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Erika GÖMÖRYOVÁ[1], Karol UJHÁZY[1], Richard HRIVNÁK[2],
Katarína STŘELCOVÁ[1], Dušan GÖMÖRY[1]*

[1] Technical University in Zvolen, Faculty of Forestry, T.G. Masaryka 24, SK-960 53 Zvolen, Slovakia
[2] Institute of Botany, Slovak Academy of Sciences, Dúbravská cesta 14, SK-845 23, Bratislava, Slovakia
* e-mail gomory@vsld.tuzvo.sk (*corresponding author*)

SOIL PROPERTIES AND MICROBIAL ACTIVITY CHANGES ALONG SPRUCE FOREST SUCCESSION IN AN ABANDONED GRASSLAND

ABSTRACT: The effects of the colonization of an abandoned grassland by forest trees and the associated microenvironmental changes on soil properties and the microbial activity of soil were studied along a 170 m transect established on a former pasture colonized by Norway spruce (*Picea abies* Karst.) in Central Slovakia. The transect with a 5×5 m grid of sampling points crosses all successional stages from a closed forest to an open grassland, representing 50 years of secondary succession. Changes of basal soil respiration, substrate-induced respiration and soil catalase activity in association with tree density, light and temperature regime were examined, and their relationships with chemical soil properties were documented. Generally, light conditions, tree influence and soil temperatures were highly significantly correlated with the distance from the lower transect edge, but the correlation coefficients were not very high ($|r|$ ranged between 0.37 and 0.70), indicating that the microsite conditions within the transect are strongly heterogeneous. With the advance of colonization, the amount of soil organic matter was found to increase, probably in association with a higher amount and a lower quality of litter. Catalase activity exhibits a linear trend along the transect, which is explained by a lower direct insolation of soils (r = 0.28***) and decreasing temperatures (r = 0.36***) in the upper part. Basal respiration is the lowest in the middle of the transect, where colonizing spruces form a dense closed stand with soil covered by a thick layer of raw litter. Both in the lower part covered by species-rich grassland communities and in the upper part, where forest herb species begin to establish, basal respiration is higher, probably due to higher amounts of easily decomposable plant material. In addition to these transect-wide trends, stationary spatial patterns were observed for most soil variables. Generally, microbial activity rates as well as chemical soil properties exhibited spatial continuity up to the distance of approx. 40 to 60 m.

KEY WORDS: soil respiration, catalase activity, soil composition, secondary succession, geostatistics

1. INTRODUCTION

Pastures in mountainous forested areas depend on permanent human interference. Secondary succession begins almost immediately after the cessation of agricultural use and is characterized by gradual changes of species composition of herb layer, structure of stands, and colonization of the site by shrubs and trees. A mosaic of several types of vegetation is gradually formed in the areas with originally more or less homogeneous grassland communities (and with more or less homogeneous ecological conditions) in the course of few decades, related to many environmental and demographical factors like radiation, temperature, moisture, nutrient cycling, competitive relationships, species' strategy etc. (cf. Grime 1979, Glenn-Lewin and van der Maarel 1992, van der Valk 1992, van Andel *et al.* 1993).

In Central-European countries, significant changes in the management of meadows and pastures occurred in the 1950s due to the collectivization of agriculture. Nevertheless, agricultural land was set aside because of the intensification of agriculture in many parts of the world. In Slovakia, the changes of agricultural management of the landscape have affected mainly mountain meadows and pastures, which were mostly small, fragmented, and surrounded by forests, where tree species spread intensively. Artificial grasslands of the volcanic Poµana Mts. (Central Slovakia), colonized mainly by Norway spruce (*Picea abies* Karst.) and juniper (*Juniperus communis* L.), represent a typical example of this process (Križová 1995, Ujházy 2003).

Gradual changes of density, age, diameter and height structure of the arboreal vegetation along a successional gradient affect environmental conditions for soil microbial communities in manifold ways. Directly, trees provide litter that is decomposed by soil microorganisms, affect access of light and precipitations to soil, height and duration of snow cover, draw water and nutrients from the rhizosphere, affect soil morphology, and their roots enter in direct (frequently symbiotic) interactions with soil microorganisms (Stoyan *et al.* 2000, Wilkinson and Anderson 2001, Phillips and Marion 2004). Indirectly, trees affect the composition of ground vegetation, which exerts similar influence on soil. Consequently, trees significantly participate in the regulation of temperature, moisture and nutrient regime of soil (Walker and del Moral 2003).

A gradient in tree stand properties is thus expected to be reflected in the composition of soil microbial communities and should produce a spatial pattern of microbial activity parameters like soil respiration and enzyme activities. Our goals were thus 1) to describe spatial patterns of soil microbial activity on an abandoned pasture colonized by trees and 2) to identify the relationships between the successional stage and the microbial activity.

2. MATERIAL AND METHODS

The study site is located in Central Slovakia at the locality Príslopy (48°38'10"N, 19°25'11"E, about 900 m a.s.l.). The area has a cold and rainy climate with the mean July temperature of 11.5–13.5 °C and 1000–1400 mm annual precipitations. The bedrock formed of andesite lava flows is covered by deep cambisols. This grassland area of about 100 ha is surrounded by a large forest complex. It was deforested around 1800 and since then it had been utilized as hay meadows until the collectivization of agriculture in 1951, when it was changed to pastures (cf. Ujházy 2003). Norway spruce (*Picea abies*) was planted along the former forest margin in 1890s. This row plantation formed the seed source for the colonization of the grassland which was gradually overgrown by spruce. At the same time, in the parts colonized by trees, cattle grazing has become more and more limited. The colonization process was followed by changes of the ground vegetation as well as genetic diversity of the participating species (Hrivnák and Ujházy 2004, Gömöry *et al.* 2006).

A research transect of 20 × 170 m (perpendicular to contour line) was established at the site in 2003 on a regular North-facing slope. The transect crosses all succession stages from the old planted spruce forest margin to a relatively open non-forest grassland area. The bottom part of the transect is formed of grassland communities with the predominance of *Avenula adsurgens* Sauer et Chmelitschek, *Avenella flexuosa* Drejer, *Carex pilulifera* L., *Nardus stricta* L. and other herb species with scattered, mostly young individuals of spruce and juniper whereas the upper part is overgrown by closed 40 to 50-years-old spruce stands almost without herb cover. The transition from a relatively open grassland to a closed forest is, however, rather smooth, and the species composition of the ground vegetation changes accordingly. The upper margin of the transect touches the former forest margin, where the old planted row of spruce started to break down and canopy became more open again. Consequently, herb cover appears again in this part, with the occurrence of beechwood species like *Galium odoratum* Scop., *Viola reichenbachiana* Jord. ex Boreau or *Oxalis acetosella* L. On the transect, a grid of 10 × 10 m was established and geodetically measured. The position (*x, y* coordinates), breast-height diameter, heights and crown projections of all trees were measured. In addition, the positions and DBHs of all trees were recorded on two neighbouring 10 m belts.

Soil sampling was done on a more detailed grid of 5 × 5 m. Since the vegetation cover varied among points, affecting the character and composition of organic soil horizons, soil samples were taken from the uppermost mineral horizon from the depth of 5–10 cm. In total, 152 points were sampled. From fresh samples, gravimetric moisture, basal soil respiration rate, substrate-induced respiration (SIR; Isermeyer in Alef 1991) and catalase activity (Khaziev 1976) were determined. A half of each sample was air-dried and used for measurement of soil acidity (pH-H_2O, pH-KCl), organic matter content (Tyurin 1951), and total N (Kjeldahl's method), P and K (Mehlich 3 extract, K – flame emission spectrometry, P – colorimetry).

To assess the effects of the colonizing tree species on soil microbial activity and to characterize the stage of colonization, we applied the concept of *Influence Potential* (Kuuluvainen and Pukkala 1989). We calculated a set of indices based on sizes of trees (defined by DBH and/or basal area) within a 5-m-neighbourhood of the soil sampling point weighted by their distances from the point. Several distance functions were tested (cf. Saetre 1999, Kühlmann *et al.* 2001), but inverse distance weighting proved to produce the closest relationships with soil parameters. To account for a possible "downslope" effect of a tree (stemflow, surface runoff, shading etc.; the trees situated above the sampling point may affect soil properties more than those below the point), the exact position of a tree in relation to the sampling point was included (Fig. 1). The following indices were finally selected:

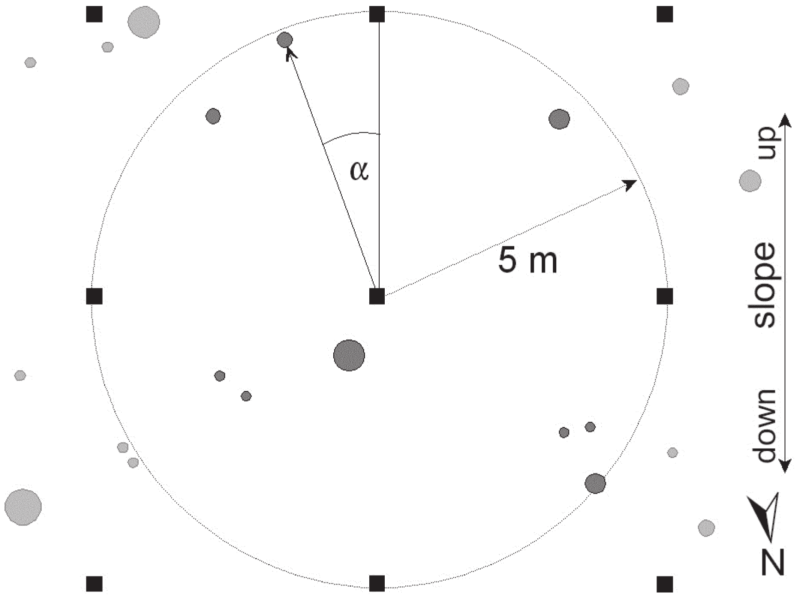

Fig. 1. Sampling scheme: black squares – soil sampling points, dark grey circles – trees within the 5-m-neighbourhood (included in the calculation of stocking indices), light grey circles – trees outside the neighborhood (omitted), circle size corresponds to tree diameter.

$IP_1 = \Sigma_i\, DBH_i / r_i$

$IP_2 = \Sigma_i\, BA_i / r_i$

$IP_3 = \Sigma_i\, DBH_i / r_i\, (1+\cos \alpha_i)$

$IP_4 = \Sigma_i\, BA_i / r_i\, (1+\cos \alpha_i)$.

where:

DBH_i and BA_i are breast-height diameter and basal area of the *i*-th tree within the 5-m-neighbourhood of the soil sampling point, respectively

r_i is the distance between the sampling point and the *i*-th tree

α is the angle between the downslope line and the sampling point → tree vector.

Since these indices reflect both density and size of trees at a particular point, we termed them stocking indices.

The light transmitted through the canopy to the soil surface was measured using canopy photographs. At each soil sampling point, vertical hemispherical photographs were taken by a Nikon digital camera with a fisheye objective from 20 cm above the soil surface. The following parameters were assessed from the photographs: canopy openness (*CO*), which is the percentage of open sky seen from beneath a forest canopy, the effective leaf area index integrated over the zenith angle 0° to 75° (*LAI*, Welles and Norman 1991), the amount of direct (R_{DIR}) and diffuse (R_{DIF}) solar radiation transmitted by the canopy. The program Gap Light Analyser 2.0 (Frazer *et al.* 1999) was used for the assessment of light variables.

The overview of the variables used in this study (microbial activity parameters, soil properties and environmental variables) in-

Table 1. Overview of the measured microbial activity parameters, soil properties and ecological variables including means, standard deviations and ranges of the observed values for the whole study period and area.

Variable		Mean	±SD	Min.	Max.	Unit
Catalase activity	*CAT*	1.40	0.39	0.25	2.70	ml O_2 g^{-1} min^{-1}
Basal respiration	*RESP*	6.41	3.25	0.52	14.76	mg CO_2 g^{-1} day^{-1}
SIR	*SIR*	28.56	10.03	4.73	64.44	mg CO_2 g^{-1} day^{-1}
Gravimetric moisture	*moisture*	41.03	6.13	25.97	65.95	% w/w
Organic matter	*OM*	8.63	2.90	0.34	16.90	% w/w
pH-H_2O	$pH\text{-}H_2O$	4.47	0.23	3.73	5.31	
pH-KCl	*pH-KCl*	3.39	0.22	2.90	4.23	
Nitrogen content	*N*	5.46	1.19	3.63	12.35	g kg^{-1}
Phosphorus content	*P*	3.68	2.08	1.05	15.26	g kg^{-1}
Potassium content	*K*	179.71	86.77	86.81	582.57	mg kg^{-1}
Canopy openness	*CO*	13.45	7.90	4.22	42.38	%
Leaf area index	*LAI*	2.45	0.62	0.74	3.63	
Direct radiation	R_{DIR}	2.85	2.59	0.37	13.83	mol m^{-2} day^{-1}
Diffuse radiation	R_{DIFF}	4.24	2.41	1.09	12.87	mol m^{-2} day^{-1}
Influence Potential[1]: IP_1	IP_1	39.70	24.79	4.41	135.39	
IP_2	IP_2	874.22	614.57	46.70	3512.00	
IP_3	IP_3	51.19	45.35	0.00	270.22	
IP_4	IP_4	1105.00	1006.00	0.10	7010.00	
Mean day temperature	T_{AVG}	7.65	0.51	6.30	10.20	°C
Temperature amplitude	T_{AMPL}	1.48	0.60	0.60	3.40	°C
Distance from the lower edge	*y*	78.44	47.89	-0.10	176.90	m

[1] see Material and Methods for explanation.

cluding their basic statistics (means, standard deviations and ranges) is given in Table 1.

To assess the spatial distribution of daily temperature course in the topsoil on the transect, soil temperatures at the depth of 2 cm were measured using soil thermometres distributed over a subset of 90 points on October 1, 2004 once per hour between 08:00 and 17:00. The average temperature (T_{AVG}) and the amplitude (T_{AMPL}) for each point were calculated.

The statistical program SAS (1998) was used for the statistical analysis of data. Factor analysis was performed for environmental variables excluding temperature data to identify common factors behind the observed variables. Factors were extracted using principal component analysis, with the squared multiple correlations of each variable with all other variables used as a prior communality estimate. The resulting factor structure was subjected first to an orthogonal varimax prerotation and subsequently to oblique rotation using the promax criterion. Factor scores were correlated with the parameters of the soil microbial activity.

Spatial patterns of soil variables were assessed using the program Variowin 2.2.1 (Pannatier 1996). Omnidirectional correlograms were calculated for 10 m distance classes.

3. RESULTS

3.1. Correlations

The *y*-axis is oriented parallel to the upslope direction, i.e., it follows the direction of the colonization of the former pasture by spruce. As expected, the *y*-coordinate is significantly correlated with the amount of light transmitted to the soil and with the size and density of trees surrounding soil sampling points as quantified by indices IP_1 – IP_4 (Table 2). At the same time, temperature regime changes along the *y*-axis, i.e. with advanc-

Table 2. Correlations between microbial activity characteristics, soil properties and ecological variables (see Table 1).

Variable	*y*[1]	*CAT*	*RESP*	*SIR*
CAT	-0.17*			
RESP	0.17*	0.35***		
SIR	–	0.38***	–	
moisture	0.18*	–	0.18*	0.38***
OM	0.17*	–	–	–
$pH\text{-}H_2O$	0.30***	–	0.18*	–
pH-KCl	0.21**	0.22**	0.22**	–
N	–	–	–	–
P	–	0.28***	0.16*	0.18*
K	–	0.22**	–	0.16*
CO	-0.62***	–	–	–
LAI	0.70***	–	–	–
R_{DIR}	-0.43***	0.28***	0.17*	–
R_{DIFF}	-0.58***	–	–	–
IP_1	0.56***	-0.23**	–	–
IP_2	0.48***	-0.28***	–	-0.16*
IP_3	0.38***	-0.15*	–	–
IP_4	0.37***	-0.21**	–	–
T_{AVG}	-0.49***	0.36***	–	–
T_{AMPL}	-0.69***	0.29**	–	–

Significance: * – $P < 0.05$, ** – $P < 0.01$, *** – $P < 0.001$

[1] The *y* axis is the axis of distance oriented parallel to the upslope direction and follows the direction of spruce colonization.

ing colonization: in the late-colonized lower part of the transect, average temperatures are generally higher, but also temperature fluctuations are bigger than in the dense forest stand in the upper half. A similar trend was observed in the case of gravimetric soil moisture, which significantly increases at more open microsites.

Surprisingly, basal respiration and SIR were found to be non-correlated. Both types of respiration rates are positively correlated with the catalase activity. Microbial activity parameters correlated positively with P, K, and partially with soil pH. Significant correlations with the other chemical soil properties were rare.

Catalase activity was consistently correlated with all variables reflecting successional stage. In the lower part of the transect with rich herbaceous vegetation, more insolated soil surface and higher soil temperatures, catalase activity was higher than in the darker and cooler upper part with an older and more closed tree stand and soil covered by a thick litter layer. Respiration rates did not exhibit any association with the successional stage. To account for a possible non-monotonous response of respiration to site conditions, we tested the relationship between respiration rates and ecological variables using polynomial (quadratic) regression. We found a significant non-linear response of basal respiration on the position on the transect (y-coordinate):

$$RESP = 7.937 - 0.0797\,y + 0.00056\,y^2$$

(R^2 = 0.17; minimum basal respiration rate was found at 71 m, i.e., in the middle of the transect).

For all soil variables, the correlations with the IP_1 and IP_2 indices were consistently higher and more significant than with IP_3 and IP_4. No downslope effect of trees on soil variables was thus observed. DBH-based and basal-area-based stocking indices yielded very similar correlations.

3.2. Factor analysis

To assess the number of common factors, we ran several analyses with numbers of factors increasing from 2 to 7. In all analyses, gravimetric moisture and organic matter content were found to be controlled by unique factors. The analysis with N_{fact} = 4 proved to give the best interpretable results (Table 3).

The first factor, which was termed *light*, had high loadings ($|r| > 0.8$) on canopy open-

Table 3 Factor structure displaying the correlations between environmental variables and the extracted factors. The highest loadings of a variable on a factor are bold-faced (see Table 1).

Variable	Factor				Communality
	Light	Stocking	Acidity	Nutrients	
Y	**−0.67**	0.45	0.32	−0.22	0.58
CO	**0.99**	−0.46	−0.03	0.08	0.98
R_{DIFF}	**0.97**	−0.47	−0.00	0.07	0.95
R_{DIR}	**0.74**	−0.32	0.16	0.20	0.61
LAI	**−0.90**	0.43	0.18	−0.02	0.84
IP_4	−0.36	**0.94**	−0.05	−0.07	0.91
IP_3	−0.35	**0.92**	0.05	−0.07	0.87
IP_1	−0.60	**0.91**	0.05	−0.01	0.87
IP_2	−0.58	**0.87**	−0.06	−0.03	0.80
$pH\text{-}H_2O$	−0.12	−0.01	**0.85**	0.01	0.73
pH-KCl	−0.01	0.02	**0.82**	0.15	0.68
P	0.03	−0.04	0.02	**0.52**	0.27
K	0.13	−0.08	0.07	**0.50**	0.26
N	0.26	−0.05	−0.11	**0.34**	0.19
moisture	0.15	−0.25	0.25	−0.17	0.17
OM	−0.02	0.01	−0.11	0.02	0.01

ness, transmitted diffuse light, and leaf area index, moderate loadings ($|r| > 0.6$) on transmitted direct insolation and the *y*-coordinate. From the other variables, indices IP_1 and IP_2 were quite closely correlated with the first factor. The second factor had high positive loadings on stocking indices IP_1 to IP_4, but it was weakly correlated ($|r|>0.3$) with the light-related variables as well. Consequently, it was termed *stocking*. The first and the second factor are correlated (to remind, oblique promax rotation yields correlated factors) and both are related to the stages of colonization. The third factor is clearly related to *soil acidity* (pH-H_2O, pH-KCl). The fourth factor had weak to moderate positive loadings on the content of nitrogen, phosporus and potassium, it was thus termed *nutrients*.

Communality values, which estimate the portion of variance explained by the extracted factors, were generally high in variables related to the succession stage (light, stocking). However, the extracted factors account for only 18 to 27% of the variance of mineral nutrient contents.

The correlations between factor scores and microbial activity parameters confirmed the relationships revealed by univariate approach (Table 4). Catalase activity was found to be significantly correlated with *light* and *stocking*, i.e., it changes with the successional stage. At the same time, it is correlated with *nutrients*, what reflects the significant correlation of catalase activity with phosphorus and potassium content. Basal and substrate-induced respiration rates depended neither from the successional stage nor from chemical soil properties (except a significant correlation of basal respiration with *soil acidity*).

3.3. Spatial patterns

Correlograms for the investigated soil variables are presented in Fig. 2. Although omnidirectional correlations were assessed, they reflect mainly directional relationships in the slope direction, at least for longer lag distances. The shape of the transect did not allow to look for possible anisotropies.

Generally, soil variables appeared to be very weakly spatially autocorrelated at the scale given by our sampling design. Nevertheless, some of them exhibit a spatial pattern. In case of nitrogen, autocorrelation steadily decreases with increasing *lag* distance. However, N exhibits a transect-wide trend (negative correlation with the *y*-coordinate). Therefore, linear regression of N on *y* was calculated and detrended N-values (residuals) were subjected to geostatistical analysis. A decrease of autocorrelations up to the distance of 40 m indicates that in addition to the overall trend, nitrogen content exhibits a short-range stationary pattern. In contrast to N, no spatial patterns could be revealed for P and K. All chemical soil properties (residuals in case of pH-H_2O) exhibit spatial continuity to some extent, with ranges of 30 to 60 m.

Among microbial activity parameters, basal respiration and catalase activity were correlated with the position on the transect (*y*-coordinate). Short-range stationary patterns were observed in case of catalase residuals and SIR (range of approx. 30 m), whereas the range of autocorrelation for basal-respiration residuals was approx. 60 m.

Table 4. Correlations between microbial activity parameters and the extracted factors.

Variable	Factor			
	Light	Stocking	Acidity	Nutrients
Basal respiration	–	0.028ns	0.191*	0.066ns
SIR	0.112ns	–0.107ns	0.136ns	0.075ns
Catalase activity	0.215**	0.248**	0.132ns	0.304***

Significance: * – *P* <0.05, ** – *P* <0.01, *** – *P* <0.001, ns – not significant.

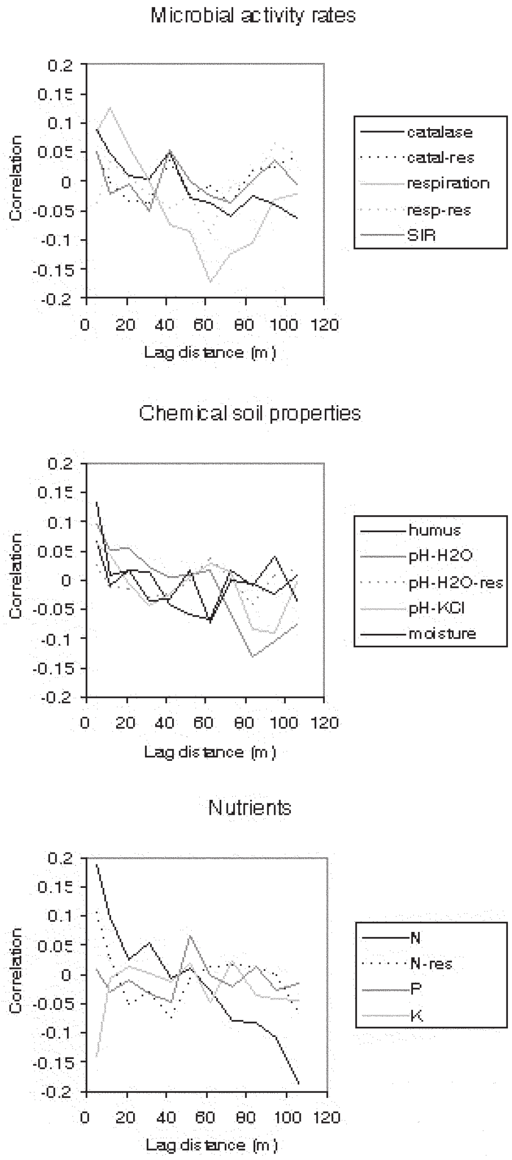

Fig. 2. Correlograms of chemical properties and microbial activity rates. N-res, catal-res and resp-res are detrended values (residuals) of nitrogen content, catalase activity and basal respiration, respectively.

4. DISCUSSION

The direction of vegetation changes in our experiment is just opposite to most studies dealing with the development of microbial communities under succession, mainly in cases when primary succession is studied. While primary succession starts on bare substrate and continues mostly over poor stages with lichens and bryophytes towards herbaceous and/or tree communities, secondary succession in our case started on species-rich pastures (the locality Príslopy exhibits the highest herb species diversity in the whole Poľana mountain range, see Ujházy 2003) and in the mid-succession stage (which is the stage in the upper half of our transect), Norway spruce forms a dense stand on a soil covered by a thick layer of poorly decomposing litter without ground vegetation or with few mosses. The effects of the advance of succession on the development of fungal and bacterial soil communities may thus differ depending on the type of succession and successional trajectories, even when the common final stage is a forest (Aikio *et al.* 2000, Mc Lean and Huhta 2002).

In our case, catalase activity decreased with the advancing colonization of the site by Norway spruce. Nevertheless, this trend need not be associated solely with the change of soil microbial community. The lower part of the transect is covered by a dense herb layer, so that the uppermost soil horizon is heavily rooted. Roots are known to contain high amounts of very active catalases (Alef 1991). Naturally, we removed all visible roots from the samples before subjecting them to the analysis. Nevertheless, in addition to enzymes active in viable bacterial and fungal cells, enzymatic activity of soil includes enzymes released from dead cells (including those of aborted roots) into soil solution or bound to soil particles (Ladd 1978). In any case, catalase activity appeared to depend from direct insolation and associated temperature regime of soil – whereas this is a direct effect or mediated through the effect of radiation and temperature on the herb layer, remains questionable. Basal respiration decreased towards the middle of the transect and afterwards increased again. This non-linear development may be associated with the breakup of the old-growth stand and the original spruce plantation along its boundary. Quite much diffuse side light enters into the upper part of the transect. Consequently, cover and species diversity of herbs increase again in the uppermost part of the transect (although the species composition differs from that of the lower part), providing plant residues of better quality than spruce needles. The quantity and quality of organic matter available for decomposition, which depend from the vegetation, not only determine humus formation (Muys *et al.* 1992), but also affect soil structure, chemical properties etc. (Graham *et al.* 1995, Vesterdal and Raulund-Rasmussen 1998). Although we have not performed an exact phytosociological investigation, spatial distribution indicates a positive relationship between the ground vegetation cover and diversity, and the respiration activity (cf. Stephan *et al.* 2000, Zak *et al.* 2003). It must, however, be mentioned that opposite trends have been observed as well. The results indicate that respiration is associated with the quality of plant residues to be decomposed.

The difference in trends of basal respiration and catalase activity over the transect may also reflect changing taxonomical composition of soil microbial communities. Actually, both parameters are quite crude indicators of the summary activity of the whole bacterial and fungal community, which need not closely correlate with its composition (Pennanen *et al.* 1999, Stephan *et al.* 2000, Yao *et al.* 2000). The same may apply to the absence of correlation between SIR and basal respiration. Only one added substrate (D-glucose) was used for the assessment of SIR. Nevertheless, soil samples showing the same summary basal respiration may differ in the representation of functional microbial groups preferring different substrates. Preliminary results based on the assessment of functional groups of microbes using the Biolog® EcoPlate system support the assumption that the composition of the microbial community changes over the transect (Gömöryová unpubl.).

Increase of soil pH towards the upper part of the transect is a surprising outcome. Density of spruce and thus the amount of spruce litter generally increases in this direction. Spruce needles were found to increase soil acidity (Augusto *et al.* 2002, 2003, Menyailo *et al.* 2002). This trend is thus associated with a possible change of the inorganic soil substrate or with the former land management rather than with the effect of trees. In fact, stocking indices, which express the influence of trees better than the position on the transect itself, are not correlated with pH. Also, the time span during which this influence is exerted (less than 50 years) may be too short for affecting soil acidity.

Spatial scale is an important matter for the assessment of any soil properties (Goovaerts 1998, Oline and Grant 2002). Soil contains many microhabitats with suitable conditions for survival and reproduction of soil microbes. Consequently, bacteria and fungi may be spatially aggregated in soil, forming hotspots of microbial activity. Nevertheless, microbial activity rates may exhibit spatial continuity not only at this microscale, but also on larger scales (Franklin and Mills 2003). Plants are known to contribute to the formation of spatial patterns of soil microbial communities. The range of variation of most soil properties as well as soil respiration rates may be very short, ranging from a few centimeters to a few meters (Jackson and Caldwell 1993, Stoyan *et al.* 2000). A sampling on a 5 × 5 m grid may thus leave much of the existing spatial continuity unrevealed.

Generally weak correlations among soil variables indicate that microbial activity rates represent complex traits. In contrast to the relationships between soil respiration or enzyme activity and environmental variables (light, stocking, temperatures), the causality of mutual interrelations between microbial characteristics and chemical soil properties is uncertain. Not only the chemical composition of soil affects the abundance and species composition of microbes, but also bacteria and fungi discharge elements bound in the organic matter into soil, resulting in a dynamic balance between microbial community and the chemical properties of the soil environment (Zhou *et al.* 2002).

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