

# Partitioning of CO<sub>2</sub> Fluxes from Coarse Woody Debris: Adaptation of the Component Integration Method

ANASTASIA V. MAMAI<sup>1</sup>, ELENA V. MOSHKINA<sup>1</sup>, IRINA N. KURGANOVA<sup>2\*</sup>, EKATERINA V. SHOROHOVA<sup>1,3,4</sup>, IVAN V. ROMASHKIN<sup>1</sup> AND VALENTIN O. LOPES DE GERENYU<sup>2</sup>

<sup>1</sup>Forest Research Institute of the Karelian Research Centre of the Russian Academy of Sciences, Pushkinskaya Str., 11, 185910, Petrozavodsk, Karelia, Russia;

<sup>2</sup>Institute of Physicochemical and Biological Problems in Soil Science, RAS, Institutskaya str., 2, Pushchino, Moscow region, 142290, Russia;

<sup>3</sup>Saint-Petersburg State Forest Technical University, 194021, Institutsky str. 5, Saint Petersburg, Russia

<sup>4</sup>Natural Resources Institute Finland (Luke), Latokartanonkaari 9, FI-00790, Helsinki, Finland

\* Corresponding author: [ikurg@mail.ru](mailto:ikurg@mail.ru)

Mamai, A.V., Moshkina, E.V., Kurganova, I.N., Shorohova, E.V., Romashkin, I.V. and Lopes de Gerenyu, V.O. 2018. Partitioning of CO<sub>2</sub> Fluxes from Coarse Woody Debris: Adaptation of the Component Integration Method. *Baltic Forestry* 24(2): 249–260.

## Abstract

Tree bark represents an important but rather poorly investigated component of coarse woody debris (CWD). We applied the component integration method to partition CO<sub>2</sub> flux from the surface of CWD into tree bark respiration and exposed wood surface respiration. Twelve large fragments of spruce (*Picea abies* (L.) Karst), birch (*Betula pubescens* Ehrh and *B. pendula* Roth), and aspen (*Populus tremula* L.) logs at various times since tree death (TTD) were collected in middle taiga old-growth forest and transported to the laboratory. CO<sub>2</sub> fluxes were measured by a closed chamber method using a portable infrared gas analyser. During the first hours after the removal of bark from the logs, we observed a pronounced increase in CO<sub>2</sub> fluxes (i.e. a respiration burst) from the exposed wood surface and cutaway bark. The TTD had an important influence on the time required for stabilization of CO<sub>2</sub> emission rates from the tree bark and exposed wood surface. The mean rate of CO<sub>2</sub> flux from undisturbed surfaces of log fragments ( $R_{\log\ surface}$ ) varied from  $23 \pm 1$  to  $45 \pm 2$  mg C m<sup>-2</sup> h<sup>-1</sup>, depending on the TTD. The bark respiration rate was significantly lower than the respiration rate of exposed wood. Tree bark of fresh logs (i.e. 0–1 y TTD) contributed a larger portion (40%) to the total CO<sub>2</sub> flux from CWD than tree bark of slightly and moderately decayed logs (15–16%). We suggest using this methodological approach for partitioning CO<sub>2</sub> fluxes from fresh and moderately decomposed CWD in both field and laboratory studies.

**Keywords:** deadwood; middle taiga; decay, carbon, tree bark, wood, respiration.

## Introduction

Forests play a key role in the global carbon cycle (Alkama and Cescatti 2016). Forest-based measures, such as reducing deforestation and increasing carbon (C) sequestration through better management of existing forests and restoration of degraded forests, are relatively cheap and easy ways to reduce greenhouse gas emissions (United Nations 2015). The degree to which forest ecosystems serve as a carbon sink or source is unclear, in part, because of the complexity of the ecological processes driving carbon dynamics and inadequate understanding of these processes. Coarse woody debris

(CWD) is a major source of uncertainty in carbon budget estimations (Russell et al. 2015).

CWD, which is generally considered as dead woody material in various stages of decomposition, includes logs, snags, stumps and large branches (Harmon et al. 1986). Logs account for a large proportion of CWD, especially in old-growth forests (Shorohova and Kapitsa 2015). The decomposition of CWD is the result of microbial decay, physical degradation (i.e. fragmentation and weathering), leaching and biological transformation. Of these, microbial decay is considered the main process (Carpenter et al. 1988, Chambers et al. 2001, Chang et al. 2017). CO<sub>2</sub> fluxes resulting from CWD decomposition

contribute 10–23% to the total annual heterotrophic respiration in boreal and temperate forests (Jomura et al. 2007, Safonov et al. 2012). This figure may increase due to global warming (Russell et al. 2015), as decomposition processes intensify with increasing temperature.

Direct measurements of CO<sub>2</sub> fluxes from CWD are labour consuming. However, they have a clear advantage over other methods, including eddy covariance techniques, used to estimate CO<sub>2</sub> fluxes in forest ecosystems (Russell et al. 2015). Despite the importance of CWD respiration for the carbon budget in forest ecosystems (Bond-Lamberty et al. 2003, Gough et al. 2007, Harmon et al. 2011), there are no commonly accepted field methods for the measurement of CO<sub>2</sub> fluxes from the surface of CWD. Measuring CWD respiration of entire log sections in situ remains a major technical challenge, for which practical solutions need to be developed (Herrmann and Bauhus 2008). In this respect, various studies have employed different techniques and sampling designs (Marra and Edmonds 1996, Chambers et al. 2001, Mackensen and Bauhus 2003, Ohtsuka et al. 2014, Kahl et al. 2015). In situ, CO<sub>2</sub> fluxes can be measured using an infrared gas analyser or soda lime with either static or dynamic closed chamber methods. Previous research demonstrated the robustness of the dynamic chamber method for measuring CO<sub>2</sub> fluxes (Rochette et al. 1992). Other studies showed that the use of small in situ chambers was an appropriate method for determining the rate of CO<sub>2</sub> evolution for whole tree stems and large log sections (Herrmann and Bauhus 2008).

Tree bark accounts for up to 25% of stem volume and 16% of stem dry mass in dominant boreal tree species (Ugolev 2005, Lestander et al. 2012). Despite tree bark being an important component of woody debris, its contribution to CO<sub>2</sub> flux during decomposition remains poorly investigated. Under field conditions of a middle boreal forest, the decomposition rate of log bark expressed as the total mass and volume loss (i.e. including fragmentation) averaged 0.147 y<sup>-1</sup> for aspen, birch and spruce and 0.291 y<sup>-1</sup> for pine (Shorohova et al. 2016). The presence of bark on logs influences the amount of CO<sub>2</sub> emitted from the surface of CWD, as it represents a natural barrier to the diffusion of CO<sub>2</sub> from decaying wood, affects the temperature and humidity of inner CWD layers and acts as a source of CO<sub>2</sub> into the atmosphere (Harmon et al. 1986, Molchanov et al. 2011).

Thus far, the contribution of log bark to the total CO<sub>2</sub> flux from logs has not been estimated. In old-growth forests, tree mortality patterns exhibit high variability. Consequently, the rates of biological fragmentation of bark also vary (Shorohova and Kapitsa 2015, Shorohova et al. 2016). Variation in bark cover attributes to high uncertainty in CO<sub>2</sub> fluxes from CWD and hampers accurate estimations of the contribution of bark to the total

CO<sub>2</sub> flux caused by the decomposition of CWD. As a rule, tree bark and wood are not considered separately in estimations of CO<sub>2</sub> fluxes from CWD (Nagel 2006, Hagemann et al. 2010, Li et al. 2012, Forrester et al. 2012, Safonov et al. 2012). However, differences in the decomposition patterns of wood and bark (Shorohova and Kapitsa 2014, 2016) suggest a need for developing an approach that can measure CO<sub>2</sub> fluxes from wood and bark separately. Partitioning CO<sub>2</sub> fluxes from the surface of CWD into two main components is crucial to reduce uncertainties surrounding the contribution of CWD to forest carbon budget.

We propose using the component integration method for direct measurements of separated CO<sub>2</sub> fluxes from tree bark and exposed wood surfaces. This method has been widely applied in environmental sciences to separate root and microbial respiration (Edwards and Harris 1977, Singh and Shekhar 1986, Larionova et al. 2003, Koo et al. 2005, Kuzyakov and Larionova 2005, Bond-Lamberty et al. 2011, Tomotsune et al. 2013) or to estimate the contribution of litter to the total respiration flux from the soil surface (Wang et al. 2009, Xiao et al. 2014, Smorkalov 2016). The component integration method is based on manual separation of different components (e.g. roots, soil and plant residues) from soil samples. To apply the component integration method to partitioning of total CO<sub>2</sub> fluxes from CWD in the field or laboratory, the following components need to be separated and measured: (1) the total respiration rate of the undisturbed surface of CWD (e.g. logs), (2) the respiration rate of cutaway bark and (3) the respiration rate of the exposed wood after bark removal. During the first few hours after disturbing the wood surface (e.g. via bark removal, cambium layer removal or sample collection), CO<sub>2</sub> emissions generally rapidly increase (Opitz 1931, Ziegler 1957, Soloviev 1983). This ‘respiration burst’ represents the external response (adaptation) of the damaged tissues to altered gas diffusion caused by disturbance of the wood surface and CO<sub>2</sub> accumulation in a substrate (Müller 1924, Chambers et al. 2001), in addition to acceleration of the respiration process due to the resulting increase in the supply of oxygen (Żelawski 1960, Soloviev 1983).

Failing to take account of the effect of the disturbance of log cohesion by bark removal on CO<sub>2</sub> fluxes can result in overestimation of the respiration rate of the separate components of CWD. To quantify the rate of CO<sub>2</sub> fluxes from CWD correctly and the contribution of various components to total CWD respiration fluxes, information is needed on the time required for stabilization of CO<sub>2</sub> fluxes from both cut bark and exposed wood surfaces. Information is also required on the role played by bark in variations in CO<sub>2</sub> fluxes from the log surface and the factors that influence such variations. To address

the aforementioned issues, a methodology needs to be developed that can estimate bark respiration in the field and separate the contributions of bark and wood to the total CO<sub>2</sub> flux from logs.

This study aimed to apply the component integration method to estimate CO<sub>2</sub> fluxes from CWD and separate these fluxes into two main components: tree bark respiration and exposed wood surface respiration. We focused on three main questions: (i) how much CO<sub>2</sub> is emitted from an undisturbed surfaces of 'fresh', slightly decayed and moderately decayed fallen logs and their components (i.e. bark and wood); (ii) when the CWD surfaces are disturbed (e.g. bark removal), how long does it take for the stabilization of CO<sub>2</sub> fluxes from the cutaway bark and exposed wood surface and (iii) what is the tree bark to exposed wood surface respiration ratio. We hypothesized that tree bark of fresh logs would contribute a larger portion to the total CO<sub>2</sub> flux from CWD than tree bark of slightly and moderately decayed logs.

We assumed that the time required for the stabilization of CO<sub>2</sub> fluxes from cutaway bark and exposed wood after disturbing the wood surface would vary, depending on the time since tree death (TTD). As the influence of various abiotic factors on CO<sub>2</sub> fluxes from CWD in situ is difficult to predict and separate from substrate attributes (Jomura et al. 2007, Fukasawa 2015), the present study was conducted in the laboratory at constant air temperature and atmospheric humidity. Given that the majority of biotic factors (e.g. the position of log fragments and tree species that affect both chemical and physical properties and the rhytidome:phloem [Rh:Ph] ratio) can be controlled in situ (Jomura et al. 2015), we believe that the main findings of our study are applicable to both laboratory and field conditions. To the best of our knowledge, no other studies have applied the component integration method to partitioning of CO<sub>2</sub> fluxes from coarse woody debris.

## Materials and Methods

### Study area

The log fragments of three tree species Norway spruce (*Picea abies* (L.) Karst, hereafter referred to as spruce, silver and downy birch (*Betula pubescens* Ehrh and *B. pendula* Roth), hereafter referred to as birch, and aspen (*Populus tremula* L.) were collected in September 2015 in a middle taiga old-growth forest located in Kivach, a strict nature reserve in the Republic of Karelia, Russia (62°28'N, 33°95'E). The study site is in the Atlantic–Arctic temperate zone region and is characterized by a maritime to continental climate. The mean annual temperature in the region is +2.4°C, the length of the growing season is 90 d, and the mean annual precipitation is 625 mm (Skorohodova 2008). Atmospheric humidity is

usually high (more than 80%). However, it can be much lower (40–55%) when the weather is sunny and dry ([https://rp5.ru/Weather\\_in\\_Kondopoga](https://rp5.ru/Weather_in_Kondopoga)). According to the classification of forest ecosystems in the Northwest of Russia (Fedorchuk et al. 2005), the forest type in the sample plot was *Piceetum oxalidosum*, with patches of *P. oxalidoso-myrtillosum*. The soils are humic-gley and superficially eluvial gleyish sandy-loamy and loamy on varved clays (Fedorets et al. 2006) or Gleysols Histic and Gleysols Dystric according to the classification of World Reference Base (WRB) for Soil Resources (Stolbovoi 2000).

### Sampling and experimental design

All logs chosen for sampling were dated using dendrochronological methods, including cross-dating growth release patterns and mechanical scars of neighbouring trees (Dynesius and Jonsson 1991). Using a chainsaw, the logs were cut into pieces (1-m long and 16–27 cm in diameter) about 1.5–2 m from the root collar. The ends of the logs were treated with a curable sealant (Neomid, Russia) to prevent CO<sub>2</sub> emission and water loss (Progar et al. 2000). They were then labelled and transported to the laboratory. In total, 12 log fragments were transported to the laboratory (3–5 samples of each species). For further analyses, the samples were combined into three groups based on the TTD: fresh (0–1 y), slightly decayed (2–5 y) and moderately decayed (6–10 y).

Two to three rectangular-shaped bark samples of 1–3 cm<sup>2</sup> were taken from each log fragment and measured in two dimensions (length × width). Wood samples in 2–3 replicates were extracted manually using a chisel and a hammer. The proportion of phloem by volume in each bark sample was estimated. Samples for bulk density measurements were oven dried at 103°C. When the samples of wood and bark were absolutely dry, they were coated with paraffin wax and placed in a water bath to estimate the volume of dry bark (or wood) using the water displacement method (Polubojarinov 1976). The dry density of bark ( $\rho_b$ , g cm<sup>-3</sup>) was calculated by dividing the dry mass by the dry volume of a sample. The bulk density of wood ( $\rho$ , g cm<sup>-3</sup>) was calculated by dividing the dry mass by the fresh volume of the sample. The area-specific mass of bark (mass per unit surface area,  $m_b$ , g cm<sup>-2</sup>) was calculated by dividing the dry mass ( $m$ , g) by the surface area of the sample ( $s$ , cm<sup>2</sup>). The average thickness of each bark sample was calculated by dividing its volume by its surface area. The concentrations of C and nitrogen (N) in the bark and wood samples were determined using an automatic CHNS Analyzer PE-2040 (Perkin Elmer, Waltham, MA, USA). The pH value was measured in water extraction (ratio bark/wood: water = 1:25) using a potentiometric pH sensor (Hanna Instruments, Vöhringen, Germany). All analytical procedures were performed in 2–6 replicates.

**Measurement of CO<sub>2</sub> fluxes**

To eliminate the effects of environmental factors (i.e. temperature and moisture variations), all the log fragments were kept in the laboratory for 2 wk at an air temperature of approximately 22°C and air moisture of approximately 45% prior to CO<sub>2</sub> flux measurements. These air temperature and air moisture conditions are similar to those observed around midday in the middle taiga forest on sunny days (Raspisaniye Pogodi 2016). The bark and wood (0–2 cm of surface wood) moisture contents of the log fragments were determined gravimetrically directly prior to CO<sub>2</sub> flux measurements. To evaluate CO<sub>2</sub> fluxes from undisturbed log fragment surfaces, exposed wood surfaces and bark samples, we used the closed chamber method, which has been widely applied in experimental studies of respiration of living trees (Molchanov et al. 2011) and CWD (Forrester et al. 2012, 2015, Progar et al. 2000, Lim et al. 2012). The preparation of the logs (bark removal and chamber installation on undisturbed and exposed wood surfaces) was carried out immediately before the CO<sub>2</sub> flux measurements. The bark was separated from the logs using an electric drill and sawing collars 108 and 111 mm in diameter. For log fragments of 6–10 y TTD, the bark was carefully removed from the surface of the log using a knife or a small saw. Polyvinyl chloride cylindrical chambers (11 cm in diameter and 12–14 cm in height) were installed on the undisturbed and exposed wood surfaces of the log fragments, taking care to maintain the integrity of the logs and intactness of the wood as much as possible. To exclude CO<sub>2</sub> losses from the surfaces of the logs during the measurements, the chambers were fixed on the undisturbed surfaces using a metallic lock with an elastic strip (Figure 1). Glazier’s putty was used as a sealer. On the ex-

posed wood surfaces, the chambers were imbedded in the surfaces at a depth of 10–15 mm. The border between the wood and the chamber was also covered by a sealer. The cutaway bark was placed in a separate chamber with a plastic bottom. The cups of all the chambers had cut membranes for connecting with a portable infrared CO<sub>2</sub> gas analyser equipped with a nondispersive infrared (NDIR) sensor (SenseAir, Sweden). This system has been used successfully for CO<sub>2</sub> flux measurements in previous studies (Carson 1997, Safonov et al. 2012, Yasuda et al. 2012). In this study, a K22 series NDIR sensor was used to measure the CO<sub>2</sub> concentration in the chamber with an accuracy of 1 ppm (Karelin et al. 2014, 2015).

The measurements of CO<sub>2</sub> fluxes from the undisturbed log surfaces started immediately after the installation of the chambers. Increases in CO<sub>2</sub> concentrations in the chamber were measured for 15–20 min (one series) at 3-min intervals (0, 3, 6, 9 min, etc). This period was considered sufficient to detect reliable and stable ΔCO<sub>2</sub> for each series. During the CO<sub>2</sub> flux measurements, air was mixed using a battery-driven internal fan to reduce spatial variations in CO<sub>2</sub> concentrations in the chamber (Herrmann and Bauhus 2008, Olajuyigbe et al. 2012, Yoon et al. 2014). The chambers were ventilated between each measurement series. We performed 2–3 series for each log fragment to make sure that CO<sub>2</sub> fluxes from the undisturbed log surfaces became nearly constant.

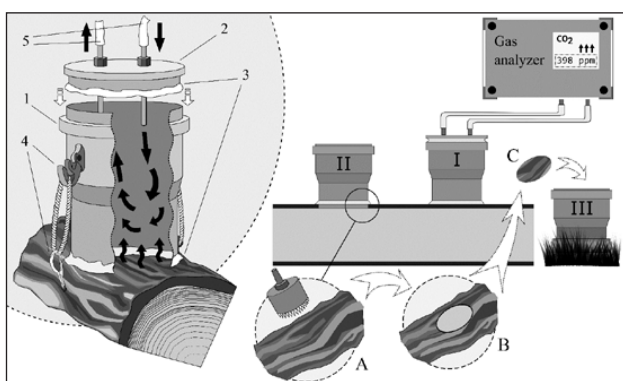
To estimate the respiration burst and the time required for the stabilization of CO<sub>2</sub> fluxes from both the cutaway bark and exposed wood surface, the measurements of CO<sub>2</sub> fluxes were started immediately after the installation of the chambers on the exposed wood surface and the placement of the cutaway bark in the chamber. After the respiration burst, CO<sub>2</sub> fluxes were measured every 5–7 h until CO<sub>2</sub> flux stabilization. Reference measurements of CO<sub>2</sub> fluxes from the exposed wood surface and cutaway bark were obtained the next day. In total, 575 measurements were obtained (i) undisturbed log surface (*n* = 104); (ii) exposed wood surface (*n* = 247); (iii) cutaway bark (*n* = 224).

**Calculations**

To calculate the change in C-CO<sub>2</sub> mass in the chamber throughout the exposition time, the following equation was used (Yoon et al. 2014):

$$R_{C-CO_2(t_2-t_1)} = \frac{\Delta CO_2 \times V_{air} \times 12 \times 273.15}{22.41 \times T_{air} \times 1000} \tag{1}$$

where  $R_{C-CO_2(t_2-t_1)}$  is the change in C-CO<sub>2</sub> mass in the chamber (mg C); ΔCO<sub>2</sub> is the change in CO<sub>2</sub> concentration in the chamber over the exposition time (t<sub>2</sub>-t<sub>1</sub>) in ppm; V<sub>air</sub> is the air volume in the chamber (m<sup>3</sup>); 12 is the molar weight of carbon (g C mol<sup>-1</sup>); T<sub>air</sub> is the air temperature (K); 22.41 is the molar volume (L mol<sup>-1</sup>) at standard tem-



**Figure 1.** Schematic diagram of the component integration method for partitioning of respiration fluxes from CWD. A) Measurement of total CO<sub>2</sub> flux from the undisturbed log surface ( $R_{log\ surface}$ ), B) exposed wood ( $R_{wood}$ ) and C) cutaway bark ( $R_{bark}$ ). In the figure, (1) is the chamber, (2) is the cup with the cut membrane, (3) is the sealer, (4) depicts the metallic lock and (5) shows the connection with the CO<sub>2</sub> gas analyser

perature (273.15 K) and pressure (1.013 bar); 273 is the correction factor to convert degrees Celsius to Kelvin (K); and 1,000 is the conversion coefficient to milligrams.

The rate of CO<sub>2</sub> flux ( $R$ , mg C m<sup>-2</sup> h<sup>-1</sup>) from the log components and undisturbed log surfaces was expressed using the following formula:

$$R = \frac{R_{C-CO_2}(t_2-t_1)}{t \times S} \quad (2)$$

where  $t = t_2 - t_1$  is the exposition time in hours (h), and  $S$  is the surface area of the bark or wood in m<sup>2</sup>.

In this study, the following two common assumptions were made regarding the component integration method: (i) the effect of physical separation on the respiration rates of all CWD components was the same, and (ii) the decrease in respiration rates after the start of the measurements was the same for each component (Kuzya-kov and Larionova 2005). We also presumed that following CO<sub>2</sub> flux stabilization, the total CO<sub>2</sub> respiration rate of the cutaway bark ( $R_{bark}$ ) and the exposed wood surface ( $R_{wood}$ ) was equal to 100%:

$$\Sigma R_{bark+wood} = R_{bark} + R_{wood} = 100\% \quad (3)$$

where  $\Sigma R_{bark+wood}$  is the sum of CO<sub>2</sub> flux rates from the cutaway bark and the exposed wood surface following CO<sub>2</sub> flux stabilization (mg C m<sup>-2</sup> h<sup>-1</sup>),  $R_{bark}$  is the rate of CO<sub>2</sub> flux from the cut bark (mg C m<sup>-2</sup> h<sup>-1</sup>), and  $R_{wood}$  is the rate of CO<sub>2</sub> flux from the exposed wood surface (mg C m<sup>-2</sup> h<sup>-1</sup>).

Hence, the contribution of the main components to the total CO<sub>2</sub> flux from the undisturbed log surface was estimated by the following equations:

$$B = \frac{R_{bark} \times 100}{\Sigma R_{bark+wood}} \quad (4)$$

$$W = \frac{R_{wood} \times 100}{\Sigma R_{bark+wood}} \quad (5)$$

where  $B$  is the bark contribution to the total CO<sub>2</sub> flux from the undisturbed log surface (%), and  $W$  is the wood contribution to the total CO<sub>2</sub> flux from the undisturbed log surface (%).

Based on the observed rate of CO<sub>2</sub> flux from the undisturbed log surface ( $R_{log\ surface}$ , mg C m<sup>-2</sup> h<sup>-1</sup>) and the contribution of the main components to this flux ( $B$  and  $W$  values), the corrected rates of CO<sub>2</sub> fluxes from the cutaway bark and exposed wood surface after CO<sub>2</sub> flux stabilization were calculated using the formulae:

$$R'_{bark} = \frac{R_{log\ surface} \times B}{100} \quad (6)$$

$$R'_{wood} = \frac{R_{log\ surface} \times W}{100} \quad (7)$$

where  $R'_{bark}$  and  $R'_{wood}$  are the corrected rates of CO<sub>2</sub> fluxes from the cutaway bark and exposed wood surface

after elimination of the effects of disturbances of the intact log surface caused by the chamber installation and bark removal.

A similar calculation algorithm was used previously to partition total soil respiration into the root and microbial respiration and to estimate their shares in the total soil CO<sub>2</sub> flux (Gloser and Tesarova 1978, Larionova et al. 2003).

To estimate the stabilization time, we calculated the standard deviation (STD) value for each measurement series for each log. Then, we compared the difference between  $\Delta$ CO<sub>2</sub> values and the STD value for the last measurement series (6 and 24 h after the beginning of the observations) until the CO<sub>2</sub> fluxes from the log and its components became constant. The stabilization time was considered the time point when the difference in  $\Delta$ CO<sub>2</sub> values no longer exceeded the STD value of the last measurement.

All the measured parameters (total and physicochemical properties of bark and wood;  $R_{log\ surface}$ ) and estimated values ( $R'_{bark}$  and  $R'_{wood}$ , stabilization period, contribution of bark/wood to the total CO<sub>2</sub> flux from logs) were analysed by groups based on the TTD (fresh, slightly and moderately decayed) using a one-way analysis of variance (ANOVA). Linear and hyperbolic regression analyses were applied to examine the relationships between  $R_{log\ surface}$  and  $R_{bark} + R_{wood}$  after CO<sub>2</sub> flux stabilization as well as between the flux stabilization time and TTD. All statistical analyses were performed using the R software package (R Core Team 2017), and  $P = 0.05$  was considered significant.

## Results

### *Physicochemical properties of the wood and bark*

The main physical and chemical characteristics of the bark and wood in the various TTD groups differed significantly (Tables 1, 2). The highest variability in the Rh:Ph ratio (from 0.3 to 2.7) was found in the 6–10 y TTD log fragment group. Wood moisture in the slightly decayed (2–5 y TTD) and moderately decayed (6–10 y TTD) groups showed the highest variability (Table 2). The  $C_0$  and  $m_b$  values, as well as the C content of the bark, decreased significantly with an increase in the TTD. The majority of physicochemical properties were significantly different in bark and wood of similar TTD (Table 2). The C content and C/N ratio in tree bark were significantly lower than those in the wood in all the TTD groups. The observed differences between bark and wood features most likely influenced CO<sub>2</sub> fluxes from these log components.

### *CO<sub>2</sub> fluxes from undisturbed log fragments*

The rates of CO<sub>2</sub> fluxes from exposed wood surfaces ( $R_{log\ surface}$ ) varied from 9–11 to 65–86 mg C m<sup>-2</sup> h<sup>-1</sup>, de-

**Table 1.** General characteristics of the log fragments in the different TTD groups. The values are means, with standard errors in brackets. The characters indicate significant differences between the various TTD groups at  $p = 0.05$  based on an ANOVA

TTD, years	n <sup>1</sup>	Diameter, cm	Mean thickness of bark, mm			Rh : Ph <sup>2</sup> Ratio
			Total	Rhytidome	Phloem	
0–1	5	21 (1) <sup>a</sup>	4.7 (0.6) <sup>a</sup>	2.3 (0.5) <sup>a</sup>	2.4 (0.2) <sup>a</sup>	1.0 (0.1) <sup>a</sup>
2–5	4	21 (2) <sup>a</sup>	5.3 (1.1) <sup>b</sup>	2.0 (0.5) <sup>a</sup>	3.3 (0.8) <sup>b</sup>	0.7 (0.2) <sup>b</sup>
6–10	3	19 (2) <sup>b</sup>	5.8 (0.6) <sup>c</sup>	3.0 (1.0) <sup>b</sup>	2.8 (0.7) <sup>ab</sup>	1.4 (0.7) <sup>c</sup>

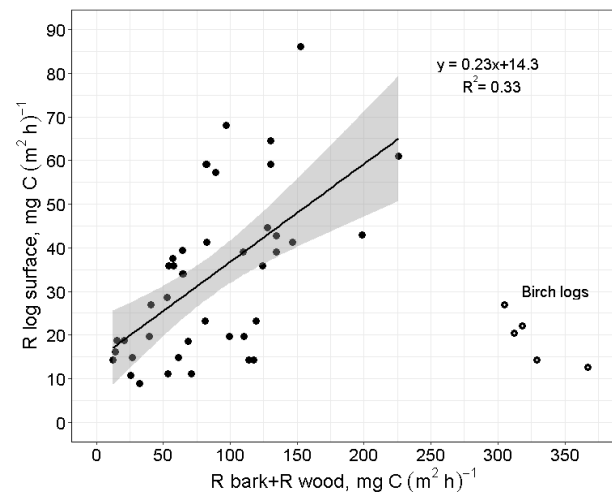
TTD (time since tree death); ANOVA (analysis of variance); <sup>1</sup> is the number of logs; <sup>2</sup> Rhytidome : Phloem ratio

**Table 2.** Physicochemical properties of bark and wood samples in the different TTD log fragment groups. The values are means, with standard errors in brackets. The letters indicate significant differences between the various TTD groups at  $p = 0.05$  estimated based on an ANOVA. \* indicates significant differences between bark and wood samples of similar TTD groups at  $p = 0.05$  based on an ANOVA

TTD, years	n <sup>1</sup>	Moisture, %	$\rho_0(\rho)^2$ , g cm <sup>-3</sup>	pH	C, %	N, %	C/N	m <sub>b</sub> , gcm <sup>-2</sup>
<b>Bark</b>								
0–1	5	63 (9) <sup>a</sup>	0.71 (0.04) <sup>a*</sup>	5.5 (0.2) <sup>a</sup>	47 (2) <sup>a*</sup>	0.67 (0.11) <sup>a*</sup>	80 (16) <sup>a*</sup>	0.32 (0.06) <sup>a</sup>
2–5	4	49 (19) <sup>b</sup>	0.67 (0.04) <sup>a*</sup>	5.4 (0.2) <sup>a</sup>	46 (3) <sup>a*</sup>	0.56 (0.03) <sup>b*</sup>	82 (3) <sup>a*</sup>	0.23 (0.09) <sup>b</sup>
6–10	3	48 (14) <sup>b*</sup>	0.63 (0.03) <sup>b*</sup>	5.7 (0.4) <sup>a</sup>	41 (2) <sup>b*</sup>	0.63 (0.04) <sup>a*</sup>	65 (4) <sup>b*</sup>	0.15 (0.01) <sup>c</sup>
<b>Wood</b>								
0–1	5	62 (14) <sup>a</sup>	0.37 (0.01) <sup>a*</sup>	5.5 (0.3) <sup>a</sup>	52 (2) <sup>a*</sup>	0.11 (0.02) <sup>a*</sup>	517 (90) <sup>a*</sup>	-
2–5	4	55 (23) <sup>a</sup>	0.33 (0.05) <sup>a*</sup>	5.7 (0.3) <sup>a</sup>	51 (1) <sup>a*</sup>	0.09 (0.02) <sup>b*</sup>	577 (104) <sup>a*</sup>	-
6–10	3	244 (109) <sup>b*</sup>	0.44 (0.09) <sup>b*</sup>	5.3 (0.4) <sup>a</sup>	52 (1) <sup>a*</sup>	0.12 (0.01) <sup>a*</sup>	459 (27) <sup>b*</sup>	-

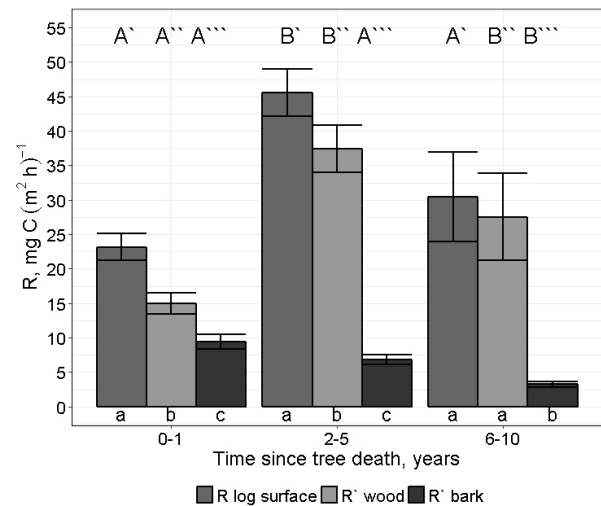
TTD (time since tree death); ANOVA (analysis of variance); <sup>1</sup>the number of logs; <sup>2</sup> $\rho_0$  for bark,  $\rho$  for wood

pending on log species identity and TTD (Figure 2). The highest mean value of  $R_{log\ surface}$  ( $46 \pm 2$  mg C m<sup>-2</sup> h<sup>-1</sup>) was found in slightly decayed log fragments, whereas the mean values of  $R_{log\ surface}$  for fresh and moderately decayed log fragments did not differ ( $23 \pm 1$  and  $31 \pm 7$  mg



**Figure 2.** Relationship between  $R_{log\ surface}$  and  $R_{bark} + R_{wood}$  after CO<sub>2</sub> flux stabilization. The measurements from birch logs were excluded from the whole dataset to fit the relationship between  $R_{log\ surface}$  and the sum of  $R_{bark}$  and  $R_{wood}$  ( $p < 0.005$ )

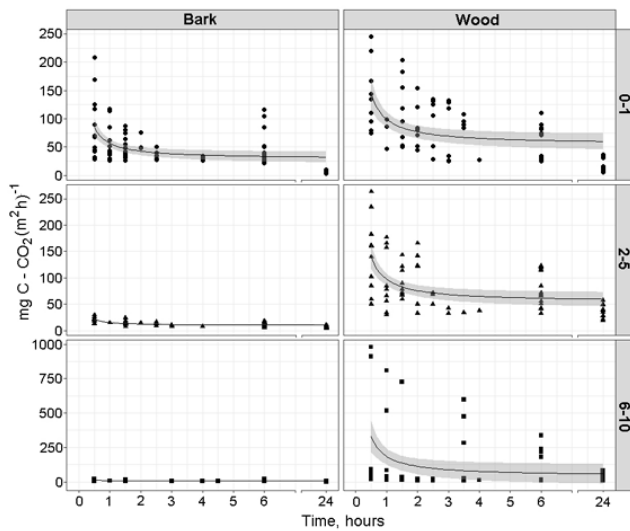
C m<sup>-2</sup> h<sup>-1</sup>, respectively) (Figure 3). Even after CO<sub>2</sub> flux stabilization, the respiration rates of undisturbed log surfaces were lower than the sum of  $R_{bark}$  and  $R_{wood}$  (Figure 2). The greatest differences (more than 10 times) between the  $R_{log\ surface}$  value and the sum of  $R_{bark}$  and  $R_{wood}$  were found in birch logs, which had the lowest Rh:Ph ratio (Fig. 2). When the birch measurements were excluded from the whole dataset, a close relationship was observed between the  $R_{log\ surface}$  value and sum of  $R_{bark}$  and  $R_{wood}$  ( $R^2 = 0.33$ ;  $p < 0.005$ ).



**Figure 3.** Measured rates of CO<sub>2</sub> flux from the undisturbed log surface ( $R_{log\ surface}$ ) and corrected rates of CO<sub>2</sub> fluxes from cutaway bark ( $R'_{bark}$ ) and exposed wood ( $R'_{wood}$ ) for log fragments in the various TTD groups after elimination of respiration burst values due to disturbance caused by sampling. The vertical bars are the standard errors of the mean. The different letters denote significant differences at  $p < 0.05$  between CO<sub>2</sub> fluxes from various components of the log fragments (undisturbed log surface, exposed wood and cutaway bark) in similar TTD groups (a, b, c) and from similar components of the log fragments in the various TTD groups (A', B'; A'', B'' etc.)

**The respiration burst and time required for stabilization of CO<sub>2</sub> fluxes from bark and wood**

The respiration burst from the exposed wood surface was generally higher than that from the cutaway bark (Figure 4). The mean values of the respiration burst (0-h time series of measurements) varied from 36 to 1,000 mg C m<sup>-2</sup> h<sup>-1</sup> for wood and from 9 to 245 mg C m<sup>-2</sup> h<sup>-1</sup> for bark. Moderately decayed log fragments (6–10 y TTD) exhibited the highest respiration burst values, reaching 725–1,000 mg C m<sup>-2</sup> h<sup>-1</sup> (Figure 4).



**Figure 4.** Stabilization dynamics of CO<sub>2</sub> fluxes from cutaway bark and exposed wood of the log fragments in the various TTD groups: 0–1 y (fresh), 2–5 y (slightly decayed) and 6–10 y (moderately decayed)

After the respiration burst from cutaway bark and exposed wood, the rates of CO<sub>2</sub> flux decreased rapidly. Some time was required for CO<sub>2</sub> flux stabilization (Figure 4). To describe the process of CO<sub>2</sub> flux stabilization from cutaway bark and exposed wood surfaces in time, an appropriate function was fitted. In all the TTD groups, the dynamics of CO<sub>2</sub> fluxes from bark and wood during the processes of CO<sub>2</sub> flux stabilization were adequately described by a hyperbolic function (Table 3). The time

**Table 3.** The parameters and adjusted *r*<sup>2</sup> values of the hyperbolic model ( $y = (a*b)/(b+x)$ ) for simulation of CO<sub>2</sub> flux stabilization (dependent variable *y*, g C m<sup>-2</sup> h<sup>-1</sup>) for various log components (bark vs. wood) and TTD. The independent variable *x* is time (h)

Log component	TTD, years	a	b	R <sup>2</sup>	F	P
Bark	0 – 1	31.81	-0.31	0.26	35.71	<0.001
	2 – 5	10.64	-0.24	0.45	59.51	<0.001
	6 – 10	5.57	-0.26	0.14	10.55	0.002
Wood	0 – 1	57.07	-0.30	0.26	28.71	<0.001
	2 – 5	63.93	-0.27	0.26	26.77	<0.001
	6 – 10	83.17	-0.38	0.13	12.55	<0.001

TTD (time since tree death)

required for the stabilization of CO<sub>2</sub> fluxes from exposed wood varied from 0.3 to 3.3 h (Figure 4). The decrease in CO<sub>2</sub> fluxes from cutaway bark was usually more rapid than that from exposed wood. The stabilization time for R<sub>bark</sub> varied between 0.17 and 2.8 h (Figure 4). Six hours after the measurements commenced, the rate of CO<sub>2</sub> from cutaway bark and exposed wood did not change significantly as compared with that of the 24-h measurements (Figure 4). The mean time of stabilization of CO<sub>2</sub> fluxes from the exposed wood surface for slightly decayed logs differed significantly from that of the other TTD groups (Table 4). For tree bark, the TTD was a key factor influencing the stabilization time of the CO<sub>2</sub> emission rate.

**Table 4.** Time (h: mean and SE) required for the stabilization of CO<sub>2</sub> flux from cutaway bark and exposed wood in the various log fragment TTD groups. The letters indicate significant differences between the various TTD groups at *p* = 0.05 based on an ANOVA. \* indicates significant differences between bark and wood of similar TTD groups at *p* = 0.05 based on an ANOVA

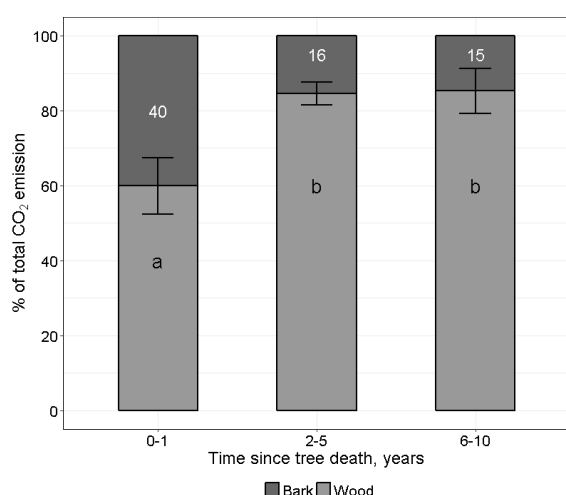
TTD, years	Bark	Wood
0 – 1	0.92 (0.25) <sup>a *</sup>	1.80 (0.51) <sup>a *</sup>
2 – 5	1.33 (0.54) <sup>b</sup>	1.38 (0.26) <sup>b</sup>
6 – 10	0.34 (0.17) <sup>c *</sup>	1.87 (0.78) <sup>a *</sup>

TTD (time since tree death); ANOVA (analysis of variance)

**Contributions of bark and wood respiration to the total CO<sub>2</sub> flux from logs**

The mean corrected rates of CO<sub>2</sub> flux from the various log components (bark vs. wood) were significantly different among the TTD groups (Figure 3). The mean corrected rate of CO<sub>2</sub> flux from the exposed wood for fresh logs was significantly lower than that for slightly and moderately decayed logs (15 ± 2 vs. 28–37 mg C m<sup>-2</sup> h<sup>-1</sup>), as shown in Figure 3. The mean rate of CO<sub>2</sub> flux from the bark of moderately decayed logs (3.2 ± 0.4 mg C m<sup>-2</sup> h<sup>-1</sup>) was much lower than that from fresh and slightly decayed logs (6.8–9.5 mg C m<sup>-2</sup> h<sup>-1</sup>). These results revealed an evident decrease in mean R<sub>bark</sub> values in relation to an increase in the TTD (Figure 3).

The contribution of bark respiration to the total CO<sub>2</sub> flux from log surfaces varied between 6 and 50%, depending on log species and TTD. The flux from the bark of fresh logs contributed the largest share to the total CO<sub>2</sub> flux from log surfaces (40 ± 5%). The contribution of bark respiration of slightly and moderately decayed logs to the R<sub>log surface</sub> was significantly lower (15 × 16%) than that of fresh logs (Figure 5).



**Figure 5.** Contribution of bark and wood to total CO<sub>2</sub> fluxes from log surfaces in the various TTD groups. For this calculation, we used the corrected rates of CO<sub>2</sub> fluxes from cutaway bark and exposed wood surfaces after elimination of respiration bursts due to disturbance caused by sampling

## Discussion

The CO<sub>2</sub> emission rates from the undisturbed log surfaces varied, depending on the TTD (Figure 3). The rate of CO<sub>2</sub> fluxes from CWD (i.e. undisturbed log surfaces) reported in the literature for the majority of tree species in boreal or temperate forests is characterized by high spatial or temporal variability, which reflects the heterogeneity of environmental factors, mainly temperature and moisture (Harmon et al. 1986, Forrester et al. 2012, Herrmann and Bauhus 2013, Mukhin et al. 2015), in addition to CWD properties, such as decay class (Marra and Edmonds 1994, Wu et al. 2010, Safonov et al. 2012), physicochemical characteristics of wood and bark (Shorohova and Kapitsa 2014, Jomura et al. 2015), and bryophyte cover and fungal species composition (Progar et al. 2000, Forrester et al. 2015). The methodology applied may also cause variability in findings on the rate of CO<sub>2</sub> flux from CWD (Herrmann and Bauhus 2008). The physicochemical and biotic features of CWD are closely interrelated. For instance, the decay class incorporates the fragmentation of bark cover, chemical composition (content of C, N, lignin, cellulose, C/N ratio) and main physical properties of bark and wood (e.g. thickness, density and moisture), as well as the composition of the decomposer community (Harmon et al. 1986; Forrester et al. 2015, Russell et al. 2015). Moreover, fungi can strongly affect the moisture contents of wood substrate during the decay process (Griffin 1977, Boddy 1983). All the aforementioned factors could possibly explain the high variability in wood moisture observed in the slightly and moderately decayed logs in the present study (Table 2).

In the present study, the TTD influenced the variation in CO<sub>2</sub> fluxes from exposed wood and cutaway bark (Figure 3). The longest TTD in the present study was 10 y, which covers only a small part of the decomposition period for CWD in boreal forests (Shorohova and Kapitsa 2016), and much more variation of CO<sub>2</sub> fluxes would be expected in situ measurements. Studies including a higher number of replicates, covering a broader range of TTD periods are needed to shed light on this variation. According to our results, the respiration of wood was greater than that of bark, although the C/N ratio in bark was 6–7 times lower than that in wood (Table 2), and a narrow C/N ratio is usually favourable for decomposition processes of various plant materials (Zimmerman et al. 1995, Hobbie et al. 2012, Larionova et al. 2017). In the present study, the enhanced respiration of wood could be explained by the much larger volume of wood versus that of bark emitting more CO<sub>2</sub>. A laboratory study on bark and wood sawdust from 28 tree species reported a similar tendency (Allison 1965). In the study, the relative amount of carbon released as CO<sub>2</sub> from wood sawdust over 60 d was 1.4 times higher than that from bark. Some researchers observed a lower decomposition rate of bark as compared to that of wood *in vitro* (Rypaček 1957, Kaarik 1974). Other than differences in volume, variations in the respiratory activity of bark and wood may be explained by different proportions of chemical compounds, anatomical structures and probably different fungal community compositions (Pittman 2005, Saunders et al. 2011). High bark resistance, mainly of the rhytidome, to decomposition can be explained by the anatomical and chemical structure of bark. Secondary bark cork tissue is composed of dead phloem and phelloderm that protects the inner layers from fungal attack (Rypaček 1957). These tissues contain a high concentration of tannins, which are toxic to wood-decaying organisms (Rypaček 1957). The moisture content of bark is also lower than that of wood (Polubojarinov 1976, Shorohova et al. 2016), and bark has a suberin layer with low water and gas permeability. These characteristics of bark may inhibit the decomposition process (Parameswaran et al. 1976). On the other hand, the decomposition of bark starts earlier than that of wood because the decomposer organisms responsible for CWD decomposition must penetrate the bark to attack wood tissues (Johnson et al. 2014). A previous study reported that decomposition rates of sugar maple and beech bark were higher than those of their wood (Johnson et al. 2014). Bark of spruce, fir, cedar and pine decomposed faster than the wood from these trees, whereas the decomposition of birch bark was slower than that of wood (Harmon et al. 1986, Shorohova and Kapitsa 2014). Therefore, environmental factors considerably affect bark and wood decomposition rates in *in situ* experiments.

In our laboratory study with a nearly constant temperature (approximately 22°C) and relatively low atmos-



pheric humidity, CO<sub>2</sub> fluxes from bark were lower than those from wood. The contribution of bark to the total CO<sub>2</sub> flux from the undisturbed surfaces of log fragments in the slightly and moderately decayed groups (2–10 y TTD) did not exceed 30%. Clearly, atmospheric humidity in the laboratory cannot imitate the diversity of field conditions. However, on dry and warm summer days, a similar level of atmospheric humidity to that applied in the laboratory has been recorded in the study region. We assume that a decrease in air temperature of 10–15°C in the relatively humid field conditions of a middle boreal forest should not considerably affect the bark to wood respiration ratio. Nevertheless, a high air temperature can result in a more pronounced decrease in bark moisture as compared with that of wood. Hence, the contribution of bark to the total CO<sub>2</sub> flux from undisturbed log surfaces can fall during a dry and warm summer in comparison with a cool and wet spring and autumn. Complementary field investigations are required to figure out natural patterns of CO<sub>2</sub> fluxes.

We demonstrated clearly that the component integration method can be used successfully for the partitioning of total CO<sub>2</sub> fluxes from fresh and moderately decomposed CWD into two components: tree bark respiration and exposed wood surface respiration. According to our results, the contribution of bark to the total CO<sub>2</sub> flux from the log surface varied greatly (Figure 5). This finding demonstrates the effect of the TTD on the  $R'_{bark}$  to  $R'_{wood}$  ratio. We showed that within the studied interval (0–10 y TTD), the contribution of CO<sub>2</sub> fluxes from bark to CO<sub>2</sub> fluxes from log surfaces decreased with an increase in the TTD, which supports our hypothesis that tree bark of fresh logs would contribute a larger portion to the total CO<sub>2</sub> flux from CWD than tree bark of slightly and moderately decayed logs. The flux from tree bark of all the studied species contributed the largest portion to the total CO<sub>2</sub> flux from fresh logs. Information on the contributions of bark and wood to total CWD respiration is very important to refine estimations of CO<sub>2</sub> fluxes of CWD in forest ecosystems. We suggest that the degree of bark fragmentation is very important for correct estimations of CWD respiration flux. In a boreal forest, especially one composed of conifer tree species, bark cover can be highly or moderately fragmented or undisturbed. Spruce and pine phloem are consumed relatively quickly by early-arriving phloem feeders, mainly bark beetles. This leads to rapid sloughing of bark from the stem, especially in standing trees (Weslien et al. 2011, Ulyshen 2016). In cases of highly fragmented log bark cover, the total flux from CWD can be overestimated due to bark respiration being lower than that of wood respiration.

As shown in the present study, measurements of immediate rates of CO<sub>2</sub> fluxes (zero measurement) from wood and bark overestimated CO<sub>2</sub> fluxes (Figure 4). The

corrected values of  $R'_{bark}$  to  $R'_{wood}$  accounted for approximately 0.52 and 0.43 of immediate CO<sub>2</sub> fluxes from bark and wood, respectively. Previous studies on decaying logs from which wood samples had been removed, thereby exposing surface areas to the atmosphere observed visible pulses of CO<sub>2</sub> (i.e. respiration bursts) due to the release of a large amount of bound CO<sub>2</sub> (Chambers et al. 2001, Yoon et al. 2014). These respiration bursts caused by the removal of the wood samples from the decaying logs levelled off after approximately 3 h. Subsequently, the CO<sub>2</sub> emission rate did not decrease significantly over time, pointing to CO<sub>2</sub> partial pressure equilibration between high CO<sub>2</sub> concentrations in the pore matrix of the wood and the atmosphere (Chambers et al. 2001). In the same study, the CO<sub>2</sub> flux from undisturbed wood was only 65% lower than the CO<sub>2</sub> flux from wood samples immediately after their removal. In the present study, the respiration rates of bark and wood after CO<sub>2</sub> flux stabilization were by 2–2.4 times less than those immediately after disturbing the logs surface and cutting of tree bark. These findings can be explained by bark cutting causing greater mechanical disturbance as compared with that of wood sample removal. Similar to our findings, in a previous study (Yoon et al. 2014), the respiration rate of cut wood samples became relatively stable and did not change significantly in the 4–122 h period after CO<sub>2</sub> flux stabilization (Yoon et al. 2014).

From our results, we can conclude that stabilization of the respiration flux from bark usually occurred faster than that from exposed wood (Table 4). The rates of CO<sub>2</sub> fluxes from cutaway bark and exposed wood after 24 h did not differ significantly from those after 6 h (Figure 4). Furthermore, there was no significant reduction in the time taken for CO<sub>2</sub> stabilization from bark of slightly and moderately decayed logs as compared with that of bark of fresh logs. Therefore, to correctly estimate the respiration rate of removed CWD fragments or separate components of CWD after mechanical disturbance, CO<sub>2</sub> fluxes should be measured no earlier than 4–6 h or on the next day after chamber installation.

It should be noted that the component integration method adapted in the present study has some limitations. We consider that this method yields correct estimates of CO<sub>2</sub> flux and is applicable to fresh and moderately decayed CWD with relatively leak-free bark and wood (i.e. tight) when installing the chamber on the CWD surface. In cases of undisturbed bark cover or low fragmentation, the component integration method may not be suitable. Another limitation of the component integration method is related to log diameter, which has to exceed the chamber diameter.

CWD is ecologically important, especially in old-growth forests. Tree bark represents a natural barrier to the diffusion of CO<sub>2</sub> from decaying wood and influences

the amount of CO<sub>2</sub> emitted from the surface of CWD. We highlight that partitioning of the total CO<sub>2</sub> flux from CWD into separate components allows estimations of CO<sub>2</sub> emissions and the carbon balance in forest ecosystems to be refined, thereby enhancing understanding of the mechanisms governing CO<sub>2</sub> fluxes from CWD.

## Conclusions

The respiration rates of bark and wood differ greatly, as do their contributions to total CO<sub>2</sub> fluxes from the surface of CWD. In the present study, the respiration rate of bark was lower than the respiration rate of exposed wood. The contribution of bark to the total CO<sub>2</sub> flux from log surfaces varied between 40 and 15%, depending on the TTD. The component integration method was successfully adapted to partition bark and wood respiration. The main limitations of the applicability of the method are the shape and decay of CWD, presence of bark, and diameter of logs. To estimate the respiration rates of the separate components of CWD correctly, CO<sub>2</sub> fluxes should be measured no earlier than 4–6 h after bark removal or the day after chamber installation. Without partitioning wood and bark respiration, in cases of highly fragmented log bark cover typical of natural taiga forests, the total flux from CWD may be overestimated due to lower bark respiration in comparison with wood respiration. The partitioning of CO<sub>2</sub> fluxes from CWD improves our understanding of decomposition processes of woody debris and their effects on the forest carbon cycle.

## Acknowledgements

*This study was financially supported by the state order of the Forest Research Institute of Russian Academy of Sciences, the Russian Science Foundation (through grant #15-14-10023) and the Programme of Presidium of RAS (through grant #51). We cordially thank the staff of the Nature Reserve "Kivach" for organizing work in the field. We are thankful to researchers from the Analytic Laboratory of the Forest Research Institute of the Karelian Research Centre of RAS for analysing the bark and wood samples. We also thank the anonymous reviewers for valuable comments, which allowed us to improve our manuscript and data presentation.*

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