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## Efficiency of Early Testing in *Pinus sylvestris* L. Grown Under Two Different Spacings in Growth Chamber

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### Abstract

An hypothesis in designing early tests was that mimicking the limiting factor occurring later in a rotation would improve the genetic correlations between early and late measurements. Seedlings belonging to 30 open pollinated families of Scots pine (*Pinus sylvestris*) were therefore grown for three growth periods at two spacings, wide and dense (9 and 36 plants per box with an area of 0.188 m<sup>2</sup>), in the growth chamber to mimic the competition for light. The wide spacing was replicated in another experiment with the same parents, and the seedlings were grown for two growth periods. Eight growth chamber characters were jointly evaluated with 20-year-old tree growth characters in four field trials with the same parents as in the growth chamber trials. The field trials were located in central

Sweden, and established with full-sib families. The additive genetic correlations between growth chamber characters and height in field tests were none or weak. The correspondence between the results from wide and dense spacing in the growth chamber was strong. Moderate genetic correlations between growth chamber characters estimated in two different experiments, established with seed collected in two different years, were probably due to differences in mating in the seed orchard. The additive genetic correlations for height between field test sites were in the range 0.26 to 0.99. The raised hypothesis that mimicking the competition for light by a dense spacing would improve the genetic correlation between early and late measurements was not supported for the tested range of growth chamber conditions. Therefore, this study does not give any support for use of early tests in operational forest tree breeding, although other experiments have resulted in high correlation between field and growth chamber experiments.

*Key words:* *Pinus sylvestris*, early tests, juvenile-mature correlations, growth trait, genetic correlation.

*FDC:* 165.3; 165.41; 181.525; 232.13; 174.7 *Pinus sylvestris*; (485).

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## Introduction

An obstacle in breeding *Pinus sylvestris* (L.) is the long generation interval. With reliable early testing and artificially induced early flowering the generation time could be shortened. This means that the genetic gain per year could be considerably improved. The effectiveness of early selection is described by juvenile-mature (J-M) genetic correlation, selection intensity and heritability of the juvenile trait (cf. JIANG, 1987). Efforts have been made in many species to find the optimal age for selection (e.g. LAMBETH, 1980).

ERIKSSON et al. (1993) summarised the results of 18 early tests in pine species. Most of them comprised J-M correlations between family means. The correlations varied considerably in the studies reviewed. A few studies support the view that mimicking early on the factors which limit growth at later stages in the field would improve J-M correlations. E.g. CANNELL et al. (1978) found the strongest family mean correlations between nursery performance and field volume at 8 years of *Pinus taeda* families when the nursery conditions resembled the field conditions. Only in a few cases early tests have been designed to vary some environmental factor in order to improve the J-M correlation. In a study with five different nutrient regimes ERIKSSON et al. (1993) found the strongest genetic correlations between field data and growth chamber data from the highest nutrient concentration and from the oldest juvenile material, i.e. when seedlings were larger. Based on the crucial role that light interception by the tree crown plays in stem wood production (CANNELL, 1989), ERIKSSON et al. (1993) hypothesised that competition for light might be the reason for the strong correlation obtained at the highest nutrient treatment and/or at the termination of the experiment.

The main objective of this investigation was to study the genetic correlation between early growth characters measured in growth chambers at two different spacings, to simulate different situations of light competition, and growth characters

measured in four field trials. In this paper we also present genetic correlations between the four field trials and between growth chamber experiments established with open-pollinated seed collected in different years. The efficiency of early versus conventional field testing is also discussed.

## Materials and Methods

### Material

The present study is one in a series of retrospective tests to examine genetic and environmental factors affecting the genetic correlation between growth chamber data and field test data for Scots pine. A series of four field progeny tests, with an age of 20 years, was available to assess the correspondence between growth chamber and field performance. The field trials were established with seed from controlled crosses. The female parents used were 36 plus-trees selected in old natural stands originating from latitude 60° 31' to 61° 43' and altitude 275 m to 650 m above sea-level. The crosses were carried out in a seed orchard in central Sweden. Four of the females were also used as males and crossed with each female. To avoid selfings a fifth plus-tree was used as male parent in four crosses. The growth chamber experiments were established with open-pollinated seed from this 30-year-old seed orchard with the same 36 parents as for the field tests. Seed for experiment 1 was collected in the autumn 1992 and for experiment 2 in the autumn 1994. The seed was collected from several grafts per clone.

### Growth chamber experiments

Two experiments were carried out in the growth chamber. Experiment 1 was established in 1993 with two different spacings, approximately 14 cm x 14 cm and 7 cm x 7 cm. The size of the boxes was 47 cm x 40 cm x 20 cm (area 0.188 m<sup>2</sup>) and the boxes were planted with 3 x 3 or 6 x 6 individuals per box. It was designed as a randomised block experiment with 30

Table 1. – Cultivation conditions during the three growth periods.

	Week no.	Night length	Temperature °C	
			Day	Night
<b>First growth period</b>				
Sowing	1-2	8 hr	25	15
Growth	3-10	6 hr	25	15
Growth retardation	11-18	gradual increase with 1 hr/wk until 14 hr	20	10
Resting stage	19-20	16 hr	20	10
	21-23	16 hr	15	5
Breaking of dormancy	24	16 hr	10	5
	25	16 hr	5	5
	26	24 hr	2	2
	27	16 hr	10	5
Second growth period	28-47	II-V repeated but only 3 wk with growth condition II		
Third growth period	48-62	II-IV repeated but only 3 wk with growth condition II		

families, each family represented by 25 individuals. Experiment 2 was established two years later with only the wide spacing. Also this experiment was designed as a randomised block experiment, this time with 36 families and 17 individuals per family. The difference in number of families represented in experiment 1 and experiment 2 was caused by the availability of seed.

The technique for cultivating pine seedlings in the growth chambers over several growth periods described in detail by JONSSON et al. (1992), is given in *table 1*. Seed was sown in a vermiculite/gravel mixture and after two weeks the germinants were transplanted to boxes filled with inert mineral wool. A balanced nutrient solution with 45 mgN per litre was used for watering.

The light source was Osram HQIE-lamps (250 W) providing an irradiation of about 320  $\mu\text{mol m}^{-2}\text{s}^{-1}$  (400 nm to 700 nm) at plant level. Light intensity was not assessed in the experiments. In a pilot study with the same spacings the light intensity within the stand of seedlings was always considerably lower in the dense spacing than in the wide spacing. The relative air humidity was kept at 75%.

The measured characters are in experiment 1 height and growth rate after the 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> growth period, and diameter after the 3<sup>rd</sup> growth period. In experiment 2 height and growth rate after the 1<sup>st</sup> and 2<sup>nd</sup> growth period, diameter after the 2<sup>nd</sup> growth period and total dry weight of needles, stem and branches at the end of the second growth period were measured.

The duration of the study was three growth periods in experiment 1 (= 62 weeks) and two growth periods in experiment 2 (= 47 weeks).

#### Field trials

The field trials (*Table 2*) were established in 1970 using single-tree plots in trial A and 4-tree square-plots in the other trials, where only the first plant in the first row was assessed. The trials were planted with 2-year-old seedlings. The single-tree plot trial had ten blocks with four randomly planted trees of each family in each block. Only 3 blocks were measured. In the trials with 4-tree-plots all ten blocks were measured. The measured characters are total height, height increment, diameter at breast height and over bark, and stem volume per tree. The stem volume of the trees was estimated using formulas presented by NÄSLUND (1947) for trees with a breast height diameter greater than 50 mm and by formulas presented by ANDERSSON (1954) for smaller trees. Approximately 25% (varying between the trials from 4% to 41%) of the trees were smaller than 50 mm.

#### Statistical analyses

Estimations of variances and covariances, and associated heritabilities and correlations, were based on multiple-trait Mixed Model Equations (MME) according to HENDERSON (1975, 1984) and Restricted Maximum Likelihood Method (REML) (PATTERSON and THOMPSON, 1971; SCHAEFFER et al., 1978) using an expectation-maximisation (EM) algorithm (DEMPSTER et al., 1977). The estimation procedure, coded in FORTRAN for this particular problem, is based on iterative solutions of two-trait MME (JANSSON et al., 1998). MME and REML are applicable in multivariate analysis in which the design matrix varies between variables as well, e.g. when, as in this case, one trait is measured on full-sib material and the other on half-sib material.

The variables measured in the different field tests were considered as two different traits. The following model was used in the analyses:

$$[1] \quad \mathbf{y}_i = \mathbf{X}_i \mathbf{b}_i + \mathbf{Z}_i \mathbf{p}_i + \mathbf{W}_i \mathbf{f}_i + \mathbf{e}_i$$

where subscript  $i$  pertains to trait  $i = 1, 2$  and

$\mathbf{y}_i$  = vector of phenotypic observations for trait  $i = 1, 2$

$\mathbf{b}_i$  = vector of fixed block effects

$\mathbf{p}_i$  = vector of random parent effects

$\mathbf{f}_i$  = vector of random family effects

$\mathbf{e}_i$  = random error vector

$\mathbf{X}_i, \mathbf{Z}_i$  and  $\mathbf{W}_i$  = design matrices pertaining to  $\mathbf{b}_i, \mathbf{p}_i$  and  $\mathbf{f}_i$ .

For random effects  $\mathbf{p}' = (p'_1, p'_2)$ ,  $\mathbf{f}' = (f'_1, f'_2)$  and  $\mathbf{e}' = (e'_1, e'_2)$ . The means and variance-covariances are assumed to be

$$\begin{bmatrix} \mathbf{p} \\ \mathbf{f} \\ \mathbf{e} \end{bmatrix} \sim \left( \begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{G} \otimes \mathbf{I} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{D} \otimes \mathbf{I} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{R} \otimes \mathbf{I} \end{bmatrix} \right),$$

where  $\mathbf{G}$  is the matrix with the parental effect (GCA) variances and covariances,  $\mathbf{D}$  is the matrix with the SCA variances and covariances and  $\mathbf{I}$  is an identity matrix. As field tests and growth chamber experiments were grown in different environments, the residuals are assumed to be uncorrelated and  $\mathbf{R}$  is a diagonal matrix containing variances only. The parents are assumed unrelated. Finally,  $\otimes$  symbolises the direct product.

The same type of model as in [1] was also used to analyse the correlation between variables measured in the growth chamber. As half-sib families were used in the growth chamber experiments the family effects were excluded from the model. To analyse the correlation between characters measured in the

*Table 2.* – Description of the field trials.

Trial	Name	Latitude	Longitude	Altitude	Site index	Survival (%)	Height (m)	Spacing (m)
A	Bogragen	60° 42'	12° 36'	350	T18	91	4.8	2.2×2.2
C	Bringsåstorpet	60° 52'	12° 29'	510	T22	82	3.9	2.5×2.5
D	Älvhöjden	60° 00'	14° 48'	340	T25	79	5.8	2.5×2.5
E	Lekvattnet	60° 12'	12° 38'	200	T18	92	4.9	2.5×2.5

growth chamber and in field trials the model in [1] was modified to include half-sib families for growth chamber characters and full-sib families for the field-trial characters.

A logarithmic transformation (JANSSON and DANELL, 1993) was used with volume and dry weight to get the values approximately normally distributed and with a homogeneous variance.

The variance and covariance components were estimated by iterating on

$$[2] \quad \hat{\sigma}_{ij}^2 = \frac{\hat{\mathbf{a}}_i \hat{\mathbf{a}}_j + tr \mathbf{C}_{ij}}{n_{ij}}$$

where

$\hat{\sigma}_{ij}^2$  = the variance if  $i=j$ , otherwise the covariance between trait  $i$  and  $j$

$\hat{\mathbf{a}}_i, \hat{\mathbf{a}}_j$  =  $\mathbf{a}$  is a vector of the parent effects, or the genetic values (BLUP) of the crosses of trait  $i$  and  $j$ , respectively

$\mathbf{C}_{ij}$  = is the submatrix pertaining to  $Cov(\hat{a}_i - a_i, \hat{a}_j - a_j)$  in a generalised inverse of the mixed model coefficient matrix

$n_{ij}$  = number of observations in trait  $i$  and  $j$  and

$tr$  = the trace operator.

The error variances were estimated as:

$$[3] \quad \hat{\sigma}_{e_i}^2 = \frac{\hat{\mathbf{e}}_i' \mathbf{y}_i}{n_i - rank(\mathbf{X}_i)}$$

where

$\hat{\mathbf{e}}_i$  = vector of residuals of trait  $i=1, 2$

$\mathbf{y}_i$  = observation vector for trait  $i=1, 2$

$\mathbf{X}_i$  = fixed effects of trait  $i=1, 2$ .

Estimates were considered to have been converged once the maximum relative changes of all the provisional variance and covariance estimates from one iteration to the next were less than  $10^{-6}$ .

When using the EM-algorithm there is no obvious method to estimate standard errors to variance components (SEARLE et al., 1992) and associated parameters. Simulations based on the actual data design, ultimate MME-fixed effect solutions and variance estimates, with which progeny records were generated as described in JANSSON et al. (1998), were therefore used for some correlations to get an indication of the range of the standard error.

#### Genetic parameters

With full-sib structure, we computed the additive ( $\hat{\sigma}_A^2$ ), dominance ( $\hat{\sigma}_D^2$ ), environmental ( $\hat{\sigma}_E^2$ ), and phenotypic ( $\hat{\sigma}_P^2$ ) variance component estimates as

$$[4a] \quad \hat{\sigma}_A^2 = 4\hat{\sigma}_p^2$$

$$[4b] \quad \hat{\sigma}_D^2 = 4\hat{\sigma}_f^2$$

$$[4c] \quad \hat{\sigma}_E^2 = \hat{\sigma}_e^2 - 2\hat{\sigma}_p^2 - 3\hat{\sigma}_f^2$$

$$[4d] \quad \hat{\sigma}_P^2 = \hat{\sigma}_A^2 + \hat{\sigma}_D^2 + \hat{\sigma}_E^2$$

With half-sib structure corresponding variance components were estimated as

$$[5a] \quad \hat{\sigma}_A^2 = 4\hat{\sigma}_p^2$$

$$[5b] \quad \hat{\sigma}_E^2 = \hat{\sigma}_e^2 - 3\hat{\sigma}_p^2$$

$$[5c] \quad \hat{\sigma}_P^2 = \hat{\sigma}_A^2 + \hat{\sigma}_E^2$$

The estimates of heritabilities ( $\hat{h}^2$ ) and genetic correlations ( $\hat{r}_A$ ) were computed as

$$[6] \quad \hat{h}^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2}$$

and

$$[7] \quad \hat{r}_A = \frac{\hat{\sigma}_{A_i A_j}}{\hat{\sigma}_A \hat{\sigma}_{A_j}}$$

#### Efficiency of indirect early selection

The target trait was assumed to be volume per area unit during a full rotation (60 to 100 years). As this is not realistic to measure in the field tests, height was used as a selection criterion for volume production. The two testing designs, growth chamber trials and field trials, were discussed in a breeding programme context. The efficiency of early selection vs. field trial selection was calculated using the ratio between correlated response per year ( $\Delta G_C$ ) based on characters assessed in the growth chamber, and direct response per year for height based on field tests ( $\Delta G_D$ ):

$$[8a] \quad \Delta G_D = r_{TI_D} i_D \sigma_{A_D} / L_D, \text{ based on results from field trials and}$$

$$[8b] \quad \Delta G_C = r_{TI_C} i_C \sigma_{A_D} r_A / L_C, \text{ based on growth chamber trials,}$$

where

$$[9] \quad r_{TI} = \sqrt{\frac{nh^2}{4 + (n-1)h^2}}$$

assuming a test with half-sib families.

$h^2$  = heritability

$n$  = number of progeny trees

$i_D, i_C$  = selection intensity with field tests and growth chamber tests, respectively

$\sigma_{A_D}$  = additive genetic standard deviation in height

$r_A$  = genetic correlation between measured variable and target trait

$r_{TI_D}, r_{TI_C}$  = correlation between true and estimated breeding value for height in field and growth chamber tests, respectively

$L_D, L_C$  = generation interval with field testing and growth chamber testing, respectively.

## Results

The mean values were higher for the wide than the dense spacing in experiment 1 (Table 3). In both wide and dense spacing in experiment 1 the heritabilities decreased with increasing age contrary to experiment 2 where it increased with increased age. The heritabilities and additive genetic coefficients of variation for measured characters in the growth chamber (Table 3) were, in general, higher than characters measured in field trials (Table 4). Transformed dry weight above ground had a heritability of 0.8, but a low coefficient of variation, 4.9%. The values of the parameters estimated from the field trials were slightly lower than in CORNELIUS' (1992) compilation of genetic parameters from 67 published papers.

As is evident from table 5 there was mostly no correlation between growth chamber characters and the height in the field trials. Correlations with height increment, diameter and volume data from the field trials showed the same tendency

(not given). The genetic correlations were in the range 0.8 to -0.4 and without any clear trends. Simulations for some of the correlations showed that the standard errors were in the range 0.2 to 0.5, correlations close to zero and/or connected to low heritability giving larger standard errors. In experiment 2 there is a tendency to increased correlation with increasing age of the seedlings in the growth chamber. This includes both total height and growth rate. Transformed dry weight of the seedlings after 2 periods in the growth chamber had in three cases a stronger correlation than total height, but probably not significantly higher. The growth chamber characters in experiment 1 seemed more strongly correlated with field characters in trial C than in the other trials, but with the large standard errors it is not possible to draw any conclusions.

Table 6 shows that the genetic correlation between performance at dense and wide spacing in the growth chamber was high. There was a tendency for the correlations after three

Table 3. – Means, heritabilities ( $\hat{h}^2$ ) and additive genetic coefficients of variation ( $C\hat{V}_A$ ) for measured characters in the growth chamber.

Character <sup>1)</sup>	Growth period	Abbreviation	Mean		$\hat{h}^2$	$C\hat{V}_A$ (%)
<i>Exp 1 wide</i>						
Height	1	H1	52.2 mm		0.45	34.8
Height	2	H2	205.6 mm		0.42	16.6
Height	3	H3	361.0 mm		0.41	14.7
Diameter	3	D3	7.97 mm		0.57	7.6
Growth rate	1	GR1	0.90 mm×day <sup>-1</sup>		0.35	24.5
Growth rate	2	GR2	3.12 mm×day <sup>-1</sup>		0.58	30.8
Growth rate	3	GR3	6.31 mm×day <sup>-1</sup>		0.41	17.6
<i>Exp 1 dense</i>						
Height	1	H1	49.9 mm		0.57	36.7
Height	2	H2	200.1 mm		0.40	17.3
Height	3	H3	304.8 mm		0.28	18.1
Diameter	3	D3	5.30 mm		0.38	23.5
Growth rate	1	GR1	0.84 mm×day <sup>-1</sup>		0.54	38.1
Growth rate	2	GR2	2.92 mm×day <sup>-1</sup>		0.56	36.3
Growth rate	3	GR3	4.59 mm×day <sup>-1</sup>		0.43	23.3
<i>Exp 2 wide</i>						
Height	1	H1	68.3 mm		0.47	22.3
Height	2	H2	176.3 mm		0.55	19.4
Diameter	2	D2	4.70 mm		0.63	10.6
Growth rate	1	GR1	0.50 mm×day <sup>-1</sup>		0.54	24.2
Growth rate	2	GR2	5.08 mm×day <sup>-1</sup>		0.35	16.3
<i>Dry weight</i>						
above ground	2	DW2	64.2 g		0.80	4.9

<sup>1)</sup> Growth rate was calculated as growth per day during the most intensive growth phase.

Table 4. – Means, heritabilities ( $\hat{h}^2$ ) and additive genetic coefficients of variation ( $\hat{CV}_A$ ) for measured characters in the field trials.

Character	Age <sup>1)</sup> (years)	Abbreviation	Mean		$\hat{h}^2$	$\hat{CV}_A$ (%)
<i>Trial A</i>						
Height	20	H20	483	cm	0.17	8.8
Height increment	14-20	HI	36	cm×year <sup>-1</sup>	0.24	10.4
Diameter	20	D20	58	mm	0.13	10.5
Volume	20	V20	10.0	dm <sup>3</sup>	0.10	21.1
<i>Trial C</i>						
Height	19	H19	388	cm	0.09	6.3
Height increment	14-19	HI	33	cm×year <sup>-1</sup>	0.11	9.2
Diameter	19	D19	56	mm	0.10	10.4
Volume	19	V19	8.6	dm <sup>3</sup>	0.13	26.0
<i>Trial D</i>						
Height	20	H20	578	cm	0.23	8.1
Height increment	14-20	HI	44	cm×year <sup>-1</sup>	0.26	9.8
Diameter	20	D20	92	mm	0.07	6.9
Volume	20	V20	26.4	dm <sup>3</sup>	0.09	16.0
<i>Trial E</i>						
Height	20	H20	488	cm	0.14	8.0
Height increment	14-20	HI	41	cm×year <sup>-1</sup>	0.29	10.0
Diameter	20	D20	59	mm	0.10	9.0
Volume	20	V20	10.5	dm <sup>3</sup>	0.09	19.0

<sup>1)</sup> Total age (from seed) at the time of measurement.

growth periods to be somewhat weaker than for the first two growth periods, i.e. for height 0.96 compared to 1.00, and for growth rate 0.84 compared to 1.00.

The genetic correlation between growth chamber data from experiment 1 and experiment 2, i.e. wide spacing, and the same families with seed collected in different years, was in the range 0.21 to 0.60 as shown in table 7.

As shown in table 8, the genetic correlations between field test data were mostly moderate or high, for height in the range 0.26 to 0.99. Total height gave a higher correlation than height increment, volume and diameter.

## Discussion

All J-M correlations were weak or even negative for the wide and dense spacing data in the growth chamber. Since earlier reports by our group have found conflicting results we shall carry out a general discussion about possible reasons for weak J-M genetic correlations according to the following:

1. *Mislabelling in field and/or growth chamber.* The first possibility of mislabelling that might occur is at the time of grafting such that the scions originate from another ortet than indicated on the tag. The harvested seeds might have been

mislabeled. At sowing in the growth chamber and transplanting, mistakes might have occurred. Any of these kinds of error would also result in low heritabilities. Since the estimates of the heritabilities were fairly high both in growth chamber and field trial we rule this out as an explanation for the low J-M correlations in our material.

2. *Low heritability at juvenile and/or mature stage.* It is self-evident that if the genetic determination is low at either juvenile or mature stage or both, the probability of revealing any J-M correlation will be limited (e.g. ABRAITIS et al., 1998). Low heritability causes a large standard error of the genetic correlation. Even if the heritabilities must be regarded as large enough to reveal genetic correlations if they existed, the standard error of the genetic correlations are too large to exclude this as an explanation.

3. *Different sets of genes expressed in juvenile and mature material.* One reason for the low genetic correlation in the present study could be that different physiological mechanisms are involved at different growth stages, which might be attributed to the expression of different genes. Such a tendency was suggested by e.g. HODGE and WHITE (1992) in field testing of *Pinus elliottii*. This can also be a possible explanation in our study.

Table 5. – Estimated genetic correlations between tree height in the field trials and characters measured in the growth chamber.

Growth chamber	Field trials			
	A	C	D	E
<i>Exp1 wide</i>				
H1	0.17	0.60	0.06	-0.13
H2	-0.01	0.52	0.07	-0.26
H3	-0.16	0.41	0.08	-0.18
D3	-0.25	0.09	-0.03	-0.42
GR1	0.19	0.60	0.05	-0.28
GR2	0.19	0.28	0.23	-0.05
GR3	0.08	0.17	0.24	0.14
<i>Exp1 dense</i>				
H1	0.08	0.80	0.22	0.00
H2	-0.19	0.54	0.23	-0.05
H3	-0.35	0.38	0.14	-0.12
D3	-0.24	0.46	0.15	-0.19
GR1	0.21	0.78	0.18	-0.12
GR2	0.30	-0.06	0.18	0.02
GR3	0.10	0.00	0.21	0.01
<i>Exp2 wide</i>				
H1	0.08	0.00	0.29	0.21
H2	0.11	0.09	0.35	0.24
D2	-0.08	-0.01	0.45	0.22
GR1	0.08	0.07	-0.04	0.13
GR2	0.45	0.22	0.56	0.26
DW2	-0.04	0.16	0.46	0.34

Table 6. – Estimates genetic correlations between the same trait at dense and wide spacing in the growth chamber study (experiment 1).

Character	$\hat{r}_A$
H1	0.99
H2	1.00
H3	0.96
D3	0.98
GR1	1.00
GR2	1.00
GR3	0.84

Table 7. – Estimates genetic correlations between the same trait assessed in experiment 1 and 2.

Character	$\hat{r}_A$
H1	0.47
H2	0.39
GR1	0.21
GR2	0.60

#### 4. Different sets of alleles giving rise to the same phenotype.

The assumption that quantitative traits are regulated by alleles at many loci and that an allele at one locus can influence the trait in a similar way as an allele at another locus means that good growth may be obtained by many different genotypes (e.g. GOLDSTEIN and HOLSINGER, 1992). If this is the case, the good performance in the juvenile material might be attributed to other alleles than those that promote good growth in the adult trees. This phenomenon is different from the situation that different genes are expressed at different ages and constitutes a general problem in develop-

Table 8. – Estimated genetic correlations between characters measured in the different trials (A, C, D, and E).

Character <sup>1)</sup>	A, C	A, D	A, E	C, D	C, E	D, E	Mean
H20	0.58	0.55	0.99	0.76	0.26	0.91	0.68
HI	0.43	0.65	0.91	0.81	0.14	0.89	0.64
V20	0.36	0.18	0.99	0.58	0.12	0.47	0.45
D20	0.48	0.03	1.00	0.60	0.24	0.30	0.44

<sup>1)</sup> In trial C age 19 years.

ment of reliable early tests. If this hypothesis about quantitative trait gene action is correct we expect a certain number of cases in which the J-M correlations are poor. Thus, different sets of alleles giving rise to the same genotype could be a possible explanation in our material.

5. *Genotype x environment interaction.* Another potential explanation is that there is a genotype x environment interaction that overrides the genetic effects causing strong J-M correlations. WELLENDORF (1979) found weak J-M correlations in *Picea abies* and stated that it probably could be attributed to the fact that correlations were confounded with genotype x environment interaction since the juvenile plants were tested under other conditions than the mature trees. Also, LAMBETH et al. (1982) found a large interaction between families and growth chamber environments and a poor correlation with field performance for the trait height increment in *Pseudotsuga menziesii*. In a study of genetic correlations of greenhouse and field performance in *Pinus contorta* WU et al. (1997) found that genotype x environment interaction had a significant impact on greenhouse-field genetic correlation. The pattern of greenhouse-field family-means and genetic correlations among four sites in their study indicated that early testing should be conducted under conditions resembling those in field.

6. *Non-genetic influences in the young field material.* Before the plants are fully established in the field trials the growth may be influenced by random events such as competition with weeds and varying micro-environments. Such influences are expected to accumulate in early stages but gradually disappear in relative terms with older ages. In the report by ERIKSSON et al. (1993), strong genetic correlations were not obtained until the age of 23. At ages 10 to 13 the genetic correlations were weak as in our case. LI et al. (1992) found a similar tendency when studying height growth of *Pinus taeda* in trees subjected to five irrigation and nutrient treatments in a closely spaced nursery test for 3 years. The height-height J-M correlations increased in size and reached a plateau at a plant height of approximately 1.5 m. Therefore, the young age (19 to 20 years) and wide spacing of our field material might be one explanation for the poor correlations in our material. However, the low correlations with growth increment in field speaks against such an interpretation.

Thus the most likely reason for the weak J-M correlations are that different sets of genes or alleles are expressed at

different ages (3 or 4 above), or that the environment in the growth chamber does not reproduce well enough the conditions in the field (5).

The correlations between wide and dense spacing were almost unity ( $r_G \approx +1.0$ ) except after three growth periods when the genetic correlation for growth rate decreased to 0.84. This may be an effect of increased competition for light that starts at this stage, but it may also be caused by sampling. After three growth periods the seedlings planted at wide spacing are approximately 18% higher than at dense spacing. Also, ST. CLAIR et al. (1991) found strong genetic correlations (close to one) between biomass measured in different competition environments for *Pseudotsuga menziesii* in a nursery test.

The genetic correlations between growth chamber data from experiment 1 and 2 were surprisingly low. One explanation may be that the pollination in the seed orchard was different between the two years (cf. JONSSON et al., 1976) or that there was pollen contamination (cf. YAZDANI and LINDGREN, 1991). Seed was collected from a limited number of grafts per clone, which might exaggerate differences in mating pattern. Seed collected in different years may also come from different ramets. The environmental conditions in the growth chamber were the same and should not have affected the results.

The genetic correlations between height in the different field trials were on average 0.68, ranging from 0.26 to 0.99. Hence suggesting that genotype x environment is only of moderate significance. HAAPANEN (1996) found the genetic correlations between progeny trials in Scots pine to be around 0.6, which is of the same size as in the present study. The study was based on eight series of 10-year-old progeny trials and the pattern of the genetic correlation was largely unpredictable.

Progeny testing provides the basis for selecting good parents in the Swedish breeding programme for Scots pine (DANELL, 1993; WILHELMSSON and ANDERSSON, 1993). Assume that by using early tests we could reduce the testing time considerably and thereby reduce the generation time to half the original time. Based on results in the present field trials and other progeny trials evaluated by The Forestry Research Institute of Sweden, the heritability for height is generally around 0.20 in field tests. Furthermore, assume that the number of tested individuals is 20 per parent, and that the selection intensity is the same in both types of tests. Then, based on equation [8] it

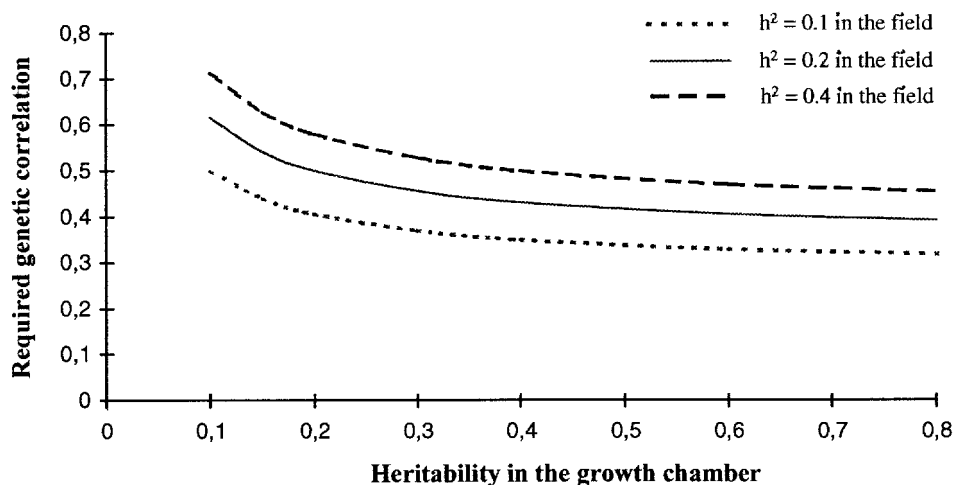


Fig. 1. – Theoretical calculation of “break even values” (equal efficiency in selection for early vs. field test results) for genetic correlations between characters measured in growth chamber and field test at different heritabilities for the two traits. The heritability ( $h^2$ ) in the field test is assumed to be 0.1, 0.2, or 0.4. The number of tested individuals is in both cases 20. The generation interval is assumed to be twice as long for field testing as for growth chamber testing.



is possible to calculate the required genetic correlation between growth chamber data and field test data in order to get the same genetic gain per year for both types of tests (Fig. 1). For example, with a heritability of 0.4 in the growth chamber data and 0.2 in the field tests, the genetic correlation needs to be at least 0.43, to make early tests superior to field tests. In the present study the correlations were mostly lower than those required in figure 1. Even the rare cases of higher estimates have a high possibility of being caused by sampling.

A genetic correlation as high as 0.5 means that only 25% of the variation is common for the two traits. With such limited genetic control it is not possible to know what the selection will lead to for characters that are not common for early and mature trees. This means that a selection criterion with such a low correlation with the actual target trait must be used with caution. If genotype x environment interaction is important between field and artificial environments, after several cycles of early selection one could develop a population that is poorly adapted to the field environment. Another issue that also has to be considered is the development of genetic diversity from one generation to the next.

This study does not give any support for use of early tests in applied tree breeding of *Pinus sylvestris*, although earlier reports have shown varying strength of J-M genetic correlations.

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