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Carbon Fluxes from Coarse Woody Debris in Southern Taiga Forests of the Valdai Upland

M. L. Gitarskiy[a], *, D. G. Zamolodchikov[b, d], V. A. Mukhin[c], V. A. Grabar[a], D. K. Diyarova[c], and A. I. Ivashchenko[d]

[a] *Institute of Global Climate and Ecology, Russian Federal Service for Hydrometeorology and Environmental Monitoring and Russian Academy of Sciences, Moscow, 107258 Russia*

[b] *Center for Forest Ecology and Productivity, Russian Academy of Sciences, Moscow, 117997 Russia*

[c] *Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*

[d] *Moscow State University, Moscow, 119234 Russia*

**e-mail: m.gitarskiy@gmail.com*

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Abstract—Studies in three typical forest biotopes of the Valdai Upland were performed to evaluate the stocks and surface area of coarse woody debris from spruce and birch (in linear transects), its colonization by xylotrophic fungi (during reconnaissance surveys), and CO_2 emission (by a chamber method). The stock and surface area were minimum in a paludal birch forest (46.4 m^3/ha and 960 m^2/ha) and maximum in a decay area of spruce forest (256.1 m^3/ha and 3761 m^2/ha, respectively). The assemblages of wood-decay fungi had a composition typically found in southern taiga forests. The total CO_2 flux varied from 145 kg C-CO_2/ha per year in the paludal birch forest to 462 kg C-CO_2/ha per year in small herb–green moss spruce forest. It is concluded that air temperature is an informative predictor of seasonal C-CO_2 flux rate from coarse woody debris.

Keywords: wood, spruce and birch, coarse woody debris, stock, decomposition, xylotrophic fungi, greenhouse gases, CO_2, flux, carbon emission

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With the adoption of the Paris Agreement on climate change (December 2015), nations across the globe have committed not only to restraining the growth of global average temperature to no more than 2°C above the preindustrial level but also to making efforts to reduce it to 1.5°C [1]. Therefore, it is necessary to reduce emissions of greenhouse gases, primarily carbon dioxide and methane, which is impossible without gaining a deeper insight into the biogeochemical cycle of carbon. Coarse woody debris (CWD) at different stages of decomposition is the second largest (after forest phytomass) terrestrial carbon source and has a major effect on carbon turnover in forest ecosystems [2–4]. During the past few decades, more detailed data have been obtained on the size of CWD pools in different zones and forest types [5–8], and intensive research has been carried out on drivers and zonal dynamics of wood necromass decomposition [9–12]. Meanwhile, being aware that dead wood decomposition is accompanied by CO_2 emission, the majority of researchers have concentrated on evaluating changes in CWD weight, while the data on instrumental measurements of CO_2 fluxes from this source are scarce [13, 14].

Gaseous emissions from CWD are an important component of the biogeochemical carbon cycle and should be taken into account in balance evaluation of carbon fluxes. This is important for accomplishing the objectives of the Paris Agreement concerning the necessity to markedly reduce atmospheric emissions of carbon-containing greenhouse gases resulting from human activities [15]. A gasometric approach is expedient for determining quantitative relationships between CWD decomposition rate and ecological factors, which has not always been possible until recently. This paper deals with the results of the study on emission fluxes of carbon in the form of CO_2 (C-CO_2) during SWD decomposition that was performed to update information on carbon expenditure budget in the main forest biotopes of the southern taiga subzone.

OBJECTS AND METHODS

The study area was in the Valdaisky National Park (the Valdai Upland, Novgorod oblast; 57°57.76′ N, 33°20.34′ E; 218 m a.s.l.). Studies were performed in forest biotopes prevailing in the southern taiga subzone: (1) a 110-year-old spruce forest of small herb–green moss type, *Piceeta parviherboso-hylocomiosa* (stand composition 9S1P, average tree diameter 37 cm, stocking density 0.4); (2) a 110-year-old paludal birch forest with spruce of herb–sphagnum type, *Betuleta herboso-sphagnosa* (6B3S1P, average tree diameter 25 cm in birch and 17 cm in spruce, stocking density 0.7); and (3) a decay area in a pure spruce stand (trees with an average diameter of 28 cm died off in 2002–2003). According to the ecofloristic classification, the spruce forest belongs to the association *Maianthemo bifoliae–Piceetum abietis*, and the birch forest, to *Climacio dendroides–Piceetum abietis*. The overstory in the decay area is absent; the understory and undergrowth (on average, 4.5 m tall, crown closure 0.4) are dominated by rowan, with insignificant proportions of spruce, birch, elder, and buckthorn; large ferns and raspberry prevail in the lower layer. There also are well-lit open patches with accumulations of CWD.

The assessment of CWD stock and measurements of CO_2 emission from it were performed as described [16], with modifications [17], in 2012 to 2014. Three linear transects extending in arbitrary directions for 40 to 180 m were established in each biotope. All fragments of CWD (no less than 2 cm in diameter) found on the transects were species-identified and examined to record their length, base and top diameters, and stage of decomposition according to Tarasov [18]:

Stage 1: bark is undamaged, needles are retained on branches, wood is without rot but sometimes blotched.

Stage 2: bark is mainly undamaged, most of thin branches are lost; core wood is usually healthy, but sap rot may be found; plant seedlings, mosses, fungal fruiting bodies occur on bark.

Stage 3: bark is falling off or absent, exposing healthy wood; stem retains its weight; some of preserved first-order branches are longer than stem diameter; dwarf shrub–moss cover is well developed, with plant roots penetrating sapwood.

Stage 4: sapwood is absent, fragment begins to lose shape; core wood is rotten, bark is lost almost completely; preserved first-order branches are shorter than stem diameter; stem loses weight and is covered by self-sown herbs, dwarf shrubs, and mosses.

Stage 5: fragment has lost structural integrity, its remains are almost buried in litter or under herb–moss vegetation and penetrated by plant roots; products of wood decomposition are humified.

The results were processed using the computer models by Grabovskii and Zamolodchikov [17] to calculate specific values of wood necromass stock and surface area at each decomposition stage.

The species composition of xylotrophic fungi was determined in the course of reconnaissance surveys and detailed censuses in July 2015, on the same CWD fragments that were used to measure CO_2 fluxes. These measurements in the spruce forest and decay area were made in April to September 2014 and 2015, and in the birch forest, in July 2014 and 2015. In each biotope, an area of no less than 0.1 ha was found that contained CWD of the dominant tree species at all stages of decomposition. Measuring chambers (nontransparent cylinders 10 cm in diameter and 9–15 cm high) were inserted in CWD fragments with a diameter close to the average tree diameter in the stand, using no less than tree fragments at each stage of decomposition. The chamber was hermetically sealed with a lid, and CO_2 concentration was measured with an AZ 7752 handheld CO_2 meter (AZ Instrument, Taiwan; resolution 1 ppm, measuring range 0–2000 ppm). Information recorded during each measurement included its duration (no less than 3 min), the initial and final CO_2 concentrations in the chamber, and temperature within the CWD fragment (no less than 6 cm from the surface), which was measured with a TM 100 digital thermometer (HM Digital, Korea) Data on air temperature were obtained from the nearby Valdai weather station.

The results were recalculated into values of C-CO_2 flux from CWD surface within the measuring chamber by the Mendeleev–Clapeyron equation [14]:

$$DC = \frac{12 \times 10^{-6} \times DM \times P \times V}{8.314(t + 273)},$$

where DC is change in the weight of carbon in the chamber, g; 12, the molar mass of carbon, g C/mol; 10^{-6}, ppm to 1/ppm conversion factor; DM, change in CO_2 concentration in the chamber, ppm; P, atmospheric pressure, Pa; V, chamber volume, m^3; 8.314, universal gas constant, Pa m^3/K mol; t, air temperature, °C; and 273, Celsius to Kelvin conversion factor.

The daily rate of carbon flux (g C-CO_2/m^2) was estimated by relating DC to the time of exposure and the base area of the chamber, and the results for each composition stage were averaged. These values and data on the surface area of CWD at corresponding stages were used to calculate the magnitude of CO_2 fluxes.

The significance of pairwise differences between the series of measurements for consecutive decomposition stages in each biotope was estimated using the Mann-Whitney U test in the IBM SPSS Statistics program package.

The CO_2 emission–temperature relationships were evaluated in the spruce forest and decay area by calculating Pearson's correlation coefficient. The dependence of emission on air temperature (according to data from the Valdai weather station) was estimated from the correlation between their daily average values. Analysis of its dependence on the temperature of CWD fragment was based on the entire series of initial measurements. If several measurements in the same chamber were made during the day, the results were averaged for analysis. The null hypotheses of nonzero correlation were tested in STATISTICA 6.1 (StatSoft Inc.).

Table 1. Results of assessment of coarse woody debris in southern taiga forest biotopes

Stage of decomposition	Small herb–green moss spruce forest		Paludal birch forest		Decay area in spruce forest	
	stock, m^3/ha	surface area, m^2/ha	stock, m^3/ha	surface area, m^2/ha	stock, m^3/ha	surface area, m^2/ha
1	15.9	226.0	5.6	102.6	53.4	789.0
2	27.6	453.9	3.7	100.0	97.5	1416.4
3	48.7	743.8	2.6	83.7	78.2	1097.4
4	25.2	483.1	19.6	382.6	21.9	335.6
5	13.4	237.2	14.9	290.8	5.1	122.6
Total	130.8	2144.0	46.4	959.7	256.1	3761.0

Table 2. Significance levels (p) in pairwise comparisons of measured C-CO_2 fluxes between consecutive stages of wood debris decomposition by the Mann–Whitney test

Biotope	p			
	st. 1 vs. 2	st. 2 vs. 3	st. 3 vs. 4	st. 4 vs. 5
Small herb–green moss spruce forest	0.008	0.008	0.002	<0.001
Paludal birch forest	0.005	0.022	0.041	0.070
Decay area in spruce forest	–	0.068	0.032	0.037

RESULTS

Table 1 shows average values of the stock and surface area of CWD at different stages of decomposition. The highest and lowest values were recorded in the decay area and in the birch forest, respectively. Xylotrophic fungi on spruce deadwood were represented mainly by *Fomitopsis pinicola* (Sw.) P. Karst. (on 54% of all CWD fragments), *Trichaptum abietinum* (Dicks.) Ryvarden (19%), and *Fomitopsis rosea* (Alb. & Schwein.) P. Karst. (9%); on birch deadwood, *Fomes fomentarius* (L.) Fr. (51%) and *Fomitopsis pinicola* (Sw.) P. Karst. (14%). The same composition of dominant xylotrophic fungi has been described for southern taiga forests of Western Siberia, where *F. pinicola*, *F. rosea*, *and T. abietinum* are the main decomposers of Siberian spruce wood, and *Fomes fomentarius* is the main decomposer of downy birch wood [19]. In our opinion, the above species of xylotrophic fungi are typical of southern taiga spruce and birch forests of Russia.

A total of 239 measurements of CO_2 emissions were made over 2 years: 133 in the spruce forest, 43 in the birch forest, and 63 in the decay area. The number of measurements (n) at individual stages of CWD decomposition varied from 4 to 46, since not all stages were present in the biotopes in different years (stage 1 was especially difficult to find). Table 2 shows significance levels (p) in pairwise comparisons of measured C-CO_2 fluxes between consecutive stages of wood debris decomposition by the Mann–Whitney U test. In most cases, differences between the fluxes from two consecutive stages are significant.

Seasonal measurements of daily average C-CO_2 fluxes in the spruce forest and decay area showed that the rate CO_2 emission started to increase in April, reached a peak in June in the decay area and in July to August in the small herb–green moss spruce forest, and decreased gradually. Similar dynamics of CO_2 emission from dead standing spruce trees were observed in a spruce forest of sphagnum–bilberry type [13].

Despite variation in the absolute values of CO_2 emission, certain tendencies could be detected in its changes depending on the stage of CWD decomposition (Fig. 1). In the spruce forest, CO_2 emission gradually decreased from a maximum at stage 1 to a minimum at stage 5, with stage 4 being out of trend (Fig. 1a). In the decay area, the rate of emission at stage 4 was also almost twice higher than at stage 5, but its values at stages 2 and 3 showed a different pattern, compared to that in the forest (Fig. 1b). This may be explained by a different course of mycogenic decomposition of spruce necromass in the decay area, where illumination level and air temperature were higher and moisture level was lower than under the forest canopy.

In the paludal birch forest, C-CO_2 emission from CWD (birch) was minimum at stage 1, increased to a maximum at stage 2, and then decreased again (Fig. 1c).

Air temperature at the time of measurements changed during the growing season from a minimum of 4.5°C in late April to a maximum of 21.6°C in mid-June, averaging 19.8°C in June, 19.7°C in August, and

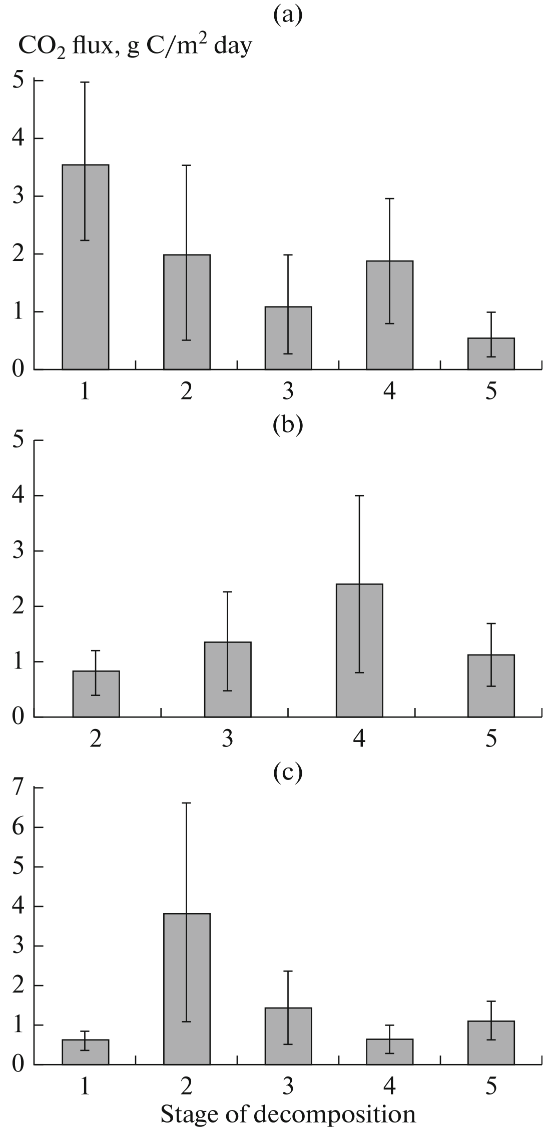

Fig. 1. Average values and variation of daily C-CO_2 fluxes from coarse woody debris at different stages of decomposition (a) in small herb–green moss spruce forest and (b) decay area (spruce wood) and (c) paludal birch forest (birch wood). Vertical lines show root-mean-square deviation.

17.9°C in September. The internal temperature of CWD (spruce) in July 2014 and 2015 varied from 13.3°C to 24.9°C under the spruce forest canopy and from 18.5°C to 30.1°C in the decay area.

DISCUSSION

Since the assessment of CWD was made on only three transects, the resulting data are insufficient for verifying the statistical significance of parameters shown in Table 1. Nevertheless, they allow us to consider trends in the accumulation of woody debris in in southern taiga forest biotopes. With regard to stock and surface area, CWD at stage 3 of decomposition is prevalent in the small herb–green moss spruce forest (≥35%), and that at stage 4, in the paludal birch forest (≥40%). In contrast, the greater part of CWD in the decay area (≥67%) is at stages 2 and 3, which is probably due to changes in illumination level and moisture supply after overstory die-off. Xylolysis of large CWD fragments in the boreal zone may continue for several decades [3, 4, 10, 18, 20]. Phytopathogens and xylophagous insects also contribute to increase in the amount of wood necromass, especially in pure spruce stands [21, 22].

The daily C-CO_2 flux from CWD is highly variable at all stages of decomposition. The observed changes in its values can be due in part to differences in assigning a given CWD fragment to a certain stage. The emission of CO_2 from woody debris is the result of respiratory activity of decomposer organisms, primarily of wood-decay fungi, which account for about 75% of its amount released to the atmosphere [7, 23, 24]. Xylotrophic fungi are a unique group of organisms that has a biospheric significance, and their role as the main decomposers of wood has not yet been fully recognized [9, 25]. Their respiratory activity and, hence, the rate of CO_2 emission from wood necromass depends on the rate of substrate colonization, temperature, moisture, and the size and location of CWD [24, 26, 27].

The lowest rate of CO_2 emission recorded for birch CWD at stage 1 can be explained by poor accessibility of freshly fallen wood to xylophagous insects and decomposer organisms. In turn, the increase in CO_2 emission upon transition from stage 3 to stage 4 of spruce CWD decomposition is a consequence of biochemical changes contributing to activation of xylotrophic fungal assemblages. The general decline of emissions at the final stages of mycogenic xylolysis is explained by decrease in the abundance of micro- and macroorganisms involved in wood decomposition because of impairment in the accessibility and nutrient properties of food substrate upon transformation of wood remains into soil detritus.

The recorded values of daily C-CO_2 fluxes from CWD agree well with those obtained under similar site conditions in southern taiga forests [13] and old-growth conifer forests of the northwestern United States, which are in the range of 2.7–8.3 g C-CO_2/m^2 [28]. The diversity of microdecomposer communities in the course of heterotrophic succession reaches the highest level at the middle stages of CWD decomposition [29], which may provide for their mutual suppression as well as to activation of the overall CO_2 flux.

Analysis of the temperature dependence of CO_2 fluxes shows that a rise in air temperature can stimulate emission from CWD: correlation coefficients between monthly average values of air temperature and C-CO_2 flux were 0.77 ($n = 12$, $p = 0.004$) in the

Table 3. Annual carbon fluxes from coarse wood debris at different stages of decomposition in southern taiga forest biotopes, kg C-CO_2/ha

Stage of decomposition	Small herb–green moss spruce forest	Paludal birch forest	Decay area in spruce forest
1	103	8	–
2	117	49	146
3	108	15	191
4	116	31	103
5	18	42	18
Total for biotope	462	145	458

spruce forest and 0.73 ($n = 11$, $p = 0.011$) in the decay area. These coefficients reflect the relationship of seasonal variation in the rate of CO_2 flux and the dynamics of temperature conditions.

The results concerning the dependence of CO_2 emission on the internal temperature of CWD are ambiguous. In the spruce forest, this temperature was found to have a positive influence on CO_2 flux: the correlation coefficient was 0.41 ($n = 77$, $p = 0.0002$). However, no significant correlation between these parameters was revealed in the decay area: the correlation coefficient was –0.008 ($n = 44$, $p = 0.957$). The absence of correlation may be explained to the simultaneous manifestation of two effects: (1) temperature stimulation of CO_2 emission in shaded CWD fragments with relatively low internal temperature and (2) inhibition of the activity of xylotrophic fungal complex by high temperatures, which were recorded in CWD fragments exposed to direct sunlight in open areas. The highest temperatures in CWD fragments from the decay area reached 30°C, compared to no more than 24°C in the spruce forest. It should be noted that measurements of the internal temperature were made only at the peak of growing season (July), and its variation was accounted for not by seasonal factors but by specific features of the location of CWD fragments. On the whole, the temperatures of air and decaying wood are informative predictors of the rate of seasonal CO_2 emission from CWD in southern taiga spruce biotopes.

The annual emission of CO_2 to the atmosphere depends not only on the rate of wood colonization by xylotrophic fungi but also on the stocks of SWD at different stages of decomposition. The frost–free period in Valdai forests is 128 days [30]. This period was taken as the duration of the annual activity cycle of wood-decay fungi for calculating annual C-CO_2 fluxes based on the data on daily average emission rates and surface area of CWD at different stages of decomposition (Table 3). The greatest contributions to the total annual C-CO_2 flux were estimated for CWD at stages 2 and 4 in the spruce forest, at stages 2 and 3 in the decay area, and at stages 2 and 5 in the paludal birch forest. The total flux was found to be the highest in the spruce forest, slightly lower in the decay area, and the lowest in the birch forest.

Old-growth forest biotopes chosen for this study are typical for the southern taiga subzone, and decomposition of fallen spruce and birch wood in these biotopes is accomplished by characteristic assemblages of xylotrophic fungi. Therefore, the reported data on the stocks and surface area of CWD and CO_2 emission from it at different stages of decomposition may be used for characterizing similar natural landscapes.

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