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Plot-scale spatial patterns of soil water content, pH, substrate-induced respiration and N mineralization in a temperate coniferous forest

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Abstract

Samples of two perpendicular transects from an even-aged Norway spruce (*Picea abies*) forest were used for geostatistical analysis of forest floor water content (WC), pH, substrate-induced respiration (SIR, a measure of microbial biomass), and N mineralization (Nmin). Nmin data did not fulfil the stationarity assumptions of geostatistics and had to be detrended prior to analysis. All variables exhibited spatial structure. The degree of spatial dependence was generally high (60%–95%). pH and SIR were isotropically distributed; WC and Nmin were anisotropic. Three different scales of spatial variability were detected at the site. (1) A fine-scale pattern with ranges < 1 m that was attributed to retarded decomposition, poor chemical and structural diversity of *P. abies* litter, and lacking bioturbatic activity of earthworms. (2) A mesoscale pattern was indicated by sinoidal periodicity of most variograms, with inflection points every 1.0–1.5 m. This periodicity probably reflected the influence of regularly spaced tree individuals. (3) Nmin and WC exhibited unexplained long-range trends that exceeded transect length.

Keywords: spatial distribution; geostatistics; variograms; autocorrelation; decomposition

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1. Introduction

Spatial heterogeneity is a dominant and conspicuous feature of temperate forest soils. Accordingly, the distribution of soil-inhabiting biota generally exhibits strong spatial structure (e.g., Schenker, 1984; Lensi et al., 1991; Gonzalez and Zak, 1994; Görres et al., 1998). Although heterogeneity seems to be of functional importance for forest soil biota, e.g., responsible for their amazingly high diversity (Anderson, 1978; Giller, 1996), more detailed information is still imperative for a deeper understanding and modeling purposes. Only few studies have explicitly quantified spatial scale and patterns, despite many attempts to characterize the phenomenon via some ''degree'' of clumping or aggregation (most notably by zoologists, e.g., Cancela da Fonseca and Stamou, 1982; Tousignant and Coderre, 1992). This may be due to the fact that adequate techniques for investigating spatial patterns have just recently found broader application in the biological sciences (Rossi et al., 1992; Liebhold et al., 1993).

Geostatistics provide powerful analytical tools to capture the horizontal variability of a property and have encountered increasing interest by soil biologists in recent years (e.g., Fromm et al., 1993; Robertson et al., 1993; Wallace and Hawkins, 1994; Wallace et al., 1993; Smith et al., 1994; Rossi et al., 1997; Görres et al., 1998). In this study, we characterized the spatial heterogeneity of biotically driven forest soil properties together with potentially controlling variables in a temperate Norway spruce stand. Meaningful spatial statistics require a large sample size (Webster, 1985; Webster and Oliver, 1992), so we limited our survey to four variables of overriding importance for microbiota and plant nutrition: microbial biomass (substrate-induced respiration, SIR), N mineralization (Nmin), water content (WC), and pH. The objectives of this study were (1) to search for patterns of spatial heterogeneity of these variables at the plot scale (range of meters); (2) to quantify and model these patterns using geostatistical techniques; and (3) to check for directional differences of the spatial distributions within the site, especially with respect to slope and stand characteristics.

2. Materials and methods

The study site was a Norway spruce (*Picea abies*) forest monoculture located near Gumpenstein, Styria, Austria (47°29′N, 14°7′E, 750 m above sea level), in the cool-temperate *P. abies–Abies alba* growth district of the Eastern Alps (Mayer, 1974). Mean annual temperatures and precipitation were 6.8°C and 1013 mm, respectively. The site was situated on a 15° inclined, west-facing slope. The forest stand was approximately 40 years old, and trees were even-aged. Tree density was 14 stems $\cdot$ 100 m^{-2}, and the average minimum distance between stems was 1.7 m. There was no undergrowth vegetation. The

soil was dystric Cambisol over quaternary sediments (silty sand), and the humus form was humimor (Green et al., 1993) with distinct L (depth ≈ 2 cm), F (≈ 2 cm), and H (≈ 6 cm) layers. The F layer was densely rooted. Chemical properties of the forest floor are summarized in Table 1. For recent studies of soil microbial–faunal interactions at the site, see Bauer et al. (1994), Bruckner et al. (1995), Kandeler et al. (1994), Vedder et al. (1996), and Zechmeister-Boltenstern et al. (1998).

The site was sampled in April 1992. We decided to orientate the sample points along transects (and not along a two-dimensional grid) to obtain spatial statistics from large (and therefore, reliable) samples. In order to capture direction-dependent differences of the spatial variability within the plot (anisotropy, see below) two intersecting 18-m transects were sampled. The *X*-transect was oriented parallel to the slope (north–south bearing), and the *Y*-transect perpendicular to it (in slope direction). Points were sampled every 10 cm along the transects with a soil auger (∅ 70 mm) to a depth of 100 mm, thus sampling the whole depth of the humus layer. 152 (*X*-transect) and 151 (*Y*-transect) of 180 possible points were successfully cored, all other points could not be sampled due to large roots, tree boles, or stumps. All data were assumed to represent point measures.

The field-moist samples were stored in plastic bags at −20°C. Within 3 days, the samples were thawed at 4°C, sieved < 5 mm, and soil microbial analyses initiated. This procedure was recommended for soil enzyme and microbial biomass measurements (Alef and Nannipieri, 1995; Schinner et al., 1996) and guaranteed a high recovery of soil microbial properties. WC (percentage of dry matter) was determined by weighing 20–30 g field-moist material and re-weighing it after drying at 105°C. The pH was measured in 0.01 M $CaCl_2$ solution. For the SIR measurement, substrate saturation and maximum initial respiration response were obtained with an amendment rate of 8.0 mg glucose g^{-1} of dry matter. CO_2 evolved was trapped in 0.05 M NaOH for a 4-h incubation at 25°C and measured by titration (Anderson and Domsch, 1978). Nmin was measured by incubating humus samples (5.0 g) under waterlogged conditions in an enclosed tube at 40°C for 7 days (Keeney, 1982). All analytical results were

Table 1
Chemical properties ($n = 5$) of the forest floor at the study site in 1992 (according to Kandeler et al., 1994)
L, F, H are litter, fermentation, and humus horizon, respectively. C_{org}: organic carbon content, N_t: total N content.

Humus horizon	C_{org} [%]	N_t [%]	pH	Ca	Mg	K
				[m equiv/100 g dry matter]		
L + F	42.2–48.9	1.45–1.79	3.0–3.4	9.9–16.7	4.5–5.8	1.0–1.3
H	27.5–45.9	1.16–1.82	2.7–3.1	2.7–5.1	1.8–6.3	0.4–0.7

calculated on the basis of oven-dry (105°C) weight of soil and are arithmetic means of two replicates.

Geostatistics provide powerful tools for the analysis and interpolation of spatially autocorrelated data (Webster, 1985; Isaaks and Srivastava, 1989; Rossi et al., 1992; Goovaerts, 1997). A property is called *autocorrelated* (or *spatially dependent*) if the probability of similar data values is higher for neighbouring sample points than for points far from each other. Thus, $z(x)$ (i.e., the value z of a property at point x) correlates to the neighboring $z(x+h)$, with h being the distance, or *lag*, between $z(x)$ and $z(x+h)$. The correlation between $z(x)$ and $z(x+h)$ expresses the *spatial structure* of the property. *h-Scatterplots* visualize the relationship between $z(x)$ and $z(x+h)$ for a given lag. All pairs of points separated by lag h are plotted against each other (Fig. 3). The *variogram* displays the change in the semivariance between sample points with increasing lag. The semivariance γ for lag h is given by

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} \left[z(x_i) - z(x_i + h) \right]^2,$$

where $z(x_i)$ is a measured sample at point x_i, $z(x_i + h)$ is a measured sample at point $x_i + h$, and $N(h)$ is the number of pairs separated by lag h. Typically, variograms are of a specific form (e.g., Fig. 2, SIR-X). The semivariance rises with increasing lag, then levels off. The lag at which the plateau is achieved is called the *range a*, the semivariance value of the plateau is the *sill C*. Points within the range can be considered spatially autocorrelated; points outside the range are spatially independent. Empirical variograms seldom pass the origin, but intersect with the ordinate. This discontinuity is the *nugget* C_0, and consists of two parts: the spatial variance of scales less than the minimum sampling distance (if present), and measurement and sample location error.

Positive definite models are fit to empirical variograms to capture the major spatial features of the property. In this study, either spherical or exponential models were fitted by eye and by minimizing an ''Indicative Goodness of Fit'' criterion (IGF), which is a standardized measure of difference between observed and model values. An IGF value close to zero indicates a good fit of the model (Pannatier, 1996).

To properly apply geostatistical techniques, a variable has to satisfy *stationarity* assumptions. In simple words, a data set fulfils the so-called ''intrinsic hypothesis'' of geostatistics, if there is no trend or *drift* of means and in the increment $z(x_i) - z(x_i + h)$ along the transect. Ecological data often do not satisfy the stationarity assumptions and have to be transformed or detrended before analysis. Deviations from the intrinsic hypothesis are indicated by non-normal univariate statistics, oblique *h*-Scatterplots, and variograms not reaching a sill.

The *structural variance* is the spatially structured proportion of the sample variance that is not random noise or measurement error (''degree of spatial

dependence'' $(C - C_0/C) \times 100\%$, Jackson and Caldwell, 1993; Görres et al., 1998). A variable is called *isotropic* (opposite: *anisotropic*) if its spatial structure (as, e.g., displayed by variograms) does not change with direction.

One suspected outlier was removed from the WC-*Y* and one from the Nmin-*X* data set, respectively, because they were outside the range $\bar{x} \pm 3$ s and differed considerably from neighboring points. We checked for normality of the data sets with frequency histograms, normal probability plots, and chi-square tests. We chose a maximum lag of $h = 100$ with a minimum number of pairs $N(h100) = 50$. At greater lags, variograms tended to be erratic. Geostatistical analyses were performed with VARIOWIN 2.2 (Pannatier, 1996), all other statistics, transformations and detrendings with the Statgraphics 3.0 package.

3. Results

The means of each variable were approximately equal for the *X*-(parallel to the slope) and *Y*-(in slope direction) transect. Data variability (coefficient of variation, CV%) was low for the abiotic properties, high for SIR, and very high for Nmin. The variability did not differ substantially between transects, except for Nmin-*X* being more variable than Nmin-*Y* (Table 2). The WC and pH data sets did not deviate significantly from normality. The SIR and Nmin frequency distributions were more or less positively skewed and steep (Table 2) and the normality assumption had to be rejected. The deviations were most pronounced for SIR-*X* and Nmin-*Y*, as revealed by frequency histograms and normal probability plots (not shown).

The local means of WC-*Y* and pH were constant along the transects (Fig. 1). WC-*X* showed a slight linear drift of means with increasing transect distance. The SIR data exhibited high local variability, but a rather constant overall mean. The Nmin data sets exhibited long-range, nonlinear drift of local means. Nmin-*X* increased almost linearly from 0 to about 15.5 m distance, then decreased steeply. Nmin-*Y* was constant over $2/3$ of the transect, then increased with a sharp step at 13.5 m (Fig. 1).

All raw data variograms exhibited spatial autocorrelation (Fig. 2). The variograms of WC-*X* and Nmin-*Y* did not reach a sill and steadily increased with distance. The variogram of Nmin-*X* leveled out at a high lag. *h*-Scatterplots of the latter variables became more or less asymmetric with increasing lag, most pronounced in Nmin-*Y* (e.g., Fig. 3, Nmin-*Y*). These two features indicated that the stationarity assumptions did not hold for WC-*X*, Nmin-*X*, and Nmin-*Y*, probably due to the abovementioned drifts of local means. The other variables (WC-*Y*, pH, and SIR) had ''well-behaved'' variograms with a clear sill and *h*-Scatterplots with more or less symmetrical, elliptical clouds of points (e.g., Fig. 3, pH-*X*). We therefore decided to use raw data of WC-*Y*, pH, and

Table 2
Summary statistics of 152 (X transect) and 151 (Y transect) forest floor cores. WC: water content, SIR: substrate-induced respiration, Nmin: nitrogen mineralization.

	WC [Percentage of dry weight]		pH		SIR [μg $CO_2 \cdot$ g dwt$^{-1} \cdot$ h^{-1}]		Nmin [mg N $\cdot$ g dwt$^{-1} \cdot$ 7 d^{-1}]	
	X	Y	X	Y	X	Y	X	Y
Mean	60.18	57.40	3.02	3.08	99.42	85.45	90.64	89.72
Median	59.66	57.05	3.02	3.09	93.70	81.55	84.55	75.51
Minimum	48.97	45.51	2.78	2.87	60.20	31.90	24.30	22.20
Maximum	70.35	71.16	3.28	3.32	188.20	144.40	169.60	209.06
Variance	22.78	25.56	0.01	0.01	565.22	577.24	985.27	1690.05
Coefficient of variation [%]	7.93	8.81	3.18	3.28	23.91	28.12	34.15	45.82
Skewness	0.22	0.41	−0.20	−0.02	1.15	0.50	0.43	1.26
Kurtosis	−0.60	−0.16	−0.12	−0.67	1.44	0.10	−0.45	0.98

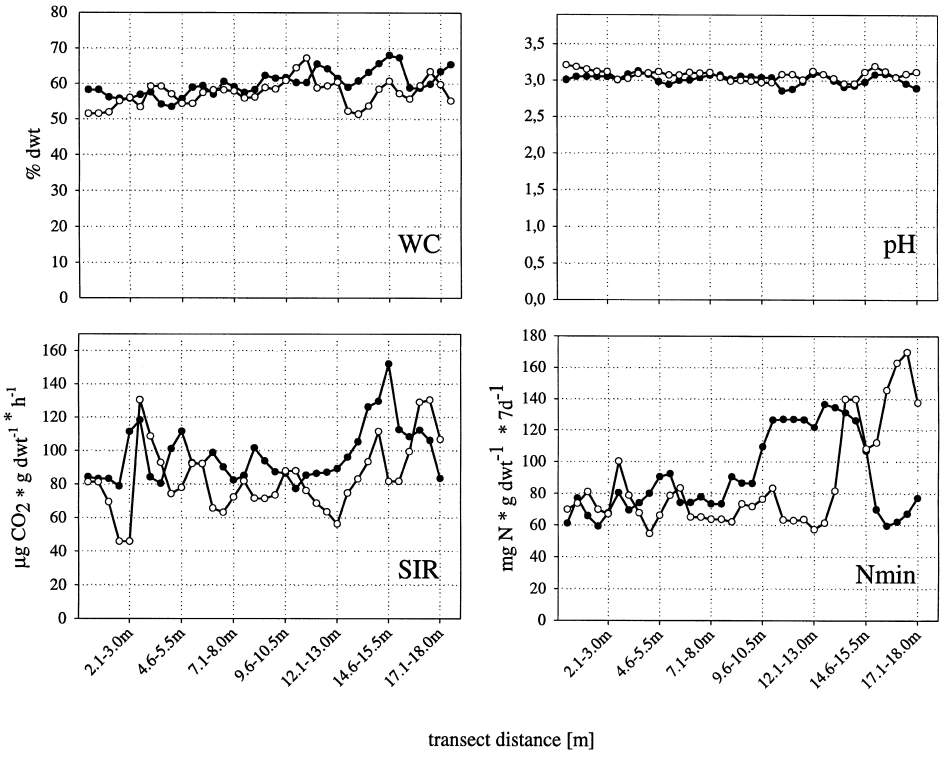

Fig. 1. Distribution of WC, pH, SIR, and Nmin along the transects (X transect: solid circles, Y transect: open circles). For better visualization, small-scale data variability is smoothed by averaging adjacent sample points with half-overlapping moving windows of size $n = 10$ (i.e., each point on the graph represents the median of 10 neighbouring sample points).

SIR for variogram modeling, and to remove the trend from WC-X, Nmin-X, and Nmin-Y.

We tried several transformations of different power ($\log_{10}$, $\log_e$, square roots, reciprocals of square roots, reciprocals) and local and general relative variograms (Isaaks and Srivastava, 1989, p.163f), but no procedure successfully adjusted for the trends in the data sets (cf. Hamlett et al., 1986). Instead, we removed trends by unweighted linear or quadratic regression of WC-X and Nmin-Y and used the regression residuals for further analysis. In the case of Nmin-X, no procedure improved the raw data variogram considerably. This variogram could only be stabilized by excluding the steeply decreasing part of the transect from the data set and linearly detrending the remaining values ($n = 127$ successful points). All further calculations are based on raw data for WC-Y, pH, and SIR, and on corrected data for WC-X and Nmin.

The overall shape of model variograms was properly described by spherical and exponential models (Table 3, Fig. 4). All variogram ranges were about 1 m

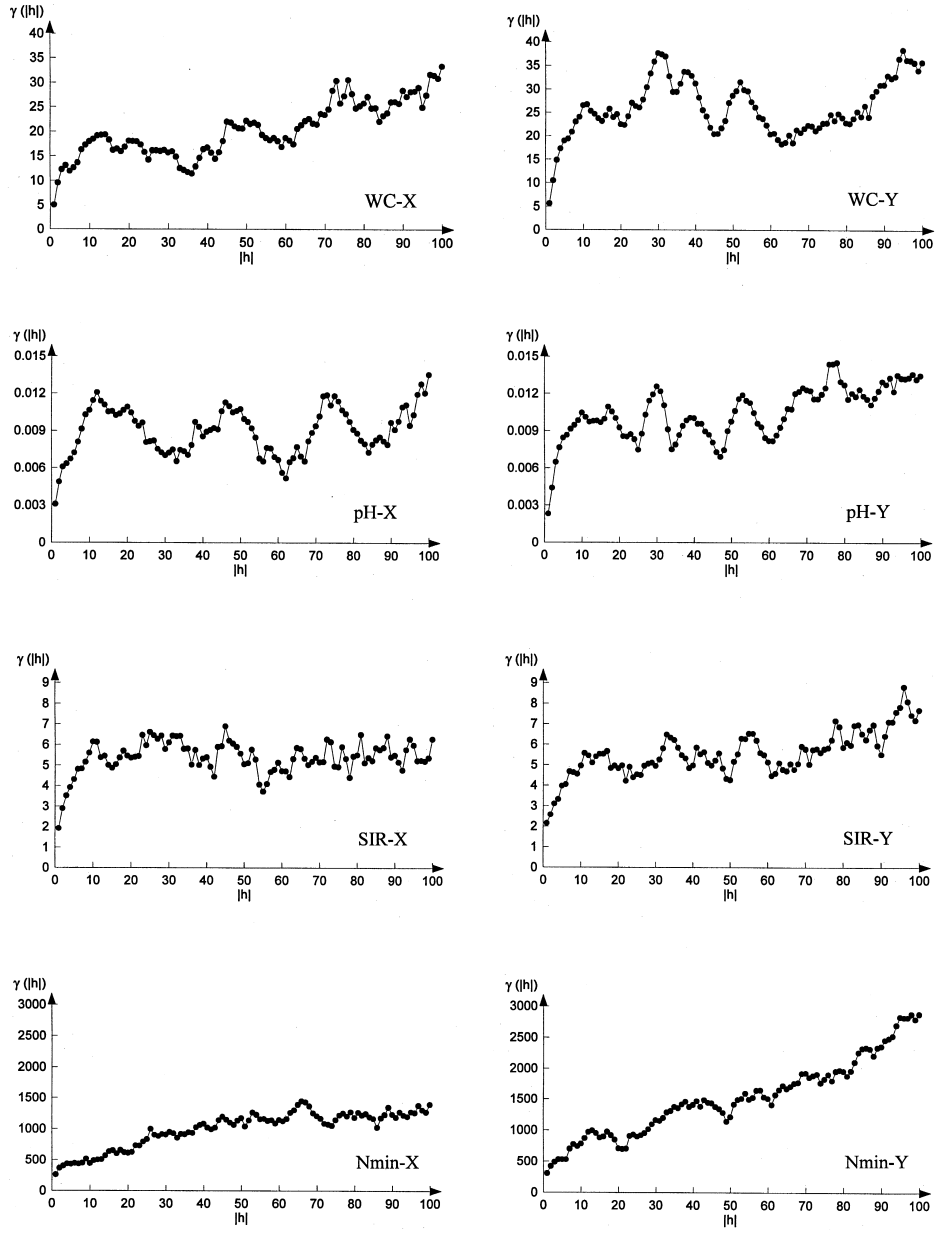

Fig. 2. Semivariograms of raw data of X and Y transects, respectively. WC, SIR, and Nmin. $|h|$ is the lag distance (in 10-cm units).

and did not differ between transects. The sill approximately equaled the total sample variance for all variables. This is evidence that there is no spatial dependence outside the range of maximum lag (Barnes, 1991; Robertson et al.,

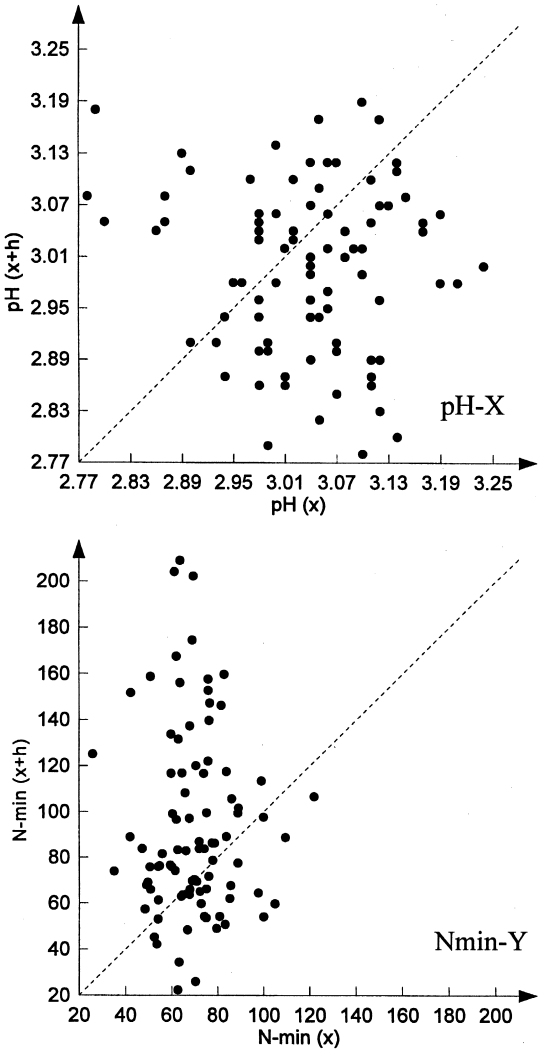

Fig. 3. *h*-Scatterplots of raw data of pH-*X* and Nmin-*Y* at lag 50.

1993). The structural variance was moderate (60%, Nmin-*X*) to very high (95%, WC-*Y*), and indicates a generally high degree of spatial structure. Most variograms had a more or less pronounced ''wavy'' appearance, i.e., the semivariance increased and declined with lag distance in a periodic cycle. The amplitude of this periodicity was different between variables, but the wavelength was roughly the same for all variables and both transects, with inflection points every 1.0–1.5 m.

The variogram sills of both transects were similar for pH and SIR, but distinctly different between WC-*X*/WC-*Y* and Nmin-*X*/Nmin-*Y*. This anisotro-

Table 3
Variogram statistics for *X* and *Y* transect data, respectively. WC, SIR, and Nmin. IGF (indicative goodness of fit criterion) is a standardized measure of difference between observed values and values of the fitted model.

	Source of data	Fitted model	Nugget (Co)	Sill (C)	Range (a) [m]	IGF	Structural variance	Sill as percentage of sample variance
WC-*X*	linearly detrended	exponential	1.97	15.99	0.86	0.08	87.67%	107.77%
WC-*Y*	raw data	exponential	1.36	27.08	1.36	0.08	94.97%	106.65%
pH-*X*	raw data	spherical	0.002	0.01	1.05	0.10	75.03%	96.09%
pH-*Y*	raw data	spherical	0.001	0.01	0.70	0.06	89.99%	98.46%
SIR-*X*	raw data	spherical	1.53	5.53	0.96	0.03	72.35%	98.54%
SIR-*Y*	raw data	spherical	1.78	5.37	1.26	0.04	66.78%	93.67%
Nmin-*X*	local data	exponential	190.01	470.61	0.68	0.04	59.62%	104.56%
Nmin-*Y*	quadratically detrended	spherical	242.32	726.39	1.05	0.07	66.64%	105.19%

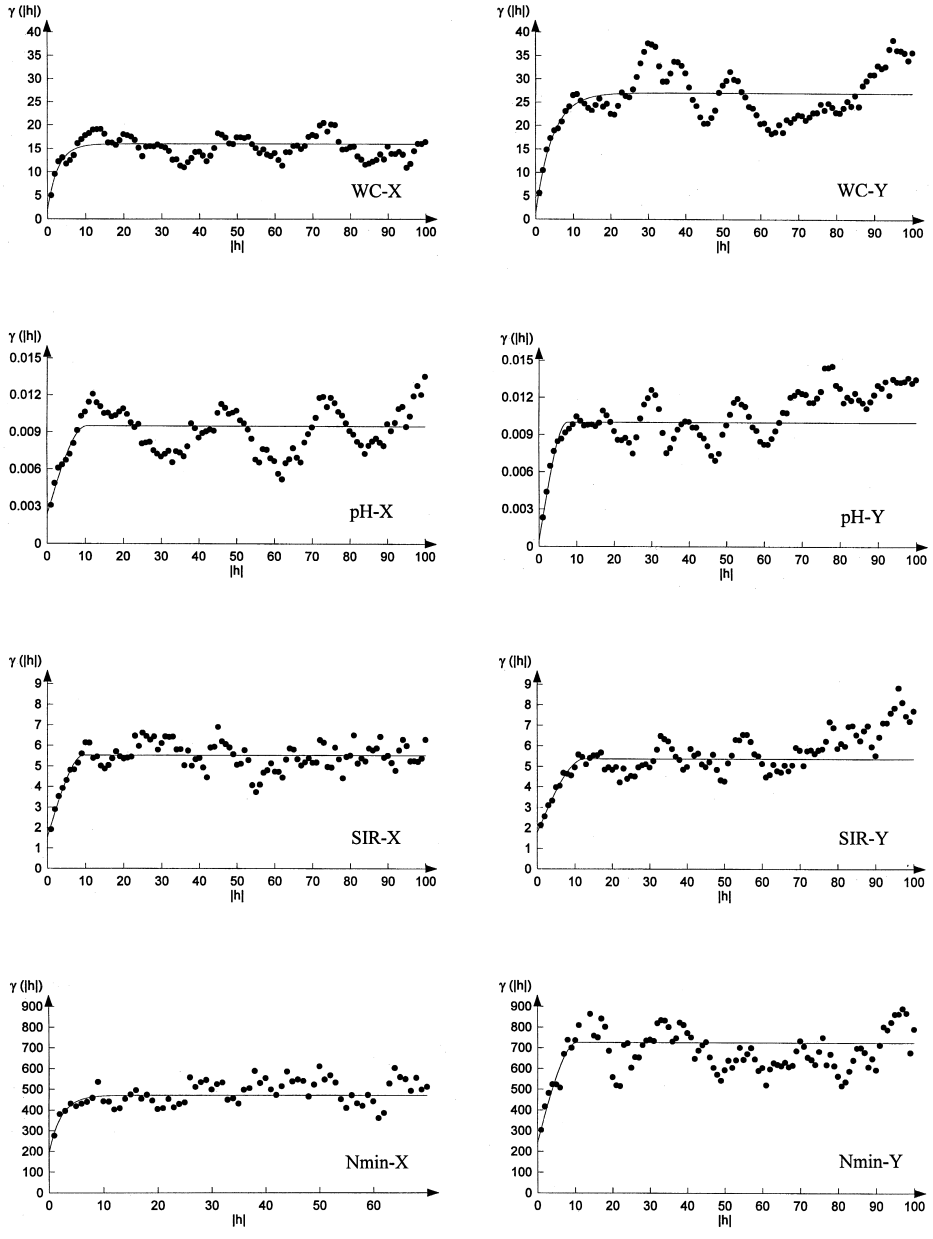

Fig. 4. Variogram models of raw (WC-*Y*, pH, SIR) and corrected (WC-*X*, Nmin) data of *X* and *Y* transects, respectively. Points indicate sample semivariances, solid lines are fitted models. WC, SIR, and Nmin. $|h|$ is the lag distance (in 10-cm units).

py (spatial structure changing with transect direction) again reflects the presence of drift in the raw data.

4. Discussion

All studied properties of the spruce forest soil *exhibited spatial structure*. Spatial autocorrelation was an important feature of all variables, since the degree of spatially structured variance was generally high (60%–95% of sill variance) and the rate of stochastic variation accordingly low.

pH and SIR were isotropic at the site, i.e., their spatial structure did not change with transect direction. WC and Nmin exhibited a slight drift of means on the *X*-transect, perpendicular to the slope. Nmin-*Y* was the only variable with a pronounced drift. We expected drift to occur frequently in slope direction due to accumulation of organic matter at the bottom of the site, but there was no general relationship between slope and spatial patterns. This is in accordance with results of Gonzalez and Zak (1994), who found N mineralization and nitrification in a tropical dry forest to be unaffected by a slope of about 15°–30°. This is surprising at first sight, since downhill surface movement of matter can be considerable on slopes (Orndorff and Lang, 1981). However, the humus layers of the study site were of tenacious consistence and made up of spruce needles and debris that were not easily moved by the action of wind and water. Therefore, topographical influences are probably negligible for this type of humus form. The reasons for the trend in Nmin-*Y* remain unexplained.

The spatial variation of all variables was displayed at roughly 1 m or less, suggesting that scales of centimeters to meters are very relevant for the studied properties. This underlying short-range structure was superimposed by long-scale trends in the WC-*X* and Nmin data, but became visible after data correction. These results underline the importance of very local phenomena for forest soil processes. Lechowicz and Bell (1991) identified the same scale as most relevant for the establishment and growth of forest herbaceous plants.

What are the reasons for the small-scale pattern? We offer three complementary explanations. In his almost forgotten, yet excellent study on the fauna of beech forest soils, Zachariae (1965) suggested that spatial patterns of animals and their activity are linked to the rate of litter decomposition: Spatial heterogeneity is highest if the period from leaf fall to complete mineralization/humification is 2–3 years. Below and above this point, permanent humus layers are either lacking or accumulating and horizontal homogeneity increases accordingly (in modern terms: the spatial scale of humus becomes finer). This hypothesis may be extended from the spatial distribution of soil fauna to forest floor properties in general. If so, the spatial scales of WC, pH, and biotic variables analogously would become finer with decelerated and accelerated decomposition. We did not measure decomposition rate at the study site, but it was certainly far beyond 2–3 years, and fine-scale patterning was therefore high.

It is difficult to substantiate this idea with other studies because literature on spatial structure of forest humus is scarce, the rate of litter turnover is not easily

assessed, and the experimental minimum lags are often too large and relevant small-scale patterns probably not detected (Riha et al., 1986; Gonzalez and Zak, 1994; Gourbiere and Debouzie, 1995). Görres et al. (1998) conducted a geostatistical investigation on soil moisture, C mineralization, and nematode numbers in a maple (*Acer rubrum*) forest with rich undergrowth and presumably rapid litter turnover. Their results strongly depended on sampling season, but, in agreement with Zachariae (1965), variogram ranges were generally one order of magnitude higher than in our study. Quian and Klinka (1995) compared the spatial variability of humus forms in three forests in Canada with poor, rich, and very rich soil nutrient regimes. Some of their results supported the above hypothesis, that is, ranges increased more or less relative to the nutrient gradient (pH, total C, total N), while other results did not (humus thickness, mineralizable N). In a pioneering attempt on the spatial variability of nutrient-poor Scots pine humus, Usher (1970) demonstrated apparent small-scale patterns of WC, pore space, total N, P, K, and Ca. It was not possible to estimate the ranges of influence of the measured variables, but the author reported (not clearly defined) ''aggregation sizes'' that indicated a rather fine-scale patterning of forest soil properties (from 16 ml for N to 750 ml for P).

A second explanation for the dominance of small-scale patterns lies in the single-species litter of the study site. Leaf litter chemistry and decomposition differs between plant species and can contribute to enhanced spatial variation in chemical and biological properties of the forest floor (Lodhi and Johnson, 1989; Gonzalez and Zak, 1994). Only Norway spruce litter was present at the study site. The poor chemical and structural diversity of this monospecific litter may favour patterning at small scales.

Finally, only very low numbers of one earthworm species (*Dendrobaena attemsi* Michaelsen, 1902) were found at the study site in 1992 (Vedder et al., 1996). The burrowing and mixing activity of Lumbricidae can disrupt the layered structure of humus and in this way increase the stochastic, nonspatial part of forest floor variability. Thus, bioturbatic effects of earthworms on the humus profile were probably negligible at the site and stochastic variability consequently low.

The most intriguing pattern is the *periodicity* of most variograms. The cycles exhibited different amplitude, but similar wavelength. A pattern of this kind arises if a property is distributed in patches of constant size, and the patches are equally spaced. We suppose that the periodicity is related to zones of influence of individual spruce trees on the forest floor. There is broad evidence that soil and humus morphology, chemistry, and biology are influenced by tree roots, local accumulation or depletion of litter, stemflow and canopy architecture (Crampton, 1982, 1984; Schenker, 1984; Turner and Franz, 1985; Liski, 1996; Scheu and Poser, 1996; among others). In an acidic Norway spruce stand, Koch and Matzner (1993) found an increase of Ca, K, and NH_4, a decrease of NO_3 and Al, and pH unchanged in the soil solution close to the trees. Results of this

kind led to the idea of the forest soil as a mosaic of profiles that are spatially and genetically associated with individual trees (Boettcher and Kalisz, 1990).

At the study site, trees were planted in lines with regular intervals between stems. This arrangement is nowadays blurred and not easily seen because of thinning activities in the past, but the planting rows probably run obliquely to slope direction. We also found some regularity of tree spacing in the two transect directions (that intersect the supposed planting lines). The frequency distributions of tree intervals peaked at around 2.0 m for the *X*-direction and 1.9 m for the *Y*-direction ($n = 50$ each, distance measurements between extrapolated stem centers). This is about twice the distance between the inflection points of the variograms and seems to contradict the idea of a tree influence. However, forest floor properties do not change linearly with increasing distance from the stem, but also depend on crown architecture. Conifer trees shed most precipitation water at the periphery of the canopy (Crampton, 1982). The soil below this zone is the moistest and even gley dynamics can occur here (Crampton, 1984). We suggest that the WC, pH, SIR and Nmin of the runoff zone are consistently different from areas outside the canopy or closer to the stem and form concentric rings around individual stems. Thus, the values of the studied properties at a certain sample point may be determined by the position of the sample relative to the canopy periphery. Taking this into account, the periodicity encountered in the variograms and the stem intervals match each other closely.

A recent summarizing paper by Frankland (1998) substantiates the hypothesis of tree influence on soil microbial variables. She and co-workers conducted an autecological analysis of the abundant non-mycorrhizal basidiomycete *Mycena galopus* in a Sitka spruce (*P. sitchensis*) stand with a very homogeneous forest floor, seemingly very similar to our study site. They found that, in analogy to fairy rings, the fruiting bodies of the fungus were predominantly arranged in concentric rings around individual trees. Accordingly, mycelial biomass of *M. galopus*, pH, NH_4^+, and depth of forest floor tended to increase towards the ring, but decrease towards the stem. This species is a frequent inhabitant of various soil types and plant litters (Frankland, 1998) and may also have been dominant at our site. Its growth pattern (and/or that of species with similar distribution) provides a plausible biological explanation of the periodicity of the SIR and Nmin variograms.

In conclusion, three different scales of spatial variability were detected in this study: a short-range pattern with a range < 1 m, a mesoscale pattern that reflected the influence of tree stems and canopy, and a long-range, unexplained pattern which exceeded transect length.

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