ISSN 1064-2293, Eurasian Soil Science, 2023, Vol. 56, No. 9, pp. 1281–1290. © Pleiades Publishing, Ltd., 2023.
Russian Text © The Author(s), 2023, published in Pochvovedenie, 2023, No. 9, pp. 1116–1127.

RESPIRATION OF URBAN SOILS

Effect of Individual Trees on Soil Respiration in Forest Ecosystems under Industrial Pollution

I. A. Smorkalov[a, b, *] and **E. L. Vorobeichik**[a]

[a] *Institute of Plant and Animal Ecology, Russian Academy of Sciences, Yekaterinburg, 620144 Russia*
[b] *Ural Federal University Named after the First President of Russia B.N. Yeltsin, Yekaterinburg, 620002 Russia*
**e-mail: ivan.a.smorkalov@gmail.com*

Received March 10, 2023; revised May 11, 2023; accepted May 12, 2023

Abstract—The effect of individual trees on soil and litter respiration in forests polluted with heavy metals from copper smelter emissions was investigated for the first time. We tested the hypothesis that the portion of spatial variability in soil respiration explained by the distance from the tree trunk decreases on polluted plots in comparison with the background area. The study was performed in the southern taiga spruce–fir and birch forests under long-term pollution from the Middle Ural Copper Smelter in the Revda City, Sverdlovsk region, Russia. Measurement points were located near spruce and birch trees at different distances from tree trunks (tree-base plot, the middle of the crown projection, and canopy gap). The total CO_2 emission, litter respiration, litter contribution to soil respiration, specific respiratory activity of litter, and litter stock were measured at each point. In the background area, soil respiration decreased from the tree trunk to the canopy gap. The hypothesis was only partially confirmed: the portion of respiration variance explained by the distance from tree trunks decreased in polluted areas in comparison with the background areas in spruce forests but did not change in birch forests. The observed change in spruce forests was related to a drop in specific respiratory activity of litter, though litter stock was considerably higher near the tree trunk than in the canopy gap. We propose to locate measurement points in the middle of the crown projection, i.e., at a sufficient distance from tree trunks and away from the canopy gaps, to reduce potential bias in soil respiration estimates.

Keywords: forest litter, spatial pattern, copper smelter, heavy metals, Stagnic Retisols

DOI: 10.1134/S1064229323601191

INTRODUCTION

Soil respiration (SR) is extremely variable in space and time, because it depends on many environmental factors. Therefore, the estimates of soil CO_2 efflux are highly uncertain [12]. It is believed that when modeling carbon dioxide fluxes, it is important to consider both spatial and temporal respiration variability [29]. Models usually explain time-dependent SR variability well (R^2 reaches 0.75–0.97). However, the results of modeling spatial SR variability are substantially poorer [12, 20]. A considerable portion of SR spatial variability in ecosystems with complicated horizontal and vertical structures, particularly in forests, remains unexplained [23]. Therefore, it is essential to analyze the factors that determine SR variability not only over time but also in space.

The analysis of time-dependent variability is relatively less complicated compared to spatial variability. The former is based on accounting for simple factors, mainly soil temperature and moisture, whereas the latter involves the analysis of complex factors. One of the main factors for forests is the distance from the tree trunk, as trees create horizontal patterns of the fields of temperature, humidity, and concentrations of chemical elements in the soil, thereby influencing the functioning of the ground vegetation and soil biota.

It has been revealed that the carbon dioxide efflux from the soil surface also depends on the distance from the tree trunk [17, 23]. Usually, there is a decrease in SR from the trunk to the canopy gap. Possible factors considered in this regard include soil moisture [23, 35], gap size [25], root stock [17], pH, concentration of ash elements [18], and organic carbon and nitrogen content [17].

All known studies on the effect of individual trees on SR have been performed in forests that have not undergone industrial pollution, which may be a strong environmental factor. The impact of pollution is usually analyzed within tens to hundreds of meters (using several test plots within the site) or within the first tens of kilometers (using several sites at different distances from the emission source) [10, 21, 22]. However, fully analyze the effect of trees on SR, studying the variation on a smaller spatial scale—within tens of centimeters or several meters—is necessary.

Long-term industrial pollution from emissions of large metallurgical factories has been observed to decrease the environmental role of trees, leading to increased micro-scale variability of soil parameters [3–5, 14]. This observation applies to various aspects, including the content of metals in the forest litter [5] and cellulose decomposition rate [4]. Hence, a question arises to whether soil respiration follows the same regularity. The purpose of this work is to analyze the effect of individual trees on the respiration of soil and forest litter in areas that have undergone long-term pollution from the emissions of a copper smelter. Two hypotheses were tested: (1) the position relative to the tree trunk significantly affects soil and litter respiration in an uncontaminated area, and (2) the impact of this factor decreases in a polluted area.

OBJECTS AND METHODS

The research area is located in the southern taiga, within the ridge of residual mountains of the axial part of the Middle Urals and its western slope. The area is classified as part of the natural region of low mountains of the Middle Urals, dominated by dark coniferous forests, according to the physical-geographical zoning of Sverdlovsk region [11]. It is also classified as part of the Konovalovsk and Kirgishansk soil areas of the Middle-Ural south-taiga soil province, according to the soil-geographical zoning [7]. The soil cover is primarily composed of soddy-podzolic variously gleyed soils with varying amounts of stone fragments, and podzolized burozems occur locally.

The Middle Ural Copper Smelter is located on the outskirts of Revda City, Sverdlovsk region, 50 km west of Yekaterinburg. The factory has been operating since 1940 and emits gaseous compounds of sulfur, fluorine, and nitrogen, as well as metals (Cu, Pb, Zn, Cd, Fe, and Hg) and metalloids (As) as its main pollutants. In the 1980s, the total emissions of the factory reached 150000–225000 tons of pollutants per year, which made it one of the largest sources of industrial contamination in Russia. However, since the early 1990s, emissions have been gradually decreasing, reaching 65000 tons/year in 1999, 27000 tons/year in 2005, and 3000–5000 tons/year after a significant factory reconstruction in 2010 [1, 2]. Despite the reduction in emissions, no vegetation recovery or natural attenuation of metals in the soil occurred near the factory at the time of the research (2013) [6]. In heavily polluted areas, metal concentrations exceeded the background levels by 1–2 orders of magnitude [2].

Field measurements were conducted in two habitat variants widely distributed in the southern taiga of the Middle Urals: spruce-fir forest (SF) and secondary birch forest (BF). Based on the status of vegetation, three pollution zones were identified: background or unpolluted (UP) (20 km to the west of the factory for BF and 30 km for SF), buffer or moderately polluted (MP) (5 km for BF and 4 km for SF), and impact or heavily polluted (HP) (1 km for BF and 2 km for SF) (Fig. S1).

Five model trees were chosen in each pollution zone and habitat variant: spruce (*Picea obovata* Ledeb.) in SF and birch (*Betula pubescens* Ehrh. or *B. pendula* Roth.) in BF. The main criterion for their selection was proximity to a gap in the forest canopy (but not to large clearings or forest edges). Model trees were chosen to be as similar in habitus as possible, with a trunk height of at least 15 m and a diameter of at least 15 cm for birch and 30 cm for spruce. Additionally, the trees had to have a well-developed crown and no visible mechanical damage. The distance between model trees within one habitat variant was 15–80 m in the background and buffer zones and 10–150 m in the impact zone.

Three lines were laid near each tree at an angle of 20°–45°, without strict orientation by the main directions. Measurements were conducted at three points within each line: the first point (Trunk) was located 10–20 cm from the trunk, the second point (Crown) was in the middle of the crown projection, and the third point (Gap) was in the gap in the tree canopy. This scheme was used to assess the effect of trees on the metal content and the rate of cellulose decomposition in the litter [3–5]. At each point (i.e., within a circle with a diameter of 10 cm), the total carbon dioxide emission (SR) and litter respiration (LR) were measured, and the litter stock (LSt) was determined. In total, 540 measurements were performed near 30 model trees.

Respiration was measured on August 23–24, 2013. The rate of CO_2 emission from the soil surface was measured using the closed dynamic chambers method with a Li-8100A gas analyzer (Li-Cor Biosciences, United States). LR was measured using the following original method [19]. After measuring SR, the litter was removed from under the chamber, placed in a plastic bag, returned to its initial place, and its respiration was measured directly in the bag after 30–40 minutes. This period allowed for respiration to stabilize after a mechanical disturbance while avoiding the strong effects of temperature fluctuations and changes in the flow of carbon dioxide due to the death of roots cut off during sampling. The specific respiratory activity of litter (LSpR) was calculated as the ratio of its respiration to the dry litter mass at the measurement point.

Data analysis was performed using R v. 4.1.2 software. In all cases, unless otherwise specified, the value at the measurement point was considered a statistical unit. The effect of the pollution zone, habitat variant, and position relative to the tree trunk was evaluated using the permutation variance analysis (PERMANOVA) implemented in the vegan package [30]. The Benjamini–Yekutieli procedure was used to control the false discovery rate (FDR) in multiple statistical hypothesis testing. Post-hoc comparisons were performed by the Tukey test. The VCA package was used to decompose the variance [31].

The response ratio (ln Response Ratio, RR) [26] was used to visualize the tree effect on a particular parameter:

$$\mathrm{RR} = \ln\left(\frac{x_{\mathrm{trunk}}}{x_{\mathrm{gap}}}\right), \text{ or } \mathrm{RR} = \ln\left(\frac{x_{\mathrm{crown}}}{x_{\mathrm{gap}}}\right), \quad (1)$$

where x_{trunk} is the value of the parameter near the trunk, x_{gap} is the parameter in the canopy gap, and x_{crown} is the parameter in the middle of the crown projection. The response ratio has the property of additivity, which is useful for interpreting the results. If a parameter can be expressed as a product of several values, then the response ratio of the resulting parameter is the sum of the response ratios of its components. Let us represent litter respiration (LR) (mg $\mathrm{C{-}CO_2/(m^2\,h)}$) as follows:

$$\mathrm{LR} = \mathrm{SR\ LContr}, \quad (2)$$

$$\mathrm{LR} = \mathrm{LSpR\ LSt}, \quad (3)$$

where SR (mg $\mathrm{C{-}CO_2/(m^2\,h)}$) is soil respiration (i.e., total $\mathrm{CO_2}$ emission), LContr (in fractions of one) is the contribution of litter respiration to total emission (i.e., LR/SR), LSpR (mg $\mathrm{C{-}CO_2/(g\,h)}$) is the specific respiratory activity of litter, and LSt ($\mathrm{kg/m^2}$) is the stock of organic matter of the litter. By combining equations (2) and (3), total $\mathrm{CO_2}$ emission from the soil surface can be expressed as:

$$\mathrm{SR} = \mathrm{LSpR\ LSt}\,\frac{1}{\mathrm{LContr}}. \quad (4)$$

Respectively, the response ratios are:

$$\mathrm{RR_{SR}} = \mathrm{RR_{LSpR}} + \mathrm{RR_{LSt}} - \mathrm{RR_{LContr}}. \quad (5)$$

Equation (5) enables us to determine which components are responsible for a change in the total soil respiration near the trunk (or in the crown projection) compared to the gap. When data are averaged for several trees, the additivity is realized only when the geometric mean is used, so it has been used in the calculations.

RESULTS

Habitat differences. In this study, differences between biotopes were identified. The litter stock increased towards the factory, while the other parameters decreased (Fig. 1, Table 1). The most considerable difference—almost an order of magnitude—was observed for the specific respiratory activity of litter between the background and impact zones. Soil respiration and specific respiratory activity of litter were higher in birch forests than in spruce forests, while litter respiration, litter stock, and litter contribution to soil respiration were greater in spruce forests. Differences in all parameters between pollution zones and habitat variants were statistically significant (Table 2).

The variability of SR (the variation coefficient and absolute and relative ranges) decreased towards the factory in spruce forests and increased in birch forests (Table 3). In both habitat variants, the variation coefficient of LR increased in polluted areas compared to the background zone, while the absolute and relative ranges decreased. Pronounced regularities were absent for the other parameters, but in most cases, the variability within the pollution zone was high: accounting for more than half of the total variability across the pollution gradient. Pollution was the main factor explaining the variance of the specific respiratory activity of litter (75%) and litter stock (14%), and the habitat variant was responsible for the contribution of litter to total soil respiration (34%) (Fig. 2).

Microbiotopic differences. The differences between individual trees were not statistically significant for all parameters, and the interaction of the factor “tree” with other factors was also insignificant. However, the position relative to the tree trunk had statistically significant effect on all parameters. The interaction of the factor “position relative to the tree trunk” with other factors was insignificant only for soil respiration. For other parameters, the position relative to the tree trunk exerted different effects, depending on the habitat variant and the pollution zone.

In all cases, soil and litter respiration were higher near the tree trunk than in the gap. Sometimes this regularity was not observed for other parameters. There was no decrease in litter stock from the tree trunk to the gap in the birch forest of the buffer zone, and there was no decrease in the litter contribution to soil respiration in the buffer and impact zones. The change in the specific respiratory activity of litter with the distance from the tree trunk was the most irregular: it did not change in both habitat variants of the background area, increased in spruce forests of the buffer and impact zones, decreased in birch forests of the buffer zone but did not change in the impact zone.

On the scale of the whole pollution gradient, the position relative to the tree trunk explains the variance of soil and litter respiration to the greatest extent and least explains the variance of specific respiratory activity of litter. The role of this factor in the explanation of variance of soil respiration decreased towards the factory in the spruce forest and did not change in the birch forest (Fig. 3). For other parameters, pronounced regularities of changes of this indicator at the transition from the background to the impact zone were absent. Differences between individual trees had the lowest importance in the variance explanation for all parameters in all cases.

The analysis of the response ratio revealed that soil respiration near the trunk could increase due to different processes (Fig. 4). In both habitat variants of the background zone, the higher emission near the trunk was attributed to an increased contribution of litter respiration resulting from its accumulation whereas

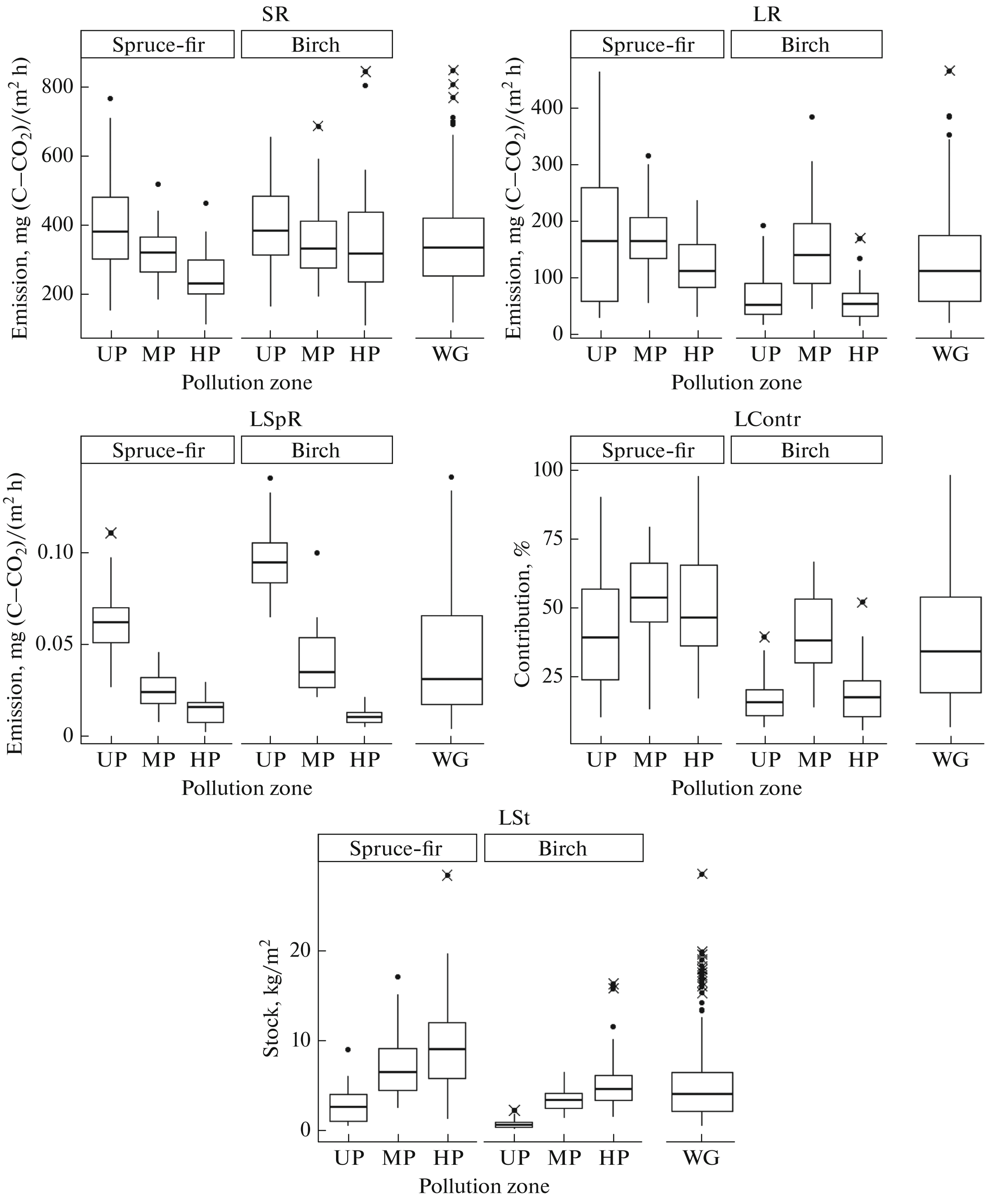

Fig. 1. The range of the studied parameters. SR—soil respiration, LR—litter respiration, LSpR—specific respiratory activity of litter, LContr—litter contribution to soil respiration, LSt—litter stock. Box-and-whiskers diagram: line—median, boxes—25–75% quartiles, whiskers—non-outlier range, points—outliers (>1.5 × interquartile range), crosses—extremes (>2 × interquartile range). Pollution zones: UP—background, MP—buffer, HP—impact, WG—the whole gradient. Spruce-fir—spruce–fir forests, Birch—birch forests.

the specific respiratory activity of litter remained constant. In spruce forests of the buffer and impact zones, soil respiration near the trunk increased to a lesser extent compared to the background, as the rise in litter stock was leveled by a decrease in its specific respiratory activity. In the birch forests of the buffer zone, soil respiration was higher near the trunk due to an increase in the specific respiratory activity of litter,

Table 1. Respiration of soil (SR) and litter (LR), specific respiratory activity of litter (LSpR), contribution of litter to soil respiration (LContr), and litter stock (LSt) in different habitats and pollution zones, depending on the position relative to the tree trunk, mean ± standard deviation ($n = 5$)

Position	Spruce-fir forest			Birch forest		
	UP	MP	HP	UP	MP	HP
Total CO_2 emission (SR), mg C–CO_2/(m^2 h)						
Trunk	493 ± 48a	359 ± 50a	270 ± 56a	499 ± 73a	475 ± 58a	442 ± 72a
Crown projection	446 ± 60a	317 ± 22a	227 ± 48a	369 ± 87ab	331 ± 47b	358 ± 118ab
Gap	263 ± 64b	279 ± 46a	231 ± 44a	315 ± 64b	264 ± 26b	231 ± 39b
Litter respiration (LR), mg C–CO_2/(m^2 h)						
Trunk	270 ± 61a	189 ± 55a	120 ± 32a	113 ± 41a	197 ± 47a	81 ± 21a
Crown projection	201 ± 61a	156 ± 27a	139 ± 37a	52 ± 17a	144 ± 29ab	45 ± 11a
Gap	53 ± 17b	161 ± 32a	96 ± 34a	42 ± 15a	94 ± 15b	44 ± 5a
Specific respiratory activity of litter (LSpR), mg C–CO_2/(g h)						
Trunk	0.055 ± 0.005a	0.016 ± 0.003a	0.008 ± 0.003a	0.093 ± 0.005ab	0.060 ± 0.008a	0.011 ± 0.003a
Crown projection	0.071 ± 0.008b	0.025 ± 0.005a	0.016 ± 0.005ab	0.090 ± 0.005a	0.038 ± 0.005b	0.011 ± 0.003a
Gap	0.057 ± 0.005a	0.036 ± 0.003b	0.019 ± 0.003b	0.101 ± 0.008b	0.027 ± 0.003ab	0.014 ± 0.003a
Litter contribution to total emission (LContr), %						
Trunk	56.5 ± 5.3a	52.5 ± 10.0a	44.4 ± 14.0ab	22.2 ± 6.4a	42.0 ± 11.9a	20.2 ± 6.5a
Crown projection	48.0 ± 16.5a	50.4 ± 8.3a	65.6 ± 15.2a	14.2 ± 3.4a	43.5 ± 7.7a	13.6 ± 4.3a
Gap	20.4 ± 1.4b	58.8 ± 6.1a	42.0 ± 17.2b	13.4 ± 4.1a	35.6 ± 6.2a	19.1 ± 1.1a
Litter stock (LSt), kg/m^2						
Trunk	4.6 ± 0.8a	10.6 ± 2.3a	15.4 ± 3.0a	1.1 ± 0.4a	3.2 ± 0.7a	7.7 ± 2.0a
Crown projection	2.6 ± 0.8ab	6.4 ± 1.2b	8.9 ± 2.7b	0.6 ± 0.2a	3.6 ± 0.8ab	4.2 ± 0.9b
Gap	0.9 ± 0.4b	4.2 ± 0.8b	4.7 ± 1.7c	0.4 ± 0.1a	3.3 ± 0.6b	3.5 ± 1.0b

Pollution zones: UP—background, MP—buffer, HP—impact. Tree is the statistical unit (arithmetic mean for three measurements). The same letters indicate the absence of statistically significant differences between the positions relative to the tree trunk for each parameter within the pollution zone and the habitat variant according to the Tukey test ($p < 0.05$).

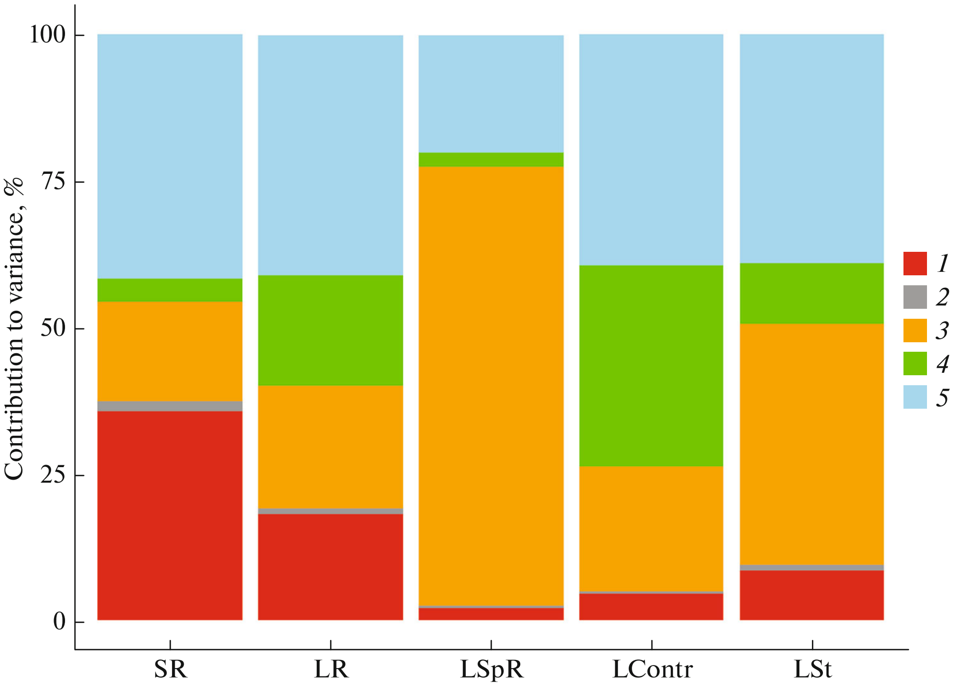

Fig. 2. Components of the variance of the studied parameters related to differences between: (*1*) positions relative to the tree trunk, (*2*) trees, (*3*) pollution zones, (*4*) habitats, (*5*) residual variance. SR—soil respiration, LR—litter respiration, LSpR—specific respiratory activity of litter, LContr—litter contribution to soil respiration, LSt—litter stock.

with no changes in its contribution to total respiration and stock. In birch forests of the impact zone, soil respiration was higher near the trunk due to an increase in the litter stock with the unchanged specific respiratory activity of litter and its contribution to respiration.

DISCUSSION

The absolute values of soil respiration in the background (214.3–604.8 mg C–CO_2/m^2 h) and polluted (159.8–561.2 mg C–CO_2/m^2 h) areas are consistent with the ranges typically observed in temperate zone forests (mg C–CO_2/(m^2 h)): to 185.8 [16], 82.1–380.2 [8], 121.0–289.4 [9], 272.2–410.4 [15], 6.0–1095.8 [21, 22], 190.1–492.5 [27], 151.2–192.1 [36], and 56.2–462.4 [20]. Similarly, the values for respiration, contribution to soil respiration, and specific respiratory activity of litter are comparable to our previous findings for spruce and birch forests [22].

The spatial variation of soil respiration in the background area closely resembles that in natural conditions [28]. The variation coefficients of soil respiration (23–43%) in both the background and contaminated areas are consistent with values typically found in

Table 2. PERMANOVA results for differences in parameters between pollution zones, habitat variants, positions relative to the tree trunk, and individual trees

Variability source	*df*	SR	LR	LSpR	LContr	LSt
Habitat	1	8.5*	50.6**	17.2**	105.1**	53.7**
Pollution zone	2	16.8**	27.5**	257.2**	32.6**	104.7**
Tree	4	0.8^{ns}	0.6^{ns}	0.9^{ns}	0.4^{ns}	1.2^{ns}
Position	2	35.7**	24.2**	6.5**	6.8**	21.8**
Habitat × zone	2	4.5^{ns}	7.1**	15.0**	11.3**	28.1**
Habitat × tree	4	0.3^{ns}	0.3^{ns}	0.4^{ns}	0.7^{ns}	0.6^{ns}
Habitat × position	2	2.5^{ns}	4.2^{ns}	12.5**	3.1^{ns}	10.1**
Zone × tree	8	1.3^{ns}	0.8^{ns}	0.7^{ns}	1.2^{ns}	1.0^{ns}
Zone × position	4	0.8^{ns}	4.8*	4.2**	4.5**	12.2**
Tree × position	8	0.3^{ns}	0.9^{ns}	0.6^{ns}	1.2^{ns}	1.4^{ns}

Values of Fisher *F*-test are given, FDR-corrected values at the significance level of: (*) $p \leq 0.05$, (**) $p \leq 0.01$; ns—$p > 0.05$; *df*—degrees of freedom of the factor; SR—soil respiration, LR—litter respiration, LSpR—specific respiratory activity of litter, LContr—litter contribution to soil respiration, LSt—litter stock.

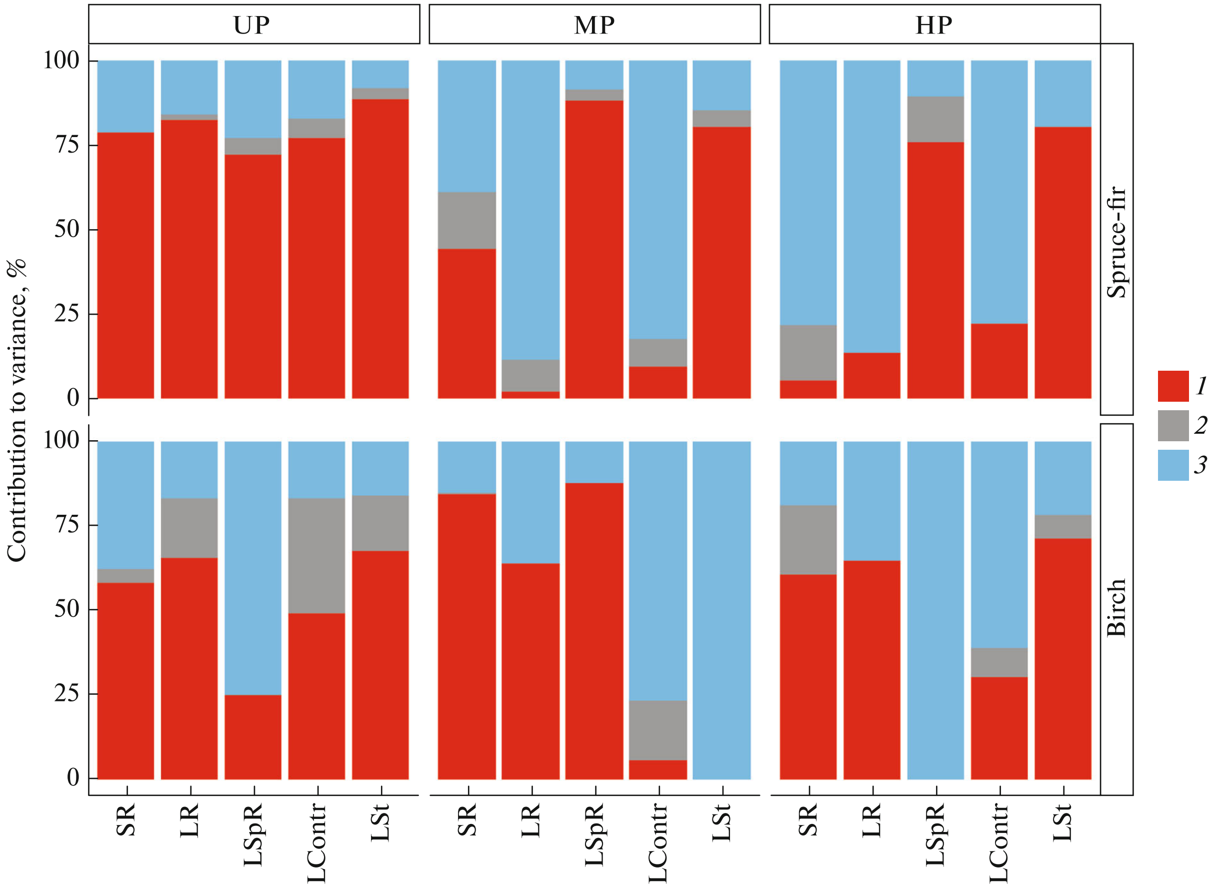

Fig. 3. Components of the variance of the studied parameters related to the differences between: (*1*) positions relative to the tree trunk, (*2*) trees, (*3*) residual variance. UP—background area, MP—buffer zone, HP—impact zone; SR—soil respiration, LR—litter respiration, LSpR—specific respiratory activity of litter, LContr—litter contribution to soil respiration, LSt—litter stock. Spruce-fir—spruce–fir forests, Birch—birch forests.

Table 3. Parameters of variation in soil respiration (SR), litter respiration (LR), specific respiratory activity of litter (LSpR), litter contribution to soil respiration (LContr), and litter stock (LSt)

Parameter	Spruce-fir forest			Birch forest			WG
	UP	MP	HP	UP	MP	HP	
Variation coefficient, %							
SR	38.6	22.7	32.3	30.6	32.6	43.2	37.8
LR	65.2	33.1	43.1	67.6	51.0	57.8	66.7
LSpR	26.1	38.3	49.3	17.4	40.5	39.1	77.4
LContr	52.1	26.6	42.5	46.0	36.9	54.9	58.8
LSt	70.0	48.9	59.3	70.5	38.2	61.2	90.9
Absolute range							
SR, mg $C{-}CO_2/(m^2\ h)$	612	334	266	488	492	734	734
LR, mg $C{-}CO_2/(m^2\ h)$	435	261	207	177	340	156	449
LSpR, mg $C{-}CO_2/(g\ h)$	0.085	0.038	0.027	0.076	0.079	0.016	0.139
LContr, %	79.8	66.3	80.7	32.8	53.0	46.3	92.1
LSt, kg/m^2	8.5	14.5	18.4	2.0	5.1	14.8	19.5
Relative range, %							
SR	83.4	45.6	36.3	66.6	67.1	100.0	–
LR	96.9	58.2	46.1	39.4	75.8	34.5	–
LSpR	60.8	27.5	19.6	54.9	56.9	11.8	–
LContr	86.6	72.0	87.6	35.6	57.6	50.3	–
LSt	43.8	74.7	94.5	10.5	26.3	75.8	–

Pollution zones: UP—background, MP—buffer, HP—impact, and WG—the whole gradient.

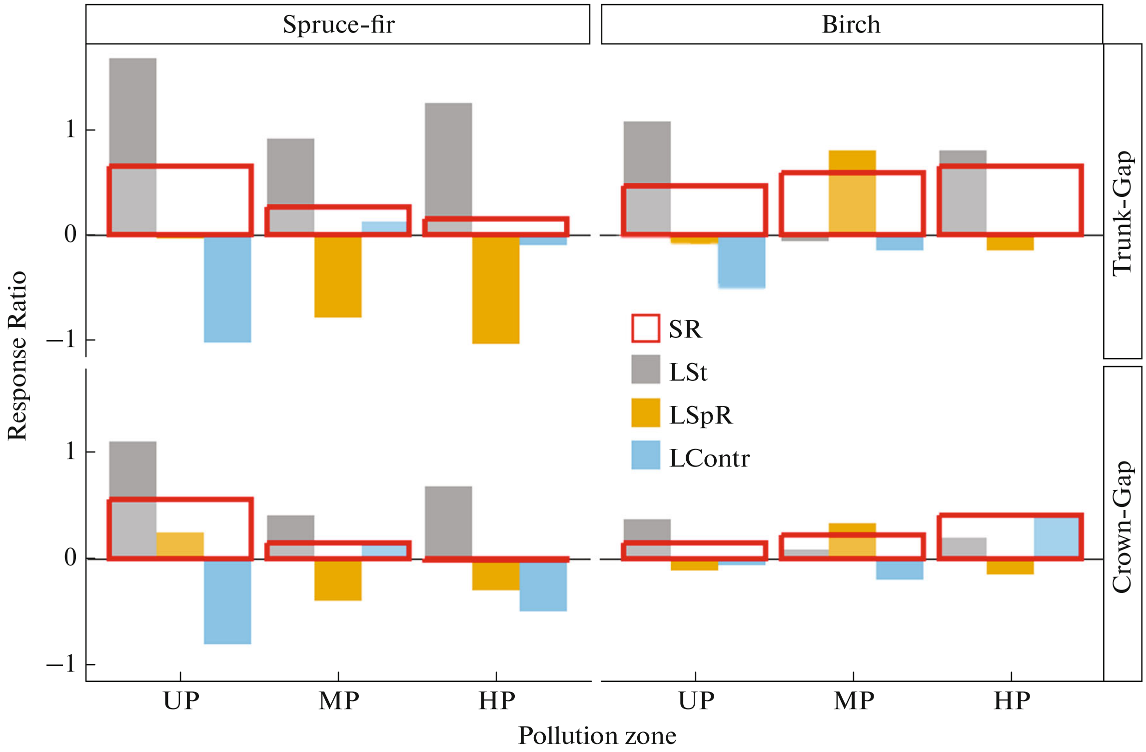

Fig. 4. The Responses Ratio of soil respiration near the trunk and in the middle of the crown projection as compared to the tree canopy gap, and the contribution of individual components to it; ln RR (LContr) is given with a negative sign according to Eq. (5). Pollution zones: UP—background, MP—buffer, HP—impact. SR—soil respiration, LSpR—specific respiratory activity of litter, LContr—litter contribution to soil respiration, LSt—litter stock. Position relative to the tree trunk: Trunk—near the trunk, Crown—the middle of the crown projection, Gap—the gap in the tree canopy. Spruce-fir—spruce-fir forests, Birch—birch forests.

coniferous (20.2–48.0%) and deciduous (21.8–61.0%) forests [13, 23].

Among all the parameters studied, the variation coefficient increases towards the emission source only for the specific respiratory activity of litter. This increase corresponds to the pronounced heterogeneity in the spatial distribution of cellulolytic activity of soil microorganisms under pollution [4]. The range within the contamination areas is comparable to the variability observed across the whole gradient for all parameters except for LSpR. The difference between the pollution zones is related to a greater portion of low values in the impact zone compared to the background.

Soil respiration is usually higher near the tree trunk than in the canopy gap [32, 34, 37]; however, respiration may not differ between these variants if the gap is small [25]. The obtained results confirm this regularity and thus testify to the validity of the first hypothesis.

It is hypothesized that soil temperature does not play a leading role in the micro-scale variation of soil respiration [23, 35]. Factors that consistently change from the tree trunk are usually considered to be the most important ones, such as soil moisture [23, 32, 35], fine root mass [25, 29, 34, 37], carbon and nitrogen content, microbial biomass [25, 29, 37], and litter stock [29, 37]. While we have not examined changes in these putative predictors of respiration, the pollution-driven transformation of ecosystems complicates the regularities of the effect of trees on soil respiration. This complexity may be the reason for only partial confirmation of the second hypothesis, as the effect of trees on SR decreases in one habitat variant and remains unchanged in the other.

In spruce forests, the role of the position relative to the tree trunk in the variability of soil respiration decreases from the background area to the impact zone due to a drop in the specific respiratory activity of litter, even though there is a substantial difference in litter stock between the trunk areas and the canopy gap. In other words, although the litter amount in the impact zone near tree trunks becomes significantly greater than in gaps, its specific activity decreases, leading to the leveling of differences in soil respiration. The specific respiratory activity of litter also decreases greatly towards the emission source.

Litter respiration is primarily related to microflora activity, as roots in this horizon comprise only 2–10% of the total root stock in the upper (0–20 cm) soil layer [33]. The change in the specific respiratory activity of litter at both scales (approaching the factory and approaching the tree trunk) is likely caused by the same mechanism: the suppression of soil microorganisms. Studies have shown that concentrations and stocks of potentially toxic metals increase in contaminated areas towards the tree trunk, and acidity also rises [3, 5]. In birch forests, the role of the position relative to the tree trunk in the variation of soil respiration is almost unchanged under the effect of pollution because the specific respiratory activity of litter is not decreased.

The need to consider the position of the measurement point relative to the tree trunk is a well-discussed phenomenon in studies on the micro-scale variation of soil respiration. However, detailed methodological recommendations are often lacking in the literature [25, 35]. Only one previous study provides such a recommendation suggesting that measurements should be taken 1.8 m to the east of the tree trunk to obtain unbiased estimates of soil respiration [24]. However, this recommendation is region-specific and overly detailed. A simpler approach to account for the micro-scale variability of soil respiration related to the effect of individual trees is to evaluate respiration within the projection of tree crowns, excluding both areas near tree trunks and gaps in the tree canopy. For the conditions of the southern taiga and relatively large trees (with a trunk diameter of more than 20 cm), the measurement points should be no closer than 1 m from the trunk. In this case, measurements likely average all positions relative to the tree trunk.

CONCLUSIONS

The change in soil respiration at the transition from the area near the tree trunk to the gap in the tree canopy is the result of a complex interaction of many dynamic and often multidirectional processes. This balance of processes may vary depending on the habitat variant (spruce or birch forest) and the pollution level (background, moderate, and heavy pollution). The study confirmed the considerable impact of trees in uncontaminated forests, supporting the first hypothesis tested: the position relative to the tree trunk explains a substantial portion of the variance in soil respiration. However, the hypothesis of a decrease in this component of variance in polluted areas was only partially confirmed, and the situation was habitat-specific: the role of the position relative to the tree trunk became smaller in the spruce forest but not in the birch forest.

In methodological terms, the results highlight the importance of considering the micro-scale variability of soil respiration. To avoid a possible estimation bias, it is recommended to locate measurement points within areas under the tree crowns, i.e., at a sufficient distance from the tree trunks and away from gaps in the tree canopy.

FUNDING

This work was supported by the Ministry of Science and Higher Education of the Russian Federation (projects no. 122021000076-9 and no. FEUZ-2023-0023).

CONFLICT OF INTEREST

The authors declare that they have no conflicts of interest.

SUPPLEMENTARY INFORMATION

The online version contains supplementary materials available at https://doi.org/10.1134/S1064229323601191.

REFERENCES

1. E. L. Vorobeichik, "Natural recovery of terrestrial ecosystems after the cessation of industrial pollution: 1. A state-of-the-art review," Russ. J. Ecol. **53** (1), 1–39 (2022). https://doi.org/10.1134/S1067413622010118
2. E. L. Vorobeichik and S. Yu. Kaigorodova, "Long-term dynamics of heavy metals in the upper horizons of soils in the region of a copper smelter impacts during the period of reduced emission," Eurasian Soil Sci. **50**, 977–990 (2017). https://doi.org/10.1134/S1064229317080130
3. E. L. Vorobeichik and P. G. Pishchulin, "Effect of individual trees on the pH and the content of heavy metals in forest litters upon industrial contamination," Eurasian Soil Sci. **42** (8), 861–873 (2009).
4. E. L. Vorobeichik and P. G. Pishchulin, "Effect of trees on the decomposition rate of cellulose in soils under industrial pollution," Eurasian Soil Sci. **44** (5), 547–560 (2011).
5. E. L. Vorobeichik and P. G. Pishchulin, "Industrial pollution reduces the effect of trees on forming the patterns of heavy metal concentration fields in forest litter," Russ. J. Ecol. **47** (5), 431–441 (2016). https://doi.org/10.1134/S1067413616050155
6. E. L. Vorobeichik, M. R. Trubina, E. V. Khantemirova, and I. E. Bergman, "Long-term dynamic of forest vegetation after reduction of copper smelter emissions," Russ. J. Ecol. **45** (6), 498–507 (2014).
7. F. G. Gafurov, *Soils of Sverdlovsk Region* (Ural. Univ., 2008) [in Russian].
8. T. V. Glukhova, S. E. Vompersky, and A. G. Kovalev, "Emission of CO_2 from the surface of oligotrophic bogs with due account for their microrelief in the southern taiga of European Russia," Eurasian Soil Sci. **46** (12), 1172–1181 (2013).
9. M. S. Kadulin and G. N. Koptsik, "Emission of CO_2 by soils in the impact zone of the Severonikel smelter in the Kola subarctic region," Eurasian Soil Sci. **46** (11), 1107–1116 (2013). https://doi.org/10.1134/S1064229313110045
10. M. S. Kadulin and G. N. Koptsik, "Carbon dioxide emission by soils as a criterion for remediation effectiveness of industrial barrens near copper-nickel plants in the Kola Subarctic," Russ. J. Ecol. **50** (6), 535–542 (2019). https://doi.org/10.1134/S1067413619060079
11. V. G. Kapustin, "Physical-geographical zoning of the Sverdlovsk Region," in *Geography and Modern Problems of Natural Science Cognition: Proceedings of the Conference* (Yekaterinburg, 2009), pp. 11–24.
12. D. V. Karelin, A. V. Pochikalov, D. G. Zamolodchikov, and M. L. Gitarskii, "Factors of spatiotemporal variability of CO_2 fluxes from soils of the southern taiga

spruce forest in Valdai," Contemp. Probl. Ecol. **7**, 743–751 (2014). https://doi.org/10.1134/S1995425514070063

13. I. N. Kurganova and V. N. Kudeyarov, "Assessment of carbon dioxide effluxes from soils of the taiga zone of Russia," Eurasian Soil Sci. **31** (9), 954–965 (1998).
14. I. V. Lyanguzova, P. A. Primak, F. S. Salikhova, E. N. Volkova, and A. I. Belyaeva, "The impact of soil pollution with heavy metals on the spatial distribution of ground cover biomass and forest litter stock in pine forests of the Kola Peninsula," Rastit. Resur. **57** (4), 340–358 (2021).
15. A. V. Mashika, "Carbon dioxide emission from the surface of podzolic soils," Eurasian Soil Sci. **39**, 1312–1317 (2006).
16. A. F. Osipov, "Effect of interannual difference in weather conditions of the growing season on the CO_2 emission from the soil surface in the middle-taiga cowberry–lichen pine forest (Komi Republic)," Eurasian Soil Sci. **51** (12), 1419–1426 (2018). https://doi.org/10.1134/S1064229318120086
17. I. V. Priputina, G. G. Frolova, V. N. Shanin, T. N. Myakshina, and P. Ya. Grabarnik, "Spatial distribution of organic matter and nitrogen in the entic podzols of the Prioksko-Terrasnyi Reserve and its relationship with the structure of forest phytocenoses," Eurasian Soil Sci. **53** (8), 1021–1032 (2020). https://doi.org/10.1134/S1064229320080128
18. O. V. Semenyuk, V. M. Telesnina, L. G. Bogatyrev, A. I. Benediktova, and Ya. D. Kuznetsova, "Assessment of intra-biogeocenotic variability of forest litters and dwarf shrub–herbaceous vegetation in spruce stands," Eurasian Soil Sci. **53** (1), 27–38 (2020). https://doi.org/10.1134/S1064229320010135
19. I. A. Smorkalov, "A new field method for measuring forest litter respiration rate," Russ. J. Ecol. **47** (5), 508–513 (2016).
20. I. A. Smorkalov, "Soil respiration variability: contributions of space and time estimated using the random forest algorithm," Russ. J. Ecol. **53** (4), 295–307 (2022). https://doi.org/10.1134/S1067413622040051
21. I. A. Smorkalov and E. L. Vorobeichik, "Soil respiration of forest ecosystems in gradients of environmental pollution by emissions from copper smelters," Russ. J. Ecol. **42** (6), 464–470 (2011).
22. I. A. Smorkalov and E. L. Vorobeichik, "Mechanism of stability of CO_2 emission from forest litter under conditions of industrial pollution," Lesovedenie, No. 1, 34–43 (2016).
23. Y. Cai, T. Nishimura, H. Ida, and M. Hirota, "Spatial variation in soil respiration is determined by forest canopy structure through soil water content in a mature beech forest," For. Ecol. Manage. **501**, 119673 (2021). https://doi.org/10.1016/j.foreco.2021.119673
24. Y. Cao, H. Xiao, B. Wang, Y. Zhang, H. Wu, X. Wang, et al., "Soil respiration may overestimate or underestimate in forest ecosystems," Sustainability **13** (5), 2716 (2021). https://doi.org/10.3390/su13052716
25. M. G. Han, M. Tang, B. K. Shi, and G. Z. Jin, "Effect of canopy gap size on soil respiration in a mixed broad-leaved-Korean pine forest: evidence from biotic and abiotic factors," Eur. J. Soil Biol. **99**, (2020). https://doi.org/10.1016/j.ejsobi.2020.103194
26. L. V. Hedges, J. Gurevitch, and P. S. Curtis, "The meta-analysis of response ratios in experimental ecology," Ecology **80** (4), 1150–1156 (1999). https://doi.org/10.1890/0012-9658(1999)080[1150:tmaorr]2.0.co;2
27. M. V. Kozlov, E. L. Zvereva, and V. E. Zverev, *Impacts of Point Polluters on Terrestrial Biota: Comparative Analysis of 18 Contaminated Areas* (Springer, Dordrecht, 2009).
28. Y. Luo and X. Zhou, *Soil Respiration and the Environment* (Acad. Press, Burlington, 2006).
29. J. G. Martin and P. V. Bolstad, "Variation of soil respiration at three spatial scales: components within measurements, intra-site variation and patterns on the landscape," Soil Biol. Biochem. **41** (3), 530–543 (2009). https://doi.org/10.1016/j.soilbio.2008.12.012
30. J. Oksanen, F. G. Blanchet, M. Friendly, R. Kindt, P. Legendre, D. McGlinn, et al., *Vegan: Community Ecology Package* (2021). http://R-Forge.R-project.org/projects/vegan/
31. A. Schuetzenmeister and F. Dufey, *VCA: Variance Component Analysis. R Package Version 1.4.2.* https://CRAN.R-project.org/package=VCA.
32. L. E. Scott-Denton, K. L. Sparks, and R. K. Monson, "Spatial and temporal controls of soil respiration rate in a high-elevation, subalpine forest," Soil Biol. Biochem. **35** (4), 525–534 (2003). https://doi.org/10.1016/S0038-0717(03)00007-5
33. I. A. Smorkalov and E. L. Vorobeichik, "Does long-term industrial pollution affect the fine and coarse root mass in forests? Preliminary investigation of two copper smelter contaminated areas," Water, Air, Soil Pollut. **233** (2), 55 (2022). https://doi.org/10.1007/s11270-022-05512-0
34. V. Suchewaboripont, M. Ando, Y. Iimura, S. Yoshitake, and T. Ohtsuka, "The effect of canopy structure on soil respiration in an old-growth beech-oak forest in central Japan," Ecol. Res. **30** (5), 867–877 (2015). https://doi.org/10.1007/s11284-015-1286-y
35. V. Suchewaboripont, M. Ando, S. Yoshitake, Y. Iimura, M. Hirota, and T. Ohtsuka, "Spatial upscaling of soil respiration under a complex canopy structure in an old-growth deciduous forest, Central Japan," Forests **8** (2), 36 (2017). https://doi.org/10.3390/f8020036
36. F. Takakai, A. R. Desyatkin, C. M. L. Lopez, A. N. Fedorov, R. V. Desyatkin, and R. Hatano, "Influence of forest disturbance on CO_2, CH_4 and N_2O fluxes from larch forest soil in the permafrost taiga region of eastern Siberia," Soil Sci. Plant Nutr. **54** (6), 938–949 (2008). https://doi.org/10.1111/j.1747-0765.2008.00309.x
37. Q. X. Tian, D. Y. Wang, Y. N. Tang, Y. Li, M. Wang, C. Liao, et al., "Topographic controls on the variability of soil respiration in a humid subtropical forest," Biogeochemistry **145** (1–2), 177–192 (2019). https://doi.org/10.1007/s10533-019-00598-x

Translated by I. Bel'chenko