REALIZED CORRELATED RESPONSES AT LATE STAGE FROM UPWARD, DOWNWARD, AND STABILIZING SELECTION AT NURSERY STAGE IN *PICEA ABIES* (L.) KARST.

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Received September 20, 1996; accepted August 26, 1997

ABSTRACT

Response to selection for height growth among four-year old seedlings in the nursery is investigated. The selection of ortets was carried out as a three-way selection, as 3 fragments were selected as upward, downward and as stabilizing selection followed by cutting propagation. The selected ortets consisted of 20 series of the tallest, an intermediate, and the smallest seedling within neighbourhoods of 100 plants in the nursery bed. In the subsequent clone trial, significant differences between the three selection groups were recorded for the following traits: height at ages 4, 9, 11, 15, and 21, height increment at ages 15–21, DBH at ages 15, 17, and 21, DBH increment at ages 17–21, flushing at age 22 and frequency of forks at ages 15 and 17. The analyses indicate that upward selection for height growth among 4-year old plants in the nursery with the applied selection intensity of 3.07 followed by vegetative cutting propagation results in a genetic gain of 7.6% for both height and DBH at age 21. The increased vigour is associated with slightly earlier flushing in spring at age 22, but not at age 4. Basic density levels estimated by the water displacement method of segment of increment cores and by Pilodyn were investigated to study correlated responses on wood quality. The basic density was adjusted for the effect of ring width and ring number, and pilodyne was adjusted for the effect of DBH. No adverse correlated response of basic density level so adjusted occurred as the result of the applied early selection for height growth, i.e. density is only affected negatively as the well known, predictable effect of wider rings associated with faster growth in Norway spruce.

Key words: *Picea abies*, clonal selection, clonal tests, early selection, correlated response, quantitative genetic parameters, ortet-ramet regressions.

INTRODUCTION

The importance of assessing characteristics at the juvenile stage and correlating them with performance at later stages of development is obvious in long living organisms such as forest trees. It is possible to select for very early growth in favourable nursery environments, but the physiological and genetic background for growth rate at early and later stages may not be identical, because stress inducing environmental factors as competition, climatic variation and scarcity of water supply accumulate at later stages. However, in breeding programs, a more accurate late selection for growth rate resulting in a higher genetic gain per generation may be outweighted by the corresponding delay in generation turn-over of the breeding population. Therefore, it is important to choose the stage for selection where the genetic gain per year is maximized. This, among other things, depends on the genetic correlation between the juvenile and the mature stage and the correlated responses of juvenile selection at the mature stage.

The objectives of the present study are (i) to determine the development of quantitative genetic parameters over time, (ii) especially to estimate genetic correlations between early growth and later stage growth, growth rhythm and wood quality traits, and (iii) –based on (i) and (ii) – to detect realized, correlated response for the observed characters at later stages as a result of selecting for height at the nursery stage. Earlier results from the investigated trial have earlier been reported (ROULUND *et al.* 1986).

MATERIAL AND METHODS

Plant material

The base population in the present experiment originates from a 2+2 commercial lot of Norway spruce seedlings from the selected seed stand "Nødebo F71i." This stand represents a well adapted local strain of west-continental origin. The seedlings were grown in the nursery of the Tree Improvement Station in Humle-

baek, Denmark. The selection of ortets was made in spring 1974.

Experimental design

20 sample plots of 100 seedlings each were demarcated in contiguous neighbourhoods of 20 seedlings selected for height growth. In each of these sample plots, two additional seedlings were selected, one representing the sample mean and another representing the slowest growing individual with the restriction, that it nevertheless should be able to deliver a sufficient amount of twigs for the subsequent cutting propagation. By this sampling procedure, three ortets were selected in each of the 20 sample plots representing upward, downward and stabilizing selection for early height growth. After cutting propagation and two years in a randomized block experiment in the nursery with three replications and 3–9 tree plots, the primary cuttings were transplanted to a field trial in the forest. This clone trial was established in the same overall environment, i.e. in sheltered conditions in Eastern Denmark on fertile soil. The field trial was laid-out as a randomized block design with two replications and 3–9 trees per plots.

Characters recorded

For the ortets total height at the 2+2 nursery stage was recorded for all 100 seedlings in each of the 20 sample plots. In each sample plot, this implied height growth of the 3 selections (the upward, the downward and the stabilizing selected ortets) plus the 97 remaining individuals of the 100-seedling sample plot.

For the ramets the characters investigated are listed in the left column of Table 3. Height was measured in the nursery experiment (age 4) and in the field trial at ages 9,11,15, and 21, whereas diameter at breast height (DBH) over bark was measured in the field trial at ages 15, 17, and 21. Based on these primary observations increment between different ages for height and DBH were derived. Direct observations on length of leader was carried out at age 21 representing height increment at age 20–21.

Flushing was scored in the nursery experiment in May 1974 (age 4) and in the field trial in May 1995 (age 22) applying the IUFRO scale 1–9 for Norway spruce (KRUTZSCH 1973). At a given date of observation, low values represent late flushing, high values early flushing.

The clones were investigated for wood basic density by two different methods: (i) using the Pilodyn instrument (COWN 1978 ,YANCHUK & KISS 1993) by firing a pin with a given force into the outer rings after removal of the bark; the Pilodyn measurements were done at ages 17 and 21; (ii) basic density was furthermore assessed on 21 of the 59 clones by the following method: Two diametrical opposite increment cores through the pith from bark to bark were taken from clear wood near breast height. The diameter of the cores were 4.2 mm. The cores were separated into segments of two annual rings numbered from the pith and the width of individual rings were measured. The basic density of each segment was recorded by the water displacement method (OLESEN 1971), and the weighted average ring width of each segment was calculated. The average ring width of each two-ring segment was weighted according to the volumen of each ring in the segment.

Quantitative genetic framework

The material is put into the framework of quantitative genetics (FALCONER 1989) in the following way: A clone consists of the ortet plus a population of ramets, where the ortet is the 4-year old initial selected individual, which subsequently was vegetatively propagated by cuttings (ramets). In this way, the ortet and the subsequent population of ramets share the same genotype. The same character recorded at early and late stages is treated as if they were different characters. These and other traits may be more or less correlated. These correlations are estimated by their phenotypic and genetic correlations. The phenotypic correlations are based on clone means. In the present case, the recorded late clonal responses to early selection of individual ortets in the nursery are interpreted as realized correlated responses. Upward and downward selection are two-way selection in opposite directions for specific traits. Selection favouring intermediate values for specific traits is termed stabilizing selection.

The statistical terms obtained in sample plots and randomized block experiments have been given the quantitative genetic interpretation presented in Table 1. Broad-sense heritability – h^2_{bs} – is in general for specified quantitative traits defined as

$$h^2_{bs} = \frac{V_G}{V_P} = \frac{V_G}{V_G + V_E}$$

Heritabilities can be defined as a parameter of a population of individuals – or as a parameter of replicated clones in a field trial. In the population of individuals, the heritability is a parameter of that particular population growing in a specific environment and is refering to variation between individuals. In the replicated clonal trial, clone means are derived and then the broad-sense heritability is a parameter of this particular population of clone means. V_P represents the pheno-

Table 1. Quantitavive genetic interpretation of statistical terms

Sample	Statistical terms		Quantitative genetic interpretation	
Populations of individuals	Within population variance	σ^2_P	Phenotypic variance	$V_P = V_G + V_E$ (assumed components)
Clonal tests laid out as randomized blocks and analyzed by two-way ANOVA with main effects clones and replications	VAR comp for clones	σ^2_{Cl}	Genetic variance	V_G
	Random error = VAR comp for plot means	σ^2_e	derived: environmental variance of clone means r = no of reps	$V_E = \frac{\sigma^2_e}{r}$
	COVAR comp for clones between trait A and B	$COV_{Cl(A,B)}$	Genetic covar between A and B	$COV_{G(A,B)}$

typic variance between clone means and V_E represents the error variance of the clone mean. In the case of application of simple two-way ANOVA of the plot means of the randomized block experiment, V_G is estimated as the variance component of clones and V_E is estimated as σ^2_e/r where σ^2_e represents the statistical error variance of individual plot means and r represents number of replications.

STATISTICAL METHODS AND DATA ANALYSES

Refering to the objectives of the investigation cited in the introduction, four types of analyses have been performed: (i) based on 4-year heights of the ortets, estimation of the selection differential and intensity of the three selection groups initiated by upward, downward and stabilizing selection; (ii) based on the clonal trials of the ramets, estimates of quantitative genetic parameters – *i.e.* variance and covariances between individual clones for the recorded traits resulting in broad-sense heritabilities of clone means and phenotypic and genetic correlations between traits; (iii) ortet-ramet regressions for successive stages of height growth based on ramet means of individual clones and the relative heights of the original 4-year old ortets; (iv) realized correlated responses at a late stage as a result of the early selection of three groups of 20 ortets each, namely the upward, downward and stabilizing selection for height growth.

Selection differential and -intensity of ortets

In each of the 20 nursery plots of 100 individuals, plot mean and phenotypic standard deviation was calculated for height at age 4. A pooled estimate of the phenotypic standard deviations in the 20 sample plots was derived. The deviation from the plot mean of the three selections, the highest, the lowest and one close to the plot mean were calculated in absolute and relative values (mean = 100). For each of the three selection groups of 20 ortets, a selection differential and a selection intensity were derived. The selection intensity was calculated as the average absolute selection differential standardized by the within-plot phenotypic standard deviation.

Quantitative genetic parameters estimated in the field trial of ramets

ANOVAs of plot means are the basic analysis. For all traits except those associated with wood density, simple averages of surviving plot members are applied. Survival was generally close to 100 %.

Basic wood density level – the water displacement method

The general framework developed by OLESEN (1976) and SILVA *et al.* (1994) is applied. The general idea is to define the density level as density adjusted for the obvious effect of ring width by regression and adjusted for ring number from the pith (the degree of juvenility) by only comparing density of rings belonging to the same ring numbers. In the present case, an analysis of covariance is applied to individuals within plots with the following model:

$$Y_{ijk} = \mu + a_i + b_j + c(x_{ijk} - \bar{x}...) + e_{ijk}$$

where: Y_{ijk} – density of individual k in ring no j in plot

i; μ – grand mean; a_i – fixed effect of plot i; b_j – fixed effect of ring no j; $c(x_{ijk}-\bar{x}...)$ – common effect of the co-variate ring width, and e_{ijk} – random error.

A transformation of ring width is applied as the relation between basic density and ring width in Norway spruce is non-linear and has been described mathematically by a hyperbolic function (OLESEN 1976):

$$R = a + \frac{b}{Rw+c} = a + b \times Rw'$$

where: R – basic density; Rw – ring width (mm); Rw' – transformed ring width (mm); a, b and c – constants.

Several values of the constant c were tried, and the lowest error mean square was obtained with the transformation involving c = 2 mm. By this approach, the adjusted plot means (LS Means in SAS) represent the density level of individual plots, i.e. basic density adjusted for the recorded effects of ring number from the pith and ring width. The so obtained basic density levels for plots are subsequently analyzed as the simple plot means for the remaining characters height, DBH , etc.

The pilodyn level

Pilodyn readings are analyzed in an analogous manner. Here only two observations are available per tree: the penetration of the pin and DBH. The model in this case is:

$$Y_{ik} = \mu + a_i + b(x_{ik}-\bar{x}..) + e_{ik}$$

where: Y_{ik} – Pilodyn reading of individual k in plot i; μ – grand mean; a_i – effect of plot i; $b(x_{ik}-\bar{x}..)$ – linear effect of covariate DBH, and e_{ik} – random error.

The obtained adjusted plot means are termed Pilodyn level and are subsequently analyzed as simple plot means as for the remaining traits, height, DBH, etc.

ANOCOV models for plot means

The aim of the following analyses is to obtain the statistical foundation for quantitative genetic estimates. Plot positions within blocks have been used as co-variates in an analysis of covariance (ANOCOV) model for each trait to reduce the systematic within-block environmental variation in the long and narrow blocks present in this particular field trial with only two replications. The initial ANOCOV was performed according to the following model:

$$Y_{ij}=\mu+A_i+b_j+dx_{1(j)}+fx_{1(j)}^2+gx_{2(j)}+hx_{2(j)}^2+lx_{1(j)}x_{2(j)}+e_{ij}$$

where: Y_{ij} – plot mean of clone i in block j, μ – grand mean, A_i – clonal effect – random; b_j – block effect – fixed; dx – linear effect of covariate x_1 within block j gx – linear effect of covariate x_2 within block j, x – plot coordinate within blocks, x – plot coordinate within blocks; e_{ij} – random error of plot means.

As not all covariates showed up to be significant, the model was simplified as much as possible with the aim to end up with a balance between simplicity and low error variance. A common model was chosen for all characters to simplify calculations of covariances between traits. Heritabilities of clone means have been calculated according to the formula:

$$H^2_{bs(clonemean)} = \frac{V_G}{V_G + V_E} = 1 - \frac{1}{F_{CL}}$$

(NANSON 1970, KUNG 1973), where: V_G – genetic variance interpreted from the variance component for clones, V_E – environmental and sampling variance of clone means; F_{CL} – F-ratio for the ANOVA test of clones against the error variance

Genetic correlations between pairs of traits A and B are estimated as

$$r_{G(A,B)} = \frac{COV_{G(A,B)}}{\sqrt{V_{G(A)} \times V_{G(B)}}} \approx \frac{COV_{Cl(A,B)}}{\sqrt{\sigma^2_{Cl(A)} \times \sigma^2_{Cl(B)}}}$$

where: $r_{G(A,B)}$ – genetic correlation between trait A and B,

$\frac{COV_{G(A,B)}}{\sqrt{V_{G(A)} \times V_{G(B)}}}$ refers to genetic variance and covariance components for traits A and B,

$\frac{COV_{Cl(A,B)}}{\sqrt{\sigma^2_{Cl(A)} \times \sigma^2_{Cl(B)}}}$ refers to clonal variance and covariance components in the ANOVA and ANOCOV analyses of trait A and B in the randomized block experiments.

For pairs of traits recorded on the same sample of trees sharing the same common environments, the clonal covariance – $COV_{Cl(A,B)}$ – is derived as the covariance component in the ANOCOV between these two particular traits. These estimates are obtained through the MANOVA option in the GLM procedure in SAS (ANON. 1990).

For pairs of traits recorded in different samples of trees not sharing any common environments, the clonal covariance is simply identical with the phenotypic covariance between clone means in the two samples. In this situation the genetic correlation can be derived as:

$$r_{G(A,B)} = \frac{r_{P(A,B)}}{H_A \times H_B} \qquad \text{(FALCONER 1989)}$$

where: $r_{P(A,B)}$ – phenotypic correlation (clonal mean level) between trait A and B; H_A, H_B – square roots of the heritabilities of clonal means for traits A and B.

In the present investigation, this option is applied for pairs of traits recorded in the nursery experiment and in the subsequent field trial.

Ortet-ramet regression

Simple linear regression between the relative heights of the individual ortets (age 4) and the relative height of the corresponding individual clones (age 21) was performed.

Comparison of selection groups and estimates of realized correlated responses to the nursery stage selection.

In order to test the realized correlated responses to early selection in the three groups, upward, downward, and stabilizing selection, nested analyses of variances were performed according to the following model:

$$Y_{ijk} = \mu + a_i + B_{j(i)} + c_k + e_{ijk}$$

where: Y_{ijk} – Plot mean of clone j within selection group i in block k; μ – grand mean; a_i – effect of selection groups – fixed; $B_{j(i)}$ – effect of clones within groups – random; c_k – effect of blocks fixed, and e_{ijk} – random error of plot means.

Correlated responses are reported directly as realized in the experiments as the raw phenotypic deviation from the grand mean and as a genetic estimate after adjusting the deviation with the clone-mean heritability.

RESULTS

Selection differential and intensity of ortets

The basic parameters of the initial selection of ortets at the nursery stage are presented in Table 2. As can be seen, the upward selection intensity has been stronger than the downward selection. This might be due to the applied sampling, where the first screening of the nursery bed for the 20 superior seedlings proceeded the lay out of the sampling plots, in which the subsequent selection of intermediate and slow growing ortets were made.

Quantitative genetic parameters

After interactive work with alternative ANOCOV models for analysis of plot means adjusted for positions within blocks in the field trial, the following common ANOCOV model was applied for all traits:

$$Y_{ij} = \mu + A_i + b_j + gx_{2(j)} + e_{ij}$$

i.e. there was a linear trend along the narrow replications which accounted for a significant part of the variation due to environment.

In Table 3 there is shown a summary of estimates of coefficients of genetic variation obtained in the two trials – the nursery trial and the subsequent field trial. Further, broad-sense heritabilities are estimated for clone means.

It is apparent from the material, that application of clonal replication by cuttings in such intensively reared field trials is able to yield high-level heritabilities of clone means for nearly all traits. However, for traits correlated to early height growth, the obtained genetic variances may be inflated because of the applied divergent early selection.

In Table 4 phenotypic and genetic correlations are presented. Genetic correlations are not accessible for correlations involving the not yet replicated ortets. In

Table 2. Average selection differential and -intensity of the three selection groups, the upward, the downward and the stabilizing selection

Selection group	Number of selections	Selection differential		Selection intensity /σ_P
		Absolute (cm)	Relative	
Upward	20	30.1	164.5	3.07
Downward	20	−17.6	62.6	−1.79
Stabilizing	20	1.5	103.4	0.15

Table 3. Summary of obtained estimates of coefficients genetic variation and broadsense heritabilities of clone means.

Trait no	Trait	Age	No. of clones investigated	CV_G	H^2 b.s. (clone mean)
2	Height 1977[2]	4	59	0.29	0.88
3	Height 1982	9	59	0.18	0.92
4	Height 1984	11	59	0.17	0.89
5	Height 1988	15	59	0.13	0.92
6	Height 1994	21	59	0.11	0.83
7	DBH 1988	15	59	0.17	0.91
8	DBH 1990	17	59	0.13	0.87
9	DBH 1994	21	59	0.13	0.78
10	Δ Height 1988–1994	15–21	59	0.11	0.73
11	Δ DBH 1990–1994	17–21	59	0.17	0 61
12	Δ Height 1993–1994	20–21	51	0.07	0.29
13	Flushing 1977	4	59	0.68*	0.92
14	Flushing 1995	22	59	0.78*	0.94
15	Pilodyne level 1990	17	59	0.10	0.89
16	Pilodyne level 1994	21	59	0.09	0.79
17	Basic density level 1990	21	21	0.06	0.90

[2] Observations from nursery experiment;
•• Square root of genetic variance in the original scale 1–9

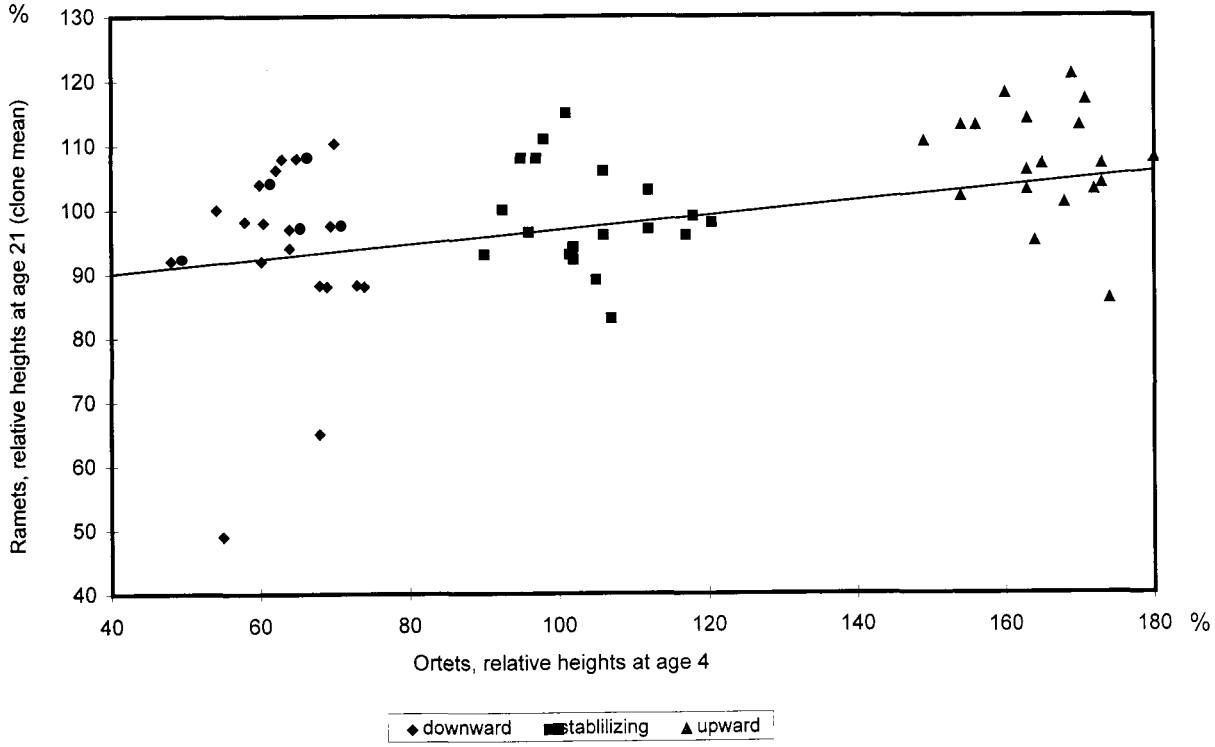

Figure 1. Ortet–ramet regression based on relative heights of 4-year old ortets and 21 year old ramets ($Y = 84.5 + 0.14\ x$; $r^2 = 0.47$)

Table 5 there is shown phenotypic correlations involv ing total heights only.

The applied three-way early ortet selection yields a better estimate of covariances between ortet heights and later expressed traits, because the over-representation of the upward and downward fractions secure an extended range of x-values in all covariance estimates involving ortet heights as x.

The obtained estimates of quantitative genetic parameters in our forest trees are accumulated in a

Table 4. Matrix of phenotypic (above diagonal) and genetic (below diagonal) correlations. The phenotypic correlations are based on clone means; significant deviation from 0 is indicated. (1) ortets in nursery bed. (2) ramets in nursery experiment (3-17) ramets in the field trial.

Trait no.	Relative ortet height 1974 (age 4)	Height 1977 (age 4)	Height 1982 (age 9)	Height 1984 (age 11)	Height 1988 (age 15)	Height 1994 (age 21)	Diameter 1988 (age 15)	Diameter 1990 (age 17)	Diameter 1994 (age 21)	Height increment 1988–1994	Diameter increment 1990–1994	Height increment 1993–1994	Flushing 1977 (age 4) [2]	Flushing 1995 (age 22)	Pilodyne 1990 (age 17)	Pilodyne 1994 (age 21)	Basic density 1990 (age 17)
1	1.00	0.52***	0.56***	0.54***	0.49***	0.47***	0.46***	0.40**	0.44***	0.32*	0.48***	0.18^{NS}	0.13^{NS}	0.19^{NS}	0.11^{NS}	0.03^{NS}	0.05^{NS}
2		1.00	0.81***	0.79***	0.69***	0.60***	0.74***	0.64***	0.56***	0.30*	0.30*	0.14^{NS}	0.10^{NS}	0.23^{NS}	0.18^{NS}	−0.10^{NS}	−0.24^{NS}
3		0.90	1.00	0.95***	0.94***	0.78***	0.88***	0.78***	0.69***	0.34**	0.44***	0.10^{NS}	0.16^{NS}	0.24^{NS}	0.17^{NS}	0.10^{NS}	−0.13^{NS}
4		0.89	0.97	1.00	0.94***	0.80***	0.89***	0.77***	0.69***	0.37**	0.44***	0.14^{NS}	0.14^{NS}	0.26*	0.19^{NS}	−0.08^{NS}	−0.10^{NS}
5		0.77	0.94	0.95	1.00	0.87***	0.91***	0.84***	0.76***	0.45***	0.52***	0.12^{NS}	0.07^{NS}	0.23^{NS}	0.19^{NS}	0.09^{NS}	−0.01^{NS}
6		0.70	0.84	0.87	0.65	1.00	0.85***	0.80***	0.85***	0.82***	0.68***	0.27^{NS}	0.13^{NS}	0.38**	0.27*	−0.05^{NS}	0.05^{NS}
7		0.83	0.88	0.88	0.90	0.92	1.00	0.94***	0.88***	0.53***	0.62***	0.15^{NS}	0.06^{NS}	0.25^{NS}	0.40**	0.10^{NS}	−0.29^{NS}
8		0.73	0.81	0.78	0.86	0.88	0.97	1.00	0.92***	0.54***	0.68***	0.17^{NS}	0.03^{NS}	0.23^{NS}	0.44***	0.19^{NS}	−0.20^{NS}
9		0.68	0.77	0.76	0.84	0.86	0.97	0.99	1.00	0.68***	0.83***	0.23^{NS}	0.01^{NS}	0.21^{NS}	0.45***	0.21^{NS}	−0.09^{NS}
10		0.37	0.49	0.53	0.61	0.85	0.72	0.72	0.76	1.00	0.65***	0.35*	0.15^{NS}	0.42***	0.32*	0.03^{NS}	0.05^{NS}
11		0.41	0.60	0.61	0.68	0.87	0.82	0.85	0.89	0.73	1.00	0.23^{NS}	−0.08^{NS}	0.10^{NS}	0.51***	0.34**	0.03^{NS}
12		0.28	0.19	0.25	0.13	0.38	0.26	0.34	0.46	0.60	0.68	1.00	0.06^{NS}	0.06^{NS}	−0.08^{NS}	−0.16^{NS}	−0.11^{NS}
13		0.11	0.17	0.15	0.08	0.15	0.07	0.03	0.01	0.18	−0.11	0.12	1.00	0.80***	−0.27*	−0.28*	0.22
14		0.25	0.27	0.29	0.27	0.43	0.29	0.28	0.27	0.48	0.13	0.17	0.86	1.00	−0.06	−0.16	−0.05
15		0.20	0.15	0.18	0.19	0.30	0.43	0.51	0.60	0.43	0.73	−0.29	−0.30	−0.06	1.00	0.80***	−0.80***
16		−0.12	−0.12	−0.09	−0.10	−0.08	0.15	0.27	0.28	0.06	0.43	−0.39	−0.38	−0.15	0.89	1.00	−0.57**
17		−0.27	−0.21	−0.15	0.01	0.01	−0.31	−0.19	−0.14	−0.11	0.01	−0.12	0.24	−0.08	−0.86	−0.70	1.00

Table 5. Age to age phenotypic correlations – r_P – for relative heights of ortets and all ages of ramets observed. Phenotypic correlations are based on clone means.

Trait	Ortet	Nursery experiment			Field trial				
	H4	H2	H3	H4	H7	H9	H11	H15	H21
H4		0.48	0.50	0.52	0.55	0.56	0.54	0.49	0.47
H2			0.87	0.89	0.78	0.73	0.72	0.63	0.58
H3				0.96	0.75	0.70	0.65	0.56	0.48
H4					0.83	0.81	0.79	0.69	0.60
H7						0.96	0.91	0.88	0.71
H9							0.95	0.94	0.77
H11								0.94	0.80
H15									0.87
H21									

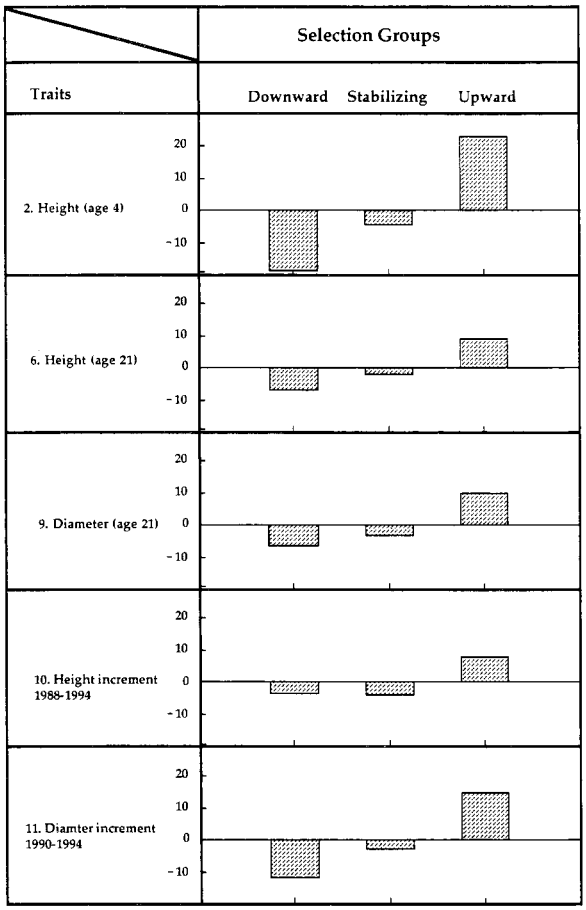

Figure 2. Realized correlated responses for late stage growth of the applied downward, stabilizing and upward selection for 4-year height growth in the nursery.

database for general use in quantitative genetic investigations (including QTLs) and development of breeding strategies in improvement programs in comparable environments.

Table 6. The slope of the ortet-ramet regression – β – and the phenotypic correlation – r_P – between relative ortet heights and relative ramet heights at ages 4, 7, 11, 15, and 21 respectively.

Age	β	r_P
4	0.35	0.51
7	0.27	0.57
9	0.29	0.56
11	0.28	0.54
15	0.18	0.49
21	0.14	0.47

Ortet-ramet regression

In Table 6 obtained slopes of regressions between relative heights of ortets and successive stages of height of the clones are presented. The dynamics of the ortet – ramet regression is demonstrated. In Fig.1 a graph of the latest stage of the ortet-ramet regression is presented. The ortets are represented by the relative height in the 100-tree sample plots in the 4-year old nursery stage, and the ramets are represented by relative phenotypic clone means at age 21.

Realized correlated responses

In Table 7 are presented the trait-for-trait ANOVA comparisons of the three groups, the upward, the downard and the stabilizing selected groups. Further, appropriate F-tests of remaining variation between clones within selection groups are presented. Finally,

Table 7. Trait-for-trait ANOVA comparison of the three selection groups initiated by upward, downward, and stabilizing selection for height growth in the 4-year old nursery stage. Realized correlated responses to the upward early selection are listed for all traits recorded in the trials. These responses are partly reported as the raw phenotypic averages, partly as the genetic estimates derived from the phenotypic after 'shrinkage' by the clone mean heritability.

Trait no	Trait	Age	ANOVA F-tests			Realized correlated response, upward selection	
			Selection groups	Clones within groups	Blocks	Raw phenotypic (%)	Genetic estimate (%)
2	Height 1977 [2]	4	12.30***	6.24***	3.72*	23.1	20.3
3	Height 1982	9	16.53***	8.07***	6.28*	16.9	15.6
4	Height 1984	11	15.26***	5.42***	8.24*	17.0	15.1
5	Height 1988	15	11.11***	7.48***	8.32*	10.2	9.3
6	Height 1994	21	11.51***	4.28***	8.29*	9.1	7.6
7	DBH 1988	15	7.89***	8.31***	18.48***	10.5	9.6
8	DBH 1990	17	5.74**	6.32***	10.21**	8.5	7.4
9	DBH 1994	21	7.87**	3.62***	17.79***	9.8	7.6
10	Δ Height 1988–1994	15–21	5.79**	3.34***	5.96*	7.7	5.6
11	Δ DBH 1990–1994	17–21	8.04***	2.13**	1.43	14.6	8.9
12	Δ Height 1993–1994	20–21	2.08	1.32	0.74	4.6	1.3
13	Flushing 1977	4	1.23	13.07***	1.28	0.20[1]	0.18[1]
14	Flushing 1995	22	3.55*	15.22***	24.86***	0.44[1]	0.41[1]
15	Pilodyne level 1990	17	0.21	8.91***	6.78*	1.2	1.1
16	Pilodyne level 1994	21	0.57	5.08**	5.73*	−1.8	−1.4
17	Basic density level 1990	21	0.07	11.53***	0.42	0.0	0.0

[1] In original scale 1–9
[2] Observations from nursery experiment

the realized correlated responses to the early upward selection are presented, partly as the raw phenotypic averages, partly as the genetic estimates derived from the phenotypic after 'shrinkage' by the clone-mean heritabilities.

In Fig. 2 histograms of the realized correlated responses for a successive number of later expressed growth traits are presented. The responses are shown for all three selection groups, the downward, the stabilizing, and the upward selections. The responses are presented as the raw phenotypic averages of each selection group. In Fig. 3 the frequencies of forking at age 17 in the three selections groups are presented. A χ^2- test of independence between selection groups and occurrence of forks are rejected at a p-level of 0.001.

Interpretation and conclusions

The applied clone testing has been effective in detecting and quantifying genetic variation between individual clones as well as between the applied selection groups. This holds true for growth characters as well as for characters associated with growth rhythm, basic wood density and occurrence of a defect as forking.

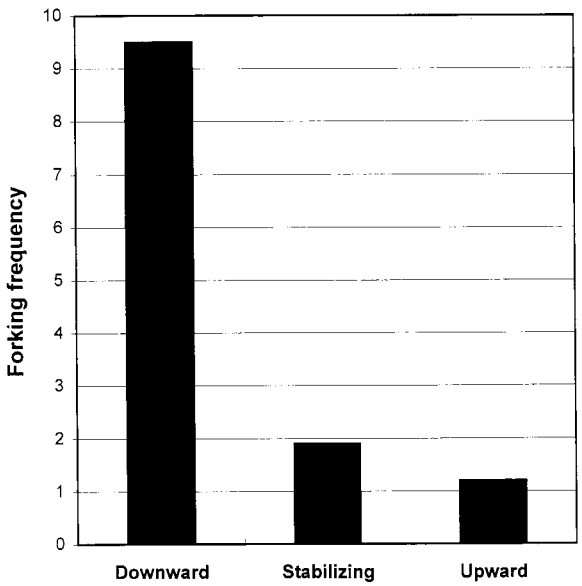

Figure 3. Frequencies of forks (%) at age 17 in the three selection groups, downward, stabilizing and upward selections established at the 4-year old nursery stage.

The applied 3-way early selection for growth has resulted in consistent realized correlated responses of

later expressed growth traits. Although the late responses for total height and DBH to a certain extend reflects a "carry-over" effect from earlier stages, the important response is the late increment in DBH in the late age span 17–21. The response in this trait is interpreted as the most sustainable for predicting long-term yield.

Concerning correlated response in flushing, no response is detected in flushing at age 4, whereas flushing at age 22 is slightly influenced in the direction of early selection for growth results in earlier flushing at this age.

Concerning correlated responses in basic wood density level, the applied early selection seems to be neutral. However, in absolute measure, wider rings will according to the general wood formation mechanisms in *Picea* results in lower density. This effect is predictable.

Concerning correlated response in frequencies of forking, early downward selection for height growth promotes forking. However, the stabilizing and upward selection groups showed almost the same low level in forking frequencies.

Concerning the risk of eroding genetic variation as a result of early selection, significant variation remains within all three selection groups each composed of 19–20 clones. This involves all recorded traits except leader length at age 20–21 (Δ height 1993–94), but this rather special trait showed only marginal genetic variation overall.

DISCUSSION

Early-late correlations detected by investigation of the same experiment at different stages have limitations concerning their overall reliability of predicting later performance at other sites (WELLENDORF *et al.* 1986, WELLENDORF 1987). Furthermore, plantation forestry may impose very different conditions at different stages of stand development, especially before and after canopy closure. The results of the present trial are judged to be only fully valid for comparable types of base populations, selection intensities and environments. Especially under more extreme ecological conditions, or with use of unadapted material, the results might be different (WELLENDORF *et al.* 1995, KLEINSCHMIDT & SAUER, 1976).

The results from the present trial indicate a promising level of early-late correlations for growth, but as certain wood quality characters (absolute basic density and branch diameter) are negatively associated with fast growth, it is not recommended to select exclusively for height growth at the nursery stage. Furthermore, several forest tree species have shown a moderate negative correlation between root / shoot ratio and height (*e.g.* LAMBETH *et al.* 1982). A reduced root / shoot ratio may during whole rotations be important for resistance against wind throw and drought.

Breeding for fast growth in an operational breeding program may therefore be restricted when the goal is to maintain or improve wood quality and avoiding unfavourable correlated responses in adaptive traits. The detected genetic variation within all selection groups (Table 7 and Fig. 1) demonstrates that genetic variation will be maintained even after applying upward selection exclusively for height growth at the nursery stage. During the long rotations of forest trees, it might be important to maintain a certain amount of genetic diversity to buffer more or less unpredictable fluctuations of environments.

However, the present study indicates, that the costs in the future for excluding breeding for growth-rate might be substantial in terms of lost opportunities for improved yield. The important challenge is to balance between conflicting goals. Wood production remains to be important in a world where the demand for wood products is ever increasing.

ACKNOWLEDGEMENTS

We are grateful to E. D. Kjær and C. Pilegaard Hansen for comments on the manuscript and to T. Kuhdal, M. Linnet and V. Jensen for technical assistance. Financial support was provided by the EEC project "Northern conifers in fast growing conditions, a step towards an adequate wood supply for industry", contract CT 920143.

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