Forest Ecology and Management 377 (2016) 36–45

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

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

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ARTICLE INFO

Article history:
Received 18 April 2016
Received in revised form 18 June 2016
Accepted 19 June 2016

Keywords:
Decay
Dead wood
Mineralization
Fragmentation
Density
Phloem

ABSTRACT

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.

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

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http://dx.doi.org/10.1016/j.foreco.2016.06.036
0378-1127/

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:

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

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 m^3 was calculated as follows:

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

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