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

Irina Kurganova[a,b,*], Valentin Lopes de Gerenyu[b], Natalia Galibina[a], Ekaterina Kapitsa[a,c], Ekaterina Shorohova[a,c,d]

[a] Forest Research Institute, Karelian Research Centre, Russian Academy of Sciences, 11 Pushkinskaya Str., 185910 Petrozavodsk, Karelia, Russia
[b] Institute of Physicochemical and Biological Problems in Soil Science, RAS, Institutskaya Str., 2, Pushchino, Moscow Region 142290, Russia
[c] Saint-Petersburg State Forest University, Institutsky str., 5, 194021 Saint Petersburg, Russia
[d] Natural Resources Institute Finland (Luke), Latokartanonkaari 9, FI-00790 Helsinki, Finland

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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

* Corresponding author at: Institute of Physicochemical and Biological Problems in Soil Science, RAS, Institutskaya Str., 2, Pushchino, Moscow Region 142290, Russia.
E-mail address: ikurg@mail.ru (I. Kurganova).

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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

distilled water or fertilizer solution to provide sufficient moisture levels of the SBSs which corresponded to ca. 80% of their full water capacity. The fertilizers (NH_4NO_3 and $Ca(H_2PO_4)_2{\cdot}H_2O$) were added with a proportion of 1% of dry bark mass for each element.

The following variants of substrates (treatments) were studied: (1) Bark + Soil, ***pure SBS or control***; (2) Bark + Soil + N, ***SBS-N***; and (3) Bark + Soil + N + P, ***SBS-NP***; (4) pure soil, ***S***. The flasks with substrates were placed in thermostats with various temperatures (2, 12, and 22 °C) and then incubated for 12 months. Every 2–3 weeks some amount of distilled water was added to each flask to sustain a constant level of moisture in soil-bark substrates. The experiment was performed in three replicates.

2.2. Measurements of the SBS decay rates

The decay rates of all substrates were estimated as the *C-CO_2 emission rates* and measured 2–5 times per week during the first 2 months of the incubation experiment and 1–2 times per week during the next 10 months. Between measurements, the flasks with substrates were covered with films permeable for air but preventing moisture evaporation and kept in thermostats. About 2–3 h before each DecR measurement, the flasks were hermetically sealed with rubber plugs to accumulate C-CO_2. Then, the samples of the gas phase were taken from the flasks with a syringe, and the increases of CO_2 concentrations in each flask were measured using an infra-red gas analyzer LiCor 820 (USA).

A DecR value of the SBS's (mg C kg^{-1} of substrate h^{-1}) was calculated according to the following equation (Kurganova et al., 2012):

$$DecR = dC{\cdot}12{\cdot}V_{flask}{\cdot}1000/m{\cdot}22.4{\cdot}t{\cdot}100 \quad (1)$$

where dC is the change in CO_2 concentration in the flask, volumetric %; V_{flask} is the flask volume, ml; t is the incubation time, hours; and m is an absolute dry weight of the substrate, kg. We observed that the DecR of pure soil was very low, and did not exceed 0.7–1.4% of the DecR values for the SBSs. Taking into account this negligible contribution of soil to the total CO_2 flux from the SBSs, we expressed the DecR for the SBSs based on the dry weight of bark (mg C kg^{-1} of bark h^{-1}).

The total C losses from SBSs (**TotL-C**, g C kg^{-1} of bark) throughout the whole experiment were estimated using the accumulative curves of DecR for each treatment during the 12-months of incubation.

2.3. Chemical and biochemical analyses

At the end of an incubation experiment, bark samples were carefully washed with distilled water and dried at room temperature. The C and N concentrations in the milled bark samples (5 replications) before and after incubation were estimated by an automatic CNHS-analyzer (LECO Corp., USA). The pH value was measured in water extraction (the bark:water ratio = 1:25) by potentiometric pH-sensor (Hanna, Germany). The content of ethanol-soluble extractives (Eth-Ext, including aliphatic and aromatic carbohydrates, terpenes, carbolic acids, resin and fatty acids, essential oils, fats, phytosterines), cellulose (Cel), and lignin (Lig) were measured gravimetrically in the bark samples before and after the 12-months of incubation. The contents of lignin and cellulose were estimated gravimetrically by Klasson's and Kürschner's methods (Browning, 1967; Dence, 1992) which were adapted in the Analytical laboratory of the Forest Research Institute of the Karelian Research Centre of Russian Academy of Sciences (Obolenskaya et al., 1991). Briefly, lignin was estimated in the extract residues after the removal of bituminous matters and treated with the 72% sulphuric acid; cellulose was extracted by the mixture of concentrated nitric acid and ethanol (volumetric ratio = 1:4). The biochemical analyses and pH measurements were not replicated.

Based on the comparison of the biochemical composition of aspen bark samples before and after the 12-months of incubation (Table 1), we estimated the shares of the residual amounts of basic organic substances (Eth-Ext, Cel, and Lig) of their initial content in aspen bark before the experiment. The changes in Eth-Ext, Lig, and Cel concentrations in the bark samples over the 12-months incubation experiment were estimated considering the changes in the C concentration in bark samples for the same period.

Table 1
Basic chemical properties of aspen bark before the experiment (mean values ± SE).

Parameter	
C, g kg^{-1} of bark	514 ± 12
N, g kg^{-1} of bark	4.30 ± 0.13
H, g kg^{-1} of bark	60.1 ± 0.3
C:N ratio	120 ± 4
C:H ratio	8.55 ± 0.17
pH (H_2O)	5.62 ± 0.10
Ethanol-soluble extractives (Eth-Ext), %	15.1
Cellulose (Cel), %	18.4
Lignin (Lig), %	22.4
Eth-Ext:(Cel + Lig)	1:2.7

2.4. Data processing and statistical analyses

The decay constant for aspen bark (k, $year^{-1}$) was estimated by fitting a single exponential model (Olson, 1963; Kätterer et al., 1998):

$$TotL\text{-}C = C_o{\cdot}(1 - e^{(-k{\cdot}t)}) \quad (2)$$

where TotL-C is the cumulative C-CO_2 loss as a result of microbial decay (g C/kg bark), C_o – is the initial content of total C in bark (g C kg^{-1} bark), k – is the decay constant, yr^{-1}; t is the incubation time (yrs). The half-life period required for 50% bark mass loss was estimated as $T_{0.5} = 2/k$, and the turnover time corresponding to the time interval when 95% of organic matter is lost was estimated as $T_{0.95} = 3/k$ (Grishina et al., 1990; Ul'yanova and Chuprova, 2015; Hu et al., 2017).

In this study, the temperature sensitivity of aspen bark *DecR* was expressed as a Q_{10} function, which indicates the change in the *DecR* for a 10 °C rise in temperature. The Q_{10} value was calculated from the formula (Chen et al., 2000):

$$Q_{10} = (DecR_2/DecR_1)^{[10/(T2-T1)]} \quad (3)$$

where $DecR_2$ and $DecR_1$ are decay rates of the SBSs at the temperatures T_2 and T_1, respectively.

A one-way ANOVA was used to separately estimate the effects of temperature and mineral addition treatment (SBS composition) on the DecR, TotL-C, and Q_{10} values for the aspen bark substrates. A two-way ANOVA was used to compare the differences in the abovementioned parameters among three treatments and three temperatures. The simple linear regression was used to identify the relationship between DecR and biochemical properties of aspen bark. The distribution of residuals was checked for normality and a test for homogeneity of variances was carried out. Statistical analyses were performed using the STATISTICA 6 Software. All statistical analyses were performed at the $\alpha = 0.05$ level of significance.

3. Results

3.1. Dynamics of DecR over the 12 months of incubation

The dynamics of DecR throughout 12 months of the experiment depended on both treatment (mineral additions) and incubation temperature (Fig. 1). The addition of mineral N resulted in the most notable increase of DecR values in comparison with pure SBS during the 1-st month of incubation. This effect was more pronounced with the simultaneous addition of mineral N and P; it was observed over the first 2–5 months and depended on the temperature. The time period of the highest response of the DecR to mineral additions at 22 °C was much

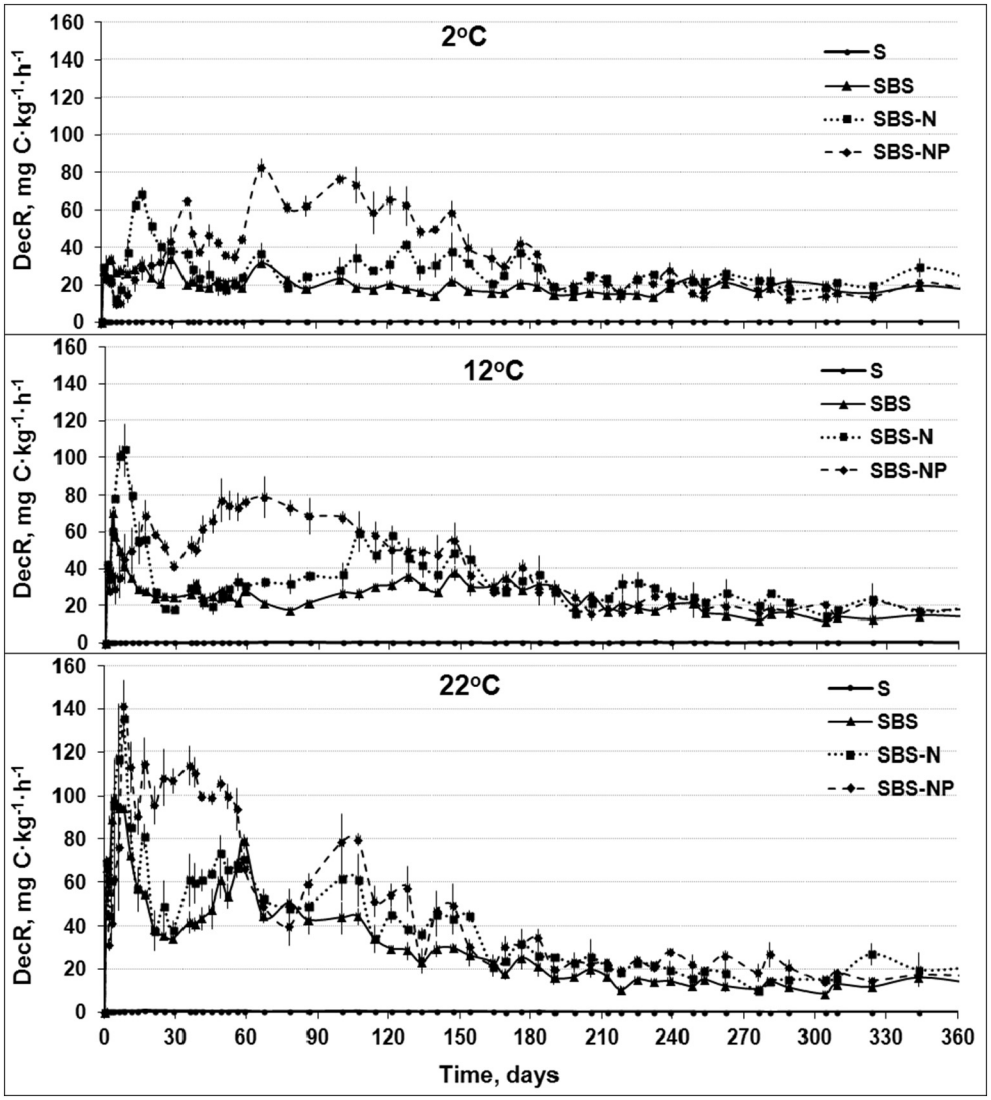

Fig. 1. Dynamics of decay rate (DecR) of various soil-bark substrates (SBSs) throughout 360 days (12 months) of incubation at different temperatures: S – pure soil; SBS – Bark + Soil; SBS-N – Bark + Soil + N; and SBS-NP – Bark + Soil + N + P.

shorter (ca. 2 months) than at 12 and 2 °C (ca. 4–5 months). The most noticeable increase in the DecR (up to 119–159 mg C kg^{-1} of bark h^{-1}) at 22 °C was observed for the SBS-NP and SBS-N treatments during the first 2 weeks. At 12 °C, the highest DecR values (89–133 mg C kg^{-1} of bark h^{-1}) were observed during the 2–4 months of incubation (Fig. 1). The dynamics of DecR at 2 °C were rather even without distinct maxima for control and the SBS-N variant, whereas the SBS-NP treatment showed rather high DecR (40–80 mg C kg^{-1} of bark h^{-1}) over the first 6 months of incubation. After 5–7 months of the experiment, differences in the DecR values caused by mineral additions became negligible at all temperatures (Fig. 1). At similar temperature, the DecR of pure soil was 70–150 times lower than the DecR of soil-bark substrates and decreased gradually during the incubation experiment. Therefore, we did not include this variant in future calculations.

3.2. *Effects of treatment and temperature on the DecR in different stages of the experiment*

Based on the temporal dynamics of DecR of soil-bark substrates (Fig. 1), we divided the 12-months period of experiment into 4 stages: 1–2, 3–4, 5–6, and 7–12 months. Mean DecR values for each treatment were estimated for each stage and for the whole incubation period (Fig. 2). At all temperatures studied, mineral additions significantly increased the DecR in all stages. As a rule, the increase in the DecR due to mineral additions was the most pronounced during the first 4–6 months of incubation and the least noticeable in the final stage of the experiment (7–12 months).

Temperature effect on the DecR diverged between the different treatments and stages of the experiment (Fig. 3). For example, the response of the DecR over the first 1–2 months of incubation to the increase of temperature was higher in the 12–22 °C temperature range (Q_{10} = 1.57–1.83) as compared to that at 2–12 °C (Q_{10} = 1.32–1.44) only for the SBS and SBS-N treatments. The inverse temperature effect on the DecR in the same treatments was observed over the 5–12 months of experiments: the Q_{10} values were higher for the 2–12 °C temperature range (Q_{10} = 0.99–1.78) in comparison with those at 12–22 °C temperature interval (Q_{10} = 0.79–0.91). In the SBS-NP treatment, the Q_{10} values were approximately the same for all stages of the experiment (Fig. 3). In general, 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 'Treatment' factor was attributed for 14% of the total variance of DecR during the first 1–2 months of experiment and then it was responsible for 76–83% of the total DecR variance (Table 2). The temperature effect was the most significant ($P < 0.0001$) only during the first 1–2 months, explaining about 83% of the mean DecR variance and

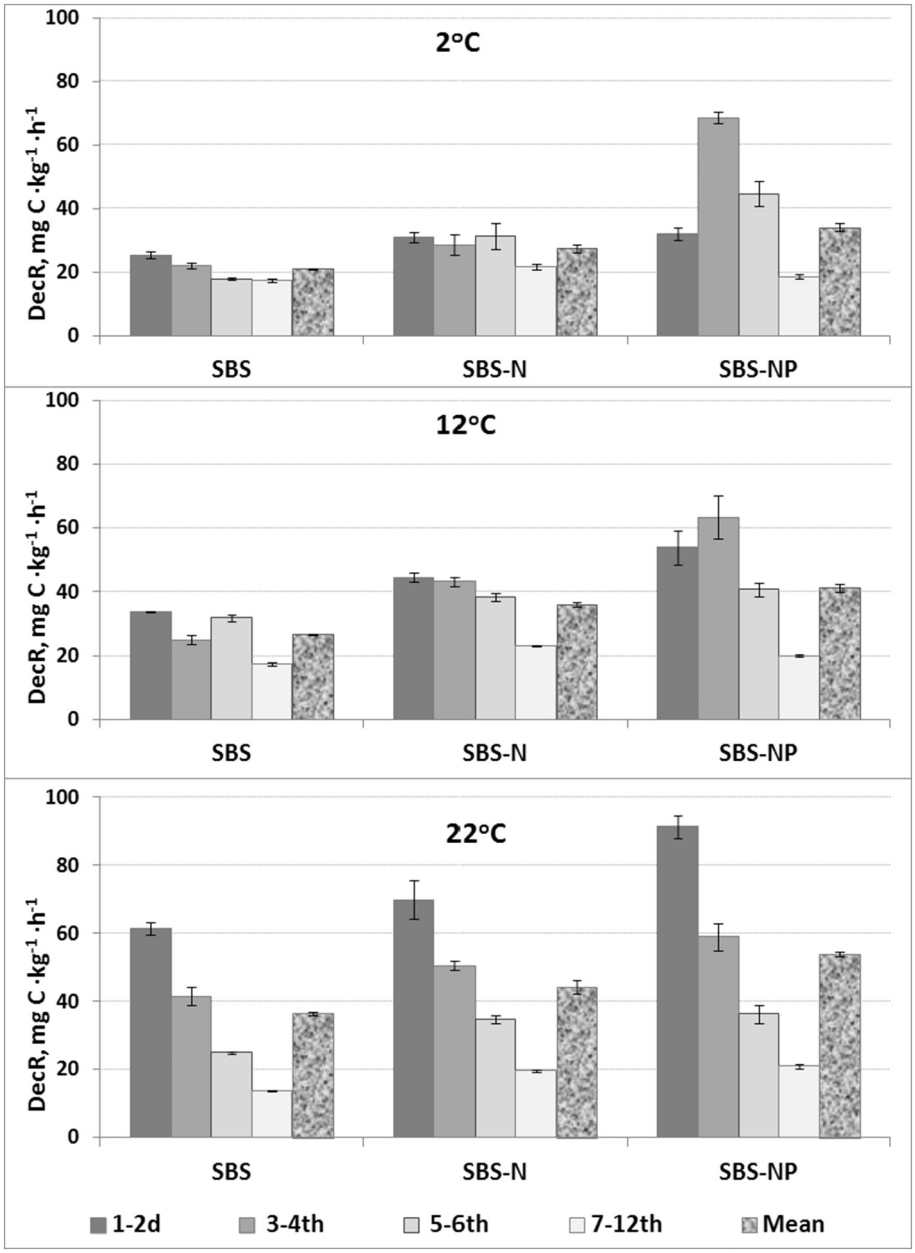

Fig. 2. Mean DecR values (bars are SEs) for various stages (months) of the experiment at different temperatures and treatments: SBS – Bark + Soil; SBS-N – Bark + Soil + N; and SBS-NP – Bark + Soil + N + P. Data for pure soil (S) was not shown because the DecR of soils were very small in comparison to the DecR of SBSs and varied negligibly during different stages of incubation (see Fig. 1).

then it was responsible only for 8–11% of the total DecR variance (Table 2). The most significant interaction of factors was detected during the 5–12 months of experiment explaining 10% of the DecR variance.

3.3. Total losses of C-CO_2 from the SBSs over the 12 months of incubation

Total C losses as CO_2 (TotL-C) from the SBSs throughout the 12 months of experiment varied from 173 to 373 g C kg^{-1} of bark depending on the temperature and treatment (Table 3). Those values corresponded to the mineralization of 34–73% from the initial (before incubation) C content in bark (514 g C kg^{-1}). The maximal values of TotL-C were attributed to the SBS-NP treatment at 22 °C and comprised 73% of the initial C content in bark. A single-factor ANOVA has shown a significant effect of temperature on the TotL-C in all treatments. Depending on treatment, TotL-C varied from 173 to 301 g C kg^{-1} of bark at 2 °C to 244–373 g C kg^{-1} of bark at 22 °C. The addition of a mineral fertilizer significantly (by 28–39%) increased TotL-C at all studied temperatures. The treatment (mineral addition) was responsible for 58% of variance in the total C-CO_2 losses from SBSs whereas the temperature was responsible for 41% of variance in the total TotL-C (Table 5).

3.4. Decay constants and turnover time of aspen bark

Decay constant of the soil-bark substrates increased with increasing temperature in the order SBS < SBS-N < SBS-NP (Table 4). Both temperature and composition of the SBSs had an important influence on k-values. Mineral additions and temperature were approximately equally responsible for the variance of the decay constants of studied substrates: 53 and 46%, respectively. The interaction between these factors did not significantly affect k variance (Table 5).

The $T_{0.5}$ (half-life time) for soil-bark substrates varied from 4.9 to 1.3 years depending on the temperature and treatments demonstrating patterns identical to those for decay constant, namely: the shortest half-life time was detected at 22 °C for the SBS-NP (Table 4), and the highest $T_{0.5}$ was attributed to pure SBS at 2 °C. The turnover time of soil-bark substrates varied from 2 to 7.3 years depending on treatment and

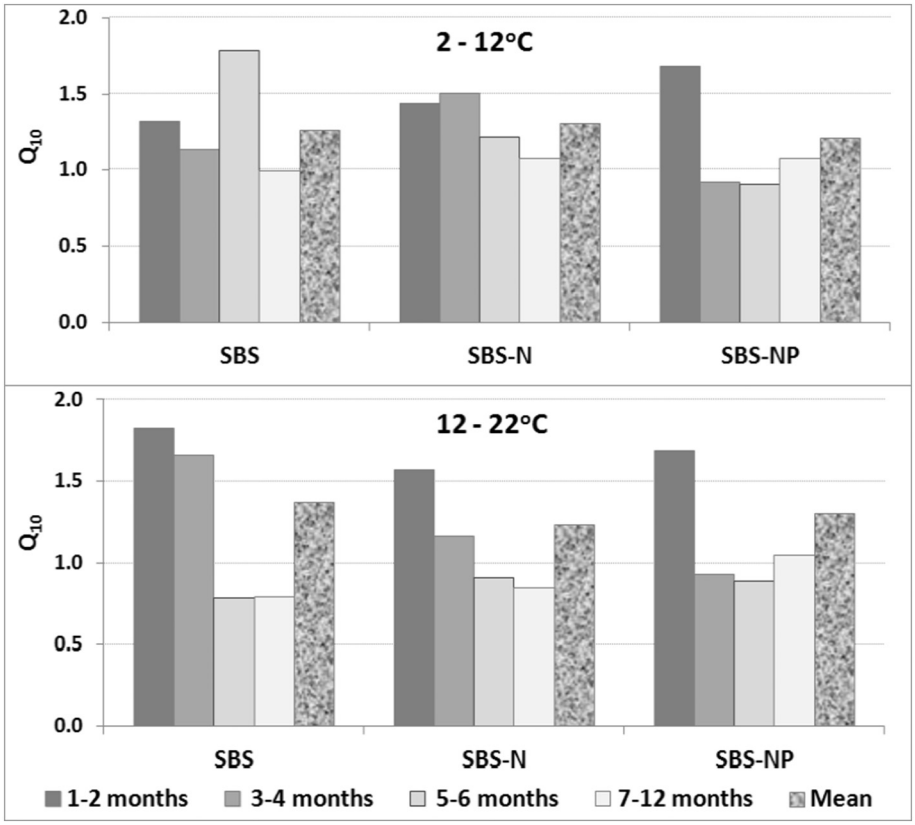

Fig. 3. Temperature coefficient Q_{10} for the decay rate (DecR) during various stages (months) of experiment at different temperatures and treatments: SBS – Bark + Soil; SBS-N – Bark + Soil + N; and SBS-NP – Bark + Soil + N + P. Q_{10} values for pure soil (S) was not shown because the changes in DecR for pure soil during incubation were negligible (see Fig. 1).

temperature.

3.5. Change in the pH and biochemical composition of the SBSs after 12 months of incubation

Initially, aspen bark was slightly acidic (pH = 5.62). Processing of pure bark with soil suspension as well as the addition of soil for the preparation of soil-bark substrates led to the alkalinization of the water SBS solution. Thus, the SBSs after the 12 months of incubation became slightly alkaline with pH varying from 7.5 to 8.4 (Fig. 4A). This tendency was more evident after an addition of mineral nitrogen to the SBS when the pH increased by 0.5 at 2 and 12 °C. After incubation of the SBSs without mineral additions at 22 °C, the pH reached 0.7–0.8.

After the 12 months of incubation, the C:N ratio in aspen bark decreased dramatically: from 120 to 57–75 and 17–30 in the SBSs without and with mineral additions, respectively. The coupled effect of N and P addition on the C:N ratio was higher than the N effect alone. We did not observe any impact of the temperature increase on the C:N ratio in the SBS and SBS-N between 2 and 12 °C and in the SBS-NP between 12 and 22 °C (Fig. 4B). The Lig:N ratio was constant before treatment and in the SBS without mineral additions at all temperatures studied. Due to N additions, the Lig:N ratio decreased twice, whereas the coupled addition of mineral N and P resulted in more than a 3-fold decline in the Lig:N ratio (Fig. 4C). The temperature effect on the Lig:N ratio was negligible. We revealed a visible increase in the Lig:Cel ratio in the SBSs after the 12 months of incubation. This effect was the most remarkable for all treatments at 22 °C and only for SBS-NP at 12 °C (Fig. 4D). A close relationship between the Lig:Cel ratio and DecR was observed during 1–2 months of incubation (R^2 = 0.86; P < 0.001) as well as between the Lig:Cel ratio and k (R^2 = 0.71; P = 0.004).

Relative residual amount of basic organic substances within the soil-bark substrates after the 12 months of incubation increased in the following order (Fig. 5A - C): Eth-Ext (12–29%) < Cel (24–70%) < Lig

Table 3
Total losses of C-CO_2 (TotL-C) from the soil-bark substrates at different temperatures throughout the 12 months of experiment (mean (SE)).

Treatment	g C kg^{-1} bark			% of initial C content in SBS		
	2 °C	12 °C	22 °C	2 °C	12 °C	22 °C
SBS	173 (3)	199 (1)	244 (2)	33.7 (0.6)	45.2 (1.9)	58.4 (1.6)
SBS-N	232 (10)	273 (3)	313 (6)	38.7(0.2)	53.1 (0.4)	63.6 (0.2)
SBS-NP	301 (8)	327 (2)	373 (4)	47.4 (0.4)	60.8 (1.2)	72.5 (0.8)

SBS – Bark + Soil; SBS-N – Bark + Soil + N; and SBS-NP – Bark + Soil + N + P.

Table 2
The results of two-way ANOVA with Eta squared (η^2) estimates for DecR values over different stages of experiment.

Factor	1–2 months			3–4 months			5–6 months			7–12 months		
	F	P	η^2, %	F	P	η^2, %	F	P	η^2, %	F	P	η^2, %
Treatment (TR)	29	< 0.0001	14	93	< 0.0001	83	34	< 0.0001	76	74	< 0.0001	77
Temperature (TE)	167	< 0.0001	83	9	0.0023	8	5	0.0190	11	11	0.0008	11
TR × TE	4	0.0112	2	9	0.0004	8	5	0.0105	10	10	0.0002	10
Error			0			1			2			1

η^2 are interpreted as the proportions of variance (%) in dependent variables attributable to effect of each factor.

Table 4
Decay constant (k), half-life period $T_{0.5}$, and full turnover time $T_{0.95}$ for SBS' at different temperatures throughout 12 months of experiment (mean (SE)). All the differences are significant at $P < 0.0001$.

Treatment	k, yr^{-1}			$T_{0.5}$, yr			$T_{0.95}$, yr		
	2 °C	12 °C	22 °C	2 °C	12 °C	22 °C	2 °C	12 °C	22 °C
SBS	0.41 (0.00)	0.53 (0.01)	0.80 (0.01)	4.85 (0.02)	3.77 (0.04)	2.52 (0.03)	7.28 (0.04)	5.66 (0.05)	3.77 (0.04)
SBS-N	0.59 (0.04)	0.77 (0.01)	1.06 (0.05)	3.42 (0.25)	2.58 (0.06)	1.89 (0.10)	5.14 (0.38)	3.88 (0.08)	2.84 (0.14)
SBS-NP	0.96 (0.04)	1.12 (0.01)	1.51 (0.01)	2.09 (0.10)	1.78 (0.03)	1.33 (0.01)	3.14 (0.15)	2.68 (0.05)	1.99 (0.02)

SBS – Bark + Soil; SBS-N – Bark + Soil + N; and SBS-NP – Bark + Soil + N + P.

Table 5
The results of two-way ANOVA with Eta squared (η^2) estimates for TotL-C and k values.

Factor	TotL-C			k		
	F	P	η^2, %	F	P	η^2, %
Treatment (TR)	194	< 0.0001	58	183	< 0.0001	53
Temperature (TE)	138	< 0.0001	41	157	< 0.0001	46
TR × TE	2.0	0.102	1	1.7	0.166	1
Error			0			0

η^2 are interpreted as the proportions of variance (%) in dependent variables attributable to effect of each factor.

(44–85%). At the end of the experiment at all temperatures studied, minimal amounts were attributed to the SBS-NP treatment (Eth-Ext, 12–15%; Cel, 24–35%; Lig 44–57%), whereas pure SBS contained the highest amounts (Eth-Ext, 21–29%; Cel, 53–70%; Lig 76–85%). The most pronounced decrease in the Eth-Ext and Cel amounts in all treatments was observed at 22 °C (Fig. 5A, B). The residual amounts of lignin were approximately the same at 2 and 22 °C and lower than those at 12 °C (Fig. 5C).

Within the 12 months of experiment, a significant change in the ratio between Cel + Lig and Eth-Ext residual amounts was also noticed. Thus, the initial content of Cel + Lig and Eth-Ext in aspen bark amounted to 71 and 29%, respectively. As a result of xylolise, the relative share of Eth-Ext within aspen bark decreased to 13–19%, demonstrating a clear tendency to decrease with the temperature increase: 15.3–19.0% – at 2 °C, 12.9–15.4 – at 12 °C and 13.0–13.4% – at 22 °C.

4. Discussion

4.1. Effects of N and P additions

Similar to the majority of plant materials, carbon is the prevailing element in the bark of all tree species (Deineko and Korbukova, 1995; Geles, 2001; Skonieczna et al., 2014). In aspen bark, the C concentration varies between 46 and 52%, whereas the nitrogen and phosphorus contents are only 0.47–0.60% and 0.015–0.07%, respectively (Faustova, 2005). Such high ratios (C:N = 77–110 and C:P = 600–3500) limit the intensity of biogenic decay of plant residues in terms of an unbalanced (for destructors) proportion of nutrients (Vedrova, 1997; Semenov and Khodzhaeva, 2006; Palviainenm et al., 2008). In our study, an addition of mineral N and P significantly increased the DecR and k of the SBSs in all stages of the experiment at all temperatures studied. The most pronounced impact of nutrient additions was observed in early stages (first 2–4 months) at 22 °C. Similar pattern – an evident increase of DecR and k due to the addition of mineral N and P to the compositions based on tree bark – was also demonstrated in the one-year laboratory experiments for aspen, pine, spruce, and larch bark (Ul'yanova et al., 2009; Ul'yanova and Chuprova, 2015). A general explanation for the mediation of decay by mineral N and P could be that these substrates are rich in C, however the N and P concentrations are less than optimal for building microbial biomass

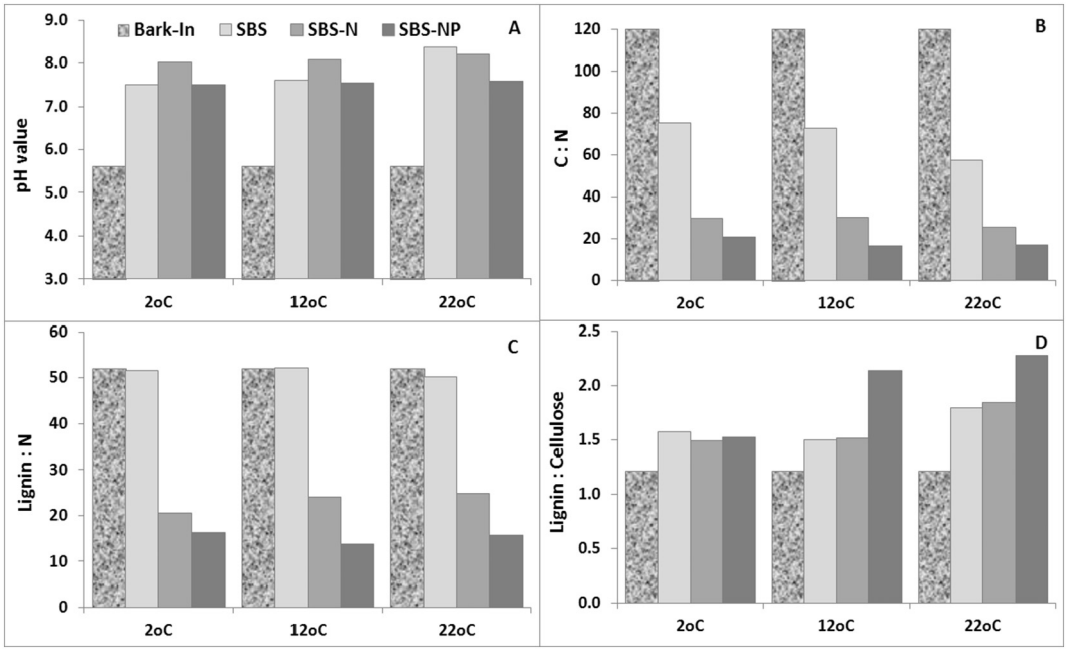

Fig. 4. Effects of mineral N and P additions on the change in pH values (A), C:N (B), Lignin:N (C), and Lignin:Cellulose (D) ratios in comparison with their initial values in aspen bark (Bark-In) after 12 months of the experiment at various temperatures. All biochemical analyses and pH measurements were not replicated.

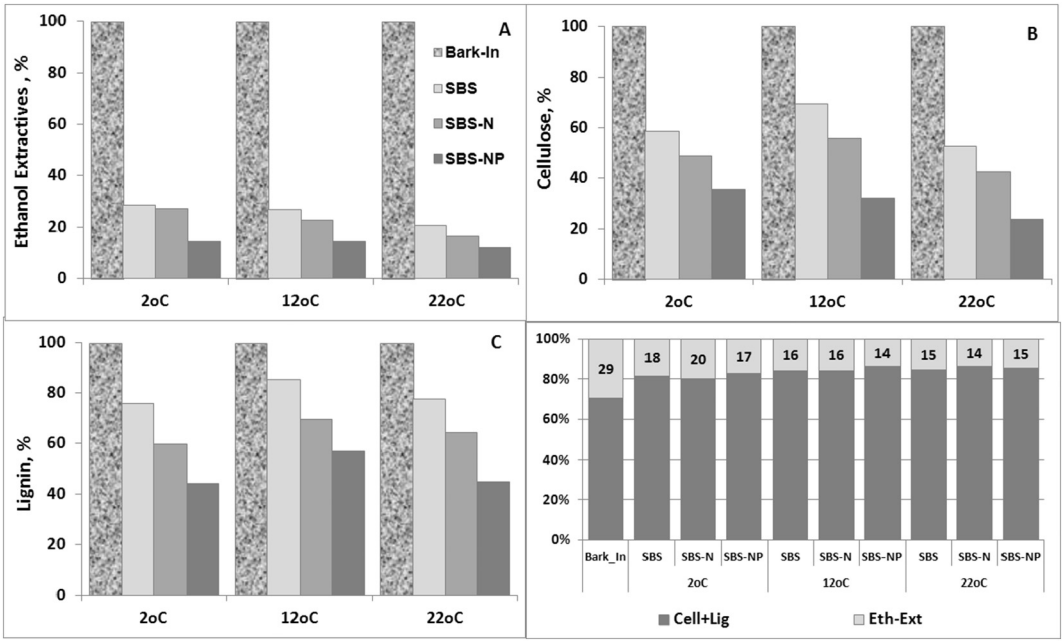

Fig. 5. Effects of mineral N and P additions on the change in the residual amounts of ethanol extractives (A), cellulose (B), lignin (C), and their ratio in comparison with their initial values in aspen bark (Bark-In) after 12 months of the experiment at various temperatures.

(Allison, 1965; Alexander, 1977; Qualls and Richardson, 2000). It was shown that after 5 months of pine bark composting with mineral N and P additions, the amount of fungal biomass increased by 5 times in comparison with pure pine bark (Ul'yanova and Chuprova, 2015). It is suggested that the decay of bark and wood tissues is directly related to the activity of cellulose and lignin-degrading enzymes through resource allocation and typically restricted by N and/or P availability (Sinsabaugh et al., 1992, 1993). At the low availability of N and P, microorganisms require more energy in a form of ectoenzyme production to obtain the needed amounts of N and P from organic sources (Sinsabaugh et al., 1992, 1993). It was revealed that within angiosperms, decay rates of wood materials positively correlated with such characteristics of wood as P and N concentrations, and C: N ratio (Weedon et al., 2009).

According to our results, the coupled positive effect of N and P addition on aspen bark decay (DecR and k) was higher than the effect of N addition alone at all temperatures studied particularly during the first 2–4 months of experiment, that almost completely supported our first hypothesis. Due to physiological difference between the microbial N and P acquisition activities, there are different patterns of gross nutrient mineralization and immobilization, with larger gross fluxes associated with phosphorous assimilation (Plante, 2005; Stefano et al., 2010). The interactions between N and P for biochemical and microbial processes are complicated, particularly for N, which is associated with nucleic acids, polysaccharides, proteins, and humic complexes (Sinsabaugh et al., 1993). An increased P availability due to P addition would mitigate an inhibitive effect of N addition during decomposition observed in some studies (Fog, 1988 c.f. Sinsabaugh et al., 1993). Although the P mitigation effect was revealed for litter decomposition in a strongly P-limited old-growth tropical forests (Chen et al., 2013), it can hold truth also for our soil-bark substrates with a very high C:P ratio.

The changes in the biochemical composition of aspen bark after 12 months of experiment observed in our study supports the first hypothesis that the coupled effect of N and P addition was more pronounced than the impact of N addition alone. Based on our results, N and P application caused more notable decreases in the residual amounts of Eth-Ext, Cel, and Lig at all temperatures studied as compared to N application only (Fig. 5). In the SBS-NP treatment, aspen bark was also characterized by lower C:N and Lig:N ratios at all temperatures studied and higher Lig:Cell ratio at 12 and 22 °C in comparison with the SBS-N treatment (Fig. 5). Therefore, the coupled effect of N and P additions resulted in the deep biochemical alterations of aspen bark composition.

In our laboratory study, we estimated decay coefficients (k) based on a cumulative curve of C-CO_2 losses during the 12 months of incubation and using a single exponential decay model. Estimating k-values for bark and wood based on the mass loss in a chronosequence of CWD or using surface litterbags approaches is more common (Zhou et al., 2007; Shorohova and Kapitsa, 2015; Dossa et al., 2016). To use correctly a chronosequence method it very important to identify accurately the age of CWD and find sites and substrates with comparable conditions (Harmon et al., 1986). The log bark decay rates estimated by a chronosequence method varied from 0.2 to 0.4 yr^{-1} for the bark of various tree species (Zhang et al., 2008) and comprised 0.074 yr^{-1} for aspen bark in an old-growth middle boreal forests (Shorohova et al., 2016). The k-values for pure aspen bark in our laboratory study at constant and sufficient moisture level were much higher (0.41–0.80 yr^{-1} depending on incubation temperature) than the reported k values estimated in the natural environment where the temperature and the water content of bark material vary significantly throughout the year. We suggest however that our approach is preferable for both studying the effects of various abiotic and biotic factors on the decay constant and parametrization of CWD-decay models due to its high accuracy and repeatability.

According to our results at all studied temperatures, mineral N increased the k-values by 1.5 times, whereas the coupled addition of mineral N and P resulted in the 2-fold increase of k (Table 4). Similar to the changes in k, half and full turnover times ($T_{0.5}$ and $T_{0.95}$) of aspen bark depended strongly on treatments and temperature. The highest rate of turnover (2 yrs) was attributed to the SBS-NP at 22 °C. In the samples with no mineral additions incubated at 2 °C, which could be the closest to natural conditions in taiga regions, full turnover time of aspen bark will be much longer (> 7 yrs). C:N ratio and $T_{0.95}$ (R^2 = 0.71; P = 0.004) were closely related, which demonstrates that N availability is the key factor for bark decay process stimulation. Similar relationships were revealed in the 12-month laboratory experiments on the composting of compositions with aspen, pine, spruce, and larch barks (Ul'yanova and Chuprova, 2015).

Therefore, substrate quality was an important factor regulating the decay process of aspen bark. Mineral N and P affected the C:N and Lig:Cel ratios during the long-term incubation of aspen bark and caused a considerable increase in the DecR, k and total carbon loss, thereby decreasing the turnover time. Due to the shift in C:N and C:P ratios towards more favorable conditions for microbial community, the coupled effect of N and P additions was higher than the impact of N addition alone.

4.2. Temperature effect

In boreal and temperate regions, the temperature is the key abiotic driver of the decay process of all components of CWD including tree bark (Rayner and Boddy, 1988; Olajuyigbe et al., 2012; Kahl et al., 2017). When there is a sufficient moisture supply, the rise of surrounding temperature results in a significant increase in the CWD respiration rate (Jomura et al., 2007, 2008; Wu et al., 2010; Forrester et al., 2012; Ohtsuka et al., 2014; Yoon et al., 2014). However, in our laboratory experiment at the constant sufficient moisture of the SBSs, a gradual rise of temperature in the interval 2 - 12 - 22 °C was responsible for the increase of DecR values only over the first 1–2 months of incubation explaining 83% in DecR variability (Table 2). Throughout the 3rd to 12th months of experiment, the temperature was responsible for only 8–11% in the DecR variance, demonstrating that the substrate quality (N and P availability) was the main determinant of the decay rate in later stages of the experiment. A possible explanation is that during the first period of incubation, aspen bark contained a sufficient amount of easily decomposable substrates to provide high decay rates of aspen bark without N and P application at all temperatures studied. Later, when the cellulose and lignin are the main substances of bark composition, the substrate quality (N and P availability) become the key driver for the decay of aspen bark. The same mechanisms govern litter decomposition in northern forests. In the early phase of forest litter decay, the concentrations of water-soluble substances decrease quickly (in a few months) before reaching relatively similar and stable levels (Berg et al., 1987). Moreover, free unshielded holocellulose is degraded in this phase, whereas the recalcitrant lignin either does not decompose yet or decomposes only at a low rate. In this early phase, the decay rate of forest litter may be related to the total concentrations of major nutrients, such as N, P and S, which often limit the decomposition rates (Berg, 2000). Apparently, during the first 2 months of aspen bark decay, the amount of nutrients in phloem tissue, which decomposes firstly, is sufficient for an active decay process.

Owing to their ability to decompose lignin and cellulose, fungi are the dominant decomposing agents of woody material, including bark (Boddy and Watkinson, 1995; Boddy, 2000). Many fungal species are mesophilous and the optimal temperature range for their growth is between 20 and 40 °C, where decomposition rates may increase by 2–3 times for every 10 °C increase (Käärik, 1974; Zhou et al., 2007). In our study, the Q_{10} values of average DecR were almost equal, varying between 1.21 and 1.37 for both temperature intervals (2–12 and 12–22 °C). Moreover, throughout the early stage of experiment (first 1–2 months), the Q_{10} values of DecR (SBS and SBS-N treatments) were higher for samples incubated at 12–22 °C than those at 2–12 °C (Fig. 3). At later stages (5–12 months of incubation), the increase of temperature from 12 to 22 °C mostly resulted in a negligible decline of the DecR values in all treatments. On the contrary, exactly for this period, the temperature rise from 2 to 12 °C mostly caused stimulation of the decay process only for the SBS and SBS-N treatments Therefore, the acquired results only partially supported our second hypothesis that the temperature increase from 2 to 12 °C leads to the more activated decay of bark in comparison with the temperature increase from 12 to 22 °C.

Recently, it was shown that temperature influences the biogenic decomposition of plant residues by coupling of direct and indirect effects (Rubenstein et al., 2017). Direct effect causes changes in the rates of enzyme-catalyzed microbial processes, whereas an indirect effect appears as a shift in the structure of microbial communities (Allison et al., 2010; Bradford, 2013). Moreover, decay activity varies considerably among fungal species, which implies that community composition is important in governing decay rates of CWD (Gessner et al., 2010; Crowther et al., 2011; Rubenstein et al., 2017). Therefore, the process of biochemical transformation of aspen bark in the SBS is very complex and reflects an interrelated effect of biotic and abiotic factors as well as direct and indirect temperature effects.

5. Conclusions

Substrate quality and temperature were important direct regulators of aspen bark decay. Mineral N and P additions affected both the dynamics of decay rate and total C-losses over the 12 months of experiment. The temperature predominantly influenced the decomposition rate of aspen bark only over the first 1–2 months of incubation, when the total amount of nutrients in phloem tissue, which decomposed firstly, did not limit the decay process. In the later phases of the SBSs decay, DecR values of aspen bark mainly depended on the total concentrations of biogenic elements N and P, which are often limiting for the decomposition of the recalcitrant components of bark – cellulose and lignin. Therefore, the coupled effect of temperature and mineral additions on the decay processes of aspen bark was non-linear and depended on the phase of decay. Modelling decay of bark and woody materials is rather complicated, since it is very difficult to decouple the effects of biotic and abiotic factors as well as direct and indirect temperature effects. Due to high accuracy and repeatability, long-term laboratory studies are preferable for both studying the effects of various abiotic and biotic factors on the decay processes and developing CWD-decay models.

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References

Alexander, M.L., 1977. Introduction to Soil Microbiology. John Wiley that and Sons, New York.
Allison, 1965. Decomposition wood and bark sawdusts in soil, nitrogen requirements, and effect on plants. In: Technical Bulletin No. 1332. Agricultural Research Service. United States Department of Agriculture.
Allison, S.D., Wallenstein, M.D., Bradford, M.A., 2010. Soil-carbon response to warming dependent on microbial physiology. Nat. Geosci. 3, 336–340.
Berg, B., 2000. Litter decomposition and organic matter turnover in northern forest soils. For. Ecol. Manag. 133, 13–22.
Berg, B., Staaf, H., Wessen, B., 1987. Decomposition and nutrient release in needle litter from nitrogen-fertilized Scots pine (*Pinus silvestris*) stands. Scand. J. For. Res. 2, 399–415.
Berglund, S.L., Ågren, G.I., Ekblad, A., 2013. Carbon and nitrogen transfer in leaf litter mixtures. Soil Biol. Biochem. 57, 341–348.
Boddy, L., 1983. Carbon dioxide release from decomposing wood: effect of water content and temperature. Soil Biol. Biochem. 15, 501–510.
Boddy, L., 2000. Interspecific combative interactions between wood-decaying basidiomycetes. FEMS. Microb. Ecol. 31, 185–194.
Boddy, L., Watkinson, S.C., 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Can. J. Bot. 73, 1377–1383.
Bradford, M.A., 2013. Thermal adaptation of decomposer communities in warming soils. Front. Microbiol. 4, 33. http://dx.doi.org/10.3389/fmicb.2013.00333.
Bradford, M.A., Warren, R.J., Baldrian, P., Crowther, T.W., Maynard, D.S., Oldfield, E.E.,

Wieder, W.R., Wood, S.A., King, J.R., 2014. Climate fails to predict wood decomposition at regional scales. Nat. Clim. Chang. 4, 625–630.
Browning, B.L., 1967. Methods of Wood Chemistry. vol. 2 Intersci. Publ, New York, London.
Chambers, J.Q., Schimel, J.P., Nobre, A.D., 2001. Respiration from coarse wood litter in central Amazon forests. Biogeochemistry 52, 115–131.
Chen, H., Harmon, M.E., Griffiths, R.P., Hicks, W., 2000. Effects of temperature and moisture on carbon respired from decomposing woody roots. For. Ecol. Manag. 138, 51–64.
Chen, H., Dong, S., Liu, L., Ma, C., Zhang, T., Zhu, X., Mo, J., 2013. Effects of experimental nitrogen and phosphorus addition on litter decomposition in an old-growth tropical forest. PLoS One 8 (12), 84101. http://dx.doi.org/10.1371/journal.pone.0084101.
Cornwell, W.K., Cornelissen, J.H.C., Allison, S.D., Bauhus, J., Eggleton, P., Preston, C.M., Scarff, F., Weedon, J.T., Wirth, C., Zanne, A.E., 2009. Plant traits and wood fates across the globe: rotted, burned, or consumed? Glob. Chang. Biol. 15, 2431–2449.
Crowther, T.W., Boddy, L., Jones, T.H., 2011. Outcomes of fungal interactions are determined by soil invertebrate grazers. Ecol. Lett. 14, 1134–1142.
Deineko, I.P., Korbukova, I.V., 1995. The group composition of ether soluble substances of the pine bark constituent part. In: 2nd International Symposium on Chemistry and Utilization of Tree Extractives. Abstracts of Papers. China, Fuzhou, pp. 197–198.
Dence, C.W., 1992. The determination of lignin. In: Lin, S.Y., Dence, C.W. (Eds.), Methods of Lignin Chemistry. Springer-Verlag, Berlin, pp. 33–61.
Dossa, G.O., Paudel, E., Cao, K., Schaefer, D., Harrison, R.D., 2016. Factors controlling bark decomposition and its role in wood decomposition in five tropical tree species. Sci. Rep. 6, 34153. http://dx.doi.org/10.1038/srep34153 1.
Faustova, N.M., 2005. Chemical composition of bark and wood of aspen *Populus tremula* L. In: Full PhD Thesis on Chemical Sciences. Sankt-Peterburg (in Russian).
Fog, K., 1988. The effect of added nitrogen on the rate of decomposition of organic matter. Biol. Rev. 63, 433–462.
Forrester, J.A., Mladenoff, D.J., Gower, S.T., Stoffel, J.L., 2012. Interactions of temperature and moisture with respiration from coarse woody debris in experimental forest canopy gaps. Forest Ecol. Manag. 265, 124–132.
Franceschi, V.R., Krokene, P., Christiansen, E., Krekling, T., 2005. Anatomical and chemical defenses of conifer bark against bark beetles and other pests. New Phytol. 167, 353–376.
Fukasawa, Y., 2015. The geographical gradient of pine log decomposition in Japan. Forest Ecol. Manag. 349, 29–35.
Ganjegunte, G.K., Condron, L.M., Clinton, P.W., Davis, M.R., Mahieu, N., 2004. Decomposition and nutrient release from radiata pine (*Pinus radiata*) coarse woody debris. For. Ecol. Manag. 187, 197–211.
Geles, I.S., 2001. Wood Biomass and Basis of Ecologically Acceptable Technologies for Its Chemico-mechanical Recycling. Karelian Sci. Centre of RAS, Petrozavodsk (in Russian).
Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hattenschwiler, S., 2010. Diversity meets decomposition. Trends Ecol. Evol. 25, 372–380.
Grishina, L.A., Koptsik, G.N., Makarov, M.I., 1990. Transformation за Organic Matter of Soils. Tutorial. MSU, Moscow.
Hagemann, U., Moroni, M.T., Gleissner, J., Makeschin, F., 2010. Disturbance history influences downed woody debris and soil respiration. For. Ecol. Manag. 260, 1762–1772.
Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res. 15, 133–302.
Harunm, J., Labosky, P., 1985. Chemical constitutes of five northeastern barks. Wood Fiber Sci. 17 (2), 274–280.
Hobbie, S.E., Vitousek, P.M., 2000. Nutrient limitation of decomposition in Hawaiian forests. Ecology 81, 1867–1877.
Hu, Z., Xu, C., McDowell, N.G., Johnson, D.J., Wang, M., Luo, Y., Zhou, X., Huang, Z., 2017. Linking microbial community composition to C loss rates during wood decomposition. Soil Biol. Biochem. 104, 108–116.
Johnson, C.E., Siccama, T.G., Denny, E.G., Koppers, M.M., Vogt, D.J., 2014. In situ decomposition of northern hardwood tree boles: decay rates and nutrient dynamics in wood and bark. Can. J. For. Res. 44, 1515–1524.
Jomura, M., Kominami, Y., Tamai, K., Miyama, T., Goto, Y., Dannoura, M., Kanazawa, Y., 2007. The carbon budget of coarse woody debris in a temperate broad-leaved secondary forest in Japan. Tellus. B. 59, 211–222.
Jomura, M., Kominami, Y., Dannoura, M., Kanazawa, Y., 2008. Spatial variation in respiration from coarse woody debris in a temperate secondary broad-leaved forest in Japan. Forest Ecol Manag. 255, 149–155.
Käärik, A.A., 1974. Decomposition of wood. In: Dickinson, C.H., Pugh, G.J.F. (Eds.), Biology of Plant Litter Decomposition. England. Academic Press, London, pp. 129–174.
Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., Buscot, F., Floren, A., Heibl, C., Hessenmöller, D., Hofrichter, M., Hoppe, B., Kellner, H., Krüger, D., Linsenmair, K.E., Matzner, E., Otto, P., Purahong, W., Seilwinder, C., Schulze, E.-D., Wende, B., Weisser, W.W., Gossner, M.M., 2017. Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. Forest Ecol. Manag. 391, 86–95.
Kätterer, T., Reichstein, M., Andren, O., Lomander, A., 1998. Temperature dependence of organic matter decomposition: a critical review using literature data analyzed with different model. Biol. Fertil. Soils 27, 258–262.
Knorr, M., Frey, S.D., Curtis, P.S., 2005. Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86, 3252–3257.
Kolattukudy, P.E., 1984. Biochemistry and function of cutin and suberin. Can. J. Bot. 62, 2918–2933.
Kuoki, J., Arnold, K., Martikainen, P., 2004. Long-term persistence of aspen – a key host for many threatened species – is endangered in old-growth conservation areas in Finland. J. Nat. Conserv. 12, 41–52.
Kurganova, I.N., Lopes de Gerenyu, V.O., Gallardo Lancho, J.F., Oehm, C.T., 2012. Evaluation of the rates of soil organic matter mineralization in Forest ecosystems of temperate continental, Mediterranean, and tropical monsoon climates. Euras. Soil Sci. 45 (1), 68–79.
Latva-Karjanmaa, T., Penttil, R., Siitonen, J., 2007. The demographic structure of European aspen (*Populus tremula*) populations in managed and old-growth boreal forests in eastern Finland. Can. J. For. Res. 37 (6), 1070–1081.
Lestander, T.A., Holmberg, C., Stenberg, L., Lehtonen, R., 2012. Towards multivariate statistical process control in the wood pellet industry. Biomass Bioenergy 45, 152–158.
Li, Q., Chen, J., Moorhead, D.L., 2012. Respiratory carbon losses in a managed oak forest ecosystem. For. Ecol. Manag. 279, 1–10.
Liu, W., Schaefer, D., Qiao, L., Liu, X., 2013. What controls the variability of wood-decay rates? For. Ecol. Manag. 310, 623–631.
Martin, R.E., Crist, J.B., 1970. Elements of bark structure and terminology. Wood Fiber Sci. 3, 269–279.
Martin, A.R., Gezahegn, S., Thomas, S.C., 2015. Variation in carbon and nitrogen concentration among major woody tissue types intemperate trees. Can. J. For. Res. 45, 744–757.
Obolenskaya, A.V., Elnitskaya, Z.P., Leonovich, A.A., 1991. Laboratory makings on chemistry of wood and cellulose. Moscow, Ecology. (in Russian).
Ohtsuka, T., Shizu, Y., Hirota, M., Yashiro, Y., Shugang, J., Iimura, Y., Koizumi, H., 2014. Role of coarse woody debris in the carbon cycle of Takayama forest, central Japan. Ecol. Res. 29, 91–101.
Olajuyigbe, S., Tobin, B., Nieuwenhuis, M., 2012. Temperature and moisture effects on respiration rate of decomposing logs in a Sitka spruce plantation in Ireland. Forestry 85 (4). http://dx.doi.org/10.1093/forestry/cps045.
Olson, J., 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44 (2), 322–331.
Olsson, M.T., 1978. Properties and Decomposition of Bark [*Norway spruce*, *Picea abies*, *Scots pine*, *Pinus silvestris*, *birch*, *Betula verrucosa*, Effect of Leachate on Soil]. 34 Swedish University of Agricultural Sciences, Uppsala (Dep. For. Soils, Rep. For. Ecol. For. Soils).
Palviainenm, M., Laiho, R., Mäkinen, H., Finér, L., 2008. Do decomposing Scots pine, Norway spruce, and silver birch stems retain nitrogen? Can. J. For. Res. 38 (12), 3047–3055.
Plante, A.F., 2005. Soil biogeochemical cycling of inorganic nutrients and metals. In: Paul, E.A. (Ed.), Soil Microbiology, Ecology and Biochemistry. Elsevier, New York, New York, USA, pp. 389–432.
Qualls, R.G., Richardson, C.J., 2000. Phosphorus enrichment affects litter decomposition, immobilization, and soil microbial phosphorus in wetland mesocosms. Soil Sci. Soc. Am. J. 64, 799–808.
Rayner, A.D., Boddy, L., 1988. Fungal communities in the decay of wood. Adv. Microb. Ecol. 10, 115–166.
Rosell, J.A., Castorena, M., Laws, C.A., Westoby, M., 2015. Bark ecology of twigs vs. main stems: functional traits across eighty-five species of angiosperms. Oecologia 178, 1033–1043.
Rubenstein, M.A., Crowther, T.W., Maynard, D.S., Schilling, J.S., Bradford, M.A., 2017. Decoupling direct and indirect effects of temperature on decomposition. Soil Biol. Biochem. 112, 110–116.
Russell, M.B., Fraver, S., Aakala, T., Gove, J.H., Woodall, C.W., D'Amato, A.W., Ducey, M.J.T., 2015. Quantifying carbon stores and decomposition in dead wood: a review. For. Ecol. Manag. 350, 107–128.
Semenov, V.M., Khodzhaeva, A.K., 2006. Agroecological functions of plants residuals in soils. Agrochimia. 7, 63–81 (in Russian).
Shorohova, E., Kapitsa, E., 2014. Mineralization and fragmentation rates of bark attached to logs in a northern boreal forest. For. Ecol. Manag. 315, 185–190.
Shorohova, E., Kapitsa, E., 2015. Stand and landscape scale variability in the amount and diversity of coarse woody debris in primeval European boreal forests. For. Ecol. Manag. 315, 185–190.
Shorohova, E., Kapitsa, E., 2016. The decomposition rate of non-stem components of coarse woody debris (CWD) in European boreal forests mainly depends on site moisture and tree species. Eur. J. For. Res. 135, 593–606.
Shorohova, E., Ignatyeva, O., Kapitsa, E., Kauhanen, H., Kuznetsov, A., Vanha-Majamaa, I., 2012. Stump decomposition rates after clear-felling with and without prescribed burning in southern and northern boreal forests in Finland. For. Ecol. Manag. 263, 74–84.
Shorohova, E., Kapitsa, E., Kazartsev, I., Romashkin, I., Polevoi, A., Kushnevskaya, A., 2016. Tree species traits are the predominant control on the decomposition rate of tree log bark in a mesic old-growth boreal forest. For. Ecol. Manag. 377, 36–45.
Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., Rayburn, L., Repert, D., Weiland, T., 1992. Wood decomposition over a first-order watershed: mass loss as a function of exoenzyme activity. Soil Biol. Biochem. 24, 743–749.
Sinsabaugh, R.L., Antibus, R.K., Linkins, A.E., McClaugherty, C.A., Rayburn, L., Repert, D., Weiland, T., 1993. Wood decomposition: nitrogen and phosphorus dynamics in relation to extracellular enzyme activity. Ecology 74, 1586–1593.
Sjöström, E., 1993. Wood Chemistry: Fundamentals and Application. Academic Press, UK.
Skonieczna, J., Małek, S., Polowy, K., Węgiel, A., 2014. Elements content of Scots pine (*Pinus sylvestris* L.) stands of different densities. Drewno Prace Naukowe Doniesienia Komunikaty. 57 (192), 77–87.
Stefano, M., Trofymow, J.A., Jackson, R.B., Porporato, A., 2010. Stoichiometric controls on carbon, nitrogen, and phosphorus dynamics in decomposing litter. Ecol. Monogr. 80 (1), 89–106.

Taylor, B.R., Parkinson, D., 1988. Aspen and pine leaf litter decomposition in laboratory microcosms. II. Interactions of temperature and moisture level. Can. J. Bot. 66, 1966–1973.
Ugolev, B.N., 2002. Wood Science and Basics of Forest Commodities. MGUL Publ, Moscow (in Russian).
Ul'yanova, O.A., Chuprova, V.V., 2015. Mineralization of bark from different tree species and bark-based fertilizer compositions. Agrochimia. 2, 33–45.
Ul'yanova, O.A., Nechaeva, A.S., Khizhnyak, S.V., 2009. Transformation of pine bark and bark-based composition. In: Vestnik Krasnoyarsky State Agrarian University. 11. pp. 126–130.
Vedrova, E.F., 1997. Decomposition of organic matter of forest litter. Pochvovedenie. 2, 216–223.
Wang, R., Goll, D., Balkanski, Y., Hauglustaine, D., Boucher, O., Ciais, P., Janssens, I., Penuelas, J., Guenet, B., Sardans, J., Bopp, L., Vuichard, N., Zhou, F., Li, B., Piao, S., Peng, S., Huang, Y., Tao, S., 2017. Global forest carbon uptake due to nitrogen and phosphorus deposition from 1850 to 2100. Glob. Chang. Biol. 23 (11), 4854–4872. http://dx.doi.org/10.1111/gcb.13766.
Weedon, J.T., Cornwell, W.K., Cornelissen, J.H.C., Zanne, A.E., Wirth, C., Coomes, D.A., 2009. Global meta-analysis of wood decomposition rates: a role for trait variation among tree species? Ecol. Lett. 12, 45–56.
Wetzel, S., Greenwood, J.S., 1989. Proteins as a potential nitrogen storage compound in bark and leaves of several softwoods. Trees 3, 149–153.
Winckler, J.P., Cherry, R.S., Schlesinger, W.H., 1996. The Q_{10} relationship of microbial respiration in a temperate forest soil. Soil Biol. Biochem. 28 (8), 1067–1072.
Worrell, R., 1995a. European aspen (*Populus tremula*): a review with particular reference to Scotland 1: distribution, ecology and genetic variation. Forestry 68, 94–105.
Worrell, R., 1995b. European aspen (*Populus tremula*): a review with particular reference to Scotland 2: values, silviculture and utilization. Forestry 68, 231–244.
Wu, J., Zhang, X., Wang, H., Sun, J., Guan, D., 2010. Respiration of downed logs in an old-growth temperate forest in north-eastern China. Scand. J. Forest. Res. 25, 500–506.
Yatskov, M., Harmon, M.E., Krankina, O.N., 2003. A chronosequence of wood decomposition in the boreal forests on Russia. Can. J. For. Res. 33, 1211–1226.
Yoon, T.K., Han, S., Lee, D., Han, S.H., Noh, N.J., Son, Y., 2014. Effects of sample size and temperature on coarse woody debris respiration from *Quercus variabilis* logs. J. For. Res. 19 (2), 249–259.
Zhang, D., Hui, D., Luo, Y., Zhou, G., 2008. Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. J. Plant Ecol. 1, 85–93.
Zhou, L., Dai, L., Gu, H., Zhong, L., 2007. Review on the decomposition and influence factors of coarse woody debris in forest ecosystem. J. For. Res. 18 (1), 48–54.
Zuo, J., Berg, M.P., Klein, R., Nusselder, J., Neurink, G., Decker, O., Cornelissen, J.H.C., 2016. Faunal community consequence of interspecific bark trait dissimilarity in early-stage decomposing logs. Funct. Ecol. 30 (12), 1957–1966. http://dx.doi.org/10.1111/1365-2435.12676.