

Inter-crown versus under-crown area: contribution of local configuration of trees to variation in topsoil morphology, pH and moisture in *Abies alba* Mill. forests

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Abstract This investigation of three *Abies alba* stands differing in stem density (338–715 per ha) and vertical structure (one-storeyed or multi-layered) explored the relations between distance from neighbouring tree stems and local canopy openness and selected topsoil properties. The null hypothesis was that in relatively densely stocked forests of close-random stem distribution topsoil morphology, pH and moisture do not differ in inter-crown and under-crown patches. In three plots 1.1 ha in area, soil samples were taken in a square grid 5.0 × 5.0 m and analysed using semivariogram estimation and spatial autocorrelation. The local configuration of trees around the sampled locations was characterised using hemispherical photography and a local stand density index based on tree locations and diameters. The largest portion of the total variation in the soil variables analysed (68–100%) was attributable to small-scale variation in scales <5 m. In all stands, irrespective of density and vertical structure, local stand density/canopy openness correlated positively/negatively with ectohumus layer thickness but negatively/positively with upper soil pH and moisture. Variation in the local configuration of trees explained up to 17% of the total variation in organic horizon thickness, up to 22–29% in topsoil pH (depending on the horizon) and up to 19–27% in topsoil moisture. The results indicate that even in stands of

random tree patterning, stem neighbourhood and small-scale variation in canopy density may contribute significantly to topsoil heterogeneity and potentially affect the functioning and structure of forest floor vegetation.

Keywords Forest soils · Micro-site · Soil heterogeneity · Ectohumus layer · Soil water dynamics · Spatial dependence

Introduction

Environmental variability can occur over various spatial scales, ranging from micrometers, to small patches at the scale of individual plants to long gradients over hundreds of metres (Ehrenfeld et al. 1997; Totsche et al. 2010). In forested ecosystems, one important source of micro-site heterogeneity is the distribution of trees and their organs in the above- and belowground space. Such tree patterning determines the light and thermic conditions in forest interiors (e.g. Canham et al. 1994; Parker 1997), modifies the amount and chemical properties of through fall (Whelan et al. 1998; Morris et al. 2003; Staelens et al. 2006) and spatially diversifies the amount of litterfall (Hirabuki 1991), rhizodeposition (Weintraub et al. 2007) and carbon input by root litter (Tingey et al. 2005).

The majority of studies carried out to date have focused on heterogeneity at micro-scales that are not applicable to forest practice (Farley and Fitter 1999; Yang et al. 2006) or on indicating differences between closed forests and relatively large, newly created gaps in an area of at least a few hundred m². The latter research has suggested that large gaps are characterised not only by more advantageous light conditions but also by more rapid decomposition of organic matter (Zhang and Zak 1995), moister topsoil (Plussi et al.

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1971; Sanesi and Sulli 1973; Collins and Battaglia 2002), a greater concentration of nutrients in soil solution (at least up to depletion of the forest floor storage) (Mlandenoff 1987; Bauhus 1996) and a minor density of tree roots (Parsons et al. 1994a, b). However, there is still little known about micro-site heterogeneity in stands that exhibit rather random distribution of trees, in spite of frequent occurrence of such structures in forest ecosystems. This void stems partly from the belief that in stands having only a slightly loosened canopy and gaps no larger than the crowns of several trees, micro-site diversity is little and heterogeneity attributable to the influence of single trees is negligible, except perhaps for single attributes like stem flow (Koch and Matzner 1993; Neary and Gizyn 1994).

Nevertheless, Kern (1966), Bouten et al. (1992) and Keim et al. (2005) have documented a significant relation between a vertically downward projected canopy structure and rain through fall distribution. Moreover, at the within-stand level, differences between the chemical properties of through fall have been found and spatially linked to the crown positions (Beier et al. 1993; Whelan et al. 1998). The investigations by Hirabuki (1991), Bartsch et al. (2002) and Penne et al. (2010) also provide evidence that the amount of woody debris is significantly higher under tree crowns than in inter-crown gaps. This small-scale variability of the amount and chemical properties of through fall and litter fall may apparently affect the decomposition rate of organic matter and thus appreciably influence ectohumus layer thickness and topsoil properties (Zinke 1962; Boettcher and Kalisz 1990; Pallant and Riha 1990). Additionally, the belowground heterogeneity of stands may be elevated by clumped distributions of roots and the resulting heterogeneity in water and nutrient uptake and release of protons (Ruark and Zarnoch 1992; Oliveira-Carvalho and Nepstad 1996; Partel and Wilson 2002). Proximity to trees may also influence the functions and diversity of soil micro-organism communities (Simard et al. 1997; Frankland 1998) and influence the species composition of forest floor vegetation (Paluch 2005a, b). Hence, distance from the tree stem appears to be a factor with considerable potential to contribute to topsoil heterogeneity even in relatively uniformly stocked stands.

Close-random distribution patterns of canopy trees are characteristic for a wide range of silvicultural systems using natural regenerative processes (e.g. shelter wood method or selection system). Over-dispersed patterns of regeneration are a common phenomenon despite the spatial homogeneity of the stand structure in such forests (Mazur 1989; Paluch 2005a, b). The success of natural regeneration partly depends on the properties of the upper soil horizons (Shelton 1995; Simard et al. 1998), which condition seed germination, root development, and establishment of relations with soil micro-flora and determine the

availability of water and nutrients. Therefore, recognising spatial variation in topsoil properties and its relation to stem distribution may contribute to an understanding of the mechanisms that form non-random spatial patterns of regeneration in evenly stocked forest stands as well.

The present study was carried out in three mature stands of *Abies alba* that grow in similar site conditions but differ in stand density and vertical structure. This species possesses a range of features that made it particularly suitable for our study: compact above-ground architecture, a considerable interception (27–80%, Otto 1994), needles that decompose with difficulty (Otto 1994, litter C/N about 24, Augusto et al. 2002; Niewinna 2010), negligible stemflow (coarse bark, crowns that conduct water towards the periphery). In addition, *Abies alba* mostly occurs on slightly acidified soils, what should facilitate the formation of pH gradients in the topsoil. The objective was to characterise the within-stand variability of three universal determinants of forest floor vegetation dynamics, i.e., the humus layer thickness, topsoil pH and moisture, and to assess to which extent this heterogeneity is attributable to the “stand density” factor, derived from local canopy density or distance from neighbouring tree stems. The “null” hypothesis was that in *Abies alba* stands, given a wide range of stand densities and vertical structures, the topsoil near and far away from the stem basis will not differ in humus layer thickness, topsoil pH and moisture.

Methods

Study sites

From among the few stands included in a research project on regenerative processes in silver fir forests in the West Carpathians (southern Poland), two pure, one-storeyed stands aged about 90 years with contrasting stem density and basal area (338 stems/ha and 34 m²/ha in the OS-I stand and 700 stems/ha and 49 m²/ha in the OS-II stand) and one, also mono-specific, multi-layered stand with a poor regeneration layer (hereafter, MS, 715 stems/ha, 35 m²/ha, with trees aged between 20 and 160 years) were selected for this study. The terrains in which the study was conducted were continuously forested. All the stands originated from natural regeneration (a shelter wood system in the OS-I and OS-II stands, an extensive single-tree selection system in the MS stand) and had not undergone intensive silvicultural treatments for the past few decades. According to local management plans, the species composition of the stands studied has not changed in 50 years, although the elimination of potentially co-occurring broadleaved species (e.g. *Fagus sylvatica* L.) by silvicultural operations seems probable in an earlier stage of

development. Between-crown gaps in the more loose OS-I stand probably originated already in young age (e.g. as effect of snow or wind damages), because stumps after fallen trees are difficult to find.

The lower montane belt zone studied here has a growing season of ca 195 days, an average annual temperature of 7°C and annual precipitation of 900, 600 mm of which occurs between April and September (Hess 1965). The selected stands were situated on western slopes (mid-slope positions) of inclination 3–5° (OS-I and OS-II stands) and 10–15° (MS stands). The stands grew on loamy, moderately stony (sandstone fragments 20–30 cm below the soil surface), eutric cambisols (IUSS Working Group, WRB 2007) developed from Flysh sediments (marlstones, sandstones and shales) with the *cambic* horizon depending on the stand between 23–29 and 57–68 cm from the soil surface and the bedrock horizon below 95–110 cm. The pH (in H₂O) increased from 4.0 to 4.4 in the humic horizon up to 6.5–7.2 at the bottom of the profiles. At the depth between 20 cm and continuous rock, base saturation (CH₃COONH₄) ranged between 51 and 67%. In the OS-II stand, about 60 cm below the soil surface, clay content increased and a gleyic colour pattern occurred.

The forests represented the association *Dentario glandulosae–Fagetum abietosum* (Matuszkiewicz 2001). The share of *F. sylvatica* L. and other less indicative tree species has probably been artificially reduced by man. The herbaceous vegetation layer was multi-species, with a common occurrence of *Dentaria glandulosa* W. K., *Dryopteris filix-mas* (L.)Schott., *Dryopteris dilatata* (Hoffm.) A. Gray., *Galeobdolon luteum* Huds., *Galium odoratum* (L.) Scop., *Lysimachia nemorum* L., *Rubus hirtus* Waldst. & Kitt. Agg. The moss layer was dominated by *Mnium* sp. The under-storey was represented by single individuals of *Lonicera nigra* L shrubs. There were no grounded deadwood logs within the study plots.

Field work

To recognise stand-level (and not only tree-level) variability in topsoil properties, the investigation was carried out on relatively large research plots 1.1 ha in area. In every stand, records were made of the stem coordinates (exact to 0.1 m, using a compass and an ultrasonic distance meter) and the diameters at breast height of all live trees above 6.9 cm in diameter. The MS stand also provided data on stump coordinates, stump diameters at 30 cm in height and decay classes (A—recently harvested stumps with slightly decomposing but still compact wood; B—old stumps or their remnants in advanced decay, supposedly recognisable up to about 40 years after the respective tree was cut down). These data were used to retrieve coordinates and diameters at breast height (via the formula given

by Bruchwald et al. 2002) of trees cut down over the past few decades. Subsequent spatial analysis (using the nearest neighbour method, Diggle 1983, pp. 16–20) revealed that the trees were randomly distributed in all the stands studied.

Canopy openness above the grid points (i.e. the fraction of open sky unobstructed by vegetation in a specified region of the canopy) was characterised based on hemispheric images. All these photos were taken in overcast conditions from 1.2 m above the ground using a Nikon E4500 camera with a Nikon FC-E8 fisheye converter fixed on a tripod and a universal O-mount with a northfinder (Régent Instruments Inc., Canada).

Soil samples were taken in a square grid 5.0 × 5.0 m that excluded an outer buffer zone 10 m wide (used to calculate the stand density indices). Shallow soil pits (242–265, depending on the stand) were dug at the grid points (5.0 × 5.0 m) except in locations that exhibited atypical characteristics like windthrow pits or old logging trails (below 5% of all the grid points), and the depth of the morphological horizons was measured with a ruler on the undisturbed pit profile exact to 0.5 cm. Soil samples were collected in plastic bags from the mineral humic (hereafter, A) horizon (about 6–8 cm), as well as from the underlying horizon down to 20 cm (hereafter, the AB horizon). All soil samples collected were marked and transported to a refrigerator where they were kept at –3°C until laboratory analysis began. The soil sampling from all the grid points was completed within 36 h. The soil samples were collected during July–August 2005 (OS-I and MS) and 2006 (OS-II) in periods when no precipitation had occurred for 1–2 weeks.

To provide insight into the dynamics of water content in the topsoil under different local stand density conditions over the growing season, two soil dielectric aqua meters (length 20 cm, model EC-20 ECHO Decagon Devices, Inc., USA) were installed in every stand in a small gap about 50 m² in area: one in the centre and one 5–6 m away, 1 m off from a neighbouring fir's trunk. In spite of similar openness for the entire hemisphere, the points at which sensors were installed differed significantly in the canopy openness determined for the zenith rings of 0–10° (0.55–0.72 and 0.03–0.11, respectively). Between 1 May and 30 September 2007, 12–13 measurements of volumetric water content were registered both in drying and rewetting conditions.

Laboratory analysis

Rather than the soil samples being sieved, the macroscopic roots and stony material were removed manually before weighing. Soil pH determination was carried out using a soil-solution suspension of 10 g of mineral soil (5 g for the

organic material) and 50 ml of 0.01 M CaCl₂ solution. After a 24-h equilibration, the pH was measured potentiometrically with a combination electrode (ROSS Ultra, Thermo Scientific, USA).

Soil moisture content was calculated on the basis of oven-dry sample weight. About 20–50 g of the soil was placed in a metal box, weighed, put into an oven to dry at 105°C for 24 h, cooled to room temperature (in a desiccator) and then weighed again. Soil moisture could then be calculated from the mass lost.

Calculation of canopy openness and local stand density

Analysis of the hemispheric photos was carried out with the WinSCANOPY Pro 2006a program (Régent Instruments Inc., Canada) using the manufacturer's camera and lens specifications. Here, the manual pixel classification method based on grey levels proved the most effective (with thresholds of about 250 on a 0–255 grey level scale). Because the gaps were rather small, determining canopy openness for a ring given by the zenith angle 0–10° appeared sufficient to properly characterise canopy closure above the grid points while still avoiding strong spatial correlation (as indicated by the variogram analysis). Specifically, assuming a stand height of about 30 m, this setting allowed capture of the canopy closure in a radius 5.3 m (ca 90 m²) around the grid points.

Local stand density (hereafter, LSD) was expressed as follows:

$$LSD_i = \sum_{j=1}^n f(D_j, u_{ij}),$$

where LSD_i denotes the local stand density at a given point i (and is expressed in dimensionless units), the summation is over all n trees in the stand, D_j is the breast height diameter of the j -th tree (in cm), u_{ij} is the distance (in m) between the j -th tree and point i , and f is the influence function. In a preliminary exploration using a threefold cross-validation technique, we tested different forms of influence functions (linear, concave or convex) and a range of distance- and (tree) diameter-scaling parameters on the power of LSD as a potential predictor of the topsoil characteristics under study (Paluch 2008). The analysis showed that (1) parameter values resulting in impact zones that were approximately smaller than the crown widths or larger than the doubled crown widths reduced the proportion of the explained variation, (2) the shape of the influence function (linear, concave or convex) had only a slight effect, and the linear influence function produced the best or almost the best results and (3) the proportion of the explained variation might be maximised if the diameter to the power of n , $n \in \langle 0.5; 1.5 \rangle$, was incorporated into the

influence function, although differences in the order of a few per cent occurred between stands and between soil variables. Here, for simplicity, a linear form of the influence function f was used:

$$f(D_j, u_{ij}) = \begin{cases} D_j - cu_{ij} & \text{if } u_{ij} < u_j \\ 0 & \text{otherwise,} \end{cases}$$

where $c = 8$ and $u_j = c^{-1}D_j$. For these settings, the potential for trees decreased linearly with increasing distance and decreasing diameter, while the zone of influence ranged between one- and twofold crown width. In the MS stand, LSD was also calculated for removed trees, with two separate calculations for the two stump decay classes, A and B.

Statistical and geostatistical analysis

The set of soil variables included the O horizon depth, the A and AB horizon pH, the content of hydrogen ions in the A and AB horizon ($10^{-\text{pH}}$) and the mineral topsoil moisture. The coefficients of variation (CV) were computed for all soil variables, and the differences in the corresponding variances were tested using Brown and Forsythe's extension of Levene's test. The relations between the soil variables were explored in scatter plots and, if relevant to this discussion, expressed as Pearson correlation coefficients.

The spatial patterning of the soil variables, local stand density and canopy openness were characterised using variography (semivariogram estimation) and spatial correlation. The semivariogram represents dissimilarity or variance, while the spatial autocorrelation measures similarity and provides a means for testing the significance of the spatial pattern. Because we found no evidence of anisotropy or non-stationarity, the spatial analyses assumed omni-directional spatial dependence. Semivariograms were calculated for distance classes of 5 m using the robust estimator recommended by Cressie (1993, p. 40). Spherical variogram models were then fitted to the empirical variograms using a weighted least squares estimation. The smoothed variance of the soil variables was decomposed into two components: small-scale variation (with a range smaller than the grid spacing) plus the measurement error (to give a so-called nugget effect) and the meso-scale variation (with a range, if one existed, larger than the grid spacing) referred to as a sill (Cressie 1993). The strength of the spatial dependence was determined by subtracting the nugget from the sill, dividing the difference by the sill and expressing the value as a percentage. Spatial autocorrelation was estimated using Moran's index (Moran's I), whose values were tested for significance using permutation tests ($n = 4,999$ permutations). Since multiple tests of autocorrelation were performed on each dataset, the P value was adjusted using the Bonferroni correction.

Because preliminary exploration showed that the relations between the soil variables and the stand density measures used can be approximated linearly, these associations were assessed using simple Pearson coefficients of correlation and slope and intercept coefficients of regression. Multiple regressions were used to assess whether inclusion of variables describing the location of trees removed in the past (from the MS stand data) increases the models’ predictive power. In many cases, the soil variables deviated slightly from a Gaussian distribution and displayed spatial dependence, which excluded any usage of conventional statistical procedures. Therefore, the coefficients of correlation were tested for significance using Monte Carlo permutation tests (4,999 simulations), and the coefficients of regression were determined as averages from 4,999 bootstrap samples. In ordinary bootstrapping techniques, an empirical distribution gives bootstrap samples via random sampling, from which bootstrap replications of a statistic of interest is calculated. In the present analysis, to avoid problems with spatial correlation of data, instead of simple permutation or bootstrapping, a moving blocks method (block length = 5 m) was used in which no single grid points but blocks of four adjacent grid points were selected (Efron and Tibshirani 1993). The coefficient of determination (i.e. R^2) was used as an estimate of the percentage of the total variation in topsoil properties that might be explained by variation in stand density (i.e. LSD or canopy openness). The analysis was performed using R statistical software, version 2.8.1 (R Foundation for Statistical Computing 2008), and Statistica, version 8.0 (StatSoft, Inc.).

Results

Spatial variation of stand density

In the OS-I, OS-II and MS stands, the CVs for local stand density amounted to 0.50, 0.44 and 0.65, respectively. For canopy openness, the values were higher: 0.94, 1.28 and 1.44, respectively. The distributions of local stand density

and canopy openness are illustrated in Fig. 1. As shown in Fig. 2, the canopy openness and LSD were characterised by significant positive spatial correlation at a scale of 5 m and the latter variable, in one-storeyed OS-I and OS-II stands, also by a negative correlation at a scale of 10 m. This finding indicates small-scale gradients in spatial structure for canopy openness and LSD. In all stands, LSD was negatively correlated with canopy openness, with the coefficients of correlation being -0.47 , -0.37 and -0.46 in the OS-I, OS-II and MS stands, respectively.

Spatial variation of soil characteristics

In the OS-II and MS stands, among the soil variables analysed, the highest variation occurred in the depth of the organic horizon (CV 0.59 and 0.89, respectively, Table 1), which varied between 0.5 and 10.0 cm. In the OS-I stand, the range of the O horizon thickness was similar (0.5–9.0 cm), but the CV was smaller than in the OS-II and MS stands (0.39, $P < 0.001$ in both cases) and comparable to the values for the A horizon depth, hydrogen-ion concentration or A horizon moisture in that stand. In the OS-II and MS stands, in contrast to other soil variables, the distribution of the O horizon depth deviated significantly from the Gaussian: in the first, the mode was markedly shifted to the left and the distribution had a long right tail, while in the second, the distribution was reversely *J* shaped, with the mode at the thin ectohumus layer values (about 0.5 cm). The O horizon depth in the OS-I stand, like other soil variables in this and the remaining stands, was characterised by a bell-shaped distribution.

The CVs for the hydrogen-ion concentration in the A and AB horizons did not differ markedly (Table 1). In the dense OS-II stand, variation in the hydrogen-ion concentration was higher than in the less dense OS-I stand ($P = 0.03$ and 0.02 for the A and AB horizons, respectively) but lower than that in the multi-layered MS stand ($P < 0.001$ for both horizons). The O horizon depth was negatively correlated with pH in the A and AB horizons, with the coefficients of correlation ranging between -0.23 and -0.44 (all significant at the 0.05 level).

Fig. 1 Distributions of local stand density (LSD) and canopy openness. For a description of the terms, see the “Methods” section

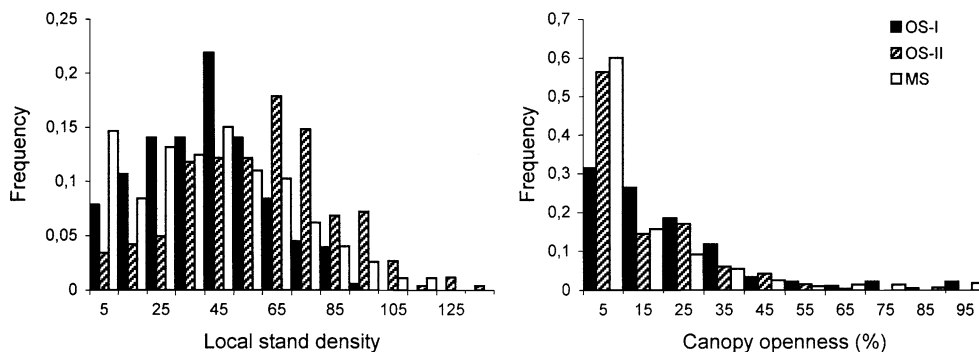


Fig. 2 Spatial correlograms of local stand density (LSD) and canopy openness. The blackened marks denote significant values at a corrected level of $0.05/10 = 0.005$

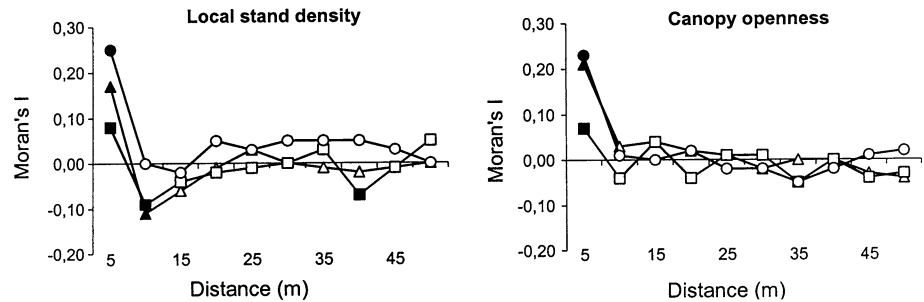


Table 1 Soil sample characteristics

Characteristics	OS-I	OS-II	MS
Sample size	242	256	265
O horizon depth (cm)			
Mean	2.9	3.6	1.9
CV	0.35	0.59	0.89
A horizon depth (cm)			
Mean	6.3	6.0	8.2
CV	0.43	0.36	0.36
A horizon pH (CaCl ₂)			
Mean	3.2	3.3	3.8
CV	0.04	0.06	0.09
A horizon H concentration (mol dm ⁻³)			
Mean	6.49×10^{-4}	4.98×10^{-4}	1.95×10^{-4}
CV	0.29	0.37	0.58
AB horizon pH (CaCl ₂)			
Mean	3.4	3.6	3.9
CV	0.04	0.05	0.10
AB horizon H concentration (mol dm ⁻³)			
Mean	4.31×10^{-4}	2.92×10^{-4}	1.68×10^{-4}
CV	0.30	0.39	0.68
A horizon moisture (%)			
Mean	43	63	37
CV	0.40	0.27	0.28
AB horizon moisture (%)			
Mean	27	46	25
CV	0.20	0.16	0.23

In all stands, the moisture determined gravimetrically decreased with soil depth (Table 1). The differences between the A and AB horizons were in the range of 12–17%. If the bulk densities of the horizons were considered (0.72 – 0.86 g cm⁻³ in the A horizons and 0.94 – 0.98 g cm⁻³ in the AB horizons), the differences decreased up to a level of 6–8%. No significant relations emerged between the O and A horizon depth and mineral topsoil moisture, and the variation in topsoil moisture was comparable in all stands. However, the CVs were higher in the A horizon than in the AB horizon.

Irrespective of the soil variables, the largest part of the total variation was the small-scale variation at lags <5 m.

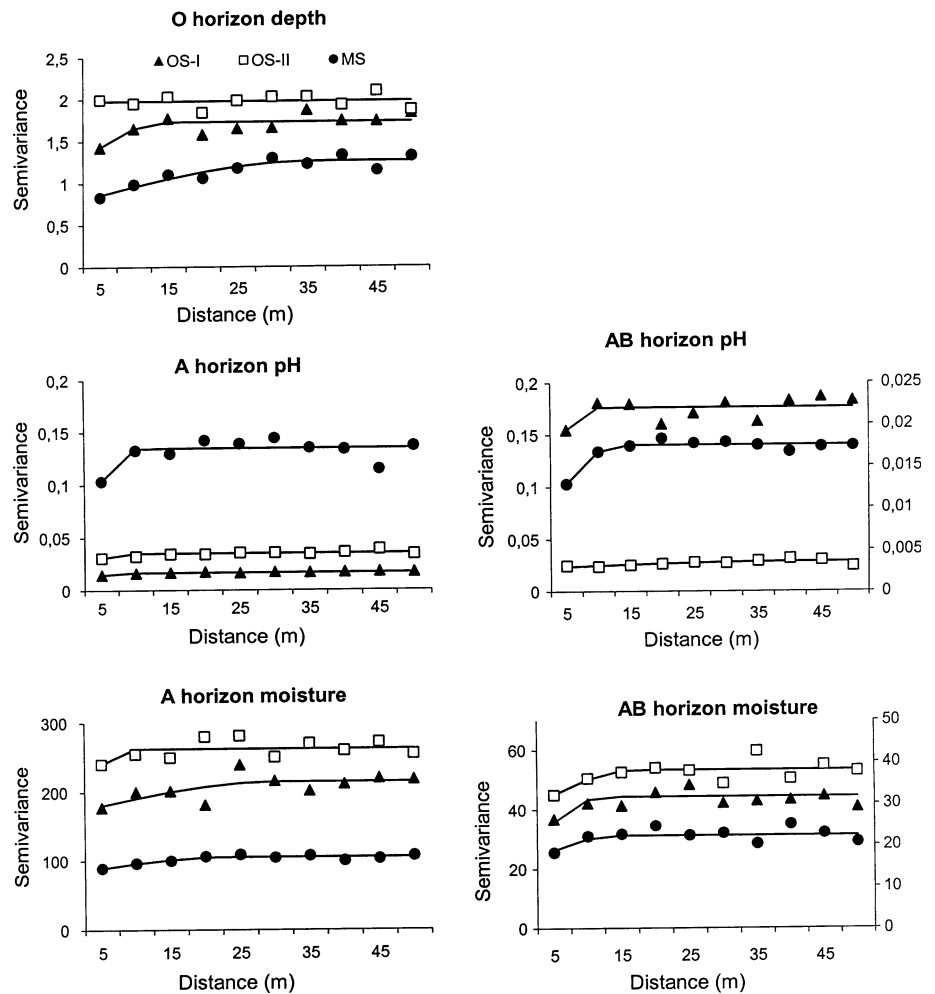
Table 2 Strength (in %) and range (in m, in brackets) of the spatial dependence of topsoil properties determined from the spherical semivariograms shown in Fig. 3

Characteristics	OS-I	OS-II	MS
O horizon depth	17 (14.5)	0 (–)	32 (35.9)
A horizon pH	13 (10.1)	12 (10.0)	23 (10.7)
AB horizon pH	12 (10.7)	14 (41.4)	27 (13.2)
A horizon moisture	16 (30.7)	8 (8.5)	15 (23.4)
AB horizon moisture	16 (14.0)	14 (17.1)	20 (12.5)

The spatial dependence for larger lags accounted for 0–32% of the total variation in the O horizon depth, 12–27% of the total variation in the A and AB horizon pH and 8–20% of the total variation in the A and AB horizon moisture (Table 2). The spatial dependence in the O horizon thickness and pH levels for both horizons tended to be stronger in the multi-layered MS stand than in the one-storeyed OS-I and OS-II stands. In the case of the O horizon depth and A horizon moisture, the spatial dependence was weaker in the more dense OS-II stand than in the OS-I stand (Table 2). We found no substantial anisotropy in the spatial data. In most cases, the differences in small-scale (<5 m) semivariances calculated in the slope line and perpendicular direction were negligible (below 5%), and the deviances occurred in the both directions (results not illustrated). However, in the MS stand, the small-scale semivariance in the slope line was 18 and 20% lower for A and AB horizons, respectively, than in the perpendicular direction. For larger distances, these differences disappeared.

The scale of the spatial dependence revealed by the variography varied considerably between the stands and soil variables, ranging from 8.5 to 41.4 m (Table 2; Fig. 3). However, the permutation tests performed at the conventional 0.05 level failed to satisfy global significance (i.e. with the *P* value adjusted using the Bonferroni correction) of the spatial autocorrelation in the dense OS-II stand for all soil variables and in the OS-I stand for A horizon pH (Fig. 4). As shown in Fig. 4, in all the statistically significant correlograms, the spatial correlation decreased with increasing distance, and no periodicity was revealed in the spatial scale investigated.

Fig. 3 Empirical variograms of the soil variables analysed and the fitted *spherical* models. For better discernability, data from the OS-I stand for pH and moisture in the AB horizon are shown on the *right axis*



Seasonal variation in topsoil moisture

The variation in topsoil moisture did change over the growing season. Although the soil moisture in the gaps was higher than in the proximity of tree trunks during the entire period (Fig. 5), the smallest differences between these locations were found at higher water content levels, that is, in the spring and/or after heavy or long-lasting precipitation. However, during drying periods, when topsoil moisture decreased, the differences deepened. The higher water content in the OS-II stand, which remained throughout the entire growing season, is mainly attributable to higher clay content in the soil on that site and probably micro-site conditions as well.

Relation between stand density and topsoil characteristics

In all stands, local stand density and canopy openness were associated with the topsoil variables analysed (Table 3). Specifically, as stand density increased (and canopy openness decreased), ectohumus layer thickness increased

and topsoil pH and moisture decreased. Examples of these relations for each soil horizon are illustrated in Fig. 6. Additionally, the percentage of the total variation in topsoil properties, which might be explainable by variation in stand density, differed among stand density measures (i.e. LSD or canopy openness), stands and, to a much lesser degree, soil characteristics. In the MS stand, the associations were closer for LSD than for canopy openness. The same tendency was found in the looser OS-I stand (Table 3) except for topsoil moisture whose correlation with canopy openness was stronger than that with LSD. In the dense OS-II stand, however, the O horizon depth and topsoil moisture correlated more strongly with canopy openness than with LSD.

The coefficients of determination (R^2) indicated that variation in the canopy openness explained between 3 and 8% of variation in the O horizon thickness, between 6 and 12% of variation in the topsoil pH (inclusive of hydrogen ion concentration) and between 4 and 21% of variation in the topsoil moisture. If stand density was expressed by LSD, the corresponding values ranged between 3 and 11% of the variation in O horizon thickness, between 7 and 29%

Fig. 4 Spatial correlograms of the soil variables analysed. The blackened marks denote significant values at a corrected level of $0.05/10 = 0.005$

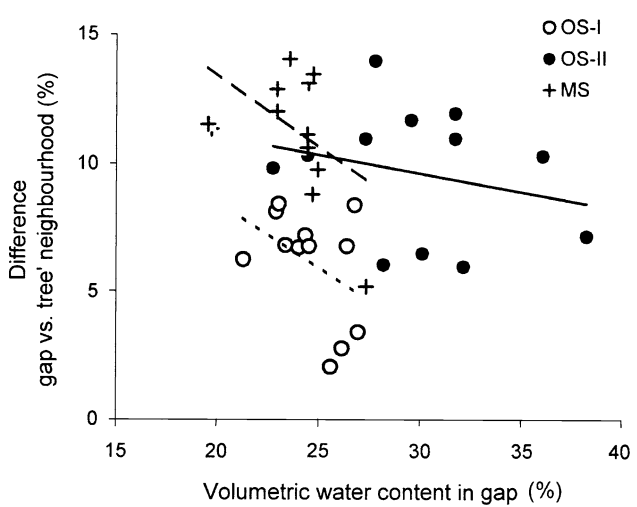
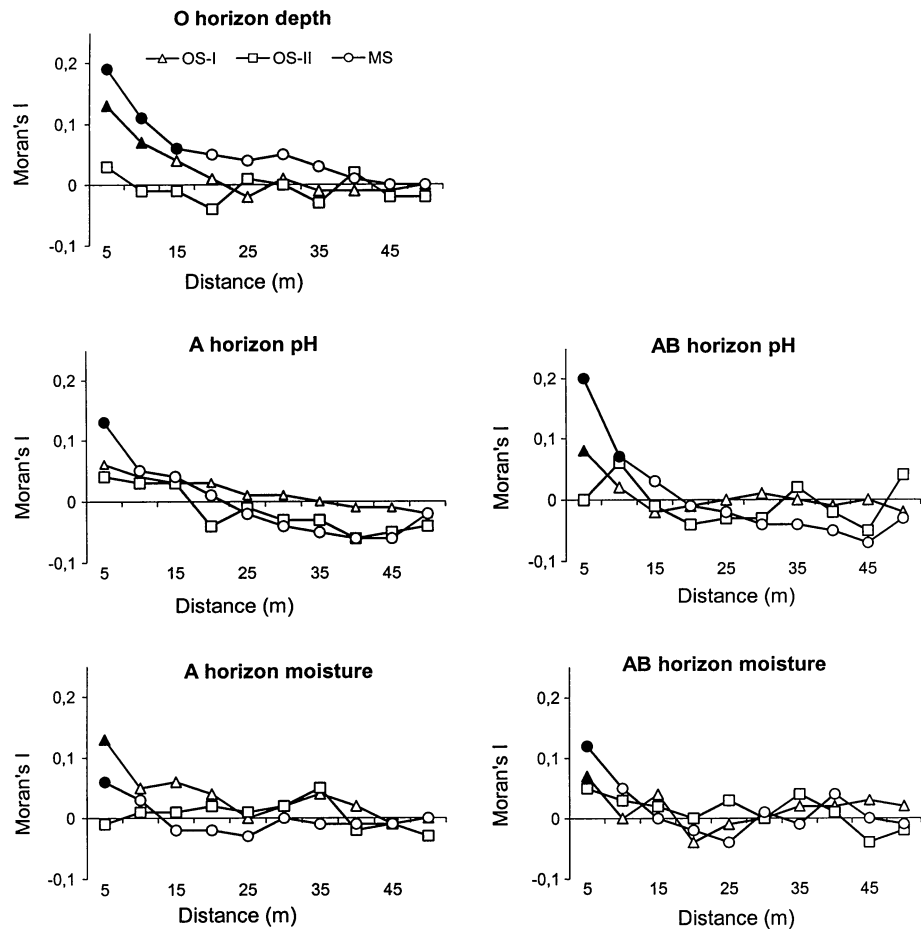


Fig. 5 Differences between volumetric water content in the centres of small gaps (ca 50 m² in area) and in the proximity of neighbouring firs. Measurements registered at the same locations between 1 May and 30 September 2007

of the variation in topsoil pH (inclusive of hydrogen-ion concentration) and between 4 and 27% of the variation in topsoil moisture. The strongest associations between LSD and topsoil pH and moisture were found in the loose OS-I

stand (R^2 between 12 and 29%). Combining LSD and canopy openness as independent variables exerted a negligible effect on the percentage of the explained variation in topsoil properties.

The rate at which the O horizon thickness increased with increasing LSD was comparable in the OS-I and MS stands (0.02 cm per 1 LSD unit) but lower in the OS-II stand (0.01 cm per 1 LSD unit, Table 4). However, although increasing LSD had a similar effect on the pH in the A and AB horizons in all stands, it was linked to a decreasing pH most clearly in the MS stand (0.005 pH unit per 1 LSD unit) and most slowly in the dense OS-II stand (0.002 pH unit per 1 LSD unit). In contrast, increasing LSD exerted a stronger effect on the topsoil moisture of the A horizon than on the AB horizon (Table 4).

The data from the MS stand enabled investigation of the relations between the locations of removed trees and the topsoil variables. Although the approximated basal area of the removed trees was considerable and accounted for 90% of the basal area of live trees (25 and 65% for the decay classes A and B, respectively), the relations between the location of the stumps and the topsoil variables were very weak and statistically insignificant (results not illustrated). One exception was the negative association between the

Table 3 Correlations between canopy openness (openness), local stand density (LSD) and topsoil properties

Characteristics	OS-I	OS-II	MS
Sample size	242	256	265
O horizon depth			
Openness	−0.18	−0.28**	−0.25**
LSD	0.33***	0.17	0.41***
A horizon pH			
Openness	0.34***	0.27**	0.28**
LSD	−0.47***	−0.27**	−0.39***
A horizon H concentration			
Openness	−0.34***	−0.27	−0.30**
LSD	0.48***	0.30***	0.37***
AB horizon pH			
Openness	0.26**	0.25**	0.27**
LSD	−0.54***	−0.3***	−0.32**
AB horizon H concentration			
Openness	−0.26**	−0.25	−0.27**
LSD	0.52***	0.27**	0.44***
A horizon moisture			
Openness	0.44***	***0.39	**0.28
LSD	−0.35***	−0.20*	−0.35***
AB horizon moisture			
Openness	0.46***	0.20*	0.29
LSD	−0.52***	−0.12	−0.32**

Note significance at the 0.05, 0.01 and 0.001 level is denoted by *, **, ***, respectively

LSD calculated for old stumps or their remnants in advanced decay (the decay class B) and the AB horizon moisture ($r = -0.21$, $P = 0.02$). Combining live trees and remnants (from decay class B) of fallen trees as independent variables in one model resulted in an increase in the adjusted R^2 from 0.10 to 0.13.

Discussion

Spatial variation in topsoil properties

The spatial variation in the physical, chemical and biological properties of soils is a natural feature attributable to a set of factors that show variation on different spatial scales and are governed by several inter-related processes. Bruckner et al. (1999), in a study of a very dense 40-year-old Norway spruce monoculture (1,400 stems per ha), identified three different scales of spatial variability of N-mineralisation, water content and pH in the ectohumus layer (0–10 cm). First, they found a fine-scale pattern with ranges of <1 m that they attributed to retarded decomposition, poor chemical and structural diversity of litter and

the absence of bioturbatic activity by earthworms. Second, they identified a mesoscale pattern that probably resulted from the influence of regularly spaced tree individuals. Third, they observed unexplained long-range trends that, however, induced much less variation in water content and pH than the fine-scale and mesoscale effects. The largest contribution of small-scale variation (below 5 m) in volumetric water content both in drying and rewetting periods was also reported by Schume et al. (2003) for a 70-year-old beech-spruce forest (988 stems/ha) growing on stagnant cambisol. At the comparable spatial scale, large variability of the soil organic carbon stock was reported also by Liski (1995) in a boreal forest, Schöning et al. (2006) in a beech forest and Spielvogel et al. (2010) in a montane spruce forests.

In general, these conclusions are concordant with the results of our study, which indicate a dominant (65–100%) contribution of the variation in scales <5 m and a much lesser contribution (0–35%) of mesoscale variation. However, contrary to Bruckner et al.'s research (1999), the stands we studied evidenced no periodicity in the spatial pattern of topsoil properties, possibly because of the close-random tree distribution. It seems that the influence of trees might contribute markedly to the variation at a scale which corresponds to the distances between stems and the centres of inter-crown openings, i.e., below 5 m (at larger scales, the spatial correlation in canopy openness disappeared). Nevertheless, groups of more closely growing trees or small gaps which usually appear at random tree patterning also have some partitioning in mesoscale gradient formation.

The spatial dependence tended to be stronger in the multi-layered MS stand and loosely stocked OS-I stand than in the densely stocked OS-II stand, which might indicate some association between forest structures or stem density and spatial topsoil variation. This observation, however, must be treated carefully because our experimental design did not consider replicates of these factors. Likewise, because the major sources of the spatial variation remain unidentified, the differences in variation of soil variables on the intra-stand level are similarly difficult to interpret.

Effect of local stem density on humus layer thickness

On the intra-stand level, the humus layer depth may be influenced by pedogenic memory, micro-topography, litter fall and decomposition rate. Apparently, the three latter factors may be somewhat associated with the spatial distribution of trees. For instance, Hirabuki (1991) found a positive relation between tree litter fall and patchy canopy structure in a mixed forest, while Penne et al. (2010) in a 55-year-old pine stand (650 stems per ha) found that the

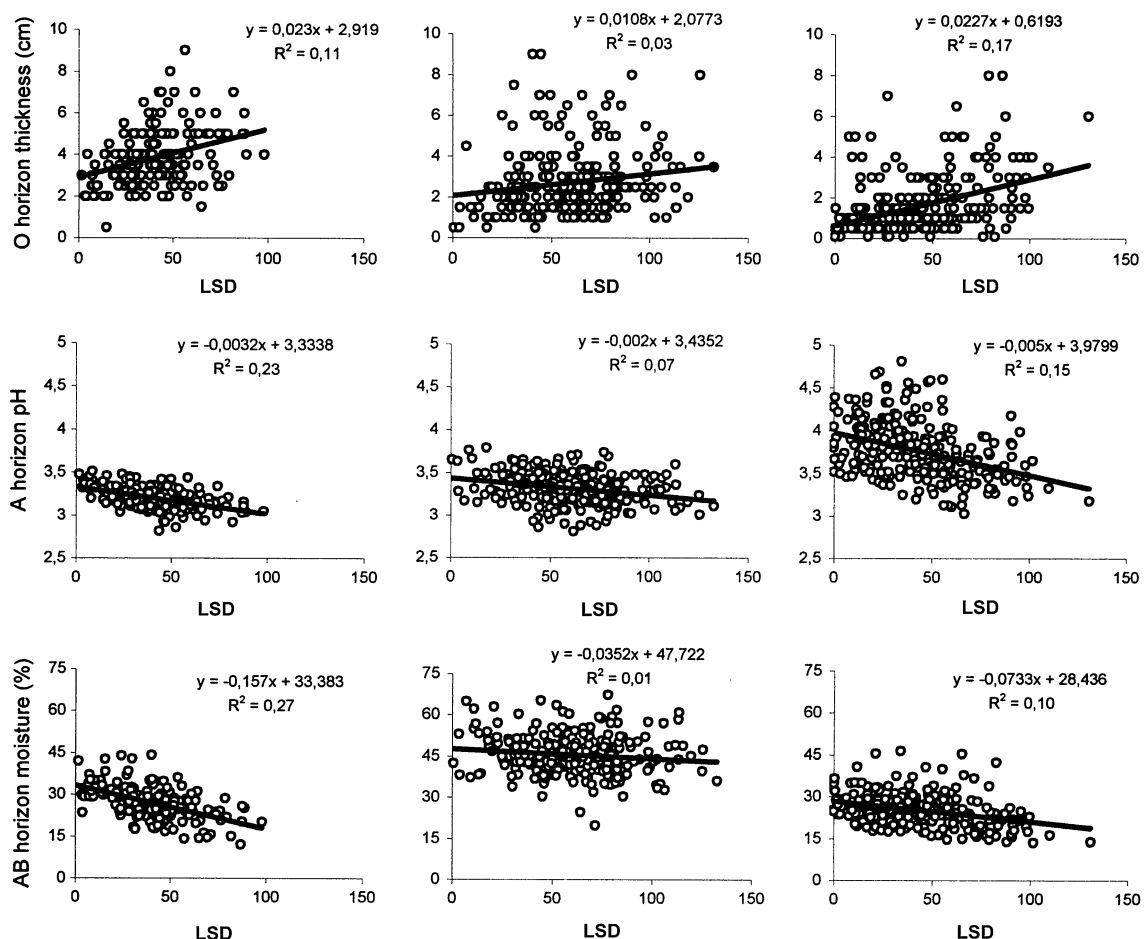


Fig. 6 Relationships between local stand density (LSD) and selected topsoil properties in the O-I, O-II and MS stands (from left to right)

needle litter fall was significantly higher directly under the tree crowns compared with the areas without direct canopy cover. Organic matter accumulation also depends on decomposition rate, which, besides tree species-dependent characteristics like hardness, morphology, lignin/N ratio, foliage longevity, and hydrosoluble component content (e.g., Aber et al. 1990; Harmon et al. 1990; Scott and Binkley 1997), might be also influenced by micro-site characteristics like biological activity and substrate moisture and temperature (Bauhus 1996; Scharenbroch and Bockheim 2007). In addition, reduced pH can negatively influence litter decomposition (Berg 1986) by affecting the abundance of soil animals (saprotrophic micro-organisms), mycorrhiza density and litter chemistry. Thus, distance from the trees, and more general, local stand density, possibly exerts influence on organic matter accumulation.

This relation was confirmed by Liski (1995) who found a thicker F and H layers and higher C density within 1–3 m radius from *Pinus sylvestris* trees. Similarly, Bens et al. (2006) found significantly higher O layer thickness around pine trees in stands with advanced age. Penne et al. (2010)

indicated on a tendency to higher carbon stocks under tree crowns, especially in the F layer, and attributed this relation to variation in needle litter fall. Staelens et al. (2003) concluded that the distribution of leaf and needle litter of isolated trees (different species and age classes) follow negative exponential functions with distance from the trees. However, in some studies carried out in deciduous or mixed forests (Riha et al. 1986; Schöning et al. 2006) or at inclined sites with a pronounced small-scale relief (Spielvogel et al. 2010), no spatial correlation was found between the distance to the nearest tree and the magnitude of the soil organic carbon stock in the forest floor.

Although in all stands studied here, a considerable variation in organic horizon depth was found and a significant positive relation observed between organic horizon depth and local configuration of trees, the contribution of this latter factor to the variation in ectohumus layer was little, only about 3–17%. As exemplified in the MS stand, this relatively low prediction level might not be increased by taking into account the stump locations of trees fallen a few decades ago, probably because of the accelerated

Table 4 Slope coefficients for the regressions between the local stand density (LSD) and soil characteristics

Characteristics	OS-I	OS-II	MS
O horizon depth			
Slope	0.023	0.011	0.023
SE	0.0049	0.0038	0.0031
A horizon pH			
Slope	−0.003	−0.002	−0.005
SE	0.0004	0.0004	0.0007
A horizon H concentration			
Slope	5.2×10^{-6}	2.1×10^{-6}	2.1×10^{-6}
SE	1.1×10^{-6}	4.3×10^{-7}	3.2×10^{-7}
AB horizon pH			
Slope	−0.004	−0.002	−0.005
SE	0.0005	0.0004	0.0009
AB horizon H concentration			
Slope	2.9×10^{-6}	1.1×10^{-6}	8.9×10^{-5}
SE	3.2×10^{-7}	2.7×10^{-7}	8.2×10^{-7}
A horizon moisture			
Slope	−0.31	−0.13	−0.14
SE	0.062	0.041	0.024
AB horizon moisture			
Slope	−0.16	−0.03	−0.07
SE	0.020	0.018	0.013

decomposition of forest floor organic matter after gap creation.

Effect of local stem density on topsoil pH

In our study, most particularly in the loose OS-I and MS stands, tree distribution pattern contributed markedly to the variation in topsoil pH. Depending on the stand and soil horizon, this variable explained 22–29% of the total variation in pH. Although the soil pH increased with depth, the slope coefficients of the regressions between the local stand density and the pH in both mineral horizons were comparable, suggesting that the impact of the trees may be observable up to at least a depth of 15–20 cm. This finding may seem surprising given the claim by many authors that alterations are confined to the uppermost soil horizons (Maciaszek et al. 2000; Ritter et al. 2002; Rothe et al. 2002; Hagen-Thorn et al. 2004). Admittedly, the highest slope coefficient was found in the multi-layered MS stand, so it may be due to the higher age of the largest trees in this stand (140–160 years) and a longer period of uninterrupted impact. However, because we found no evidence for the influence of the neighbourhood of older stumps on topsoil pH, such an impact is probably rapidly overlapped.

Earlier studies have also reported reduced pH in the vicinity of tree stems, especially coniferous species (Zinke

1962; Boettcher and Kalisz 1990; Pallant and Riha 1990). This effect probably has several origins (Augusto et al. 2002): the capacity to intercept atmospheric deposition that is potentially acidic, the acidity of litter, the number of protons released after tree uptake of cations, the higher amounts of acids with lower pK released under some tree species and the modification of soil micro-climate.

Effect of local stem density on topsoil moisture

The topsoil moisture was negatively associated with stand density as expressed by local stand density index and canopy openness, although this effect diminished in lower soil horizons. This influence could result from reduced water input due to interception in the crowns, the buffering of mineral soil from large amounts of summer rainfall by organic layers (Leuschner 2002) or water extraction by tree roots (Schume et al. 2003). In fact, a positive correlation between interception rates and stand density has been documented repeatedly (Raat et al. 2002). For instance, Olszewski (1984) and Kozłowski (2003) found that the highest through fall in conifer and mixed stands occurred under crown edges and the lowest near the stem, with average differences amounting to over 100% of direct precipitation.

Most particularly, the monitoring of topsoil moisture showed that although the lower topsoil moisture in the neighbourhood of the stems was maintained over the whole growing season independently from precipitation, the differences deepened in drying periods. Such increasing variation in topsoil (0–30 cm) water content during drying periods also emerged from Schume et al.'s (2003) extensive data on beech-spruce forest on stagnic cambisol developed from Flysch sediments, although the differences were rather small (CV 0.12 for volumetric water content 20.3% and 0.09 for 33.0, respectively). More specifically, Schume et al. (2003) reported an erratic pattern of water content after high intensity rainfall on dry soil, which they attributed to a macro-pore system usually found in soils with a high clay content capable of randomly distributing water over longer distances. Because the topsoil moisture displays spatiotemporal variation dependent on drying and rewetting history, the predictive value of stand density as determined in our study (in which the best stand-level predictors might explain up to 12–27%) is a very rough approximation.

Other sources of soil variability

The impact of trees might explain only a minor part of the total variation in the topsoil properties analysed. Potential contributory factors to the unexplained variation are pedogenic memory (pits and mounds of snow- and

windthrows, enrichment in organic matter from coarse woody debris), micro-relief and fine-scale variation in mineral soil texture and measurement errors. It might also be expected that, because of small-scale soil erosion and accumulation processes, organic layer thickness would be smaller on crests but higher in depressions or in the presence of hindrances like coarse woody debris, protruding roots or stony materials (Mueller and Pierce 2003; Spielvogel et al. 2010). Increased organic carbon stocks in such patches would affect other soil properties, including acidity and water storage capacity. However, although, on slopes tree stems and stumps may catch flowing-down organic matter and thus likely to increase variation in slope direction, in the MS stand growing on an inclined site, we found no evidence of directional differences in the O horizon thickness. Possibly such differences may admittedly occur at smaller spatial scales than the grid spacing used in our research. However, in the MS stand, small-scale variation in the topsoil pH tended to be lower on the slope line than in the perpendicular direction. This effect may be attributable to a dominant down-slope direction of surface flow and percolation.

Nor can we substantiate any stronger relation between stump location and topsoil pH. Surprisingly, association of that variable with the AB horizon moisture was also negative, although, in the neighbourhood of decaying stumps, increased amounts of accumulated organic carbon, mineral-bound dissolved organic carbon and concomitant lower pH and higher water content might be expected (Auerswald and Weigand 1996; Spielvogel et al. 2010). Such effects, however, may only be discernible at small distances between the sampling point and woody debris or coarse decomposing roots. Additionally, the lower moisture of the AB horizon in the neighbourhood of the stumps could result from a denser canopy in such patches, which at present consist of the crowns of trees from a lower stand layer that has been intentionally released by cutting. Another study has provided evidence of a positive spatial dependence between the stumps and clumps of smaller trees, including those in the MS stand (Paluch 2006).

Conclusions

Unlike most prior research, which compares closed stands with large gaps or clear-cuts, this study investigated three stands of different stand density and vertical structure but a random distribution pattern of trees. In all stands, irrespective of density and vertical structure, local stand density correlated positively with ectohumus layer thickness and negatively with upper soil pH and moisture. The variation in local stand density provided maximal explanation up to 17% of the total variation in organic horizon

thickness, up to 22–29% in topsoil pH (depending on the horizon) and up to 19–27% in topsoil moisture, although on the single-stand level, these amounts differed considerably. Because this present research used a simple yet probably sub-optimal way of expressing stand density, it remains an open question whether using more sophisticated predictors, e.g., those that take into account non-additive effects, might enhance the predictive power of data on the spatial pattern of trees or local canopy density. Nevertheless, our study does provide an illustration that, even given a rather wide spectrum of stand densities and structures, tree neighbourhood and small-scale variation in canopy density may contribute significantly to topsoil heterogeneity. For silvicultural practice, our results indicate that in *Abies alba* stands under shelterwood or individual selection systems over-dispersion of regeneration density at a scale corresponding with crown widths may be a natural phenomenon attributable to spatial topsoil variation and tree patterning.

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References

- Aber JD, Melillo JM, McLaugherty CA (1990) Predicting long term patterns of mass loss, nitrogen dynamics and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. *Can J Bot* 68:2201–2208
- Auerswald K, Weigand S (1996) Ecological impact of dead-wood hedges: release of dissolved phosphorus and organic matter into runoff. *Ecol Eng* 7:183–189
- Augusto L, Ranger J, Binkley D, Rothe A (2002) Impact of several common tree species of European temperate forests on soil fertility. *Ann For Sci* 59:233–253
- Bartsch N, Bauhus J, Vor T (2002) Effects of group selection and liming on nutrient cycling in European beech forest on acidic soils. In: Dohrenbush A, Bartsch N (eds) *Forest development. Succession, environmental stress and forest management. Case studies*. Springer, Berlin, pp 109–166
- Bauhus J (1996) C and N mineralization in an acid forest soil along a gap-stand gradient. *Soil Biol Biochem* 28:923–932
- Beier C, Hansen K, Gundersen P (1993) Spatial variability of through fall fluxes in a spruce forest. *Environ Poll* 81:257–267
- Bens O, Buczko U, Sieber S, Hüttl RF (2006) Spatial variability of O layer thickness and humus forms under different pine beech-forest transformation stages in NE Germany. *J Plant Nutr Soil Sci* 169:5–15

- Berg B (1986) The influence of experimental acidification on nutrient release and decomposition rates of needle and root litter in the forest floor. *For Ecol Manag* 15:195–213
- Boettcher SE, Kalisz PJ (1990) Single-trees influence on soil properties in the mountains of eastern Kentucky. *Ecology* 71:1365–1372
- Bouten W, Heimovaara TJ, Tiktak W (1992) Spatial patterns of through fall and soil water dynamics in a Douglas fir stand. *Water Resour Res* 28:3227–3233
- Bruchwald A, Rymer-Dudzińska T, Dudek A, Michalak K, Wróblewski L, Zasada M, Tomusiak R (2002) Tablice miąższości grubizny drzewa oparte na średnicy pniaka. *Sylvan* 146(1):5–16
- Bruckner A, Kandeke E, Kampichler C (1999) Plot-scale spatial patterns of soil water content, pH, substrate-induced respiration and N mineralization in a temperate coniferous forest. *Geoderma* 93:207–223
- Canham CHD, Finzi AC, Pacala SW, Burbank DH (1994) Causes and consequences of resource heterogeneity in forests: inter-specific variation in light transmission by canopy trees. *Can J For Res* 24:337–349
- Collins BS, Battaglia LL (2002) Microenvironmental heterogeneity and *Quercus michauxii* regeneration in experimental gaps. *For Ecol Manag* 155:279–290
- Cressie NAC (1993) *Statistics for spatial data*. Wiley, New York
- Diggle PJ (1983) *Statistical analysis of spatial point patterns*. Academic Press, London
- Efron B, Tibshirani RJ (1993) *An introduction to the bootstrap*. Chapman and Hall/CRC, New York
- Ehrenfeld JG, Han X, Parsons WFJ, Zhu W (1997) On the nature of environmental gradients: TEMPORAL and spatial variability of soils and vegetation in the New Jersey pinelands. *J Ecol* 85:785–798
- Farley RA, Fitter AH (1999) Temporal and spatial variation in soil resources in a deciduous woodland. *J Ecol* 87:688–696
- Frankland JC (1998) Fungal succession: unravelling the unpredictable. *Mycol Res* 102:1–15
- Hagen-Thorn A, Callesen I, Armolaitis K, Nihlgård B (2004) The impact of six European tree species on the chemistry of mineral topsoil in forest plantations on former agricultural land. *For Ecol Manag* 195:373–384
- Harmon ME, Baker GA, Spycher G, Greene SE (1990) Leaf-litter decomposition in the picea/tuga forests of olympic national park, Washington, USA. *For Ecol Manag* 31:55–66
- Hess M (1965) Piętra klimatyczne w polskich Karpatach Zachodnich. *Zeszyty naukowe UJ*, 115. *Prace Geogr* 11:1–258
- Hirabuki Y (1991) Heterogenous dispersal of tree litterfall corresponding with patchy canopy structure in a temperate mixed forest. *Vegetation* 94:69–79
- IUSS Working Group (WRB) (2007) World reference base for soil resources 2006, first update 2007. World soil resources reports 103. FAO, Rome
- Keim RF, Skaugset AE, Weiler M (2005) Temporal persistence of spatial patterns in through fall. *J Hydrol* 314:263–274
- Kern K (1966) Wachstum und Umweltfaktoren im Schlag- und Plenterwald. *Schriftenreihe d Forstl Abt d Univ Freiburg*, vol 5, p 232
- Koch AS, Matzner E (1993) Heterogeneity of soil and soil solution chemistry under Norway spruce (*Picea abies* Karst.) and European beech (*Fagus sylvatica* L.) as influenced by distance from the stem basis. *Plant Soil* 151:227–237
- Kozłowski R (2003) Przestrzenne zróżnicowanie opadu podokapowego w drzewostanie jodłowo-bukowym w centralnej części Gór Świętokrzyskich. *Kieleckie Towarzystwo Naukowe, Regionalny monitoring środowiska przyrodniczego* 4:99–106
- Leuschner C (2002) Forest succession and water resources: soil hydrology and ecosystem water turnover in early, mid and late stages of a 300-yr-long chronosequence on sandy soil. In: Dohrenbush A, Bartsch N (eds) *Forest development. Succession, environmental stress and forest management. Case studies*. Springer, Berlin, pp 1–68
- Liski J (1995) Variation in soil organic carbon and thickness of soil horizons within a boreal forest stand: effect of trees and implications for sampling. *Silva Fennica* 29:255–266
- Maciaszek W, Gruba P, Januszek K, Lasota J, Wanic T, Zwydak M (2000) Degradacja i regradacja gleb pod wpływem gospodarki leśnej na terenie Żywiecczyzny. *Akademia Rolnicza im. H. Kołłątaja w Krakowie, Kraków*
- Matuszkiewicz J (2001) *Zespoły leśne Polski*. Wydawnictwo Naukowe PWN, Warszawa
- Mazur M (1989) Structure and dynamics of silver fir (*Abies alba* Mill.) population in fores communities of the Świętokrzyski national park. *Acta Soc Bot Pol* 58:385–407
- Mladenoff DJ (1987) Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* 68:1171–1180
- Morris DM, Gordon AG, Gordon AM (2003) Patterns of canopy interception and throughfall along a topographic sequence for black spruce dominated forest ecosystems in northwestern Ontario. *Can J For Res* 33:1046–1060
- Mueller TG, Pierce FJ (2003) Soil carbon maps: enhancing spatial estimates with simple terrain attributes at multiple scales. *Soil Sci Soc Am J* 67:258–267
- Neary AJ, Gizyn WI (1994) Throughfall and stemflow chemistry under deciduous and coniferous forest canopies in south-central Ontario. *Can J For Res* 24:1084–1100
- Niewinna M (2010) Wielkość opadu i tempo rozkładu ściółki w wybranych drzewostanach Bieszczadów. *Roczniki Bieszczadzkie* 18:59–73
- Oliveira-Carvalho K, Nepstad DC (1996) Deep soil heterogeneity and fine root distribution in forests and pastures of eastern Amazonia. *Plant Soil* 182:279–285
- Olszewski JL (1984) Intercepcja i jej wpływ na wysokość opadów atmosferycznych docierających do powierzchni gruntu w lesie. *Zeszyty Postępów Nauk Rolniczych* 288:245–270
- Otto HJ (1994) *Waldökologie*. Verlag Eugen Ulmer, Stuttgart
- Pallant E, Riha SJ (1990) Surface soil acidification under red pine and Norway spruce. *Soil Sci Soc Am J* 54:1124–1130
- Paluch J (2005a) Spatial distribution of regeneration in west-carpathian uneven-aged silver fir forests. *Eur J For Res* 124:47–54
- Paluch J (2005b) The influence of the spatial pattern of trees on forest floor vegetation and silver fir (*Abies alba* Mill.) regeneration in uneven-aged aged forests. *For Ecol Manag* 205:283–298
- Paluch J (2006) Factors controlling the regeneration process in unevenly aged silver fir forests: inferences from the spatial pattern of trees. *J For Sci* 52(11):510–519
- Paluch J (2008) Czynniki kształtujące przestrzenną zmienność procesów odnowieniowych w drzewostanach jodłowych. *Sprawozdanie z grantu nr 2 P06L 017 28*, Kraków
- Parker GG (1997) Canopy structure and light environment of an old-growth Douglas-fir/western hemlock forest. *Northwest Sci* 71:261–270
- Parsons WFJ, Knight DH, Miller SL (1994a) Root gap dynamics and forest disturbance theory in lodgepole pine forests: nitrogen transformations in gaps of different size. *Ecol Appl* 4:354–362
- Parsons WFJ, Knight DH, Miller SL (1994b) Root gap dynamics in lodgepole pine forests: ectomycorrhizal and nonmycorrhizal fine root activity after experimental gap formation. *Can J For Res* 24:1531–1538
- Partel M, Wilson SD (2002) Root dynamics and spatial pattern in prairie and forest. *Ecology* 83:1199–1203

- Penne C, Ahrends B, Deurer M, Böttcher J (2010) The impact of the canopy structure on the spatial variability in forest floor carbon stocks. *Geoderma* 158:282–297
- Plussi P, Sanesi G, Sulli M (1971) Osservazioni sull'umidità del suolo nella foresta di Vallombrosa. *Annali Istituto Sperimentale per la Selvicoltura* 2:299–320
- Raat KJ, Draaijers GPJ, Schaap MG, Tietema A, Verstraten JM (2002) Spatial variability of through-fall water and chemistry of forest floor water content in a Douglas fir forest stand. *Hydrol Earth Syst Sci* 6:363–374
- Riha SJ, James BR, Senesac GP, Pallant E (1986) Spatial variability of soil pH and organic matter in forest plantations. *Soil Sci Soc Am J* 50:1347–1352
- Ritter E, Vesterdal L, Grundersen P (2002) Changes in soil properties after afforestation of former intensively managed soils with oak and Norway spruce. *Plant Soil* 249:319–330
- Rothe A, Kreutzer K, Küchenhoff H (2002) Influence of tree species composition on soil and soil solution properties in two mixed spruce-beech stands with contrasting history in southern Germany. *Plant Soil* 240:47–56
- Ruark GA, Zarnoch SJ (1992) Soil carbon, nitrogen and fine root biomass sampling in a pine stand. *Soil Sci Soc Am J* 56:1945–1950
- Sanesi G, Sulli M (1973) Variazioni dell'umidità e temperatura del suolo in zone diverse all'interno un'abetina. *Annali Istituto Sperimentale per la Selvicoltura* 4:167–179
- Scharenbroch BC, Bockheim JG (2007) Impacts of forest gaps on soil properties and processes in old growth northern hardwood-hemlock forests. *Plant Soil* 294:219–233
- Schöning I, Totsche KU, Kögel-Knabner I (2006) Small scale spatial variability of organic carbon stocks in litter and solum of a forested luvisol. *Geoderma* 136:631–642
- Schume H, Jost G, Katzensteiner K (2003) Spatio-temporal analysis of the soil water content in a mixed Norway spruce (*Picea abies* (L.) Karst.): European beech (*Fagus sylvatica* L.) stand. *Geoderma* 112:273–287
- Scott NA, Binkley D (1997) Foliage litter quality and annual net mineralisation: comparison across north American forest sites. *Oecologia* 111:151–159
- Shelton MG (1995) Effects of the amount and composition of the forest floor on emergence and early establishment of loblolly pine seedlings. *Can J For Res* 25:480–486
- Simard SW, Perry DA, Smith JE, Molina R (1997) Effects of soil trenching on occurrence of ectomycorrhizas on *Pseudotsuga menziesii* seedlings grown in mature forests of *Betula papyrifera* and *Pseudotsuga menziesii*. *New Phytol* 136:327–340
- Simard MJ, Bergeron Y, Sirois L (1998) Conifer seedling recruitment in a southwestern Canadian boreal forests: the importance of substrate. *J Veg Sci* 9:575–582
- Spielvogel S, Prietzel J, Auerswald K, Kögel-Knabner I (2010) Site-specific spatial patterns of soil organic carbon stocks in different landscape units of a high-elevation forest including a site with forest dieback. *Geoderma* 152:218–230
- Staelens J, Nachtergale L, Luyssaert S, Lust N (2003) A model of wind-influenced leaf litterfall in a mixed hardwood forest. *Can J For Res* 33:201–209
- Staelens J, De Schrijver A, Verheyen K, Verhoest NEC (2006) Spatial variability and temporal stability of throughfall water under a dominant beech (*Fagus sylvatica* L.) tree in relation to canopy cover. *J Hydrol* 330:651–662
- Tingey DT, Phillips DL, Johnson MG, Rygielwicz PT, Beedlow PA, Hogsett WE (2005) Estimates of Douglas-fir fine root production and mortality from minirhizotrons. *For Ecol Manag* 204:359–370
- Totsche KU, Rennert T, Gerzabek MH, Kögel-Knabner I, Smalla K, Spiteller M, Vogel HJ (2010) Biogeochemical interfaces in soil: the interdisciplinary challenge for soil science. *J Plant Nutr Soil Sci* 173:88–99
- Weintraub MN, Scott-Denton LE, Schmidt SK, Monson RK (2007) The effects of tree rhizodeposition on soil exoenzyme activity, dissolved organic carbon, and nutrient availability in a subalpine forest ecosystem. *Oecologia* 154:327–338
- Whelan MJ, Sanger LJ, Baker M, Anderson JM (1998) Spatial patterns of throughfall and mineral ion deposition in a lowland Norway spruce (*Picea abies*) plantation at the plot scale. *Atmos Environ* 20:3493–3501
- Yang J, Hu Y, Bu R (2006) Microscale spatial variability of redox potential in surface soil. *Soil Sci* 171:747–753
- Zhang Q, Zak JC (1995) Effects of gap size on litter decomposition and microbial activity in a subtropical forest. *Ecology* 76:2196–2204
- Zinke PJ (1962) The pattern of influence of individual forest trees on soil properties. *Ecology* 43:130–133