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ECOLOGY

Changes in the Spatial Structure of the Destruction Process under the Conditions of Atmospheric Pollution of Forest Ecosystems

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Abstract—Contamination of the southern taiga forests (Middle Urals) by from cooper smelters (heavy metals combined with SO_2) not only decreases the mean rate of decomposition of pure cellulose, but also radically changes the spatial structure of the destruction process. Heterogeneity of distribution of the destruction rate is sharply increased near the source of emission due to differentiation of the space into microsites with high and low destruction rates. The range of spatial heterogeneity amounts to several tens of centimeters and the distribution of microsites with a high rate is random within several tens of meters. A hypothesis has been put forward that the described changes in the spatial structure of the destruction process are related, above all, to disturbed colonization of the substrate by soil microfungi.

INTRODUCTION

Inhibition of the organic matter destruction in the case of contamination of terrestrial ecosystems by heavy metals and sulfur dioxide has been well documented (Strojan, 1978; Coughtrey *et al*., 1979; Freedman and Hutchinson, 1980; Killham and Wainwright, 1981; Grodzinski *et al*., 1990; Zwolinski, 1990; Berg *et al*., 1991; Vorobeichik, 1991, 1995). However, mainly changes in average rates under the conditions of moderate pollution were studied, while the information about spatial distribution of the activity of organisms-destroyers is almost absent. Meanwhile, this aspect is essential both for understanding the patterns of functioning of the soil biota under extreme conditions and solving some methodical problems in order to correctly estimate the destruction process.

When analyzing the changes in the rate of pure cellulose destruction in the southern taiga forests contaminated by polymetallic dust, we found very significant differences in the spatial variation of this index: the coefficient of variation increased almost by one order of magnitude with the approach to the source of emission—from 16.9 ± 2.2% on the background territory to 136.9 ± 17.7% on the strongly polluted territory (Vorobeichik, 1991). This study was aimed at a more detailed analysis of such significant changes in the spatial distribution of the destruction rate.

REGION OF STUDIES

Studies were carried out near the Sredneural'skii copper smelter located at Revda, Sverdlovsk District (subzone of southern taiga). The main ingredients of emission: SO_2 and polymetallic dust, in which Cu, Pb, Cd, Zn, and As predominate. Permanent (about 60 years) contamination of the environment by heavy metals combined with soil acidification produced a powerful toxic load, which lead in the long run to almost full degradation of the forest ecosystems. The patterns of technogenic transformation of the soil, and plant cover in the region of studies have already been described in detail (Vorobeichik *et al*., 1994; Vorobeichik, 1995).

Plots were laid down in the impact (1 km to the west of the smelter), buffer (4 km), and background (20 km) zones in trans accumulative landscapes (lower part of slopes) in spruce-fir forests of different associations on grey forest soil (Table 1). In the buffer zone as compared to the background zone, processes of tree stand disintegration were activated (standing crop was reduced and proportion of dead trees increased from 2 to 14%), projective cover and species richness of the grass-shrub and moss cover diminished (from 31 to 23 and from 24 to 10 species, respectively), and decomposition of the litter is significantly inhibited (its thickness increased two to three times). The impact zone is a classical example of a technogenic desert: the tree stand is preserved as fragments of weakened or dead trees, the species richness of the grass-shrub layer decreases to one–seven species (horsetails, tufted hair-grass, bent, meadow-grass, rose bay, salad burnet, etc.), monospecific (explerent species *Pohlia nutans*) moss cover is well developed (projective cover reaches 70%), litter is almost not decomposed (its burials 10 to 15 cm thick occur in depressions), and a marked water erosion takes place in a part of the territory, which washes away the upper soil horizons, including horizon B.

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Table 1. Characteristics of plots and territory pollution

Index	Zone of load		
	background	buffer	impact
Composition of tree stand	8F2S + B, Asp	6F4S + B, Asp	8F2S +B, Asp
Association	Motley-grass-wood-sorrel	Horsetail-grass	Moss-horsetail
Soil	Grey forest heavy-loamy	Grey forest heavy-loamy with signs of gleying	Technozem of grey forest medium-loamy gley
Litter thickness, cm	1.6 ± 0.2	6.4 ± 0.3	6.1 ± 0.3
Litter pH_{water}	5.2 ± 0.1	4.7 ± 0.2	4.1 ± 0.1
Fallout, mg/m^2			
Cu	25.9 ± 4.3	112.2 ± 27.4	208.4 ± 28.2
Pb	6.6 ± 1.4	24.8 ± 4.8	50.5 ± 4.7
Cd	0.5 ± 0.1	1.9 ± 0.8	3.5 ± 0.5
Zn	28.8 ± 3.4	74.8 ± 16.5	112.2 ± 31.1
Concentration in litter, μg/g			
Cu	134.3 ± 10.9	3635.7 ± 441.4	5164.1 ± 430.6
Pb	83.5 ± 4.7	1516.1 ± 106.6	1532.1 ± 82.4
Cd	5.3 ± 0.4	8.8 ± 1.7	13.6 ± 2.6
Zn	379.9 ± 47.7	502.2 ± 88.8	559.3 ± 128.2

Note: Litter thickness is the mean of 30 measurements; concentrations of heavy metals were measured on an AAS-3 atomic-absorption spectrophotometer (Carl Zeiss, Germany); acid-soluble forms were determined in the soil with 5% HNO_3 as an extractant, fallout was estimated by the metal content in the snow cover (mean of five samples). Designations: (Asp) aspen, (B) birch, (F) fir; (S) spruce.

METHODS OF STUDY

The rate of destruction was measured by the loss of air-dry mass of pure cellulose (laboratory filter paper) exposed to the natural conditions for a fixed period of time. The paper was placed in net bags (5×10 cm) with three mesh sizes: *a*–5.0 mm; *b*–0.5 mm; *c*–0.14 mm. The bags were placed inside the litter or, if the litter was very thin, at the litter boundary with the humus-accumulating horizon in June; the duration of exposure was one year.

The experimental plots were arranged in a line at equal distances. Two spatial scales were used: macroscale (at 1.0–1.2 m) and microscale (at 10 cm). Each load zone contained 76 macroscale plots and 30 microscale plots. In each plot, bags with different mesh size were placed close to each other, but not in contact. For microscale, the plots were located in two variants of micirobiotopes: crown projection (series nos. 1 and 2, 10 plots in each) and intercrown spaces (series no. 3: 10 plots). In the impact zone, where the patchyness of soil-plant cover is very high, qualitative characteristics of phytocoenotic conditions were given for each macroscale plot, such as distance from tree trunk and presence of moss cover.

RESULTS

Macroscale. Spatial distribution of the rate of cellulose destruction at a given space scale is illustrated by the variant with a 0.14 mm mesh (Fig. 1). Spatial variability was markedly increased under the conditions of pollution, as compared to the background territory. In the background territory, almost all plot had a destruction rate close to maximum: in the range of 80–100% per year, only one plot was below 50% per year. In the buffer zone, the major part of the territory also had a high rate of destruction (the upper limit of the range remained at the level of 100% per year, while the lower limit was decreased to 60–70%). At the same time, microsites appeared with a very low rate (10–30% per year), but their proportion was small (about 8%). In the impact zone, it was as if the spatial structure of the destruction process changed to a mirror reflection of the buffer zone: the major part of the territory had a very low rate of destruction (10–20% per year), while there were microsites with a very high rate, comparable to that in the background territory: up to 97% per year. The proportion of such microsites with respect to the total area of plots is relatively small: 10–15%.

MANOVA (grades of the first factor: “peritrunk region”, “crown projection”, and “intercrown space” and grades of the second factor: “moss grove” and “moss-free litter”) has shown the absence of a significant effect of these factors: for different variants of mesh size, $p = 0.63$–095 for the main effects and $p = 0.82$–0.99 for the interaction of factors. Hence, the position of microsites with high rates of destruction is not connected with certain structural elements of phytocoenosis.

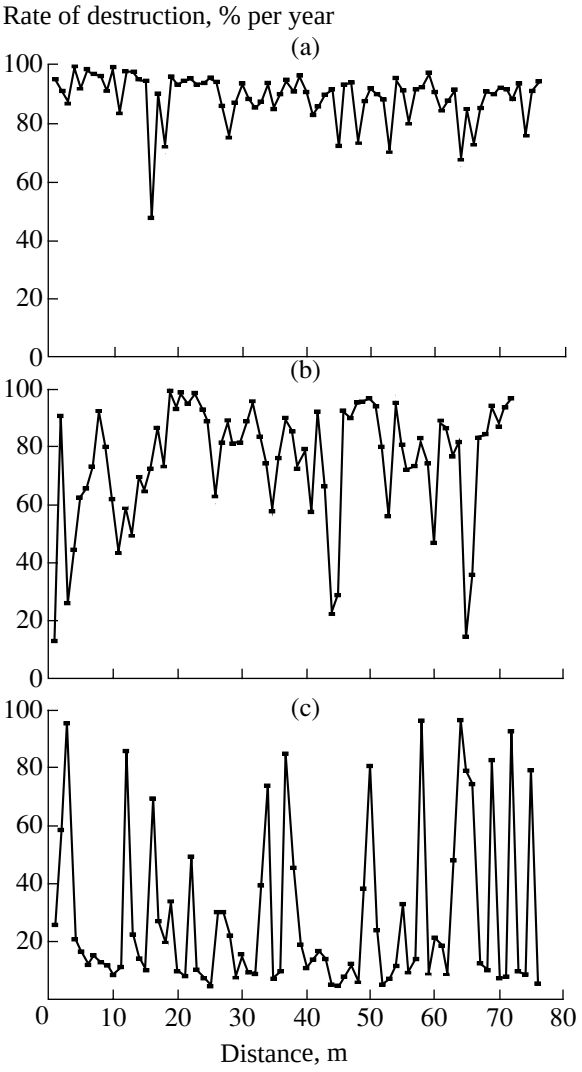


Fig. 1. Spatial distribution of the rate of cellulose destruction (0.14 mm mesh) at macroscale in the background (a), buffer (b), and impact (c) zones.

The frequency distribution of the destruction rate is presented in Fig. 2 and the main statistical parameters are listed in Table 2. Right-hand distributions "flow" regularly to the left-hand ones upon transition from the background territory to the impact zone and from lesser mesh size to the bigger one (correspondingly, skewness changes from negative to positive). In all cases, the distributions significantly differed from the normal and log-normal distributions (according to Kolmogorov–Smirnov test, $p < 0.15$–0.01). In the background zone, this is related to the distributions being truncated on the right: most plots had the rate close to the upper limit of measurements because of a long exposure. In the impact zone, it appears to be a mixture of two distributions with the centers in the areas of low and high rates. Significant deviations of distributions from the normal distribution make us consider with caution the standard statistical procedures and determine the displacement of accent towards nonparametric estimates.

The mean rates of destruction were decreased 3.2–3.7 times and the coefficients of variation increased 6.8–10.6 times upon transition from the background zone to the impact one. The differences between the zones are highly significant ($p \ll 0.00001$) according to the Kruscall–Wallis ANOVA by ranks at all variants of mesh size. In all zones, the mean rates increased upon transition from a larger mesh size to a lesser one (p = 0.0025, 0.0065, and 0.00001 in the impact, buffer, and background zones, respectively).

For comparison of the coefficients of variation, we used a modification of Student's *t*-test which takes into account nonzero values of skewness and kurtosis (Zhivotovskii, 1991):

$$U = \frac{|\ln C_1 - \ln C_2|}{\sqrt{V_1 + V_2}},$$

$$V_i = \frac{1 + 2C_i^2 + E_i/2 - A_i C_i}{2n_i}, \quad i = 1, 2,$$

where C_i, E_i, and A_i are coefficients of variation (in portions of unity), kurtosis, and skewness of the ith sample and n is the sample volume. All paired differences of the coefficients of variation between the zones are highly significant ($p \ll 0.0001$) at all variants of mesh size. Paired differences of the coefficients of variations between all combinations of mesh size are significant only in the background zone ($p < 0.01$), while in the buffer and impact zones, the differences in pair *b*–*c* are insignificant, while in pairs *a*–*b* and *a*–*c*, they are significant ($p < 0.001$).

The use of various order estimates (see Table 2) amplifies the picture. The greatest differences between the zones were noted for the minimum; upon transition from lower percentiles to the higher ones, the differences between the zones are gradually obliterated and disappear, when the maximum is considered. The median (C_m), quartile (C_q), and decile (C_d) coefficients of variation (Zhivotovskii, 1991) allow estimation of the contribution of different parts of frequency distribution to the total variability:

$$C_m = 1.481\tilde{s}/\tilde{x}, \quad C_q = 0.741R_q/\tilde{x},$$

$$C_d = 0.39R_d/\tilde{x},$$

where $\tilde{s}$ is the median deviation, $\tilde{x}$ is the median, and R_q and R_d are interquartile and interdecile ranges, respectively. In the background and buffer zones, all coefficients of variations were practically identical (for specific mesh size), while in the impact zone, they significantly increased from the median to the decile coefficients. Hence, the distribution tails make the main contribution to the total variability. Thus, analysis of the changes in order estimates suggests that a sharp increase in spatial variability of the destruction rate in

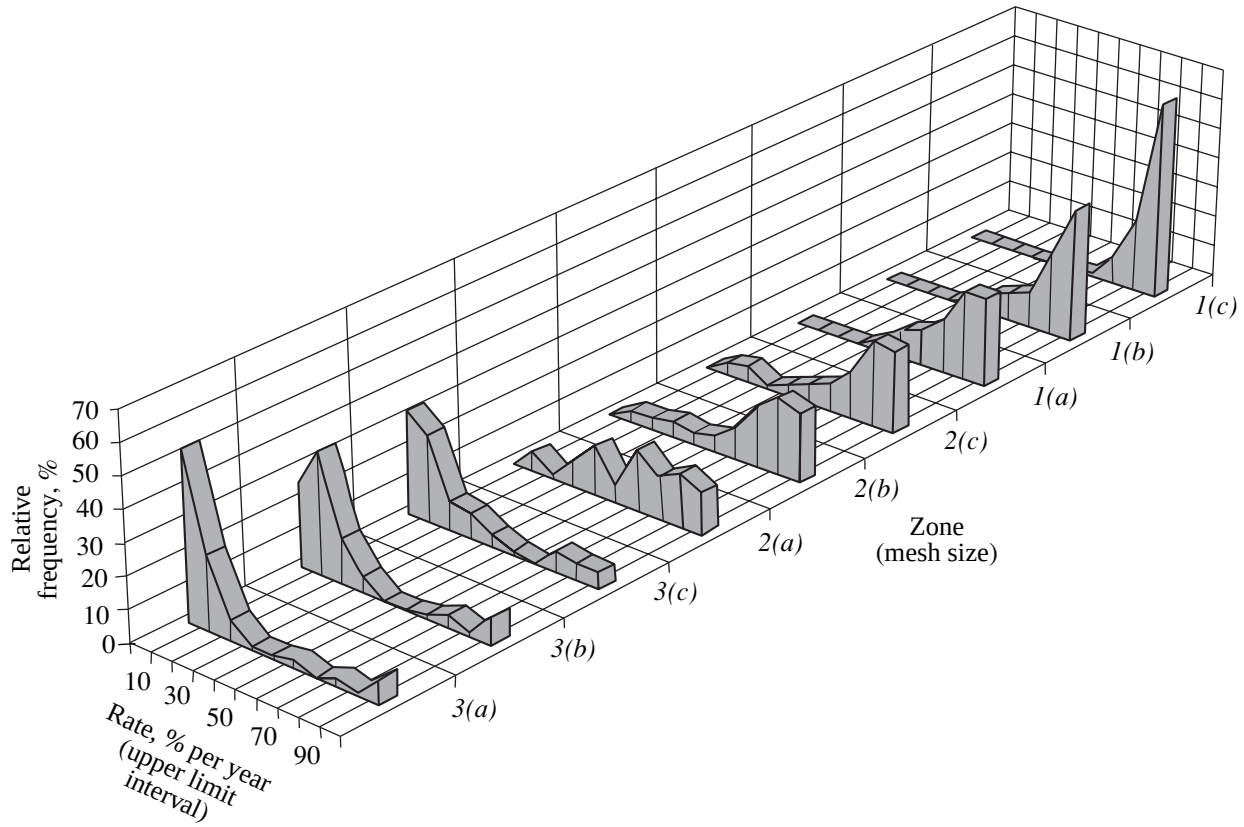


Fig. 2. Frequency distributions of the destruction rate at macroscale in the background (*1*), buffer (*2*), and impact (*3*) zones at different variants of meshs size (*a*—5.0 mm, *b*—0.5 mm, *c*—0.14 mm).

the polluted environment is due to division of the space into two types of microbiotopes: with very low and very high rates.

A modified version of the index of homogeneity we proposed earlier (Vorobeichik, 1986) was used as a measure of closeness of the empirical series to such a model:

$$K = \sqrt{\frac{D}{(X_m - X)(X - X_0) + fD_m + (1 - f)D_0}},$$

$$f = \frac{X - X_0}{X_m - X_0},$$

where D and X are the variance and mean of the sample, and X_m (D_m) and X_0 (D_0) are estimates of the mean (variance) using subsamples of high and low values, respectively. The coefficient changes from zero, when spatial variation is absent, to unity, when the sample consists of values of only two types (high and low) and its variance reaches a maximum possible value in this case. The values X_m (D_m) and X_0 (D_0) are considered to be common for all zones and were determined from 30 maximum values of rates in the background zone (with a variant of 0.14 mm mesh) and 30 minimum values in the impact zone (with a variant of 5 mm mesh), respectively.

In the impact zone, the index of homogeneity was significantly higher than in the background or buffer zone and was close to unity (see Table 2), which confirms the validity of the "focal" model of spatial structure of the destruction process in a polluted environment.

Microscale. Distribution of the destruction rate at microscale is presented in Fig. 3. The pattern of changes in spatial structure of the destruction process is similar to that at macroscale: a minimum variation was recorded in the background territory, a maximum variation in the impact zone, while the buffer zone occupied an intermediate position.

Analysis of frequency distribution was restricted to calculation of only some indices due to a small sample volume (Table 3). The absolute values varied, as it could be expected, to a lesser extent than at macroscale and their differences between the zones of load and mesh size variants were not that regular. Most likely, this is due to a small size of series and, hence, a significant role of the random factor. This can also explain the differences between the series. Thus, according to the Kruscall–Wallis test, the differences between the series were significant in all zones and all variants of mesh size (at least, with $p < 0.01$, 0.04, and 0.001 in the background, buffer, and impact zones, respectively). In

Table 2. Parameters of frequency distributions of the rate of cellulose destruction (% per year) at macroscale in different zones and at different variants of meshs size (*a*—5 mm, *b*—0.5 mm, *c*—0.14 mm)

Parameter	Zone and mesh size								
	background			buffer			impact		
	a	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
Analytical estimates:									
arithmetic mean	79.54	84.00	89.30	64.15	72.25	73.78	21.40	26.42	28.18
standard deviation	14.37	13.05	8.47	22.87	22.82	22.27	27.26	27.88	28.22
coefficient of variation, %	18.07	15.54	9.48	35.65	31.59	30.19	127.39	105.49	100.14
index of homogeneity	0.42	0.44	0.37	0.54	0.58	0.58	0.80	0.74	0.73
skewness	−0.60*	−1.16**	−2.19**	−0.57*	−1.13**	−1.27**	1.98**	1.77**	1.34**
kurtosis	−0.60	0.33	6.79**	−0.39	0.47	0.90*	2.56**	1.70**	0.38
Order estimates:									
median	84.02	89.20	91.41	67.55	78.63	80.73	9.33	14.76	14.08
mode (rounded to integer)	85.00	89.00	91.00	66.00	83.00	81.00	5.00	11.00	9.00
minimum	45.00	47.09	48.28	11.58	12.00	13.25	1.04	4.28	4.14
10% decile	58.91	62.20	76.14	35.25	31.12	35.70	5.15	7.23	6.90
25% quartile	68.11	77.91	86.92	46.74	62.77	64.19	6.63	9.79	8.82
75% quartile	90.55	93.27	94.76	81.65	89.41	91.22	19.33	25.36	35.81
90% decile	96.61	96.05	96.63	91.07	95.32	94.72	78.54	86.27	80.86
maximum	99.77	99.74	99.50	99.26	99.18	97.96	99.74	98.64	96.50
range:									
interlimit	54.77	52.65	51.22	87.68	87.18	84.71	98.70	94.36	92.36
interdedcile	37.70	33.85	20.49	55.83	64.20	59.03	73.39	79.04	73.96
interquartile	22.43	15.36	7.84	34.91	26.65	27.04	12.70	15.56	26.99
median deviation	9.54	5.43	3.59	17.38	11.66	12.08	3.47	6.25	6.90
coefficients of variation, %									
median	16.82	9.01	5.82	38.11	21.96	22.15	55.14	62.70	72.59
uartile	19.78	12.76	6.36	38.30	25.11	24.82	100.93	78.13	142.00
decile	17.50	14.80	8.74	32.23	31.84	28.52	306.84	208.85	204.79

Note: Significance of difference from zero of coefficients of skewness and kurtosis: * $p < 0.05$, ** $p < 0.001$.

the absolute values, the differences between the mean indices were 7- and 1.2-fold in the impact and background zones, respectively.

Geostatistical analysis. The methods of geostatistics make it possible to estimate the range of spatial heterogeneity. Conventionally, (Clark, 1979), they are based on the plotting of a variogram: semivariance $\gamma(h)$ as a function of lag h (lag is the distance between the plots in question). Semivariance is intimately related to the autocorrelation function:

$$\gamma(h) = \frac{1}{2m(h)}\sum_{i=1}^{m(h)}(x_i - x_{i+h})^2,$$

where $m(h)$ is the number of compared pairs at lag h, x_i is the recorded index. The lag value, at which semivariance reaches the stationary level ("sill") equal to the sample variance is taken as the range of heterogeneity.

The stationary state of spatial series, i.e., equality of the mean (first-order stationarity) and variance (second-order stationarity) over the entire area of plotting is a condition of correct geostatistical analysis. In order to check the condition of the stationary state, the macroscale lines were divided into three successive subsamples, with 25 plots in each. In the buffer and impact zones, the differences between the subsamples according to the Kruscall–Wallis test were absent ($p = 0.366$–0.973); hence, these series could be considered stationary. However, in the background zone, the differences between the subsamples were significant (as a minimum $p < 0.005$). Regression analysis revealed a linear trend (slope differed significantly from zero, $p < 0.005$). Therefore, in further analysis of the background zone,

the values after the subtraction of the linear trend were used.

Macroscale variograms have similar horizontal shapes for all zones (Fig. 4): semivariance at all lags was equal to the stationary level. Such a shape of the variogram is interpreted as the absence of spatial autocorrelation and is determined by a so-called "nugget effect", when the range of spatial heterogeneity is significantly less than the chosen distance between the plots. In the buffer zone alone, there was a weak trend of decrease of semivariance at small lags.

Microscale variograms (all series are combined to one sample) are of a "reconnaissance" character, since the application of geostatistical analysis in this case cannot be considered as fully justified because of the small volume of the sample and the evident nonstationary state of the series. In the buffer and impact zones, the variograms had classical shape: semivariance gradually reached a stationary level, while in the background zone, the variogram shape, as at macroscale, may be interpreted as the absence of autocorrelation, which is related to an almost zero scattering of rates.

The next step of analysis was the selection of a theoretical equation for description of the variogram shape. In all cases, the best approximation was achieved using the most popular in the geostatistics spherical model:

$$\gamma(h) = \begin{cases} \frac{1}{2}C\left[3\frac{h}{a} - \left(\frac{h}{a}\right)^3\right] + \gamma_0 \text{ for } h \le a, \\ C + \gamma_0 \text{ for } h > a, \end{cases}$$

where $\gamma(h)$ is semivariance, h is lag, C is sill (stationary level of semivariance), a is range of heterogeneity, and γ_0 is the coefficient of the "nugget effect" (intersection of semivariance with ordinate axis at $h = 0$). The coefficients of the model were found by Markwardt numerical estimation: all of them are significant, at least with $p < 0.05$.

In the impact zone, the range of heterogeneity for a 0.14 and 0.5 mm mesh were 63 ± 0.5 cm (95% confidence interval from 52 to 73 cm) and 76 ± 0.7 cm (60 to 909 cm), respectively. Analysis of variograms for the buffer zone provided the range of heterogeneity 100 ± 24 cm (44 to 158 cm), which does not contradict the results of analysis of the macroscale variogram (2.8 ± 1.4 m with interval of 0 to 5.8 m), but the heterogeneity contrast in the buffer zone was considerably less than in the impact zone. Thus, the ranges of spatial heterogeneity of the destruction process in the impact and buffer zones were 60–80 and 100 cm, respectively. The position of microsites with high rates in the scale of sample site can be considered random.

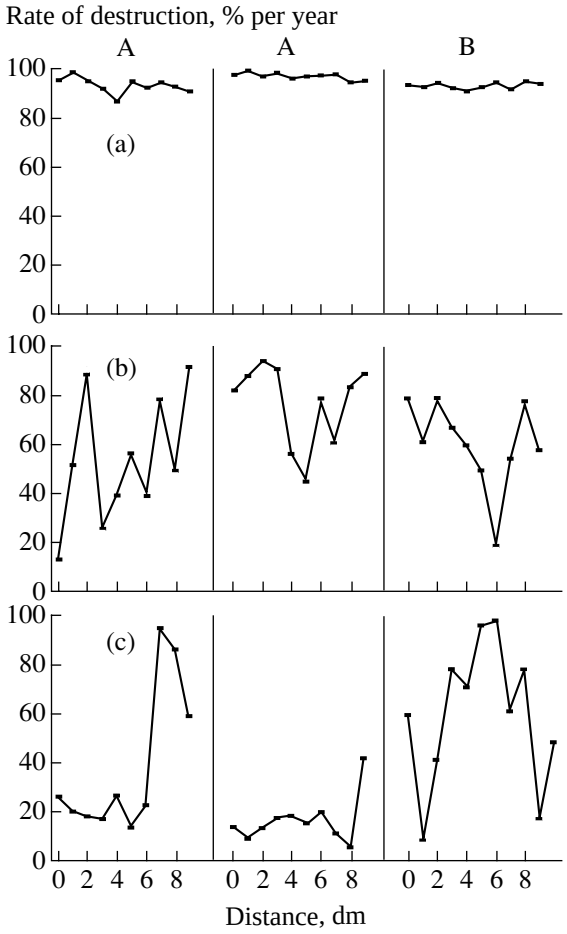


Fig. 3. Spatial distribution of the rate of cellulose destruction (0.14 mm mesh) at microscale in the background (a), buffer (b), and impact (c) zones and in different structural elements of phytocoenosis (A—crown projection, B—intercrown space).

DISCUSSION

When considering possible causes of sharply increased spatial heterogeneity of the destruction process we described, several hypotheses can be proposed (scheme). The first of them looks the most probable. It is known that soil microfungi, which play the dominant role in organic matter mineralization in the taiga forests, are tolerant to a certain extent to a high content of heavy metals (Gadd and Griffiths, 1978; Kobzev, 1980; Babich and Stotzky, 1985). Therefore under the conditions of heavy contamination they can either preserve their functioning at a high level, but either spore production decreases, or the processes of their spreading and/or germination become disturbed. As a result, the territory is differentiated into microsites colonized and not colonized by microfungi: if spores germinate, a "hot spot" with a high rate is formed in the territory with a low rate.

It is essential that in a polluted territory, the abundance of soil fauna decreases. Microarthropods (Moore

Table 3. Parameters of frequency distributions of the rate of cellulose destruction (% per year) at microscale in different zones and at different variants of mesh size (*a*—5 mm, *b*—0.5 mm, *c*—0.14 mm)

Parameter	Zone and mesh size								
	background			buffer			impact		
	a	*b*	*c*	*a*	*b*	*c*	*a*	*b*	*c*
	Series no. 1 (crown projection)								
X	82.75	91.53	93.53	60.53	51.65	53.15	20.92	37.08	38.38
CV, %	20.00	3.57	3.00	23.92	41.20	45.78	99.20	64.59	74.34
Min	42.46	85.60	87.50	33.19	14.49	13.25	5.83	17.86	13.80
Max	99.76	96.76	98.50	83.89	82.82	90.80	80.53	91.57	93.76
R	57.31	11.17	11.00	50.70	68.32	77.55	74.71	73.71	79.96
	Series no. 2 (crown projection)								
X	98.14	94.68	97.12	71.38	78.46	76.16	8.58	14.53	12.89
CV, %	1.16	7.38	1.22	14.09	14.33	20.28	39.11	37.14	34.28
Min	96.94	74.29	94.86	52.03	63.46	46.04	3.17	8.01	5.46
Max	99.77	99.73	99.04	84.25	97.10	93.12	13.30	22.68	18.93
R	2.83	25.44	4.18	32.21	33.64	47.08	10.14	14.67	13.47
	Series no. 3 (intercrown space)								
X	86.22	93.25	93.52	50.24	57.14	59.66	59.91	59.61	59.47
CV, %	11.20	3.99	1.20	29.77	34.61	27.86	50.07	51.89	48.70
Min	64.44	84.20	91.63	22.76	15.80	19.00	10.71	11.91	8.60
Max	99.01	97.75	95.33	68.50	78.65	78.18	95.58	95.50	97.13
R	34.57	13.55	3.70	45.74	62.85	59.18	84.86	83.59	88.53

Note: *X* is arithmetic mean, *CV* is coefficient of variation, min is minimum, max is maximum, *R* is range.

and Walter, 1988) and earthworms (Striganova, 1980) play an important role in the inoculation of the soil with microorganisms. The impact zone of our studies was located in the territory of "lumbricid desert", while in the buffer zone, earthworms occurred rarely (Vorobeichik, 1998). The data on the abundance of microarthropods are absent but, by analogy with other regions of chemical pollution (Kuznetsova and Potapov, 1997), it

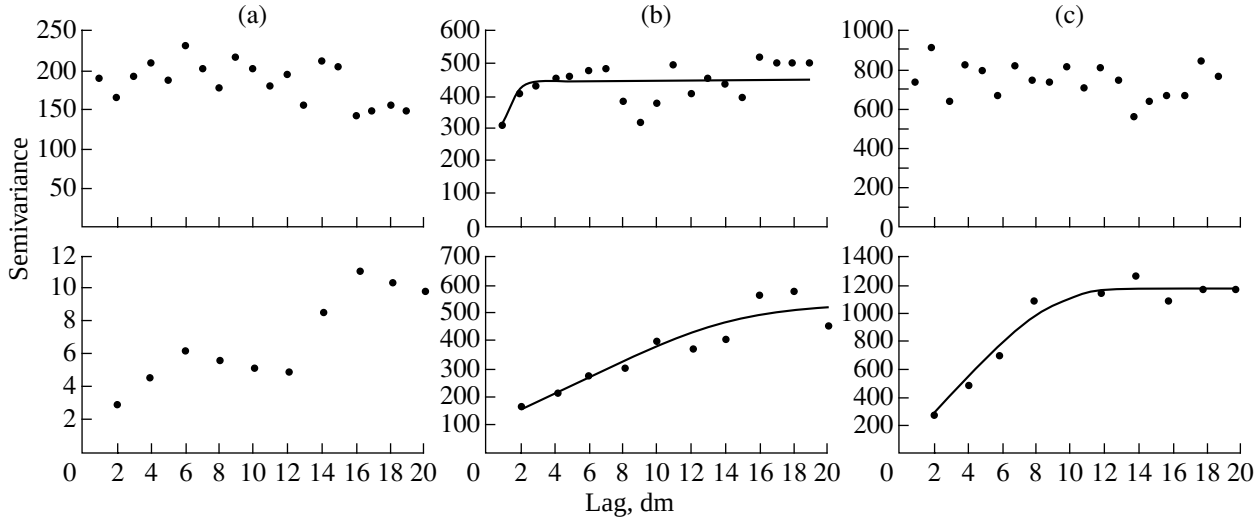
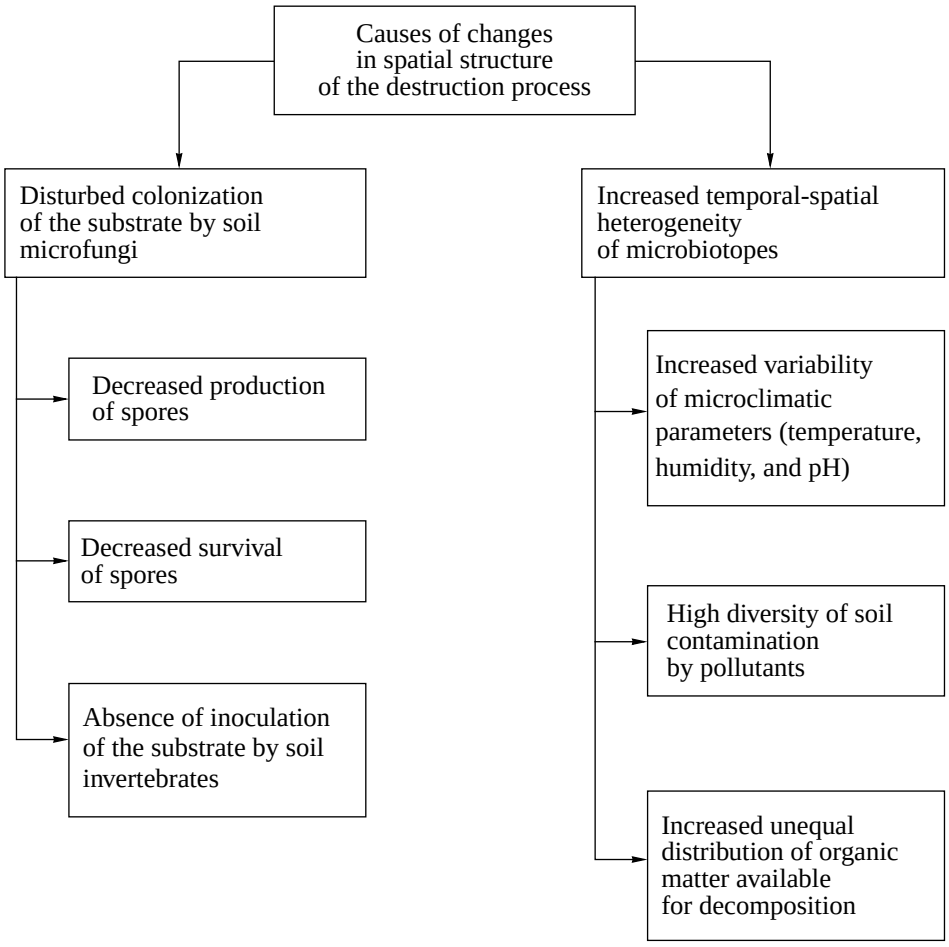


Fig. 4. Variograms of spatial distribution of the destruction rate (0.14 mm mesh) in the (a) background, (b) buffer, and (c) impact zones at macroscale (upper part) and microscale (lower part). Curve designates approximation of semivariance by the spherical model.



Scheme 1. Possible causes of disturbed spatial structure of the destruction process.

can be proposed that this group was strongly suppressed. Hence, the absence of the main agents of inoculation is an additional factor of increase in heterogeneity.

There is indirect evidence in favor of this hypothesis. Since according to the method we used, the bags with different mesh size were located in every plot in direct vicinity to each other, they can be considered as "replicates" for measuring the destruction rate in a region of about 10×20 cm. In all zones (Table 4), especially in the impact zone (Fig. 5), a very intimate relationship was found between the variants with different mesh size. In other words, a microsite of, at least, 10×20 cm represents a homogenous "hot spot" of a high activity of microfungi. This relationship is a certain assurance that the phenomenon we described is not an artifact caused, for example, by microbial contamination of some bags with filter paper by the experimenter.

Random, in the scale of tens of meters, distribution of the microsites with high rates and the absence of their connection with definite elements of the phytocoenotic mosaic can also be considered as an expression of the above described mechanism of formation of the "hot spot" of the activity of soil fungi.

The "focal" hypothesis is also confirmed by a significantly increased coefficient of variation of the abundance of soil microorganisms, which reaches 200% in a polluted territory (Levin *et al*., 1989). Estimation of the abundance by colony forming units using cultures on selective media is, actually, an estimate of distribution homogeneity of the spores of microorganisms. In addition, it is known that the life cycle stages of soil fungi related to spore production and germination are most sensitive to various factors (Marfenina *et al*., 1991), including chemical pollution (Marfenina and Popova, 1988).

The real situation is, in all likelihood, much more complicated because of the interference of several processes. In the impact zone, the activity of soil bacteria and actinomycetes can be suppressed, which plays the main role in the formation of soil fungistasis (Lockwood, 1977). This, as well as a possible direct stimulation of elevated acidity on the development of fungal mycelium (Lockwood, 1977) facilitate the formation of active zones from germinated spores.

Table 4. Coefficients of linear correlation between the destruction rate in bags with different mesh size (for microscale, all series are united in one sample)

Compared variants	Zone		
	background	buffer	impact
	Macroscale		
a–b	0.55***	0.69***	0.94***
a–c	0.49***	0.62***	0.87***
b–c	0.63***	0.83***	0.91***
	Microscale		
a–b	0.36*	0.65***	0.84***
a–c	0.23	0.45**	0.75***
b–c	0.06	0.66**	0.94***

Note: Significance of the coefficients of correlation: * $p < 0.05$; ** $p < 0.001$; *** $p \ll 0.0001$.

Increased variability of microclimatic and physicochemical parameters of the biotope, is, in our opinion, a modifying, rather than the key, factor of disturbance of the spatial structure of the destruction process. A stable relationship between the mean rates and their variation in variants with different mesh size is most likely related to the differences in microclimatic conditions: in the bags with smaller mesh size, the conditions are more stable and, hence, optimal for the functioning of the microflora. However, the difference between the variants is not comparable to the total range of spatial variability in the impact and buffer zones, as well as to the level of variability of soil and litter contents of heavy metals. According to our data, the coefficient of variation of acid-soluble forms of Cu, Cd, Pb, and Zn in the impact zone was 30–50% (Bezel' *et al*., 1994). Taking into account that the metal content exceeds the background levels by one or two orders of magnitude, this could hardly explain such a significant spatial variability of the destruction rate. On the one hand, bioavailability of metals and, hence, their toxicity for microorganisms depends, to a great extent, on various soil factors (Giller *et al*., 1998); therefore, spatial variation of bioavailable forms can markedly exceed the observed one.

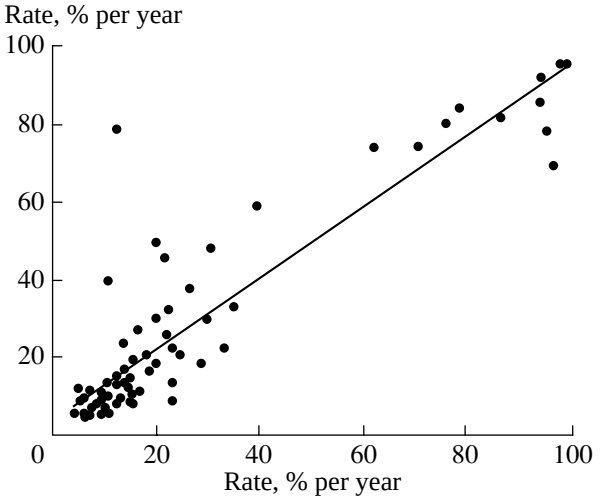


Fig. 5. The rate of cellulose destruction in the impact zone as a function of mesh size (abscissa: 0.5 mm; ordinate: 0.14 mm).

Other possible explanations (not included in the scheme), such as local increase of nonenzymatic catalytic activity of the soil or local distribution of pollutant-resistant species or strains of fungi in the impact zone, are still less likely, although additional studies are needed to exclude them.

There is an analogy between the phenomenon we described and great spatial variability of the activities of wood-decay fungi in the northern ecosystems. According to Mukhin (1993), the coefficient of variation of the wood destruction rate increased from 13–41 to 43–87% upon transition from southern taiga biotopes optimal for xylotrophic basiodiomycetes to the pessimal (thermodeficient and/or hydroexcessive) northern taiga or forest-tundra biotopes. In this case, both chemical pollution and pessimization of the hydrothermal regime lead to a similar result: differentiation of the space in two types of microsites with sharply different rates. The heterogeneity of colonization of the wood samples treated by various antiseptics with wood-decay fungi significantly increases (Belenkov, 1991). These antiseptics can be considered as analogs of technogenic pollutants. In both cases, disturbed colonization of the substrate by fungi is considered as the most probable cause of increased heterogeneity.

Another analogy is the existence of stable (in time) "hot spot" of soil denitrification, whose position also does not correlate either with the pattern of plant cover, or with the microclimatic conditions (Christensen and Tiedje, 1988). The coefficients of variation of spatial distribution of the intensity of denitrification within several square meters reach 100–500%; the contrast of hot spot is very pronounced: 85% of the process intensity are concentrated in less than 1% of the soil volume (Parkin, 1991). This analogy concerns the external expression, rather than the mechanisms of formation of "focal" biological activity of the soil.

It may well be that the differentiation of the space in the two types of microsites we described is responsible for discrepancies of the data on the relationship between the rate of cellulose destruction and the level of soil pollution: in some case such a relationship was not found (Evdokimova *et al*., 1984; Umarov and Azieva, 1980). Given a small sample volume, the mean values of destruction will heavily depend on a possible distortion of the true ratio between plots characterizing microsites with such sharply different rates.

Variation of the rate at macroscale determines the correctness of estimates in standard plots, since their common size (25×25 m) causes their position within 1–3 m. The information about the level of variation allows determination of the volume of a sample necessary for correct estimates of the destruction rate. The results of calculations by standard formulas (Zaitsev, 1984) are as follows. In the background territory at 10% error and 5% level of significance, the number of plots can be restricted by 4–15; in the buffer zone, the number of plots should be increased to 30–40; and in the impact zone, their number should be 350–400. With the error increased to 20%, the sample volume can be reduced in the latter case to about 100. It is probably more reliable and informative to operate with portions of the number of plots with high and low rates, rather than with just the mean rates. In our case (see Fig. 3), the portions of plots with the rates below 30% and above 80% were: 0 and 90.7, 7.4 and 45.6, and 67.0 and 12.4% in the background, buffer, and impact zones, respectively.

CONCLUSION

Inhibition of destruction upon technogenic pollution is usually presented as a sufficiently "smooth", spatially homogenous process, which can be satisfactorily described by changes in the mean values. The methodical approach we used in this study allowed us to reveal a much more complicated picture: even under the conditions of maximum contamination, in the territory of technogenic desert, with destruction almost fully blocked everywhere, there were microsites with a very high rate. This is why spatial heterogeneity of the destruction process in the impact zone is very high: the coefficient of variation reaches 130% and the observed range approaches the theoretically possible (100% per year).

Chemical pollution of the forest ecosystems radically changes the spatial structure of the destruction process. The territory under the toxic load is clearly differentiated into two types of microbiotopes: with very low and very high rates. The size of "hot spot" with a very high destruction rate is 20 to 60–80 cm and their position within the scale of several tens of meters can be considered random and not connected with any elements of the phytocoenotic mosaic.

As concerns the hypothesis proposed in this paper, which explains the described changes in spatial structure of the destruction process by disturbed colonization of the substrate with soil fungi, the following comments are pertinent. The weakest point of this study is that it can be classified as "microbiology without microbes." Therefore, all considerations about the mechanisms of the phenomenon described are speculative and require substantiation by standard methods of soil microbiology.

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