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ORIGINAL PAPER

The decomposition rate of non-stem components of coarse woody debris (CWD) in European boreal forests mainly depends on site moisture and tree species

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Abstract The decomposition rate of CWD is a key missing link for a quantitative understanding of forest ecosystem functioning. We examined factors influencing decomposition rates of bark, roots and branches from aspen (*Populus tremula*), birch (*Betula pendula*, *B. pubescens*), fir (*Abies sibirica*), spruce (*Picea abies*, *P. obovata*), Scots pine (*Pinus sylvestris*) and Siberian pine (*Pinus sibirica*) CWD in three primeval European boreal forests. The chronosequence approach with estimates of single exponential decomposition rate (k) based on calculation of mass loss was used. The k of non-stem parts increased in the order: branches ($0.006\ \text{year}^{-1}$ for *P. sibirica* and $0.020\ \text{year}^{-1}$ for other species), roots in poorly drained sites ($0.025\ \text{year}^{-1}$), roots in well-drained sites ($0.034\ \text{year}^{-1}$) and bark (0.110 and $0.138\ \text{year}^{-1}$ and 0.147 and $0.255\ \text{year}^{-1}$ under poorly and well-drained conditions and from 1 to 3 m and >3 m above the root collar, respectively). Our results predict that the rate of decomposition of whole CWD pieces in European boreal forests is a function of vegetation zone, site conditions, tree species and size.

Keywords Decay · Roots · Branches · Bark · Dead wood · Fragmentation · Biodiversity · Carbon

Introduction

Coarse woody debris (CWD) represented by standing dead trees, downed woody debris and stumps (Harmon et al. 1986) has been acknowledged as an important component of forest biodiversity, carbon and nutrient cycling (Laiho and Prescott 2004; Palviainen et al. 2011; Stokland et al. 2012; Dittrich et al. 2014). It has also been used as an indicator of forest ecosystem services (Helfenstein and Kienast 2014). The aboveground volume of CWD stem parts in European boreal forests can reach over one thousand $\text{m}^3\ \text{ha}^{-1}$ (Shorohova and Kapitsa 2015) with the residence time varying from tens to more than 500 years (Shorohova and Kapitsa 2014b). Non-stem components can double the aboveground CWD pools of organic matter and nutrients. For example, the volume of bark, branches and roots can vary from 8 to 17 %, from 4 to 10 % and from 18 to 30 %, respectively, of the stem volume of the dominant boreal tree species (Tetioukhin et al. 2004).

Decomposition of woody debris is the result of microbial decay, physical degradation (i.e., fragmentation and weathering), leaching and biological transformation. Of these, microbial decay is considered the main process (Chambers et al. 2001; Bond-Lamberty and Gower 2008). There have been many studies in European boreal forests that estimate regional decomposition rates of stem wood (Krankina and Harmon 1995; Harmon et al. 2000; Yatskov et al. 2003; Mäkinen et al. 2006), whereas less is known about decomposition rates of non-stem components (Yin 1999; Palviainen and Finér 2015).

The estimates of microbial respiration and fragmentation rates of aboveground stem parts are used for calculating carbon budgets on the country level (Mackensen and Bauhus 1999; Kudeyarov et al. 2007; Zamolodchicov et al. 2011) and in vegetation and climate models (Cramer et al.

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2001). Less frequently, belowground roots and branches on the forest floor are included in the models (Beets et al. 2011; Garrett et al. 2012). The lack of information on coarse root decomposition rates and C pool changes has been identified as one of the biggest source of errors in forest C-stock reporting (Tobin et al. 2007). Considering all CWD components separately, taking into account ecosystem attributes, would improve those models significantly. In general, uncertainties in predicting the rate of CWD decomposition can lead to uncertainties in our understanding of forests and their role in the sequestration and emission of CO_2. Those uncertainties, in turn, result in an inability to develop appropriate strategies for achieving deadwood-related objectives, including climate change mitigation, biodiversity protection and procurement of forest bioenergy feedstocks (Russell et al. 2015).

In boreal zones, over a narrow range of conditions, the climatic effects on the decomposition rate of stem wood have been shown to be less important or nonsignificant compared to site and substrate characteristics (Yatskov et al. 2003; Mäkinen et al. 2006; Shorohova and Kapitsa 2014a, b). On an ecosystem scale, higher decomposition rates were observed for stem wood on sites with moderate moisture compared to those on dry and moist sites (Shorohova and Kapitsa 2014a, b) and can be hypothesized for non-stem CWD components as well.

Data on the decomposition rate of belowground coarse roots are scarce and show the same, faster and slower root decomposition rates compared to aboveground material (Fahey et al. 1988; Janisch et al. 2005; Olajuyigbe et al. 2011; Shorohova et al. 2012; Palviainen and Finér 2015). These contradictions can be explained by the interplay between differences in moisture content and oxygen concentration below and above ground. The influence of soil drainage may be a significant driver of decomposition rates, particularly for roots, where decomposition can be retarded under the saturated conditions of very poorly drained soils or facilitated under well-drained conditions, where the availability of moisture and nutrients for decomposing fungi can be improved (Erickson et al. 1985). The decomposition of roots above ground, as part of uprooted trees, has not been studied yet. The decomposition rates of roots below ground and above ground for different tree species, different regions and different tree mortality modes (i.e., snags and snapped trees as well as of other aboveground CWD parts) need to be compared under well and poorly drained site conditions in different parts of boreal zone.

The decomposition of branches and the fungal communities associated with them have been studied mainly when they were attached to standing trees under a forest canopy (Boddy and Rayner 1983; Boddy et al. 1987) or on the forest floor (Miller 1983; Erickson et al. 1985; Mukhin 1993; Hyvönen et al. 2000; Garrett et al. 2012). When branches start to decompose when a tree is alive, complete decay of sapwood can occur in the canopy if it is supported by heartwood, but if not, branches and twigs will fall to the floor, where decay continues (Boddy and Heilmann-Clausen 2008). Knowledge of the decomposition of the side branches, or branches attached to logs, is very limited (Ganjegunte et al. 2004).

Decomposition rates of bark have been shown to differ from those of wood. However, the character of this difference depends on tree species and environmental conditions influencing microbial respiration (mineralization) rates as well as on fragmentation induced by biotic agents (Rypaček 1957; Parameswaran et al. 1976; Ganjegunte et al. 2004; Shorohova and Kapitsa 2012, 2014b) and requires further research.

In this study, we aimed at estimating the decomposition dynamics of non-stem CWD components and whole CWD pieces in primeval European boreal forests using a chronosequence approach. Our specific objectives were to: (1) estimate the initial conditions and mass loss of non-stem CWD components: roots, branches and bark; (2) calculate the decomposition rates of CWD components depending on vegetation zone, soil moisture, CWD tree species, tree mortality mode and log size; and (3) estimate the CWD piece scale decomposition rates of the dominant tree species in European boreal forests. We hypothesized that the substrate moisture during decomposition influenced by position of CWD component and soil conditions, together with initial density and mass, are the most important predictors of the decomposition rate. We hypothesized that the decomposition rate at the CWD piece scale would increase from north to south and would be higher under better than poor soil drainage. Comparing an assumed higher, equal and lower decomposition rate of bark, roots and branches, respectively, to stem wood and relative weight proportion of each component, we hypothesized that the decomposition rate of whole CWD pieces would be higher than that of stem wood alone.

Materials and methods

Study sites and sample plots

The studies were carried out from 1997 to 2009 in three primeval old-growth forests located in Russia (Fig. 1). Mean annual temperatures vary from −3.0 to +3.6 °C, and mean annual precipitation varies from 600 to 750 mm. The forested areas of Vepssky forest (VF1) and Central Biosphere Forest Reserve (CFR) landscapes are dominated by Norway spruce (*Picea abies* Karst., *P. fennica*) with an admixture of birch (*Betula pubescens* Ehrh. and *Betula*

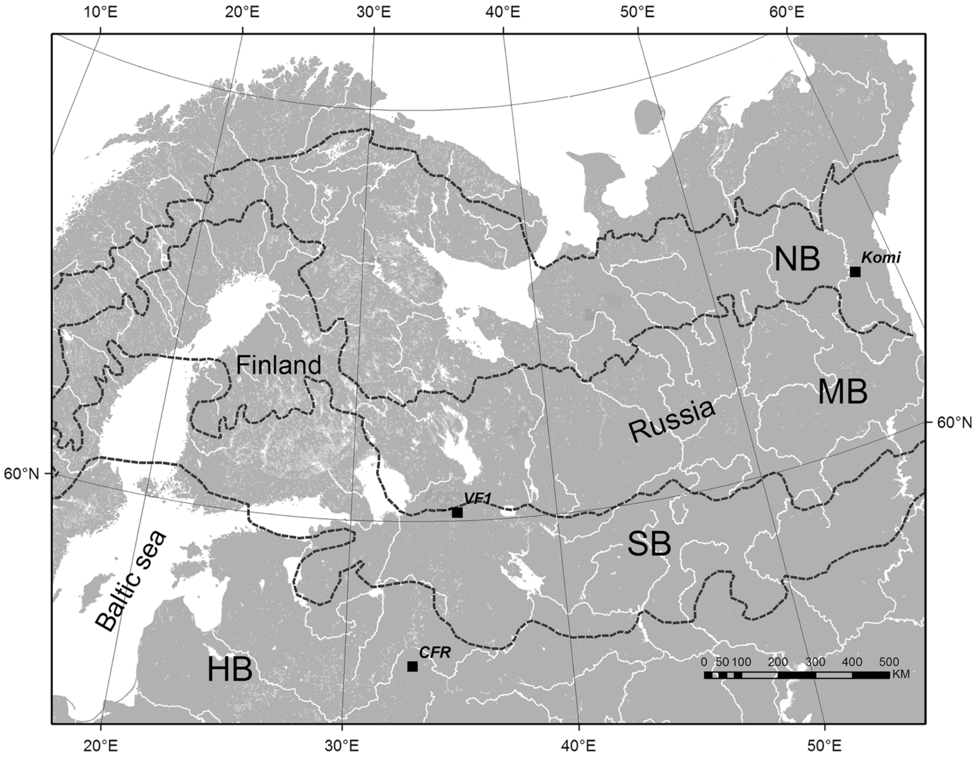


Fig. 1 Location of the study sites. Komi—Yugyd-va National Park, VF1—Vepssky forest, Saint-Petersburg region, CFR—Central Forest State Natural Biosphere Reserve, Tver region. NB, MB, SB and HB—northern, middle, southern boreal and hemi-boreal zones, respectively, according to the forest vegetation zoning mapped for the natural vegetation of Europe (Bonh et al. 2000, 2000/2003)

pendula Roth.), aspen (*Populus tremula* L.) and Scots pine (*Pinus sylvestris* L.). In the CFR, the broadleaved species Norway maple (*Acer platanoides* L.) and European white elm (*Ulmus laevis* Pall.) also occur. The forests of Yugyd-Va National Park sites (Komi) are mixed Siberian spruce (*Picea obovata* Ledeb.), Siberian fir (*Abies sibirica* Ledeb.), Siberian pine (*Pinus sibirica* Du Tour or (Loudon) Mayr) and birch. According to the information from the archives, the forests of all sampled sites have never been commercially harvested. Standing growing stock varied from 0 in the gap left by stand-replacing windthrow in CFR to 502 m^3 ha^{-1} in an over-mature mixed even-aged stand in VF1. All forest stands were uneven-aged with the tree age ranging from 1 to 460 years. The period of time since last disturbance (determined by dating fire scars or uprooted trees) varied from 1 to 380 years. The CWD stocks varied greatly among the plots, ranging from 46 to 1267 m^3 ha^{-1}, depending on the natural disturbance regime. Maximum CWD values were found after stand-replacing windthrows in highly productive forests in CFR.

The main forest types in the study sites were herb-rich, Oxalidosum, Equisetum, Hylocomioso-Myrtillosum, Myrtillosum, Ledosum, Polytrichoso-Myrtillosum and Sphagnoso-Myrtillosum according to the classification of forest ecosystems in the northwest of Russia (Fedorchuk et al. 2005). The forest types herb-rich, Oxalidosum and Myrtillosum are classified as well-drained; the forest types Equisetum, Ledosum and Sphagnoso-Myrtillosum are classified as poorly drained.

Sampling, calculations and data analysis

The non-stem components of logs larger than 8 cm in DBH of the following tree species were sampled: Norway spruce and Siberian spruce, hereinafter referred to as spruce; Scots pine, birch, aspen and Siberian fir, hereinafter referred to as fir; and Siberian pine. The CWD formed after the death of mature trees ranged from 60 to a few hundred years old. We used a chronosequence approach to estimate the dynamics of CWD decomposition. The dating of CWD pieces was determined from permanent plot records (VF1, 14–34 year period, CFR, 22–37 year period), year of windfall (CFR, 7–64 year period) and dendrochronological methods of cross-dating, growth release patterns and mechanical scars of neighboring trees (Komi, period covered up to 168 years). Undecayed wood of roots and branches and log bark were sampled from trees that died in the current year or 1 year before sampling to serve as controls. In total, 1768 samples were taken (Table 1). When the year of windthrow was known, the determination of time since death (i.e., time elapsed from the date of tree death to the date of sampling) was precise. Permanent plot inventories had been conducted every 3–5 years, so the accuracy of time since death estimates averaged 2 years.

Table 1 Number of samples by sites and CWD components

Site	Number of sampled CWD pieces		
	Bark	Branches	Roots
Control samples			
Komi	62	32	31
VF1	35	19	25
CF	104	42	31
Samples for decomposition rate			
Komi	303	151	161
VF1	191	83	128
CF	56	46	67

Three to five "representative" roots and branches with diameters ranging from 4 to 15 cm were selected by CWD piece. The roots were sampled aboveground from (1) trees after windthrow when a tree was uprooted (49 trees), (2) trees that died standing and then fell down so that the root system turned up totally or partly aboveground (15 trees) and (3) trees that were damaged by wind or snow so that part of their root system remained belowground and part of it emerged aboveground (67 trees). Belowground roots were not excavated; thus, only the decomposition of roots that decomposed totally or partly aboveground was studied. Side branches were sampled at a minimum distance of 20 cm from the place of attachment to a log. We did not study the branches that fell from live trees or any CWD that decomposed on the forest floor.

Cross sections from side branches and roots were extracted by a chain saw and axe or knife and debarked. The samples from branch and root wood were taken at ca. 0.5 m from the stem. At this distance, bulk density of branch and root wood reaches their mean values (Polubojarinov 1976). The proportional area in different degrees of decomposition was visually estimated on a scale of 1–4, from intact to completely decomposed wood, respectively, with white and brown rot considered separately. An adjustment for volume losses during decomposition was made; the initial shape of fragmented and highly decomposed fractions was reconstructed. Holes due to fragmentation or complete decomposition were counted as well. Small samples of regular shape up to 100 cm^3 in size were taken from each cross section according to degree and type of rot. Their length, width and thickness of the samples were measured. The area percentage was assumed to correspond to the proportional volume for each sample. Samples were oven-dried at 103 °C for 48 h and weighed. Bulk density (ρ, g m^{-3}) was calculated by dividing the dry mass by the fresh volume of the sample. A weighted average for bulk density (as weighted by the proportion of different degrees of decomposition represented in the sampled cross sections) was calculated for each root or branch piece.

We studied only the decomposition of bark attached to logs. Bark on the ground or in litter was not considered. The decomposition of bark was analyzed based on mass loss per surface area. The length of all logs (L, m) was measured, and diameters were recorded at the stem base, at 1.3 m and the top of all logs. The lateral surface area of logs (S, m^2) was calculated by the formula:

$$S = \pi L(R + r) \tag{1}$$

where R and r are, respectively, the maximum and minimum radii at opposite ends of a broken log segment in m, and L is a slant height of a log in m.

To account for the loss of bark fragments by mechanical damage or insects, the percent cover of bark remaining on a log (f) was visually estimated. Two to three regularly shaped bark samples of a few cm^2 were taken from the stem base and the middle of each log and measured in two dimensions. Then, the area-specific mass of bark (mass unit per surface area) was calculated as:

$$M_b = m/s \tag{2}$$

where M_b is the area-specific mass of bark (g m^{-2}), m is the dry mass of a bark sample (Mg), and s is the area of sample (m^2).

In order to determine the total area of remaining bark (S_f), the lateral surface area of log (S) was multiplied by the percent of remaining bark (f):

$$S_f = Sf \tag{3}$$

The total mass of log bark (M_{sb}) was calculated as:

$$M_{sb} = S_f M \tag{4}$$

In order to separate the factors controlling the rate of decomposition from the factors controlling initial bulk density and mass (as measured in the control samples), we first analyzed the bulk density of roots and braches as well as the initial mass per surface area and total mass from the bark of trees that died in the year of observation or the year before. An analysis of variance (ANOVA) type III sum of square for unbalanced design, when the numbers of observations for different groups were unequal (Shaw and Mitchell-Olds 1993), and Duncan post hoc multiple comparison tests (Statistica 6.0) were implemented to estimate the effect of: (a) vegetation zone (northern boreal, southern/middle boreal, hemi-boreal); (b) soil moisture (well-drained vs. poorly drained); (c) tree species; (d) component (root vs. branch); (e) log part (0–3 m above root collar vs. >3 m above root collar for bark); (f) log at breast height, or 1.3 m (DBH) (expressed as three categories: 0–20, 21–40 and >41 cm); and (g) the interrelationship of some of the above factors on the initial bulk density and mass variation.

We calculated the percent dry mass remaining (M, %) based on the loss of the bulk density (ρ, g m^{-3}), area-specific (M_b) and total (M_{sb}) mass of bark related to the initial density (ρ_0), and specific (M_{b0}) and total (M_{sb0}) mass, respectively. The initial parameters were calculated based on the results of ANOVA, i.e., the values were grouped when the differences were not statistically significant. The remaining mass was adjusted to 100 % when ρ exceeded ρ_0, M_b exceeded M_{b0}, and M_{sb} exceeded M_{sb0}. The annual decomposition rates (k, year^{-1}) were calculated based on a single exponential model (Olson 1963).

Factorial ANOVA (type III sum of square test for unbalanced design) and Duncan tests were implemented to estimate the effects of vegetation zone (northern boreal, southern/middle boreal, hemi-boreal), soil moisture (well-drained vs. poorly drained), tree species, tree mortality mode (uprooted, died standing, broken), component (roots, branches, bark), log part (0–3 m above root collar vs. >3 m above root collar), log DBH (expressed as three categories: 0–20, 21–40 and >41 cm) and the interrelation of some of the above factors on the variation in k. The effect of log DBH on k variation was also analyzed using linear regression analysis. All graphs were created in R (R Core Team 2013).

The decomposition rates for whole CWD pieces were estimated as follows. First, mean DBH and height for sampled CWD pieces were calculated by tree species, vegetation zones and site conditions. The volumes of those mean stems with bark were calculated using taper functions (Tetioukhin et al. 2004). The volumes of stems without bark were acquired by subtracting the proportion of bark estimated depending on tree species and DBH (Tetioukhin et al. 2004). Second, the initial mass of CWD components was estimated. The stem mass was calculated by multiplying the volumes of mean trees by mean bulk density of control samples (Shorohova and Kapitsa 2014b). The initial bark mass from this study was used. The tree species and age-specific biomass expansion factors depending on vegetation zone (Zamolodchicov et al. 1998) were applied to calculate the initial mass of roots and branches related to the volume of a mean tree. Finally, mean decomposition rate of CWD pieces was calculated as a sum of the decomposition rate for each component multiplied by its mass proportion in the total mass of a CWD piece.

Results

Roots

Initial density of root wood did not depend on tree species. The decomposition of roots depended on soil moisture regime and tree species independently of tree mortality mode and log size (Table 2; Fig. 2). Aspen roots decomposed at the fastest rate and fir roots decomposed at the slowest rate (Table 3).

Branches

Before decomposition, the wood of branches was denser than that of roots independent of vegetation zone and site conditions. Initial wood bulk density of branches depended on tree species, with the highest values for fir and spruce. The decomposition rate of branches depended only on the tree species. Branches of Siberian pine decomposed at the slowest rate (Table 2; Fig. 3).

Bark

The area-specific mass and total mass of bark before decomposition were higher at the stem base than at the top and increased with log diameter. The regional climate and site conditions did not influence the initial bark mass. The rate of area-specific mass loss of bark increased with log diameter (Table 3; Fig. 4). The percent of bark left on the sampled stems decreased with time since tree death and averaged 94, 76, 68 and 41 % for aspen and birch, fir and spruce, Siberian pine and Scots pine, respectively. The rate of bark decomposition estimated as a total mass loss, i.e., including fragmentation as sloughing from logs and mineralization, depended on the log part and site moisture regime. It increased with the distance from the root collar. Higher fragmentation and consequently decomposition rates were recorded on well-drained sites compared to poorly drained ones (Table 3; Fig. 5).

The CWD piece scale decomposition rates varied depending on vegetation zone, moisture regime and tree species. The slowest rates were found for Siberian pine in northern boreal forest under poorly drained conditions. The fastest decomposition rates were found for spruce on well-drained southern boreal sites. In general, the decomposition of whole CWD piece was faster than decomposition of stem wood (Table 4; Fig. 6).

Discussion

Range of variability in the decomposition rates of CWD components and decomposition factors

Our results concur with the results from our previous studies and with information found in the available literature (Polubojarinov 1976). The initial density of woody CWD components increases in the order: roots, stems and branches. With some exceptions, the wood density of a component determines its decomposition rate. This result

Table 2 Results of ANOVA tests for k of mass loss of roots, branches and bark

Variable	Factors	F	p	df	Groups significantly different at $p < 0.05$
Decomposition of roots' wood (k_r)	Tree species	6.490	**<0.001**	5	(Aspen), (spruce and birch), (Scots pine, fir and Siberian pine)
$N = 335$	Log diameter	1.210	0.300	2	
	Mortality mode	0.223	0.637	1	
	Tree species × mortality mode	1.485	0.196	5	
	Vegetation zone	7.274	**<0.001**	2	(Northern), (southern/middle, hemi-boreal), not sign. within the species groups
	Soil moisture	13.972	**<0.001**	1	(Well-drained), (poorly drained)
	Soil moist. × mortality mode	1.953	0.163	3	
	Soil fertility	10.314	**<0.001**	2	(poor), (moderate and fertile)
Decomposition of branches' wood (k_{br})	Tree species	3.061	**0.011**	5	(Siberian pine) and (aspen, fir, Scots pine and spruce)
	Log diameter	2.664	0.073	2	
$N = 253$	Vegetation zone	5.4312	**0.005**	2	(Northern) and (southern/middle, hemi-boreal)
	Soil moisture	0.614	0.434	1	
	Soil fertility	0.009	0.991	2	
Mineralization of bark (k_b)	Tree species	6.154	**<0.001**	5	
$N = 332$	Diameter[a]	10.788	**<0.001**	2	No differences within the DBH groups
	Log part	0.587	0.444	1	(<20), (21–40), (>41) cm
	Tree species × Log part	0.833	0.527	5	
	Diameter × Log part	0.651	0.522	2	
	Vegetation zone	3.045	**0.049**	2	(Hemi-boreal), (southern/middle, northern), not sign. within the DBH groups
	Soil moisture	2.197	0.139	1	
	Soil fertility	1.289	0.277	2	
Decomposition of bark (k_{Sb})	Tree species	8.939	**<0.001**	5	
$N = 332$	Diameter[b]	0.020	0.888	2	
	Log part	13.095	**<0.001**	1	(0–3), (>3) m above root collar
	Tree species × log part	0.755	0.583	5	
	Diameter × log part	0.134	0.875	2	
	Tree species × diameter	4.811	**<0.001**	7	(Scots pine, 0–3 m above root collar, log DBH < 20 cm), (other)[c]
	Vegetation zone	7.623	**<0.001**	2	(Northern), (southern/middle, hemi-boreal), >3 m above root collar[d]
	Soil moisture	12.908	**<0.001**	1	(Well-drained), (poorly drained)
	Soil fertility	4.404	**0.013**	2	

Factors significant at the $p < 0.05$ level are denoted by bold font

[a] The mineralization rates of bark linearly depended on the log DBH ($F = 9.466$, $p = 0.002$). However, the adjusted r^2 of the model was only 0.022. The decomposition rates of bark for different log diameter groups were independent of tree species

[b] The linear regression between bark decomposition rates and log diameter was not significant either ($F = 0.380$, $p = 0.242$, $r^2 = 0.002$)

[c] This group was not considered separately because of small sample sizes (only 3 Scots pine logs <20 cm in DBH)

[d] The northern boreal zone was represented by Komi sites; the site conditions on all sample plots are classified as poorly drained. Thus, the difference in decomposition rates in this case can be explained by moisture conditions, not by climate

supports an earlier study on the negative interrelationship between initial density and decomposition rate (Harmon et al. 1995).

The decomposition rates of CWD components differed greatly. Local ecosystem characteristics and substrate attributes were more important predictors of decomposition

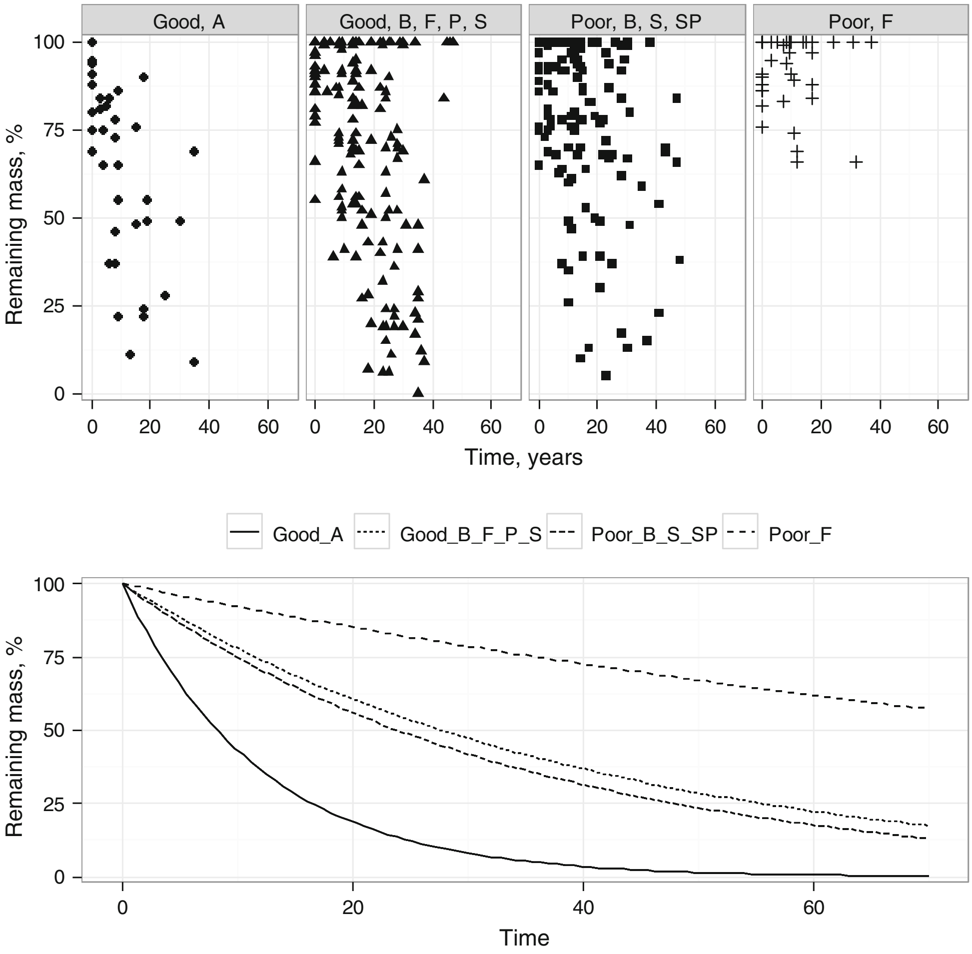


Fig. 2 Decomposition of roots over time. The *dots* represent remaining mass of roots; *lines* are models based on calculated mean decomposition rates for the following cases: good_A—roots of aspen under well-drained conditions; good_B, F, P, S—roots of birch, fir, Scots pine and spruce under well-drained conditions; poor_B, S, SP—roots of birch, spruce and Siberian pine under poorly drained conditions; and poor_F—roots of fir under poorly drained conditions

rates than vegetation zone. This confirms the conclusion that the common assumption that climate is a predominant control on decomposition is supported only when local-scale variation is aggregated into mean values (Mackensen and Bauhus 1999; Bradford et al. 2014).

Roots

Our estimates of root decomposition rates in boreal forests were of the same order of magnitude as reported in the literature (Tarasov and Birdsey 2001; Melin et al. 2009; Palviainen and Finér 2015). The decomposition rates of roots under well-drained soil conditions were comparable with the regional averages for decomposition rates of log wood of the same tree species (Krankina and Harmon 1995; Harmon et al. 2000; Tarasov and Birdsey 2001; Yatskov et al. 2003; Mäkinen et al. 2006; Shorohova and Kapitsa 2014b). The decomposition rates of roots under poorly drained conditions in this study were much lower than regional averages of the same tree species. As we hypothesized, soil moisture regime had a strong effect on the decomposition rates of root wood. Under poorly drained conditions, the lack of oxygen necessary for decomposers (Rayner and Boddy 1988) can explain the slow decomposition rates observed in our study. The influence of tree species on decomposition rates was only marginal and related to soil moisture. Only the decomposition rate of aspen and fir root wood was different from that of other tree species. Globally, there were clear differences found for decomposition rates of stem wood of gymnosperms compared to angiosperms (Weedon et al. 2009). Case studies from North America suggest that decomposition rate of woody roots varied between coniferous tree species either strongly (Janisch et al. 2005) or marginally (Chen et al. 2001). There was no variation between 80 native and non-native species in deciduous forest species (Jo et al. 2016). The effect of species traits and log diameter on the decomposition rates of woody roots is probably dominated by other effects such as moisture and aeration. Tree mortality mode did not influence the decomposition rate of root wood. This means no difference in the root decomposition rate was observed when decomposition started belowground when a tree died standing and then was blown down, or if a tree was first

Table 3 Exponential model parameters for the mass loss of bark and wood of roots and branches

	k (year^{-1})	SE	N	$T_{0.95}$ (years)
Decomposition of roots' wood				
Poorly drained mean	0.025	0.003	141	120
Fir	0.008	0.002	26	375
Birch, spruce, Siberian pine	0.029	0.003	115	103
Well-drained mean	0.034	0.003	194	88
Aspen	0.084	0.013	27	36
Birch, fir, Scots pine, spruce	0.025	0.003	167	120
Decomposition of branches' wood				
Siberian pine	0.006	0.002	26	*
Aspen, birch, fir, Scots pine, spruce	0.020	0.002	227	*
Mineralization of bark				
<20 cm	0.048	0.003	136	63
21–40 cm	0.072	0.005	201	42
>40 cm	0.087	0.010	38	34
Decomposition of bark including fragmentation				
0–3 m above root collar mean	0.120	0.008	177	25
Poorly drained	0.110	0.010	113	27
Well-drained	0.138	0.014	64	22
>3 m above root collar mean	0.177	0.012	160	17
Poorly drained	0.147	0.012	116	20
Well-drained	0.255	0.028	44	12
Decomposition of logs' wood[a]				
Aspen and birch	0.066	0.002	670	45
Fir and spruce mean	0.032	0.001	678	94
Fir and spruce leaning	0.018	0.002	406	167
Fir and spruce fallen	0.032	0.001	272	94
Scots pine	0.027	0.001	702	111
Siberian pine	0.014	0.004	26	214

k decomposition rate (year^{-1}), N sample size

[a] From Shorohova and Kapitsa (2014b)

* Cannot be calculated because the model is restricted to 30 years, the time when most braches are attached to logs

broken and then blown down, or when decomposition started aboveground in case of uprooting. Probably, the high initial moisture content of roots partly covered by soil or in many cases by mosses predetermines quick colonization of the substrate by wood-decomposing organisms which start the decay process.

Branches

The decomposition rates of attached and elevated side branches in this study were much lower than regional averages of stem wood for the same tree species (Krankina and Harmon 1995; Harmon et al. 2000; Tarasov and Birdsey 2001; Yatskov et al. 2003; Mäkinen et al. 2006; Shorohova and Kapitsa 2014b) and lower than the decomposition of branches of the same tree species on the forest floor (Mukhin 1993). As in the case with roots, decomposition rate of branches only slightly depended on tree species and did not depend on log diameter. Side branches decomposed at a common rate except Siberian pine, which showed the lowest decomposition rate. No significant differences were found between decomposition rates of deciduous tree branches in a mixed deciduous woodland (Swift et al. 1976). This evidence suggests that neither species traits nor log size is an important predictor of decomposition rates of attached branches.

Bark

The decomposition rate of bark attached to logs determined in this study is within the range reported for the decomposition rates of stumps (Shorohova et al. 2012)

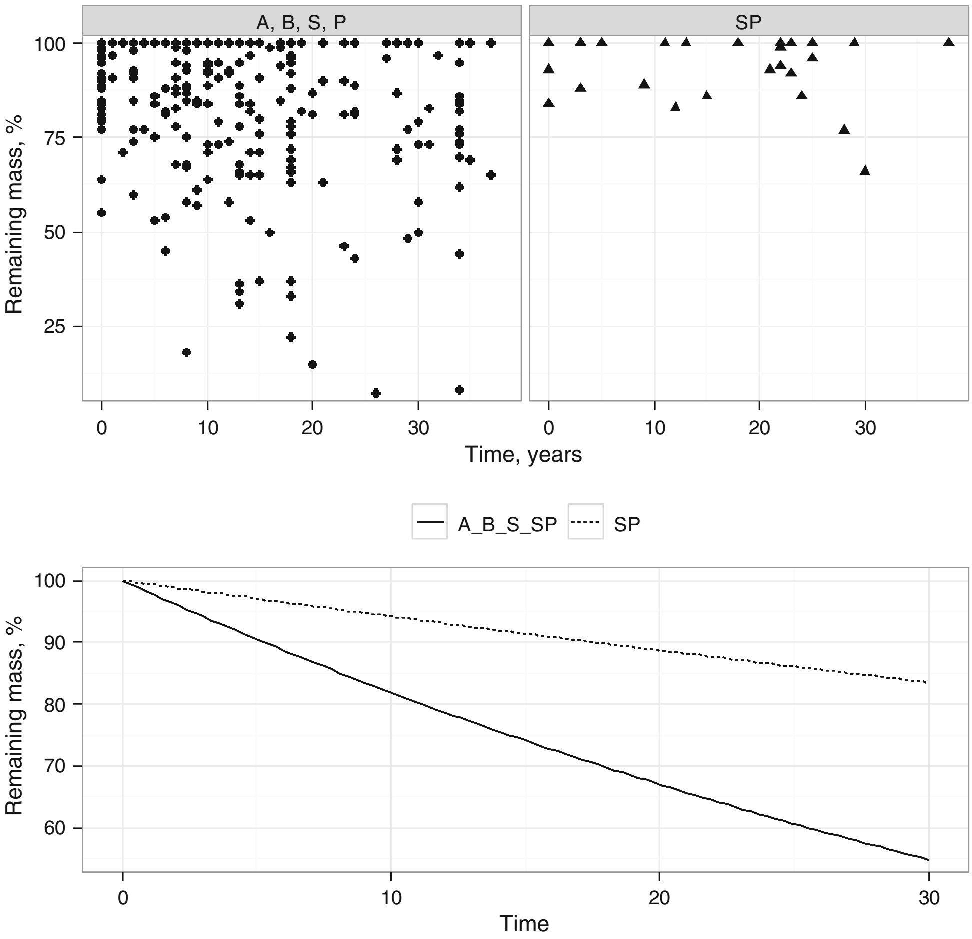
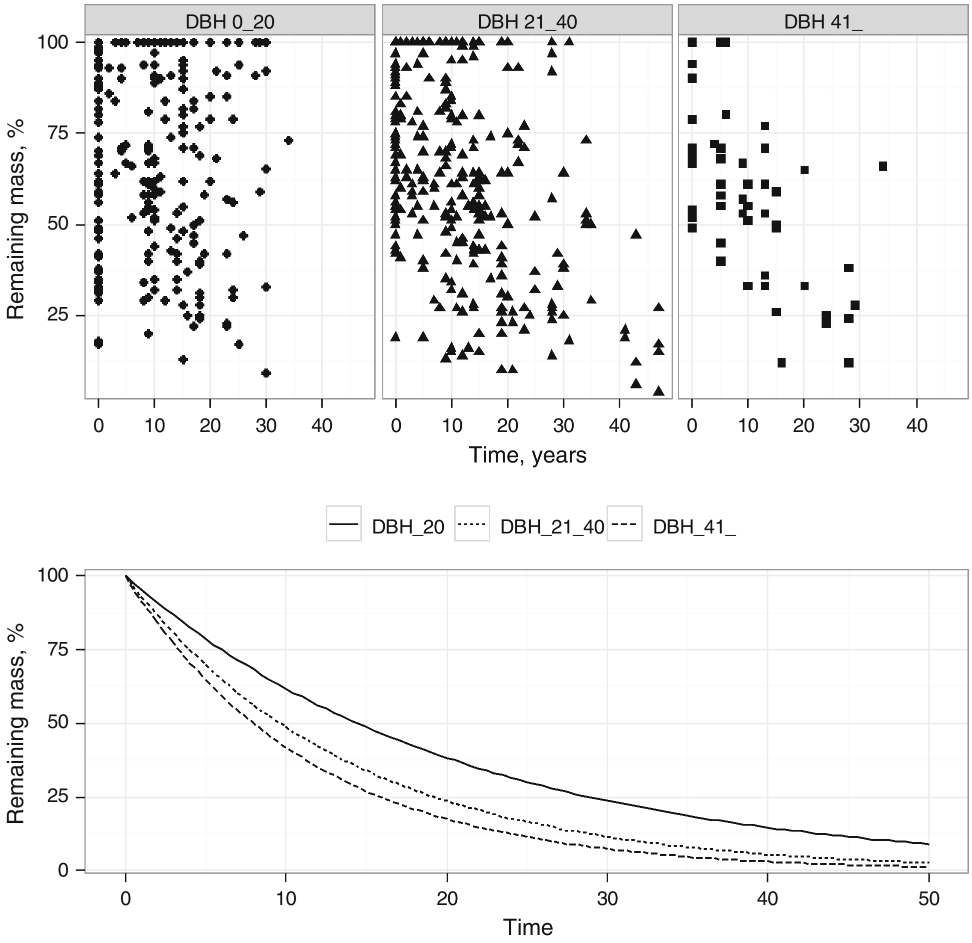


Fig. 3 Decomposition of branches over time. The dots represent remaining mass of branches; lines are models based on calculated mean decomposition rates of branches of A, B, S, P (aspen, birch, spruce and Scots pine) and SP (Siberian pine)

and log bark (Shorohova and Kapitsa 2014a) in European boreal forests. The much higher decomposition rates of bark compared to wood may be one of the reasons that our estimates of decomposition rates for whole CWD pieces were in the upper limit of the regional ranges for CWD decomposition rates. Moisture regime has both direct and indirect influence on CWD decomposition rates. When losses due to fragmentation are considered, the decomposition rate of bark becomes significantly higher on well-drained sites compared to poorly drained ones. This result can lead to an assumption of higher activity of bark-boring insects under more favorable site conditions compared to poor conditions. In wet forests in Komi sites, bark cover of coniferous trees slowly decreases during decomposition (Shorohova and Kapitsa 2014a). In this study, when Komi sites are combined with more well-drained CF and partly VF1 sites, many trees have already been affected by bark beetles before death. The bark of such trees sloughs from logs relatively quickly. Stem diameter negatively influenced the mineralization and fragmentation rates of the bark of all tree species showing the importance of the initial substrate quality for decomposition. The area-specific mass loss of bark caused by mineralization and volume loss was faster compared to decomposition of wood. Likewise, when considering the whole CWD piece and taking into account fragmentation, bark decomposed faster than other components.

With a few exceptions for some tree species, the decomposition rate increased in the following order, from slowest to fastest: branches, roots in poorly drained sites, leaning logs, fallen logs and roots in well-drained sites and bark. The slowest rate of decomposition of side branches among other CWD components was recorded also for *Pinus radiata* CWD due to unfavorable microclimate conditions (most of the side branches were not in contact with soil even after a few years of decomposition). Polyphenol and greater lignin concentrations may also have been a factor (Ganjegunte et al. 2004). The same study showed the faster decomposition of *Pinus radiata* log wood compared to bark; however, bark fragmentation was not taken into account.

Fig. 4 Loss of area-specific mass of bark over time. The *dots* represent remaining area-specific mass of bark; *lines* are models based on calculated mean mass loss rates of bark from stems with DBH < 20 cm (DBH_0_20), 21–40 cm (DBH_21_40) and >41 cm (DBH_41_)



Methodological considerations and uncertainties

Most uncertainties in our estimates of decomposition rates are related to the chronosequence approach, as discussed earlier for ecological studies in general (Johnson and Miyanishi 2008) and for decomposition studies in particular (Shorohova and Kapitsa 2014a, b; Palviainen and Finér 2015).

Initial substrate condition is unknown, and decomposition rates are overestimated in cases where decomposition starts and/or bark sloughs before tree death. In this study, we tried to select CWD pieces without traces of rot caused by biotrophic fungi. Logs without bark were not sampled either.

The trees that decomposed most slowly are measured at the extreme end of time since death, hence underestimating the decomposition rate. The processes of bark and wood colonization by decomposing organisms and leaching are not separated from fragmentation and mineralization. In general, uncertain predictions for CWD decomposition rates, and their global C-cycle implications, will persist until interactions of CWD microbial communities are better understood (Liu et al. 2013). In chronosequence studies, including this one, CWD pieces which were decomposed by different fungal species are combined in the same dataset.

When estimating the whole CWD piece decomposition rates, we used the biomass expansion factors acquired from different case studies. The length of time when branches are attached to logs remains uncertain. This leads to uncertainties in estimating the whole CWD piece decomposition rate. In addition, our estimates of CWD decomposition rates cannot be scaled up for buried wood (Moroni et al. 2015).

Conclusions

Assessments of CWD decomposition need to take into account fragmentation effects and differences among components. The different decomposition rates of wood and bark suggest that if wood and bark together are considered as one substrate, the rate of decomposition will likely be underestimated. Attached branches decomposed at the slowest rate compared to other components and cannot be associated with branches on the forest floor. The whole CWD piece decomposition rate can be predicted as a

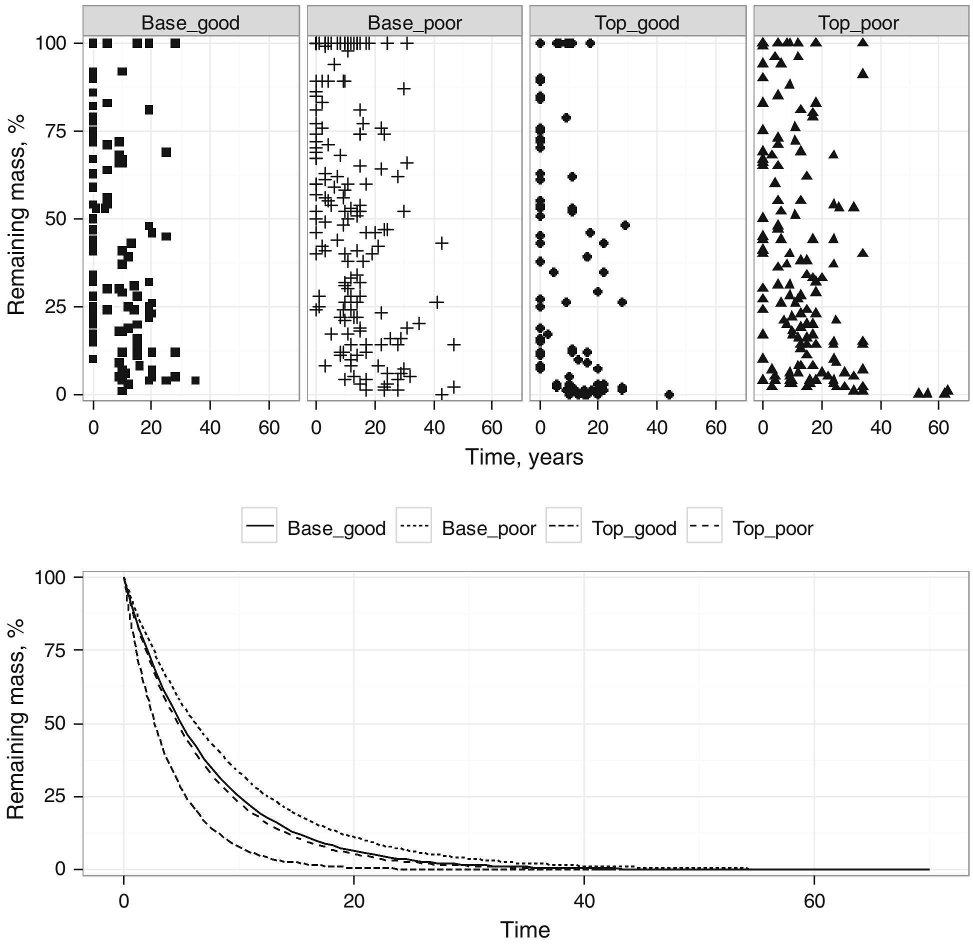


Fig. 5 Decomposition of bark over time (including fragmentation). The *dots* represent remaining total mass of bark; *lines* are models based on calculated mean decomposition rates for the following cases: Base_good_—bark from 0 to 3 m from the stem base under well-drained conditions; Base_poor—bark from 0 to 3 m from the stem base under poorly drained conditions; Top_good—bark from >3 m from the stem base under well-drained conditions; and Top_poor—bark from >3 m from the stem base under poorly drained conditions

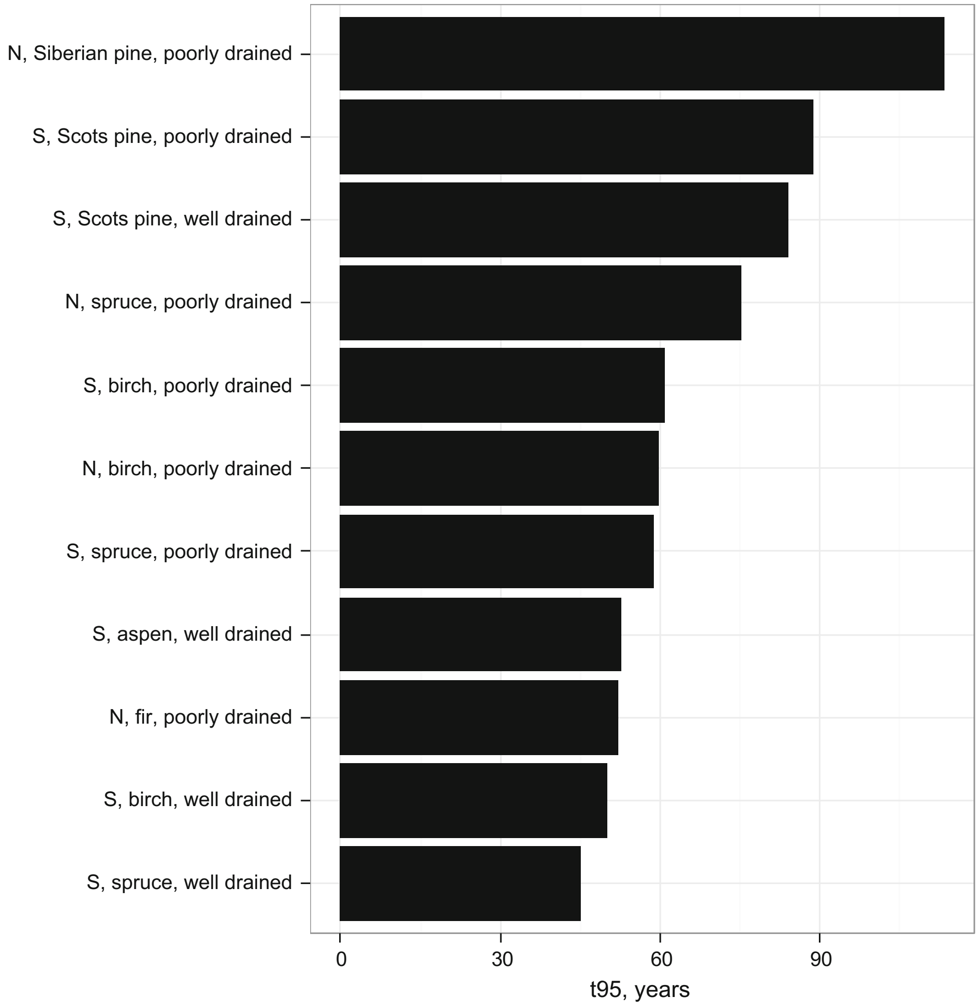
Table 4 Mean ecosystem and CWD attributes and exponential decomposition rate for the mass loss of whole CWD piece

Tree species	Vegetation zone	Moisture regime	Mean height (m)	Mean DBH (cm)	k (year^{-1})	$T_{0.95}$ (years)
Aspen	Southern and hemi-boreal	Well-drained	28	40	0.057	53
Birch	Northern	Poorly drained	14	19	0.050	60
	Southern and hemi-boreal	Well-drained	19	25	0.060	50
		Poorly drained	15	21	0.049	61
Fir	Northern	Poorly drained	14	17	0.058	52
Scots pine	Southern and hemi-boreal	Well-drained	22	27	0.036	83
		Poorly drained	19	19	0.034	88
Siberian pine	Northern	Poorly drained	17	33	0.026	113
Spruce	Northern	Poorly drained	16	25	0.040	75
	Southern and hemi-boreal	Well-drained	19	22	0.067	45
		Poorly drained	13	19	0.051	59

function of vegetation zone, site conditions, tree species and size in European boreal forests.

CWD decomposition rates and turnover time affect the quality and persistence of this substrate in forest ecosystems and, consequently, its role for carbon and nutrient storage and as a substrate for deadwood-dependent organisms (Stokland et al. 2012). Thus, our results can be applied in modeling carbon dynamics and for predicting the quality of CWD in biodiversity studies in European boreal forests.

Fig. 6 The whole CWD decomposition time, t_{95}, depending on vegetation zone, site conditions and CWD tree species. *N* northern boreal zone, *S* middle and southern boreal zones and hemi-boreal zone



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