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DEGRADATION, REHABILITATION, AND CONSERVATION OF SOILS

Effect of Trees on the Decomposition Rate of Cellulose in Soils under Industrial Pollution

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Abstract—The effect of spruce and birch on the spatial distribution of the decomposition rate of pure cellulose in the region of the Middle Urals copper smelter near the town of Revda in Sverdlovsk oblast (southern taiga) was studied. The contamination of the soil by heavy metals (Cu, Pb, Cd, and Zn) decreased the decomposition rate by 2.7 (spruce-fir forests) to 5.4 (birch forests) times and increased its spatial variation (the coefficient of variation reached 80–226%). The trees in the forests could not be considered as the main determinants of the horizontal structure of the soil microbocenosis, because the position of a test point with respect to the tree stem explains less than 10% of the total spatial variance of the cellulolytic activity. The decomposition rate of the cellulose in the spruce-fir forests was higher than in the birch forests; it was higher in the undercrown areas than in the forest canopy gaps. It was supposed that this was related to the buffering role of the litter, which smoothed the fluctuations of the water content. Under the pollution conditions, the differences between the coniferous and deciduous biotopes increased, and those between the undercrown areas and canopy gaps decreased.

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INTRODUCTION

The analysis of the effect of the trees on the soil is a classic problem of forest soil science [9, 14, 64, 77], which is closely related to the study of the rain interception by the crowns and the changes in their chemistry [55, 56] and the characterization of the effect of the trees on the microclimate and the underlying vegetation [12, 15]. The effect of the trees on the soil biota is less understood than the morphological and physicochemical parameters of the soil. Studies were done of microarthropods [16, 50, 52, 60, 69], large soil animals [34, 67], and soil microflora [1, 19, 23], including its functional parameters [1, 22, 50, 60, 61, 65, 76].

Studies of this issue are most frequently performed in background areas without high anthropogenic loads. There are a few works in which the edifying role of trees in the gradient of contamination from the point sources of industrial emissions was considered [1, 6, 10, 18, 19, 78, 79]. At the same time, the lack of such information does not allow characterizing the role of trees under technogenic pressure. It should be emphasized that the interest in the study of technogenic territories goes far beyond purely applied research related to the hazard for human health and the conservation of nature. The areas subjected to pollution from local emission sources are suitable models for studying the effect of strong external impacts on ecosystems. In fact, long-term field experiments established beyond the will of researchers at the start-up moment were implemented on them. The results of such unprompted experiments are promising for the basic ecology, because they allow revealing the mechanisms of the ecosystem resistance to stressing factors, examining the consequences of theoretical constructions, and verifying the models of the response to external impacts [5, 53, 54].

The decomposition of organic matter is a key process ensuring the return of biogenic elements to the soil and determining the productivity of terrestrial ecosystems [30, 71]. This work examines the decomposition rate of pure cellulose, which is frequently used as a suitable relative index characterizing the decomposition rate of organic matter in terrestrial and aquatic ecosystems [32]. The main agents of cellulose decomposition in boreal forests are the soil and litter saprotrophic fungi and cellulolytic bacteria [11, 30, 71].

Many authors noted the inhibition of organic matter decomposition under the contamination of soil by heavy metals and sulfur compounds [2, 4, 7, 25, 27, 33, 39, 40, 42, 58, 62, 70, 80], which is primarily related to the suppression of soil biota. However, there is almost no information on the changes in the edifying role of trees with respect to destroying organisms under pollution conditions.

The aim of this work was to analyze the effect of trees on the cellulolytic activity of the soil microflora under strong industrial pollution. In the course of the work, we tested the working hypothesis that the impact of the trees on the biological activity of the soil in technogenic territories decreases compared to undisturbed

areas. The hypothesis follows from the well-documented inhibition of woody plants under pollution conditions, which is manifested in the decrease in tree and crown densities [47]. The distribution of the cellulolytic activity was studied in two contrasting biotopes (coniferous and deciduous forests).

The study of the edifying role of trees is usually based on several methodological approaches. In one approach, the studied parameters are recorded at a large number of regularly arranged sampling points with replicated measurements of the tree-related environmental parameters at each point [9, 61, 74]; in another approach, microplots at different distances from the stems of model trees are compared [6, 12, 22, 52, 69]; in the third approach, a closed canopy is compared to canopy gaps [26, 65, 76] or woodless areas [64]. This work is based on the second and, in part, third approach: representative samples of model trees were used, around which the effect of the phytogenic (Uranov [15]) or ecological [74] field is well pronounced and, hence, its gradient can be studied in the pure form. In other words, a series of microsites with decreasing strength of the phytogenic field (the near-stem area ⟶ crown-projection area ⟶ canopy gap) around a model tree at different distances from the stem was presented. A canopy gap and a closed canopy were also compared.

AREA STUDY

The studies were conducted in the region affected by the Middle Urals copper smelter (**MUCS**) located in the town of Revda in Sverdlovsk oblast 50 km to the west of Yekaterinburg. The plant has been in operation since 1940; this is one of the most significant sources of atmospheric pollution in Russia: the total emission was more than 140000 t/yr in the late 1980s and decreased to 30000 t/yr in the middle 2000s. The main ingredients of the emission are sulfur dioxide and dust particles with sorbed toxic elements (Cu, Pb, Cd, Zn, Fe, As, Hg, etc.).

The long-term impact of the plant resulted in the formation of zones with different degrees of ecosystem damage, whose shapes partially coincide with the predominant wind direction in the region (from west to east). The local gradient of contamination is more spread to the east and is overlapped by the impact zone of the Yekaterinburg urban agglomeration; therefore, the studies were conducted to the west of the MUCS. Two types of biotopes prevalent in the southern taiga of the Middle Urals were selected: spruce-fir forests and secondary birch forests. The soil cover in the studied plots consists of combinations of mountain-forest brown, soddy-podzolic, and gray forest soils differently transformed by technogenic factors. According to the state of the higher plants, three load zones were separated: the impact zone (1 km from the plant for the birch forests and 2 km for the spruce-fir forests), the buffer zone (5 km from the plant for the birch forests and 4 km for the spruce-fir forests), and the background zone (20 km from the plant for the birch forests and 30 km for the spruce-fir forests).

A detailed description of the pollution levels and changes in the ecosystems under the effect of the contamination was reported earlier [7, 13]. The contents of the mobile heavy metals in the forest litter on the polluted area significantly exceeded the background levels: by 2 (Zn) and 18 (Cu) times in the buffer zone and by 3 (Zn) and 50 (Cu) times in the impact zone; the litter's acidity increases under the effect of the contamination by 0.7–1.2 pH units [7].

The following aspects of the technogenic degradation of the forest are notable: the inhibition of the woody layer (a decrease in the density and reserves of the tree stand, an increase in the portion of dry stands, and a decrease in the crown density) and the grass-dwarf shrub layer (a decrease in the abundance and species diversity), as well as the double-to-triple increase in the thickness of the forest litter because of the suppressed activity of the saprotrophic soil biota, primarily large soil saprobes. In the impact zones, the decrease in the abundance of the grass-dwarf shrub layer is accompanied by an increase in the projective cover of mosses (up to 70% in some places).

MATERIALS AND METHODS

The decomposition rate of pure cellulose was measured from the decrease in the weight of a standard sample (laboratory filter paper) exposed under natural conditions for a specific time period. The papers were placed in bags 5 × 10 cm in size made of Capron net with meshes of 0.5 mm; the initial sample weight was 3.513 ± 0.009 g (mean ± error, $n = 2160$) with a variation range of 2.752–4.340 g. The bags were placed into the litter layer no deeper than 3–4 cm from its surface; if the litter was very thin, the bags were placed at the boundary with the humus-accumulative horizon. Every effort was made to minimize the disturbance of the ground cover. The samples were exposed from May 28 or June 17 through September 26–30, 2005; i.e., the time of exposition was 104–125 days. After the end of the exposure, the samples were thoroughly cleaned with a scalpel and a brush from soil particles and fine roots. Before weighing, the original and exposed samples were dried in a drying oven at 105°C for 2 h. All the weighing operations were performed on an HR-120 analytical balance (Japan) with an accuracy of 0.001 g; all the calculations were based on the oven-dry weight. The rate of the decomposition was expressed in the percentage of the weight loss per day.

Cellulose samples were exposed near model trees: spruce (*Picea obovata* Ledeb.) in the spruce-fir forest and downy birch (*Betula pubescens* Ehrh.) or white birch (*B. pendula* Roth.) in the birch forest. The main selection criterion was the closeness to a canopy gap (but not to large forest clearings or edges). To reduce the interferences, model trees with maximally similar

habits were selected (height no less than 15 m; trunk diameter no less than 15 cm for birch and 30 cm for spruce; well-developed crown without visible mechanical damage). Three plots with five model trees each were selected from each load zone and each biotope. The distance between the neighboring plots was 400 m on the average (200–1000 m) in the background and buffer zones and 300 m on the average (50–1000 m) in the impact zone. Within a plot, the distance between the neighboring model trees was 10–20 m.

A circle with a radius of 4–6 m around the model tree stem bounded a circular plot within which 24 bags with cellulose were exposed. The points of exposure were arranged in three microsites: near the trunk (at 0.2–0.4 m from the stem), in the middle of the crown projection (1.2–1.8 m), and in the canopy gap (3.8–5.3 m). In addition, bags were also placed under the closed forest canopy on the opposite side from the gap (2–3 m from the stem). In each of the four types of microsites, six bags were exposed; for three treatments (crown projection, canopy gap, and closed forest canopy), the points were arranged along arcs of the same radii at 50-cm intervals; in the near-trunk zone, they were arranged in a circle around the trunk at 25–40 cm intervals. A total of 2160 bags were exposed around 90 model trees; 27 bags were lost during the withdrawal; hence, a total of 2133 decomposition rate measurements were performed.

Two expressions for the relative difference (***RD***) between the sites under the crowns and those beyond the crowns were used as parameters characterizing the direction and value of the tree effect on the distribution of the cellulose decomposition rate:

$$RD_1 = \frac{c_i - w_i}{c_i + w_i} \times 100 \quad \text{and} \quad RD_2 = \frac{f_i - w_i}{f_i + w_i} \times 100,$$

where c_i is the parameter value in the ith circular plot under the crown (the average value for the near-trunk plot and the crown projection), w_i is the parameter value in the ith plot in the canopy gap, and f_i is the parameter value in the ith plot under the forest canopy. The relative difference lies in the range from –100% (when the parameter under the crown or under the canopy is zero) to +100% (when the parameter in the canopy gap is zero). This parameter was considered best for the solution of an analogous problem (the characterization of the interaction between the species in a community [24]) because of the symmetric contributions of the positive and negative differences.

In the statistical analysis, the sample sets were formed by two methods: in one of them, an individual sample was considered as an accounting unit; in the other method, this was a circular plot (the arithmetic mean for 6 or 24 samples). In the ANOVA, square rooting was used for the transformation of the variable (the exact value of the Box–Cox transformation parameter for the different methods of the sample set formation was 0.49–0.61). The partition of the variance into components was performed according to Snedecor.

The characterization of the weather conditions was based on the data for 8 measurements daily from the nearest meteorological station (Revda) provided by the All-Russian Research Institute of Hydrometeorological Information in Obninsk.

RESULTS

The weather conditions during the period of the exposure. The distribution of the precipitation among the months significantly differed from the long-term average (Fig. 1a). In June, the precipitation was higher by 78.3 mm (two showery rains in the first week of the month made up more than half of it); the precipitation in July, August, and September was lower than the mean by 49.5, 4.3, and 30.1 mm, respectively (in total for three months, lower than the mean by 83.9 mm). In June–September of 2005, precipitation was absent for 61 days, while the mean value was 51 days.

The temperature conditions of 2005 were close to the long-term average (Fig. 1b). The mean temperature in August and September was higher than the mean value by 1.1 and 1.3°C , respectively. The maximum air temperature was higher than 25°C during 27 out of 125 days of the exposure. The Selyaninov hydrothermal coefficient (the ratio between the total precipitation and the sum of the temperatures above 10°C divided by 10) was 1.80 for the entire period of the exposure and only 1.15 for July–September, which was lower than the long-term averages (1.94 and 2.02, respectively). Hence, the exposure period of the cellulose in 2005 can be characterized as warm but nonuniform in terms of the precipitation distribution and relatively droughty for the most part.

Biotope differences. The highest rate of the cellulose decomposition was recorded in the spruce-fir forest of the background zone, and the lowest rate was found in the birch forest of the impact zone (Table 1). The results of the three-way ANOVA (with circular plots as accounting units) showed a significant effect of all three considered factors: the load zone ($F_{2;\,334} = 215.4$, $p \ll 0.0001$, and it explains 60.0% of the total variance within the entire variation range), the biotope ($F_{1;\,334} = 19.9$, $p < 0.0001$, 3.5% of the variance), and the position relative to the stem ($F_{3;\,334} = 3.7$, $p = 0.0126$, 1.0% of the variance).

In the background zone, the average rate of the cellulose decomposition in the spruce-fire forests was higher than that in the birch forests for all the positions relative to the stem, but the difference was no higher than 0.05% per day. When the contamination increased, the difference between the biotopes retained the sign and increased to 0.07% per day in the buffer zone and to 0.18% per day in the impact zone; the interaction of the factors "load zone × biotope" was significant ($F_{2;\,334} = 12.1$, $p < 0.0001$). The con-

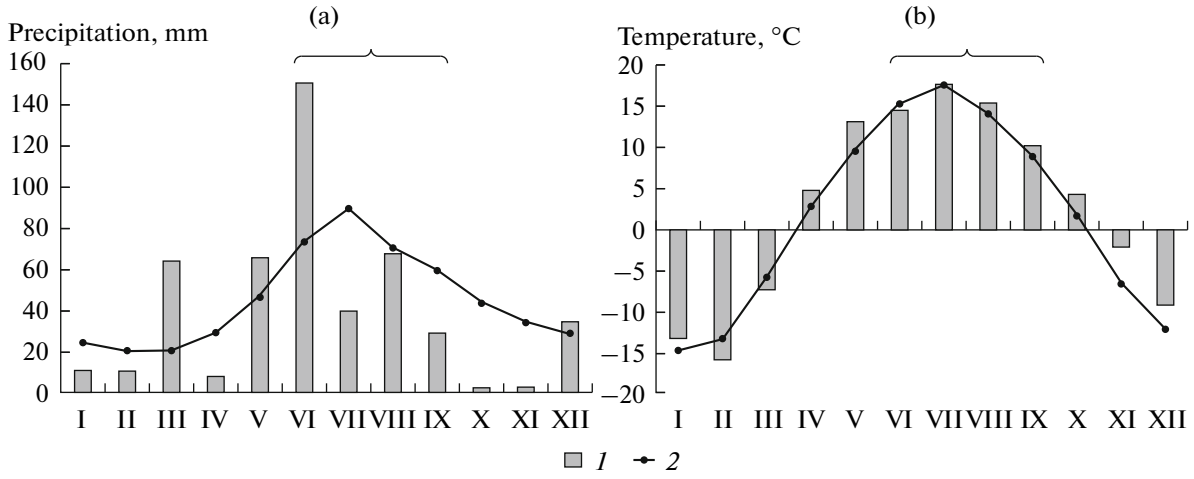

Fig. 1. (a) Monthly precipitation and (b) average monthly air temperature in the region under study: (*1*) data of 2005; (*2*) long-term data (1959–2008); (Roman numerals) the number of the month; the period of the cellulose exposure is denoted by a curly bracket.

tamination significantly decreased the intensity of the decomposition processes: for the spruce-fir forests, the average cellulose decomposition rate in the impact zone was lower than in the background zone by 2.7 times; for the birch forests, the difference was even higher (by 5.4 times); the cellulose decomposition rate in the buffer zone was lower than in the background zone by 1.4 times for both biotopes.

Microbiotope differences. With the forest canopy being excluded from the consideration, significant differences in the cellulose decomposition rate between the microsites were observed only in the spruce-fir forest of the background (one-way ANOVA, circular plots as accounting units, $F_{2;42} = 3.3$, $p = 0.0463$) and buffer ($F_{2;42} = 5.5$, $p = 0.0079$) zones; in the other cases, the effect of the position relative to the stem was insignificant ($F_{2;42} = 0.3–1.1$, $p = 0.35–0.73$). The highest value of the microbiotopic difference was recorded in the spruce-fir forest of the buffer zone (Table 1): the cellulose decomposition rate in the can-

Table 1. Decomposition rate of cellulose (% per day) in different biotopes, load zones, and positions relative to the tree stem

Microbiotope	Load zone		
	background	buffer	impact
	Spruce-fir forest		
I	0.52 ± 0.02 (0.01–0.76) [90]	0.46 ± 0.03 (0.00–0.82) [85]	0.17 ± 0.01 (0.02–0.69) [90]
II	0.54 ± 0.01 (0.22–0.77) [88]	0.39 ± 0.03 (0.01–0.82) [83]	0.16 ± 0.02 (0.00–0.80) [90]
III	0.44 ± 0.02 (0.08–0.81) [90]	0.26 ± 0.02 (0.01–0.80) [90]	0.18 ± 0.02 (0.01–0.74) [90]
IV	0.53 ± 0.01 (0.13–0.81) [90]	0.37 ± 0.03 (0.00–0.79) [84]	0.25 ± 0.02 (0.00–0.77) [90]
V	0.51 ± 0.01 (0.01–0.81) [358]	0.37 ± 0.01 (0.00–0.82) [342]	0.19 ± 0.01 (0.00–0.80) [360]
	Birch forest		
I	0.49 ± 0.02 (0.10–0.84) [90]	0.39 ± 0.02 (0.04–0.86) [89]	0.07 ± 0.01 (0.00–0.40) [90]
II	0.49 ± 0.02 (0.16–0.86) [90]	0.34 ± 0.02 (0.02–0.81) [89]	0.14 ± 0.03 (0.00–0.94) [89]
III	0.44 ± 0.02 (0.14–0.86) [89]	0.30 ± 0.02 (0.04–0.83) [88]	0.08 ± 0.02 (0.00–0.91) [90]
IV	0.50 ± 0.02 (0.12–0.86) [90]	0.39 ± 0.02 (0.05–0.86) [90]	0.07 ± 0.01 (0.00–0.57) [89]
V	0.48 ± 0.01 (0.10–0.86) [359]	0.36 ± 0.01 (0.02–0.86) [356]	0.09 ± 0.01 (0.00–0.94) [358]

Note: Here and in Table 2, the microsites are as follows: (I) near-stem area; (II) crown projection; (III) canopy gap; (IV) forest canopy; (V) all the treatments. The mean ± errors are given followed by the minimum and maximum values in the parenthesis and the number of samples in square brackets; the individual samples are used as the accounting units.

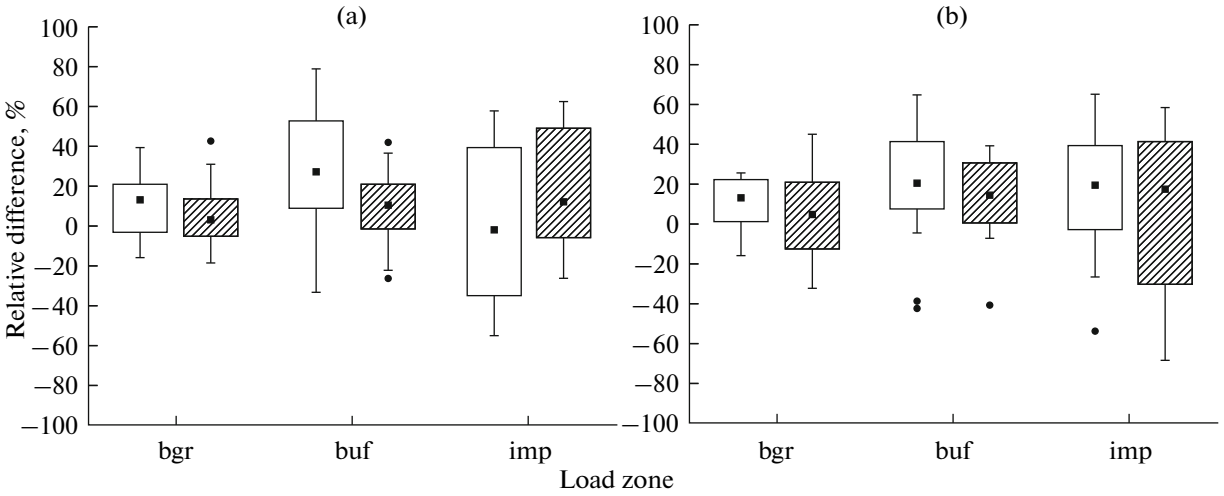

Fig. 2. Relative difference (*RD*) in the decomposition rate (a) between the undercrown area and the canopy gap and (b) between the forest canopy and the canopy gap in spruce-fir forests (unshaded rectangles) and birch forests (shaded rectangles) in the background (bgr), buffer (buf), and impact (imp) zones. The accounting unit: a circular plot ($n = 15$). Here and in Fig. 4: (full square) median; (rectangle) upper and lower quartiles; (vertical lines) range without outliers; (full circles) outliers (deviated from the quartiles by more than the interquartile range).

opy gap was 0.20% per day lower than in the near-stem plot and 0.13% per day lower than in the crown projection; for the background zone, the corresponding values were 0.08 and 0.11% per day. In the birch forest, the absolute differences between the microsites were lower than in the spruce-fir forests: the cellulose decomposition rate in the canopy gap of the background and buffer zones was lower than that under the crown by 0.04–0.09% per day. In the impact zone, there were almost no differences between the different positions relative to the stem in both the spruce-fir and birch forests. Similar tendencies were observed when the canopy gap was compared to the closed forest canopy.

The relative difference between the plots under the crowns and those beyond the crowns varied in a wide range from negative to positive values; for all the load zones, the *RD* median was close to zero (with a maximum of 27%), and the range reaches more than half the entire potential variation range of the parameter (Fig. 2). The high variation resulted in the absence of significant difference in *RD* values between the zones and biotopes (Kruskal–Wallis test, $H(2, 44) = 1.3–5.1$, $p = 0.08–0.52$).

Spatial variation. The range of the cellulose decomposition rate varied along the gradient of the contamination lower than the average values (Table 1). The maximum values were similar in all the zones, including the impact zone, and reached 0.80–0.94% per day, which corresponded to the almost 100% degradation of the original sample. The zero rate corresponding to the absolute absence of the substrate degradation (within the error of the measurements) was recorded only in the buffer and impact zones, while the minimum rates in the background zone were 0.01–0.22% per day.

Although the variation range of the cellulose decomposition rate along the contamination gradient was relatively stable, the frequency distributions radically differed between the load zones (Fig. 3, Table 2). When going from the background to the impact zone, the symmetric or slightly right-skewed distributions changed into strongly left-skewed ones (correspondingly, the asymmetry changed the sign from negative to positive). In some cases (the spruce-fir forest of the buffer zone and the birch forest in the background and buffer zones), the bimodality of the distributions (negative excess) was well pronounced, which indicated similar proportions of low and high values in the set of samples.

The contamination significantly increased the relative variation of the cellulose decomposition rate (Table 2). The variation coefficient calculated from the set of individual values indicated a moderate variation (23–40%) in the background zone, a high variation (54–85%) in the buffer zone, and a very high variation (80–226%) in the impact zone. The values of the variation coefficient calculated from the averaged values were lower (18–33%) in the background zone but increased in the buffer (36–63%) and especially impact (50–177%) zones. Such high values of the variation coefficient were due to the retention of the variation range at the decrease in the the average decomposition rate, which was observed even when the averaged values for the circular plots were considered (Fig. 4). The relative variation of the cellulose decomposition rate was either similar for the different microsites or higher for the canopy gap (the spruce-fir

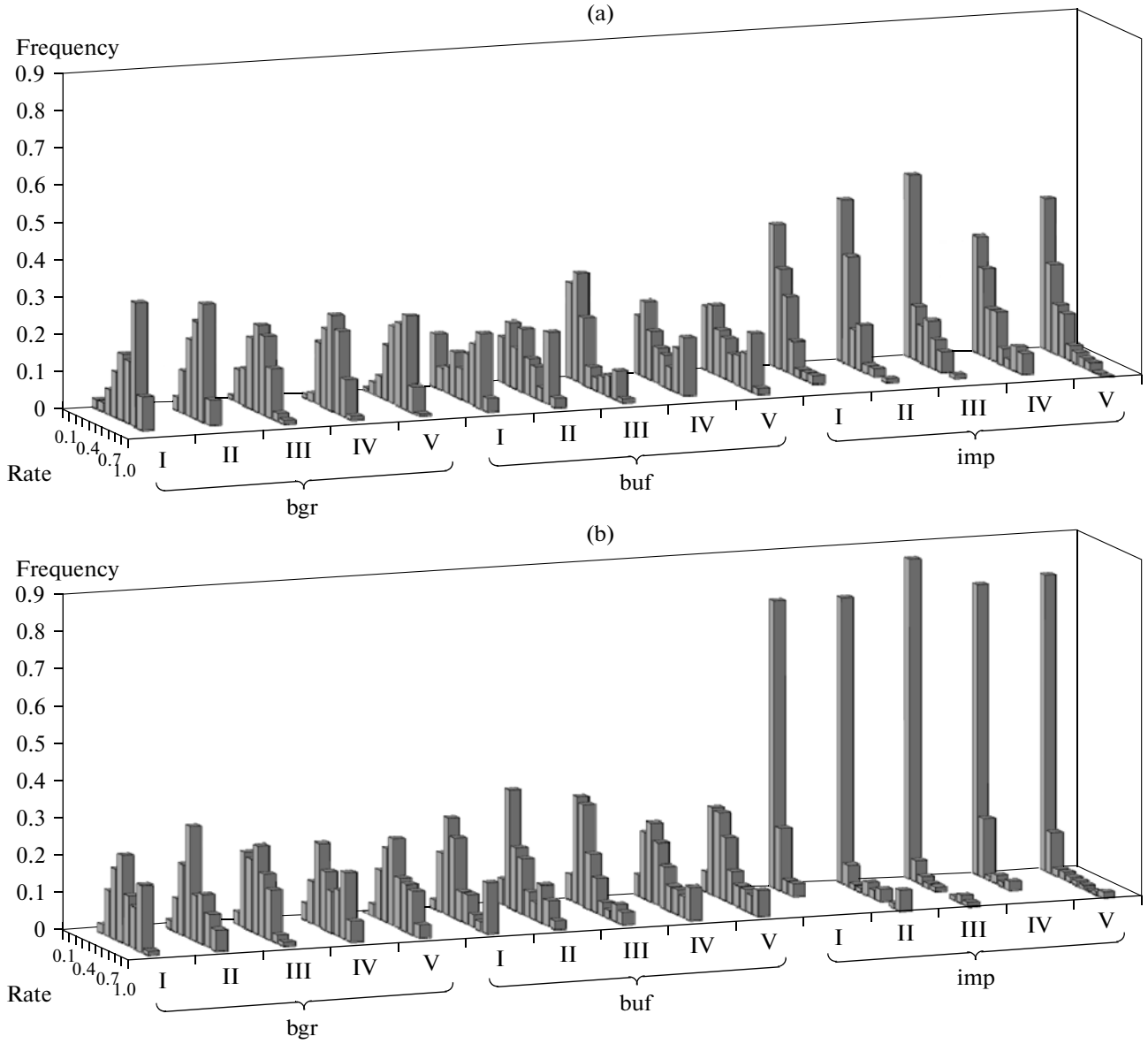

Fig. 3. Frequency distributions of the cellulose decomposition rate (% per day) in (A) the spruce-fir and (B) the birch forests in the background (bgr), buffer (buf), and impact (imp) zones. The accounting unit: a sample (the *n* values are given in Table 1); the microsites: (I) near-stem area; (II) crown projection; (III) canopy gap; (IV) forest canopy; (V) all the treatments.

forest in the background and buffer zones, the birch forest in the impact zone).

Spatial variance components. The contribution of the trees to the microscale spatial variation of the cellulolytic activity can be quantitatively estimated by the partitioning of the total spatial variance into components. Our methodological approach allowed partitioning of the variance into three components: the variance related to the position of the test point relative to the trunk, the variance related to the difference between the separate trees, and the residual variance. The first component can be interpreted as the effect of the trees' phytogenic field gradient on the activity's distribution; the second component characterizes the spatial heterogeneity (spottiness) at the scale of the load zone; the third component characterizes the variance due to random sources and not related to the above factors.

From the results of the two-way ANOVA, the position relative to the trunk and the differences between the trees in all the cases significantly affected the distribution of the cellulose decomposition rate (most frequently, $p \ll 0.0001$; at the least, $p < 0.03$). However, the effects of these factors were different. The position relative to the stem in all the zones explained the very low portion of the spatial variance (Fig. 5): no more than 9.5% in the spruce-fir forest and 3.5% in the birch forest. In the spruce-fir forests, this parameter

Table 2. Parameters of the empirical frequency distributions of the decomposition rate in different load zones, biotopes, and microsites

Load zone	Microsites	Spruce-fir forest			Birch forest		
		Cv	As	Ex	Cv	As	Ex
Accounting unit: sample							
Background	I	31.98	−0.81**	0.31	37.03	0.11	−0.93**
	II	23.02	−0.58**	−0.20	33.88	0.38	−0.45
	III	36.75	−0.21	−0.62	34.57	0.22	−0.56
	IV	25.50	−0.27	−0.30	39.86	0.13	−1.15**
	V	30.13	−0.57**	−0.09	36.85	0.25*	−0.77**
Buffer	I	54.01	−0.43*	−1.13**	58.82	0.85**	−0.40
	II	62.09	0.27	−1.27**	65.26	0.78**	−0.65*
	III	85.99	1.14**	0.03	64.51	1.29**	1.13*
	IV	68.63	0.26	−1.34**	58.79	0.67**	−0.68*
	V	68.28	0.28*	−1.35**	62.30	0.87**	−0.31
Impact	I	80.80	1.43**	2.16**	122.23	2.17**	5.06**
	II	96.69	1.56**	3.27**	182.89	2.13**	3.26**
	III	93.83	1.05**	0.21	227.51	3.66**	13.05**
	IV	86.80	1.10**	0.19	151.76	2.93**	9.40**
	V	91.79	1.36**	1.51**	194.85	3.38**	11.63**
Accounting unit: circular plot ($n = 15$)							
Background	I	23.56	−0.52	−0.07	25.63	0.18	−1.44*
	II	18.99	−0.56	−0.81	24.19	1.64**	4.07**
	III	27.81	−0.29	0.55	27.39	0.07	−0.40
	IV	20.24	−0.60	0.50	34.12	0.22	−1.27
	V	16.44	−1.75**	4.47**	19.63	0.43	−0.19
Buffer	I	37.14	−0.89*	−0.64	53.10	1.21*	0.90
	II	47.50	0.33	−0.29	54.63	1.00*	−0.02
	III	65.01	0.76	−0.77	56.20	2.01**	5.25**
	IV	55.59	0.07	−0.81	50.66	1.01*	0.59
	V	36.62	0.40	−0.10	46.53	1.48**	2.55**
Impact	I	50.84	0.49	−0.82	95.54	1.63**	2.12**
	II	72.74	0.58	−0.71	183.54	2.39**	5.41**
	III	75.62	1.00*	−0.10	187.94	3.08**	9.97**
	IV	69.49	1.45**	2.67**	146.46	2.95	9.82**
	V	48.60	0.63	−1.27	139.36	1.96**	2.97**

Note: (Cv) coeffi cient of variation; (As) asymmetry; (Ex) excess; significance of the difference from zero: (*) $p < 0.05$; (**) $p < 0.01$. The number of samples is given in Table 1.

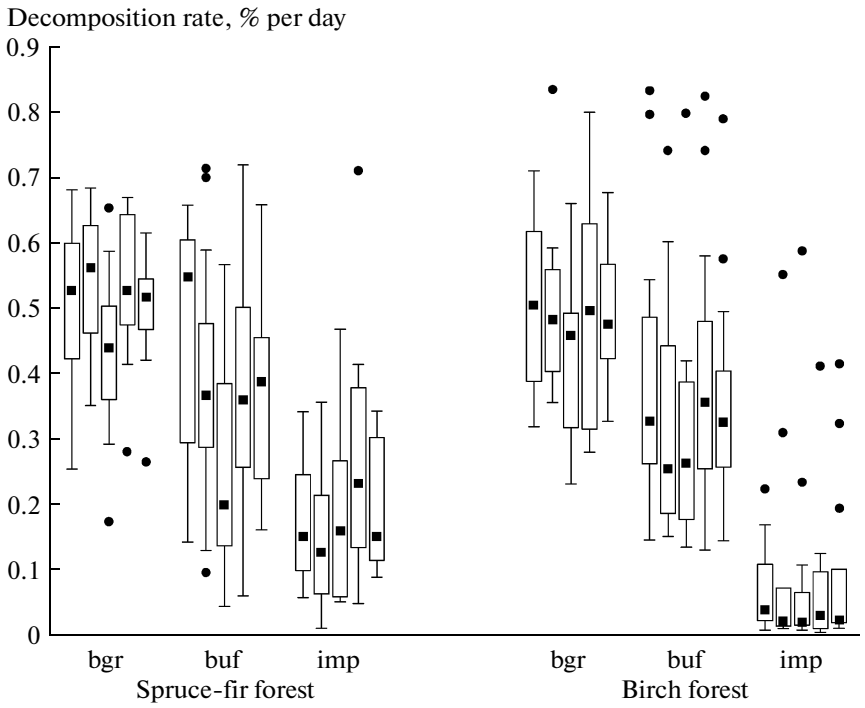

Fig. 4. Cellulose decomposition rate in the background (bgr), buffer (buf), and impact (imp) zones. Accounting unit: circular plot ($n = 15$); from left to right in each group: near-stem area, crown projection, canopy gap, forest canopy, average for all the microsites.

decreased when going from the background and buffer zones to the impact zone, where it reached the minimum value (4%); no similar trend was observed for the birch forests. A significantly higher portion of the spatial variance was related to the differences between the separate trees: this factor explained about 26–27% of the variation in the spruce-fir forests of all the load zones; in the birch forests, this factor explained from 23% in the background zone to 56% in the impact zone. In all the biotopes and zones, the major part of the spatial variance (42–75%) was not related to the factors considered.

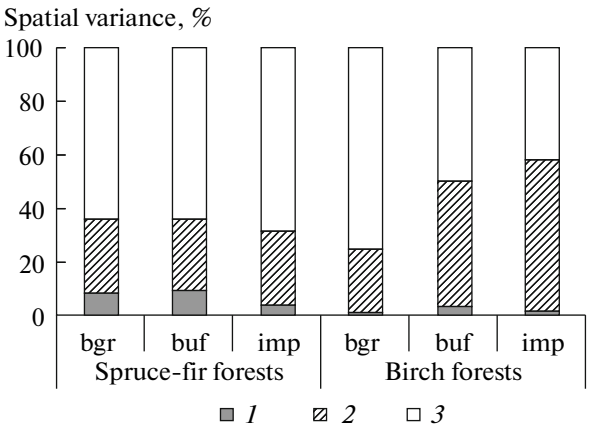

Fig. 5. Spatial variance components of the cellulose decomposition rate in the different biotopes of the background (bgr), buffer (buf), and impact (imp) zones. The variances due to (*1*) the position of the test point relative to the tree stem, (*2*) the differences between the trees, and (*3*) the effect of unaccounted for factors (residual variance).

DISCUSSION

The abundance peak of the micromycetes playing the key role in the decomposition of the plant material is confined to the forest litter [11, 30]. Correspondingly, the laying of cellulose samples within this horizon allowed us to estimate the maximum decomposition rate for the entire soil profile and better simulated the microclimatic conditions of the degradation compared to another conventional method: the placement of samples on the litter surface.

The direct comparison of the absolute values obtained for the decomposition rate of the pure cellulose with the data of the other authors is difficult because of the different experimental conditions (the initial sample weight, the duration of the exposure, the depth of the sample placement, etc.). Nonetheless, our estimates of the average cellulose decomposition rate in the background zone (0.44–0.54% per day) are close to the values reported by other authors for exposures shorter than a year. For example, the decomposition rate of pure cellulose was 0.45–1.70% per day in the background biotopes of Silesia (56 days of exposure) [28], 0.51–0.57% per day in oak and beech for-

ests of the Caucasus region (98–120 days) [38], 0.50–1.39% per day in beech and mixed forests of the Carpathian low mountains (70 days) [36], and 0.50–0.62% per day in birch plantations on heath lands of Scotland (120 days) [60].

The average decomposition rates of the cellulose in the impact zone (0.06–0.25% per day) were close to the values that we obtained earlier for the MUCS region (0.03–0.30% per day) [4]. They corresponded to the values recorded under natural pessimal conditions, e.g., in the stony tundra of Spitsbergen (0.04–0.09% per day) [29], the semi-deserts and steppes of the Caspian Lowland (0.20–0.35% per day) [38], and the Carpathian high mountains (0.31–0.62% per day) [36].

Our interpretation of the results discussed below is based on the prevailing opinion in soil biology that the degradation of organic matter under natural conditions is determined by three groups of factors: the substrate's quality, the physicochemical conditions of the habitat, and the soil biota activity [30, 71]. The use of pure cellulose (standardized homogeneous material) in this work allowed excluding the first of them; hence, the differences between the localities are determined by the two other groups of factors. It was shown in many works that the temperature and moisture are the key physicochemical parameters, and the role of other factors (acidity, supply with biogenic elements, etc.) is less important [11, 71]. In the region of low values, moisture is more important than the temperature [31, 35].

Undoubtedly, the inhibition of degradation in the MUCS impact zone, as well as near other sources of emission [27, 33, 39, 40, 58, 62, 70, 80], is primarily related to the extremely high content of heavy metals, whose toxicity is enhanced by the increased acidity. Although the minimum active concentrations of a metal causing recorded negative effects on soil microorganisms reported by different authors can differ by two–three orders of magnitude [25, 42], the levels of contamination noted in the impact zone [2, 4, 6] significantly exceed them in all the cases. An additional factor is the vegetation degradation, which affects the microclimatic conditions of the habitat.

It is generally accepted that the decomposition rate of the plant litter in deciduous forests is higher than in coniferous forests [30, 71]. However, we recorded an inverse ratio of biotopes from the decomposition rate of pure cellulose, although the absolute difference was low (Table 1). Other authors also noted analogous situations [20, 45]. This is most probably related to the more favorable microclimatic conditions for the functioning of micromycetes created in coniferous forests in some years: it is logical to suppose that, in the relatively droughty year of 2005, the water content of the litter was higher and its dynamics was more stable in the spruce-fir forests compared to the birch forests. It is also cannot be excluded that the micromycetes of the spruce-fir forests, which are accustomed to the difficulty degradable coniferous substrate, more rapidly utilize the pure cellulose free from lignin, monoterpenes, and other phenolic compounds than the micromycetes of birch forests, which are spoilt by the readily degradable leaf debris. This is indirectly confirmed by the data on the more efficient utilization of the readily available carbon by the microorganisms of the coniferous forests compared to the deciduous forests [63].

Forest trees are efficiently functioning "ecosystem engineers" [49] significantly affecting the physical and chemical parameters of the environment around them. Therefore, it could be expected that the trees will be powerful determinants of the horizontal structure of the soil microbocenosis. However, this is not the case: the position of the test point relative to the tree stem explains a very small portion of the spatial variance even under the background conditions (Fig. 5). This indicates that either the trees change the environment around them in a too narrow range to limit the propagation and development of micromycetes or their effect spreads to the entire biotope territory, including the intercrown areas.

The sign of the difference between the decomposition rates in the undercrown areas and the canopy gaps recorded in our work was also opposite to the expected one. Under tree crowns, the soil water content is usually lower and the acidity is higher, as well as the content of polyphenolic compounds, macroelements, and heavy metals [6, 9, 12, 14, 55, 56, 64, 69, 75, 77]. Taking into consideration this distribution of the factors, we supposed that the cellulolytic activity will also be higher under the crowns. An additional basis for this supposition was the prevalent opinion that the undercrown areas under increased local environmental pollution can be considered as models for studying the effect of pollutants on the soil because of the stemflow and throughfall [18, 34, 52, 67, 69, 75]. In addition, the results of the field experiments on the establishment of special roofs under the forest canopy to simulate the effect of crowns showed that the decomposition rate of the plant litter decreased because of the reduced precipitation and the lower soil temperature [43]. However, our results attested to the inverse: either the undercrown and intercrown microsites did not differ in the decomposition rate (in the deciduous forest), or the rate was higher under the crowns (in the coniferous forest).

Contradictory data are available in the literature about the effect of trees on the activity of destructors. Some authors noted a decrease in the activity under the crowns compared to the canopy gaps. In the coniferous forests of Japan, the decomposition rate of the plant litter was lower near the tree trunks [50]. Analogous results were obtained in beech forests of Austria [52], as well as (with the use of pure cellulose) in oak, spruce, and pine forests of European Russia [20]. The trophic activity of large soil saprobes was also significantly decreased near tree trunks in the beech forests of Germany [67] and the oak forests of France [34]. In beech forests of Denmark [65] and Germany [26], the

decomposition rate of the plant litter was slightly higher in specially formed canopy gaps.

In other cases, on the contrary, a higher cellulolytic activity was recorded under the crown. So, in the Taimyr mountains, the degradation of pure cellulose and plant litter was significantly higher (by 1.7–4.5 times) in the near-stem areas of larch and birch compared to the intercrown areas [22]. Pure cellulose was degraded more rapidly under single birches compared to the forestless area of the Scotland heath lands [60]. In subtropical forests of China, the maximum rate of the leaf decomposition was recorded under the canopy compared to the canopy gaps [76].

However, even the low effect of trees observed in the background zone of the MUCS changed to almost no effect in the impact zone. This can be considered as proof for our working hypothesis about the decreased edifying role of trees in the technogenic areas. Only sparse and contradictory data about the effect of trees on the soil biota under pollution are available in the literature. In the Kola Peninsula, the differences in the microbial biomass between the undercrown and intercrown microplots, which were well pronounced in undisturbed forests [23], were leveled under the effect of polymetal contamination [1, 19]. In the spruce-fir forests of the MUCS impact zone, on the contrary, collembolans were more abundant near the tree stems compared to the canopy gaps, while no differences between these microsites were observed in the background area [16]. In Switzerland, the decomposition rate of beech leaves under increased acid precipitation was slightly higher near the tree stems compared to the canopy gaps; in the absence of contamination, the microsites were almost similar [69].

In the discussion of the possible reasons for the differences between the coniferous and deciduous biotopes and between the undercrown and intercrown microplots, attention should be given to the buffer role of the litter, which suppressed the abrupt variations in the temperature and moisture; the thicker the litter layer, the more efficient the buffer. In the region under study, the litter in the spruce-fir forests is twice as thick as that in the birch forests [3, 7]. In the near-stem areas, the litter is thicker than in the canopy gaps by 3–4 times in both types of biotopes [6]. Consequently, it can be supposed that more favorable moistening conditions are created in the localities with thicker litter during the periods of hot dry weather. Direct measurements show lower fluctuations in the soil moisture under the forest canopy compared to the open areas [48].

The dynamics of the moisture, rather than that of the temperature, are of leading importance for the degradation of organic substrates. It was shown in laboratory experiments that the decomposition rate of plant material under constant moisture conditions was similar in the treatments with constant and fluctuating temperatures [72, 73]; at the same time, the operations leveling the moisture variations positively affected the decomposition rate [73]. An unusual effect of the mesh size on the degradation of cellulose [2, 45] and plant litter [68] was noted in some field experiments: a higher rate was recorded in bags with finer mesh. This was most probably related to the fact that the moistening conditions were more stable and, hence, the period of the destructor activity was longer in the former treatment [57]. It cannot be excluded that the leveling of the moisture fluctuations shifts the species composition of the micromycetes [59]. In some aspects, the results of these experiments simulate the situation with litter layers of different thicknesses.

Along with climatic factors, the distribution of mosses, whose metabolites inhibit the development of micromycetes, can also contribute to the differences between microsites. In spruce forests, the moss cover is usually better developed in the canopy gaps [10, 12], which enhances the pessimality of intercrown spaces.

Of special importance is the abrupt increase in the spatial variation of the cellulolytic activity under industrial pollution, which we observed at two scales: at the levels of separate samples and circular plots. In our opinion, this is the key factor which masks the effect of the trees on the distribution of the destructor activity.

We previously described the development of a focal spatial structure of the degradation process under industrial pollution [2], which included the retention of loci with the high activity typical for the background habitats in the impact areas under almost complete blocking of degradation. The differentiation of the area into the plots with very low and very high decomposition rates entails an abrupt increase in the variation coefficient. It was shown that the typical size of the loci with high activity is several to some tens of centimeters, and their spatial localization is stable during the vegetation period [4]. This spatial structure indicates the resistance of at least several micromycete species to high levels of contamination, which is ensured by numerous protection mechanisms from the toxic effect of heavy metals [17, 25, 41, 42].

The decomposition rate of cellulose in a specific point of the space depends on three factors: (1) the presence of spores and/or mycelium in this point, (2) the capacity of the spores/mycelium to germinate/grow, and (3) the rate of degradation of the colonized cellulose sample by hydrolase enzymes. Hence, the increase in the spatial variation of the cellulolytic activity can be related to the nonuniform distribution of micromycetes or their interference with other groups of soil biota [51], as well as to the spatial variation of the physicochemical parameters of the litter affecting the metabolism of microbes. We proposed the following mechanism to explain the focal spatial structure [2, 4]. It is known that soil micromycetes form colonies in favorable loci; in their absence, they can actively overpass the pessimal area by means of mycelial cords [11, 17, 66]. Each of the exposed cellulose samples, all other conditions being equal, is a potential favorable locus for micromycetes, which is

actively colonized and almost completely utilized. Under chemical contamination, the sensitive micromycete species are eliminated, the amount of active mycelium decreases, and the life cycle is disturbed [17]; therefore, the total colonization potential of micromycetes decreases, and most samples remained not colonized. Thus, the spatial distribution of the decomposition rate of pure cellulose at the end of the exposure under contamination primarily reflects the process of colonization, i.e., represents a combination of successfully colonized and uncolonized cellulose samples rather than the distribution of the utilization rate of simultaneously colonized substrates. Under background conditions, most samples are colonized during the early exposition period, and the rate distribution primarily characterizes the distribution of the metabolic activity of the micromycetes. In principle, colonization is a largely stochastic process. If the proposed mechanism is valid, the gradient of the tree phytogenic field only slightly affects the spatial distribution of the cellulolytic activity of the micromycetes.

The high variation of the decomposition rate at another spatial scale (circular plots) can depend on the microrelief and the features of specific trees, whose crown size and structure determine the microclimatic differences between the particular localities. The antibiotic effect of tree metabolism products can be an additional factor. It was shown that for coniferous trees, the composition and amount of secondary metabolites, including monoterpenes, are genetically controlled and strongly differ among the specific trees, which can affect the structure of the underlying vegetation [46]. Taking into consideration the pronounced fungicidal and bactericidal effects of monoterpenes, it can be supposed that this factor contributes to the differences in the destructor activity among the specific trees [44].

CONCLUSIONS

The contamination of the environment by emissions from the copper smelter decreases the decomposition rate of pure cellulose by 3–5 times and abruptly increases its spatial variation, which is more pronounced in deciduous forests compared to coniferous ones. It was unexpectedly found that the trees' crowns under the background conditions cannot be considered as the leading determinants of the horizontal structure of the soil microbocenosis: even in the case of a strong edifier (spruce), less than 10% of the spatial variance is related to the position of the test point relative to the tree stem. Under pollution conditions, the edifying role of trees with respect to cellulolytic activity is almost absent, which confirms our working hypothesis.

It was also found that the decomposition rate of pure cellulose in spruce-fir forests was higher than in birch forests and higher in undercrown areas than in canopy gaps. We related this to the buffer role of the forest litter leveling the variation of the moisture content: in the relatively droughty year of the experiments, more favorable conditions for cellulose degradation were created in the loci with thicker litter.

In the interpretation of the results, it should be taken into consideration that we used a simplified model for the test substrate. At the same time, the degradation mechanism of pure cellulose significantly differs from that of plant litter by the range of destructors and the set and sequence of the process steps. The degradation of pure cellulose reflects the colonizing potential of micromycetes to a greater extent than the conditions for the utilization of organic matter by the destroyers. On the one hand, this simplification of the actual situation can be considered as a shortcoming, because it is difficult to directly go to the absolute estimates of the decomposition rate of plant litter. On the other hand, it can be considered as an advantage, because the use of a standardized substrate allows analyzing the spatial structure of the decomposition process in a pure form.

Interest in the spatial ecology of soil organisms has risen recently, and the progress in the development of soil biology is related to this field of study [21, 37], including for polluted areas [8]. At the same time, there are many white spots in the spatial ecology of soil micromycetes [66]. Our results indicate that such a strong disturbing action on the forest ecosystem as the polymetal pollution from a point source of emission radically changes the spatial distribution of the cellulolytic activity of soil micromycetes.

It follows from our results that the model of concentric impact zones of an individual tree, which is traced back to the work of Zinke [77], has limited applicability to the spatial distribution of the cellulolytic activity of micromycetes even in undisturbed ecosystems. In the works based on the methodology of geostatistical analysis, the characteristic size of the spatial heterogeneity for different parameters of the biological activity of the soil in a forest is usually estimated in the range from 3–4 to 8–10 m [37, 61] and is related to the local effect of individual trees. Our results indicate that this interpretation of the reasons for the formation of this heterogeneity should be treated with reserve.

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