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Properties of Top Soil and the Relationship between Soil and Trees in a Boreal Scots Pine Stand

Timo J. Hokkanen, Erkki Järvinen and Timo Kuuluvainen

Hokkanen, T.J., Järvinen, E. & Kuuluvainen, T. 1995. Properties of top soil and the relationship between soil and trees in a boreal Scots pine stand. Silva Fennica 29(3): 189–203.

A one hectare plot in a Scots pine (*Pinus sylvestris*) forest was systematically sampled for surface soil characteristics: humus layer thickness, soil carbon and nitrogen content, pH, electrical conductivity and respiration were determined from 106 samples. The effects of large trees on the plot were mapped and their joint influences at the locations of soil sampling were described as the influence potential, derived from the ecological field theory, and were calculated based on the locations and dimensions of trees. The range of variation of soil characteristics was from three to sevenfold; no spatial autocorrelation was detected. The calculated influence potential of trees, as determined by their size and spatial distribution, was related to the spatial variation of top soil properties. Top soil properties were also related to thickness of the humus layer but they were poorly correlated with underlying mineral soil characteristics. Humus layer thickness, with the calculated influence potential of trees, may provide a means to predict top soil characteristics in specific microenvironments in the forest floor.

Keywords *Pinus sylvestris*, organic matter, carbon, nitrogen, respiration, ecological field theory, spatial patterns.

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Main terms and abbreviations

IPOT	influence potential; the estimated relative influence of all adjacent canopy trees in a given location in the understorey as defined in Kuuluvainen and Pukkala (1988)
C_{tot}	total carbon in top soil (%)
N_{tot}	total nitrogen in top soil (%)
OM	refers to organic matter; the amount of OM is expressed as per cent in top soil ($g\ g^{-1}$, estimated by loss on ignition)
Humus	is the amorphous, decomposed form of organic matter
Top soil	refers to the top 5 cm layer of soil beginning from the amorphous humus layer (litter and live plants are excluded); if the humus layer is less than 50 mm, also some mineral soil is included in the top soil

1 Introduction

The spatial variation and heterogeneity of soil properties in forest ecosystems has recently received considerable attention. For example, small scale variation of the forest floor has been studied both in hardwood forests (e.g., Boerner and Koslowsky 1989, Bringmark 1989, Beniamino et al. 1991), and in coniferous forests (e.g. Riha et al. 1986a, b, Nykvist and Skyllberg 1989 and Ilvesniemi 1991). The spatial heterogeneity of the forest soil has a profound influence on many essential ecosystem characteristics, such as the regeneration of plant species (Bell et al. 1991, Bell and Lechowicz 1991, Lechowicz and Bell 1991) and the distribution and species diversity of plants (Beatty 1984).

The spatial influence of trees on soil characteristics is apparently one of the main causes of soil heterogeneity in forests (e.g. Björkman and Lundeberg 1971, Walter and Breckle 1989). Especially mature, isolated forest trees appear to exert a strong effect on the soil (e.g. Zinke 1962, Boettcher and Kalisz 1990, Escudero et al. 1991). Trees also influence soil through above and belowground litter production, varying quality and distribution of litter, shading, interception etc. (e.g. Facelli and Pickett 1991, Hirabuki 1991).

One approach to model these spatial influences of trees is proposed in the ecological field theory (Wu et al. 1985, Walker et al. 1989). In this approach an individual plant is considered to be surrounded by a circular field of influence – the zone of influence – which depends on plant size. The field of influence of a tree is described in terms of the combined effect of crown, stem and root influences upon the spatial distribution of resources, i.e., water, nutrients and light (Wu et al. 1985). The joint effects of all trees at a point estimate the amount of resources available for, e.g., a seedling.

The ecological field theory was initially used to model competitive interferences among plants but we believe that this approach can be valuable also in describing the effects of trees on soil because trees influence strongly the accumulation, turnover and quality of forest floor organic matter (OM) (e.g., Escudero et al. 1991). OM thus provides a dynamic link between trees and soil. To describe the properties of OM some key characteristics were chosen for this study keeping in mind that chemical and microbiological properties of the surface soil play an essential role in natural establishment and growth of Scots Pine (*Pinus sylvestris* L.) seedlings. Respiration rate and C/N-ratio of OM describe the process of forest floor decomposition (e.g., Swift et al. 1978). Soil solution pH and electrical conductivity are important criteria for predicting the capability of soils to support microbial reactions (Paul and Clark 1989); these characteristics also give an estimate of the ion supply in the soil (see Rhoades 1982).

Our objectives in this study are (i) to describe the within-site variation of top soil properties, (ii) to study if top soil characteristics can be related to the influence of trees by applying the theory of ecological fields, and (iii) to study if the influence of mineral soil properties can be detected in humus layer depth and characteristics. The study is part of a research project aiming at quantifying the patterns of ground vegetation, seedling establishment and seedling growth in terms of consumption, accumulation and release of resources in a spatially heterogeneous soil-vegetation system of a Scots pine stand.

2 Material and Methods

2.1 Site Description and Sampling

Soil samples were collected in 1989 from a sander-delta situated in a wide, glaciofluvial, marginal-interlobate complex of Jaamankangas (Kontiolahti, Finland; 62°40' N, 29°45'E; 105 m a.s.l.). The one hectare study area was in a patchy Scots pine forest. Most of the large trees were approximately 70 years old, but a small portion (gap) of the plot consisted of about 20 year old trees. The ground vegetation was fairly uniform, and consisted mainly of dwarf shrubs (*Calluna vulgaris* Hull, *Vaccinium myrtillus* L., *V. vitis-idaea* L.), mosses (*Pleurozium schreberi* Mitt., *Dicranum* sp.) and lichens (*Cladonia* sp.).

The trees were mapped (location) and measured (height, diameter) within a plot of 180 m × 150 m, i.e., 2.7 ha (including a buffer zone for the central 100 × 100 m area). Trees from the whole area were considered when calculating tree influences in the central area. A more detailed description of the forest stand is provided in Kuuluvainen et al. (1993).

Composite soil samples were taken systematically at 20 m intervals along lines spaced five metres apart. In case a tree or other large obstacle occurred in a designated soil sample location, soil sampling was moved to the next possible location. One composite soil sample consisted of six cores each of 25 cm^2 cross-sectional area and taken to the depth of 5 cm from the humus layer surface. Each composite sample was designed to represent a one m^2 sample plot used in the vegetation mapping. The samples were taken by depth because, first, the humus layer in some samples in the area was very thin and did not allow sampling by horizons (there was too little humus for the various analyses). Secondly, the aim to study the growth of seedlings (Kuuluvainen et al. 1993) motivated us to take samples by depth, since the effective environment of a seedling's root system consists of various amounts of humus and mineral soil depending on the characteristics of a specific microsite.

Humus layer thickness was measured from each soil core. Litter and living plants were removed in the field. Soil cores were put into polythene bags and transported to a cold room (4 °C) within a few hours. The total number of samples was 106.

The samples were homogenised and sieved (2 mm mesh) and the visible root fragments were removed in the laboratory. Part of the sieved soil was dried for pH, electrical conductivity, total nitrogen and carbon determinations (55 °C), and for loss on ignition and water content measurements (105 °C). Calculations (C, N) were done on the 105 °C dry weight basis. The rest of the soil was kept at field moisture level in plastic bags for eight weeks in a cold room (4 °C) for decomposition studies.

2.2 Analyses

Soil acidity was determined (duplicate samples) in 0.01 M $CaCl_2$ (1:2.5 soil:liquid) after one hour of shaking in a rotary shaker (30 rpm)(see e.g. Conyers and Davey 1988). Soil solution *electrical conductivity* was measured (duplicate samples) from an aqueous solution (1:2.5 soil:liquid) after one hour of shaking in a rotary shaker (30 rpm) with a Radiometer cell. *Soil organic matter* was determined by loss on ignition (550 °C, 12 hrs; duplicate samples) from dried and ground soil samples. *Total nitrogen* was determined in duplicate by Kjeldahl-distillation (Page et al. 1983). *Total carbon* was determined in duplicate with a Carlo-Erba Elemental Analyser Mod 1106 (Carlo-Erba Strumentazioni, Milan, Italy) from ground samples.

CO_2 evolution: Sieved soil samples were moistened to approximately 60 % of the water holding capacity (WHC) and preincubated in 15 °C for one week to equilibrate the moisture and respiration rate. To moisten the samples, WHC (ml g^{-1} d.wt) was first determined from a series of extra samples containing a varying mixture of organic matter (from 5 to 60 %) and mineral soil. A curve of about 60 % WHC was produced. The amount of water needed to moisten the samples was calculated by subtracting the initial amount of water (ml g^{-1} d.wt) from the approximated 60 % WHC (ml g^{-1} d.wt, derived from the experimental curve according to the OM content of the sample). After the preincubation, subsamples of 3–4 g (n = 4 per sample) were put into 60 ml measuring bottles, which were left open to equil-

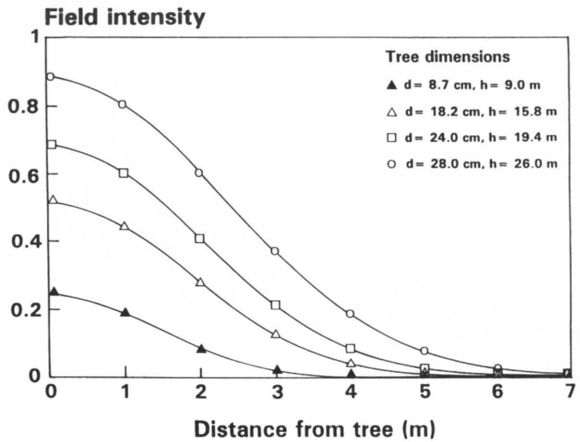

Fig. 1. The effect of individual trees of different size on influence potential in a tree's vicinity, according to Equation 1.

ibrate for one hour in 15 °C. The bottles were then closed with septum-stoppers and incubated at 15 °C. Soil respiration was measured from 1.0 ml serial gas samples withdrawn from the bottles with a syringe (see e.g. Mikola and Komppula 1981). CO_2 concentration in the headspace air was determined with an infrared gas analyser at intervals of 24 hours. Soil respiration was calculated per dry weight of the soil (105 °C) and per soil organic matter.

2.3 Mineral Soil Properties

Mineral soil (10–15 cm deep layer) from the same area has been studied by Järvinen et al. (1993). In the present study we use some variables from the mineral soil data of Järvinen et al. (1993) to examine the relationships between top soil and mineral soil properties. The mineral soil variables used here are: mean particle size, proportions of fine sand and coarse sand, degree of sorting, specific surface area of mineral soil fine grain fractions, loss on ignition, Mg_{tot}, Ca_{tot}, and K_{tot}.

2.4 Calculation of Tree Influences

It was assumed *a priori* that many influences of large trees are approximately symmetrically distributed and distance dependant so that the influence decreases with the distance from the tree (Fig. 1). The concept of influence potential (IPOT) is used to refer to the relative influence of all trees in the 2.7 ha plot at a given point of sampling in the inner one hectare plot (Wu et al. 1985). Influence potential ranges from the maximum of 1 (one) near a big tree to the minimum of 0 (zero) at greater distances apart from the trees. The effect of one tree on the influence potential was described with one function (Equation 1). This function was taken from the study of Kuuluvainen and Pukkala (1989), which analysed the effect of Scots pine seed trees on the density on seedlings and understorey vegetation on a similar site with trees of approximately the same age as in the present study. The function is:

$$\phi_i(s) = \phi_i(O)\exp(-b_i s^2) \tag{1}$$

where

$\phi_i(s)$ = influence potential of tree i at distance s (m) from the tree, s = the distance from the tree to the calculation point, $\phi_i(O)$ = the effect of tree i at the point of tree location,

b_i = parameter. Parameters $\phi(O)$ and b depended on tree size as follows: $\phi_i(O) = d / 35$ and

b = $1 / (0.4h)$, where d is breast height diameter (cm) and h is the height (m) of the tree.

The effect of all trees within the plot on influence potential at a given point is computed with the aid of growth potential (GPOT), which is the inverse of influence potential. Growth potential has been used to estimate the amount of growth resources (Wu et al. 1985). Growth potential at each point of sampling (p) is obtained as a product of the influences of all individual trees (n) on the plot:

$$\mathrm{GPOT}_i(p) = \prod_{i=1}^{n}\left[1-\phi_i\left(s_i(p)\right)\right] \tag{2}$$

The influence potential (IPOT) is then defined as:

$$\mathrm{IPOT}_i(p) = 1 - \mathrm{GPOT}_i(p) \tag{3}$$

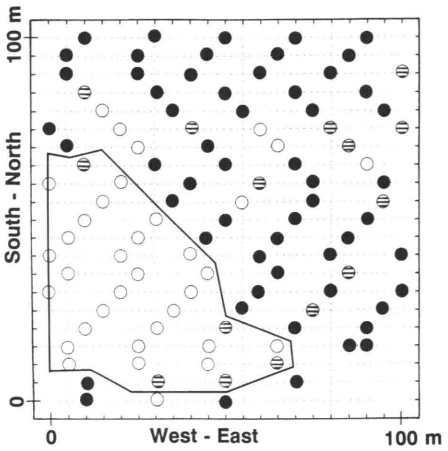

Fig. 2. The distribution of tree influence potential (IPOT) classes in the studied one hectare area in Jaamankangas. The area separated by the thick line roughly represents the younger part of the stand. Open circle: IPOT = 0.00–0.40; Hatched circle: IPOT = 0.40–0.59; Black dot: IPOT = 0.60–1.00.

2.5 Statistical Analyses

Analysis of spatial autocorrelation was carried out using semivariogram analysis which is a basic tool in geostatistics (e.g. Burrough 1983, Legendre and Fortin 1989, Nielsen and Alemi 1989). The semivariogram is useful in detecting and quantifying spatial autocorrelation in spatially explicit sample data (e.g. Riha et al. 1986b, Robertson et al. 1988). We used the computer programs presented by Robertson (1987) to calculate semivariances for sample points ranging from 5 to 50 m apart. Log-normally distributed variables were transformed to normalise the distribution.

The influence of trees on soil properties was tested by dividing the sample locations into three arbitrary classes according to the calculated influence potential of trees: IPOT = 0.0–0.4, low or no influence; IPOT = 0.4–0.6, intermediate influence; IPOT 0.6–1.0 = high influence of trees (Fig. 2). The differences between classes were tested with analysis of variance and the means were compared pairwise with the method of least significant difference (LSD) at 95 % level of probability. The amount of organic matter was used as a covariate when testing C_{tot} (of OM), C/N, electrical conductivity and pH.

Factor analysis was used to determine and group the variables in the top and mineral soil that are most closely associated with each other. Regression was used to derive a model to explain the variation in soil respiration.

3 Results

3.1 Variability of Soil Characteristics

The studied Scots pine stand in Jaamankangas included a great deal of variation in the top soil (0–5 cm) properties (Table 1). Thickness of the humus layer varied from 1 mm to 47 mm with the coefficient of variation of 32.3 %. The other measured top soil properties were strongly affected by the variation in the thickness of the humus layer. The range of variation was from three to sevenfold. Nitrogen concentration of organic matter (OM) varied from 0.57 to 1.81 %. The

Table 1. Top soil (0–5 cm) properties and their ranges of variation in Jaamankangas study area (n = 106).

	Mean	sd [a)]	Min	Max	CV-% [b)]
Respiration (μg CO_2-C g^{-1}(OM) h^{-1})	14.22	3.55	6.59	23.14	25.0
Humus layer thickness (mm)	25.3	7.60	1.0	47.0	32.3
Loss on ignition (%)	13.78	5.54	6.70	35.80	40.2
N_{tot} (%)	0.18	0.06	0.07	0.38	31.7
N (% of OM)	1.38	0.20	0.57	1.81	14.5
C_{tot} (%)	7.05	2.23	3.42	15.07	31.6
C (% of OM)	54.10	3.94	45.36	64.10	7.3
C/N	41.6	6.2	15.7	66.7	14.9
Electrical conductivity (mS m^{-1})	9.2	2.5	3.7	18.5	27.2
pH ($CaCl_2$)	3.38	0.24	2.77	3.93	7.1

[a)] sd = standard deviation
[b)] CV-% = ((sd / mean) · 100)

coefficient of variation in the variables ranged from 7.3 % in carbon concentration of OM to 40.2 % in humus layer thickness (Table 1). The distribution of humus layer depth in the sample points over the area is illustrated in Fig. 3.

3.2 Spatial Variation of Soil Properties

The semivariogram analysis was used to examine possible spatial autocorrelation in the measured soil properties. No clear spatial dependence within distances from 5 to 50 m was detected in the examined variables. However, in some variables such as humus thickness and related loss on ignition, there was a slight general increase with increasing lag-distance as displayed by the semivariogram in Fig. 4. This suggests that points closer to each other are slightly more similar than points further away. The failure to detect significant spatial autocorrelation in the analysis may be largely due to the short-scale variability which was not detected by the applied sampling scheme. In general, the results show remarkable spatial variation in thickness of the humus layer and the associated top soil properties.

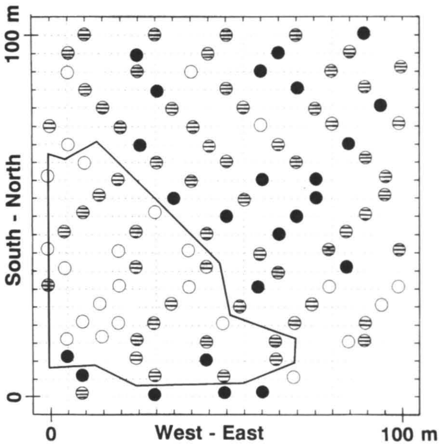

Fig. 3. Spatial distribution of Jaamankangas humus layer thickness classified into three classes: Open circle = humus < 20 mm; Hatched circle = humus 20–30 mm; Black dot = humus > 30 mm (n = 106).

3.3 Tree Influence Classes

The sampling locations belonging to the low-IPOT class, indicating low influence of trees, had a significantly lower amount of organic matter in the top soil than sampling points in the high-IPOT class. This can be seen in humus layer thickness and thus also in the amount of OM (Table 2). Total carbon was significantly lower in the low-IPOT class, but nitrogen concentration per organic matter was higher. There was no statistically significant difference in organic matter carbon concentration between the IPOT classes. Electrical conductivity was about 20 % higher near the trees (high-IPOT class), but no difference was seen in pH (Table 2). In general, differences between the IPOT classes were quite small.

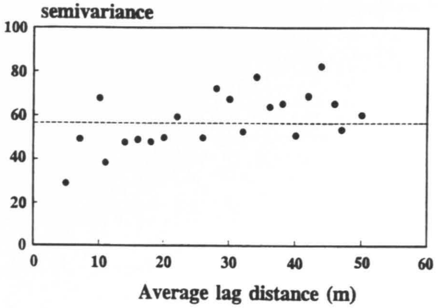

Fig 4. Omnidirectional semivariogram of humus layer thickness within Jaamankangas plot. The dashed line shows general variance of the data.

3.4 Grouping Analysis of Top Soil Properties

The factor analysis solution represented the data fairly well and about 84 % of the total variance could be explained with the extraction of two factors (Table 3). Most of the variables were tightly intercorrelated and situated in factor 1, which explained 54.7 % of the variance. Factor 1 included the variables that are closely coupled with the total amount of organic matter: loss on ignition, total C, pH and electrical conductivity had a factor loading of at least 0.75. The first factor can be interpreted as "the amount of top soil organic matter".

Correlation analysis (table not presented) confirmed that all intercorrelations between the main variables in the first factor (factor loading > 0.56) were high (r > 0.68), and significant (p < 0.001 for every pair of variables).

Factor 2 accounted for 29.2 per cent of the variance. This factor can be explained as "the humus quality factor", because nitrogen concentration of OM and C/N ratio had a high factor loading (Table 3). Correlations between variables in factor 2 were weaker than those between variables ranked high in factor 1 (table not pre-

Table 2. The mean values of the top soil (0–5 cm) properties in the calculated influence field classes (IPOT) of the trees. The tree influence classes are: little or no influence = IPOT 0.00–0.39 (n = 36); intermediate influence = IPOT 0.40–0.59 (n = 15); high influence of trees = IPOT 0.60–1.00 (n = 56). The values followed by the same letter do not differ at the 95 % probability level (LSD-test).

	Tree influence class		
	Little influence	Inter-mediate	High influence
Respiration (μg CO_2-C g^{-1}(OM) h^{-1})	13.37a	14.90a	13.91a
Humus layer thickness (mm)	21.4a	26.8b	27.2b
Loss on ignition (%)	11.7a	15.5b	15.0b
N_{tot} (%)	0.16a	0.21b	0.19b
N (% of OM)	1.43b	1.35ab	1.30a
C_{tot} (%)	6.29a	8.35b	7.87b
C (% of OM)	53.48a	53.94a	52.08a
C/N	38.03a	40.55a	41.61a
Electrical conductivity (mS m^{-1})	8.1a	9.6ab	10.2b
pH ($CaCl_2$)	3.44a	3.32a	3.36a

Table 3. Factor loadings matrix of top soil (0–5 cm) properties in Jaamankangas (nfactor = 2, rotation = varimax, n = 106).

	Factor 1	Factor 2
Electrical conductivity	**0.90**	0.06
pH ($CaCl_2$)	**–0.89**	0.01
Loss on ignition	**0.78**	0.43
Humus layer thickness	**0.57**	0.09
N (% of OM)	–0.15	**0.93**
C/N	0.23	**0.91**
Respiration (per OM)	0.19	–0.43
C (% of OM)	0.30	–0.11
Percentage of total variance explained	54.7	29.2

sented), but several correlations were statistically significant, e.g., $r = 0.749$, $p < 0.001$) between N (% OM) and C (% OM).

3.5 Grouping Analysis of Select Top Soil and Mineral Soil Properties

A factor analysis solution with three factors extracted (including both top and mineral soil properties) explained only 61.5 % of the variation in the data (Table 4). Soil properties were divided roughly into factor 1, representing top soil, and factor 2, representing mineral soil. The only mineral soil property to attain a noteworthy factor loading in factor 1 was total magnesium (factor loading –0.312). A negative correlation was observed between Mg_{tot} and respiration ($r = -0.410$; $p < 0.01$).

Factor 3 contained properties from both top and mineral soil layers. This factor could be interpreted as "the interaction factor". This factor explained only 15.3 % of the variance and we accordingly conclude that the interactions between the two soil layers are weak (Table 4). In factor 3 the greatest factor loading in absolute terms was found for coarse sand (0.746) and for respiration per organic matter (–0.550). A weak, barely significant negative correlation was observed between coarse sand and respiration per OM ($r = -0.236$; $p < 0.05$).

Table 4. Factor loadings matrix of select top soil and mineral soil properties from Jaamankangas (nfac = 3, rotation = varimax, n = 106).

	Factor 1	Factor 2	Factor 3
Loss on ignition	**0.920**	–0.081	0.104
Electrical conductivity	**0.894**	–0.001	–0.058
pH ($CaCl_2$)	**–0.815**	–0.023	0.065
N (% of OM)	**–0.618**	–0.140	–0.379
Mean particle size [1)]	0.091	**0.784**	–0.240
K_{tot} [1)]	–0.163	**0.722**	0.431
Loss on ignition [1)] (mineral soil)	0.021	**0.711**	0.077
Fine sand [1)]	–0.064	**–0.710**	**–0.533**
Degree of sorting [1)]	0.189	**0.649**	–0.302
Ca_{tot} [1)]	–0.052	**0.585**	0.129
Mg_{tot} [1)]	–0.312	**0.571**	**0.592**
Coarse sand [1)]	0.022	0.348	**0.746**
Respiration (per OM)	0.049	0.142	**–0.550**
C/N	0.291	–0.080	**0.536**
Specific surface area [1,2)]	–0.075	0.062	**0.391**
Percentage of total variance explained	25.7	20.5	15.3

1) from Järvinen et al. (1993)
2) from <0.06 mm grain size fraction

3.6 Respiration versus Soil Characteristics

Respiration rate illustrates differences in organic matter decomposition. We used linear regression analysis to examine the effect of top soil pH on the variation in respiration per organic matter. The calculated model explained only 4.2 % of the variation in respiration ($F = 3.93$; $p < 0.05$). Moreover, the slope was negative, suggesting that the higher the pH, the lower the respiration. This result is largely due of the fact that the more mineral soil there was in a sample of fixed weight, the less was the amount of humus, and that increasing the amount of mineral soil raised the pH of the humus/mineral soil mixture. In Table 2 it was seen that the nitrogen concentration of organic matter was higher in places where IPOT was low and humus layer was thin. This suggests that the organic matter was more decomposed in places with a thin humus layer than in places with a thick one. Accordingly, to be able to estimate the actual influence of humus pH on respiration, the effect of varying amount and quality of humus in samples was considered.

To exclude the effect of the varying amount of mineral soil in samples from the analysis the following measures were taken. First, the influence of mineral soil on pH was estimated by using linear regression: The amount of mineral soil explained 48.1 % of the variation in pH ($F = 83.33$; $p < 0.001$). Second, a reciprocal regression model ($1 / y = a + bX$) between organic matter nitrogen concentration and respiration per organic matter explained 18.3 % of the variation in respiration ($F = 15.95$; $p < 0.001$). Third, the residuals of these two regression models were plotted against each other, and a linear regression (Equation 4) was calculated:

$$\text{Respiration (per OM)}_{\text{corrected}} = 1.007 \cdot 10^{-3} + 0.0472\ \text{pH}(CaCl_2)_{\text{corrected}} \quad (4)$$

This model explained 17.8 % of the residual variation in respiration per organic matter ($F = 14.905$; $p < 0.001$). This relationship indicates that the increase in soil pH is related to increase in respiration.

4 Discussion

4.1 Variation in Soil Properties

The studied Scots pine stand had a great deal of variation in top soil properties, but no clear spatial patterns were detected. This can be because there is no detectable autocorrelation, or that – most probably – the examined variables are autocorrelated within shorter distances than the minimum of five metres between sample locations used in this study. In an old field Robertson et al. (1988) found spatial autocorrelation in pH and nitrification occurring within distances less than 20 m. However, the resolution of autocorrelation may be substantially smaller in forests than in field soils because trees increase the variability of forest soil properties by, e.g., changing the distribution of rain and dissolved ions (Zinke 1962, Helmisaari and Mälkönen 1989; see also Boettcher and Kalisz 1990, Beniamino et al. 1991). Especially soil pH is highly variable at both short and long distances. For example, Oliver and Webster (1987) detected spatial dependence (an increasing trend in semivariograms) in pH of deciduous forest soils within lag distances from about 5 to 70 m. Riha et al. (1986a) found no spatial dependence in the pH from Norway spruce, sugar maple and red pine plantation soils, even in samples 20 cm apart. Furthermore the results of Riha et al. (1986b) and Nykvist and Skyllberg (1989) indicate that to find spatial autocorrelation in the pH of forest soils, the distance between separate samples must be short, at least less than 2 m.

Probably the spatial autocorrelation in soil pH is so fine-grained that it is difficult to detect. This condition may be due to the highly variable pH of litter from trees, understorey and ground vegetation (Mikola 1954, Howard and Howard 1980, Fyles and McGill 1987) with the uneven fall and accumulation of litter (e.g. Facelli and Pickett 1991, Hirabuki 1991). If the variation in pH is very fine grained (within distances less than 1 m) then our method of taking composite samples, as required to describe the characteristics of a one square metre plot, hides a large part of the natural variation in soil pH.

Classifying the sample points according to the calculated influence potential of trees revealed, however, a weak but significant segregation in soil properties according to the proximity of large trees. Electrical conductivity of soil and the amount of organic matter was highest near the trees where IPOT was highest, but N_{tot} of OM was highest in the low-IPOT class, i.e. farther away from the trees (see also Boettcher and Kalisz 1990). Forest soil organic matter cation exchange capacity is high (e.g. Pritchett and Fisher 1987), and apparently the higher amount of organic matter near the trees explains part of the difference in electrical conductivity among the IPOT classes. However, high electrical conductivity was not only due to the thicker layer of humus, because the analysis of variance with the amount of OM as a covariate did not change the results presented in Table 2. Obviously the ion-rich throughfall from the canopy has raised the ionic concentration near the trees (Helmisaari and Mälkönen 1989). Soil solution electrical conductivity rises nearly linearly when ionic concentration rises (Rikala and Jozefek 1990, Alva et al. 1991, Walworth 1992).

There was also a non-significant tendency for C_{tot} of OM to be higher and C/N lower in sample points belonging to the low-IPOT class compared to higher IPOT class. High N_{tot} of OM in low-IPOT samples suggests that the decomposition has been more rapid and the proportion of old organic material with high content of N is higher (Alexander 1977, Berg 1986, Persson and Wirén 1989) in the areas where the influence of trees is weaker . In spite of the significantly lower N_{tot} in low-IPOT samples, nitrogen might be more easily available there, because N_{tot} of OM is high and C/N is low. In general, availability of nitrogen is better in areas under early stages of secondary succession, as in the younger part of the studied stand (see Vitousek et al. 1989).

Some previous studies concentrating on, e.g., througfall chemistry (Helmisaari and Mälkönen 1989, Beniamino et al. 1991, Boettcher and Kalisz 1991) suggested that soil pH might be lower under the trees where the influence potential of trees is high. However, we found no significant differences in soil pH in different IPOT-classes, even when organic matter content was used as a covariate. This may be because our composite sample procedure has cancelled at least part of the high spatial variability of pH as created by the influences of trees (Riha et al. 1986a, 1986b).

4.2 Organic Matter in Top Soil

Factor analysis and the corresponding correlation analysis of top soil properties showed the particular importance of the amount of organic matter on top soil chemical and microbiological properties. The more organic matter, the more carbon, nitrogen and other ions (Vaughan and Ord 1985). Accumulating organic matter also contains increasingly of exchangeable acidity. Humus is incompletely decomposed organic matter and contains lots of acidic, functional groups (e.g. Swift et al. 1978, Stevenson 1985).

Decomposition is the process that leads to the release of nutrients to be used by plants, and differences in decomposition thus play a distinct role in determining the fertility status of soil. The method we used to measure respiration standardises moisture and temperature, which are the most important abiotic factors influencing decomposition (Bunnell et al. 1977). The quality of litter greatly affects decomposition too (Mikola 1954, Rosswall 1975, Fyles and McGill 1987). However, the chemical characteristics we measured did not predict well the variation in respiration. Organic matter nitrogen concentration explained respiration best, but the relationship was weak and less than 20 % of the variance was explained. In several studies substrate nitrogen concentration has been the best predictor for organic matter decomposition rate (e.g., Gilmour et al 1985), but the relationship is not always straightforward. For instance, Fyles and McGill (1987) failed to find a consistent relationship between material chemical composition and decay rate.

Persson and Wirén (1989) found that for the same type of humus material there was a positive correlation between pH and CO_2 evolution at similar N concentrations. Our sampling technique (core samples of fixed depth) required the use of corrections, to reveal the influence of pH on respiration rate. After standardization of respiration for concentration of N, our results also are in agreement with those of Persson and Wiren (1989): correlation between pH and respiration was 0.422 ($p < 0.001$). However, most of the variation in respiration remained unexplained, again demonstrating the variability of forest humus material.

The thickness of the humus layer within the study area varied manifoldly. This is ecologically significant because the humus layer integrates information about input of organic matter, quality of the environment and the humus itself. In other words, the amount of humus shows the sum of interactions in input of organic matter (high or low), environmental conditions (favouring or restricting decomposition) and substrate quality (easy or difficult to degrade). Accumulation of humus indicates environmental conditions restricting decomposition, and/or poor quality of the material (from the standpoint of decomposers), and/or high input rate of the organic material. The effect of trees on humus layer thickness is undeniable, and the mechanisms may be through (i) the amount of litter, which is higher near the trees, (ii) the quality of litter (bark, and cone litter are less decomposable than twigs and needles (see, e.g., Edmonds 1987), (iii) shading, competition and throughfall, which favour less decomposable plants as mosses (Mikola 1954, Rosswall et al. 1975, Fyles and McGill 1987).

4.3 Relationships between Top Soil and Mineral Soil

When separate sites and forest types are compared, top soil characteristics indicate the differences in mineral soil quality (e.g., Westman 1990, Tamminen 1991). For example, Sepponen et al. (1979) found a weak but significant dependence between humus horizon thickness and sand or fine gravel in separate mixed pine stands and spruce stands in northern Finland. In our study

area mineral soil particle sizes vary remarkably. Järvinen et al. (1993) reported coefficient of variation from 22 to 99 percent for different mineral soil particle size fractions. The coefficient of variation for fine gravel was 51 %. Our results are similar to those of Sepponen et al. (1979) and indicate that the within-site relationships between mineral soil and top soil properties are weak. In the factor analysis total magnesium was the only mineral soil property to gain a reasonable – but negative – factor loading on factor one, which represented the humus layer. Tamminen (1991) compared separate stands and presented a factor solution, where humus layer thickness, mineral soil extractable magnesium and humus layer total and extractable magnesium were all positively correlated and situated on factor 1. We assume that the negative factor loading for magnesium in our factor analysis solution is due to the sampling procedure which includes some mineral soil in top soil samples. Magnesium is abundant in the mineral soil in the study area (Järvinen et al. 1993) and the amount of mineral soil – also magnesium – is greater in the samples taken from locations where the humus layer is thin.

In our factor analysis solution factor 3 included mineral soil and top soil properties which were related to each other and this factor was denoted as the interaction factor (Table 4). Respiration and C/N were the most important top soil properties and coarse sand, fine sand and magnesium represented mineral soil best. These interaction factor properties indicate that mineral soil and humus properties may be more closely connected than suggested by the lack of correlation between top soil organic matter and mineral soil properties. One indirect link is via trees and field layer vegetation, which are influenced by the mineral soil and which, in turn, influence the amount and characteristics (e.g., decomposability) of humus at a point. In the present site Järvinen et al. (1993) found that mineral soil properties are autocorrelated within distances less than 20 m in the area and that mineral soil properties thus vary gradually. Also roots of plants and litter production vary gradually around each individual plant. Large trees are obviously most important in production of litter in pine ecosystems (e.g. Prescott et al. 1989). These facts imply that the changes in soil properties around trees are not abrupt, and the interactions between mineral soil and humus are smooth and not easily detected.

4.4 Top Soil Variability and Influence of Trees As Related to Pine Regeneration and Seedling Growth

The germination of pine seeds and the early development of small seedlings are determined by a small effective environment on and beneath the surface of the top soil (e.g. Yli-Vakkuri 1961). Subsequently, this environment which affects the microclimate of seedlings and from which the seedlings have to extract nutrients, gradually expands. When the humus layer is thin, mineral soil lies very near the surface and can be reached even by roots of a tiny seedling. Moreover, in glaciofluvial soils magnesium has been shown to be especially important for trees in determining the fertility of soil (Viro 1951). We found that, in general, where IPOT is low and consequently the influence of trees is weak, the humus layer is thin and the concentration of nitrogen is high. A thick humus layer generally restricts pine regeneration (Sarvas 1950) and the critical nitrogen concentration for mineralisation to occur is about 1.6–1.8 % for decomposing forest litter (e.g., Aber and Melillo 1980, Berg and Staaf 1981). Accordingly, it seems that in locations with low IPOT (small gaps in the forest) many prerequisites for successful tree regeneration are fulfilled. Our results imply that the IPOT approach may be useful in determining which gaps offer space and resources enough for seedlings to grow and survive. In addition, when small pine seedlings are considered, the thickness of humus layer may also be used as a direct indicator of the supply of mineral nutrients for the seedlings.

4.5 Methodological Remarks

The soil characteristics in a stand result from long time of interaction between soil and vegetation. Variation of forest soil properties depends on many forest stand characteristics, such as the age and structure of the tree layer, but also depends on factors like aspect, topography etc. Apparently, the IPOT approach was successful in predicting top soil properties because large trees are important in describing site quality. The size of the trees was also considered when calculating IPOT. The use of the approach is, however, inevitably restricted to relatively undisturbed forest stands that have developed naturally for prolonged periods. For example, it is unreasonable to expect that rapid changes in IPOT due to the removal of trees can be seen in soil properties. In some soil properties as the pH, the influence of a single tree on the soil can be sometimes detected even years after the tree has been removed (Pallant and Riha 1990). Dead, standing trees and windthrows also cause noticeable variation in soil properties, but in our study site there were no conspicuous signs of either ones to be seen.

Our sampling procedure (composite samples; mixture of humus and mineral soil) was a compromise determined by the objectives of the research project, especially those related further analyses concerning field and bottom layer vegetation in relation to soil properties (Hokkanen et al. 1995, Kuuluvainen et al. 1993). The thickness of the humus layer evidently characterizes many top soil properties, but the small-scale variation of soil properties could not be satisfactorily accounted for by humus thickness. Especially the variation in soil pH evidently occurs within distances of less than one metre, and our pH-values are means for one square metre.

5 Conclusions

Spatial variability of humus thickness and organic matter properties was coupled with the influences of large trees. The calculated influence potential of the trees appears to provide a method to predict the long-term spatial effects of trees on top soil characteristics. However, for a more rigourous test of the method, sampling should be more intensive than undertaken in this study.

Composite soil samples, which were used due to the other objectives of the research (study of vegetation composition and seedling growth in relation to soil properties), cannot be recommended for the detailed study of spatial variation in forest soil microhabitats because of the loss in resolution.

Humus layer thickness provided a simple, integrative measure of many forest floor characteristics of the studied Scots pine stand. Humus organic matter content, pH, carbon and nitrogen content and respiration followed closely the variation in humus layer thickness.

Factors dependent on organic matter quality (C/N, concentration of carbon and nitrogen and respiration per organic matter) showed considerable spatial variation but their interdependencies were weak. Increasing nitrogen concentration in humus organic matter was the best general predictor for the increasing degree of decomposition.

The within-site interaction between the humus layer and the underlying mineral soil was weak and we found no consistent trends. The interactions between mineral soil and humus chemical characteristics may be revealed with more intensive mapping and separate samples for mineral soil and humus, as suggested by C/N and N_{tot} of OM (see also Ilvesniemi 1991).

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References

Aber, J.D. & Melillo, J.M. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Canadian Journal of Botany 58: 416–421.

Alexander, M. 1977. Introduction to soil microbiology. 2nd edition. John Wiley & Sons, New York. 467 p.

Alva, A.K., Sumner. M.E. & Miller, W.P. 1991. Relationship between ionic strength and electrical conductivity for soil solutions. Soil Science 152: 239–242.

Beatty, S.W. 1984. Influence of microtopogaphy and canopy species on spatial patterns of forest understory plants. Ecology 65: 1406–1419.

Bell, G. & Lechowicz, M.J. 1991. The ecology and genetics of fitness in forest plants. I. Environmental heterogeneity measured by explant trials. Journal of Ecology 79: 663–685.

— , Lechowicz, M.J., & Schoen, D.J. 1991. The ecology and genetics of fitness in forest plants. III. Environmental variance in natural populations of Impatiens pallida. Journal of Ecology 79: 697–713.

Beniamino, F., Ponge, J.F. & Arpin, P. 1991. Soil acidification under the crown of oak trees I. Spatial distribution. Forest Ecology and Management 40: 221–232.

Berg, B. 1986. Nutrient release from litter and humus in coniferous forest soils – a mini review. Scandinavian Journal of Forest Research 1: 359–369.

— & Staaf, H. 1981. Leaching, accumulation and release of nitrogen in decomposing forest litter. In Clark, F.E. & Rosswall, T. (eds.). Terrestrial nitrogen cycles. Ecological Bulletin (Stockholm) 33: 163–178.

Björkman, E. & Lundeberg, G. 1971. Studies on root competition in a poor pine forest by supply of labelled nitrogen and phosphorus. Studia Forestalia Suecica 94: 1–16.

Boerner, R.J. & Koslowsky, S.D. 1989. Microsite variations in soil chemistry and nitrogen mineralization in a beech-maple forest. Soil Biology and Biochemistry 21: 795–801.

Boettcher,S.E. & Kalisz, P.J. 1990. Single-tree influence on soil properties in the mountains of eastern Kentucky. Ecology 71: 1365–1372.

Bringmark, E. 1989. Spatial variation in soil pH of beech forests in relation to buffering properties and soil depths. Oikos 54: 165–177.

Bunnell, F.L., Tait, D.E.N., Flanagan, P.W. & van Cleve, K. 1977. Microbial respiration and substrate weight loss: I. A general model of the influences of abiotic variables. Soil Biology and Biochemistry 9: 33–40.

Burrough, P.A. 1983. Multiscale sources of spatial variation in soil. I. The application of fractal concepts to nested levels of soil variation. Journal of Soil Science 32: 577–597.

Conyers, M.K. & Davey, B.G. 1988. Observations on some routine methods for soil pH determination. Soil Science 145: 29–36.

Edmonds, R.L. 1987. Decomposition rates and nutrient dynamics in small-diameter woody litter in four forest ecosystems in Washington, U.S.A. Canadian Journal of Forest Research 17: 499–509.

Escudero, A., Hernandez,M.M. & Del Arco, J.M. 1991. Spatial patterns of soil composition around isolated trees. In: Berthelin, J. (ed.). Developments in geochemistry 6. Diversity of environmental biogeochemistry. Elsevier, Amsterdam–Oxford–New York–Tokyo. p. 507–517.

Facelli, J.M. & Pickett, S.T.A. 1991. Plant litter: its dynamics and effects on plant community structure. Botanical Review 57: 1–32.

Fyles, J.W & McGill, W.B. 1987. Decomposition of boreal forest litters from central Alberta under laboratory conditions. Canadian Journal of Forest Research 17: 109–114.

Gilmour, J.T., Clark, M.D. & Sigua, G.C. 1985. Estimating net nitrogen mineralization from carbon dioxide evolution. Soil Science Society of America Journal 49: 1398–1402.

Helmisaari, H-S. & Mälkönen, E. 1989. Acidity and nutrient content of throughfall and soil leachate in three Pinus sylvestris stands. Scandinavian Journal of Forest Research 4: 13–28.

Hirabuki, Y. 1991. Heterogenous dispersal of tree litterfall corresponding with patchy canopy structure in a temperate mixed forest. Vegetatio 94: 69–79.

Hokkanen, T.J., Järvinen, E. & Kuuluvainen, T. 1995. Relationships between ground vegetation, canopy trees and soil properties in a patchy boreal Scots pine stand. (Submitted to Journal of Vegetation Science).

Howard, D.M. & Howard, P.J.A. 1980. Effect of species, source of litter, type of soil, and climate on litter decomposition. Oikos 34: 115–124.

Ilvesniemi, H. 1991. Spatial and temporal variation of soil chemical characteristics in pine sites in southern Finland. Silva Fennica 25: 99–108.

Järvinen, E., Hokkanen, T.J. & Kuuluvainen, T. 1993. Spatial heterogeneity and relationships of mineral soil properties in boreal Pinus sylvestris stand. Scandinavian Journal of Forest Research 8: 435–445.

Kuuluvainen, T. & Pukkala, T. 1989. Effect of Scots pine seed trees on the density of ground vegetation and tree seedlings. Silva Fennica 23: 156–167.

— , Hokkanen, T.J., Järvinen, E. & Pukkala, T. 1993. Factors related to seedling growth in a boreal Scots pine stand: a spatial analysis of a vegetation – soil system. Canadian Journal of Forest Research 23: 2101–2109.

Lechowicz, M.J. & Bell, G. 1991. The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. Journal of Ecology 79: 687–696.

Legendre, P. & Fortin, M-J. 1989. Spatial pattern and ecological analysis. Vegetatio 80: 107–138.

Mikola, P. 1954. Kokeellisia tutkimuksia metsäkarikkeiden hajaantumisnopeudesta. English summary: Experiments on the rate of decomposition of forest litter. Communicationes Instituti Forestalis Fenniae 43. 50 p.

Mikola, J. & Komppula, J. 1981. Respiratory activity of milled peat: a rapid method of measurement and observations on the effects of moisture, temperature, pH and peat quality. Soil Science 131: 156–162.

Nielsen, D.R. & Alemi, M.H. 1989. Statistical opportunities for analyzing spatial and temporal heterogeneity of field soils. Plant and Soil 115: 285–296.

Nykvist, N. & Skyllberg, U. 1989. The spatial variation of pH in the mor layer of some coniferous forest stands in northern Sweden. Scandinavian Journal of Forest Research 4: 3–11.

Oliver, M. A. & Webster, R. 1987. The elucidation of soil pattern in the Wyre Forest of the West Midlands, England. II. Spatial distribution. Journal of Soil Science 38: 293–307.

Page, A.L., Miller, R.H. & Keeney, D.R. (eds.). 1983. Methods of soil analysis. Part 2. Chemical and microbiological properties. 2nd edition. Agronomy 9. American Society of Agronomy, Inc. Madison, Wisconsin USA. 1159 p.

Pallant, E. & Riha, S.J. 1990. Surface soil acidification under red pine and Norway spruce. Soil Science Society of America Journal 54: 1124–1130.

Paul, E.A. & Clark, F.E. 1989. Soil microbiology and biochemistry. Academic Press, Inc., San Diego. 273 p.

Persson, T. & Wirén, A. 1989. Microbial activity in forest soils in relation to acid/base and carbon/nitrogen status. In: Braekke, F.H., Bjor, K. & Halvorsen, B. (eds.). Air pollution as stress factor in the Nordic forest. Norsk Institutt for Skogforskning NISK, Ås. p. 83–95.

Pickett, S.T.A. & White, P.S. 1985. (eds.). The ecology of natural disturbance and patch dynamics. Academic Press. 472 p.

Platt, W.J. & Strong, D.R. 1989. (eds.). Special feature – treefall gaps and forest dynamics. Ecology 70: 535–576.

Prescott, C.E., Corbin, J.P. & Parkinson, D. 1989. Input, accumulation, and residence times of carbon, nitrogen, and phosphorus in four Rocky Mountain coniferous forests. Canadian Journal of Forest Research 19: 489–498.

Pritchett, W.L. & Fisher, R.F. 1987. Properties and management of forest soils. Second Edition. John Wiley & Sons, New York. 494 p.

Rhoades, J. D. 1982. Soluble salts. In: Page, A.L. (ed.). Methods of soil analysis. Part 2. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, Wisconsin, USA. p. 167–179.

Riha, S.J., Senesac, G. & Pallant, E. 1986a. Effects of forest vegetation on spatial variability of surface mineral soil pH, soluble aluminum and carbon. Water, Air and Soil Pollution 31: 929–940.

— , James, B.R., Senesac, G.P. & Pallant, E. 1986b. Spatial variability of soil pH and organic matter in forest plantations. Soil Science Society of America Journal 50: 1347–1352.

Rikala, R. & Jozefek, H.J. 1990. Effect of dolomite lime and wood ash on peat substrate and development of tree seedlings. Silva Fennica 24: 323–334.

Robertson, G.P. 1987. Geostatistics in ecology: interpolating with known variance. Ecology 68: 744–748.

— , Huston, M.A. & Evans, F.C. 1988. Spatial variability in a successional plant community: patterns of nitrogen availability. Ecology 69: 1517–1524.

Rosswall, T., Veum, A.K.& Kärenlampi, L. 1975. Plant litter decomposition at fennoscandian tundra sites. In: Wielgolaski, F.E. (ed.). Fennoscandian tundra ecosystems, Part I: Plants and microorganisms. Springer-Verlag, Berlin. p. 268–278.

Sarvas, R. 1950. Tutkimuksia Perä-Pohjolan harsimalla hakattujen yksityismetsien luontaisesta uudistumisesta. Summary: Investigations into the narural regeneration of selectively cut private forests in northern Finland. Communicationes Instituti Forestalis Fenniae 38. 84 p.

Sepponen, P., Lähde, E. & Roiko-Jokela, P. 1979. On the relationship of the forest vegetation and the soil physical properties in Finnish Lapland. Folia Forestalia 402. 31 p.

Stevenson, F.J. 1985. Geochemistry of soil humic substances. In: Aiken, G.R., McKnight, D.M., Wershaw, R.L. & MacCarthy, P. (eds.). Humic substances in soil, sediment and water. Geochemistry, isolation and characterization. John Wiley & Sons, New York–Chichester–Brisbane–Toronto–Singapore. p. 13–52.

Swift, M.J., Heal, O.W. & Anderson, J.M. 1978. Decomposition in terrestrial ecosystems. Studies in Ecology, Volume 5. Blackwell Scientific Publications, Oxford. 372 p.

Tamminen, P. 1991. Expression of soil nutrient status and regional variation in soil fertility of forested sites in southern Finland. Folia Forestalia 777. 40 p.

Vaughan, D. & Ord, B.G. 1985. Soil organic matter – a perspective on its nature, extaction, turnover and role in soil fertility. In: Vaughan, D. & Malcolm, R.E. (eds.). Soil organic matter and biological activity. Developments in Plant and Soil Sciences 16: 1–35.

Viro, P.J. 1951. Nutrient status and fertility of forest soil. I. Pine stand. Selostus: Maan ravinnesuhteet ja viljavuus. I. Männiköt. Communicationes Instituti Forestalis Fenniae 39. 54 p.

Vitousek, P.M., Matson, P.A. & van Cleve, K. 1989. Nitrogen availability and nitrification during succession: Primary, secondary, and old-field seres. Plant and Soil 115: 161–171.

Walworth, J.L. 1992. Soil drying and rewetting, or freezing and thawing, affects soil solution composition. Soil Science Society of America Journal 56: 433–437.

Walker, J., Sharpe, P.J.H., Penridge, L.K. & Wu, H. 1989. Ecological field theory: the concept and field tests. Vegetatio 83: 81–95.

Walter, H. & Breckle, S-W. 1989. Ecological systems of the geobiosphere. 3. Temperate and polar zonobiomes of northern Eurasia. Springer-Verlag, Berlin. 581 p.

Westman, C.J. 1990. Metsämaan fysikaaliset ja fysikaalis-kemialliset ominaisuudet CT-OMaT kasvupaikkasarjassa. Summary: Soil physical and physico-chemical prosperties of Finnish upland forest sites. Silva Fennica 24: 141–158.

Wu, H., Sharpe, P.J.H., Walker, J. & Penridge, L.K. 1985. Ecological field theory: A spatial analysis of resource interference among plants. Ecological Modelling 29: 215–243.

Yli-Vakkuri, P. 1961. Kokeellisia tutkimuksia taimien syntymisestä ja ensi kehityksestä kuusikoissa ja männiköissä. Summary: experimental studies on the emergence and initial development of tree seedlings in spruce and pine stands. Acta Forestalia Fennica 75. 110 p.

Zinke, P.J. 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43: 130–133.

Total of 66 references