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CO₂ Efflux from the Stem Surface of Scots Pine under Various Growing Conditions

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Abstract—Evaluating temporal variability of CO_2 efflux from the tree trunks of Scots pine (*Pinus sylvestris* L.) are presented. The field measurements were performed by the chamber method in a swampy cotton grassy—sphagnum pine forest in Yaroslavl region and in a highly productive grassy—bilberry pine forest on well drained sandy soils in the Serebryaniy Bor forest service area in Moscow region. Tree trunk respiration was measured during several growing seasons under different weather conditions and groundwater level depths. The results showed that the CO_2 emission of living tree trunks in the southern European taiga forests exhibited clear seasonal and diurnal variation and it was a highly sensitive to changing ambient conditions (air temperature and groundwater level). The differences in the trunk respiration rate of trees of various growth classes for a swampy pine forest were also revealed.

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INTRODUCTION

The modern climate change and observed sustained growth of global temperature are attributed by most researchers to an increase of greenhouse gas concentration, and especially carbon dioxide (CO₂), in the atmosphere (IPCC, 2013). Terrestrial ecosystems, in particular forests, not only absorb and accumulate CO₂ from the atmosphere, but they are also an active source of CO₂ in the atmosphere (Luyssaert et al., 2007). CO₂ emission from the soil surface and plant canopy is determined by a number of biotic and abiotic factors and varies widely depending on the type of plant communities and their growing conditions (Malhi et al., 1999; Falge et al., 2002; Ibrom et al., 2006; Alferov et al., 2017; Zamolodchikov et al., 2017; etc.).

It is generally accepted that the CO_2 emission from the soil surface including the respiration of soil biota and plant roots, as well as the respiration of the aboveground photosynthetic biomass is the main natural source of CO_2 for the atmosphere in forest ecosystems (Lavigne et al., 1997; Law et al., 1999; Malhi et al., 1999). A significant contribution to the total ecosystem respiration can be also exerted by CO_2 emissions from the decomposition of dead wood (Molchanov et al., 2011; Safonov et al., 2012). The contribution of non-photosynthetic elements of living trees to the total emission of the above-ground forest phytomass is often ignored, although it can be large and range from 5 to 22% (Tselnicker et al., 1993; Zha et al., 2004). The temperature of vascular cambium of trees and the air temperature in the forest canopy are usually considered as the main factors affecting the rate of CO₂ emission from the surface of living tree trunks (Linder and Trong, 1981; Goulden et al., 1996). It has also been reported that the tree growing conditions (solar radiation regime, soil structure, groundwater level) and the rate of biomass growth can significantly affect the respiration rate of tree trunks (Molchanov et al., 2011). Based on an analysis of the pine growth dynamics under various growing conditions, Edwards and Zollins (1973) showed that the respiration rate of Scots pine trunks of growth class IV (suppressed trees) is about four times lower than that of trees of growth class I (with maximum growth rate). Some differences in the rate of CO_2 emission from the surface of tree trunks can be observed at different growing sesons. Particularly, it was shown for Siberian pine a clear dependence of the stem respiration rate in the summer months on leaf and shoot growth phenology (Zabuga and Zabuga, 2013).

Similar results were obtained for tree trunk respiration of Scots pine forests in eastern Finland (Zha et al., 2004), as well as in the pine forests of the central part of European Russia (Tselnicker et al., 1993). It was shown that the respiration rate of tree trunks changes little during the day in the autumn varying around $0.3 \,\mu$ mol CO₂/(m² s); however, the differences between night and day values can be quite large in summer, varying from 0.8 to 1.1 at night and from 1.0 to 1.7 μ mol CO₂/(m² s) in the daytime (Zha et al., 2004). Thus, the mean summer respiration rate of pine trunks can reach ~1.2 μ mol CO₂/(m² s).

A rather wide range of respiration variability of nonphotosynthetic parts of woody plants under various growing conditions and a significant lack of experimental data on CO₂ efflux in forest ecosystems still remain the main reasons to obtain new data on the spatial and temporal variability of tree trunk respiration of different species growing under various ambient conditions, as well as their dependence on environmental factors. They can be used not only for more detailed study of the CO₂ budgets in forest ecosystems, but also for interpretation of the existing data on ecosystem CO₂ fluxes obtained using modern monitoring systems, including those based on eddy covariance technique (Goulden et al., 1996; Ibrom et al., 1996; Falge et al., 2002; Luyssaert et al., 2007; Burba et al., 2016). In addition, there remains a need for adequate parameterization of the dependence of the CO₂ emission rate of woody plants on environmental factors for their further application in the carbon cycle models of local and regional scales (De Pury and Farquhar, 1997; Olchev et al., 2008, 2017; Kurbatova et al., 2008, 2009; Oltchev et al., 2008; Korzukhin, 2015).

The main goal of this study is to obtain new data on the seasonal and diurnal variability of CO_2 emissions from the trunk surface of Scots pine *Pinus sylvestris* L. growing under various conditions, as well as to develop a simple model describing the dependence of the respiration rate of Scots pine trunks on environmental factors.

MATERIALS AND METHODS

The measurements of Scots pine trunk respiration were carried out in the Serebryanii Bor forest service area of the Institute of Forestry, Russian Academy of Sciences, in Moscow region (from May to October 2011 and in May and November 2012), as well as at the Northern Forest Experimental Station "Gorodishche" of the Institute of Forestry of RAS, in Yaroslavl region (in May and June 2009, as well as in June and August 2011). In the Serebryaniy Bor forest station, the measurements were carried out in a 140-year-old grassy-bilberry pine forest of growth class I, growing on sod-weakly podzolic sandy loam soil at very deep soil groundwater level (GWL) ranged between 2.0 and 2.5 m. Trees of growth class I with a height of 26–29 m and a diameter of 40-45 cm were chosen for tree trunk respiration measurements.

At the Gorodishche forest station, the measurements were conducted in a swampy very suppressed cotton grassy–sphagnum pine forest of growth class Vb with a shallow-walled surface microtopography. The thickness of the peat deposit in the study area was ~1 m. The root necks of old pines were immersed in peat to a depth of 40–60 cm. The cotton grassy–sphagnum pine forest consisted of two generations of trees with an average age of 144 and 54 years and mean tree crown cover of ~30%. To study the CO₂ gas exchange from the tree trunk surface, the trees of different growth classes, i.e., the trees with high growth rate (growth class I) up to 13 m tall with bole up to 18 cm in diameter at breast height and the trees with very low growth rate (growth class IV) with a height of 7 m and diameter of 12 cm, were selected.

The CO_2 emission rate from the surface of the tree trunks was measured at both sites by the open chamber method (Edwards and Sollins, 1973; Rayment and Jarvis, 1997; Pumpanen et al., 2004; etc.). Sealed rectangular chambers from transparent plastic film with a base area of 200-250 cm² and a volume of 140-210 cm³ were installed on selected trees at a height of ~1.3 m on the north side of the tree to protect the chambers from heating by direct sunlight (Molchanov, 2010). The chambers were attached to the trees with plasticine of 0.8-1.0 cm thick. The inlet and outlet openings for the connecting tubes were located in the frame of the chambers from their different sides, which ensured uniform mixing of the air inside the chambers. The position of each chamber on the tree did not change during the entire observation period. A constant flow of ambient air through the chambers was maintained throughout the experiment at an average rate of 1 L/min. The air flow rate through each chamber was measured and corrected using a RS-3A flow meter (Russia).

The CO_2 emission rate from the stem surface was calculated as a function of the CO₂ concentration difference between outlet and inlet air, the air flow rate through the chamber, and the surface area of the chamber adjacent to the tree trunk (Molchanov, 2010; Molchanov et al., 2017). CO₂ concentrations were measured at 5 s time intervals using an LI-820 portable infrared gas analyzer (LI-COR Biosciences, United States). The data were stored with a 20 s averaging by the EMS data logger (Czech Republic) together with data on the soil and air temperature, air relative humidity, and incoming solar radiation. The serial connection of the measuring chambers to the gas analyzer was made using an automatic channel switching system based on a three-way switch that provided continuous air pumping through the chambers throughout the entire measurement period, preventing stagnation of air in the chambers during periods when gas exchange measurements were not carried out (Molchanov, 2010, 2014).

Date	GWL, m	Number of measurements	CO ₂ emission from μmol CC	the trunk surface, $D_2/(m^2 s)$	
Grassy-bilberry pine forest					
			Tree of growth class I		
25-31.05.2011	>2.0	120	1.19 ± 0.41		
27-31.07.2011	>2.0	231	2.06 ± 0.43		
01-09.08.2011	>2.0	408	1.72 ± 0.47		
06-15.10.2011	>2.0	111	0.91 ± 0.38		
28.04-21.05.2012	>2.0	1120	1.94 ± 0.58		
15-18.11.2012	>2.0	127	0.62 ± 0.11		
Cotton grassy-sphagnum pine forest					
			Tree of growth class IV	Tree of growth class I	
27-28.05.2009	0.04	58	1.22 ± 0.21	1.34 ± 0.18	
17-18.06.2009	0.07	48	0.91 ± 0.67	3.23 ± 0.72	
24-25.06.2011	0.15	230	1.55 ± 0.32	2.76 ± 0.68	
22-24.08.2011	0.43	60	0.58 ± 0.22	2.13 ± 0.49	

Table 1. Mean values and standard deviations of CO_2 emission from the surface of tree trunks in the grassy-bilberry and cotton grassy-sphagnum pine forests

GWL is the groundwater level.

RESULTS

Seasonal and Diurnal Variation in the Respiration of Pine Trunks

The results of CO₂ efflux measurements from Scots pine trunks indicate their pronounced seasonal variability. In the grassy bilberry pine forest (Serebryaniy Bor forest station) under sufficient soil moisture conditions during the entire growing season, the CO₂ emission from the trunk surface reached minimum rates in spring and autumn and the maximum rates in summer (Table 1). Whereas the average stem respiration rate in the spring at 20–25°C was $1.19 \pm 0.41 \,\mu$ mol CO₂/(m² s), it increased slightly to $2.06 \pm 0.43 \,\mu$ mol CO₂/(m² s) in summer months. In the fall, there was a steady decrease in CO₂ emissions down to $0.62 \pm 0.11 \,\mu$ mol CO₂/(m² s) in November.

In the swampy cotton grassy–sphagnum pine forest at the Gorodishche forest station, the seasonal dynamics of CO₂ emission changed from year to year, reaching maximum values in May–June (1.3– 3.2μ mol CO₂/(m² s) for trees of growth class I, and $0.9-1.8 \mu$ mol CO₂/(m² s) for trees of growth class IV) and gradually decreasing in July–August simultaneously with lowered GWL (Table 1). The stem respiration for trees of growth class I decreased in August to $2.1 \pm 0.5 \mu$ mol CO₂/(m² s), and for trees of growth class IV to $0.58 \pm 0.2 \mu$ mol CO₂/(m² s), respectively. At the same time, there was no significant difference between the CO₂ emission from the trunk surface of trees of growth class I in the cotton grassy–sphagnum and grassy–bilberry pine forests.

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The diurnal variability of CO₂ emission from the tree trunk surface for both stands was mainly influenced by daily temperature variation. The minimum values of the stem respiration rate were found in the cotton grassy-sphagnum pine forest at night and in the morning, and the maximum values were measured in the afternoon (2 p.m.) (Fig. 1). The minimum respiration rates in the grassy-bilberry pine forest were also observed at night and in the morning, while the CO_2 efflux maximum was shifted to a later time (with the first maximum at 3-5 p.m., and the second maximum in the evening). In the diurnal course, a close relationship between the trunk respiration and the air temperature was found for both experimental sites. There were also significant differences between the respiration rates of pine trunks belonging to different growth classes in the swampy cotton grassy-sphagnum pine forest. It was found, that the average CO_2 efflux rate from the stem surface of the Scots pine in the daytime under GWL >40 cm was almost three times higher for trees of growth class I than for trees of growth class IV $(2.4 \pm 0.6 \text{ and } 0.9 \pm 0.2 \text{ } \mu\text{mol CO}_2/(\text{m}^2 \text{ s}), \text{ respec-}$ tively) (Fig. 1).

The Dependence of the Respiration of Pine Trunks on Environmental Factors

The results of field measurements showed also that whereas the trees in the grassy-bilberry pine forest are characterized by well pronounced dependence of the respiration rate of tree trunks on the air temperature only (Fig. 2), the trees in the swampy cotton grassy– sphagnum pine forest depends on both the air tem-



Fig. 1. The diurnal course of air temperature and CO_2 emission from the Scots pine trunk surface in (a) the grassy-bilberry pine forest and (b) the cotton grassy-sphagnum pine forest in trees of growth classes I and IV with GWL of 48 cm. The average values of parameters and standard deviations from the mean value are shown. (1) Air temperature, (2) CO_2 emission from the trunk surface in the grassy-bilberry pine forest, (3) CO_2 emission from the trunk surface in the cotton grassy-sphagnum pine forest of growth class I at GWL of 48 cm, (4) CO_2 emission from the tree trunk surface in the cotton grassy-sphagnum pine forest of growth class I at GWL of 48 cm.

perature and GWL, that can be considered as an indicator of water supply for trees in the swampy pine forest. Moreover, the effect of GWL on the respiration rate is manifested differently for trees of various growth classes (Fig. 3). The minimum values of the respiration rate are found for trees of growth classes I and IV under water-logged conditions. The stem respiration increases in trees of growth class I simultaneously with an increase of GWL, and reaches its maximum at GWL ~10 cm. Observed slight decrease of the respiration rate at GWL ~20-30 cm is varied depending on the air temperature. At the same time, the maximum respiration rates of pine trunks for trees of growth class IV are observed at GWL of 15-20 cm. With a further increase in GWL, trees of this growth class exhibit a sustained and stronger decrease in the rate of respiration of tree trunks in all temperature ranges (Fig. 3).

An analysis of the temperature dependence of the rate of CO_2 emission from the stem surface in both grassy-bilberry and cotton grassy-sphagnum pine forests showed a pronounced increase in the respiration rate with the temperature growth from 6 to 28°C,

as well as a relatively weak temperature dependence of the respiration rate at the air temperatures above $28^{\circ}C$ (Fig. 3). In this case, the temperature dependence of the trunk respiration in the cotton grassy–sphagnum pine forest for the trees of growth class IV differed significantly from the temperature dependence for the trees of growth class I both at the shallow (GWL = 3–5 cm) and at a deeper groundwater level (GWL = 45 cm).

Parameterization of the Pine Trunk Respiration dependence on the Temperature and GWL

A simple multiplicative model, taking into account the dependence of the respiration rate on the air temperature and GWL, was developed using the results of CO_2 efflux measurements in selected forest stands under various environmental conditions. GWL was chosen as an indicator of moisture availability in root zone of the trees.

To describe the response of the respiration rate of pine trunks to the air temperature change, a nonlinear model allowing to describe both an exponential increase of the respiration rate in the temperature



Fig. 2. Dependence of CO_2 emission from the surface of pine trunks on the air temperature in the grassy–bilberry pine forest (July–August 2011) (a) and the cotton grassy–sphagnum pine forest for trees of growth classes I and IV (*1* and *2*, respectively) at different GWLs ((b) 48, (c) 16, and (d) 2–5 cm). The dashed curves correspond to model approximations (Eq. (1)) obtained using the parameters from Table 2.

range up to 25°C and its possible gradual decrease when the air temperature increase above some threshold value determined by the species-specific features of the trees under various growing conditions was suggested. The shape of selected nonlinear function is similar to e.g. the functional dependence used to describe the response of key photosynthetic parameters of plant leaves to temperature changes in biochemical models (e.g. De Pury and Farquhar, 1997). The dependence of the respiration rate of pine trunks on GWL takes into account the respiration reduction under abnormally high and low GWL, which was revealed in the swampy cotton grassy–sphagnum pine forest (Fig. 3). For forest stands in well-drained soils (grassy–bilberry pine forest), the effect of GWL on the stem respiration was ignored.

In general terms, the equation for describing the response of stem respiration (R_{stem}) to changes in air temperature (T_a) and GWL can be written as

$$R_{\text{stem}} = R_{\text{stem}(T_a=25^{\circ}\text{C})} f_{R_{\text{stem}}}(T_a) f_{R_{\text{stem}}}(Z_W),$$

$$f_{R_{\text{stem}}}(T_a) = \exp\left[\frac{E_{a,R_{\text{stem}}}(T_a-298)}{298\Re T_a}\right]$$

$$\times \left[1 + \exp\left(\frac{298\Delta S_{R_{\text{stem}}} - H_{d,R_{\text{stem}}}}{298\Re}\right)\right] / \left[1 + \exp\left(\frac{T_a\Delta S_{R_{\text{stem}}} - H_{d,R_{\text{stem}}}}{T_a\Re}\right)\right],$$
(1)

where $R_{\text{stem}(T_a=25^{\circ}\text{C})}$ is the value of R_{stem} at the air temperature of 25°C in μ mol/(m² s), $E_{a,R_{\text{stem}}}$ is the activation energy, which determines the rate of exponential rise of R_{stem} with increasing temperature (at tempera-

tures below the temperature optimum for the respiration rate) in J/mol; $\Delta S_{R_{\text{stem}}}$ is the factor determining the entropy of the temperature dependence of R_{stem} in J/(K mol); $H_{d,R_{\text{stem}}}$ is the parameter determining the

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Fig. 3. Dependence of CO_2 emission from the surface of pine trunks on air temperature and GWL in the cotton grassy–sphagnum pine forest for trees of growth classes (a) I and (b) IV.

rate of decrease of R_{stem} at temperatures above the optimum in J/mol; \Re is the universal gas constant ($\Re = 8.314 \text{ J/(mol K)}$; $f_{R_{\text{stem}}}(T_a)$ is the function describing the dependence of R_{stem} on the temperature; $f_{R_{\text{stem}}}(Z_W)$ is the function describing the dependence of R_{stem} on GWL (Z_W) and ranging from 0 to 1. For the grassy-bilberry pine forest $f_{R_{\text{stem}}}(Z_W)$ is assumed to be equal to one.

The equation for describing the limiting effect of GWL on the respiration rate of the trunks was written as follows:

$$f_{R_{\text{stem}}}(Z_W) = \{0.5 \tanh[(Z_W - d_1/2.5)/0.045] - 0.5 \tanh[(Z_W - (d_2 + 0.2))/0.1]\}^m,$$
(2)

where d_1 and d_2 determine the GWL range within which it is not a limiting factor for R_{stem} , and *m* determines the rate of attenuation of R_{stem} at $Z_W < d_1$ and $Z_W > d_2$. The values of d_1 and d_2 for trees of growth class I in the cotton grassy–sphagnum pine forest at the air temperature of 25°C were 0.10 and 0.24 m, and for pines of growth class IV—0.12 and 0.22 m, respectively. The parameter *m* was taken equal to 0.2 for trees of growth class I and 0.3 for trees of growth class IV. The model parameters describing the dependence of the stem respiration rate on temperature and GWL were estimated by the non-linear least square method based on the Levenberg-Marquardt algorithm (Gill et al., 1985). The parameters $\Delta S_{R_{stem}}$ and $H_{d, R_{stem}}$ were determined only on the basis of experimental data obtained in the grassy-bilberry pine forest mainly due to available data of respiration rate measurements for a fairly wide temperature range, including temperatures >30°C. To parameterize the respiration of pine trunks in the cotton grassy-sphagnum pine forest, these parameters were taken equal to the values of $\Delta S_{R_{stem}}$ and $H_{d, R_{stem}}$ obtained for the grassy-bilberry pine forest.

Comparisons of $E_{a,R_{stem}}$ for different types of pine forests showed their significant differences. Stable growth of $E_{a,R_{stem}}$ with an increase in GWL is observed for cotton grassy-sphagnum pine forest of growth class IV. At GWL 48 cm $E_{a,R_{stem}}$ reaches 36878 J/mol; i.e., it is almost two times higher than at GWL 3–5 cm ($E_{a,R_{stem}} = 18733$ J/mol). Quite high values of $E_{a,R_{stem}}$ are found for the cotton grassy–sphagnum pine forest of growth class I at GWL of 15 cm. They significantly exceed not only the values of $E_{a,R_{stem}}$ for higher and lower GWL (Table 2), but also the values of $E_{a,R_{stem}}$ in

GWL, cm	$R_{\text{stem}(T_a=25^{\circ}\text{C})}$, µmol CO ₂ /(m ² s)	$E_{\mathrm{a},R_{\mathrm{stem}}},\mathrm{J/mol}$			
Grassy-bilberry pine forest, trees of growth class I					
>200	2.18	23954			
Cotton grassy-sphagnum pine forest, trees of growth class I					
3-5	1.39	25920			
15	5.80	72504			
48	2.89	44160			
Cotton grassy-sphagnum pine forest, trees of growth class IV					
3-5	1.26	18733			
15	2.45	27361			
48	0.93	36878			

Table 2. The values of $R_{\text{stem}(T_a=25^{\circ}\text{C})}$ and $E_{a, R_{\text{stem}}}$ in Eq. (1) for calculating the rate of CO₂ emission from the surface of a Scots pine trunk depending on the air temperature (at $H_{d, R_{\text{stem}}} = 202\,000 \text{ J/mol}, \Delta S_{R_{\text{stem}}} = 652 \text{ J/(K mol)})$

 $R_{\text{stem}(T_a=25^{\circ}\text{C})}$ is the pine trunk respiration rate at temperature of 25°C; $E_{a, R_{\text{stem}}}$ is the activation energy, which determines the rate of exponential increase of trunk respiration with increasing temperature (at temperatures below the temperature optimum for the respiration rate); $H_{d, R_{\text{stem}}}$ is the parameter that determines the rate of the respiration rate decrease at temperatures above the optimum; $\Delta S_{R_{\text{stem}}}$ is the factor determining the entropy of the temperature dependence of stem respiration.

the cotton grassy–sphagnum pine forest of growth class IV for the entire range of GWL changes. Comparing the values of $E_{a,R_{stem}}$ for different types of pine trees, it may be noted their insignificant differences between grassy–bilberry ($E_{a,R_{stem}} = 23954$ J/mol) and cotton grassy–sphagnum pine forests of growth class IV under mean GWL ($E_{a,R_{stem}} = 27361$ J/mol) and growth class I under very high GWL ($E_{a,R_{stem}} = 25920$ J/mol).

The results of modeling experiments showed that, despite the different responses of the respiration rate for various types of pine trees on the temperature and GWL, the proposed nonlinear model (Eqs. (1) and (2)) allows us to describe adequately the dependence of the respiration rate on environmental factors (Fig. 3, Table 2). The determination coefficient (r^2) between the simulated and measured respiration rates varied from 0.46 (p < 0.05) for the grassy–bilberry pine forest to 0.54 (p < 0.05) for the cotton grassy–sphagnum pine forest.

DISCUSSION

The results of CO_2 efflux measurements of Scots pine trunks under various growing conditions shows their significant variability. Moreover, the respiration rate of tree trunks in different phenological stages can be comparable with the rates of dark respiration of photosynthesizing leaves (Zha et al., 2002). It is also confirmed by data obtained by Molchanov (2007) showing that the nocturnal respiration of needles, fine roots, and the trunk of Scots pine, as well as soil heterotrophic respiration, accounts for 8, 26, 23, and 16% of the total CO_2 absorption by the pine forest stand of growth class Ia, respectively. Thus, the contribution of

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 CO_2 emission from the surface of pine trunks to ecosystem respiration is comparable with the contribution of autotrophic root respiration and may exceed the contribution of heterotrophic soil respiration for the forest ecosystems under study, which indicates the importance of taking this component into account when calculating the total ecosystem flux of CO_2 .

The revealed high sensitivity of the respiration rate of pine trunks to temperature variation has been reported in many studies (Goulden et al., 1996; Zha et al., 2004; Zabuga, 2006). In particular, the response of respiration rate to temperature growth for the temperature range below 25°C are in good agreement with the measurement data of Molchanov et al. (2011) obtained in Tver region in a mature Norway spruce forest stand and showing a twofold increase in the respiration rate of spruce trunks in the period from June to early August simultaneously with an increase of the air temperature from 10 to 20°C. Zha et al. (2004) found a stable seasonal variability of the temperature response of trunk respiration of the Scots pine trees in Finland. In this case, the growth of respiration rate under raised temperature, determined by the temperature coefficient (Q_{10}), reached maximum in the summer ($Q_{10} = 1.98$, that corresponds to an increase in the respiration rate by 1.98 times with an increase in temperature by 10°C). Similar results were obtained by Goulden et al. (1996) for a number of deciduous and coniferous trees in the Harvard Forest, consisting mainly of Red oak and maple with admixture of Canadian tsuga and White pine.

The differences between the rates of CO_2 emission from the surface of pine trunks in the stands of growth classes I and IV of the cotton grassy–sphagnum pine forest may be caused by a combination of different factors, among which an essential role belongs to the differences in the radial increment of trees of different growth classes (Zabuga, 2006; Zabuga, V.F. and Zabuga, G.A., 2013, 2014). The radial growth of tree trunks of growth class IV is *a priori* much lower than that of trees of growth class I, which provides lower stem respiration rates, as well as its weaker sensitivity to changes of environmental factors (Fig. 2). Differences in the water regime can also result in different respiration rates of pine trunks of various growth classes.

An important point that attracts attention when analyzing the temperature dependences of the rate of CO_2 emission from the surface of living pine trunks is the weak sensitivity of the stem respiration to temperature changes at temperatures of 26–28°C and higher. Such temperature dependences were reported earlier mainly in the studies of the temperature response of key photosynthesis parameters determined by the biochemical and biophysical processes in plant leaves (Leuning, 1995). When considering the temperature dependences of CO₂ emission from the surface of a pine stems, this tendency may be associated with a slowdown of pine assimilation processes in the afternoon under partial stomata closure due to high air and canopy temperatures, a high water vapor pressure deficit, and weak moisture availability of shoots. For cotton grassy-sphagnum pine forest, this tendency can also be strengthened by a decrease in the GWL, which leads to reduced root water supply, especially for trees of growth class IV. It is important to note that under extremely high GWL, the differences in the CO_2 emission from the trunk surface in trees of different growth classes in cotton grassy-sphagnum pine forest are almost completely absent. This may be due to a lack of oxygen in the root zone of trees under high GWL, which usually leads to a decrease in the rate of assimilation (Molchanov, 1993) and, as a result, to a reduction in the respiration rate of nonphotosynthetic parts of woody plants.

The parameterization of respiration response to temperature changes proposed in this study is a modification of currently widely used model approaches based on the Arrhenius equation (Medlyn et al., 2002; Oltchev et al., 2008) and the Vant-Goff rule, which implies a two- to fourfold increase in the plant respiration rate with a temperature increase of 10°C (Lloyd and Taylor, 1994). Incorporated in both approaches the infinite exponential increase of the rate of CO_2 emission by the temperature rise makes it possible to describe fairly well the temperature response of the respiration rate of the nonphotosynthetic parts of plants to the temperature changes between 0 and 30° C. However, at higher temperatures ($35-40^{\circ}$ C) under thermal stress, the representativeness of this approach is questionable, which is confirmed by the results of this study. The nonlinear function used in the study (De Pury and Farquhar, 1997) allows us to describe the deceleration and attenuation of CO₂ emissions at high temperatures, and it is, in our opinion, more representative if we take into account the possible significant overheating of the surface of the photosynthetic and nonphotosynthetic parts of trees in summer and the close relationship of the respiration rate of tree trunks with assimilation processes occurring in woody plants.

The inclusion of a multivariable dependence of the respiration rate of pine trunks on GWL in the model algorithm allowed us to take into account multidirectional changes in the CO_2 emission of pine trunks under extremely high and very low GWL. Despite the relative complexity of used GWL parameterization, it relies on a small number of key parameters that describe the rate of stem respiration reduction under water-logged conditions and the GWL range, in which the effect of GWL on the respiration rate is completely absent. All these parameters can be easily estimated in the field for various types of wetland forests.

The model parameterizations was developed using rather limited experimental data obtained in two types of pine forests under different growing conditions. It is obvious, that the data are not sufficient to derive all possible variety of the trunk CO_2 efflux in forest communities on a regional scale. The need for further verification of the model and its optimization using new experimental data on the respiration of tree trunks of different species under various growing conditions is obvious.

CONCLUSIONS

The results of field experiments to derive the temporal variability of respiration of Scots pine trunks in different types of forests under different air temperatures and soil moisture conditions showed, on the one hand, the presence of a fairly pronounced their seasonal and diurnal variability, and on the other hand, a clear dependence of the respiration rate of the tree trunks on the air temperature and on GWL for swampy cotton grassy-sphagnum pine forest. Significant differences in the rate of CO_2 emission from the surface of tree trunks in a swampy pine forest between trees of different growth classes were also revealed. At the same time, trees of growth class I turned out to be more sensitive to changes in the air temperature and less sensitive to changes in GWL in comparison with more suppressed trees of class IV. In addition, with a decrease in GWL <40 cm the respiration rate of trees of growth class I was close to the stem respiration rate in the grassy-bilberry pine forest, which may be due to various factors, including the similar net photosynthesis rates in these types of pine forests. All found differences are in good agreement with available experimental data for forest sites located in other geographical regions. The developed empirical model based on the results of field measurements allowed us to describe the dependence of trunk respiration on the air temperature for pine trees of various growth classes in a wide range of GWL changes. The found relationships can be used to parameterize the processes of CO_2 exchange in models of the biogeochemical cycle of the Earth's surface on local and regional scales. Its further improvements are possible, in particular, using information on e.g. the vertical distribution of the roots of trees of different growth classes, various water supply, the mineral composition of different soil horizons, and the age of forest stands.

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COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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