DYNAMICS OF *PICEA ABIES* MORTALITY AND CO_2 AND CH_4 FLUXES FROM SPRUCE TREES DECOMPOSITION IN THE SOUTHWEST OF THE VALDAI UPLAND, RUSSIA

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A mass decline of *Picea abies* (hereinafter – spruce), often associated with outbreaks of *Ips typographus*, is one of the main reasons for the reduction of spruce forests. In turn, dry and fallen trees can be both stock and source of greenhouse gases at various stages of decomposition. In our study, using an unmanned aerial vehicle, we evaluated the dynamics of spruce decline in two forest types in the southwest of the Valdai Upland (Central Forest State Nature Reserve, Russia), namely *Sphagnum*-bilberry forests and nemoral spruce forests. It was found that the rate of decline in *Sphagnum*-bilberry spruce forest was much higher than in nemoral spruce forest. By the fourth year after a windfall on 0.13 km^2, 913 spruce individuals had withered in *Sphagnum*-bilberry forest and 66 ones in the nemoral spruce forest. Based on direct measurements of greenhouse gas fluxes by chamber method on dead trunks and coarse woody debris, it was found that in relative values the highest amount of CO_2 is emitted by coarse woody debris of the decay classes 3–4 (800–1800 mg $CO_2 \times m^{-2} \times h^{-1}$). Deadwood and coarse woody debris from the first decay classes are assumed to be a source of CH_4 (0.0008–0.0070 mg $CO_2 \times m^{-2} \times h^{-1}$), and from classes 3–5 they are a stock (from -0.0070 mg $CO_2 \times m^{-2} \times h^{-1}$ to -0.0009 mg $CO_2 \times m^{-2} \times h^{-1}$). When converted to the total surface areas of deadwood and coarse woody debris of the study sites, it was found that coarse woody debris of the decay classes 3–5 (2.3–13.6 kg $CO_2 \times h^{-1}$) made the highest contribution to the integral CO_2 emission, and deadwood (67 mg $CH_4 \times h^{-1}$) made the highest contribution to the CH_4 emission. Significant differences in greenhouse gas fluxes were found both between deadwood and decay classes of coarse woody debris, and between fluxes from deadwood and coarse woody debris of individual decay classes in various forest types. The results have shown the importance of considering deadwood and all available decay classes of coarse woody debris when estimating greenhouse gas fluxes from dead timber and the contribution of debris to the carbon cycle in forest ecosystems.

Key words: carbon dioxide, chamber method, coarse woody debris, methane, spruce forest, unmanned aerial vehicle

Introduction

Deadwood and coarse woody debris are the second largest carbon reservoir in forest ecosystems after living phytomass (Kudeyarov et al., 2007). Large woody debris (LWD) contains up to 8% of the biogenic carbon of the world's forest ecosystems (Pan et al., 2011). The decomposition of debris by fungi, which can provide up to 75% of the CO_2 emission flux in boreal forests, and microorganisms emits carbon in the greenhouse gases CO_2 and CH_4 (Burova, 1986; Mukhin & Voronin, 2007; Mukhin et al., 2010). If CO_2 fluxes from dead timber are purely emissive, then depending on the prevalence of aerobic or anaerobic conditions of decomposition of coarse woody debris (CWD), it can serve as both source and stock of methane (Warner et al., 2017; Mukhortova et al., 2021). It should be noted that coarse woody debris is a very dynamic pool, constantly open to both inflow and loss, due to its decomposition. With massive forest mortality occurring worldwide (Johnson et al., 1986; Allen et al., 2010; Kharuk et al., 2015; Young et al., 2017; Sippel et al., 2018), an increase in aboveground and belowground dead timber pools in forests can lead to changes in the carbon balance structure of forest ecosystems (Schmid et al., 2016; Karelin et al., 2020).

Studies of greenhouse gas fluxes caused by decomposition of coarse woody debris have been conducted for some time, but most of the research has been done in North America. Flux estimates have mostly been obtained under laboratory conditions (Wang et al., 2002; Rinne-Garmston et al., 2019) or by indirect computational methods (Kapitsa et al., 2010; Harmon et al., 2011). Meanwhile, there are relatively few studies of CO_2 fluxes from large woody debris and deadwood under natural conditions in the Eurasian boreal zone (e.g. Molchanov et al., 2011; Safonov et al., 2012; Kahl et al., 2015; Gitarskiy et al., 2017), and the authors have not found any direct measurements of methane fluxes from debris in the Russian Federation. To fill this gap in the southwestern part of the Valdai Upland, we conducted experimental studies aimed to assess the fluxes of methane and carbon dioxide between the atmosphere, coarse woody debris and deadwood.

Material and Methods

Experimental studies were performed under natural conditions on the territory of the Central Forest State Nature Reserve – CFSNR (Russia, Tver Region, Nelidovsky district). The CFSNR is located in the southwestern part of the Valdai Upland (56.61°–56.42° N, 32°72°–33.03° E) in a region of moderate continental climate. The average annual (1963–2016) temperature is 4.4°C; the average monthly temperature is -8.5°C in January and +17.2°C in July; the average annual rainfall is 750 mm. According to Aleksandrova & Yurkovskaya (1989), the CFSNR is located in the Severodvinsk-Verkhnedneprovskaya subprovince of the North European taiga province, in the southern taiga forest belt.

The average monthly temperature in June, July and August 2021 was 17.8°C, 19.4 °C and 16°C, respectively, which is 16%, 13% and 4% higher than the long-term average value. The total monthly precipitation of the summer period (243 mm) was 4% below the multiyear average value. Thus, the weather conditions of the study period can be characterised as hot and close to the climatic norm in terms of moisture conditions.

Observations of gas exchange were carried out in two forest types (Fig. 1) with domination of *Picea abies* (L.) H.Karst. (hereinafter – spruce), namely paludified spruce forest (PSF) and nemoral spruce forest (NSF). PSF is under conditions of considerable overwatering with a high-water table during the summer season (40–50 cm), and it is located in a depression of a flat watershed. Peaty-gley soils (Albeluvisols Histic) have a peat horizon of 30–50 cm and a well-defined gley horizon. The canopy of the woody vegetation is represented mainly by spruce with a small amount of *Betula pendula* Roth. Spruce belongs to the fourth class of bonitet. Taking into account the undergrowth, the average diameter at breast height (1.3 m) (hereinafter – DBH) of spruce is 21 cm, the height is 16.6 m. The density of the spruce stand is 60 000 specimens/km^2. The area of the spruce community is 0.13 km^2.

NSF is located 2 km southwest of PSF in a more drained environment with a 1.5–2.0-m water table. Soils are sod-pale-podzolic (Albeluvisols Umbric). In addition to spruce, *Acer platanoides* L. and *Sorbus aucuparia* L. dominate the forest stand (Table 1). Spruce has the second class of bonitet. Including undergrowth, the average DBH of spruce is 24.4 cm, the height is 17.1 m. The density of the spruce stand is 9000 specimens/km^2. This site is considerably larger than in PSF, so a circle-shaped area equal in size to PSF (0.13 km^2) with a diameter of 406 m and centered at the Eddy covariance 2019 microclimatic station was chosen to compare the amount of deadwood in the two types of spruce forests (Mamkin et al., 2019).

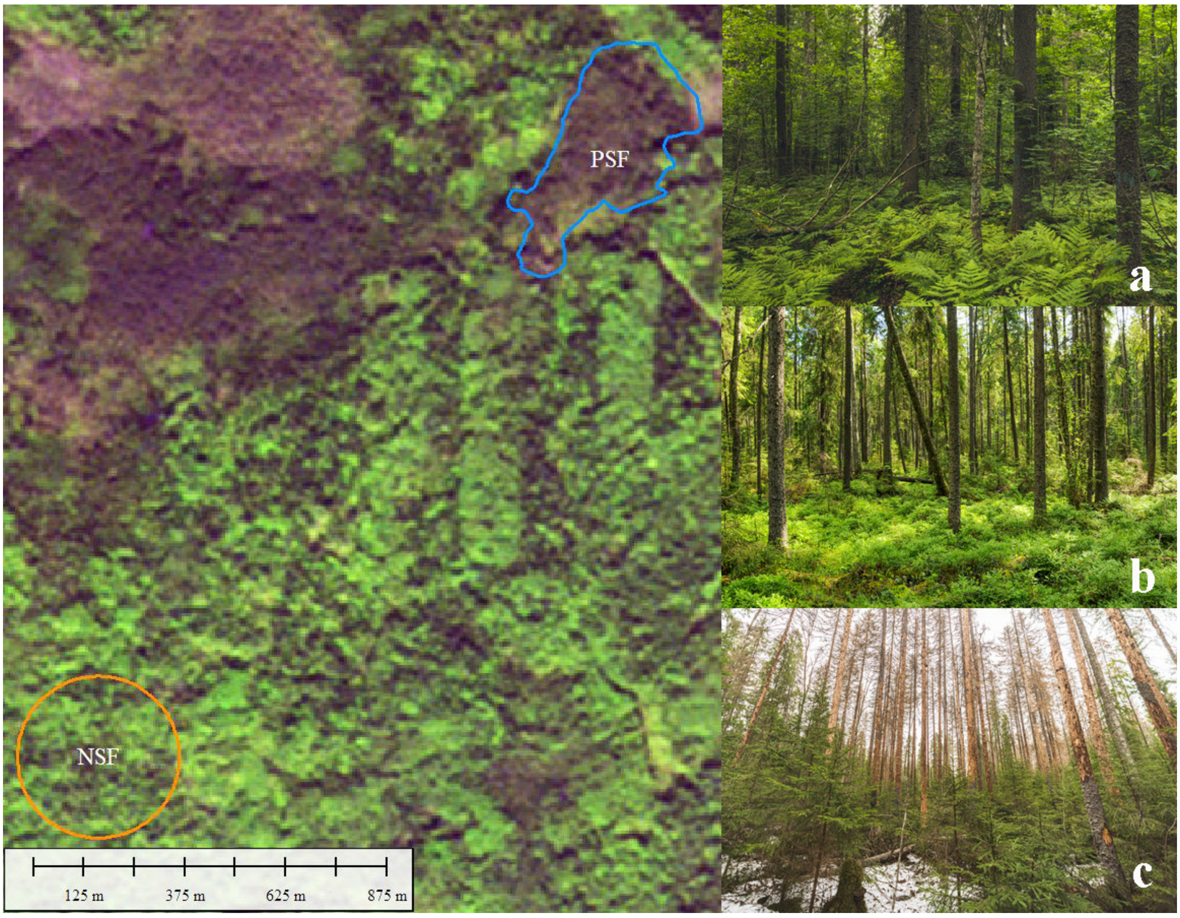

Fig. 1. Scheme of the location (RapidEye) and photos of the observation objects. Designations: a – nemoral spruce forest (NSF), b – typical paludified spruce forest (PSFt), c – decline of the paludified spruce forest (PSFd) in the Central Forest State Nature Reserve, Russia.

Table 1. Predominant vegetation in two spruce forest types in the Central Forest State Nature Reserve, Russia

Site	Canopy and understory	Herb layer	Coarse woody debris
PSF	*Picea abies* (L.) H.Karst.	*Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L., *Carex globularis* L., *Sphagnum girgensohnii* Russow, *S. angustifolium* (Warnst.) C.E.O. Jensen, *S. divinum* Flatberg & K. Hassel (moss coverage 90%)	*Sphagnum angustifolium* (Warnst.) C.E.O. Jensen, *S. divinum* Flatberg & K. Hassel., *Pleurozium schreberi* Willd. ex Brid., *Hylocomium splendens* (Hedw.) Schimp.
NSF	*Picea abies* (L.) H.Karst., *Acer platanoides* L., *Populus tremula* L., *Sorbus aucuparia* L.	*Galeobdolon luteum* Huds., *Dryopteris cristata* L., *Oxalis acetosella* L.	*Oxalis acetosella* L., *Pleurozium schreberi* Willd. ex Brid., *Dicranum scoparium* Hedw., *Plagiomnium cuspidatum* (Hedw.) T. Kop.

Note: PSF – paludified spruce forest, NSF – nemoral spruce forest.

The hurricane that passed through the CFSNR area in 2017 led to a general weakening of trees, due to damage to the root system (oral report of employees of the scientific department of the CFSNR). This could be one of the reasons for the observed drying out of spruce since 2019, with further loss of individual trees to coarse woody debris.

The degree of decomposition of coarse woody debris was determined according to the classification of Tarasov (2002). Two spruce stands had no coarse woody debris of the first class (freshly fallen spruces). Spruces that had fallen in the previous few years, with partially preserved bark and mostly small branches, were classified as coarse woody debris of the second class (DC2). Spruces without bark, partially covered with mosses, only with skeletal branches were attributed to the third class (DC3). Spruces with a soft trunk, fully covered with moss, without branches were classified to the fourth class (DC4). Spruces, classified to the fifth class (DC5), had a strongly decomposed trunk, covered with moss, the shape of which is determined only by the general outline (Fig. 2).

The number of coarse woody debris of various degrees of decomposition was estimated in 2021 according to Grabovsky & Zamolodchikov (2012). In spruce forests, parallel 100-m transects were laid, being oriented from north to south (Fig. 3). Four transects were laid in PSF. Two of them passed through an area with a mass decline of spruce (PSFd), and two (background) sites passed through typical paludified spruce forest (PSFt). In the NSF, due to the insignificant amount of deadwood, two transects were laid, which passed through representative forest areas, including those with deadwood. The length as well as the minimum and maximum diameters of coarse woody debris of all decay classes higher than 5 cm in diameter were measured along transects for the coarse woody debris crossing it.

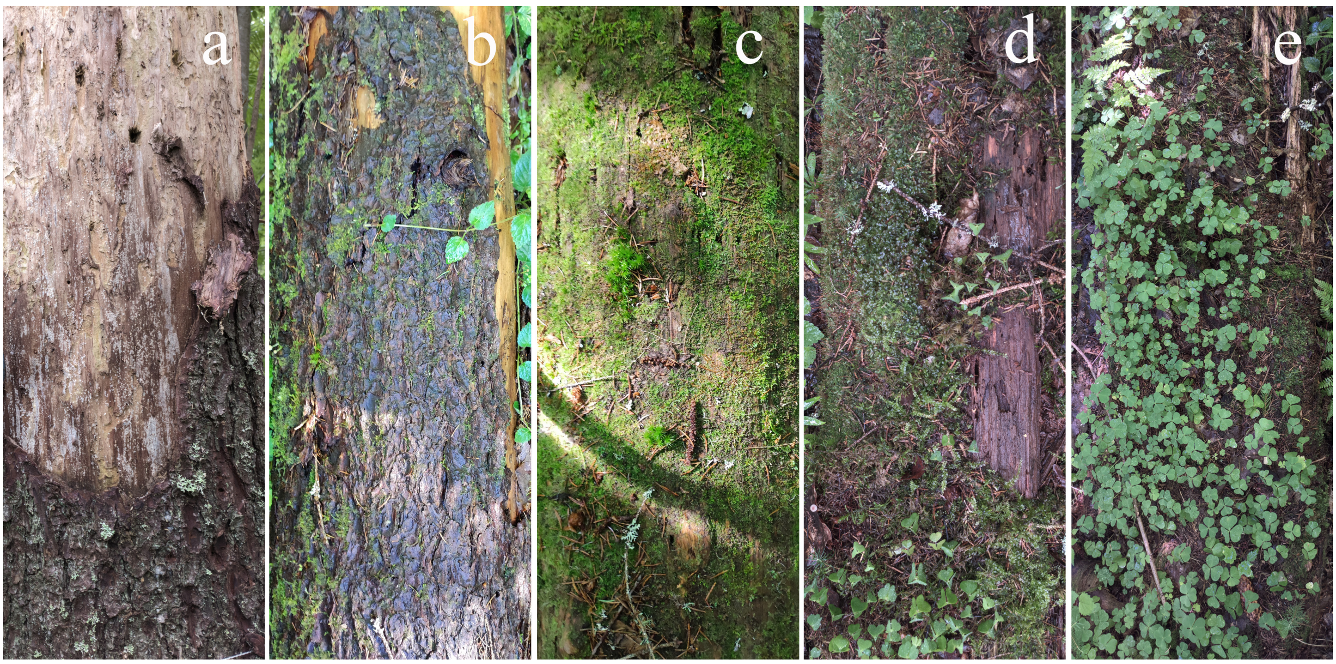

Fig. 2. Examples of objects for measurements of greenhouse gas fluxes in nemoral spruce forest (a – deadwood, b–e – coarse woody debris of decay classes 2–5) in the Central Forest State Nature Reserve, Russia.

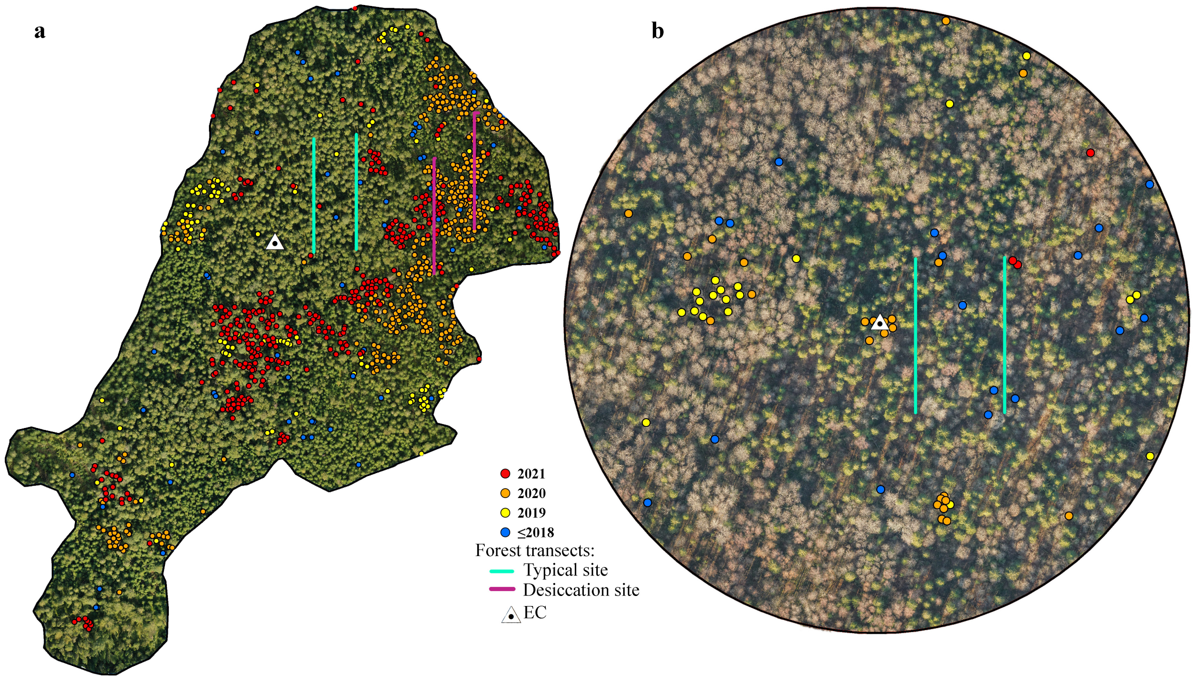

Fig. 3. Dynamics of spruce decline during 2019–2021 on orthophotos taken in PSF (paludified spruce forest) on 24.08.2021 (a) and in NSF (nemoral spruce forest) on 02.11.2021 (b) in the Central Forest State Nature Reserve, Russia. Designations: EC – Eddy covariance tower.

The total volume, surface area, and carbon stocks in coarse woody debris were calculated according to a model which main input parameters are: belonging to a species group (coniferous, hardwood, softwood), trunk length, maximum and minimum trunk diameters, decay class, transect length, prevailing wind direction and wind speed (Grabovsky & Zamolodchikov, 2012). The surface area of deadwood was estimated based on the average values of height and DBH of spruces in each forest type using the cone surface area formula. The wood density was measured by volume weight method. The wood humidity was measured with a Bosch Universal Humid moisture meter (Bosch, Germany). Data on spruce stand density and spruce decline dynamics were obtained from analysis of orthophotos taken in 2019–2021 using the Mavic 2 Pro unmanned aerial vehicle (DJI, China) in the Agisoft Photoscan Professional 1.4.5 software package (Agisoft LLC, Russia).

To measure CO_2 and CH_4 fluxes between deadwood, coarse woody debris of decay classes 2–5, and the atmosphere, we used plastic tubes of 20 cm in length and 10 cm in diameter, which were incised into the wood to a depth of 1–3 cm. The measurements have been performed in four replications for each class. To measure the fluxes, the mortise tube was closed with a cover equipped with a fan to ensure uniform mixing of air and a thermometer to measure the air temperature. CO_2 and CH_4 concentrations inside the chamber were measured using Li-7810 gas analyser (Li-Cor Inc., USA). Fluxes were calculated with the Table Curve 2D software (Systat Software Inc., USA) and based on the determination of CO_2 and CH_4 concentration change rate, using an exponential function (e.g. Ivanov et al., 2017). To calculate methane fluxes, coefficients of its molar mass and the conversion of ppb to ppm were used. Greenhouse gas fluxes were measured twice a month from June through August 2021 (24 measurements for each class) at 13:00–15:00. Data analysis has been carried out with the STATISTICA 12 (StatSoft Inc., USA) software.

Results

Dynamics of spruce decline and coarse woody debris parameters

The dynamics of spruce decline in the two forest types is shown in Fig. 4. Analysis of orthophotos of 2019–2021 show that in a 0.13 km^2 area in 2019, i.e. two years after the mass windfall of 2017, 155 dry spruces were observed in the paludified spruce forest, given an average crown projection area of 13 m^2, totaling an area of about 0.002 km^2. Of these, 53 spruces dried out in the previous year; this was determined by the remaining skeletal branches only. In 2020, the number of deadwood increased to 541 trees (0.007 km^2). In 2021, the area of spruce decline in PSF increased by 61% over 2020 to 0.0113 km^2 (913 trees), with 45 trees fallen to coarse woody debris. The average height of dry spruce trees was 24 ± 3 m; the DBH of spruce was 28 ± 7 cm.

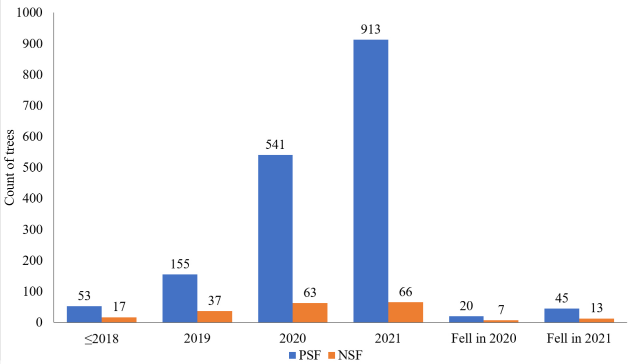

Fig. 4. The number of spruce trees declined and fallen in 2019–2021 in PSF (paludified spruce forest) and NSF (nemoral spruce forest) in the Central Forest State Nature Reserve, Russia.

A total of 37 dead trees (0.0005 km^2) were observed in the nemoral spruce forest in 2019, of which 17 ones had previously dried out. In 2020, the number of deadwood increased to 63 trees (0.0008 km^2), and to 66 trees in 2021, of which 13 ones are previously dead dry spruces fallen to coarse woody debris. The average height of deadwood in nemoral spruce forest was 31 ± 5 m; the DBH of trunks was 41 ± 12 cm.

In the species structure of coarse woody debris, spruce accounted for 75% in the background site and 89% in the dry site of the waterlogged spruce forest, and only 45% in the nemoral spruce forest. The area and volume of spruce coarse woody debris on the dried site exceed the ones in nemoral spruce forest by 3.1 times and 2.4 times, respectively, and by 3.8 times and 5.3 times, respectively, on the background site.

Calculations based on the model showed that the largest area, volume, and carbon stock correspond to the coarse woody debris of decay classes 2–5 on the windfall and dry site in PSFd (Table 2). The coarse woody debris stocks on the PSFt and NSF background sites were close in values and about 2–5 times lower than in PSFd. On all experimental sites, the highest amount of coarse woody debris belonged to decay class 4, while the minimum amount belonged to decay class 2.

Greenhouse gas fluxes

The results of measurements of CO_2 and CH_4 fluxes from the surface of deadwood and coarse woody debris at various stages of decomposition are shown in Fig. 5. The highest CO_2 fluxes were observed on coarse woody debris of decay class 3 in the waterlogged spruce forest (1278 mg $CO_2 \times m^{-2} \times h^{-1}$) and class 4 in the nemoral spruce forest (1825 mg $CO_2 \times m^{-2} \times h^{-1}$). The CO_2 fluxes from deadwood and from the surface of coarse woody debris of other decay classes were two or more times lower.

Measurements taken over three months showed no pronounced intra-seasonal dynamics of CO_2 fluxes from deadwood and coarse woody debris in all decay classes. During the summer season, in the two types of spruce forests, methane emission from deadwood and coarse woody debris of classes 2–3 and absorption in decay classes 4–5 was generally observed during the decomposition process. The absolute values of methane fluxes were close to zero, increasing negatively only for coarse woody debris of decay class 5.

Table 2. Model estimates of the parameters of spruce coarse woody debris of various decay classes in two types of spruce forest in the Central Forest State Nature Reserve in 2021

Decay class	2	3	4	5	Total
PSFt					
Surface area (m^2/km^2)	1.1	4.2	4.6	2.3	12.2
Volume (m^3/km^2)	0.02	0.15	0.16	0.11	0.45
Carbon stocks (t/km^2)	0.003	0.015	0.013	0.005	0.037
PSFd					
Surface area (m^2/km^2)	9.6	13.0	12.8	11.0	46.4
Volume (m^3/km^2)	0.46	0.60	0.66	0.65	2.37
Carbon stocks (t/km^2)	0.059	0.060	0.053	0.032	0.205
Wood density (g/cm^3)	0.42 ± 0.06	0.31 ± 0.06	0.30 ± 0.16	0.28 ± 0.16	–
NSF					
Surface area (m^2/km^2)	2.7	3.6	5.7	2.7	14.8
Volume (m^3/km^2)	0.22	0.22	0.37	0.16	0.97
Carbon stocks (t/km^2)	0.029	0.022	0.029	0.008	0.088
Wood density (g/cm^2)	0.45 ± 0.06	0.37 ± 0.15	0.30 ± 0.20	0.27 ± 0.15	–

Note: PSFt – typical paludified spruce forest, PSFd – declining paludified spruce forest, NSF – nemoral spruce forest.

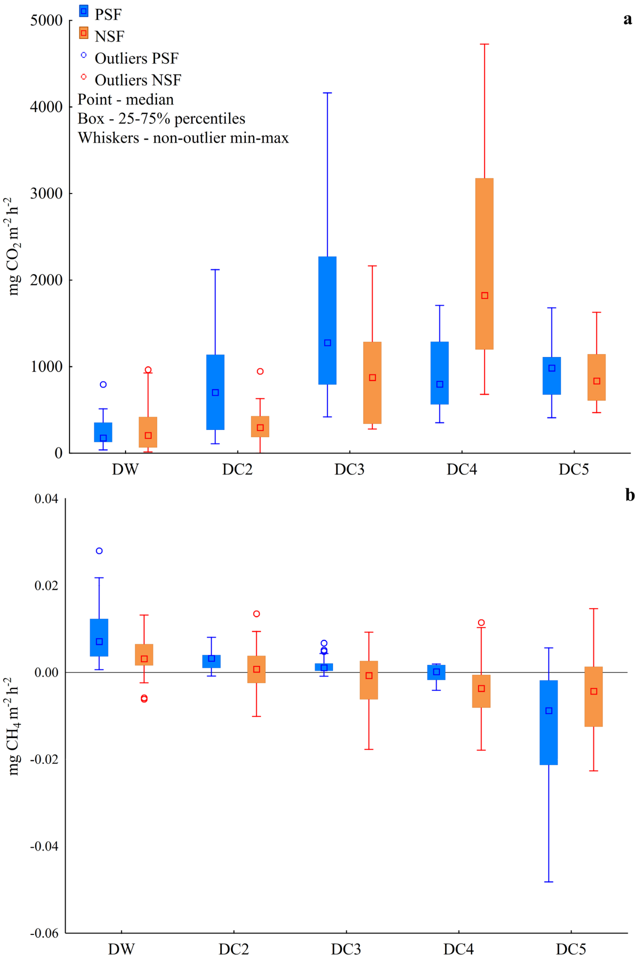

Fig. 5. Median fluxes of CO_2 (a) and CH_4 (b) from deadwood and coarse woody debris on the experimental sites during the 2021 summer season in the Central Forest State Nature Reserve, Russia. Designations: PSF – paludified spruce forest, NSF – nemoral spruce forest.

Table 3 summarises the significance level (*p*) achieved in a paired comparison of CO_2 and CH_4 fluxes in the two types of spruce forests using the Mann-Whitney U-criterion for adjacent stages of the decomposition process. In the waterlogged spruce forest, CO_2 fluxes differed significantly between all adjacent decay classes, except for differences between class 4 and class 5. CH_4 fluxes were not significantly different, only between decay class 2 and class 3. In the nemoral spruce forest, there were no significant differences in CO_2 fluxes, only between deadwood and coarse woody debris of decay class 2, and methane fluxes did not differ significantly for all adjacent decay classes. In the pairwise comparison of fluxes from deadwood and coarse woody debris of classes 2–5 between two forest types (Table 4), it was found that the differences were reliable for classes 2–4 for CO_2, and for deadwood and decay class 4 for CH_4.

For an integral area estimate of greenhouse gas fluxes from the coarse woody debris surface, the median flux values were multiplied by the total surface areas of coarse woody debris of various classes and deadwood separately for all experimental sites PSFt, PSFd, and NSF. The highest CO_2 emissions (2.3–5.3 kg $CO_2 \times h^{-1}$) were obtained on all sites for coarse woody debris of decay classes 3–5 with a maximum of 13.6 kg $CO_2 \times h^{-1}$ for decay class 4 in NSF. Also, the total values of CO_2 emissions from deadwood in the nemoral spruce forest were low.

Table 3. Significance level (*p*) for the Mann-Whitney U-criterion comparison of greenhouse gas fluxes from deadwood and coarse woody debris of decay classes 2–5 for various forest types in the Central Forest State Nature Reserve, Russia

	DW–DC2	DC2–DC3	DC3–DC4	DC4–DC5
PSF (CO_2)	**0.000233**	**0.001444**	**0.009772**	0.321730
NSF (CO_2)	0.279017	**0.000102**	**0.000021**	**0.000004**
All (CO_2)	**0.000480**	**0.000001**	0.107997	0.004526
PSF (CH_4)	**0.000935**	0.059202	**0.001377**	**0.000633**
NSF (CH_4)	0.074490	0.105525	0.197493	0.718216
All (CH_4)	**0.000740**	0.063233	**0.004728**	**0.003717**

Note: PSF – paludified spruce forest, NSF – nemoral spruce forest, DW – deadwood, DC2–DC5 – coarse woody debris of decay classes 2–5.

Table 4. Significance level (*p*) for the Mann-Whitney U-criterion comparison of greenhouse gas fluxes from deadwood and coarse woody debris between two forest types in the Central Forest State Nature Reserve, Russia

	DW	DC2	DC3	DC4	DC5
CO_2	0.862161	**0.010616**	**0.004501**	**0.000003**	0.775768
CH_4	**0.009969**	0.093047	0.246507	**0.012367**	0.184524

Note: DW – deadwood, DC2–DC5 – coarse woody debris of decay classes 2–5.

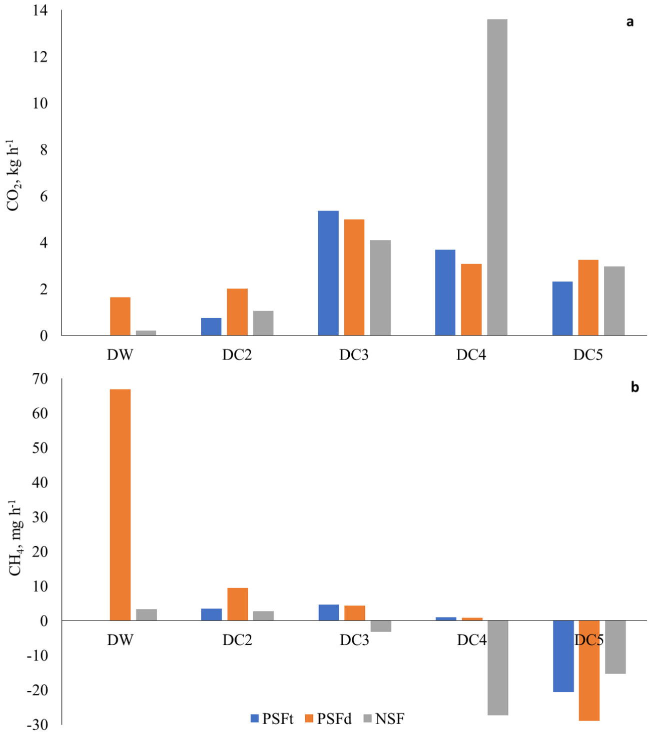

Fig. 6. Integral fluxes of CO_2 (a) and CH_4 (b) from deadwood and coarse woody debris in 2021 in the Central Forest State Nature Reserve, Russia. Designations: PSFt – typical paludified spruce forest, PSFd – declining paludified spruce forest, NSF – nemoral spruce forest, DW – deadwood, DC2–DC5 – coarse woody debris of decay classes 2–5.

The integral methane fluxes at the experimental sites differed in both values and direction (Fig. 6). The maximum positive values of methane fluxes were determined for deadwood in the waterlogged spruce forest (67 mg $CH_4 \times h^{-1}$). Lower (1–9 mg $CH_4 \times h^{-1}$) methane fluxes were obtained for DC2–DC4 in PSFt and PSFd, and DW and DC3 in NSF. The maximum integral values of methane oxidation were noted in DC5 in all forest types and in DC4 in NSF, the minimum integral values were found in DC3 in NSF.

The dependence of CO_2 and CH_4 fluxes on environmental factors was observed only for individual decay classes of coarse woody debris, namely for CO_2, r = 0.79 for density in DC3 and r = 0.63 for moisture in DC5, as well as for CH_4, r = -0.54 for density in DC4, and r = -0.6 for moisture in DW. In other cases, the values of the correlation coefficient were considerably lower. The overall correlation coefficients of wood moisture for all classes of coarse woody debris and deadwood in both forest types were r = 0.42 for CO_2, and r = -0.36 for CH_4. The dependence on air temperature was noted only for CO_2 and CH_4 fluxes from deadwood, where the correlation coefficients were r = 0.50 and r = 0.60, respectively. The dependence on wood temperature was observed in DC5 (r = 0.59) for CO_2, and in deadwood (r = 0.73) for CH_4.

Discussion

A mass decline of spruce forests, often associated with outbreaks of *Ips typographus* (Linnaeus, 1758) (Malakhova & Lyamtsev, 2014), is one of the main reasons for the reduction of spruce forest areas (Ulanova, 2000; Pukinskaya, 2016). A large number of authors attribute the dramatic increase in *Ips typographus* abundance to various climatic extremes, such as summer droughts (Solberg, 2004; Kharuk et al., 2015; Gessler et al., 2018) and hurricanes followed by windfalls (Wichmann & Ravn, 2001; Lindroth et al., 2009; Økland et al., 2016). In addition, one of the reasons is the primary weakening of trees by phytopathogens (Zhigunov et al., 2007). The CFSNR experienced summer droughts in 2015, 2018, and 2021, with a total precipitation of 40–75% of the average annual norm. There were also massive windfalls following hurricanes in late 2017 and 2021. According to Pukinskaya (2016) study, related to five-year observations in the Gladyshevsky Sanctuary (Leningrad Region, Russia) after the windfall of 4000 m^2, this forest gap expanded due to the focal decline in its edges, the merging of foci and the fall of deadwood, thereby increasing the area of the fall by 15 times over ten years. For eight years, the spruce stand on an area of 37 km^2 was affected in the Bavarian Forest National Park (Wermelinger, 2004). Our results have shown high differences between the number of dead trees in PSF, where spruce accounted for 80–90% of the forest stand of the upper tier, and in NSF, where spruce occupies no more than 19%. Over four years, the number of affected spruces increased by 17 times in PSF, and by 4 times in NSF, while in NSF spruce trees were approximately of the same age as the trees in PSF (i.e. 110–130 years). Abrazhko (1988, 1994), studied the effects of the 1972 and 1992 droughts in the CFSNR on close sites, did not find selectivity of spruce decline by age, too. Wermelinger (2004) also noted that the resistance of spruce to *Ips typographus* infestation is directly related to the bark thickness, which increases with an increasing of the DBH of trunks. The average diameter of the upper tier spruce trunks was 26 ± 7 cm in PSF, and 39 ± 12 cm in NSF.

The flat topography and location of the CFSNR in the watershed area affect temporary overwatering more than soil decline. Therefore, the highest destruction of the forest stand (solid fallout) here is associated with hurricanes during periods of overwatering, rather than with a decline during periods of drought, which is partially confirmed by Knohl et al. (2002). Abrazhko (1988), Pugachevsky (1992), and Bobrov et al. (1999) pointed out that spruce trees dry out from root soaking in abnormally wet years. The thin root layer of soil is a contributing factor to decline, too. According to Zolotarev (1950), when the root layer is thin, any deviation from the normal moisture regime often leads to a spruce decline.

Decline and decay of spruces contribute significantly to coarse woody debris accumulation, carbon stock redistribution and greenhouse gas emissions (Karelin et al., 2021). Measurements of coarse woody debris and deadwood respiration conducted on these sites in 2011 (Molchanov et al., 2011) showed considerable variation in CO_2 emissions for PSF (4–147 mg $CO_2 \times m^{-2} \times h^{-1}$, median: 20 mg $CO_2 \times m^{-2} \times h^{-1}$) and for NSF (10–926 mg $CO_2 \times m^{-2} \times h^{-1}$, median: 131 mg $CO_2 \times m^{-2} \times h^{-1}$), and it was noted that respiration of trunks with a larger diameter was more intense than those with a smaller diameter. In our study, in both forest types, scatters were close to NSF in 2011, and medians were higher in both cases than in 2011, namely 176 mg $CO_2 \times m^{-2} \times h^{-1}$ for PSF, and 207 mg $CO_2 \times m^{-2} \times h^{-1}$ for NSF, which also confirmed the higher CO_2 emissions from the larger diameter trunks. Additionally, the higher emission values are probably related to the warmer year of 2021 and measurements on large trunks. In the study of Molchanov et al. (2011), a maximum CO_2 emission has also been observed on coarse woody debris of classes 3–4, but the values obtained in it were 2–10 times lower than in our study. The studies carried out in the Novgorod Region, Republic of Karelia, and Primorsky Krai also show large variations in CO_2 emission values from coarse woody debris of decay classes 1–5, ranging from 84–165 mg $CO_2 \times m^{-2} \times h^{-1}$ (Mamai et al., 2018) to 60–1346 mg $CO_2 \times m^{-2} \times h^{-1}$ (Gitarskiy et al., 2017; Ivanov et al., 2018). Emissions from coarse woody debris of classes 2–3 were 300 ± 20 mg $CO_2 \times m^{-2} \times h^{-1}$ in spruce plantations in the United States of America (Vanderhoof et al., 2013), and 90–475 mg $CO_2 \times m^{-2} \times h^{-1}$ in spruce stands in Canada (Bond-Lamberty et al., 2002; Hagemann et al., 2010). In most cases, these results were also considerably lower than values established in our study for classes 2–5, namely 110–4160 mg $CO_2 \times m^{-2} \times h^{-1}$ (median: 890 mg $CO_2 \times m^{-2} \times h^{-1}$) in PSF, and 70–4730 mg $CO_2 \times m^{-2} \times h^{-1}$ (median: 845 mg $CO_2 \times m^{-2} \times h^{-1}$) in NSF.

Unfortunately, we have not found data on measurements of methane fluxes from trunks and coarse woody debris of spruce from the territory of the Russian Federation. Therefore, results of fluxes from other forest types have been taken for comparison. CH_4 fluxes from dead trunks (probably *Acer rubrum* L.) standing in water measured by Carmichael et al. (2018) were also mostly positive, but two orders of magnitude higher than our results (0.4 mg $CH_4 \times m^{-2} \times h^{-1}$), and CO_2 was 2.0–2.5 times lower (114.6 mg $CO_2 \times m^{-2} \times h^{-1}$) than our results. At the same time, Carmichael et al. (2018) noted that dead trunks acted as channels for methane from the water, which is probably confirmed by our data, because the methane release in PSF was 2 times higher than in NSF, and the groundwater level under trees in PSF was about 30–60 cm below the surface, compared to 1.5–2.0 m in NSF. According to Warner et al. (2017), hardwood trunks of coarse woody debris were primarily a source of methane during the first stages of decomposition (from -0.006 mg CH4 $\times m^{-2} \times h^{-1}$ to 0.052 mg CH4 $\times m^{-2} \times h^{-1}$), and stock during the later stages of decomposition (from -0.006 mg CH4 $\times m^{-2} \times h^{-1}$ to -30 mg CH4 $\times m^{-2} \times h^{-1}$), with average flux values of 18 ± 15 mg CH4 $\times m^{-2} \times h^{-1}$. CO_2 emission from the same coarse woody debris was 160–635 mg $CO_2 \times m^{-2} \times h^{-1}$, which was also close to our values in both cases. CO_2 fluxes from coarse woody debris of *Fraxinus nigra* Marshall were 2075 ± 315 mg $CO_2 \times m^{-2} \times h^{-1}$ according to Noh et al. (2019).

Considerable differences in carbon dioxide fluxes at various decomposition stages can be explained both by changes in such physical characteristics of wood as moisture capacity, density, and porosity, and by the number and species composition of wood-destroying organisms. Thus, in the early decomposition stages, CO_2 emissions are much lower than in stages 3–4 of the decomposition process, while the wood retains a high density and a small number of xylophages.

During the decomposition process, dead spruce wood goes from the source to the methane stock. At the same time, while in the wet PSF spruce becomes stock only at the fifth stage, in NSF it gradually passes to methane absorption already at the third stage of the decomposition. Probably, this explains the lack of statistical differences between the decay classes in NSF.

Conclusions

It was found that in recent years in the CFSNR there was a mass spruce decline, which may lead to a change in structure of the carbon balance between forest ecosystems and atmosphere. Measurements of greenhouse gas fluxes of CO_2 and CH_4 between the surface of deadwood and coarse woody debris in two types of spruce forests have shown that debris is a significant source of CO_2 for atmosphere. At the same time, depending on the stage of decomposition, debris can be both stock and source of methane. At the ecosystem level of averaging, taking into account the assessment of debris stocks and the forest types studied, the main source of CO_2 is coarse woody debris of decay classes 3–4, and the source of CH_4 is deadwood and coarse woody debris of decay classes 2–3.

The forest types selected for the study are typical for the southern taiga subzone of European Russia. The obtained estimates of parameters of deadwood and spruce coarse woody debris, as well as the fluxes of CO_2 and CH_4 between atmosphere and dead timber of various decomposition stages can be used in estimations of the carbon balance in spruce ecosystems located in similar climatic and edaphic conditions.

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ДИНАМИКА УСЫХАНИЯ *PICEA ABIES* И ПОТОКИ CO_2 И CH_4 ПРИ РАЗЛОЖЕНИИ ЕЛОВОГО ДРЕВОСТОЯ НА ЮГО-ЗАПАДЕ ВАЛДАЙСКОЙ ВОЗВЫШЕННОСТИ, РОССИЯ

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Массовое усыхание *Picea abies* (далее – ель), часто связанное со вспышками численности *Ips typographus*, является одной из основных причин сокращения площадей еловых лесов. Сухие и выпавшие деревья в свою очередь могут быть как стоком, так и источником парниковых газов на разных стадиях разложения. В данной работе с использованием беспилотного летательного аппарата были проведены оценки динамики усыхания ели в двух типах леса на юго-западе Валдайской возвышенности (Центрально-Лесной заповедник, Россия) – сфагново-черничном и неморальном ельниках. Было установлено, что скорость усыхания в сфагново-черничном ельнике была гораздо выше, чем в неморальном. К четвертому году после ветровала на 0.13 км^2 в сфагново-черничном усохло 913 елей, в неморальном – 66. На основе прямых измерений потоков парниковых газов камерным методом на сухих стволах и валеже ели было выяснено, что в относительных значениях наибольшее количество диоксида углерода выделяется валежом 3–4-го классов разложения (800–1800 мг CO_2 × м$^{-2}$ × ч$^{-1}$). Сухостой и валеж первых классов разложения предположительно является источником метана (0.0008–0.0070 мг × CO_2 м$^{-2}$ × ч$^{-1}$), а начиная с 3–5 класса – стоком (от -0.0070 мг × CO_2 м$^{-2}$ × ч$^{-1}$ до -0.0009 мг × CO_2 м$^{-2}$ × ч$^{-1}$). При пересчете на суммарные площади поверхности сухостоя и валежа исследуемых участков, было установлено, что в интегральной эмиссии диоксида углерода наибольший вклад оказывает валеж 3–5 классов разложения (2.3–13.6 кг CO_2 × ч$^{-1}$), а в эмиссии метана – сухостой (67 мг CH_4 × ч$^{-1}$). Были найдены достоверные различия в потоках парниковых газов как между сухостоем и классами разложения валежа, так и между потоками из сухостоя и валежа отдельных классов разложения в разных типах леса. Полученные результаты показали важность учета сухостоя и всех доступных классов разложения валежа при оценке потоков парниковых газов из мертвой древесины и вклада дебриса в углеродный цикл лесных экосистем.

Ключевые слова: беспилотный летательный аппарат, диоксид углерода, еловый лес, крупные древесные остатки, метан, метод камер