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Coupled effect of temperature and mineral additions facilitates decay of aspen bark

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ABSTRACT

Tree bark represents a substantial component of coarse woody debris (CWD) in boreal forests. Estimating its decay rates improves our understanding of decomposition processes of woody debris and their effects on the forest carbon cycle. The atmospheric deposition of nitrogen (N) and phosphorus (P) from aerosols and gases has notably grown during the last century. We examined the effect of mineral N and P additions and temperature on the decay rate of aspen (*Populus tremula*) bark in a long-term incubation experiment at constant and sufficient moisture level.

Fresh aspen bark with natural moisture was mixed with local soil (*Haplic Phaeozems*) in proportion of 2:1 by dry mass to prepare the soil-bark substrates (SBSs). Mineral elements (N and P) were added to the SBSs with a proportion of 1% of dry bark weight (for each element). The following treatments of SBS's were studied: (1) Bark + Soil, *pure SBS* (*control*); (2) Bark + Soil + N; (3) Bark + Soil + N + P and (4) pure soil, ***S***. The SBSs were incubated in thermostats at 2, 12 and 22 °C for 12 months. The decay rate of SBSs (DecR, mg C kg^{-1} h^{-1}) was measured by an infrared gas analyzer at least 1–2 times per week. Total carbon losses (TotL-C, g C kg^{-1} of bark) were estimated using the accumulative curves of DecR throughout the experiment for each treatment. The decay constants (k) were calculated based on the single exponential model. The temperature sensitivity of the DecR was estimated using the temperature coefficient Q_{10}.

Mineral N and P additions decreased the C:N and increased the Lignin : Cellulose ratios during the long-term incubation of aspen bark and caused a considerable increase in the DecR, k values, TotL-C values, and consequently a decrease of the turnover time. The maximal values of TotL-C were attributed to the SBS-NP treatment at 22 °C and comprised 72% of the initial C content in bark. The turnover time of soil-bark substrates varied from 2 to 7.3 years depending on the treatment and temperature. The increase of the incubation temperature from 2 to 12 °C and from 12 to 22 °C caused a similar effect on the DecR over 12 months of the experiment, and the Q_{10} in different treatments varied negligibly: from 1.21 to 1.37. The temperature effect was most significant only during the first 1–2 months of experiment, explaining ca. 83% of the mean DecR variance whereas the 'Treatment' factor was attributed for 76–83% of the mean DecR variance in later stages (3–12 months) of decay of aspen bark. A close relationship between the Lig:Cel ratio and DecR was observed during 1–2 months of incubation. We conclude that the effect of mineral additions on the decay rate of aspen bark is more important than the effect of temperature. The coupled effect of N and P additions was more pronounced than the effect of N addition alone.

Abbreviations: C, carbon; N, nitrogen; P, phosphorous; CWD, coarse woody debris; DecR, decay rate; TotL-C, total losses of C; SBSs, soil-bark substrates; SBS, pure Bark + Soil; SBS-N, Bark + Soil + N; SBS-NP, Bark + Soil + N + P; S, pure soil; Eth-Ext, ethanol-soluble extractives; Cel, cellulose; Lig, lignin; k, decay constant; $T_{0.5}$, half-life period; $T_{0.95}$, the full turnover time

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1. Introduction

Decomposition of coarse woody debris (CWD) represents a set of several interrelated processes: physical degradation (i.e., fragmentation and weathering), leaching, biological transformation, and microbial decay (Harmon et al., 1986; Zhou et al., 2007; Russell et al., 2015). Providing ca. 76% of total carbon (C) loss, the microbial decay is considered the main process in the decomposition of CWD (Chambers et al., 2001). Hence, acquiring its quantitative characteristics is crucial for the estimation of its share in the C cycle on local and global levels (Liu et al., 2013; Russell et al., 2015).

Bark is the outer layer beyond the living cambium, which often has corky structure and consists of living tissues of phloem, phellema, pheloderma, and dead cells of rhytidome (Martin and Crist, 1970; Rosell et al., 2015). Tree bark is an important but the most poorly investigated component of CWD (Shorohova et al., 2012, 2016). Making up 25% of the stem volume and 16% of the stem dry mass in the dominant boreal tree species, tree bark forms a substantial component of woody litter in some forests (Ugolev, 2002; Lestander et al., 2012). Moreover, bark can potentially affect the rate of wood decomposition, altering the access for decomposers, microclimate and chemical conditions within decaying logs (Dossa et al., 2016; Zuo et al., 2016). Until now, our knowledge on bark decomposition has been rather scanty since tree bark and wood were often integrated together for estimating decay rates of CWD (Yatskov et al., 2003; Hagemann et al., 2010; Li et al., 2012). However, bark and wood are markedly dissimilar in chemical composition and structure (Sjöström, 1993). For instance, bark lignin differs considerably from wood lignin by its poorer solubility and higher heterogeneity (Käärik, 1974). Bark also contains higher C and nutrient concentrations than wood (Wetzel and Greenwood, 1989; Franceschi et al., 2005; Martin et al., 2015). Hence, the decay rates of bark and wood are rather different, and the character of this difference depends on tree species and environmental conditions, influencing microbial respiration rates, as well as on fragmentation induced by biotic agents (Ganjegunte et al., 2004; Shorohova and Kapitsa, 2014, 2016). Nutrient dynamics during decomposition also differ between bark and wood (Johnson et al., 2014). Bark's protective function is provided by its structure and chemical properties, especially by the high content of bark lignin and extractives, which may inhibit the growth of microorganisms. Biochemical composition of bark varies strongly depending on tree species (Harunm and Labosky, 1985). E.g. the bark of *Pinus sylvestris* and *Picea abies* contains 50–60% of carbohydrates, mainly cellulose, 30–40% of lignin and 2–3% of suberin (Olsson, 1978). Reduction of desiccation and inhibition of microorganism attacks are among the functions attributed to suberin (Kolattukudy, 1984).

Many biotic and abiotic factors are responsible for the decomposition of bark and wood under natural conditions. Climate is the key abiotic determinant of decomposition rates on a global scale, whereas biotic factors are determinants on local and regional scales (Berglund et al., 2013; Bradford et al., 2014; Fukasawa, 2015). At the same time, it is well documented that in a local forest ecosystem, the microbial decay rate of most plant materials, including CWD, generally increases with increasing temperature (T) within a certain range (Boddy, 1983; Harmon et al., 1986; Taylor and Parkinson, 1988; Winckler et al., 1996). It was also shown that in a 'warming' experiment, lignin and polyesters such as cutin and suberin responded differently to the temperature (Cornwell et al., 2009). The moisture dependence of the decay rate of CWD is more complicated than its temperature sensitivity. For instance, both high and low humidity can restrict the activity of wood inhabiting organisms (Zhou et al., 2007). Biotic factors mainly include decomposing organisms and substrate quality (Cornwell et al., 2009; Hu et al., 2017). Although the concentrations of main biophilic and mineral elements in bark and wood vary widely, the high carbon to nitrogen (C:N) and carbon to phosphorus (C:P) ratios are attributes for all tree species (Skonieczna et al., 2014). In boreal and temperate forests, N and P addition has been shown to stimulate litter decomposition in the N- and P-limited forests (Hobbie and Vitousek, 2000; Knorr et al., 2005). Since 1850, due to the dry and wet deposition of aerosols and gases containing N and P, the atmospheric deposition of N and P has notably grown, increasing an importance of quantifying their impact on forest C uptake (Wang et al., 2017). However, a fertilization effect of N and P on CWD decomposition has not been yet estimated. Until now, the experimental data on the impact of N and P additions on the bark decay rate at different temperatures is missing.

Due to a complex interrelationship between biotic and abiotic factors in field studies, a laboratory incubation approach is preferable when studying mutual impact of several factors on the decay process. In this study, we examined the effect of mineral N and P additions on the decay rate (DecR) of aspen bark at a wide range of temperatures under laboratory conditions. For our experiment, we have chosen aspen tree bark since aspen is a native species to the most of the Northern Hemisphere (Worrell, 1995a). European aspen (*Populus tremula*, L.) has high ecological value as a keystone species for biodiversity in a boreal forest: it provides a habitat and food for a wide variety of mammals, birds, insects, and fungi (Latva-Karjanmaa et al., 2007). Nutrient-rich alkaline aspen litter is an important resource for a range of soil inhabiting organisms as well. E.g., > 150 species are known to be exclusively associated with European aspen in the boreal forest in Finland (Kuoki et al., 2004). Since aspen can sprout from existing roots and its suckers grow faster than new slower growing conifers, aspen can be a dominant early successional tree species for many years. Due to the fast growth rate and ability to regenerate from sprouts, aspens have got an increased popularity in forestry, making the reforestation after harvesting much cheaper, since no planting or sowing is required (Worrell, 1995a). Aspen plays an important role in production of wood for renewable energy and for various wood industries (products): pulp and paper, lumber and matches, plywood and flake boards (Worrell, 1995b). A promising way for recycling of aspen bark remaining after wood utilization could be a composting of aspen bark with various mineral additions for horticultural applications.

Thereby, our specific objectives were to: 1) explore the DecR dynamics of aspen bark with and without N and NP additions at a wide range of temperatures (T = 2, 12 and 22 °C) throughout the 12-month long incubation experiment; 2) estimate the effect of mineral additions and T on the total losses of C-CO_2 and bark decay constants; 3) quantify the T-sensitivity of mean DecR for various time intervals using Q_{10} values; 4) track changes in the chemical composition of aspen bark for the 12-months of incubation. We tested two hypotheses: (1) the coupled effect of N and P additions on the decay rate of aspen bark will be higher than the impact of N addition alone; (2) an increase of incubation temperature from 2 to 12 °C will lead to the more pronounced stimulation of bark decomposition in comparison with the temperature increase from 12 to 22 °C. The obtained estimations of the decay rates of tree bark allow us to narrow the uncertainties in C losses due to the decomposition of CWD. Optimizing decay conditions by the use of mineral additions is needed for the recycling of bark residues in wood industry.

2. Materials and methods

2.1. Sample preparation and experimental design

Bark was removed from the middle part of aspen (*Populus tremula*) stem with the diameter at breast height of 30 cm. The tree was windblown ca. 1 month before sampling. The removed bark material was cut into small pieces (< 2 × 2 cm) using clippers and placed into 500 ml flasks. For incubation experiments, local soil (*Haplic Luvisols*; C = 13.4 ± 0.9 g C kg^{-1} soil; N = 1.01 ± 0.10 g N kg^{-1} soil; pH_{KCl} = 5.90 ± 0.01) was added to milled bark in proportion of 10:1 by volume (or ca. 2:1 by dry mass) and mixed carefully. The obtained soil-bark substrates (SBSs) were wetted by the addition of 5 ml of