Singh, S.P., Rawat, Y.S., Bargali, S.S., 2000. Fine root decomposition and nitrogen mineralisation patterns in Quercus leucotrichophora and Pinus roxburghii forests in central Himalaya. For. Ecol. Manag. 131, 191–199. https://doi.org/10.1016/s0378-1127(99)00213-3.

Vasander, H., Laine, J., 2008. Site type classification on drained peatlands. Finland-Fenland: research and sustainable utilisation of mires and peat. Finnish Peatland Society Maahenki, pp. 146–151.

Vogt, K., 1991. Carbon budgets of temperate forest ecosystems. Tree Physiol. 9, 69–86. https://doi.org/10.1093/treephys/9.1-2.69.

Westman, C.J., Laiho, R., 2003. Nutrient dynamics of drained peatland forests. Biogeochemistry 63, 269–298. https://doi.org/10.1023/a:1023348806857.

Wieder, R.K., Lang, G.E., 1982. A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63, 1636. https://doi.org/10.2307/1940104.

Xia, M., Talhelm, A.F., Pregitzer, K.S., 2015. Fine roots are the dominant source of recalcitrant plant litter in sugar maple-dominated northern hardwood forests. N. Phytol. 208, 715–726. https://doi.org/10.1111/nph.13494.

Xia, M., Talhelm, A.F., Pregitzer, K.S., 2018. Long-term simulated atmospheric nitrogen deposition alters leaf and fine root decomposition. Ecosystems 21, 1–14. https://doi.org/10.1007/s10021-017-0130-3.

Yuan, Z.Y., Chen, H.Y.H., 2010. Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: literature review and meta-analyses. Crit. Rev. Plant Sci. 29, 204–221. https://doi.org/10.1080/07352689.2010.483579.

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

Zhang, X., Wang, W., 2015. The decomposition of fine and coarse roots: their global patterns and controlling factors. Sci. Rep. 5, 9940. https://doi.org/10.1038/srep09940.

Zhuang, L., Yang, W., Wu, F., Tan, B., Zhang, L., Yang, K., He, R., Li, Z., Xu, Z., 2018. Diameter-related variations in root decomposition of three common subalpine tree species in southwestern China. Geoderma 311, 1–8. https://doi.org/10.1016/j.geoderma.2017.09.041.