Tree species traits are the predominant control on the decomposition rate of tree log bark in a mesic old-growth boreal forest

Ekaterina Shorohova [a,b,*], Ekaterina Kapitsa [b,a], Igor Kazartsev [d,b,a], Ivan Romashkin [a], Aleksei Polevoi [a], Helena Kushnevskaya [a,c]

[a] Forest Research Institute of the Karelian Research Centre, Russian Academy of Science, Pushkinskaya Str. 5, Petrozavodsk 185910, Russia
[b] Saint-Petersburg State Forest Technical University, Institutsky Str. 5, St. Petersburg 194021, Russia
[c] Saint-Petersburg State University, University Embankment, 7-9, St. Petersburg 199034, Russia
[d] All-Russian Institute of Plant Protection, Podbelskogo shosse, 3, St. Petersburg 196608, Russia

A B S T R A C T

Decomposition of coarse woody debris (CWD) bark is characterized by complex and poorly understood dynamics with unclear implications for carbon and nutrient cycling and biodiversity. We examined changes in cover and physical parameters through decomposition of bark attached to logs of the main tree species in an old-growth middle boreal forest. In a 66 yrs long chronosequence after tree death and fall, we analyzed changes in the following parameters of log bark: cover, moisture, area-specific mass, total mass, dry bulk density, thickness and proportion of phloem. The percent of bark left on the sampled stems decreased with time since tree death and averaged 38%, 61% and 86% for Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), and silver and downy birch (*Betula pubescens* and *Betula pendula*) = aspen (*Populus tremula*), respectively. Bark moisture increased along with succession of epixylic vegetation on logs that progressed similarly for all studied tree species. On average, no vegetation was recorded on logs 3 yrs after tree death. In 9 yrs, logs were characterized by the first stage of sparse vegetation cover. The closed groups of the second stage, with cover of not less than 70%, consisted mainly of non-epigeous species, and developed an average of 19 yrs after tree death. The third stage was dominated by ground cryptogam species without a significant contribution of vascular plants, and the fourth stage, when the wood was completely overgrown by the establishment and spread of vascular plants, was observed and average of 30 yrs after tree death. The exponential rate of total mass loss of bark increased at rates of 0.068, 0.110, 0.197 and 0.312 yr^{-1} for birch, aspen, spruce, and pine, respectively. The highest rate of bulk density loss was recorded for aspen (0.024 yr^{-1}) and did not differ for birch, pine and spruce (0.009 yr^{-1}). The decomposition rate was expressed as a rate of bark mass loss divided by initial volume (integrating losses due to bark mineralization, peeling, consumption by insects and sloughing from logs). It averaged 0.147 yr^{-1} for birch, aspen and spruce and 0.291 yr^{-1} for pine, independent of stem section, log diameter and decay class. In old-growth forests, where CWD volumes may reach hundreds of cubic meters, the accurate portrayal of bark decomposition patterns is crucial for estimating the role of CWD in carbon and nutrient cycles and the diversity of CWD-dependent organisms with different habitat requirements.

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1. Introduction

Tree bark is a highly complex, heterogeneous material composed of tissues external to vascular cambium (Corder, 1976). It makes up 25% of the stem volume and 16% of the stem dry mass in the dominant boreal tree species (Ugolev, 2002; Lestander et al., 2012). The inner (phloem) and outer (rhytidome) tree bark tissues differ significantly in physical properties, chemical composition, anatomical and morphological characteristics from each other and from wood (Corder, 1976; Polubojarinov and Sorokin, 1992, 1997). The proportion of inner and outer bark varies with tree species, age and tree section (Polubojarinov et al., 2000).

After tree death, all bark tissues undergo decomposition processes either in fragmented pieces as a litter component, or attached to wood, as a component of woody debris (WD) (Harmon et al., 1986). Mineralization, as a transformation of

organic substances into inorganic compounds (Schlegel, 1985) and mechanical or biological fragmentation are the most important processes for decomposition of tree bark (Harmon et al., 1986) and the release of its nutrients into the soil (Barber and van Lear, 1984; Holub et al., 2001; Spears et al., 2003). Narrowing the uncertainties in decomposition rates of bark as a WD component can significantly improve our understanding of the role of WD in carbon and nutrient cycling and biodiversity in forest ecosystems (Laiho and Prescott, 2004; Palviainen et al., 2011; Stokland et al., 2012).

The decomposition rate of coarse woody debris (CWD) bark is different from that of wood. It depends on substrate attributes and environmental conditions influencing microbial respiration and substrate mineralization as well as on fragmentation induced by biotic agents (Ganjegunte et al., 2004; Shorohova et al., 2012; Shorohova and Kapitsa, 2014b, 2016). However, variation in CWD bark decomposition patterns and the factors influencing it in boreal forests require further research.

Stimulated by forest industry needs, the initial physical characteristics of bark are relatively well studied (Tsyvin, 1973; Corder, 1976; Geles et al., 1981). Ecologically meaningful changes in bark parameters during decomposition under natural conditions have been incompletely studied and do not incorporate all mass and volume losses. The rate of mass per surface area of bark, or area-specific mass loss of bark characterizes bark mineralization rates and rates of peeling and fragmentation by insects. Total bark mass loss rate also takes into consideration the role of fragmentation as bark sloughs from logs (Shorohova et al., 2012; Shorohova and Kapitsa, 2014b). However, decomposition of bark characterized only by mass loss does not account for all thickness and volume losses. The rate of bark bulk density loss, based on estimates of bark volume measured in three dimensions in the lab (Ganjegunte et al., 2004; Shorohova et al., 2012), does not account for volume losses either, as it does not account for peeling losses. Thus, described patterns of specific and total mass, as well as density losses, underestimate the decomposition rate of CWD bark.

In intensively managed southern and northern boreal forests, the area-specific mass loss rate differs for spruce, birch and pine stump bark, and, in the case of spruce and pine, depends on stump size (Shorohova et al., 2012). In an old-growth northern boreal forest, the area-specific mass loss rate of log bark depends neither on log diameter nor on stem section. Nor does it differ among fir, spruce and Siberian pine log bark (Shorohova and Kapitsa, 2014b). In a combined dataset of log bark sampled in northern-, middle-, and hemi-boreal old-growth forests, the area-specific mass loss rate increases with log diameter independently of tree species (Shorohova and Kapitsa, 2016). Given these findings in different parts of the boreal forest belt, the influence of tree species, log size and distance from the stem base on bark areaspecific mass loss rate needs to be tested within one landscape under similar growing conditions.

Total mass loss of stump and log bark is species-specific. The influence of CWD size on mass loss of bark is different for stumps and logs. In most cases, bark fragmentation and consequently mass loss are more intense on smaller than on larger stumps (Shorohova et al., 2012). For log bark, diameter can have the opposite effect: larger logs have higher fragmentation and mass loss rates of bark than smaller ones. This tendency was observed for Siberian pine (*Pinus sibirica* Du Tour or (Loudon)) bark (Shorohova and Kapitsa, 2014b). Patterns of mass and volume loss of CWD bark require more research. Changes in log bark moisture, density, thickness, ratio of phloem to rhytidome as factors in the decomposition process may better explain mass and volume losses of bark. Factors, influencing variation in initial bark properties and their change due to decomposition of CWD need to be identified and quantitatively estimated.

We examined changes in the cover and physical parameters of bark attached to logs of the main European boreal tree species in a chronosequence of decomposition covering a period up to 66 yrs after tree death in a mesic old-growth middle boreal forest. Our specific objectives were to: (1) identify initial bark parameters before decomposition: area-specific mass (mass per surface area), total mass, dry bulk density, moisture, thickness, proportions of phloem and rhytidome; (2) analyse changes in those parameters through decomposition and the growth of epixylic vegetation; (3) estimate mass and volume losses due to fragmentation; (4) calculate decomposition rates of bark as a result of mineralization with adjustments for fragmentation, thickness losses, and losses due to bark sloughing from the log; and (5) estimate variation in bark decomposition rates according to tree species, log diameter, stem section, and wood decay class. We hypothesized that in a given forest type species-specific bark traits predetermine its decomposition rate.

2. Materials and methods

2.1. Study area and sample plots

The studies were carried out in summer 2015 in the middle boreal old-growth forest located in the State Strict Nature Reserve 'Kivach' in the Republic of Karelia, Russia (62°28′N, 33°95′E). The mean annual temperature is +2.4 °C, the length of the growing season is 90 days, and the mean annual precipitation is 625 mm (Skorohodova, 2008).

In order to find logs of all tree species typical of the middle boreal forest, two sample plots located ca. 300 m apart were established. The forest stands consisted of Norway spruce (*Picea abies* Karst.), silver and downy birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth.), trembling aspen (*Populus tremula* L.) and Scots pine (*Pinus sylvestris* L.). According to the classification of forest ecosystems in the Northwest of Russia (Fedorchuk et al., 2005), the forest type in the first sample plot was *Piceetum oxalidosum* with patches of *Piceetum fontinale* and *Piceetum oxalidoso-myrtillosum*. The soils are humic-gley and superficially eluvial gleish sandy-loamy and loamy (Fedorets et al., 2006).

Mean basal area of living trees by species age cohorts was calculated from ten relascope plot measurements. The age cohorts were identified visually; three trees were randomly selected from each cohort and cored to estimate tree ages. Mean DBH and height of the three measured trees were calculated for each tree species cohort. The volume of each tree cohort was calculated by multiplying basal area by mean species-specific height (Tetioukhin et al., 2004). Finally, all the volumes were summed.

Line intercept sampling was used in the downed wood (fallen and leaning logs) inventory (Ståhl et al., 2001). The volume of downed wood was calculated as:

$$V = \left(\frac{\pi^2}{8} \sum d_i^2 S\right) \sum L_j \qquad (1)$$

where V is the volume of the downed wood of the i-th decay class, d_i is the diameter of the i-th wood unit at the point of interception of the survey line, L_j is the length of the survey line (in our case 50 m for each sample plot), and S is the area of the stand.

The standing dead trees (snags) and stumps were measured on the two 4-m wide and 50 m long transects. The height, base and top (at breast height) diameters of all stumps (snags) were measured. Assuming a conical shape for each stump, its volume (V_{St}) in m³ was calculated as follows:

$$V_{st} = \frac{\pi h}{3}(R^2 + Rr + r^2) \qquad (2)$$

where h is the height of the stump in m; R and r are respectively the maximum and minimum radii in m.

The snag volumes (V_{sn}) were calculated using the formula:

$$Vsn = SHF \qquad (3)$$

where S is the snag basal area at breast height, m^2, HF is the species-specific height, m (Tetioukhin et al., 2004).

The tree stand volume was 347 m^3 ha^{-1}. It was distributed among tree species as follows: 60% Norway spruce (90–160 yrs. old), 20% birch (40–90 yrs), 20% aspen (80 yrs) + Scots pine (90–120 yrs). The volume of CWD was 52 m^3 ha^{-1}. The second sample plot was established in *P. oxalidoso-myrtillosum* on podzolic sandy-loam soils. The tree stand volume of 369 m^3 ha^{-1} was distributed among tree species as follows: 40% Norway spruce (120–160 yrs), 30% Scots pine (120–160 yrs), 20% birch (50–60 yrs), 10% aspen (70 yrs). The volume of CWD was 43 m^3 ha^{-1}.

2.2. Sampling and calculations

The bark attached to 73 logs from 16 to 80 cm in diameter at breast height (DBH) of the following tree species was sampled: Norway spruce, Scots pine, birch and aspen (Table 1). The CWD formed after the death of trees ranging in age from 60 to a few hundred years old. We used a pseudo-chronosequence approach to estimate the dynamics of bark decomposition. The dating of CWD pieces was determined using dendrochronological methods of cross-dating, growth release patterns and mechanical scars of neighboring trees for a period of up to 66 yrs. Undecayed log bark was sampled from trees that died in the current year or one year before sampling to serve as controls. The decay class for each log

Table 1
Characteristics of the sampled logs.

Time since tree death	Tree species	Number of sampled logs
0	Aspen	8
	Birch	8
	Spruce	6
	Pine	3
1–5	Aspen	4
	Birch	2
	Pine	2
	Spruce	6
6–10	Aspen	10
	Birch	4
	Pine	8
	Spruce	8
11–15	Aspen	2
	Birch	2
	Pine	–
	Spruce	4
16–20	Aspen	–
	Birch	2
	Pine	4
	Spruce	–
21–25	Aspen	2
	Birch	6
	Pine	2
	Spruce	4
26–30	Aspen	2
	Birch	–
	Pine	4
	Spruce	–
31–35	Aspen	2
	Birch	–
	Pine	–
	Spruce	–
>36	Aspen	2
	Birch	–
	Pine	6
	Spruce	2

was recorded according to the CWD decay class system described in Shorohova and Shorohov (2001). Briefly, these five decay classes can be characterized as: (1) Volume of decomposed wood is 0–10%; the remaining wood is sound. Bark may be present or absent due to bark beetle activity, sporocarps of wood decay fungi are absent. Only epiphytic lichens may be present. (2) Slightly decomposed wood accounts for 10–100% of the log, the remaining wood is sound. Sporocarps of wood decay fungi and epixylic mosses may be present. (3) Decayed wood accounts for 10–100%, remaining wood is slightly decayed or sound. Inclusions of mycelium, small pits and cracks occur. Wood may be crumbled or broken. Sporocarps of wood decay fungi occur. Coverage of mosses, lichens and higher plants can be up to 100%. Tree seedlings may be present. (4) All wood is well decayed. Wood samples of white rot are fragmented into separate fibres. Humification processes are beginning in the brown rot wood. Some pieces of wood have been lost via fragmentation and complete decomposition. Other features are the same as in decay class 3. (5) Types and borders of rot are difficult to distinguish. Pieces of CWD have significantly changed shape. Humification is continuing. Sporocarps of wood decay fungi are absent or very old. Vegetation on the trunk is similar to the ground vegetation, but with a higher number of tree seedlings.

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 for a truncated cone's lateral surface area:

$$S = \pi L(R + r) \qquad (4)$$

where R and r are, respectively, the maximum and minimum radii at opposite ends of a broken log segment in m, L is the 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 rectangular shaped bark samples of a 1–3 cm^2 were taken from 0 to 3 m and >3 m from the stem base of each log and measured in two dimensions (length × width). Whole samples and their phloem and rhytidome parts separately, when possible, were weighed. In the laboratory, they were oven-dried at 103 °C and weighed again. The moisture of bark in % was calculated based on the field and laboratory mass measurements in the natural and absolutely dry conditions, respectively. The moisture was estimated on the 23–27th of June, 2015 at temperatures ranging from 13 to 18 °C. According to the data from the Kondopoga meteorological station, during the measurement period, 18 mm of rainfall was accumulated after a week without precipitation.

The stage of vegetation succession on decaying logs was identified for the stem section where the bark samples were taken. Those stages were classified by using the features of epixylic vegetation as a baseline (Kushnevskaya et al., 2007). The zero stage means no plants were found growing on a log. The earliest first stage is characterized by a sparse vegetation cover, formed by clumps of the bryophyte-lichen groups. The closed groups with cover of ⩾70% formed by mainly non-epigeous species were treated as the second stage. Dominance of ground cryptogam species without significant contribution of vascular plants was considered diagnostic of the third stage. The overgrowing of wood is completed by establishment and spread of vascular plants, which indicated the fourth stage.

The area-specific mass of bark (mass per unit surface area, m_b, g cm^{-2}) was calculated by dividing the dry mass of a bark sample (m, g) by the surface area of sample (s, cm^2).

In order to determine the total area of remaining bark (S_f) the lateral surface area of each log (S) was multiplied by the percent of remaining bark (f). The total mass of log bark (M_{sb}) was calcu-

lated by multiplying the total area of remaining bark (S_f) by the specific mass of bark (m_b).

In the laboratory, the completely dried samples were coated with paraffin wax and put into water. Their dry volume was estimated using water displacement method (Polubojarinov, 1976). The dry bulk density of bark (ρ, g cm^{-3}) was calculated by dividing the dry mass by the dry volume of the sample. The average thickness of bark samples was calculated by dividing their volume by surface area. The proportion of phloem by volume was visually estimated for each bark sample.

2.3. Data analysis

In order to separate the factors controlling the rate of decomposition from the factors controlling initial physical characteristics of bark, we first analyzed the initial moisture, thickness, proportion of phloem, area-specific mass, total mass and bulk density from the bark of trees that died in the year of observation or the year before. An analysis of variance (ANOVA) incorporating type III sum of squares for an 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) tree species; (b) stem section (0–3 m above root collar vs. >3 m above root collar); and (c) log DBH (expressed as three categories: 0–20, 21–40 and >41 cm) on the variation in initial dry bulk density, mass, thickness and moisture content of bark.

For bark samples from all trees that died ⩾2 yrs before sampling, we calculated the percent of dry mass (M, %), density (ρ, %), thickness and proportion of remaining phloem based on the loss of the specific (m_b) and total (M_{sb}) mass, bulk density (ρ), thickness and proportion of phloem of bark relative to the corresponding initial characteristics. 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 initial parameters of a given bark sample exceeded the mean initial parameters. The annual rates of change over time (k, year^{-1}) were calculated based on a single exponential model (Olson, 1963) for the following parameters of bark: specific (k_m) and total mass loss (k_{Mb}), bulk density loss (k_ρ), thickness loss (k_t) as well as for the loss of phloem volume (k_{ph}). The rate of decrease of bark cover due to its sloughing from logs (k_f) was also calculated based on single exponential model. The decomposition rate takes into account all processes of mass and volume loss (k_D) including mineralization, thickness loss due to peeling and insect consumption and fragmentation as sloughing from stems. It was calculated as a bulk density loss on the basis of volume losses estimated so that the bark thickness was constant, multiplied by the percent cover of bark remaining on a log (f).

Factorial ANOVA (based on a type III sum of squares test for an unbalanced design) and Duncan tests were implemented to estimate the effects of (a) tree species, (b) stem section (0–3 m above root collar vs. >3 m above root collar), (c) log DBH (expressed as three categories: 0–20, 21–40 and >41 cm), (d) wood decay class on the variation in k values. The variation in bark moisture was analyzed using ANCOVA with decomposition time as a covariate and the same variables listed above, plus stage of succession, as categorical predictors. The moisture-log diameter relationship was tested with simple linear regression analysis. All graphs were created in R (R Core Team, 2013).

3. Results

The minimum values of area-specific mass of bark before decomposition were found for spruce and pine, and the maximum values were found on aspen logs with >41 cm in DBH. The total initial mass of bark increased with log diameter. The initial bulk density, thickness, proportion of phloem and moisture depended only on tree species. The effect of log diameter on the above variables was non-significant for bark of different tree species when evaluated separately. The lowest values of initial bulk density were found for pine bark. The initial bark thickness increased in the following order: spruce < birch = pine < aspen. The initial proportion of phloem increased in the following order: pine < spruce < aspen < birch. In control logs, aspen and spruce bark was characterized by higher moisture than birch and pine bark (Table 2).

The rate of change in all parameters was species-specific (Table 3). The rate of area-specific mass loss influenced by the loss of thickness because of bark peeling, insect consumption and shrinkage was greater on the top than on the stem base, and the greatest rate was recorded for pine bark (Table 3 and Fig. 1a). The percent of bark left on the sampled stems decreased with time since tree death in the following order: aspen < birch < spruce < pine (Table 3) and averaged 38%, 61% and 86% for pine, spruce, and birch = aspen, respectively (data not shown). The rate of total mass loss of bark increased in the following order: birch < aspen < spruce < pine (Table 3 and Fig. 1b). The rate of bulk density loss was the greatest for aspen (Table 3 and Fig. 1c). The differences between diameter groups were not significant within two species groups (aspen; birch + pine + spruce). The phloem layer disappeared faster from aspen, pine and spruce bark as compared to birch bark (Table 3).

Moisture of bark increased along with succession of epixylic vegetation on logs (Table 4 and Fig. 2) that in turn progressed over time (Fig. 3) in a similar manner for all tree species (Table 5). In the zero stage of epixylic succession, cover of epiphytic lichens varied from 0.5 to 5%. *Hypogimnia physodes*, *Platismatia glauca*, *Parmeliopsis ambigua* dominated on spruce, pine and birch logs. *Pylaisia polyantha*, *Sanionia uncinata* and *Peltigera praetextata* dominated on aspen logs. In the first stage of succession, *Ptilidium pulcherrimum* as well as *Cladonia* sp. (the primary thallus) established on conifer logs. In the second stage, the abundance of these species reached 70%. At the same time, mosses *Dicranum fucescens*, *Dicranum scoparium* and small hepatics *Lophozia* spp., *Cephalozia* spp., and *Anastrophyllum hellerianum* spread on conifer logs. In the first and second stage of succession on birch and aspen logs, *S. uncinata* dominated. Associated species were *P. pulcherrimum*, *Sciurohypnum reflexum*, *Sciuro-hypnum oedipodium*, *D. scoparium*, *Plagiomnium cuspidatum*. In the third stage of epixylic succession *Pleurozium schreberi* dominated on all logs. Its cover was up to 90%. Associated species with cover up to 50% were *Hylocomium splendens*, *Ptilium crista-castrensis*, *Rhytidiadelphus triquetrum*. In the fourth stage, the same moss species dominated. However, their cover decreased to 30% and lower. Vascular species typical for surrounding ground vegetation *Linnea borealis*, *Oxalis acetosella*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea* formed the next layer of vegetation on logs on the final fourth stage of succession. Aspen bark was characterized by exceptionally high moisture at the initial stages. At later stages, pine bark was characterized by lower moisture than other species (Fig. 2). Bark moisture also marginally depended on log diameter in a linear relationship (Table 4). Total decomposition rate was the greatest for pine bark (Fig. 4) independent of stem part (Table 3). The differences between diameter groups were not significant within two species groups (pine; aspen + birch + spruce). Most of the above bark parameters were not related to decay class of CWD (Table 3). The thickness loss rate of bark did not depend on decay class when considered separately for the stem base and top. The bulk density loss rate did not depend on decay class when considered separately for different tree species, with the exception that phloem loss rate differed between CWD of the 1st decay class (0.206 ± 0.037 yr^{-1}) and the 2–5th decay classes (0.080 ± 0.012 yr^{-1}).

Table 2
Initial physical parameters of tree bark depending on log characteristics. ANOVA F values significant at the p < 0.05 level are denoted by **bold font**.

Variable	Factors	F	p	df	Means (SE) for groups significantly different at p < 0.05				
Specific mass, m_{b0}, g cm^{-2}	Tree species	12.2	**<0.001**	3	Spruce, pine	Aspen < 40[a]	Birch		Aspen > 41
	Log diameter	12.7	**<0.001**	2	0.257 (0.021)	0.389 (0.009)	0.446 (0.057)		0.836 (0.160)
	Stem section	<0.1	0.915	1					
Total mass, M_{sb0}, kg	Tree species	4.0	**0.020**	3	Base[b], 0-40[a]	Top[c], 0-20	Top, 20–40	Base, >41	Top, >41
	Log diameter	10.4	**0.001**	2	9.87 (1.418)	8.94	40.98 (5.796)	41.74 (6.090)	265.55 (106.852)
	Stem section	10.9	**0.003**	1					
Dry bulk density, ρ_0, g cm^{-3}	Tree species	7.2	**0.001**	3	Pine		Aspen, birch, spruce		
	Log diameter	0.7	0.512	2	0.498 (0.072)		0.673 (0.015)		
	Stem section	3.1	0.092	1					
Thickness, cm	Tree species	14.2	**<0.001**	3	Spruce		Birch, pine		Aspen
	Log diameter	17.5	**<0.001**	2	0.353 (0.010)		0.614 (0.050)		1.100 (0.179)
	Stem section	0.6	0.553	1					
Proportion of phloem, %	Tree species	11.2	**<0.001**	3	Pine	Spruce		Aspen	Birch
	Log diameter	0.3	0.718	2	21 (10)	32 (5)		56 (6)	71 (3)
	Stem section	2.8	0.109	1					
Moisture, %	Tree species	9.1	**<0.001**	3	Birch, pine		Aspen, spruce		
	Diameter	3.4	0.052	2	61 (3)		88 (3)		
	Log section	2.5	0.128	1					

[a] Log DBH, cm.
[b] Bark from 0 to 3 m from the stem base.
[c] Bark from >3 m from the stem base.

Table 3
Mean annual rates k (yr^{-1}) of change in physical parameters of bark depending on log characteristics. ANOVA F values significant at the p < 0.05 level are denoted by **bold font**.

Variable	Factors	F	p	Means (SE) for groups significantly different at p < 0.05			
Area specific mass loss, k_m	Tree species	4.1	**0.009**	Base[a]	Top[b], aspen, birch, spruce		Top, pine
	Log diameter	0.1	0.776	0.060 (0.007)	0.074 (0.010)		0.153 (0.032)
	Stem section	5.7	**0.019**				
	Decay class	1.2	0.3				
Total mass loss, k_{Mb}	Tree species	8.2	**<0.001**	Birch	Aspen	Spruce	Pine
	Log diameter	2.2	0.140	0.068 (0.023)	0.110 (0.019)	0.197 (0.028)	0.312 (0.045)
	Stem section	3.9	0.050				
	Decay class	0.9	0.5				
Bulk density loss, k_ρ	Tree species	5.1	**0.003**	Birch, pine, spruce		Aspen	
	Log diameter	4.7	**0.034**	0.009 (0.002)		0.024 (0.004)	
	Stem section	<0.1	0.855				
	Decay class	3.1	**0.019**				
Thickness loss, k_t	Tree species	2.4	0.072	Base	Top, aspen, birch, spruce		Top, pine
	Log diameter	2.4	0.128	0.052 (0.008)	0.076 (0.011)		0.157 (0.034)
	Stem section	9.0	**0.003**				
	Decay class	3.2	**0.017**				
Decrease of bark cover, k_f	Tree species	13.0	**<0.001**	Aspen	Birch	Spruce	Pine
	Log diameter	2.4	0.095	0.021 (0.006)	0.028 (0.015)	0.070 (0.012)	0.155 (0.031)
	Stem section	1.9	0.165				
	Decay class	6.3	**<0.001**				
Decrease in the volume proportion of phloem, k_{ph}	Tree species	8.3	**<0.001**	Birch		AsSen, pine, spruce	
	Log diameter	0.1	0.730	0.030 (0.008)		0.140 (0.020)	
	Stem section	<0.1	0.969				
	Decay class	4.5	**0.003**				
Decomposition as a total mass and volume loss, k_D	Tree species	11.1	**<0.001**	Aspen, birch, spruce		Pine	
	Log diameter	5.7	**0.019**	0.147 (0.015)		0.291 (0.071)	
	Stem section	0.7	0.400				
	Decay class	1.3	0.285				

[a] Bark from 0 to 3 m from the stem base.
[b] Bark from >3 m from the stem base.

4. Discussion

The values of the initial properties of bark found in this study fell into the range of corresponding values reported for boreal forests (Simonov, 1962; Leontiev, 1967; Sosunov, 1967; Tsyvin, 1973; Polubojarinov and Sorokin, 1992, 1997; Stängle et al., 2016).

In this study, the initial area-specific properties of bark varied only subject to tree species, indicating relatively uniform radial growth of tree bark independently of the stem section. Reported patterns of bark accumulation along the stem differ considerably depending on tree species and tree growth conditions and marginally on tree age (Gusev, 1981; Nahabtsev, 1989; Laasasenaho et al., 2005; Vais, 2015). In the northern boreal forest, the initial area-specific bark mass increases with the distance from the stem base similarly for spruce, birch and Siberian pine (Shorohova and Kapitsa, 2014b). Similar patterns were observed for bark density of Norway and Sitka spruce (*Picea sitchensis*) in northern Norway (Dibdiakova and Vadla, 2012). Higher mass of birch bark compared
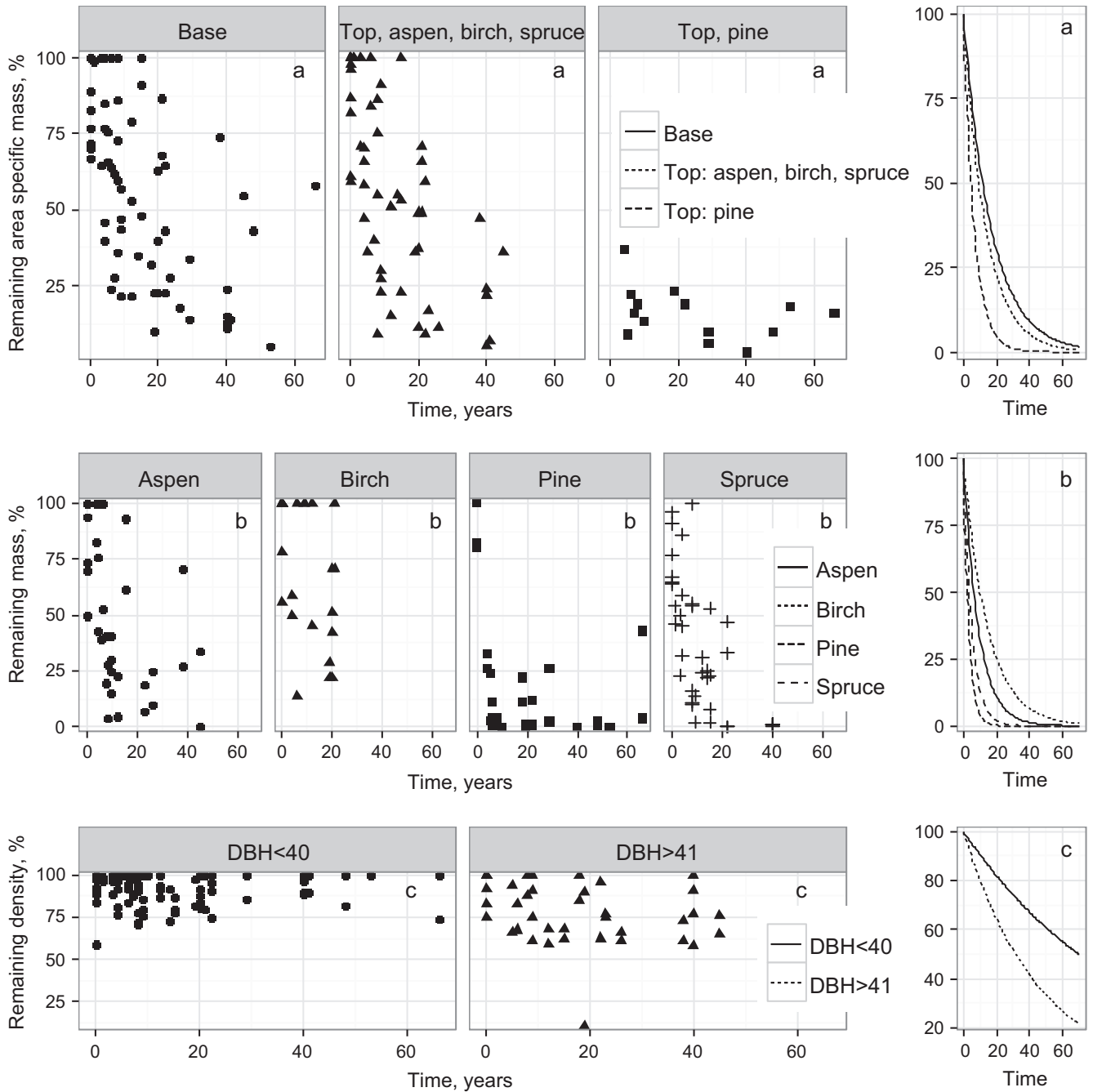
Fig. 1. Change of physical parameters of bark over time. (a) Loss of area-specific bark mass over time. The dots represent remaining specific mass of bark; lines are drawn based on single exponential models with calculated mean rates of area-specific bark mass loss from stems for the following cases: Base – bark from 0 to 3 m from the stem base; Top: aspen, birch, spruce – bark from >3 m from the stem base for aspen, birch and spruce; and Top: pine - bark from >3 m from the stem base for pine. (b) Loss of total bark mass over time. The dots represent remaining total mass of bark; lines are drawn based on models with calculated mean rates of bark mass loss from stems of aspen, birch, pine and spruce. (c) Loss of bark bulk density over time. The dots represent remaining bulk density of bark; lines are drawn based on the models with calculated mean rates of bark bulk density loss from logs with DBH < 40 cm and >41 cm.

to that of spruce and pine bark may be attributed to better growth conditions, as this difference was not found in northern sites. Higher proportions of birch bark in large trees were found also in Middle Siberia (Vais, 2015). Aspen is characterized by the most massive bark layer among boreal tree species (this study, Table 1; Polubojarinov et al., 2000) and thus diverges from other tree species by its bark properties.

The observed species-specific differences in the initial specific properties of bark disappear at the whole-log level: total bark mass

depended only on log size. The influence of initial total amount of bark depending only on log diameter and stem section as recorded in this study also was observed for logs in the northern European boreal forest (Shorohova and Kapitsa, 2014b). Bark moisture on logs after fall was lower that on freshly cut logs (Leontiev, 1967) and higher than that in a growing tree (Polubojarinov, 1976; Dibdiakova and Vadla, 2012). Higher water content of bark at the tree top than at the tree base as reported for freshly cut logs (Tsyvin, 1973; Wästerlund, 1986; Dibdiakova and Vadla, 2012)

Table 4
The moisture of bark related to time since tree death and log characteristics. ACNOVA F values and linear regression r^2 significant at the $p < 0.05$ level are denoted by **bold font**.

Variable	Factors	F	p	df	a[a]	b	r²
Moisture, %	Time	0.2	0.653	1			
	Tree species	12.0	**<0.001**	3			
	Log diameter	14.4	**<0.001**	2	2.5	20.6	**0.202**
	Stem section	0.1	0.773	1			
	Stage of succession	18.2	**<0.001**	4			
	Tree species * stage of succession	2.2	**0.019**	11			
	Decay class	2.1	0.094	4			

[a] Coefficients of linear regression model.
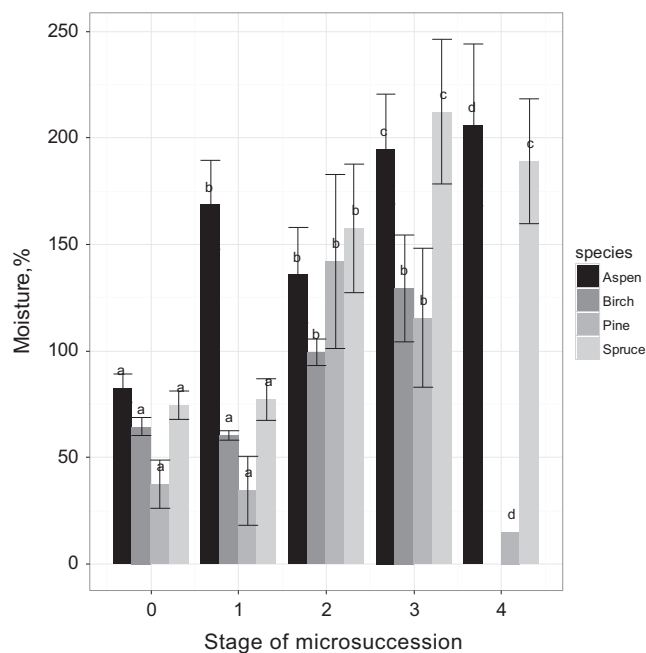
Fig. 2. Change in moisture of bark samples depending on stage of succession of epixylic vegetation. The dots are means, whiskers are SE. Letters indicate differences between groups, significant at $p < 0.05$.

Fig. 3. Succession of epixylic vegetation related to time since tree death. The zero stage means no plants were found growing on a log. The earliest first stage is characterized by a sparse vegetation cover, formed by clumps of the bryophyte-lichen groups. The closed groups with cover of ⩾70% formed by mainly non-epigeous species were treated as the second stage. Dominance of ground cryptogam species without significant contribution of vascular plants was considered diagnostic of the third stage. When wood is completely overgrown by vascular plants, this indicates the fourth stage. Dots are mean times for each stage of succession, whiskers are SE.

Table 5
Variation in the time since tree death related to the stage succession of epixylic vegetation. ANOVA F values significant at the $p < 0.05$ level are denoted by **bold font**.

Variable	Factors	F	p	df
Time since tree death	Stage of succession	38.5	**<0.001**	4
	Tree species * stage of succession	20.6	0.816	11

was not confirmed for bark from fallen logs in this study. These results raise a question about the requirements for control logs when studying the dynamics of bark moisture during decomposition, i.e. should bark from living trees, snags, fresh or 'old' logs be sampled for control.

The rates of area-specific and total mass loss of bark in this study exceeded the range reported for that of stump and log bark in European boreal forests (Shorohova et al., 2012; Shorohova and Kapitsa, 2014b). These results can be explained by differences in methodology, peculiarities of the study sites and substrate. In the above-mentioned studies, the annual mass loss of bark was calculated as a mean k for exponential models fitted to the dynamics of remaining bark mass over time. Such an approach does not take into account the fact that the annual decomposition rate of individual samples decreases non-linearly over time (Shorohova and Kapitsa, 2014b). Shorohova et al. (2012) calculated mean k based on the dynamics of bark mass over time, i.e. without separation of variation in the initial bark mass from the variation in bark mass loss through decomposition. Relatively favourable site conditions in this study may have promoted high initial specific mass and thickness of bark, and a greater proportion of quickly decomposable phloem, all of which probably positively influenced the rate of mass loss. Greater log bark fragmentation leads to a higher mass loss rate in
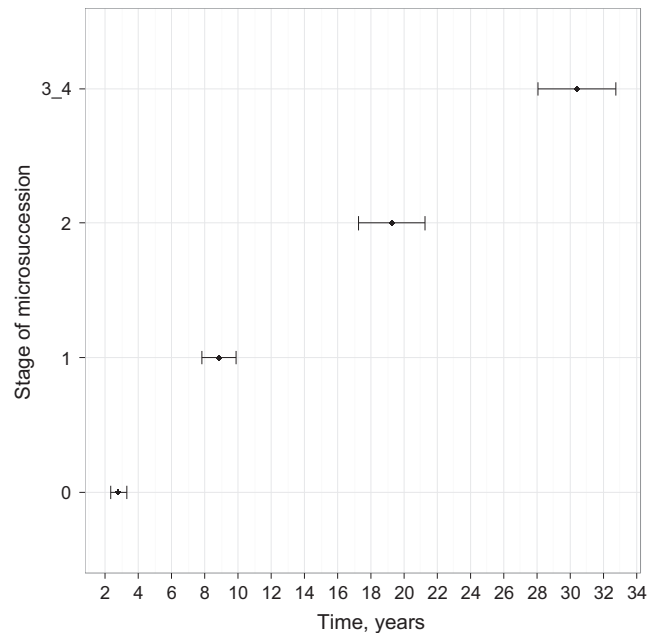
this study compared to rates found in northern European boreal forests (Shorohova and Kapitsa, 2014b).

Increasing total bark mass loss rate in the order of birch, aspen, spruce, pine reflects a similar trend in fragmentation rates, and may be partly explained by increasing bark consumption by insects during the initial stages of decay. Bark density loss rate was lower compared to the area-specific mass loss rate, indicating high rates of thickness loss especially from the top section of stems.

The slowest phloem loss rate was recorded for birch. In contrast with other studied tree species, birch phloem is denser than its rhytidome (Polubojarinov and Sorokin, 1992) and consists of sclereids with highly thickened, lignified walls (Lotova, 1999). Phloem of aspen, pine and spruce decomposes at the same rate, influenced by initial substrate attributes and biological agents. Scots pine phloem is characterized by the lowest thickness (this study, Polubojarinov and Sorokin, 1997; Polubojarinov et al., 2000), lowest density (Polubojarinov and Sorokin, 1997; Polubojarinov et al., 2000) and highest nutrient content (Skonieczna et al., 2014) compared to aspen, birch and spruce. Aspen phloem has the lowest decay-resistant lignin content than phloem of other species (Faustova, 2005). Spruce and pine phloem is consumed rather quickly by early-arriving phloem-feeders, mainly bark beetles. This leads to rapid sloughing of the bark from the stem, especially in standing trees (Weslien et al., 2011; Ulyshen, 2014).
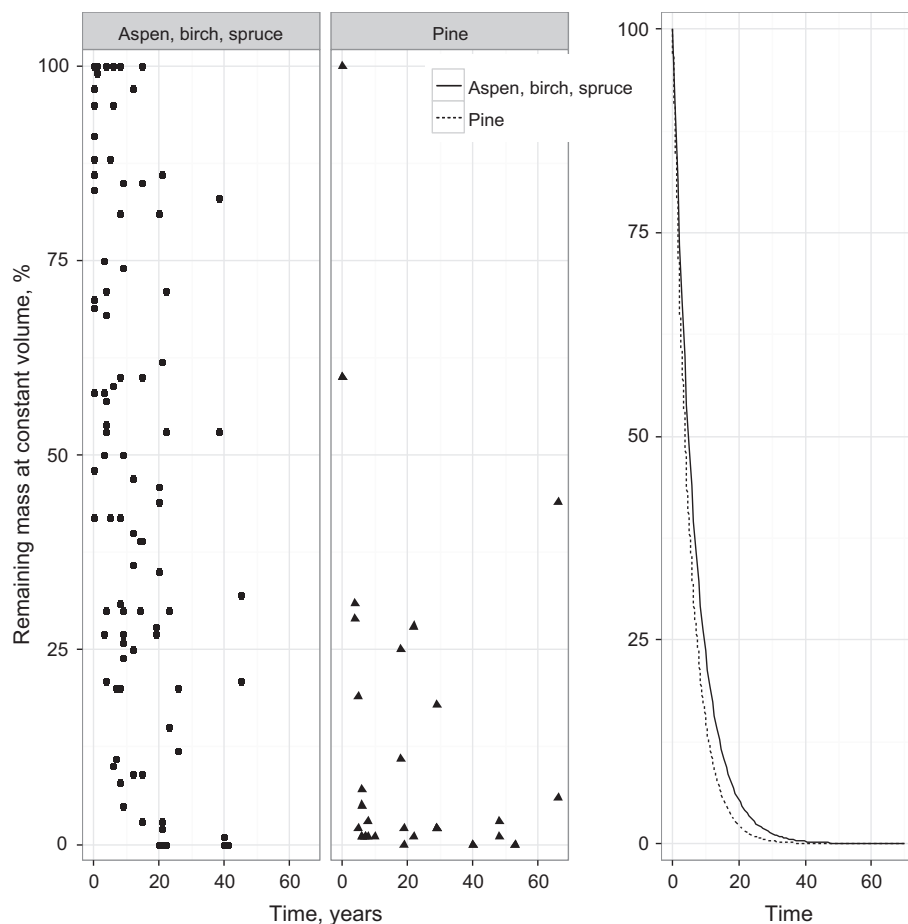
Fig. 4. Decomposition of bark over time. The dots represent remaining total mass of bark at constant volume, lines are drawn based on the models with calculated mean decomposition rates of bark mass and volume loss for aspen, birch, pine and spruce.

The absence of a relationship between the rates of bark mass, volume and density loss and CWD decay class indicate the relative independence of wood and bark decomposition processes. This restricts our possibilities in predicting bark decomposition patterns based on the data on CWD decay class.

Variation in bark moisture and of the growth of plants on logs affects decomposition rates. The high mass and density loss rate of aspen bark can be explained by its high moisture at the initial stages of decomposition. Aspen tree stems are in most cases covered by epiphytes that keep bark moist after trees fall. In general, mosses absorb water at levels hundreds of times more than their dry mass (Dilks and Proctor, 1979; Glime, 2007). The water absorption capacity of bryophyte clumps increases in parallel with the increase of size and density of clumps. In our study, this leads to an increase in bark moisture, which may positively influence the decomposition rate of bark. The phenomenon of deadwood being overgrown and buried by bryophytes (Moroni et al., 2015) is not typical for mesic forests hosting bryophyte species growing in clumps with good aeration and relatively high turnover rates. Bryophytes release chemicals that change the pH of the substrate on which they grow (Vitt and Weider, 2009), they may inhibit activity of some fungal species (Üçüncü et al., 2010; Klavina et al., 2015) and influence composition of fungal communities (Davey et al., 2014). This may have implications to the decomposition rates of bark observed in this study.

The decomposition rates of log bark acquired in this study are higher than decomposition rates of wood under similar favourable site conditions reported by Shorohova and Kapitsa (2014a). The bark on aspen, birch and spruce logs decomposes ca. three times

faster than wood, whereas pine log bark decomposes ca. 16 times faster than wood. In our study area of the Kivach reserve, the annual rate of litter decomposition in the 130 yr old spruce forest averages 39% (Germanova, 2009), which is ca. two times higher than the decomposition rate of log bark if ignoring non-linearity of the processes.

In the estimates of decomposition rates of bark, uncertainties related to the chronosequence approach (Johnson and Miyanishi, 2008) are even greater than for wood decomposition studies (Shorohova and Kapitsa, 2014a, 2016; Palviainen and Finér, 2015). Initial bark condition is unknown. Bark pieces, which initially differed by density, mass, moisture, thickness and proportion of phloem and then decomposed by different fungal species, are combined in the same dataset. Besides, the decomposition rates can be overestimated in cases where decomposition starts and/or bark sloughs before tree death, which is difficult to detect in its later stages under moss cover. Bark cover for logs covered by plants is often impossible to estimate, which creates an uncertainty for estimates of the total bark mass loss rate.

5. Conclusions

In mesic boreal forests with relatively good tree growth conditions, species-specific patterns of stem radial growth determine variation in initial bark parameters and its decomposition rates.

As initial parameters of bark are even more variable than those of wood, the variation in initial bark parameters and their change through decomposition need to be studied separately. Assessments

of CWD bark decomposition need to take into account all processes of mass and volume loss. Decomposition rate of bark expressed as a rate of its mass loss divided by its initial volume integrates losses due to bark mineralization, peeling, consumption by insects and sloughing from logs.

The decomposition rate of bark is relatively independent of that of wood and cannot be predicted based on the data on CWD decay class.

In old-growth forests, where CWD volumes may reach hundreds of cubic meters (Shorohova and Kapitsa, 2015), the role of bark as a CWD component can thus be especially important. Accurate portrayal of bark decomposition patterns is crucial for estimates of the role of CWD in carbon and nutrient cycles and in supporting a diversity of CWD-dependent organisms having different habitat requirements (Stokland et al., 2012). From forest management, conservation and restoration perspectives, our results support the importance of mimicking natural disturbance patterns with a gradient of log types with different bark cover in time and space, Such a management approach would increase variability in decomposition rates of bark and consequently provide valuable substrates for different deadwood dependent organisms.)

Acknowledgements

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