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Seasonal Changes in the Spatial Distribution of Cellulolytic Activity of Soil Microflora under Conditions of Atmospheric Pollution

E. L. Vorobeichik

Institute of Plant and Animal Ecology, Ural Division, Russian Academy of Sciences, ul. Vos'mogo Marta 202, Yekaterinburg, 620144 Russia
e-mail: ev@ipae.uran.ru

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Abstract—Spatial variation in the cellulolytic activity of the soil microflora during the growing season (from May to September) has been studied in spruce–fir forests exposed to emissions from the Middle Ural Copper-Smelting Plant. It has been shown that the average rate of decomposition of pure cellulose in polluted areas is significantly reduced, with its spatial variation being markedly increased. The spatial pattern of cellulolytic activity remains stable during the growing season, and the integrated parameters of frequency distributions in zones with different pollution levels change with time in the same direction.

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Key words: cellulose decomposition, soil microorganisms, micromycetes, spatial structure, dynamics, industrial pollution, heavy metals, forest ecosystems, southern taiga, the Middle Urals.

Decomposition of dead organic matter is the key process providing for the return of biogenic elements to the soil and determining the productivity and stability of terrestrial ecosystems. To date, specialists have accumulated abundant information on organic matter decomposition, including data on its main agents, stages, characteristic rates, and specific features of progression in different biomes and ecosystem types (*Biology…*, 1974; Swift et al., 1979). However, some aspects of this process remain unclear. In particular, this concerns trends in the horizontal distribution of the functional activity of soil saprotrophs, as the attention of specialists in soil biology has been concentrated mainly on the vertical component of its spatial structure (Zvyagintsev et al., 2005). Interest in this problem is by no means casual. Previously, spatial variation in the properties of natural objects was usually regarded only as an obstacle to correct statistical estimation of the parameters of interest, but this attitude has changed recently: an increasing number of researchers consider that spatial structure is an essential property of ecosystems that needs detailed analysis (Goovaerts, 1998, 1999; Heuvelink and Webster, 2001; Ettema and Wardle, 2002).

Many authors have shown that organic matter decomposition is retarded in ecosystems exposed to pollution with heavy metals and sulfur compounds, attributing this phenomenon primarily to a reduced activity of the soil biota (Strojan, 1978; Coughtrey et al., 1979; Freedman and Hutchinson, 1980; Baath, 1989; Berg et al., 1991; Vorobeichik et al. 1994; Giller et al., 1998; McEnroe and Helmisaari, 2001; Chew et al., 2001; Vorobeichik, 2002a, 2002b, 2003). However, information on changes in the spatial distribution of destructor organisms in the polluted environment is virtually absent, although this aspect is important both for understanding trends in their functioning under pessimal conditions and for solving certain methodological problems (Gongal'skii et al., 2003; Irmler, 1998).

In my previous study (Vorobeichik, 2002a), I described the phenomenon of focality in the spatial structure of cellulolytic activity under conditions of industrial pollution: the foci of very high cellulolytic activity characteristic of undisturbed habitats proved to be preserved in an area with an extremely high contents of pollutants, where organic matter destruction was virtually blocked. Similar changes in the spatial structure were revealed along an altitudinal gradient, upon transition from the mountain taiga to the mountain tundra belt (Vorobeichik, 2002b). This phenomenon makes us take a different look on the inhibition of organic matter decomposition under the effect of unfavorable factors, as it can no longer be regarded as a spatially uniform process. This study is devoted to the problem concerning how stable in time the spatial distribution of cellulolytic activity is.

STUDY REGION

Studies were performed near the Middle Ural Copper-Smelting Plant (MUCP) located in the suburbs of

the city of Revda, Sverdlovsk oblast (the southern taiga subzone). The main components of emissions from the plant are SO_2 and suspended polymetal particles consisting mainly of the compounds of Cu, Pb, Cd, Zn, and As. Long-term heavy metal and acid pollution (since 1940) has resulted in almost complete degradation of forest ecosystems near the source of emissions. Characteristics of technogenic load and ecosystem transformation in the study region were described in detail previously (Vorobeichik et al., 1994; Voroveichik, 2003).

Test plots were established in spruce–fir forests growing on soddy podzolic soils, in the lower parts of slopes, in the impact, buffer, and background zones located 1, 4, and 30 km west of the plant, respectively. In the buffer zone, compared to the background, tree stand degradation is manifested (timber volume is reduced, and the proportion of dead standing trees is greater); the species richness of the herb–dwarf shrub and moss layers decreases from 31 to 23 and from 24 to 10 species, respectively; and decomposition of the litter is markedly retarded, with its depth being two to three times greater (5–7 cm vs. 2–3 cm in the background zone). The impact zone is characterized by a fragmentary tree stand consisting of weakened or dying trees; the herb–dwarf shrub formed by only one to seven species, depending on the site *(Equisetum sylvaticum, E. pratense, Deschampsia caespitosa, Agrostis* sp., *Poa pratensis, Epilobium angustifolium, Sanguisorba* sp., and *Tussilago farfara*); and a well-developed monospecific moss cover consisting of *Pohlia nutans*, a pioneer species that usually colonizes mechanically disturbed areas. Its coverage reaches 70%. The litter is virtually not decomposed, and its depth in depressions and near tree trunks may reach 10–15 cm.

MATERIAL AND METHODS

The cellulolytic activity of the soil biota was estimated from the decomposition rate of pure cellulose. This parameter was determined by calculating the daily decrement (%) of the absolutely dry weight of standard filter paper samples (initial weight 0.79 ± 0.06 g) placed in nylon mesh bags (mesh size 0.5 mm) and exposed under natural conditions for specified periods of time. The bags were placed within the forest litter or, when the litter was very thin, at the litter–humus horizon boundary so as to cause the minimum possible damage to the ground vegetation.

Three test plots located at distances of 70 to 170 m were established in each of the tree zones with different pollution levels. In each plot, 50 bags with cellulose were arranged in a line at 50-cm intervals. The cellulose sample in each point of the line was exposed for 23–25 days; thereafter, it was removed, and another sample was immediately put in exactly the same place. On the whole, 2250 cellulose samples were tested for the decomposition rate over five periods of exposure: (I) from May 26, (II) from June 18, (III) from July 15, (IV) from August 7, and (V) from September 1 to September 26, 2003. Information on weather conditions (eight measurements per day) was received from the Revda weather station.

In each zone, samples of the forest litter were taken from 25 plots (10×10 m) more or less uniformly distributed over an area of approximately 500×500 m. Six samples per plot were taken; thus, a total of 450 samples from three zones were analyzed. Each sample was placed in an individual plastic bag. In the laboratory, the litter was rid of large inclusions (branches, cones, pieces of bark, etc.), dried to an air-dry state, and ground. The resulting powder was suspended in water at a ratio of 1 : 25 (w/v) to measure pH. Movable and exchangeable forms of metals were extracted, respectively, with 5% HNO_3 and 0.05 M $CaCl_2$ (1 : 10 w/v) with subsequent filtration through a paper filter. Their concentrations were measured on an AAS 6 Vario atomic absorption spectrometer (Analytic Jena AG, Germany).

Frequency distributions were analyzed, and Spearman's rank correlation coefficients were calculated on the basis of concrete values recorded at certain points in certain periods of exposure; in ANOVA, the mean value for a plot was used as an accounting unit. In addition to traditional parameters of variation, the coefficient of homogeneity K was calculated to estimate the degree of similarity between the observed spatial distribution and the theoretical, maximally nonuniform distribution (Vorobeichik, 2002a):

$$K = [D/\{(X_m - X)(X - X_0) + fD_m + (1 - f)D_0\}]^{\frac{1}{2}}, \quad f = (X - X_0)/(X_m - X_0),$$

where D and X are the variance and mean value of the test parameter in the whole sample and $X_m(D_m)$ and $X_0(D_0)$ are the means (variances) in subsamples with large and small values of the parameter, respectively. This coefficient is 0 when there is no spatial variation and increases to 1 when parameter values in the sample fall into two distinct groups, high and low, and its variance reaches the highest possible level. The $X_m(D_m)$ and $X_0(D_0)$ values were calculated for each plot and period of exposure on the basis of the five highest and five lowest values, respectively. General concordance in the spatial distribution of test parameters in all periods of exposure was estimated for each plot using the Kendall–Smith coefficient of concordance (a function of Spearman's rank correlation coefficients for all combinations).

RESULTS

Both heavy metal contents and acidity of forest litter had markedly different values in the background, buffer, and impact zones (Table 1). The difference in acidity between the background and impact zones reached almost one pH unit (Table 1). Compared to the background, the contents of movable metal forms in the

Table 1. Acidity and heavy metal content of forest litter in zones with different pollution levels

Parameter	Zone		
	background	buffer	impact
pH_{water}	5.41 ± 0.06	4.76 ± 0.04	4.53 ± 0.05
Movable forms, mg/kg:			
Cu	48.88 ± 2.46	1948.45 ± 106.19	3109.56 ± 158.33
Cd	2.99 ± 0.10	14.35 ± 1.12	12.30 ± 0.99
Pb	86.67 ± 2.29	964.35 ± 43.97	1485.26 ± 44.49
Zn	242.37 ± 9.13	590.74 ± 41.66	539.53 ± 44.59
Exchangeable forms, mg/kg:			
Cu	3.42 ± 0.17	31.20 ± 3.30	100.83 ± 9.92
Cd	0.57 ± 0.04	5.55 ± 0.36	5.80 ± 0.38
Pb	0.47 ± 0.04	5.46 ± 0.50	11.95 ± 1.08
Zn	27.64 ± 2.05	164.97 ± 12.79	215.65 ± 13.67

Note: Mean values and their standard deviations for 25 plots in each zone are shown, with one plot (the average value for six samples) being taken as an accounting unit.

Table 2. Weather conditions in different periods of exposure

Period	Daily air temperature, °C			Precipitation, mm
	average	minimum	maximum	
I	11.5 ± 0.6 (4.2–16.6)	5.6 ± 0.7 (0–12.2)	17.2 ± 0.7 (6.7–22.7)	111.8
II	18.2 ± 0.7 (9.2–22.3)	12.5 ± 0.6 (6–16.1)	23.7 ± 0.7 (11.2–28.4)	65.0
III	18.4 ± 0.6 (12.8–24.5)	11.9 ± 0.6 (5.8–16.3)	24.8 ± 0.8 (17.6–31.7)	16.2
IV	18.7 ± 0.6 (13.5–24)	13.5 ± 0.5 (8.1–18.3)	24.7 ± 0.8 (16.1–32.3)	117.8
V	10.4 ± 1.0 (1.6–24.1)	6.5 ± 1.0 (–1.5…+17.9)	15.6 ± 1.4 (5.4–31.3)	31.4

Note: Mean values with standard deviations and, in parentheses, the minimum and maximum values over the period are shown.

impact zone increased by factors of 2 (Zn) to 60 (Cu) and the content of exchangeable metal forms increased by factors of 8–10 (Cd and Zn) to 25–30 (Pb and Cu). In the background zone, the proportions of exchangeable forms relative to movable metal were small: 0.5% for Pb, 7% for Cu, 11% for Zn, and 19% for Cd. In polluted areas, the respective proportions increased to 0.6, 2, 28, and 39% in the buffer zone and to 0.8, 3, 40, and 47% in the impact zone.

Weather conditions varied during the growing season (Table 2): periods I and V were relatively cold, whereas periods II, III, and IV were relatively warm, with the minimum and maximum precipitation being characteristic of periods II and IV, respectively. The most contrasting temperatures were characteristic of period V: at its end, air temperature decreased below 0°C. The greatest differences between the periods concerned the minimum air temperature.

The frequency distributions of cellulolytic activity significantly differed between the zones and, to a lesser extent, between the periods of exposure (Fig. 1). Upon transition from the background to the impact zone or, within the zone, from warm to cold periods, the centers of distributions consistently shifted toward lower values. The greatest asymmetry and sharpest peaks were characteristic of frequency distributions in the impact zone (Table 3). The average rates of cellulose decomposition in the background and impact zones in the same periods differed by factors of 4.3 to 16.0, and the maximum rates differed by factors of 1.2 to 3.3. Within the zone, differences between the rates of cellulose decomposition in different periods were most distinct in the impact zone (by a factor of 10 for the average rate and by a factor of 4.9 for the maximum rate), markedly smaller in the background zone (by factors of 3.0 and 2.2), and intermediate in the buffer zone (by factors of 2.9 and 5.3, respectively).

Zero rates of cellulose decomposition in the buffer and impact zones were recorded in all periods of exposure; in the background zone, they were recorded only in periods I and III. The maximum rates recorded in the same periods were always higher in the background and buffer zones than in the impact zone. However, the rates recorded in the impact zone in the warm periods II and

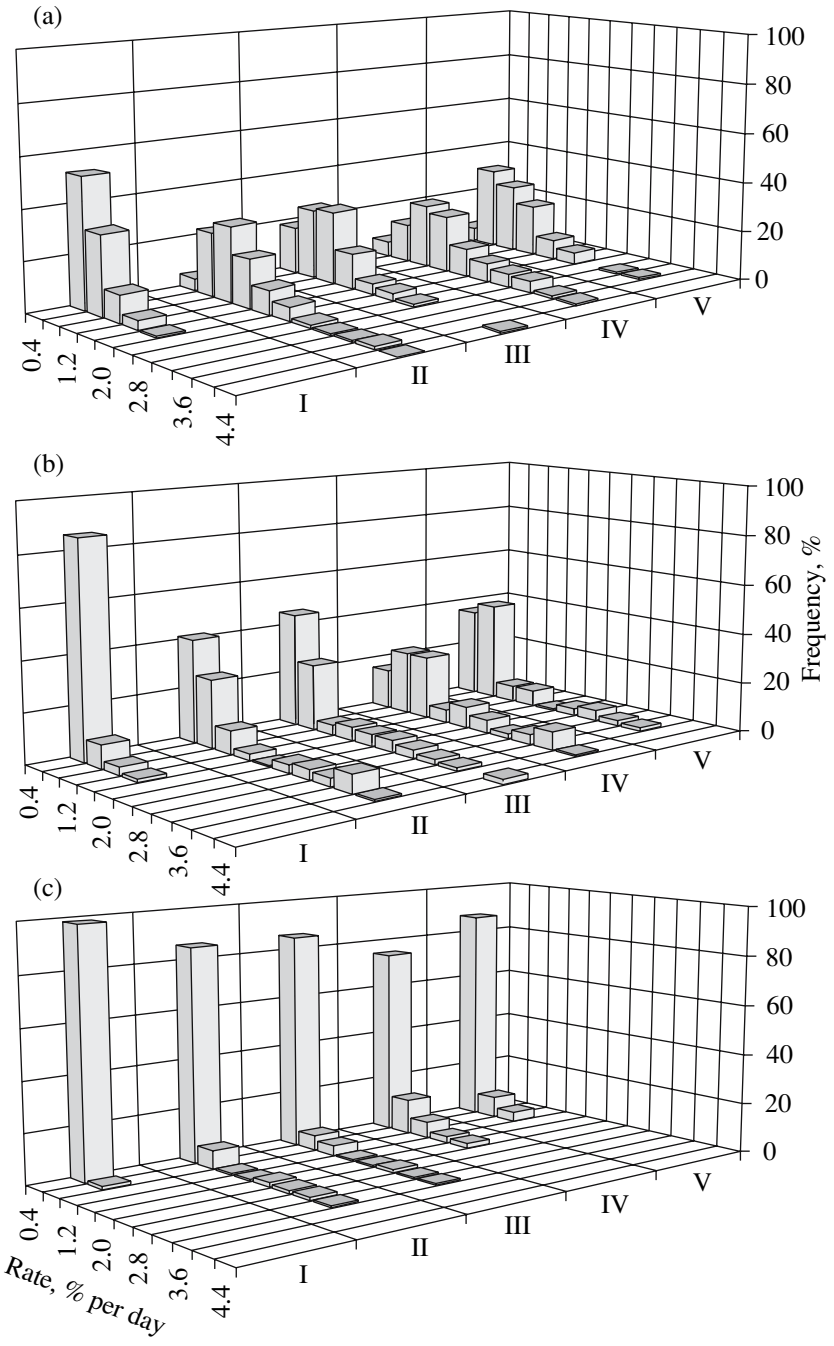

Fig. 1. Frequency distributions of cellulose decomposition rate (the upper limit of the range) in (a) background, (b) buffer, and (c) impact zones in different periods of exposure (I–V).

III were higher than those in the background and buffer zones in the cold period I. The maximum rates exceed the average rates by factors of 2.8–4.5 in the background zone, 3.0–6.0 in the buffer zone, and 5.8–20.3 in the impact zone. The decile range (characterizing the extent of variation without regard to distribution tails) in the same period of exposure (except for period I) was greater in the buffer than in the background zone and in the background than in the impact zone. Moreover, there was no range overlap between the impact and other zones, unlike the situation with the maximum values. Assuming that the boundary between high and low rates of cellulose decomposition in a certain period lies at the 10% percentile of the corresponding frequency distribution in the background zone, we obtain that high rates in the impact zone were recorded at 7.3% of points in period I, 12.0% of points in period II, 22.7% of points in period III, 15.3% of points in period IV, and

Table 3. Parameters of empirical frequency distributions of cellulose decomposition rate (percent per day) in zones with different pollution levels

Zone	Period	Minimum	Average	Maximum	Decile range	Coefficient			
						variation, %	homogeneity	asymmetry	curtosis
Background	I	0.00	0.47	1.85	0.93	76.60	0.58	1.13	1.14**
	II	0.07	1.18	3.70	1.55	55.44	0.55	1.33	2.66**
	III	0.00	0.90	4.07	1.39	66.53	0.54	1.46	4.74**
	IV	0.24	1.40	3.86	1.90	52.60	0.56	0.85	0.52
	V	0.23	1.05	3.46	1.32	52.21	0.56	1.13	2.17**
Buffer	I	0.00	0.23	1.38	0.50	109.83	0.53	2.25	5.91**
	II	0.00	0.93	3.66	2.74	111.50	0.66	1.51	0.84*
	III	0.00	0.79	4.09	2.15	120.24	0.65	1.73	2.41**
	IV	0.00	1.23	3.70	2.75	78.76	0.59	1.14	0.33
	V	0.00	0.76	3.50	1.90	101.44	0.57	1.95	3.06**
Impact	I	0.00	0.03	0.61	0.07	256.69	0.48	4.52	23.39**
	II	0.00	0.24	3.00	0.61	219.60	0.71	3.48	12.29**
	III	0.00	0.21	2.86	0.59	228.75	0.76	3.52	13.50**
	IV	0.00	0.30	1.76	0.86	125.15	0.65	1.93	3.59**
	V	0.00	0.17	1.03	0.47	125.45	0.62	2.04	3.76**

Note: Asterisks indicate that coefficients of curtosis significantly differ from zero at * $p < 0.05$ or ** $p < 0.01$; all coefficients of asymmetry significantly differ from zero at $p < 0.01$. The coefficients of homogeneity are shown as average values for three plots.

12.0% of points in period V; in the buffer zone, the respective proportions were 67.3, 48.7, 68.7, 76.0, and 59.3%.

The highest and lowest values of the variation coefficient, which differed from each other in the same period by a factor of 2.3–4.0, were recorded in the impact and background zones, respectively; the buffer zone was intermediate in this respect. The coefficients of homogeneity in the same periods of exposure (except for period I) were higher in the impact zone than in the buffer zone and in the buffer zone than in the background zone.

According to the results of two-way ANOVA, all integrated parameters of frequency distributions significantly differed depending on the zone of pollution (Table 4). The period of exposure also had a significant effect on most parameters (except for the coefficient of asymmetry, curtosis, and homogeneity). The factor "zone of pollution" accounted for 24–75% of the total variance of these parameters, whereas the factor "period of exposure" accounted for only 7–34% (with the smallest values pertaining to the variation coefficient). The interaction of factors "zone of pollution" × "period of exposure" had an insignificant effect on the parameters studied, as the direction of their changes during the growing season was the same in all zones.

To estimate how stable in time the spatial distribution of cellulolytic activity is, relationships between cellulose decomposition rates in different periods of exposure were analyzed. In all zones, a close positive correlation between these rates in two successive periods of exposure was revealed. For example, Fig. 2 shows this correlation for the contrasting periods IV and V. The strength of correlations was estimated from the absolute values of Spearman's rank correlation coefficient (Fig. 3). There were 10 such coefficients (for all asymmetrical combinations) calculated for each plot and, hence, 30 coefficients for each zone. The strength of correlations was maximum in the impact zone, with correlation coefficients for all periods of exposure averaging 0.599 and those for successive periods (I and II, II and III, III and IV, and IV and V) averaging 0.698; it decreased in the buffer zone (0.516 and 0.616) and was minimum in the background zone (0.300 and 0.359, respectively). In the impact zone, 29 out of 30 correlation coefficients significantly differed from zero at $p < 0.05$; in the buffer zone, there were 27 such coefficients and their number in the background zone decreased to 15. The coefficients of concordance for individual test plots were 0.64, 0.66, and 0.74 in the impact zone; 0.51, 0.60, and 0.72 in the buffer zone; and 0.27, 0.41, and 0.64 in the background zone. All these coefficients (except for the minimum value) significantly differed from zero according to the χ^2 test, with $p \ll 0.001$ at $n = 50$ and $k = 5$.

DISCUSSION

Considerable differences between the zones of pollution concerned the contents of both movable and

Table 4. Results of two-way ANOVA for differences in the parameters of frequency distributions of the cellulose decomposition rate between pollution zones and periods of exposure

Parameter	Source of variation					
	pollution zone		period of exposure		zone × period	
	$F_{2;\,30}$	p	$F_{4;\,30}$	p	$F_{8;\,30}$	p
Arithmetic mean*	72.26 (0.60)	<0.00001	19.67 (0.26)	<0.00001	1.18	0.34465
Lower decile**	89.45 (0.71)	<0.00001	12.16 (0.15)	0.00001	1.51	0.19602
Upper decile*	32.85 (0.45)	<0.00001	13.97 (0.30)	<0.00001	1.52	0.19157
Limit range*	9.74 (0.24)	0.00055	8.31 (0.34)	0.00012	0.73	0.66793
Decile range*	23.51 (0.38)	<0.00001	11.64 (0.30)	0.00001	1.78	0.12166
Coefficient of variation*	61.67 (0.75)	<0.00001	4.18 (0.07)	0.00829	0.46	0.87301
Coefficient of asymmetry	19.96 (0.55)	<0.00001	0.96	0.44507	1.06	0.41622
Coefficient of curtosis	11.92 (0.35)	0.00016	1.02	0.41219	2.02	0.07806
Coefficient of homogeneity	34.01 (0.65)	<0.00001	2.15	0.09888	1.13	0.37491

Note: $F_{n;\,k}$ is Fisher's test, with n and k being the numbers of degrees of freedom for the factor and error, respectively; p is the significance level; values in parentheses show the proportion of variance explained by the factor (calculated according to Snedecor). To normalize variance, variables were transformed by computing their logarithms (*) or square root (**).

exchangeable forms of heavy metals, with the latter being regarded as most toxic for soil microorganisms (Kunito et al., 1999). Their minimum effective concentrations inhibiting the functioning of these microorganisms may differ by two to three orders of magnitude, depending on the metal (Baath, 1989; Giller et al., 1998), but the concentrations recorded in the impact zone exceed these minimum values in all cases. This is evidence that chemical pollution is the key factor responsible for the observed retardation of cellulose decomposition.

In taiga forests, the main role in cellulose decomposition belongs to soil micromycetes. These organisms are most abundant in the forest litter, which, therefore, is regarded as the most biologically active soil horizon (Zvyagintsev et al., 2005). Thus, placing the samples of cellulose within the litter allows us to estimate the maximum possible rates of its decomposition. Moreover, natural microclimatic conditions of litter decomposition in this case are simulated better than in experiments with cellulose samples placed on the litter surface. A direct comparison of the absolute rates of cellulose decomposition with those recorded by other authors is difficult because of differences in the conditions of field experiments (the initial weight of samples, the period of exposure, the depth of sample placement, etc.). However, the average decomposition rate of samples exposed for less than one year in the background zone (0.47–1.40% per day) is close to the values reported by other authors. For example, the daily rate of cellulose decomposition in weakly disturbed biotopes of Silesia (56-day exposure) was estimated at 0.45–1.70% (Bienkowski, 1990a); in oak and beech mountain forests of the Caucasus (98- to 129-day exposure), at 0.51–0.57% (Fischer et al., 2006); and in Carpathian beech and mixed forests at low elevations (70-day exposure), at 0.50–1.39% (Drewnik, 2006). However, when the standard one-year period of exposure is used, the calculated daily rates are usually lower: in conifer forests of Finland, for example, they range from 0.03 to 0.24% (Kurka et al., 2000). The cause of this situation is well known: the initial substrate (sample) has a small mass and is decomposed almost completely within a relatively short time, and, therefore, the daily decomposition rate calculated over the whole period of exposure is systematically underestimated. Thus, at the highest daily rate recorded in this study (4.07%), almost all cellulose (93.6%) should be decomposed within 23 days; at a 1.00% rate (the average value for all periods of exposure in the background zone), complete decomposition will take 100 days if this process is linear; if the process conforms to the most conservative exponential model, 95% decomposition will take 264 days (both these period are shorter than one year).

The average daily rates of cellulose decomposition in the impact zone (0.03–0.30%) correspond to those recorded under pessimal conditions in nature: 0.04–0.09% in the stony tundra in Spitsbergen (Bienkowski, 1990b), 0.20–0.35% in deserts and steppes of the Caspian Lowland (Fischer et al., 2006), and 0.31–0.62 in high-mountain regions of the Carpathians (Drewnik, 2006).

It is generally accepted that organic matter decomposition in nature is determined by three factors: substrate properties, physicochemical conditions in the habitat (temperature, moisture, acidity, etc.), and activity of the soil biota (Swift et al., 1979). As this study was performed with a standard, homogeneous material (pure cellulose), the effect of the first factor was excluded. Therefore, differences in the decomposition

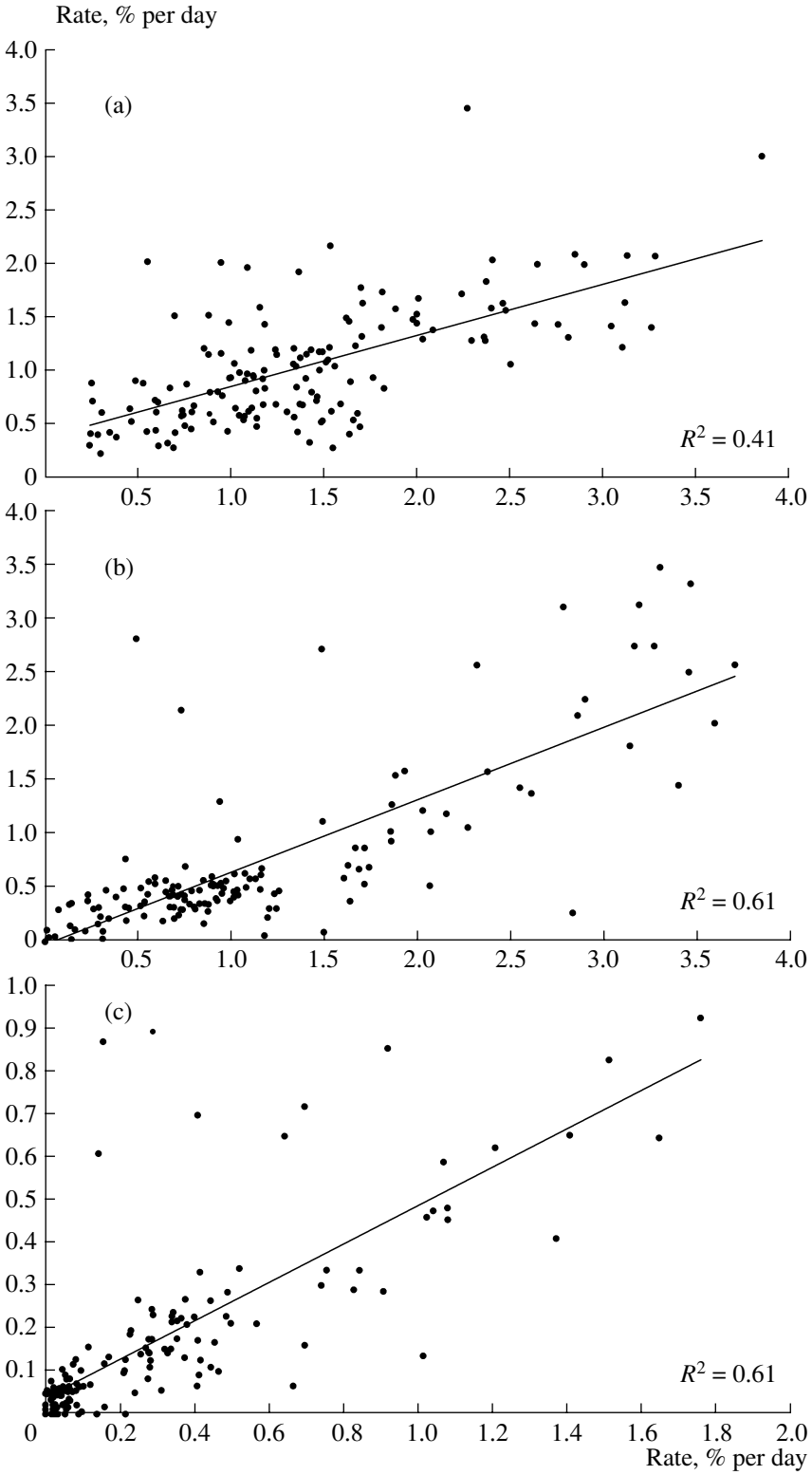

Fig. 2. Relationship between cellulose decomposition rates in two successive periods of exposure in (a) background, (b) buffer, and (c) impact zones.
X–IV axis, period IV; Y axis, period R^2 is the proportion of variance explained by the linear regression equation.

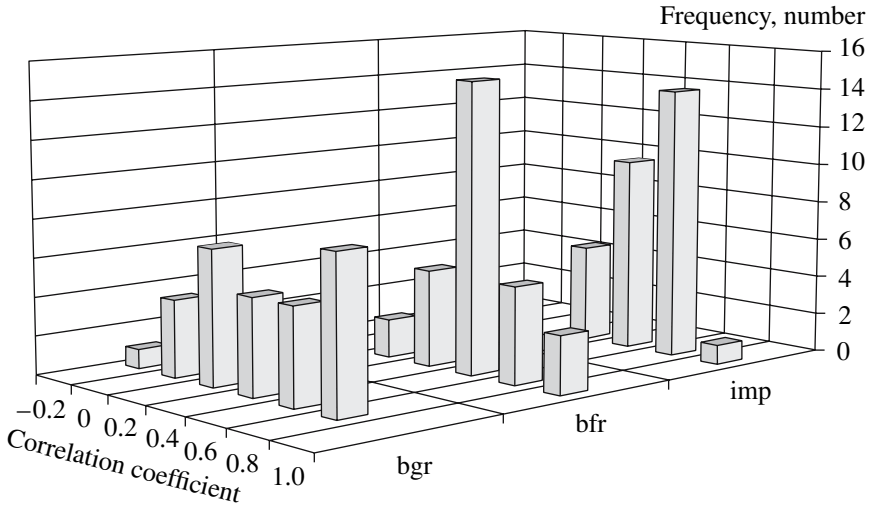

Fig. 3. Frequency distributions of Spearman's rank correlation coefficients (the upper limit of the range) for cellulose decomposition rates in different periods of exposure in the background (bgr), buffer (bfr), and impact (imp) zones.

rate between test points were determined by the remaining two factors. Its results confirm the phenomenon revealed in our previous study: the space of pessimal habitats is differentiated into two types of microbiotopes characterized by either high or low rates of cellulose decomposition. The difference between these microhabitats in the impact zone is considerable, with the maximum and average decomposition rates differing by a factor of up to 20. The peaks of cellulolytic activity are not singular: 7–23% of points in the impact zone are characterized by decomposition rates that are as high as those in the background zone. An increase in relative indices of variation (the coefficients of variation and homogeneity) is a logical consequence of this spatial differentiation. A high rate of cellulose decomposition in individual sites is evidence that micromycete species (at least, some of them) are tolerant of high pollution levels. This tolerance, accounted for by numerous mechanisms of protection from the toxic action of heavy metals (Gadd, 1993), was repeatedly noted in different situations (Baath, 1989; Giller et al., 1998; Marfenina, 2005).

An increase in the spatial variation of cellulolytic activity may be accounted for by a nonuniform distribution of soil micromycetes or their interference competition with other groups of the soil biota, such as mycorrhizal fungi (Koide and Wu, 2003), on the one hand, and by spatial variation in physicochemical parameters of the litter, on the other hand. The experimental design of this study does not allow us to separate the effects of these factors. As a hypothesis, the following explanation may be proposed. Soil micromycetes are known to form colonies in sites with conditions favorable for their development, moving there through pessimal areas with the aid of mycelial strands (Zvyagintsev et al., 2005; Marfenina, 2005). Each cellulose sample placed in the site where physicochemical conditions are not extreme is a potential favorable locus for micromycetes. Having "located" this locus, they actively colonize and, eventually, fully utilize it. Chemical pollution leads to elimination of sensitive micromycete species, the amount of active mycelium decreases, and changes in the micromycete life cycle take place. In particular, they include the retarded growth of mycelium, its lysis prior to spore formation, a decrease in spore germination rate, and cessation of germ tube development (Marfenina, 2005). Correspondingly, the general colonization potential of micromycetes decreases and the majority of samples remain "vacant." Thus, the spatial distribution of cellulose decomposition rates by the end of exposure reflects primarily the process of colonization of cellulose samples by micromycetes (i.e., the pattern of successfully colonized and noncolonized samples).

Experiments on the decomposition rate of plant remains are usually performed by exposing several test samples at one site and then removing them after certain periods of time. This scheme is not instrumental in assessing the temporal dynamics of activity of the soil biota, since different stages of organic matter decomposition are accounted for by different groups of organisms (*Biology…*, 1974; Swift et al., 1979). The seasonal component of decomposition dynamics may be estimated by complementing the above standard scheme with a symmetrical scheme: new samples are placed in the same site at certain intervals to be removed simultaneously at the end of the exposure period (Herlitzius, 1983). This fairly complex approach allowed specialists to reveal the presence of a seasonal component in the dynamics of decomposition of plant remains (Herlitzius, 1983; Berg et al., 1998; Gunadi et al., 1998).

Experiments with pure cellulose allow a direct analysis of the temporal dynamics of decomposition. However, experimental schemes similar to that used in this study, with several samples consecutively exposed at the same site for short periods of time over the growing season, are rarely used in practice, although one of the first studies with pure cellulose as a test substrate for measuring its decomposition rate (Golley, 1960) was performed according to such a scheme. The results described above provide evidence for distinct seasonal dynamics of cellulose decomposition in the background zone, where its rates in certain periods of exposure differed by a factor of three. Other authors also revealed considerable changes in the rate of cellulose decomposition in different seasons (French, 1988; Fischer et al., 2006) and during the same growing season (Golley, 1960; Witkamp and van der Drift, 1961; Brown and Howson, 1988). In a temperate climate, the peak of the decomposition rate is usually observed in late summer and early autumn. Under chemical pollution, seasonal changes in the decomposition rate increase, with its values in the impact zone differing by an order of magnitude. This may be explained by a decrease in the species richness of micromycetes and, therefore, higher responsiveness of their communities to fluctuations of temperature and humidity, on the one hand, and by increasingly contrasting microclimatic conditions in the impact zone, on the other hand.

In contrast to changes in the average decomposition rate, the dynamics of its spatial variation is leveled off: differences between the values of the variation coefficient in different periods of exposure were no more than twofold. An important fact is that the relationship between zones with different pollution levels with respect to the degree of variation remains unchanged throughout the growing season. Close positive correlations between parameters of cellulolytic activity in different periods of exposure indicate that when a high decomposition rate was recorded at a given point in a certain period of time, it is highly probable that this rate at the same point was also high in other periods. This is evidence that the general spatial pattern of cellulolytic activity and the distribution of points with a high decomposition rate remain relatively constant in time (at least, throughout the growing season). This stability of the spatial structure is more distinct in polluted areas than in the background zone, which may be accounted for by the same mechanisms that are responsible for differentiation of space into the loci with high and low decomposition rates: developed colonies of resistant micromycete species are capable of self-maintenance over long periods of time, on the one hand, but a reduced colonization potential does not allow them to occupy new areas.

CONCLUSIONS

In this study, I continued analysis of the phenomenon of sharply increasing spatial variation in the cellulolytic activity of soil microflora upon deterioration of environmental conditions. Under industrial pollution, destruction processes are almost completely blocked in the greater part of the impact zone, but there are some foci in which cellulolytic activity remains as high as in the background zone. The main conclusion drawn from the results of this study is that the foci of high cellulolytic activity retain a constant location throughout the growing season, with the general spatial pattern of cellulolytic activity also remaining relatively stable in time. This stability is manifested more distinctly in the area with the highest pollution level. The temporal dynamics of integrated parameters of spatial variation (coefficients of variation and other indices) in different zones of the pollution gradient have the same direction. This fact is important from the methodological standpoint, as it shows that comparisons between the zones examined in different periods of the growing season are correct.

The problem concerning the mechanisms of formation of spatial structure and its modification under the effect of pollution needs special analysis and is not considered here. It fact, this study concerns the final results of the functioning of a cellulolytic microbial community formed after the introduction of pure cellulose samples into the forest litter. An analysis of the taxonomic structure and dynamics of this community, its modification under the effect of pollution, and the life cycles of its constituent species may shed light both on the causes of differential distribution of cellulolytic activity in space and on the factors providing for the stability of this distribution pattern in time.

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