Growth of Beech, Oak, and Four Conifer Species Along a Soil Fertility Gradient

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Callesen, I., Raulund-Rasmussen, K., Jørgensen, B. B. and Kvist-Johannsen, V. 2006. Growth of Beech, Oak, and Four Conifer Species Along a Soil Fertility Gradient. *Baltic Forestry,* 12 (1): 14–23.

Abstract

Growth of beech, oak, and four coniferous species (Norway spruce, Douglas-fir, Larch and Sitka spruce) was compared in a 33-year-old tree species trial on eight field soils in Denmark. Height and volume growth were fitted in difference equations, and parameter estimates $a(H_{100})$ and $a(V_{tot})$ were tested as biotic site quality indicators against climate and soil fertility indicators. Site quality indicators for height $a(H_{100})$ and volume growth $a(V_{tot})$ increased significantly with soil nutrient availability (PC1) for Sitka spruce, Norway spruce and oak (height), and oak and beech (total volume). Principal component analysis explained 64% of total variance in soil and climate variables by the first component (PC1), which was interpreted as a gradient in soil nutrient availability. The volume growth of oak and beech responded stronger to increasing soil nutrient availability than the conifers, and the correlation was stronger. Conifers were able to maintain a high production on very nutrient poor soils in contrast to oak and beech. Therefore, volume growth $a(V_{tot})$ of conifers as an indicator for soil fertility is inappropriate within the study area, as conifer growth does not reflect soil nutrient availability. However, the correlations observed in growth-site-soil variables in this study suggest that soil information should be used in forecasting growth performance e.g. in planning afforestation of arable land.

Key words: Tree species trial - soil-site relationship, soil nutrient regime – afforestation – set-aside farmland

Introduction

Growth-site-soil relationships for tree species grown on agricultural sites are in request due to contemporary afforestation policies, which recommend mixed stands and extended use of indigenous broadleaves. Innovation in soil mapping techniques, *e.g.* detailed soil texture maps and quantitative approaches in soil classification based on databases for physical and chemical soil properties (O'Connel *et al.* 2000), have increased the demand for and potential use of growth-site-soil studies.

Tree height at a reference age may be termed site index and used in evaluation of site quality, defined as the potential of a site to produce biomass (Carmean 1975). Physical and chemical soil properties are used in soil quality evaluation such as soil fertility rating (Seybold *et al.* 1998) along with biological indicators as *e.g.* site index. Assessment of site quality from tree growth and the correspondence with soil variables will be analysed in this paper. Water and nutrient availability may be related to growth, provided that genotypes are adapted to climate within a region including extreme climatic events, and appropriate parameters are identified and measured.

Field investigations of site index relationships with soil and site variables describing soil moisture regimes and soil nutrient regimes deal with the challenge of keeping other factors constant, while studying the factor of interest, e.g. influence of physical or chemical soil properties on growth across climate gradients. Studies based on inventory data may not have soil and climate factors represented in a crossed design, and the genotype component is not controlled, while designed experiments often have inadequate number of replicates to give statistical evidence.

Growth-soil-site studies for single species across gradients in soils and climate for northern Europe have been published *e.g.* for Norway spruce (Tamminen 1993, Hägglund and Lundmark 1977, Köhler 1984), and for Douglas-fir (Curt *et al.* 2001). Carmean (1975) provided an extensive review of soil-site evaluations identifying soil properties, which predict site index for broadleaved and conifer species in the US. Topsoil depth, subsoil texture, drainage, aspect, and slope position are commonly used predictors of site index in the reviewed investigations (Carmean 1975).

Few Danish studies investigate relationships between the growth and quantitative soil properties and climate parameters. Henriksen (1958) relates Sitka spruce yield class to soil clay content, and Magnussen (1983) constructs a regional Norway spruce yield table for "loamy calcareous tills in coastal south-eastern Denmark", characterized by rapid initial growth, high production and early height growth decline. M¸ller (1954) suggests Norway spruce productivity to be related to extractable phosphorus (0.2 N H_2SO_4) in soils.

We investigate the growth of six tree species in relation to growth environment to evaluate absolute and relative biomass accumulation of different tree species on different soils. This knowledge is useful in forest management planning for both carbon and nutrient budgets. The use of biotic and abiotic site quality indicators are discussed in this context. The following questions are examined:

i) is attained height (H_{100}), total volume (V_{tot}), and biotic site quality parameters for height and volume of six species related to growth environment, and ii) which species are the better indicators for soil nutrient availability ?

Sites and methods

Denmark is characterized by a cool temperate humid climate. The mean annual temperature is 7-8° C, with an average temperature in January of 0° C, and in July 16° C. Mean annual precipitation ranges from 600 to 1000 mm (Scharling 2000). A Danish tree species trial was used to study tree growth in relation to climate and soil parameters, while keeping age and genotype constant. 3-4-year-old seedlings of climate-adapted provenances of Beech (*Fagus sylvatica* L.), pedunculate oak (*Quercus robur* L.), Norway spruce (*Picea abies* (L.) Karst.), Sitka spruce (*Picea sitchensis* (Bong) Carr.), coastal Douglas-fir (*Pseudotsuga menziesii var. menziesii* Mirb. Franco), and Japanese larch (*Larix kaemferi* (Lamp.) Carr.) were planted in adjacent plots of size 0.2 – 0.3 ha in the fall of 1964 and the spring of 1965 in 13 blocks (sites) (Holmsgaard and Bang 1977). The location of tree species plots was randomised within site. Each plot had a buffer zone of 2 to 3 metres. The site selection for this study was restricted to eight sites of formerly cultivated soils, because this study is aimed at decision support to afforestation schemes. More vigorous early growth has been recorded on abandoned fields than on uncultivated soils in Sweden (Karlsson *et al.* 1997, Johansson 1995) and is experienced at local forest districts on poor sandy soils in western Jutland (pers. comm. Ulborg State District foresters). This justifies the choice of field soils in this study. Precise additional details on site history are not available (Holmsgaard and Bang 1977). The sites were mapped in a soil survey by a qualitative description of soil morphology to a depth of 2 m in each plot. All sites were nearly level or gently sloping. One representative soil profile from each site was analysed by genetic horizons for texture, total carbon and nitrogen by dry combustion, extractable phosphorus (P) by 0.2 N H_2SO_4, pH in 0.01 M $CaCl_2$ (soil:water 1:2.5), and exchangeable calcium (Ca), magnesium (Mg) and potassium (K) by 1 M NH_4NO_3 (Stuanes *et al*. 1984).

Soils were classified according to World Reference Base (1998) as Orticaclic Luvisol (Christianssæde, CHR), Cutanic Luvisol (Skjoldenæsholm, SKJ and Frederiksborg, FRE), Hyperalbic Luvisol (Frijsenborg, FRI), Hyperdystric Arenosol (L¸venholm, L¨V), Anthric Podsol (Palsgaard, PAL), Arenic Gleysol (Hanherred, HAN), and Arenic Umbrisol (N¸rlund, N¨R).

Height (15 per plot) and diameter at breast height (DBH) of all the planted trees within each plot was recorded approximately every 3 to 5 years from stand closure, starting about 1980 up to 1998.

Abiotic site quality indicators

Soil nutrient concentrations were converted to contents by soil volume and bulk density in genetic horizons, and summed to nutrient pools (kg ha^{-1}) in 0-100 cm depth. Monthly climate data from 1965-1998 were interpolated from local climate stations (Finn Plauborg Hansen, Danish Institute of Agricultural Sciences, personal communication). The mean precipitation surplus from April 1 to October 1 was calculated as precipitation minus potential evaporation, which was calculated by Makkink's formula (Aslyng and Hansen 1982), and averaged for 1965 – 1998. Soil and site variables were: Soil texture, *i.e.* average clay, silt and fine sand per cent (% w) in 50-100 cm soil depth weighted by horizon thickness, element pools in the top 100 cm mineral soil (kg ha^{-1}) of P, K, Ca and Mg, maximum pH in the subsoil (B or C horizon), C:N ratio of the top mineral soil (0-15 cm depth), drainage class, annual mean temperature, and precipitation surplus (mm) in the growing season (Table 1).

Biotic site quality indicators

Stand height (H_{100} – mean height of the 100 thickest trees in each stand) were estimated by a Näslund Height - Diameter model:

$$H[dm] = (DBH / c_1 + c_2 \times DBH)^{c_3+13}$$

(DBH~diameter at breast height) at each measurement year based on pairs of measured heights (N=20) and corresponding diameters (Näslund 1936). Stand values of total stem volume (m^3 ha^{-1}), and total volume including branches (beech and oak) were calculated from single tree height, DBH, and volume functions for each species including thinned volumes.

Table 1. Abiotic climate and soil variables for water and nutrient availability, and scores of the first principal component, PC1. N=8

Site	T	Surpl.	Drain.	Clay	Silt	Fine sand	pH	P	K	Ca	Mg	C:N	PC 1
	[°C]	[mm]			[% (w)]				[kg ha^{-1}]				
CHR	8.1	-147	5	13	18	46	7.7	2518	660	29041	789	10	3.3
FRI	7.5	-77	5	17	13	48	4.1	1918	546	2420	257	17	0.1
LØV	7.4	-116	4	4	10	46	4.8	1531	176	789	57	13	-0.9
PAL	7.3	-3	6	3	2	29	4.0	72	137	1495	119	17	-3.3
SKJ	7.7	-110	4	17	12	37	7.7	3422	851	12684	840	11	2.6
FRE	7.8	-83	4	23	29	45	5.5	2639	1107	12344	1547	8	3.3
HAN	7.3	-49	6	2	1	54	4.1	423	238	77	20	17	-3.2
NØR	7.3	-61	2	4	9	43	4.4	628	220	1067	59	18	-1.8

T: Mean annual temperature, average for 1964-1998.
Surpl.: Precipitation surplus in growing season (month 4-9 incl.) calculated as precipitation - potential evaporation- (P-Ep).
Drain. Drainage class: (2) well drained, (4) moderately well drained, (5) imperfectly drained, (6) poorly drained.
Texture: Subsoil clay 0-2 mm, silt 2-20 mm, fine sand 20-200 mm, % (w) weighted by horizon thickness at 50-100 cm soil depth.
pH: Subsoil pH (maximum in soil depth 50-100 cm) in 0.01 M $CaCl_2$.
P: Extractable Phosphorus in 0.2 N H_2SO_4.
K, Ca, Mg: Exchangeable nutrients (1 M NH_4NO_3) calculated for soil depth 0-100 cm.
C:N Ratio of carbon to nitrogen pools at 0-15 cm soil depth.
PC1 Score of the first principal component.

Height and volume growth were assessed by fitting difference equations for H_{100} (1) and V_{tot} (2), in steps from time t_1 to t_2 thereby eliminating effects of slow early growth (Johannsen 1999). Each plot had been measured 4 to 6 times at 3 to 5 year intervals.

(1) Height growth $\Delta H = a\hat{H}^{b} e^{-c\hat{H}}$

(2) Volume growth $\Delta V = a\hat{V}^{b} e^{-c\hat{V}}$

ΔH and ΔV refer to growth from t_i to t_{i+1} (i being measurements), $\hat{H}$ and $\hat{V}$ are estimated height or volume at t_i, and a, b and c are fitted parameters. b and c are fixed for each tree species, whereas "a" is estimated for each species grown in one stand on each site, and thus an indicator for site quality for that particular species.

The variables a(H_{100}) and a(V_{tot}) may be regarded as biological indicators for site quality as they describe the height and volume growth rate (Johannsen 1999). Between-plot-differences in "a" for the same species are not linearly proportional with corresponding differences in attained height or volume because the difference equations are non-linear. Equation parameters were fitted by iteration for each stand using the SAS procedure Proc Model (SAS 2000). Estimates for a, b, and c were fitted for each species in accordance with eq. (1) and (2), and were chosen to be dependent on each other within species. Thus, relative species differences were studied after standardisation by mean and standard deviation of "a" for each species to yield mean 0 and standard deviation 1.

Statistical analysis

We interpret a close correlation between biotic and abiotic site quality indicators as a stable growth response to a gradient in the environment. To study growth in relation to soils and site, assumed causal relationships with selected variables published in similar studies, or a best fit approach for a large number of variables could be used in simple or multiple regressions. If abiotic variables are closely correlated, however, multiple regression is not appropriate, and variable selection among soil and climate parameters could be flawed. Here, the number of dimensions (variables) exceeded the number of sites (Table 1). Therefore, principal component analysis (PCA) was applied to investigate if the numerous soil and climate variables could be replaced by one or two independent variables that were linear combinations of the set of original variables (Sharma 1996).

Abiotic soil and site variables were log-transformed if necessary and mean corrected to achieve approximate normal distribution prior to PCA analysis. Analyses were carried out using SAS procedures IML, PRINCOMP, CORR and GLM (SAS 2000).

The growth of each species in relation to the environment was analysed in a homogeneity-of-slopes analysis, including an intercept for species, $\alpha_{species}$, a continuous environment parameter, $\beta_{environment}$, selected in exploratory correlation analysis, and an interaction term with species, $\beta_{species\ x\ environment}$ to test if slopes were different (3).

$$(3)\; H_{100}, V_{tot}, a(H_{100}) \text{ or } a(V_{tot}) \;\square\square_{species} \;\square\square_{environment} \;\square\square_{species\ x\ environment} \;\square\square$$

Results

Soil and stand characteristics

The range in the annual mean temperature was 7.3 – 8.1 ˚C, and the range in the mean precipitation surplus -3 to -147 mm (Table 1). Subsoil texture and subsoil pH ranged from coarse sand to loam and from acid to neutral pH. Ca pools to soil depth 100 cm ranged from 77 kg ha^{-1} to 2.9 x 10^4 kg ha^{-1}, whereas P, K, and Mg pools varied by factor 10-20 and about factor 50 for P. Some sites had low pools of P (PAL), while other sites were low in Mg (L¨V, HAN, N¨R). C:N ratios in 0-15 cm mineral soil were generally low (8 to 18) probably owing to the former agricultural use.

Attained average heights (H_{100}) in 1998 at age 33 years from planting were 14.0 and 14.4 m for beech and oak respectively, while those of Sitka spruce, Douglas-fir, larch and Norway spruce ranged from 19.2 m to 22.9 m (Table 2). Beech and oak did not reach the height of the conifers on any of the sites. Average volume produced (V_{tot}) was highest in Sitka spruce, 704 m^3, followed by Norway spruce, Douglas-fir, and larch, and lowest in beech and oak stands with 269 m^3 and 239 m^3, respectively.

Table 2. Number of plots (N), height of dominant trees (H_{100}) and total volume (V_{tot}) at age 33 years from planting. Conifer species: stem volume; beech and oak: total volume including branches

	Plots	H_{100}			V_{tot}		
Species	N	mean [m]	std[1] [m]	range [m]	mean [m^3]	std [m^3]	range [m^3]
Sitka spruce	8	22.9	2.3	19.8 - 25.8	704	146	508 - 872
Douglas-fir	8	20.5	3.3	14.2 - 23.7	506	170	273 - 754
Norway spruce	8	19.2	3.2	12.7 - 22.2	575	180	175 - 748
Larch	8	19.7	2.7	14.5 - 23.0	464	133	244 - 581
Beech	8	14.0	3.2	9.8 - 17.8	269	137	92 - 494
Oak	7	14.4	3.1	9.0 - 17.8	239	93	118 - 377

[1]std~standard deviation

Temperature, clay and silt were significantly (up to r~95%, P<0.05) positively correlated with pH and nutrient pools (Table 3). Moisture surplus was negatively p-correlated with pH and P pools, and Ca, Mg and K pools were correlated with each other, and with clay and silt.

Table 3. Pearson correlation matrix of log-transformed (Ca, Mg and K), and mean corrected climate and soil variables. Variable names as in Table 1. Significant correlation (P < 0.05) in bold. N=8

r	T	Surpl.	Dr	Clay	Silt	Fine sand	pH	P	K	Ca	Mg
T											
Surpl.	**-0.75**										
Drain.	0.07	0.34									
Clay	**0.71**	-0.44	-0.14								
Silt	**0.75**	-0.55	-0.33	**0.86**							
Fine sand	0.10	-0.37	-0.10	0.07	0.19						
pH	**0.85**	**-0.76**	-0.02	0.51	0.46	-0.10					
P	0.69	**-0.87**	-0.45	**0.74**	**0.73**	0.44	0.65				
K	**0.80**	-0.56	-0.07	**0.95**	**0.81**	0.21	0.67	**0.81**			
Ca	**0.86**	-0.57	-0.14	**0.77**	**0.74**	-0.31	**0.78**	0.58	**0.74**		
Mg	**0.84**	-0.47	-0.04	**0.91**	**0.81**	-0.23	**0.71**	0.61	**0.87**	**0.95**	
C:N	**-0.83**	0.67	0.04	**-0.71**	**-0.78**	0.01	**-0.78**	-0.69	**-0.76**	**-0.76**	**-0.81**

Site quality parameters for growth

Correlation between height or total volume and soil and climate variables differed by species (correlation matrices not shown). Height and total volume of larch were not significantly correlated with any of the investigated variables in Table 1, whereas Douglas-fir was positively correlated with silt. In contrast to them, height and total volume of beech were positively correlated with all variables, except fine sand. In oak, both height and total volume were correlated with Ca, and height also with temperature, clay and Mg. Height and total volume of Sitka spruce and Norway spruce were negatively correlated with C:N ratio and positively correlated with Ca. In Norway spruce stands, also Mg was significant, and in Sitka spruce V_{tot} was negatively correlated with moisture surplus. Thus, correlation of H_{100} and V_{tot} for different species with abiotic variables showed similarities, but also inconsistencies.

Correlation between biotic site quality variables $a(H_{100})$ and $a(V_{tot})$, and abiotic site quality variables were found for Sitka spruce, Norway spruce, beech and oak (correlation not shown). For $a(H_{100})$ these were temperature (oak), clay (oak), silt (oak and Sitka spruce), and nutrient pools, especially Ca and Mg, (oak and Norway spruce), K (oak) or P (beech), and C:N ratio (Sitka spruce, beech and oak).

Volume growth, $a(V_{tot})$, was correlated in a similar way for oak (excluding clay, silt and K, but including subsoil pH), whereas beech had more significant variables, also including clay, P, K, Ca , and Mg. Among conifers $a(V_{tot})$ estimates were positively correlated with silt (Douglas-fir) and Ca and Mg (Norway spruce).

Abiotic variables in PCA

The inconsistent univariate correlation between biotic and abiotic variables, and the strong correlation between abiotic variables suggested a multivariate approach reducing the number of variables used in characterization of each site. For this purpose we used the PCA analysis. The first axis (PC1) explained 64 % of total variance in the soil and climate data. PC1 was influenced almost equally by temperature (+), clay and silt (+), soil nutrients (+), moisture surplus (-) and C:N ratio (-), judged by the first Eigen vector and loadings, *i.e.* the correlation of each variable with PC1 (Table 4). The second axis (PC2) that explained 15 % of total variance was mainly influenced by fine sand (-). The score plot of PC1 versus PC2 (Figure 1) revealed a clear differentiation of sites along PC1 with increasing temperature, clay, silt, subsoil pH and nutrient pools and decreasing C:N ratio, and precipitation surplus (cf. Table 1). Along PC2, Palsgaard (PAL) was different from the other sites, owing to the low fine sand content. Due to strong correlation between abiotic variables, PC1 was used in ANOVA, and subsequent regression analysis of the relationships between biotic and abiotic site quality variables.

Table 4. Eigen-vectors and loadings (correlation of PC scores with abiotic variables). Significant correlation in bold (P < 0.05). Variable names explained in Table 1

Env. variable	PC1	PC2	$r_{Env\ x\ PC1}$	$r_{Env\ x\ PC2}$
T	0.33	0.08	**0.92**	0.11
Surpl.	-0.28	0.31	**-0.76**	0.42
Drain.	-0.07	0.41	-0.19	0.55
Clay	0.32	0.04	**0.88**	0.06
Silt	0.31	-0.09	**0.87**	-0.11
Fine sand	0.03	0.64	0.09	**-0.85**
pH	0.29	0.12	**0.81**	0.16
P	0.31	-0.36	**0.85**	0.48
K	0.33	-0.02	**0.92**	-0.02
Ca	0.32	0.27	**0.89**	0.35
Mg	0.33	0.27	**0.91**	0.36
C:N	-0.32	-0.09	**-0.89**	-0.12

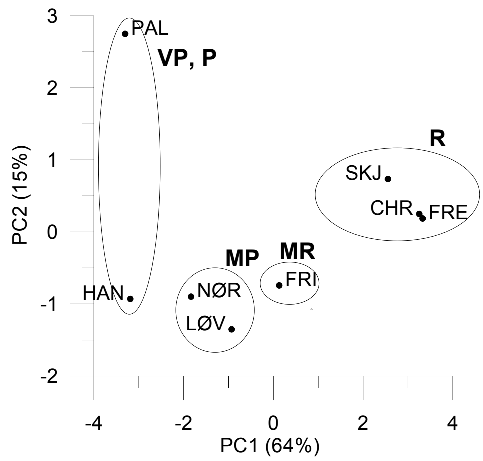

Figure 1. Score plot of PC1 versus PC2. Similar sites along PC1 are encircled. PC1 is soil nutrient availability gradient. Abbreviations refer to location (Table 1) and soil nutrient regimes: Very poor (VP), poor (P), medium poor (MP), medium rich (MR), rich (R), and very rich (VR)

H_{100}, $a(H_{100})$, V_{tot} and $a(V_{tot})$ depended significantly on PC1 (*P<0.0002*), but no further explanation attributable to individual tree species was significant (*P-values* in the range 0.42 – 0.90 ^{NS} for $\beta_{species\ x\ PC1}$), after accounting for the significant positive effect of β_{PC1} common to all tree species. Only $a(H_{100})$ for oak and $a(V_{tot})$ for oak and beech were significantly correlated to PC1 (Figure 2 and 3). The indication that not all tree species responded positively to PC1, allowed testing of a model excluding the main effect of soil nutrient availability, β_{PC1}. In this model $\beta_{species\ x\ PC1}$ was highly significant, and the parameters for each species were estimated in separate regressions (Figure 2 and 3). The growth of Sitka spruce, beech and oak were considerably related to PC1 for three out of four biotic variables. For Sitka spruce V_{tot} but not $a(V_{tot})$ was significantly related to PC1, whereas for oak $a(V_{tot})$ was correlated but not V_{tot}. The growth of Douglas-fir and larch were unrelated to increasing values of PC1. Slopes of $a(V_{tot})$ with PC1 was steeper for beech (β_{PC1} ~ 0.30) and oak (β_{PC1} ~ 0.27), than for conifers (β_{PC1} in the range 0.12 - 0.21, Figure 2 and 3).

Discussion

The soil and climate variables included in Table 1 may all add causal explanations to growth variation in the six studied species, but only few univariate correlations between growth and site were found. However, much insignificant correlation between biotic and abiotic parameters pointed in the same direction. Furthermore, the correlation between abiotic variables made interpretation of single soil and site variables unjustified. Instead, the PCA analysis should be used to represent the numerous dimensions at the limited number of sites. No single variable is likely to control the growth along the studied gradient in soil fertility.

The gradient in climate is small compared to the gradient in soils. In respect of precipitation surplus, the climate gradient is contradictory to the gradient in soil nutrient availability. Available nutrients for root uptake during the growing season depend on both nutrient pools and soil moisture. These parameters are more favourable in loamy tills as compared to sandy podsolized soils within the range of soils stud-

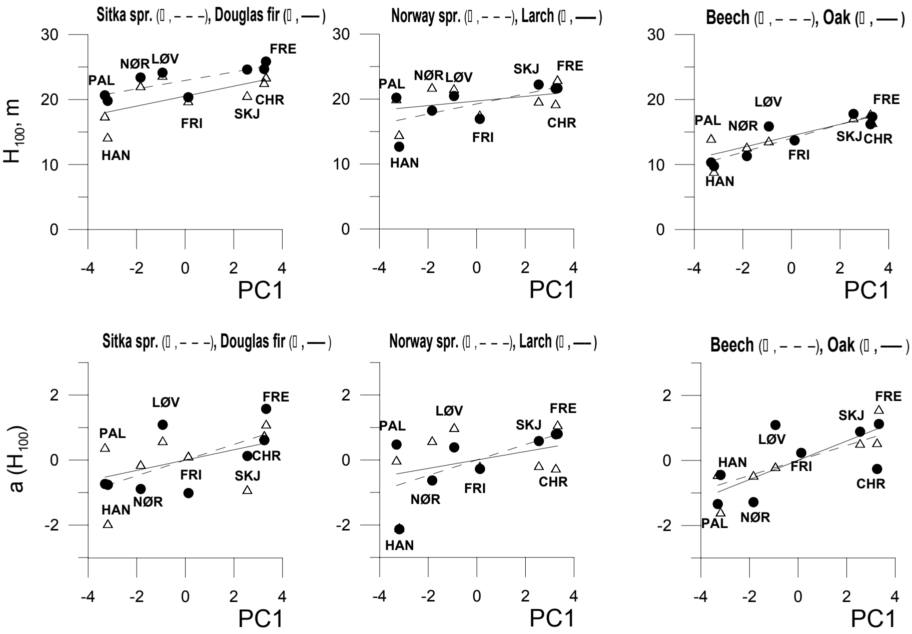

Figure 2. Top height (H_{100}, height of the 100 thickest trees per hectare) at 33 years from planting, and site quality for height growth, a(H_{100}), versus a linear combination of abiotic variables, PC1. PC1 is correlated with increasing element pools (+), clay and silt per cent (+), pH (+), annual mean temperature (+), mean water precipitation surplus in growing season (-), and C:N ratio (-). The positive relationship of $H_{100}$with PC1 was significant for Sitka spruce ($P<0.05$, $R^2\sim0.61$), beech ($P<0.01$, $R^2\sim0.83$) and oak ($P<0.01$, $R^2\sim0.74$). For a(H_{100}) the *P*-levels and coefficient of determination were: Sitka spruce ($P<0.05$, $R^2\sim0.44$), Norway spruce ($P<0.05$, $R^2\sim0.43$), and oak ($P<0.01$, $R^2\sim0.78$)

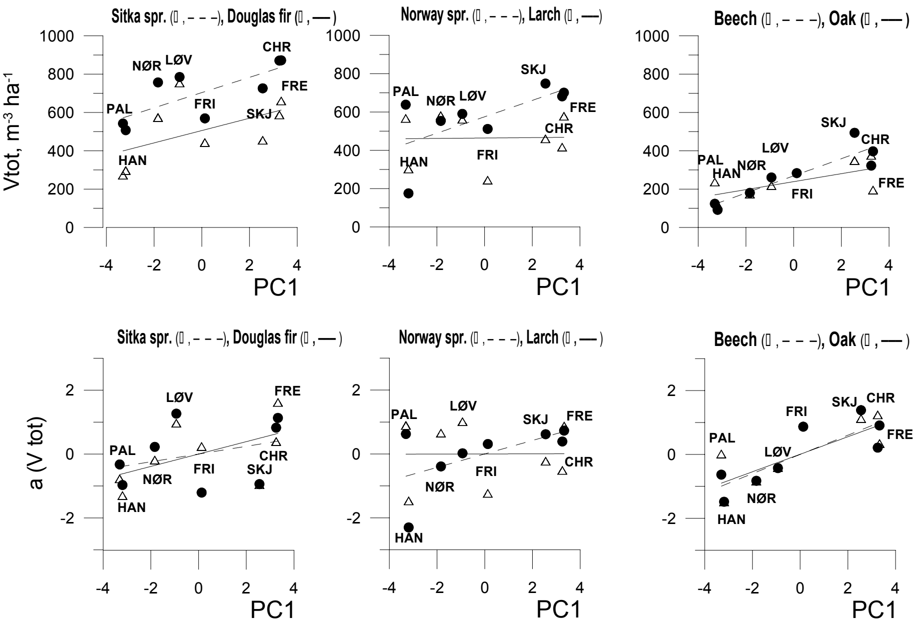

Figure 3. Total stem volume, V_{tot}, (conifers) and total volume (beech and oak) produced at 33 years from planting, and volume growth site quality (V_{tot}), versus PC1. The positive relationship with total volume, V_{tot}, with PC1 was significant for Sitka spruce ($P<0.05$, $R^2\sim0.57$), and beech ($P<0.01$, $R^2\sim0.82$) and for a(V_{tot}) with beech ($P<0.01$, $R^2\sim0.69$) and oak ($P<0.05$, $R^2\sim0.67$)

ied. Nitrate availability is higher in loamy soils in comparison with sandy soils (Callesen *et al.* 1999). Observed C:N ratios below 15 in loamy soils in contrast to ratios >15 in sandy soils suggest higher N availability on the loamy sites (Table 1). Unstable water supply caused by lower available water capacity in sandy soils as compared to loamy soils may explain the clear co-variation of summer precipitation and annual ring width observed in low-productive Danish Norway spruce stands. In contrast to this, weaker correlation between the ring width and precipitation was observed on sites with higher production class (Holmsgaard *et al.* 2001). Here, observed differences in site quality was attributable to the gradient in availability of soil nutrients and water. Therefore, soil differences are more important than the climate factor in this regional study with limited climate variation.

The low sampling intensity of just one soil profile per site could be justified by the broad range in soil nutrient pools, subsoil texture, and subsoil pH. Andersen *et al.* (2002) found that tree planting on these sites changed top soil properties during the time course of the experiment, causing a lowered pH, and decreased concentrations of exchangeable base cations. Subsoil properties have not been influenced by tree species after 33 years (Andersen *et al.* 2002). Nutrient pools to a fixed soil depth representing most of the root volume seem to be robust indicators for abiotic site quality. It was illustrated by the range in nutrient pools and texture among sites (cf. Table 1), and the amount (64%) of total variation explained by the first principal component, PC1.

The linear increase in the growth of beech with PC1 is unlikely to continue beyond the maximum subsoil clay content of 23% in our data, as poor internal drainage caused by insufficient pore space may impair root growth and thus nutrient availability in heavy clay soils. Clay-rich Danish tills approximately contain up to 30 % clay, and lacustrine deposits up to 50 clay %, representing sites, where *e.g.* beech does not thrive well (personal observation). Adequate soil aeration and favourable conditions for root penetration are important to soil nutrient availability in beech stands.

Positive relationships between the growth and abiotic site indicators for Norway spruce (Hägglund and Lundmark 1977, Köhler 1984, Johansson 1995, Stendahl *et al.* 2002) and also Douglas-fir (Curt *et al.* 2001, Dunbar *et al.* 2002) are reported in the literature. Stem diameter at breast height and basal area are positively correlated with Ca-pools in a soil-site study of twelve 23-year-old Norway spruce stands in Lower Saxony (Köhler 1984). Among other chemical properties, site index depends on exchangeable mineral soil Ca concentrations in a soil-site study of Norway spruce stands growing on substrates rich in weatherable minerals in central Sweden (Stendahl *et al.* 2002). The correlation between the site index (height at reference age 100 years) and exchangeable Ca in mineral soil in Scots pine (*Pinus sylvestris* L.) stands, but not in Norway spruce stands, is seen in southern Finland (Tamminen 1993). Here, the correlation with Ca for Norway spruce was significant and positive, in line with cited studies (Köhler 1984, Stendahl *et al.* 2002). A soil-site study of Douglas-fir in Ireland on former agricultural soils finds soil parent material to be indicative for site quality (Dunbar *et al.* 2002) in a study of 120 stands, also including physiography and climate as predictors of site class. Thus, the eight experimental sites used here were insufficient in demonstrating an expected statistical inference for Douglas-fir.

A Danish investigation of 14 oak stands with an age from seed in the range of 30 to 75 years planted on soils with 3 to 32% clay showed correlation between the growth rate for height and basal area; and silt, fine sand content, and temperature. The correlation between the growth rate and clay was not found (Johannsen 1999). In our study temperature was positively related to oak growth, but the increase in nutrient availability along PC1 also contributed (pH, Ca, Mg, C:N, Table 3). These relationships cannot be separated in the present data set. For beech, the positive response in growth rate seems to be related to soil nutrient availability, as suggested by the relationship with clay and other soil nutrients related to the clay content (P, K, Ca, Mg, and also C:N ratio).

The significant increase in height and volume growth with PC1 in beech and oak may be interpreted as sensitivity to stress on poor sites and/or stronger response to increasing soil nutrient availability along the soil nutrient gradient. The poorest sites (HAN and PAL) had the lowest nutrient pools, and low soil pH, suggesting that nutritional stress cannot be excluded as a reason for slow growth. The sites also had high ground water tables and a sandy soil texture. However, in years with low precipitation, water stress may also impair nutrient uptake. Sitka spruce is adapted to coastal sites with high deposition of sea salt, whereas Norway spruce is intolerant of salt spray (Saxe 1993). The height of Sitka spruce exceeded that of Norway spruce on the Hanherred site (HAN, Figure 2). Lack of salt tolerance, and wind deformation could be the explanation for heights lower than predicted for all other species than Sitka spruce on the Hanherred site.

Early summer frost could have retarded height growth of beech at Palsgård as compared to oak, and red deer browsing and weeds were a severe problem on the Frijsenborg site in particular, causing a slow initial growth of the seedlings (Holmsgaard and Bang 1977). On poor sites N¸rlund and Palsgård (apart from Hanherred), oak was taller than beech, suggesting better adaptation to recurring spring frosts and nutrient poor conditions. Slow growth may be caused by adverse climate and insufficient nutrient and water availability. Site quality parameters $a(H_{100})$ and $a(V_{tot})$ for beech, oak, Sitka spruce, and Norway spruce reflect the soil nutrient availability gradient, although confounding variation in climate and deposition like wind and salt cannot be separated from the gradient in soil nutrient regime. The lack of significant relationships between the growth rate and soil fertility for Douglas-fir and larch underline that not all tree species show the same response.

In the search for inexpensive indicators for soil quality with respect to soil nutrient regime and site quality for tree growth, the parameters in Table 1 were evaluated. The subsoil clay content, and soil reaction are site specific parameters, which may be evaluated in the field at low cost. These are highly correlated with nutrient pools (Table 1), and, in general, with C:N ratio of the top mineral soil (Callesen *et al.* in review).

Biotic and abiotic site quality indicators may be used to group sites into classes of soil nutrient regime (Figure 1). SKJ, CHR and FRE could be termed *rich* or *very ric*h non-acid or slightly acid loamy tills, followed by the *medium rich* acid loamy till FRI, *medium poor* fine sandy acid brown soils N¨R and L¨V, *poor* fine sandy weakly developed HAN, and the *very poor* coarse sandy podsolized PAL. This classification is in accordance with the long-term capability for nutrient release as determined by simulated weathering of the same soils, controlled by soil texture (Callesen and Raulund-Rasmussen 2004). Thus, the apparent nutrient availability gradient is also a gradient in potential long-term nutrient availability by weathering. Lack of nutrient sustainability may be an issue for productive species at very poor to medium poor sites with minimal exchangeable nutrient pools, since depleted nutrients cannot be replaced by weathering or would only be replaced at extremely slow rates (Callesen and Raulund-Rasmussen 2004). However, input-output nutrient budgets based on ecosystem fluxes of elements must be calculated for specific species and sites to assess nutrient sustainability, also taking deposition of Ca, Mg and K into account. Beech and oak produced less volume than conifers (Table 2) up to the age of 33 years from planting years especially on the nutrient poor sites (Figure 2 and 3). Negative element mass balances (inputs < outputs) are seen in conifer plantations on poor soils in the region (Hovmand and Bille-Hansen 1999). Silviculture using broadleaves may thus be a strategy to prevent depletion of available soil nutrient pools, but this hypothesis requires examination of element balances for the broadleaved species.

The results of our study underline the need to distinguish and specify the terms “site quality” for e.g. biomass production and “soil fertility”. The site quality (height or volume growth) is particular for each tree species. Soil fertility is focused on e.g. nutrient sustainability and should be evaluated independent of tree species.

Height and volume growth (or biomass production) are supposedly closely related parameters, but for beech, $a(V_{tot})$ was significantly related to PC1, whereas $a(H_{100})$ was only near-significant (P = 0.06). The situation was opposite for Norway spruce and Sitka Spruce. Therefore, height growth may not be generalised as an indicator for site productivity, Figure 2 and 3.

Conclusions

We conclude that investigation of the relationships between biotic and abiotic site quality indicators require stratified sampling with respect to all factors significant to water and nutrient availability (*i.e.* soils, climate, deposition etc.).

It was not achieved in the present experiment, and is rarely achieved in field experiments across regions. However, the experimental design allowed relative comparison of species across a soil nutrient availability gradient, which is unique. Definition and delimitation of the study area is important in soil-site studies (Carmean 1975) to evaluate their general applicability. We studied a strong gradient in soil nutrient availability that excluded heavy clay soils. The climate gradient was weak, although confounded with the soil nutrient gradient. Dimension reduction by the principal component analysis was useful in treating the multidimensional growth environment, and thereby establishing significant relationships between biotic and abiotic site quality variables as an overall result for all species, although species responded differently. Sitka spruce, beech and oak showed the strongest response in volume growth to increasing nutrient availability, whereas larch showed no significant response to increasing soil nutrient status. Inexpensive parameters such as the subsoil clay content and soil reaction (pH) may be used as indicators for nutrient availability (cf Table 3). We acknowledge that empirical indicators only in part represent cause-effect relationships between the growth and growth environment in the study region. The site indicators for growth of beech and oak as well as attained height and volume at age 33 could be used as indicators for soil nutrient availability whereas coniferous species were less useful. This conclusion may be useful in the forecasting of stand growth based on soil information when agricultural land is afforested.

Acknowledgements

The study was part of the Strategic research centre “Changing Landscapes” (http://www.sdu.dk/Hum/ForandLand/English/Index.htm). We acknowledge financial support from The Danish Environmental Research Programme 1999-2001, and Aage V. Jensens Fonde. We thank the forest districts that hosted the experiments and provided manpower for mensuration.

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Received 10 October 2005
Accepted 26 May 2006

РОСТ БУКА, ДУБА И ЧЕТЫРЕХ ХВОЙНЫХ ПОРОД НА ПОЧВАХ РАЗНОГО ПЛОДОРОДИЯ

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Резюме

Рост бука европейского (*Fagus silvatica* L.), дуба черешчатого (*Quercus robus* L.) и четырех хвойных пород - ели европейской (*Picae abies* (L.) Karst.) и ситхинской (*Picea sitchensis* (Bong.) Carr), лжетсуги тиссолистной (*Pseudotsuga menziesii var. menziesii* (Mirbю) Franco) и лиственницы японской (*Larix leptolepsis* (Gord.) Murr.), сравнивался в 33-летних опытных культурах, растущих на различных восьми почвах Дании. Высота и объем насаждений были введены в ряд уравнений, а параметры этих показателей роста - тестированы для индикации качества условий произрастания в сравнении с такими индикаторами как климат и плодородие почвы. В целом установлено, что с увеличением доступных растениями питательных веществ в почве, в насаждениях значительно повышается высота ели и дуба, а общий объем – в насаждениях дуба и бука. Применение основного компонентного анализа показало, что 64% общей изменчивости почвенных и климатических показателей отражает градиент доступных питательных веществ в почве. Также выявлено, что по сравнению с хвойными, рост дуба и бука значительно более положительно реагирует на плодородие почв. Хвойные насаждения могут отличаться высокой продуктивностью и на неплодородных почвах, поэтому их объем в большинстве случаев не отражает содержание доступных питательных веществ. Не смотря на это, выявленные корреляционные связи между показателями роста насаждений и почвенными условиями произрастания подтвердили необходимость применения информации о плодородии почв для прогнозирования продуктивности лесных насаждений, например, при планировки облесения пахотных земель.

Ключевые слова: различные древесные породы, почвенные условия произрастания, плодородие почв, облесение, пахотные земли