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From deadwood to forest soils: quantifying a key carbon flux in boreal ecosystems

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Abstract Deadwood represents a dynamic carbon pool in forest ecosystems where microbial decomposition causes fluxes of CO_2 to the atmosphere through respiration and organic carbon to the soil through leakage and fragmentation. This study characterises different stages of deadwood of Norway spruce (*Picea abies*). 35 Norway spruce trees were sampled and categorized on a 0–5 decay scale. For the 14 trees in classes 0–3, two stem discs were collected from two heights. For the 21 trees in classes 4 and 5, a single sample per tree was taken, because decay was relatively uniform throughout the stem. The relative amount of hemicellulose and cellulose declined moderately from decay class 1 to 3 and substantially from decay class 3 to class 4 but small amounts were still present in decay class 5. The relative lignin proportion increased substantially from decay class 3 to 4 and dominated in decay class 5. Relative carbon content increased from 50 to 56% during the decomposition process due to the increasing accumulation of lignin residuals being a typical signature of brown rot decay. A laboratory experiment including three species of brown rot fungi verified decomposition close to 70% of Norway spruce biomass and resulted in 55% carbon content. This was similar to the carbon content in decay class 4 and 5. A novel approach is presented to quantify the carbon flux from deadwood to the soil. First, we calculated the residual proportion of carbon in decayed wood compared to the initial carbon content of live trees. Subsequently, we extended the calculation to determine the amount of remaining carbon from non-decayed wood that was transferred to the soil during each decay class. The approach showed that Norway spruce wood decomposition under field conditions transfers at least 39–47% of the initial wood carbon to the soil carbon pool, depending on soil type. This strengthens the previously under-communicated fact that the carbon flux from deadwood to soil is higher from brown rot decomposition in boreal forests than the corresponding carbon flux in temperate and tropical forests where deadwood is more influenced by white rot fungi.

Keywords Brown rot · Carbon content · Chemical composition · Norway spruce · White rot · Wood density

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Introduction

Boreal forests comprise about a third of the global forest cover (FAO 2006) and contain an estimated one third of the terrestrial carbon stocks (IPCC 2007; Pan et al. 2011). According to Pan et al. (2011) boreal forest ecosystem account for 20% of the global forest carbon sink for atmospheric CO_2. Some studies indicate that the sink strength is weakening (Stephens et al. 2007; Bonan 2008; Hayes et al. 2012) while other studies indicate a stable (Pan et al. 2011) or even increasing (Watts et al. 2023) sink strength over time. A distinct feature of boreal forests is that most of the carbon stock resides in the soil (93%) while the remainder (7%) is plant biomass; contrasting with tropical rainforests with 49% in the soil and 51% in live plants (Scharlemann et al. 2014).

Reliable knowledge about carbon pools and fluxes is fundamental to develop government policies for resource utilisation and climate change mitigation across boreal forests. This is the background for nations reporting their contribution to the global carbon cycle through annual greenhouse gas (GHG) national inventory reports. The IPCC guidelines state that nations should report forest carbon stock changes in four separate pools: aboveground biomass, litter, deadwood and soil organic carbon. A typical approach in GHG inventories is to translate deadwood volumes and biomass into carbon stocks, typical with conversion factors for five decay classes (Sandström et al. 2007; Weggler et al. 2012; Stakėnas et al. 2020; Romashkin et al. 2021).

It is often implicitly assumed that all wood is decomposed completely above-ground. However, in boreal forest a significant proportion of medium-strongly decayed wood is overgrown by the ground vegetation and incorporated into the soil humus layer, i.e. becomes buried (Moroni et al. 2015; Stokland et al. 2016). Wood decomposition slows down significantly when buried in upland well-drained soils (Moroni et al. 2010) and it appears to be permanently arrested in wet organic soils (Eckstein et al. 2009). The reduced decomposition rate can result in significant buried stores of wood components. It seems to be a gap in forest carbon inventories as carbon from such buried deadwood is generally not quantified.

In boreal forest ecosystems conifers are the dominating forest forming species. The primary coniferous wood degraders are brown rot fungi (Arantes and Goodell 2014). Briefly, brown rot fungi utilize a non-enzymatic system during initiation of decay that rapidly depolymerizes cell wall components prior to degradation by cellulases and hemicellulases (Wei et al. 2010; Korripally et al. 2013; Arantes and Goodell 2014; Zhang et al. 2016; Goodell et al. 2017; Zhang and Schilling 2017). Further support for this two-step mechanism has been provided by gene expression and secretome studies (e.g. Zhang et al. 2016). Brown rot does not degrade lignin but induce chemical modifications to lignin such as demethylation and an increase in truncated lignin structures (Filley et al. 2002; Yelle et al. 2011). The stability of this brown rot modified lignin needs further investigation. While brown rot fungi tend to dominate the decomposition of conifer wood in boreal forests, white rot fungi are the main wood decomposers in temperate and tropical forests where broadleaved trees tend to dominate (Curling et al. 2002; Arantes and Goodell 2014). In contrast to brown rot fungi white rot fungi degrade lignin. Thus, one can expect that contrast in dominating decay mechanisms in boreal versus temperate and tropical forests produce different carbon fluxes from deadwood to the soil carbon pool in these forest ecosystems. This difference is probably reinforced by insects being more important wood decomposers in temperate and tropical forests than in boreal forests (Seibold et al. 2021).

Most of the carbon from wood decomposition seems to be released back to the atmosphere as CO_2 from respiration and this flux seems to be larger in tropical than in boreal forests (Chambers et al. 2001; Bond-Lamberty and Gower 2008). However, it has become evident that there also is a significant carbon flux from deadwood to soil in the form of dissolved organic carbon (Hafner et al. 2005; Kuehne et al. 2008; Bantle et al. 2014; Stutz et al. 2017; Błońska et al. 2019a) and fragmentation of particulate wood residuals (Stutz et al. 2017; Lagomarsino et al. 2021). Numerous studies have documented increased amount of organic carbon in soil directly below deadwood compared to reference points few meters away from the wood (Kahl et al. 2012; Pichler et al. 2013; Bai et al. 2017; Wambsganss et al. 2017; Błońska et al. 2017; Błońska et al. 2019b; Stutz et al. 2019; Piaszczyk et al. 2019; Minnich et al. 2021; Shannon et al. 2022; Nazari et al. 2023 but see Spears et al. 2003). Hardly any of these studies have quantified the total amount or proportion of carbon from deadwood

that enter the soil carbon pool except Lagomarsino et al. (2021). This is confirmed by Tatti et al. (2018) who states "…the study of deadwood in a broader ecosystemic context remains relatively untouched …, especially when linked to humus systems made of dominant wood under transformation by wood-feeding animals and/or wood-rotting fungi."

The aim of the study was to profile all five decay classes of Norway spruce in a boreal Norwegian forest with focus on later decay classes and changes in wood polymer and carbon content. Our null hypothesis was that the decomposition of coniferous wood in boreal forests does not provide carbon transfer to the soil carbon pool. The following parameters were quantified: decay class (0–5), wood density, hemicellulose, cellulose, lignin, carbon, nitrogen and C/N ratio. Decay class was used to stratify the samples for further analysis to document the loss of different wood components during decomposition and the remaining residuals being transferred to the soil in the final decay stage(s).

Materials and methods

Decay characterisation of stem discs

In total 35 Norway spruce trees were sampled from the from a ICP Forests intensive monitoring site (Level II) in Hurdal, Viken, Norway (DEIMS-SDR 2023) May 2021. The monitoring site in Hurdal is 0.103 hectars, stand age 97 years and is situated in blueberry-dominated Norway spruce forest at approximately 275 m above sea level (Timmermann et al. 2023, Supplementary material 1 in Verstraeten et al. 2023). Within the stand we randomly selected deadwood from downed trees representing different decay stages. Decay classes were defined on a 0–5 scale (Table 1) to stratify the wood samples. For some samples, the wood was in transition from one decay class to the next. We grouped such samples to the earlier decay class (except in Fig. 1 where samples in transition from decay class 3 to 4 are illustrated separately). For 14 trees in decay classes 0–3 we typically collected two 5 cm thick stem discs from each tree using a chain saw, one near the root end, and another 4–5 m further along the stem (Table 1). For 21 trees in decay classes 4 and 5 we typically collected one sample per tree because the decay was regarded as homogenous throughout the stem (Table 1). In addition, we included a wood sample from a Norway spruce tree

Table 1 Definition of decay classes and number of sample trees and subsamples used in this study

Decay class	No. of trees	No. of samples	Definition
0	1	2	Recently windthrown (0–3 months), still with green needles
1	2	3	Recently deadwood (0–3 years), bark still firmly attached or recently loose after intensive bark beetle attacks. Hard sapwood
2	5[a]	9	Loose bark with incipient to well-developed fungal mycelium between bark and wood. Starts to soften 0–3 cm into the wood
3	7[a]	11	More or less rotten > 3 cm into wood where it can be picked apart with a knife. The core is still hard
4	12[b]	13	The wood is rotten throughout and has elliptic cross-section, can be picked apart by hand and is floating out on the ground in places. No inner hard core. Often somewhat overgrown
5	10[b]	10	Wood fragments only, often covered by ground vegetation, contours of completely decomposed trunk

The total number of trees is 35, but in two trees had different decay classes within the same tree

[a]11 trees altogether in decay class 2 and 3, but one tree had a sample with decay 2 and another with decay 3. Hence, the tree with two decay classes is allocated to both categories

[b]21 trees altogether, but one tree had a sample with decay 4 and another with decay 5. Hence, the tree with two decay classes is allocated to both categories

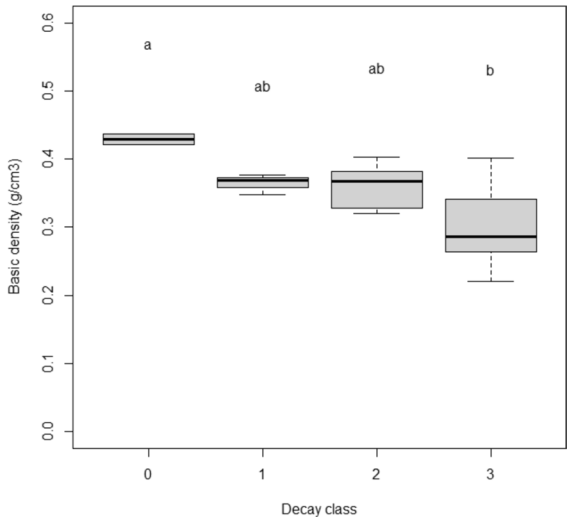

Fig. 1 Basic density relative to decay class from field samples of dead Norway spruce logs. Decay class 0 represents samples from a harvested tree and a newly fallen tree with green needles. Different letters above boxplots represent statistical different group means

directly after harvest. The mean sample disc diameter was 16.6 cm (range 9.4–21.0 cm). The same day as sampling was performed all wood samples were stored in a freezer at − 20 °C until further use.

Disc diameter was recorded for all stem discs in decay classes 0–4 except two fragmented discs in decay class 4. Samples in decay class 5 were too decomposed to measure diameter.

Five subsamples (2×2 × 2 cm) were collected from each stem disc for density analysis. The subsamples were from the four cardinal directions in the disc sapwood and one in the heartwood core. Subsample 1 was always from the upper side of the log (marked with chain saw in the field) while sample 5 always was from the heartwood core. For the remaining of the stem discs the bark was removed (using a knife and hammer), and the wood was milled and sieved with a 8 mm mesh. The material was kept frozen at − 20 °C for further analyses.

Density

When possible mean basic density was calculated from five subsamples of each stem disc. Samples in decay class 4 and 5 were too decomposed to measure density (i.e. after sampling we had no stem disc but only wood fragments). Basic density was calculated as:

$$p_0 = m_0 / V_{max}, \quad (1)$$

where m_0 is the mass (g) of the dry sample and V_{max} is the volume of the sample at fibre saturation (cm^3).

Wood polymer characterisation

The 8-mm-sieved wood fraction described above was milled to 1 mm. An aliquot of the material was extracted with acetone previously described in (Ekeberg et al. 2006) with some modifications. 7 g of the material was extracted for 8 h using Soxtec Avanti 2050 (Foss-Tecator, Foss North America, MN, USA). The extracted material was vacuum dried at 60 °C for 4 days. Cellulose was quantified in extracted and vacuum dried material according to the Seifert method (Browning 1967) using acetylacetone (Merk), 1,4-dioxane (Merk), hydrochloric acid (VWR 37%), methanol (VWR) and diethyl ether (Merk). Klason lignin was determined in extracted and vacuum dried material according to (TAPPI 2006), using 95–97% sulfuric acid (Merk). An aliquot of the material was used for hemicellulose quantification according to Gao et al. (2014). The method included a one-step acid hydrolysis of the wood using 87 ml 4 wt % sulfuric acid (Merk) in autoclave at 121 °C for 1 h and sugar analysis on a HPLC 1260 Infinity II system with a refractive index detector (Agilent Technologies, Hewlett-Packard-Strasse 8, Waldbronn, Germany). The amount of sugar content was calculated according to NREL (Sluiter et al. 2012).

C/N analyses

A combustion method, also known as The Dumas method, was used to quantify nitrogen and carbon according to ISO 13878. Samples of 10 mg (1 mm sized milled wood) was weighed into tin foil boats. The boats were closed and compressed before introduction into the instrument. The samples were combusted at an oven temperature of 950 °C. The resulting gasses were quantified using a Elementar Vario EL Cube (Elementar Analysensysteme GmbH, Langenselbold, Germay) and a thermal conductivity detector.

Laboratory wood decomposition test

To establish a link between mass loss and carbon content a laboratory decay test was performed with wood blocks inoculated with basidiomycete monocultures: three brown rot fung—*Fomitopsis pinicola* (NIBIO strain 2000-67/10), *Fomitopsis rosea* (NIBIO strain 1998-746/1) and *Rhodonia placenta* (FPRL 280), and one white rot fungus *Trametes versicolor* (CTB 863 A). All four species are found in the boreal forest in Norway, but the two latter are also regarded as model organisms, i.e., frequently included in standards and different fungal decay experiments. Wood material was from the reference tree and wood block sample size was 5 × 10 × 30 mm based on Bravery (1978). The samples were dried at 60 °C for 76 h and cooled down in a desiccator before initial dry weight was measured and the dry dimension of the samples were measured with a Mitutoyo Digimatic digital caliper. The samples were climatized to stable weight at 65% RH/20 °C before it was sterilised in an autoclave at 20 min/120 °C. Sterile soil was used instead of malt medium as substrate to facilitate a prolonged incubation phase. The sterile soil was a mix of 1/3 garden compost (leaves and gras) and 2/3 sandy soil and it was sterilised in an autoclave 2 × 60 min/120 °C. Two specimens were added to each Petri dish containing 20 g sterile soil and a plastic mech separating the specimens from direct soil contact. Liquid cultures of the test fungi were homogenised with a Ultraturax (IKA). Under sterile conditions 1 ml fungal inoculum was added to each wood block. The total weight of the Petri dishes was measured before incubation at 70% RH/ 22 °C. Every third week the weight of the Petri dishes was recorded, and sterile water added to the soil when needed to make sure the moisture content remained stable. To profile the decay development samples were harvested at different intervals. The time of incubation was based on previous experience with these species and strains and the aim was to keep the experiment running until the decay rate levelled out: *F. pinicola* and *F. rosea*—harvest every second week, 12 weeks in total, *R. placenta* harvest every fourth week, 20 weeks in total, and *T. versicolor*—harvest every fourth week, 32 weeks in total. Six replicates were collected for each fungus at each harvest point. At each harvest point mycelia on the surface of the samples were removed before dry weight were recorded. Mass loss was calculated as:

$$\left(m_0 - m_1/m_0\right) * 100, \tag{2}$$

where m_0 is initial dry weight and m_1 is dry weight after fungal decay.

For the C/N quantification we analysed specimens with increasing levels of mass loss (i.e. n = 20 for *F. pinicola*, n = 13 for *F. rosea*, n = 12 for *R. placenta*, n = 12 for *T. versicolor* and n = 1 for reference sample).

Carbon flux to the soil

We introduce a novel approach to calculate the carbon flux from the deadwood pool to the soil carbon pool. This approach combines two equations.

First, using our own and published data we calculate, for each decay class, the remaining proportion of carbon in decayed wood relative to the initial carbon content of wood in live trees. In the following equations wood density indicates the weight of oven-dried wood samples divided by the fresh wood volume (i.e. before drying). Two alternative equations can be used, depending on whether the wood density of decay class 0 is known (Eq. 3a) or not (Eq. 3b):

$$C_d = \left(CP_d/CP_0\right) * 100 * DD_d/DD_0, \text{ or,} \tag{3a}$$

$$= \left(CP_d/CP_0\right) * 100 * DD_d/\left(DD_1/(1 - il)\right), \tag{3b}$$

where

C_d: is the remaining carbon in decay class d as a percentage of the carbon in a wood unit at the mortality event (i.e. non-decayed wood).

CP_0: is the carbon percentage in non-decayed wood.

CP_d: is the carbon percentage in decay class d.

DD_0: is the wood density in non-decayed wood. DD_1/(1-*il*) : is used as a proxy when DD_0: is not reported in the study (Eq. 3b).

DD_d: is the wood density in decay class d.

il: is the initial wood density loss from non-decayed wood to decay class 1.

Studies documenting wood density of decayed wood are typically silent about the wood density of sound (i.e. non-decayed) wood. Based on a typically reported density of non-decayed Norway spruce wood of 0.41 g/cm^3 (mean value based on six Norwegian studies from Fischer 2016) and mean wood density for decay class 1 = 0.38 g/cm^3 (Table S1), we use

0.07 as a constant for *il* and thus divided DD_1 values by 0.93 to obtain a proxy for DD_0.

For CP_d and CP_0: we used our own data as derived from Fig. 3a. Due to very similar mean and range values for CP_4 and CP_5, we used the same value of 56% for both decay classes.

Second, we calculated, for each decay class, how much of the initial carbon in non-decayed wood that is transferred to the soil during this decay class using the following equation (Eq. 4):

$$BC_d = b_d * C_d \quad (4)$$

where BC_d is the percentage of initial carbon in non-decayed wood buried in decay class d, b_d is the proportion of all logs that become buried in decay class d, C_d is the remaining carbon in decay stage d as calculated in Eqs. 3a and 3b. Buried in this context means that the log is overgrown by ground vegetation and incorporated into the soil humus layer.

We derived b_d values from Fig. 2 in Stokland et al. (2016) who analysed burial status for more than 11 000 downed logs in a Swedish NFI dataset covering the whole boreal zone. The Swedish decay classification system deviates somewhat from the standard 5-class system being used in our study and the studies listed in Table S1, specifically that the Swedish decay class D3 corresponds to decay class 3 in Tables S1 and S2, while the Swedish class D4 comprise both decay class 4 and 5 in Tables S1 and S2 (Aakala and Heikkinen 2024). The proportion of buried logs (defined as > 50% of the log incorporated into the humus layer) increased from 6–22% in decay class D1-D2 to 51% in decay class D4 (Stokland et al. 2016). Since the definition of burial included logs that are still somewhat exposed, we assumed that no complete burial occurred in decay class D1-D2 and subsequently we reduced the burial proportions by ca. 10 percentage points from the percentages of predominantly buried logs entering a decay class (from 22 to 10% entering decay class D3 and from 38 to 30% entering decay class D4 on mineral soils, and from 39 to 30% entering both decay class D3 and D4 on organic soils). Hence, we adopted a conservative approach for burial percentages and used the following b_d values in Eq. 4: 0, 0, 0.1, 0.3 and 0.6 for decay class 1–5 on mineral soils and 0, 0, 0.3, 0.3 and 0.4 for decay classes 1–5 on organic soils (Table S3). The b_d values for decay class 5 (i.e. 0.6 and 0.4) represent the remaining logs not buried in earlier decay classes. (Specifically: the values for decay class 5 are calculated as $1 - (0.1 + 0.3)$ for mineral soils and $1 - (0.3 + 0.3)$ for organic soils). Thus, we assume that unburied logs entering decay class 5 (typically partly buried) become buried during this final decay class.

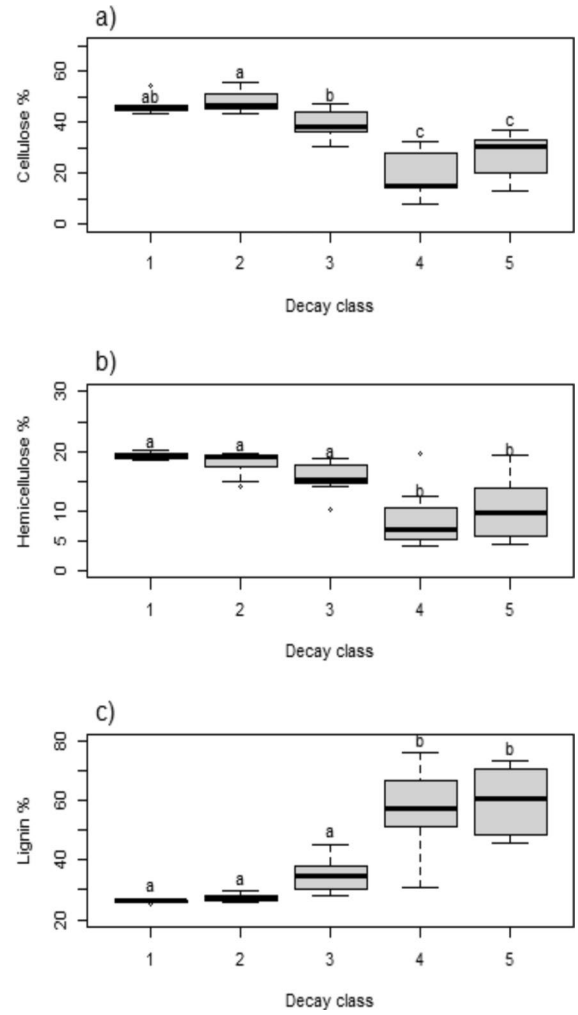

Fig. 2 The relative proportions of main wood polymers sampled in the field samples across five decay classes for **a** cellulose, **b** hemicellulose and **c** lignin. Different letters above boxplots represent statistical different group means. Note differences in scale

Statistical analysis

We used ANOVA and Tukey's HSD test for multiple comparisons to evaluate statistical significance

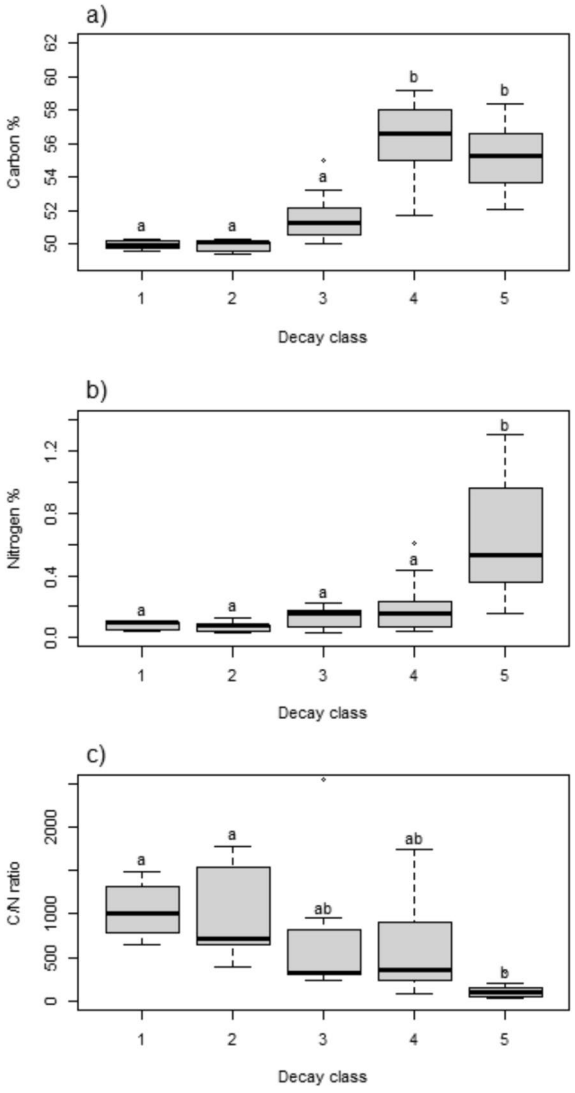

Fig. 3 The proportions of C, N and C/N in wood across five decay classes sampled in the field for **a** carbon content, **b** nitrogen content and **c** C/N ratio. Different letters above boxplots represent statistical different group means

of different wood properties across the decay classes. We used a probability of 0.05 as a statistical type-I error level. Further, regression was used to assess linear fit between mass loss vs. carbon or nitrogen content.

All data analysis were performed in R version 4.2.3 (R Core team 2023).

Results

Density loss across decay classes

The wood density of logs sampled in the field decreased with increasing decay class. Specifically, the basic density dropped from 0.43 to 0.29 g/cm^3 between decay class 0 and decay class 3 (Fig. 1). Two logs in decay class 3 were in transition to decay class 4 and had a median basic density of 0.23 g/cm^3 (53% of initial basic density).

Wood components across decay classes

The relative amount of hemicellulose and cellulose decreased with increasing decay class while the relative amount of lignin increased with increasing decay class (Fig. 2a–c). Variation increased with increasing decay class, but chemical characterisation could distinguish between decay class 1–3 and 4–5, i.e., hemicellulose and cellulose content was significantly lower in decay class 4 and 5 than in decay class 1–3, while the lignin content was significantly higher in decay class 4 and 5 than in decay class 1–3.

Carbon and nitrogen content across decay classes

The carbon content was 50.0 ± 0.3% in intact wood (decay class 0 + reference tree), and decay class 1–3 showed low variation and no significant difference (decay class 1 49.8 ± 0.03, decay class 2 49.9 ± 0.3 and decay class 3 51.6 ± 1.4). In decay class 4 and 5 the carbon content was significantly higher than in decay class 1–3 (Fig. 3a), i.e. decay class 4 56.3 ± 2.4 and decay class 5 55.2 ± 2.1. Further, no significant increase in nitrogen content was found until decay class 5 (average 0.5%) (Fig. 3b). The C/N ratio tended to decrease with increasing decay classes (Fig. 3c), but the variation was high for most decay classes. The only significant difference was found between decay class 1 and 2 and decay class 5.

Mass loss vs. carbon content experiment on basidiomycete monocultures

The laboratory tests showed that the three brown rot fungi caused a nearly linear mass loss of the wood blocks that levelled out after 10–16 weeks of incubation (Fig. 4a–c). Although the mass loss over

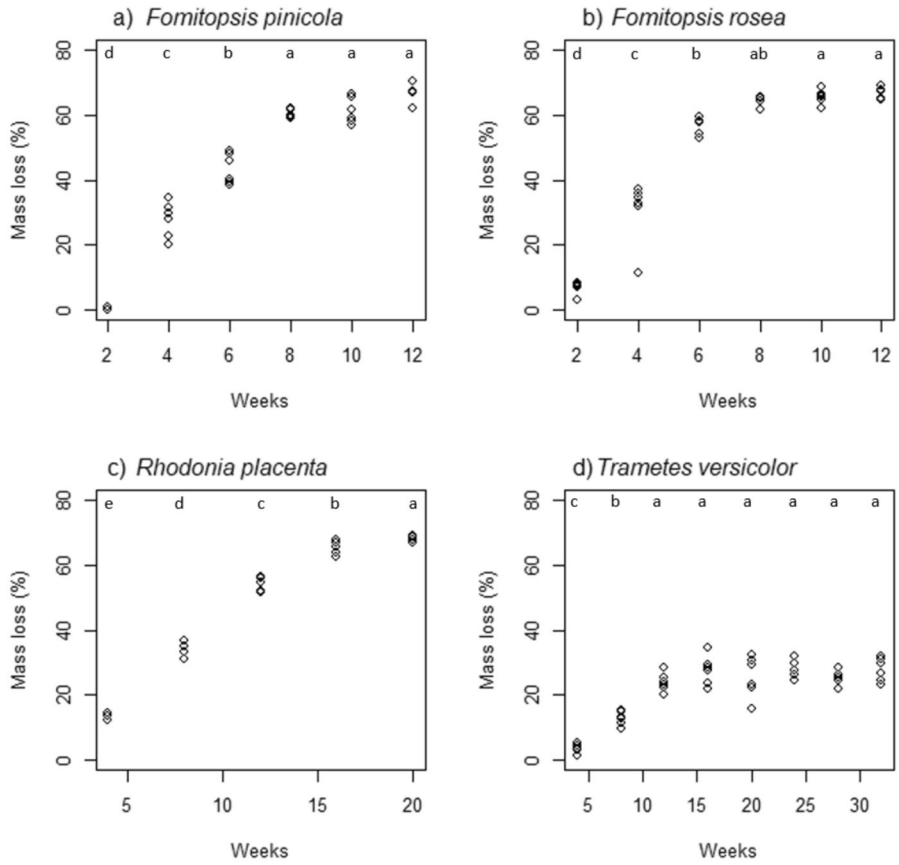

Fig. 4 Mass loss vs. weeks of incubation of Norway spruce wood blocks depolymerised by different monocultures of wood-decaying fungi in the laboratory experiments. Different letters above plots represent statistical different group means

time differed somewhat, the mass loss levelled out close to 70% of the initial mass for all three brown rot species (Fig. 4a–c). The white rot species also caused an initial linear mass loss that levelled out after 16 weeks of incubation, but for this species the mass loss levelled out at 30% of the initial mass (Fig. 4d). For all four species the mass loss from 0 to 40% (30% in the white rot species) caused a linear drop in wood density from 0.4 to 0.3 g/cm^3 (not illustrated).

The three brown rot fungi on one hand and the white rot fungus on the other had quite different effects on the chemical composition of the wood with advancing mass loss (advancing decay). The relative carbon content increased from 47 to 55% for all brown rot fungi during mass loss (Fig. 5a–c). The white rot species, a simultaneous white rot, had no effect on the relative carbon content that remained constant at 47% during the incubation period (Fig. 5d).

Carbon flux to the soil

The wood density dropped with increasing decay class from 0.38 g/cm^3 in decay class 1 to 0.11 g/cm^3 in decay class 5 (Fig. 6a, Table S1). The corresponding remaining carbon percentage dropped monotonically from 93% in decay class 1 to 30% in decay class 5 (Fig. 6b, Table S2). Expanding on this using Eq. 4 we calculated the carbon flux from the deadwood pool to the soil carbon pool. Here we adopted a conservative approach for burial rate, resulting in a carbon flux from deadwood to the soil carbon pool of 39% on mineral soils and 47% on organic soils (Table S3).

Discussion

This study documents the carbon dynamics of decaying coniferous wood in boreal forests. Our study

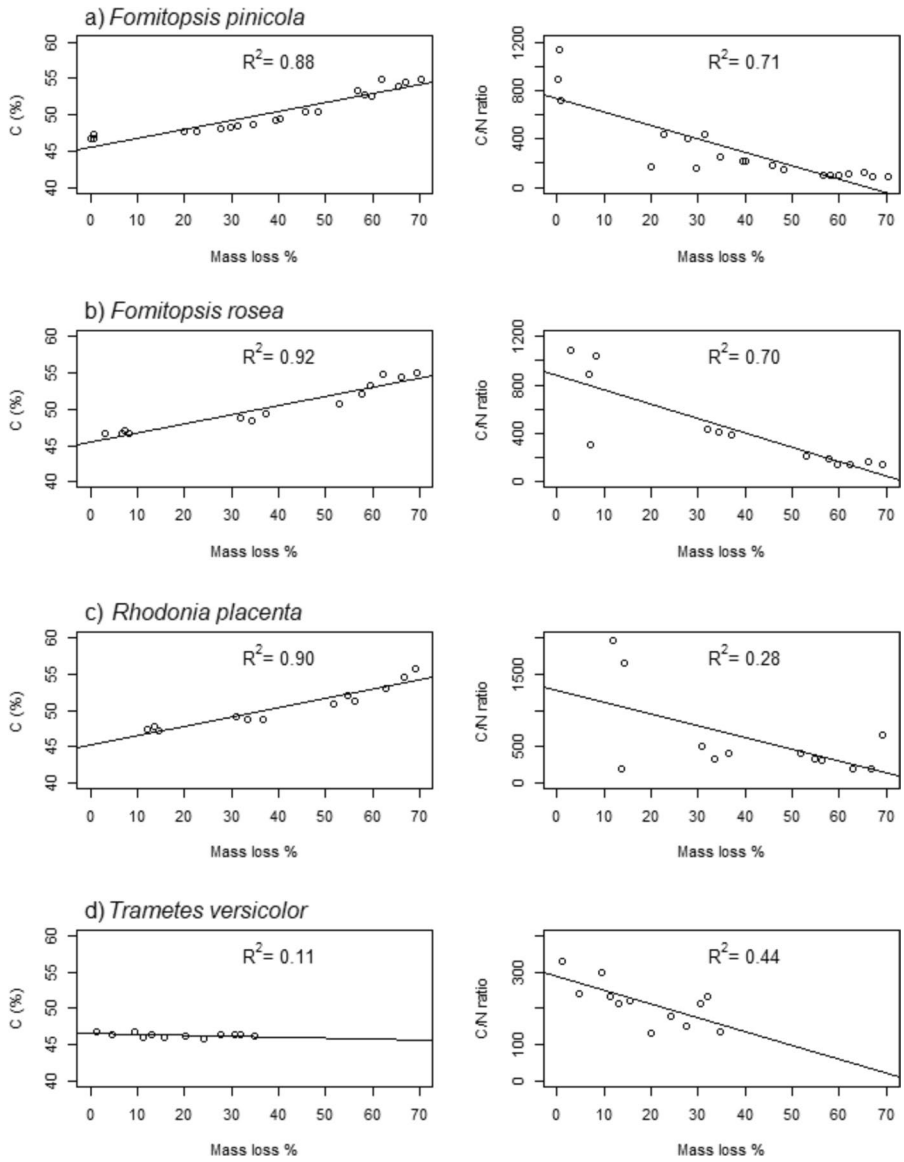

Fig. 5 Carbon content (left panels) and C/N ratio (right panels) relative to mass loss of Norway spruce wood blocks decomposed by different monocultures of wood-decaying fungi in the laboratory experiments. Lines represent the linear regression model of the responses relative to mass loss %

quantifies the carbon content and chemical composition of such deadwood in transition to the soil carbon pool.

Carbon content across decay classes

We found that the wood density decreased monotonically from 0.42 g/cm^3 in decay class 0 (recent windfall, still green needles) through decay class 1 to 3. The mean wood density at the transition from stage 3 to 4 was 0.23 g/cm^3 or 55% of the initial wood density. This finding corresponds well with other studies of wood density reduction across decay classes of Norway spruce. Six European studies revealed an initial average Norway spruce wood density of 0.38 g/cm^3 in decay class 1, and subsequent reductions to 0.27 g/cm^3 in decay class 3 and 0.11 g/cm^3 in decay class 5 (Table S1). Wood decomposition in boreal forests is primarily, driven by brown rot fungi (Renvall 1995) that enrich the content of modified lignin in the decaying wood (Yelle et al. 2011; Arantes and Goodell 2014). This decomposition process creates a potentially significant carbon flux from deadwood to the forest soil due to burial of downed wood by

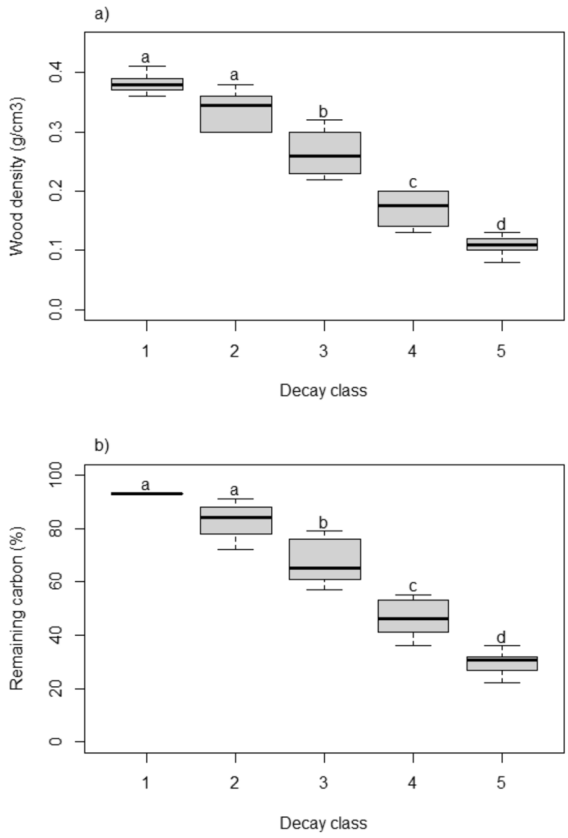

Fig. 6 Wood density across decay stages for Norway spruce wood (derived from the literature, Table S1) and remaining carbon as percentage of the carbon in non-decayed wood (derived from Table S2). Different letters above boxplots represent statistical different group means

the ground vegetation (Moroni et al. 2015; Stokland et al. 2016). Several studies have quantified carbon content across decay classes to summarize deadwood carbon stocks in greenhouse gas accounting systems (Sandström et al. 2007; Weggler et al. 2012; Seedre et al. 2013; Di Cosmo et al. 2013; Harmon et al. 2013; Köster et al. 2015; Stakėnas et al. 2020; Martin et al. 2021). Such studies typically produce conversion factors to translate deadwood volumes to carbon quantities and facilitate calculations of carbon stock changes from repeated deadwood inventories. Alternatively, one can interpret the decay classes as documenting the progression of decomposition in deadwood, which is the purpose of our study.

Our study showed a statistically significant increase in carbon concentration from 50% of the biomass in decay class 1 to 56% of the biomass in decay class 4 and 5. This increase corresponds with other studies showing invariably increasing carbon concentration in decaying Norway spruce wood, although with slightly lower values, from around 48% in decay class 1 to 51% in decay class 5 (Sandström et al. 2007; Weggler et al. 2012; Köster et al. 2015; Stakėnas et al. 2020). This concentration increase seems to be a common pattern in decaying conifer wood (typically decayed by brown rot fungi), contrasting with broadleaved wood that show stable carbon concentration during the decomposition process (Harmon et al. 2013). The underlying mechanism is the enrichment of lignin by brown rot fungi, and that lignin has a higher carbon concentration (60–70%) compared with that of cellulose (40–44%) (Pettersen 1984; Ma et al. 2018). A combination of relative density reduction and the increased carbon concentration suggest that 46% and 30% of the initial carbon is still present in decay class 4 and 5, respectively (Table S2).

The elevated concentration of carbon in late stages after brown rot decomposition has implications for the carbon flux from deadwood to the soil carbon pool. A comprehensive national forest inventory study from boreal forests shows that nearly every second log in decay class 4 is covered by ground vegetation or litter on mineral soils, and thus in transit to the soil carbon pool (Stokland et al. 2016). This transition rate was even higher in swamp forest on organic soils (Stokland et al. 2016). Using the above-ground-to-soil transition rates from Stokland et al. (2016) we conservatively estimated that 39% of the initial carbon amount in coniferous deadwood is transferred to the soil carbon pool on mineral soils and 47% on organic soils (Table S3). Hence, we reject the null hypothesis of our study.

The observed difference in carbon flux rate between forests on mineral soils and organic soils highlights that wood burial is an ecosystem feature rather than an aspect of wood decay as such. The phenomenon is common in boreal forests with high abundance of feathermosses (e.g. *Hylocomium* sp., *Ptilium* sp., *Pleurozium* sp.) and increases further in swamp forests with *Spahgnum* moss growth (Moroni et al. 2015) while studies from temperate forests typically observe far less wood burial (Spears et al. 2003; Moroni et al. 2015). Thus, we call for more studies quantifying the carbon flux rates from wood to the soil C pool in different forest types.

Carbon profile across decay classes

The composition of the main wood components changed profoundly across the decomposition stages of the field samples. The average initial fractions (decay 1) of the mass were 46% cellulose, 19% hemicellulose, and 27% lignin. In the final stage (decay 5), the cellulose and hemicellulose fractions of the current/remaining mass had declined substantially (to 30% and 10%, respectively), while the lignin fraction more than doubled to 60% of the remaining mass. These findings correspond with the well-established knowledge of lignin enrichment in brown-rotted wood from laboratory studies. Yet surprisingly few studies have documented this change across decay classes under field condition in coniferous forests. Our findings correspond to those of Romashkin et al. (2021) from Karelia in Russia. They found that the fraction of cellulose in spruce wood decreased from 52 to 5% of the remaining mass from decay class 1 to 5, while the fraction of lignin increased from 26 to 72% of the remaining mass. Also, Petrillo et al. (2016) and Herrmann and Bauhus (2018) found similar trends for decaying spruce wood in Italian alps and southern Germany, but they used decomposition time rather than decay class for data classification. It is, however, evident from these studies that a) that the lignin dominates (60–70% of the remaining mass) strongly decayed Norway spruce wood in decay class 5, and b) at least some hemicellulose and cellulose residuals remain in such strongly decayed wood.

Our laboratory decomposition experiment, using Norway spruce as a model for conifer wood with low fungal decay resistance, i.e. durability class 4–5, slightly durable—not durable according to EN 350 (2016), revealed a consistent pattern across three brown rot fungus species that caused the dry density reduction to level out close to 70% mass loss after 12–20 weeks (*F. pinicola* 67% 12 weeks, *F. rosea* 67% 12 weeks, *R. placenta* 68% 20 weeks). This result is almost identical with the laboratory study by Filley et al. (2002) who tested Red spruce (*Picea rubens*) decomposition by *Postia placenta* (current valid name *Rhodonia placenta*) and another brown rot fungus (*Gloeophyllum trabeum*). They observed a dry density reduction that levelled out at 70% mass loss after 16–32 weeks. Furthermore, they demonstrated that this mass loss corresponded to a complete consumption of all polysaccharides (cellulose and hemicellulose) while the lignin was demethylated and mildly oxidized.

Evidently, brown rot fungi can decompose all the wood polysaccharides under favourable physical (temperature, moisture, oxygen availability) and competition-free conditions in laboratory tests. Such conditions are never present in large trunks decomposing under natural forest conditions, decomposer community and decomposition pathways might differ substantially between logs. We found large variation across field sampled logs in decay class 5, as cellulose varied in the range 13–37%, hemicellulose in the range 4–20%, and lignin in the range 46–75%. A large variation in remaining cellulose (0–32%) and lignin (28–69%) was also observed in field-derived samples of Norway spruce wood in decay class 4 and 5 by Petrillo et al. (2016).

It was evident from the field samples that the changes in cellulose, hemicellulose and lignin fractions mainly took place from decay class 2 to decay class 4 (Fig. 2). The cellulose fraction seemed to start declining somewhat before hemicellulose (from stage 2 to stage 3) whereas both polysaccharide fractions declined substantially until decay class 4. In parallel the lignin fraction increased slightly from decay class 2 to 3, and substantially until decay class 4. All three wood components showed minimal further changes in average values from decay class 4 to 5 (Fig. 2). These findings correspond closely to those of Romashkin et al. (2021) with one exception. Romashkin et al. observed a further increase in the lignin fraction and decline in the cellulose fraction from decay class 4 to 5. This difference might be a result of sooner wood burial in our study area where some decay 4 wood and all decay 5 wood were completely overgrown by vascular plants, whereas vascular plant appeared to start establishment and spread on decay 5 wood in the Romashkin study. The burial due to vascular plants (mainly *Vaccinium myrtillus*) and mosses can possibly reduce oxygen availability and slow down wood decomposition by brown rot fungi (Moroni et al. 2010), thus preventing further loss of polysaccharides in our study.

Wood decomposition of coniferous and broadleaved trees

Our study primarily deals with brown rot of Norway spruce wood as a model system for conifer

wood decomposition. In the lab experiment we also tested one white rot fungus (*Trametes versicolor*) under the same conditions as the three brown rot fungi. This species only degraded 30% of the Norway spruce biomass after 32 weeks. Thus, it was far less effective in conifer wood degradation compared to the brown rot fungi. This might seem surprising, given that the species is a simultaneous white rot fungus and in theory is capable of degrading both polysaccharides and lignin. On the other hand, *T. versicolor,* like most white rot fungi, has a strong selective preference for decaying broadleaved trees (Ryvarden and Gilbertson 1993; Niemelä 2005). Likewise, most brown rot fungi have a strong selective preference for coniferous trees (Ryvarden and Gilbertson 1993; Niemelä 2005).

The general pattern that conifer trees are predominantly decomposed by brown rot fungi and broadleaved trees by white rot fungi is most likely an effect of lignin differences and the evolutionary history of these tree clades. Gymnosperm trees that include the conifers are minimum 310 million years old (Stokland 2012a) and conifer wood has rather high lignin content (25–33%) primarily built up of coniferyl subunits (Sjöström and Westermark 1999; Stokland 2012b). Broadleaved trees are evolutionary much younger (130 million years or less), and they have significantly lower lignin content (18–25%) composed of other subunits than the conifers (Sjöström and Westermark 1999; Stokland 2012b). It appears advantageous to have developed a brown rot mode among conifer wood decay fungi, and evolutionary origins of the brown rot fungi are repeatedly coupled with conifer exclusivity (Hibbett and Donoghue 2001). The advantage of brown rot mode over white rot mode in conifer wood decomposition is clearly demonstrated in our laboratory test.

Although some white rot fungi may occur in conifer wood (e.g. some *Trichaptum* and *Phellinus* species), field studies show that conifer wood typically is decomposed by a brown rot mechanism resulting in increasing lignin fraction and carbon concentration during the decomposition (Petrillo et al. 2016; Herrmann and Bauhus 2018; Romashkin et al. 2021, this study). Broadleaved wood, on the other hand, is characterized by a somewhat lower and stable lignin fraction as well as a stable carbon concentration during the decomposition process (Harmon et al. 2013). This is both an effect of lower initial lignin concentration (see above) and the dominance of white rot fungi that degrade both cellulose, hemicellulose and lignin.

The connection between wood type (conifers vs. broadleaved trees) and decay mechanisms (brown rot vs. white rot) translates to a similar connection between forest types across bioclimatic regions and functional decomposition of deadwood. In boreal forests wood decomposition is primarily driven by brown rot fungi in contrast to temperate and tropical forests where white rot fungi dominate (Zhou et al. 2011; Wu et al. 2021). This has fundamental implications for the carbon flux from deadwood to the soil carbon pool in these forest ecosystems.

Wood residuals transferred to soil

The contrasting fungal decay mechanisms of coniferous and broadleaved wood create different types of residual carbon being transferred to forest soils during decomposition. Already in the early phase of decomposition microbially modified carbon leaches from the wood as dissolved organic carbon, both from broadleaved and coniferous wood (Bantle et al. 2014). This flux increases substantially (up to more than tenfold) towards the final decomposition stage for broadleaved wood (Hafner et al. 2005; Kuehne et al. 2008; Błońska et al. 2019a). Also, from conifer wood the carbon leakage increases towards the final decomposition stage but to a lesser degree (about twofold, Błońska et al. 2019a).

Not surprisingly, several studies have documented increased levels of soil organic carbon below decaying broadleaved wood as compared with adjacent control points without deadwood (Wambsganss et al. 2017; Stutz et al. 2017, 2019; Błońska et al. 2019b; Piaszczyk et al. 2019; but see Kahl et al. 2012). Similar increased levels of soil organic carbon have been observed below coniferous wood (Bai et al. 2017; Błońska et al. 2017; 2019b; Stutz et al. 2017; Piaszczyk et al. 2019). Detailed chemical analyses demonstrate, however, that soil carbon originating from white rot decayed broadleaved wood is dominated by oxidized, water-extractable lignin-derived phenolic matter, while soil below brown-rotted coniferous wood is primarily enriched by particulate (not dissolved) lignin-derived carbon (Stutz et al. 2017, see also Bantle et al. 2014 showing distinctly different leached metabolites from conifer and broadleaved wood in early decay phase). Thus, both wood

classes enrich the soil carbon stock but the residuals from conifer and broadleaved wood are quite different with implications for soil carbon stability and long-term soil carbon accumulation. When tree species is controlled for, the respective dominating decay mechanism still produce different effects on forest soils. Brown rot produces less dissolved organic matter with lower aromaticity than white rot of *Populus tremuloides* (Mosier et al. 2017), while brown rot resulted in higher total soil carbon than white rot of *Abies nephrolepsis* (Bai et al. 2017).

These leaching studies and the soil carbon imprint studies clearly indicate that broadleaved wood (typically decomposed by white rot fungi) is decomposed more completely above-ground and hence might indicate that carbon is respired to the atmosphere to a larger extent than from conifer wood. Furthermore, the residual carbon that enters the soil from brown-rotted conifer wood (in contrast to white-rotted broadleaved wood) is mainly composed of particulate, weakly modified lignin with prolonged residence time in forest soils (Filley et al. 2002; Stutz et al. 2017). These findings have clear implications for modelling and forecasting carbon fluxes from decaying wood as well as for soil carbon stability and long-term soil carbon accumulation.

Ecosystem implications

Very few studies have tried to separate and quantify the total carbon fluxes from decaying wood through respiration (to the atmosphere), leaching (to the soil) and fragmentation (to the soil). We calculated that 39% of the carbon from boreal coniferous deadwood is transferred to the mineral soil carbon pool as strongly decayed wood mainly composed of lignin residuals. We did not quantify carbon transfer through leaching but assume that some leaching occurs as well, albeit in small quantities. This suggests that minimum 40% of the carbon from coniferous deadwood is transferred to the soil while up to 60% is respired to the atmosphere. Bond-Lamberty and Gower (2008) found similar values in Canadian boreal forests where they calculated that respiration accounted for roughly 60% mass loss from decaying wood and fragmentation for 40% (two-thirds that from respiration, they assumed leaching = 0).

Studies from temperate broadleaved forests suggest that less carbon is transferred from deadwood to the soil. Fragmentation accounted for 10% of deadwood mass loss in a North American *Acer* spp. forest (Chueng and Brown 1995) and leaching plus fragmentation accounted for about 33% of total mass loss in a North American mixed hardwood (i.e. broadleaved) forest (Mattson et al. 1987). Chambers et al. (2001) predicted that 76% of the carbon loss from deadwood is emitted as CO_2 in an Amazonian Forest.

The differences in carbon fluxes from decaying wood across forest biomes agree very well with the detailed leaching and soil carbon imprint studies documenting conifer and broadleaved wood decomposition. This knowledge strongly indicates that decaying wood generate an important carbon flux to forest soils and that this flux is larger in boreal forest than in temperate and tropical forests.

Methodological considerations

Our method and estimates of carbon flux from deadwood to the soil carbon pool has some uncertainties.

First, some of the decaying wood can be lost via fragmentation before the decomposing log eventually becomes incorporated in the soil. One type of fragmentation is direct consumption by insects tunnelling the wood. This is quantified by Seibold et al. (2021) who found the effect to be significant (40% of the density loss) in the tropics but virtually zero in boreal forests. There are boreal wood tunnelling insects but they create minimal density loss compared to the termites (non-existing in boreal forests) causing major wood degradation in the tropics. Volume losses caused by insects mainly occur early in the decomposition process. Another type is physical fragmentation (pieces falling off or being removed by woodpeckers/mammals searching for insects) that occurs frequently in boreal forests. Such fragments fall to the ground, however, and rapidly become covered by mosses and litterfall. This kind of fragmentation rather increases the carbon transfer to the soil prior to the final integration of the log residuals in the humus layer. We cannot say that such physical fragmentation completely offset carbon loss through insect wood consumption, but we consider the combined effect to be minimal.

A second uncertainty is the phenomenon that some mass/volume can disappear completely as decomposition progresses. This occurs when the sapwood decomposes faster than the remaining heartwood

(especially in pines) or when heartwood rot creates hollow trees (common in large temperate broadleaved trees, uncommon in boreal broadleaved trees). Such differential volume loss partly results in wood fragments beneath the trunk or inside the trunk cavity, and partly in a volume loss due to complete wood decomposition. The latter volume loss would indicate the presence of white-rot fungi capable of complete wood decomposition. We found a non-significant variation in carbon and lignin concentrations in more advanced decay classes of our spruce logs, which could indicate a presence of white-rot fungi. We encourage studies to quantify the frequency of partial volume loss from dead trees across tree species and tree sizes and ideally sort this loss into a fragment portion and a volume loss portion. We further encourage molecular studies to elucidate rot type crating such partial volume loss.

A third uncertainty in our methodology is the proportion of the wood that is buried in each decay class. We used a large dataset from Sweden to quantify this (Stokland et al. 2016). That dataset defined logs as buried when more than half of the log was covered by ground vegetation (i.e. not completely buried), but we compensated for this by disregarding that some logs actually became predominantly buried in decay classes 1 and 2, and by reducing the burial proportions by ca. 10 percentage points in decay classes 3 and 4 (see Material and methods). We consider that these adjustments translate the Swedish data to conservative burial rates.

Still another methodological consideration is the validity of our study. We consider our carbon flux rates to be generally valid for brown-rotted coniferous wood in boreal forests. Logs from broad-leaved and coniferous trees have similar burial rates across decay classes in boreal forests (Stokland et al. 2016), but unlike brown-rotted wood the white rot mode does not increase the carbon concentration in the remaining wood. Hence, the carbon flux rates from white-rotted wood to the soil is probably 2–4 percentage points lower than from brown-rotted wood, due to lacking carbon concentration increase.

Conclusions

This study quantifies the density (biomass) loss and biochemical transformation of Norway spruce wood throughout the whole decomposition process until the wood falls apart and disintegrates. Based on a novel approach we demonstrate that nearly 40% of the carbon from the above-ground wood is transferred to the boreal soil carbon pool on mineral soils and nearly 50% on organic soils. This transferred carbon is mainly composed of slightly modified lignin residuals with a higher carbon concentration than intact wood, features being typical of fungal brown rot decay.

The carbon flux from deadwood to the soil carbon pool appears to be higher in boreal forests than in temperate and tropical forests, an ecosystem difference that we ascribe to predominantly different decay mechanisms (brown rot versus white rot) in the respective forest ecosystems.

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Data availability Enquiries about access to data should be directed to the authors.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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