

Relation between Soil Properties and Tree Species Composition in a Scots pine–Norway spruce Stand in Southern Finland

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It is commonly known in Finland that Scots pine (*Pinus sylvestris* L.) is a tree of dry soils and Norway spruce (*Picea abies* (L) Karst.) is a tree of fresh soils. However, the concepts of dry and fresh soils still lack a precise definition. Consequently, the discussion on which soil/site is a pine or spruce habitat has continued over several decades. Moreover, in forest regeneration, the practice of tree species selection between the pine and the spruce has varied. We investigated the relationship between soil properties and pine–spruce species composition in a mature, naturally regenerated stand in southern Finland. We applied spatial analysis to divide the stand area up into 3–7 classes based on selected soil properties and then investigated the variations in species composition among those classes. The pine–spruce basal area ratio (BA of pines / BA of spruces) increased along with increasing mean particle size and proportion of coarse sand and gravel particle size fraction (0.6–20 mm) of mineral soil, and was lowest in classes, with the highest proportions of fine texture fractions. The results suggest that in southern Finland on sorted soils, pine is more competitive in regeneration and growth than spruce when mean particle size is above 0.44 mm or percentage of coarse sand and gravel is higher than 50%.

Keywords Scots pine, Norway spruce, tree species composition, soil texture, soil-water retention, spatial variability

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1 Introduction

Scots pine (*Pinus sylvestris* L.) or Norway spruce (*Picea abies* (L.) Karst.) most often dominates mature natural tree stands in Finland. On mineral soils, forest sites are classified according to the site-type classification presented by Cajander (1949). The system classifies sites by the species composition of the understorey vegetation. The most common site types in southern Finland are Calluna (CT), Vaccinium (VT), Myrtillus (MT) and Oxalis-Myrtillus (OMT), in order of increasing site fertility. Pine always dominates on the least fertile CT sites, and spruce usually dominates on the most fertile OMT sites, but both species may dominate on sites of medium fertility (VT and MT), which cover 60 per cent (12 million ha) of forestry land in Finland (Finnish Statistical Yearbook... 2000).

It is a commonly known fact in Finland that pine is a tree of dry soils and spruce is a tree of fresh soils. However, the concepts dry soil and fresh soil are inaccurate and subjective. Thus, the reasons for the pine or spruce dominance on the medium fertility MT-VT sites are still fairly unknown. Consequently, owing to the uncertainty about the site-demands for pine or spruce, there have been considerable changes in the practice of the choice between the two species (Finnish Statistical Yearbook... 2000). In the 1970s the area regenerated for pine increased from 72% to 86% of a total of approximately 100 000 ha/year. Correspondingly, the area regenerated for spruce decreased from 27 to 12 percent. However, during the following decades this trend was reversed, and by 1994 the area regenerated for pine had decreased to 64%, while the area regenerated for spruce had increased to 25%.

Few, if any, ecological constraints causing one or the other of the two species to dominate have been presented in the literature. Aaltonen (1936) states that spruce is a tree of fresh soils, but mentions that the relationship between soil and pine–spruce composition is unclear. He also notes that spruce is an intruder in pine stands. Kalela (1949) states that succession leads to pure or nearly pure spruce stands on fresh soils and to pure pine stands on dry soils. However, Kalela does not define fresh and dry soils, although he asserts that on gravel, coarse sand and fine sand

soils (mean particle size 0.2–20 mm), only pine is capable of growing and regenerating. Sarvas (1951) declares that VT covers a wide range of sites, from genuine spruce sites (MT) to genuine pine sites (CT). He concludes that on VT sites the growth of pine is considerably faster than the growth of spruce, and when selecting species for these sites, pine should be favoured at the expense of spruce, although the latter is apt to colonise also VT sites.

Keltikangas (1959) declares that what he calls genuine VT sites (however without any clear definition) are not colonised by spruce, and that those VT sites described by Sarvas (1951) should actually be classified as a separate forest site-type: the *Pleurozium-Vaccinium*-type (PIVT). According to Keltikangas, such PIVT sites are, in hydrological sense, intermediate types between the dry VT and fresh MT. However, he calls for more research to define the minimum demand of spruce with respect to site fertility, and on the relationship between soil properties and the vegetation society formation.

Keltikangas's objective is still unachieved, and only few research articles concerning the causal relationships between soil properties and the tree species composition on pine–spruce stands are available. Most of this research has been conducted in the Finnish Lapland. Sepponen et al. (1979) demonstrated that in the Lapland pine stands are found on more coarse-grained soils than spruce stands. They also pointed out that it is difficult to express soil texture with one single value, and consequently did not suggest any particular soil texture classes as suitable for either pine or spruce. Sutinen et al. (1996) and Penttinen (2000) have studied the relationship between soil moisture and tree species composition in pine–spruce stands on till soils in the Lapland. They state that species composition seems to be associated with soil water content, and that pine is restricted to dry, coarse-textured sites having a dielectric coefficient (which has a strong positive correlation with soil-water content) less than 13 in the topsoil (15 cm). Penttinen (2000) suggests that spruce require fresh soils with a dielectric coefficient over 10 and that the regeneration of pine might be a risk on soils with a dielectric coefficient exceeding 15. Heiskanen and Mäkitalo (2002) found that water content of mineral soil in

the field capacity was significantly larger on the natural spruce stands (32.5%) than on the natural pine stands (22.5%) in the Finnish Lapland.

The aim of this study is to investigate the relationship between soil properties and tree species composition in a mature, naturally established, unmanaged stand covering a site type range from dry pine dominated VT via intermediate MT to moist spruce dominated OMT. To do so we first applied spatial analysis to selected soil properties to partition the forest area into edaphically homogenous habitats. Finally we investigated the relation between the mean soil property of such habitats and corresponding tree species composition.

2 Material and Methods

2.1 Study Site and Tree Stand

The study site located in the Ruovesi municipality, in southern Finland (61°50'N, 24°22'E), about 200 km north of Helsinki. The average annual mean temperature and precipitation in the region is 2.9 °C and 709 mm, respectively. The stand area was on a south-facing slope with an average inclination of 3.4% and a mean elevation a. s. l. of 152 m (Figs. 1 and 2). The soil was glacio-fluvial sorted sand with a mean particle-size of 0.43 mm. The soil order was a Spodosol, and the soil-group a Typic Haplocryod (Soil Survey Staff 1992). The average thickness of the organic, eluvial, and illuvial horizons were 45, 52 and 176 mm, respectively. The forest site type changed along the slope, from dry VT on top of the slope, over a mesic MT to moist OMT at the bottom (Cajander 1949). The ground water table level (measured monthly in four ground water wells along the slope) ranged between 3.2 and 5.1 m below ground surface during the growing season 1997 (Fig. 1).

The forest on the site was clearcut in February 1998 prior to soil sampling (summer 1998) and surface vegetation description (summer 2000). The harvested stand on the site was a naturally established Norway spruce–Scots pine forest. The tree species distribution in the forest was obtained by counting each stump by tree species, and

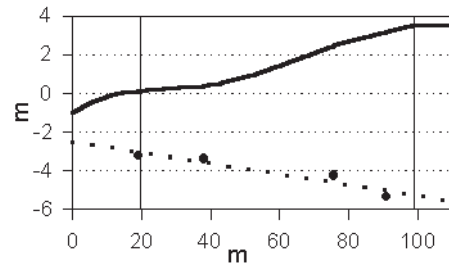


Fig. 1. The slope surface (solid line) and average ground water table (dotted line) on the study site in summer 1997. Big dots represent the average water table level of the four ground water wells. The actual location of the analysed area is indicated with vertical lines, and the course of the horizontal-axis is shown in Fig. 2. Zero of the vertical axis is 150 m a.s.l.

measuring the diameter from two perpendicular directions. The number of spruce and pine stems was 589 and 203 ha⁻¹, respectively. There was an evident trend from pine-dominated forest on the upper slope to spruce-dominated forest on the lower slope, but there was no concomitant change in stand density. The diameter at breast height (1.3 m) (DBH) of each tree was then obtained from the stump diameter by applying transfer functions. DBH was used to calculate the basal area and stem volume of each tree (Laasasenaho 1982). The stem volume was 240 m³ ha⁻¹, out of which 63% was Norway spruce and 37% Scots pine. The age of the trees was fairly uniform being some 130–140 years and there were no such variations in the year-ring width that obviously indicate thinnings.

The surface vegetation species composition and coverage (%) was determined on 80 systematically distributed points (0.25 m² squares). The entire site was mapped by the aid of a geodimeter. The locations of all trees (stumps), points for surface vegetation analysis and soil sampling, and the elevations of 120 evenly distributed points were recorded.

2.2 Soil Sampling and Analyses

A total of 72 soil samples were taken from evenly

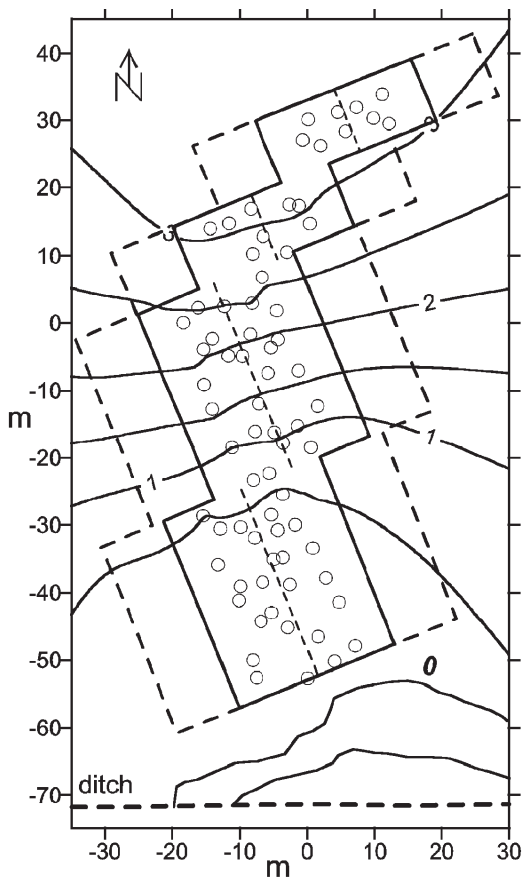


Fig. 2. The study site with 0.5-m-elevation contours (0=150 m a.s.l.). Soil sampling points are represented by dots; the borders of the 2000-m² and 3600-m² size mapping areas are indicated with dashed and solid lines, respectively. The short-dashed line in the middle of the mapping areas indicates the course of the horizontal-axis of Fig. 1.

distributed points in the approximately 80 m long and 15 m wide area, parallel to the slope inclination (Fig. 2). The area had the shape of a series of somewhat meandering rectangles. Sampling was done with an auger (Westman 1995), the length of which and inner diameter were 500 and 46 mm, respectively.

Soil cores were divided into organic (O), elluvial (E), illuvial (B) and unaltered subsoil (C) horizons. The B-horizon was further divided into

the top 50 mm (B1) and the remainder (B2). The thickness and colour (Munsell soil color charts 1992) of each soil horizon were determined from the fresh sample in a laboratory. Each horizon was separately dried in an oven at 105 °C for 24 h, and then weighed for dry mass.

Particle-size distribution was determined for the E-horizon and the B1-layer. Gravel (>2 mm) and coarse sand (0.6–2.0 mm) were determined by dry sieving. The size distribution of particles smaller than 0.6 mm was analysed with laser-diffractometry (COULTER-LS230, Coulter Corporation, Miami, USA) from a soil paste obtained by moistening the soil with a 0.05 M Na₄P₂O₇-solution. Soil texture was then described by calculating mean particle-size, and fractions of silt plus clay jointly (<0.06 mm), fine silt (0.002–0.02 mm), and coarse sand plus gravel jointly (0.6–20 mm). Values were calculated for particles smaller than 2 mm, with the exception of the fraction of coarse sand and gravel, which was calculated for particles smaller than 20 mm.

The total organic carbon content of E-horizon and B1 and B2 layers was measured with a LECO-analyser (LECO CSN-1000, Leco Corporation, St. Joseph, USA) after powdering the sample (fraction < 2 mm) in a mechanical mortar. The ammonium oxalate extractable Al (Al_{OX}) and Fe (Fe_{OX}) of the same layers were determined according to Wang (1981) from the fraction smaller than 0.6 mm.

2.3 Calculations and Statistical Analyses

The storage potential of plant-available water was calculated for the uppermost 30-cm layer of mineral soil. To do so, soil water retention curves for the E-horizon, and upper and lower B-horizon of each soil sampling point were first estimated using regression models (Mecke et al. 2002). These models predict volumetric water content at selected matric potentials with particle-size distribution, oxalate extractable Al and Fe, total organic carbon content, and bulk density as explanatory variables. Water content (m³ × m⁻³) at matric potentials of 1000 cm and 31.6 cm was then estimated for each horizon from the retention curves, and the plant-available water taken as the difference between these two contents. Finally the

potential water storage of the 30-cm topsoil layer was obtained by calculating the weighted (according to the thickness of layers) average of the storage in different layers. In the calculations, as the particle size distribution of the B2-layer was not determined the particle-size distribution of the B1-layer was applied to the B2-layer. In the case that the thickness of E and B-horizons together was less than 30-cm the retention curve of the E horizon was used also for the C-horizon.

The redness of the E-horizon and B1-layer was quantified with the index called redness rating (RR) (Torrent et al. 1980):

$$RR = [(10 - H) \times \text{chroma}] / \text{value} \tag{1}$$

where, $H=0.0, 2.5, 5.0, 7.5$ and 10.0 , corresponding to the Munsell-hues 10R, 2.5YR, 5YR, 7.5YR and 10YR, respectively, chroma=Munsell-chroma, and value=Munsell-value (Munsell soil color charts 1992).

To study the relation between soil properties and pine–spruce species composition, the study area was partitioned into map units (classes) based on a set of selected soil properties. Map units were thus bounded by the isobar-lines of soil property values. The properties used were: 1) the mean particle-size of B1-layer soil, 2) the fraction of silt and clay in B1-layer soil, 3) the fraction of fine-silt in B1-layer soil, 4) the fraction of coarse sand plus gravel in B1-layer soil, 5) the potential plant-available water storage, 6) the RR of E-horizon soil, 7) the RR of B1-layer soil, and 8) the thickness of humus layer.

First, a semi-variance analysis (Bailey and Gatrell 1995) was conducted for each soil property in order to determine the nature of its spatial covariance structure. The width of lags and the maximum active lag distance were set so that each lag comprised a minimum of 100 pairs of sampling points. The information obtained was then used in creating soil property grids covering

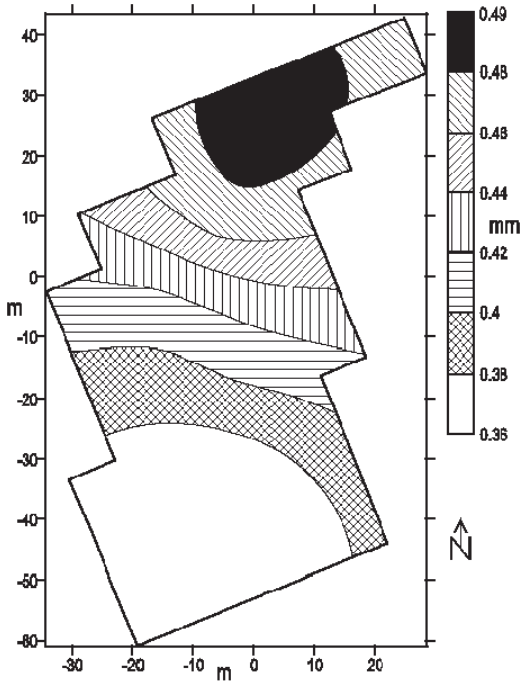


Fig. 3. The study area partitioned into a seven-class map on the basis of the mean particle size of the B1-layer soil.

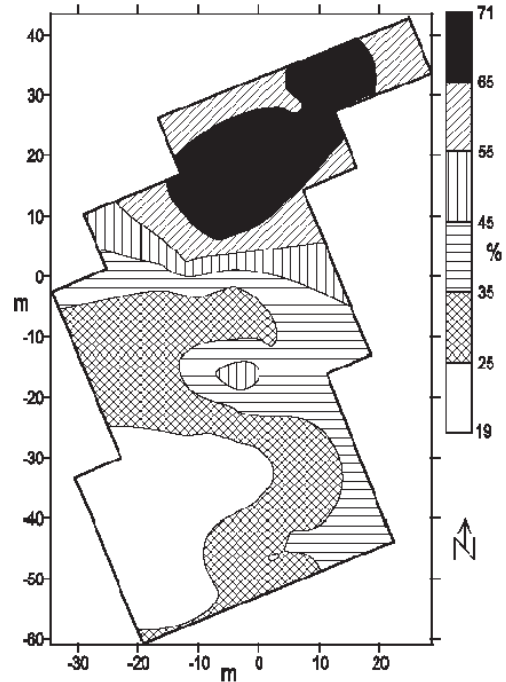


Fig. 4. The study area partitioned into a six-class map on the basis of the joint fraction of coarse sand and gravel (0.6–20 mm) in the B1-layer soil.

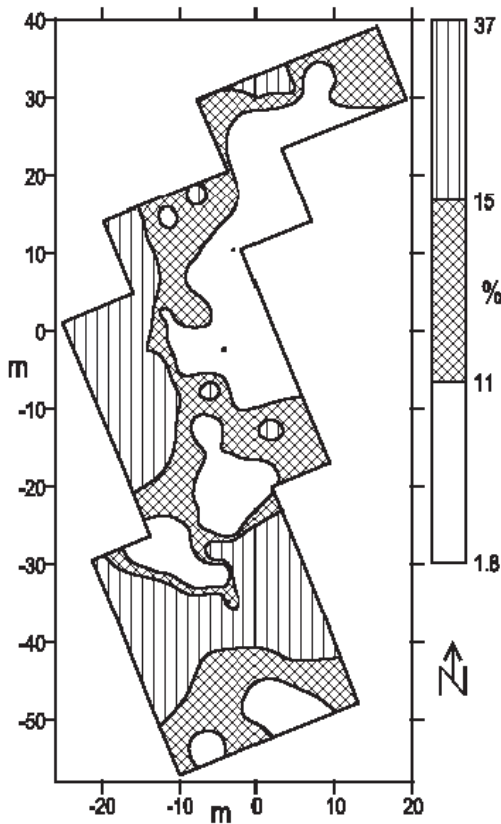


Fig. 5. The study area partitioned into a three-class map on the basis of the joint fraction of silt and clay ($< 0.06\text{ mm}$) in the B1-layer soil.

the studied site. The kriging-interpolation method (Bailey and Gatrell 1995, Golden Software inc. 1999) was used to calculate grids. A linear model was used for all soil properties, with the exception of the mean particle-size and the fraction of coarse sand and gravel, which were spatially auto-correlated. For the mean particle size and the coarse fraction the grids were fitted with the spherical variogram models (2 and 3, respectively) having following parameters (Bailey and Gatrell 1995, Golden Software inc. 1999):

$$\text{Nugget}=0.0227\text{ mm}^2, \text{ sill}=0.0513\text{ mm}^2, \text{ range}=100\text{ m}, \text{ and } R^2=0.683 \quad (2)$$

$$\text{Nugget}=122\% ^2, \text{ sill}=853\% ^2, \text{ range}=93.9\text{ m}, \text{ and } R^2=0.754 \quad (3)$$

The map grid covered the sampled area symmetrically and took the similar meandering rectangular shape that determined the area from which the soil samples were taken (Fig. 2). In the case of mean particle size and fraction of coarse sand and gravel, which were spatially auto-correlated and gently fluctuating variables, the map grid could be extended to cover a 3600 m^2 area (Fig. 2). This mapping area allowed the partitioning of the area into a sufficient number of map units for statistical testing. Thus, the area was partitioned into seven equal-interval soil property value classes (map units) based on the mean particle size, and into six equal-interval soil property value classes based on the fraction of coarse sand and gravel (Figs. 3 and 4). In cases of linear kriging-interpolation in the grid calculation for non-auto-correlated variables a reasonable kriging area was 2000 m^2 , which was then divided into no more than three equal-sized areas, as further division resulted into many discrete spots of unreasonably small areas (Fig. 5).

The Pearson correlation coefficients (r) were calculated for the linear relationships between the mean particle size of the B1-layer, the fraction of coarse sand and gravel of the B1-layer, and stand attributes: the total BA, BA of pine, BA of spruce and pine–spruce BA ratio (BA of pine/BA of spruce). In the analysis, the mean values of the mean particle size and the coarse sand and gravel fraction of each map unit were compared with the measured stand attributes of the same areas.

The Canoco program (ter Braak and Smilauer 1998) was used to perform canonical correspondence analysis (CCA) (Jongman et al. 1987) of the understory vegetation and stand attributes in map units partitioned on the basis of the mean particle size of the B1-layer. Areas of the map units were treated as sites, while the total BA, BA of pine and BA of spruce were treated as environmental variables.

3 Results

3.1 Total Basal Area (BA)

There was only minor variation in total BA within the stand. Consequently, total BA did not correlate

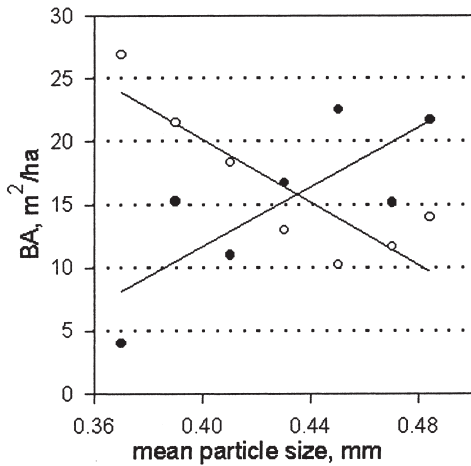


Fig. 6. The relation between the mean particle size of the B1-layer soil and the basal areas of pine (filled dots) and spruce (empty dots). The solid lines are linear fits to the data.

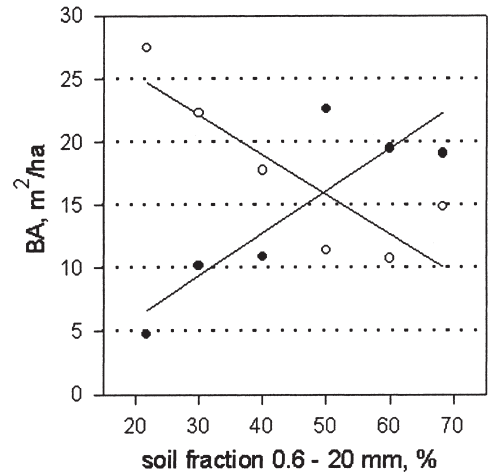


Fig. 7. The relation between the joint fraction of coarse sand and gravel (0.6–20 mm) in the B1-layer soil and the basal areas of pine (filled dots) and spruce (empty dots). The solid lines are linear fits to the data.

with the mean particle size or the coarse sand and gravel fraction of the B1-layer (Tables 1 and 2). Neither were there any uniform trends in the total BA among the classes of silt and clay fraction of the B1-layer, potential plant-available water storage, RR of the E-horizon and thickness of the organic horizon (Table 1). There was a decrease in total BA with an increasing fine silt fraction and RR of the B1-layer (Table 1), but the range of variation in total BA was only 17% among mapping units based on the fine silt fraction and only 24% among units based on RR of B1-layer.

3.2 Soil Texture and Pine–spruce Composition

There was an obvious relation between soil particle-size distribution and tree species composition in the stand. The BA of pine and the pine–spruce BA ratio correlated positively, and the BA of spruce negatively, with the mean particle size of the B1-layer (Fig. 6, Table 2). Also, the coarse sand and gravel fraction in the B1-layer correlated positively with the BA of pine and negatively with the BA of spruce (Fig. 7, Table 2). The

pine–spruce BA ratio tended to increase with an increasing coarse sand and gravel fraction, and the trend was almost significant ($p=0.059$, Table 2). Consistently, the BA of pine and pine–spruce BA ratio decreased with an increasing fraction of silt and clay in the B1-layer (Table 1), and the BA of spruce increased with an increasing fraction of silt and clay (Table 1). Among the map units partitioned on the basis of fine-silt fraction of the B1-layer, there was a uniform downward trend in the BA of pine as the fine-silt fraction increased (Fig. 8, Table 1). However, there were no uniform trends in the BA of spruce and in the pine–spruce BA ratio (Fig. 8, Table 1), although the BA of spruce was highest and the pine–spruce BA ratio lowest in the map unit having the highest fine-silt fraction.

3.3 Potential Plant-Available Water Storage, Thickness of Organic Layer and Pine–spruce Composition

The BA of pine and the pine–spruce BA ratio decreased with increasing potential plant-available water in the top 30 cm of mineral soil (Fig.

Table 1. The mean values of kriging-interpolated soil properties and corresponding stand attributes of map units partitioned according to different soil properties.

Measurement unit and the mean value of the map unit (class mean)	Total BA, m ² /ha	Number of stems per hectare	BA of pine, m ² /ha	BA of spruce, m ² /ha	BA of pine / BA of spruce
mm	Mean particle size of B1-layer soil				
0.370	30.9	856	3.98	26.9	0.16
0.390	36.8	839	15.2	21.5	0.76
0.410	29.3	781	11.0	18.4	0.67
0.430	29.7	725	16.7	13.0	1.4
0.450	32.7	709	22.5	10.2	2.3
0.470	26.8	684	15.1	11.6	1.5
0.484	35.7	917	21.7	14.0	1.8
%	Fraction of coarse sand and gravel in B1-layer soil (0.6–20 mm)				
21.8	32.2	990	4.78	27.5	0.17
30.0	32.5	773	10.2	22.3	0.46
40.0	28.7	690	10.9	17.8	0.61
50.0	34.0	843	22.6	11.4	1.98
60.0	30.3	646	19.5	10.7	1.81
68.3	33.9	920	19.1	14.8	1.29
%	Fraction of silt and clay in B1-layer soil (< 0.06 mm)				
6.40	32.4	860	13.3	19.1	0.75
13.0	31.0	732	11.3	19.7	0.63
26.0	32.2	821	10.1	22.2	0.49
%	Fraction of fine silt in B1-layer soil (0.002–0.02 mm)				
0.630	34.5	867	14.4	20.1	0.71
3.30	32.5	793	14.0	18.5	0.76
7.15	28.7	764	6.29	22.4	0.28
m ³ /m ³	Potential plant available water of top 30 cm of mineral soil				
0.101	34.1	841	15.7	18.5	0.85
0.155	26.4	708	11.9	14.5	0.83
0.220	35.1	863	6.87	28.2	0.24
RR	Redness rating of E-horizon soil (Torrent et al. 1980)				
0.410	35.2	879	8.43	26.8	0.33
0.855	26.4	671	7.30	19.2	0.41
1.28	34.0	874	18.8	15.2	1.40
RR	Redness rating of B1-layer soil (Torrent et al. 1980)				
3.48	34.9	875	13.9	21.0	0.72
5.53	34.3	831	12.0	22.3	0.58
8.65	26.6	708	8.74	17.8	0.53
mm	Thickness of organic layer (mm)				
22.9	27.5	762	4.2	23.3	0.18
43.8	34.8	785	17.3	17.5	0.99
71.7	33.0	865	12.7	20.3	0.63

Table 2. The Pearson correlation coefficients and corresponding p-values for the relations between mean particle size in B1-layer soil and stand attributes, and between fraction of coarse sand and gravel in B1-layer soil and stand attributes.

Soil property	n	BA of pine / BA of spruce		BA of pine		BA of spruce		total BA	
		r	p-value	r	p-value	r	p-value	r	p-value
Mean particle size	7	0.799	0.031	0.785	0.037	-0.869	0.011	-0.077	0.870
Fraction of coarse sand and gravel	6	0.794	0.059	0.866	0.026	-0.860	0.028	0.176	0.739

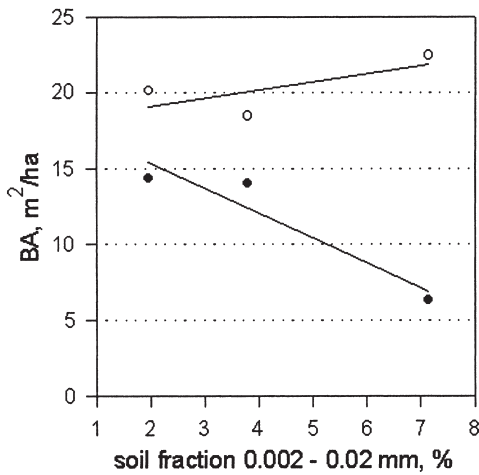


Fig. 8. The relation between the fraction of fine-silt (0.02–0.02 mm) in the B1-layer soil and the basal areas of pine (filled dots) and spruce (empty dots). The solid lines are linear fits to the data.

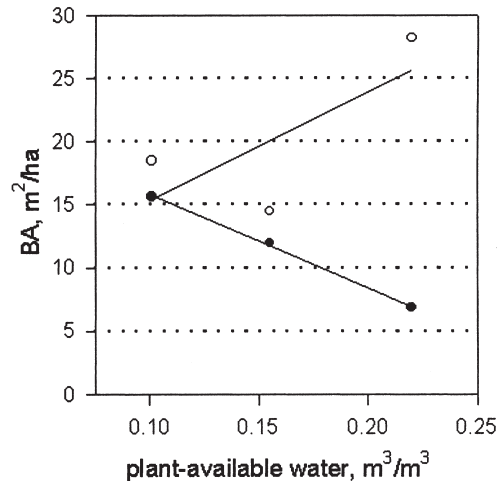


Fig. 9. The relation between the potential plant-available water in the top 30 cm of mineral soil and the basal areas of pine (filled dots) and spruce (empty dots). The solid lines are linear fits to the data.

9, Table 1). There was no uniform trend in the BA of spruce among the map units partitioned on the basis of plant-available water (Fig. 9, Table 1). However, the BA of spruce was highest when the plant-available water was highest, in which case the pine–spruce BA ratio was no larger than 0.27. There were no trends in the stand attributes in the classes of organic horizon thickness (Table 1).

Redness of the E-Horizon and B1-layer and Pine–spruce Composition

Among map units based on E-horizon redness, a

linear decrease in the BA of spruce and a concomitant increase in the pine–spruce BA ratio were associated with an increasing redness (Table 1). There was no corresponding trend in the BA of pine, although it was highest in the map unit of highest redness (Table 1). This was the only case among map units made in the three-class partitions of the study area in which the BA of pine exceeded that of spruce. Contrary to redness of E-horizon the BA of pine and the pine–spruce BA ratio decreased with increasing redness of the B1-layer (Table 1). There was no uniform trend in the BA of spruce, but it also was the smallest in the map unit with the highest redness (Table 1).

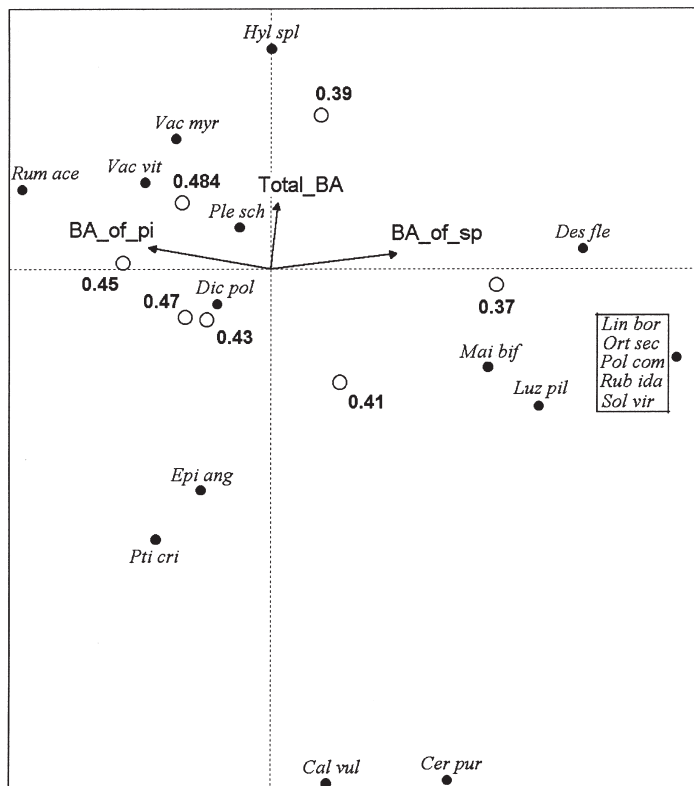


Fig. 10. Canonical ordination (CCA) diagram of the understorey vegetation and map units partitioned on the basis of the mean particle size of the B1-layer soil. The plant species are represented by filled dots and the map units by empty dots. The five plant species inside the box have exactly the same location in the ordination diagram. The total basal area and basal areas of pine and spruce are plotted in the diagram as environmental variables and represented by arrows. The full scientific names of plant species are: Cal vul = *Calluna vulgaris*, Cer pur = *Ceratodon purpureus*, Des fle = *Deschampsia flexuosa*, Dic pol = *Dicranum polysetum*, Epi ang = *Epilobium angustifolium*, Hyl spl = *Hylocomium splendens*, Lin bor = *Linnaea borealis*, Luz pil = *Luzula pilosa*, Mai bif = *Maianthemum bifolium*, Ort sec = *Orthilia secunda*, Ple sch = *Pleurozium schreberi*, Pol com = *Polytrichum commune*, Pti cri = *Ptilium crista-castrensis*, Rub ida = *Rubus idaeus*, Rum ace = *Rumex acetosella*, Sol vir = *Solidago virgaurea*, Vac myr = *Vaccinium Myrtillus*, Vac vit = *Vaccinium vitis-idaea*.

Understorey Vegetation

According to the outcome of the CCA-ordination of map units distinguished on the basis of the mean particle size of the B1-layer (Fig. 10), the tree species composition of the stand is closely associated with the first (horizontal)

ordination axis. The BAs of pine and spruce are strongly correlated with axis ($r = -0.91$ and 0.96 , respectively). Thus, the ordination diagram may be interpreted as an indication that species and map units on the right side of the diagram are associated with high BAs of spruce, while species and map units on the left side of the diagram are

associated with high BAs of pine. The second (vertical) ordination axis is mainly correlated with total BA ($r=0.54$), indicating that species and map units in the upper part of the diagram are associated with a higher total BA than those in the lower part, but this interpretation is probably not as evident as the previous one.

4 Discussion

The tree species composition of a mature stand is a result of a variety of dynamic processes affecting stand establishment and development. Such processes are in the early phase seed production, dispersal, germination and seedling establishment and growth, and later competition of growth factors, self-thinning and various damaging agents like wind-throw, snow breakdown, pests etc. In addition to the natural succession, various mankind activities recently in particular tree harvesting as part of forest management, have influenced on development of the tree stands.

The age of our experimental forest was about 130–140 years, and since there is no time series of the stand development covering this period available, we are not able to evaluate how various processes have influenced the present tree species composition of the forest. The land area where the experimental forest is situated has during early half of the stand development been a relatively sparsely inhabited frontier area certainly with minor if any forestry management. Based on observations, no cuttings have either been performed in the forest over the recent 40-year period prior to the clearcut. We also couldn't observe any obvious thinning-effects in the year-ring widths. In conclusion, we believe that a substantial fraction of the variation in tree species composition of our experimental forest is related to the variation in edaphic site properties.

Our findings indicate that soil texture explains a substantial part of the variation in tree species composition in the stand. The fraction of pine increased (increasing pine–spruce BA ratio) along with increasing mean particle-size and fraction of coarse material in soil. On the opposite, the fraction of Norway spruce was the highest in those parts of the forest where the amount of the fine-

soil material (e.g. silt and clay) was the highest. The result is on general level similar to several earlier studies (Lähde 1974, Sepponen et al. 1979, Sutinen et al. 1996, Penttinen 2000). However, not only pine, but also spruce may regenerate and be competitive on fine sand (0.2–0.6 mm) soils, which is conflicting with Kalela's (1949) findings.

It is suggested that pine is more sensitive than spruce to excess water during the establishment phase (Lähde 1974, Jonsson 1996, Heiskanen and Mäkitalo 2002). The soil texture greatly determines the water retention characteristics of the soil (Mecke et al. 2002) and, as the topography of our site was quite even, also the spatial variation of soil water content on the site. The site index of pine generally increases with the percentages of fine soil fractions unless the site is paludificated (Viro 1947, 1962, Hägglund and Lundmark 1977, Tamminen 1993), and there were no signs of paludification on our site. In addition, pine on average grows faster than spruce on the forest site types occurring on our stand (Gustavsen 1980). Therefore, there is no reason to believe that spruce has been more competitive than pine at the growth phase on our site, and we believe that spruce dominance on locations where soil is at its finest has been produced in the establishment phase. This is supported by that we found rapidly appearing high coverage of *Deschampsia flexuosa* to be linked to preceding spruce dominance. Accordingly, Jonsson (1999) found that 14 years after clearcut the survival of pine seedlings was negatively correlated with the coverage of *Deschampsia flexuosa*, while it had no influence on the survival of spruce.

Sutinen et al. (1996), Penttinen (2000), and Heiskanen and Mäkitalo (2002) suggest that spruce require more moist soil for regeneration and optimum growth than pine. It is probable that drought have caused mortality of spruce seedlings in the stand establishment phase on the map units where the soil is coarsest (pine dominated), although the germination ability of the two species shouldn't have differed considerably (Yli-Vakkuri 1961). Droughts may also have deteriorated the growth of established spruces in these units (Alavi 1996). However, because we observed some small spruces in these map units that were considerably younger (about age of 80

years) than dominant trees, it seems that in some stage of the succession the site conditions have become more suitable for the establishment of spruce. Thus, the spruce possibly has gradually started to colonise also these parts of the stand.

Although the pine–spruce BA ratio increased (competitiveness of spruce decreased) as the silt and clay (< 0.06 mm) content in soil decreased, the range of variation in the species composition within the silt and clay classes was small. Consequently, differences in BAs of pine and spruce were also small among the three classes. This may arise from the rather small fraction of silt and clay in the soil of the mapped area, the class-means of the mapping units were: 6.4, 13 and 26%. Lähde (1974) concluded that in Finnish Lapland, good regeneration results with pine might be expected, if the silt and clay fraction is less than 25%. He also found that on average pine grow naturally on soils with a silt and clay fraction of 16%, but that pine also grows on soils with the fraction exceeding 27%. Penttinen (2000) classified tills according to their silt and clay content into fine-textured (35–50%) and coarse-textured (17–35%) soils, pointing out that the former are supporting stands dominated by spruce and the latter mixed spruce–pine stands. The climate at the growing season is more humid in the Lapland than in the southern Finland where our stand is located (Solantie 1974). Thereby, the upper limit of silt and clay fraction of soils carrying natural pine stands should be even higher in our stand than in Lähde's (1974) or Penttinen's (2000) sites.

Partitioning the stand according to the fraction of fine-silt (0.002–0.02 mm) showed that in the map unit having the highest class-mean (7.2%), the BA of pine was less than half of that in other map units. The range of variation in species composition was much larger than in map units partitioned on the base of silt and clay. Repo and Valtanen (1994) suggest that pine should not be regenerated on soils having a silt and clay fraction over 30%. In addition, they state that particularly fine-silt is a troublesome texture fraction because it causes high water retention, but do not compose secondary structure and thereby facilitate soil aeration, as clay does. Therefore, soils with a large fine-silt fraction are actually more suitable for pine the higher the clay fraction they have, and the percentage of silt and clay is not always

a good measure for the soil aeration.

Partitioning the stand on the basis of the potential plant-available water in the top 30-cm soil layer showed corresponding results to those, obtained on the basis of the soil texture. In the map unit having the highest plant-available water content, the pine–spruce BA ratio was very low. This suggests pine to be less competitive than spruce when surface soil has high water retention capacity.

The relation between soil water conditions and tree stand composition was also reflected by soil type properties. Thus the BA of spruce decreased linearly with increasing redness of the E-horizon, in fact the map unit having the highest redness was the only one among all the three-class partitions where BA of pine exceeded the BA of spruce. The reddish colour of spodic soils originates from oxidised iron mainly in the form of hematite (Torrent et al. 1983). We presumed that on our stand the mineralogy of the parent material was quite uniform. Therefore, the E- and B-horizons would be the redder the more oxidised and less water-saturated the soil conditions are as Mokma and Sprecher (1994) report from a hydro-sequence on a spodosol. However, there was no relation between the pine–spruce BA ratio and the redness of the B1-layer. Thus, on sorted spodosol-soils attention might be rational to focus on E-horizon properties when estimating the ecological demands of pine or spruce or soil-water conditions (Evans and Mokma 1996).

5 Conclusions

On the basis of our results we conclude that competitiveness of Scots pine and Norway spruce is related to soil texture and related hydraulic properties, and in naturally developing forests such variables explain a substantial part of the variations in the tree species composition. Our results suggest that the natural regeneration of pine may fail on the VT and MT forest site types in the glacio-fluvial deposits in southern Finland if the mean particle size is near to the lower limit of fine sand (0.2 mm). Urvás and Erviö (1974) reported that in southern Finland 25 and 42% of MT and VT sites, respectively, are on sorted

soils (about 2 million of the total of 11 million ha) (Urvas and Erviö 1974, Finnish Statistical Yearbook... 2000).

In addition our results suggest that in southern Finland on this kind of glaciofluvial soils pine is more competitive than spruce if the mean particle size is near to the upper limit of fine sand (0.6 mm). However, we studied only one site in southern Finland, which must be kept in mind when evaluating our results. In northern Finland, for example, the climate is more humid than on our site at the growing season (Solantie 1974), and the soil having same physical properties and the same topography is thereby more moist than on our site. It must also be considered that although the soil texture greatly determines the water retention capacity (Mecke et al. 2002) the topography has a great influence on in situ soil moisture (Nyberg 1996). Therefore, the soil-type properties (e.g. soil-type, colours of mineral horizons), which summarise the soil conditions, might be the most interesting topic for the future research when considering the relation of site properties and the success of different tree species.

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Total of 37 references