As the Sikhote Alin and Low Amur mountain range populations have comparable levels of variation to south Korea's, it may serve as confirmation of the hypothesis of longterm existence of Korean pine within these areas (*Figure 2*). The lower values of genetic variation within the Maliy Khingan – Kukan mountain range populations are likely evidence of recent colonization of these territories by *P. koraiensis* and/or of the influence of geographic barriers.

Interestingly the present expansion of the species range (URUSOV, 1995) or a continued expansion of Korean pine (NEISHTADT, 1957) to the north have been suggested by both hypotheses. The discovered lower values of genetic variation in the Maliy Khingan – Kukan mountain range populations do not contradict these assuptions, at least for this part of the *P. koraiensis* range.

Were we to compare the obtained results with the history of the studied species in the recent period of climate cooling, a lack of Sikhote Alin Korean pine refugium would have been corroborated by low  $F_{\rm ST}\left(Table\ 3\right)$  and D values (Table 4).

At the same time in order to reconstruct a more correct model of *P. koraiensis* diversity distribution it is nessesary to research the populations in China and north Korea.

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## Juvenile-Mature Correlations and Selection Effects on Clone Level After Stratified Family and Individual Selection of *Picea abies* (L.) KARST. Seedlings

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## 1. Abstract

A set of 130 clones of *Picea abies* planted in three field sites has been studied after 8 years. The ortets were representatively selected in 5 full-sib families. Estimates of ortet (nursery) – ramet (field) correlation were significant but low, r = 0.23. Correlation estimates vary dramatically between families.

Different degrees of adaptation on family level are discussed as one possible explanation.

Clone x field site interaction components were significant and twice the size of the clone component for height increment, which is larger than found in other studies.

The gain in height increment in the field after selection for the 20% best ortets in the nursery was only 5.6%, which is only 15% of the gain achieved after field tests. That is considered too low to justify nursery selection. The selection response showed a large variation between full-sib families.

The conclusion of the study is that nursery selection of young ortets is too unprecise. Field testing on clonal level is required to obtain a sufficient genetic gain.

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Key words: Clone, genotype x site interaction, juvenile x mature correlation, selection gain.

FDC: 165.3; 165.441; 165.6; 232.13; 561.1; 174.7 Picea abies; (485).

#### 2. Introduction

The long rotation age of species like *Picea abies* is a great constraint to genetic gain per year. One way to overcome this constraint is to develop reliable early testing, i.e. to obtain strong juvenile-mature (JM) correlation. However, the JM correlation will be low if there are different sets of genes operating at the juvenile and mature stages. Similarly the differences in growth conditions at juvenile and mature stages might cause poor JM relationships.

Picea abies can readily be vegetatively mass propagated from juvenile material (Kleinschmit et al., 1973). Therefore, the effects of early selection in nurseries can be better studied in this species by the aid of cuttings than by seedlings. Thus, it will allow testing of the effects of selection among as well as within families

Mass selection for clones among commercial seedling stocks followed by clone testing in field trials and mass propagation have been a widely used method (KLEINSCHMIT and SCHMIDT, 1977; BENTZER, 1993; KARLSSON, 1993). In order to estimate the efficiency of early selection for later mass propagation, several studies have been presented, some of which show promising results while other are less encouraging. ROULUND et al. (1986) showed 17% gain in height after 10 years in field tests of cuttings of ortets selected from the better third of 4-year old seedlings of Norway spruce compared with random selection from the same seedlings. Skrøppa and Dietrichsson (1986) report large variation among 58 cutting-propagated full-sib families of Norway spruce for height growth and thus concluded that selection of families should be an effective strategy. GREENWOOD and VOLKAERT (1992) concluded after studying reports from several conifer species that nursery height is the best trait to predict later field performance. They suggested, due to the knowledge that G x E interaction is more pronounced for full sib families and clones, that early selection of full sib families and clones is less reliable than selection of half-sib families.

The purpose of this study was to estimate JM correlation between nursery and field performance of clones selected in the nursery for height at family level as well as within families. At both levels the selection was carried out to represent the entire variation. Estimates of potential gain following selection of plants in the nursery was also aimed at.

## 3. Material and Methods

A total of 16 full sib families were sown at Röskärs experimental station in 1975. The seedlings were planted in 1976 in

a randomised block design with 9 seedlings in each of 8 replications. Traits from measurements carried out in the nursery during 1977 to 1979 are listed in *table 1*.

A weighted index for bud-break (D10W) for individual ortets was created by assigning the same typical standard deviation to assessments for both years. For D90 values an index (D90W) was created in an analogous way.

In order to neutralise block differences for correlation estimates and calculations of selection effects, a rescaled ortet value for H5 (H5W) was calculated by multiplication of each ortet observation with a quotient between a chosen within-block standard deviation and the actual standard deviation for the block.

In 1980, the best, the worst and three average families were selected for total height growth (H5). Data for the selected families are found in *table 2*. In each of 6 replications the seedlings were vegetatively propagated by cuttings. Since the first propagation resulted in too few cuttings/clone a second propagation was carried out in 1984 with cuttings from the first cycle ramets. For the field test, 26 clones/family were representatively selected concerning H5, with the restriction that the number of ramets had to be enough for two test sites.

Table 2. – Mating design for the families and latitude for the parents.

Family	Me	other	Father		
no.	Id	Latitude	Id	Latitude	
6	W2023	61° 28	Westerhof 2	52° ¹	
7	W2023	61° 28	S3024	59° 36	
10	W2004	61° 13	P2001	58° 56	
12	Z2004	62° 37	Neuf Chateau 25	50° ¹	
15	Z3008	64° 17	AC1008	64° 35	

<sup>1)</sup> Approximate latitude.

In 1988, the 4-year old rooted cuttings were planted out in field trials at three test sites ( $Table\ 3$ ). The design was a randomised block design with 4-tree plots (2 x 2) and 4 replications.

Table 3. - Description of test sites.

Name	Latitude	Longitude	Altitude (m)
Vitmossen	59° 00'	15° 54'	60
Hall	59° 09'	17° 41'	30
Röskär	59° 25'	18° 10'	20

In the autumn of 1996 an assessment of the trials was carried out. The traits measured are shown in *table 1*.

Anova for nursery measurements was carried out using Proc GLM (SAS Institute Inc., Cary, NC, USA), model:

Table 1. – Traits measured on seedlings in the nursery and on cuttings in the field trials. For growth start and termination 1977 and 1978, the day count was started May 1.

Trait	Abbreviation	Unit	Description
Growth start 1977	D1077	days	Time to reach 10% of final leader length 1977
Growth termination 1977	D9077	days	Time to reach 90% of final leader length 1977
Height 1977	H1	mm	Total height at the end of 1977
Growth start 1978	D1078	days	Time to reach 10% of final leader length 1978
Growth termination 1978	D9078	days	Time to reach 90% of final leader length 1978
Leader length 1978	H2	mm	Total leader length 1978
Height 1979	H5	cm_	Total height at the end of 1979
Height 1993	H8	dm	Height at the end of 1993 in field trials. Age 8 years.
Height 1996	H11	dm	Height at the end of 1996 in field trials. Age 11 years.
Increment 1994-1996	INC	dm	Height increment 1994-1996 (3 years) in field trials.
Frost damage	FR	0-1	Frost damage in field. Transformed to Normal score.

$$y_{ijk} = \mu + nb_i + f_j + e_{ijk}$$

 $y_{ijk}$  = Value of the ijkth observation  $\mu$  = mean value of the population  $nb_i$  = fixed effect of nursery block i $f_i$  = fixed effect of family j

 $\vec{e}_{ijk}$  = random error term  $(N, \sigma^2)$ 

Least square means were calculated for families.

The analysis of variance for individual field trials was carried out using Proc Mixed (SAS Institute Inc., Cary, NC, USA) and the following model was assumed:

$$y_{ijklm} = \mu + nb_i + b_j + f_k + c_{l(k)} + e_{ijklm}$$

## Where:

 $y_{ijklm}$  = Value of the ijklmth observation  $\mu$  = mean value of the population  $nb_i$  = fixed effect of nursery block i $b_i$  = fixed effect of field trial block j $f_k$  = fixed effect of family k $c_{l(k)}$  = random effect of clone l in family k (N,  $\sigma^2$ )  $e_{ijklm}$  = random error term (N,  $\sigma^{2}_{\rho}$ )

Genetic parameters were interpreted as:

$$\sigma_G^2 = \sigma_c^2$$
$$\sigma_E^2 = \sigma_e^2$$

 $\sigma_G^2$  = the genotypic variance  $\sigma_E^2$  = the environmental variance

Broad sense heritability  $(H^2)$  on an individual ramet basis was calculated as the ratio between  $\sigma_G^2$  and  $\sigma_G^2$  +  $\sigma_E^2$  (FALCO-NER, 1981).

Best linear unbiased predictors for clones (BLUP-values) were calculated using software by Danell (1988). The following equation was assumed:

$$y_{ijkl} = \mu + nb_i + b_j + c_k + e_{ijkl}$$

## Where:

 $y_{ijkl}$  = Value of the ijklth observation  $\mu = \text{mean value of the population}$  $nb_i$  = fixed effect of nursery block i $b_i$  = fixed effect of field trial block j $c_k$  = random effect of clone k (N,  $\sigma_c^2$ )  $e_{iikl}$  = random error term  $(N, \sigma_{\rho}^2)$ 

Correlation between traits in the nursery and trials were estimated as Pearson's product-moment correlation (SAS Institute Inc., Cary, NC, USA) between BLUP-values from trials and ortet data from the nursery. Therefore, they are not strictly genetic correlations.

REML variances for the complete experiment series were estimated using Proc Mixed (SAS Institute Inc., Cary, NC, USA). In order to avoid interaction caused by scale effects or unequal genetic variation, the observation values of each trial were rescaled so that all trials achieved the same genetic variance by multiplication of the observed values with the quotient between a chosen genotypic standard deviation and the estimated genotypic standard deviation from the individual trial analysis. The model for the analysis was:

$$y_{ijklmn} = \mu + \mathrm{nb}_i + \mathrm{s}_j + \mathrm{b}_{k(j)} + \mathrm{f}_k + c_{m(l)} + c \mathrm{s}_{jm(l)} + e_{ijklmn}$$

 $y_{ijklmn}$  = value of the ijklmnth observation  $\mu$  = mean value of the population  $nb_i$  = fixed effect of nursery block i

 $s_i$  = fixed effect of site j

 $b_{k(j)}$  = fixed effect of block k in site j

 $f_k$  = fixed effect of family k

 $c_{m(l)}$  = random effect of clone m in family l (N,  $\sigma^2$ )

 $sc_{im(l)}$  = random interaction effect of site j and clone m in family  $l(N, \sigma_{cs}^2)$ 

 $e_{ijklmn}$  = random error term (N,  $\sigma^2$ )

Genetic parameters were interpreted as:

$$\sigma_{G}^{2} = \sigma_{c}^{2}$$

$$\sigma_{GE}^{2} = \sigma_{cs}^{2}$$

$$\sigma_{E}^{2} = \sigma_{e}^{2}$$

Broad sense heritability  $(H^2)$  on an individual ramet basis over the experimental series was calculated as:

$$H^2 = \sigma_G^2/(\sigma_G^2 + \sigma_{GE}^2 + \sigma_E^2)$$

## 4. Results

### 4.1 Nursery assessment

Significant differences between families were found for all nursery traits (Table 4) which indicates that family differences existed at an early stage.

Table 4. - Probability values and least square means from analysis of nursery measurements. Nb = Nursery block.

	Family	H5	D10W	D90W
	id	(cm)	(days)	(days)
Prob(Nb)		0.0001	0.0362	0.5850
Prob(Fam)		0.0001	0.0001	0.0001
	Mean	65.4	34.3	70.5
	6	68.7	35.4	75.9
	7	76.2	33.8	71.0
	10	56.9	32.4	68.6
	12	67.7	38.4	74.8
	15	61.4	29.3	63.8

## 4.2 Field trial assessments

Significant differences between clones were found in all trials and  $H^2$ -estimates between 0.17 and 0.28 were obtained (Table 5). Family differences are significant for all traits at Vitmossen and for H11 and INC at Hall but for none of the traits at Röskär.

Table 5. - Results from analysis of field experiment characters.

Site		H8	H11	INC
Vitmossen	Mean (dm)	8.0	17.7	8.7
	Prob(Nb)	0.0011	0.0049	0.0171
	Prob(Block)	0.0000	0.0000	0.0000
	Prob(Fam)	0.0000	0.0000	0.0000
	Prob(Clone)	0.0000	0.0000	0.0000
	$H^2$	0.27	0.27	0.24
Hall	Mean (dm)	9.3	17.8	8.50
	Prob(Nb)	0.1794	0.3265	0.5689
	Prob(Block)	0.0000	0.0000	0.0000
	Prob(Fam)	0.1150	0.0249	0.0019
	Prob(Clone)	0.0000	0.0000	0.0000
	$H^2$	0.28	0.25	0.17
Röskär	Mean (dm)	7.2	15.3	8.1
	Prob(Nb)	0.3432	0.4540	0.5424
	Prob(Block)	0.0000	0.0000	0.0000
	Prob(Fam)	0.4709	0.3975	0.1546
	Prob(Clone)	0.0000	0.0000	0.0000
	$H^2$	0.22	0.23	0.21

#### 4.3 Nursery (ortet)-field (ramet) correlation

The correlation estimates between nursery height of the ortets and weighted BLUP-values for field trial traits were generally low (*Table 6*). In *table 7*, it is shown that families 7 and 15 correlate positively significant, 6 and 10 positively but weak, and family 12 shows a weak negative estimate. The pattern seem to be the same at all sites.

Table 6. – Correlation estimates and probability-values (p<) between nursery observations and weighted BLUP-values from the field trials. W = Weighted over trials, N = Normal score values.

	WNSU	WH8	WH11	WINC	WNFR
D10W	0.05	0.08	0.14	0.20	-0.20 0.0218
p<	0.5906	0.3565	0.1224	0.0279	0.0218
D90W	0.06	0.22	0.27	0.31	-0.25 0.0041
p<	0.5242	0.0143	0.0025	0.0004	0.0041
H5W	-0.11	0.15	0.23	0.29	-0.13
p<	0.2099	0.0792	0.0100	0.0010	0.1522

Table 7. — Within-family correlation estimates between H5W in the nursery and BLUP-values for height increment (INC) in field trials. d.f. = 14 at Röskär and 24 at the other sites and for the weighted BLUP-values.

Family	Vitmossen	Hall	Röskär	Weighted
6	0.24	0.02	0.13	0.14
7	0.24	0.38	0.48	0.49
10	0.02	0.11	0.31	0.16
12	-0.08	-0.01	-0.21	-0.17
15	0.27	0.49	0.39	0.48

## 4.4 Clone x site interaction - Correlation between field trials

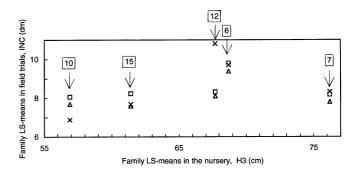
Table 8 show that the variance components for clone x site interaction are significant for all traits in the field trials. Indications of existing interaction are verified by the significant but rather low correlation estimates between BLUP-values for the same trait in different trials (Table 9). The highest estimates were found between Röskär and the other two sites while estimates between Vitmossen and Hall were lower.

## 4.5 Family selection effects

The ranking for families in the nursery correlated well with weighted BLUP-values except for family 7 (Fig. 1). Although it is the superior family in the nursery, its result in field tests is about average. Looking at D10W and D90W (Table 4), this family shows average means, which indicates that the family is not an extreme as far as phenology is concerned.

## 4.6 Effects of clone selection within family

The gain when selecting ortets in all families in this study is shown in *figure 2*. The discrepancy between that selection and a selection done on the weighted BLUP-values for INC after



 $\label{eq:hall-constraint} $$ \blacksquare \text{Hall-chinossen $\Delta$ R\"{o}sk\"{a}r$}$ Figure 1. — Plot of nursery — field performance on family basis. Boxed numbers indicate family number.}$ 

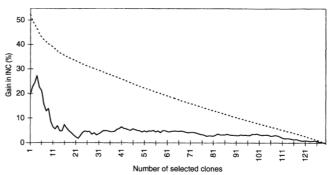


Figure 2. – Calculation of genetic gain on the basis of weighted BLUP-values for INC (increment) after selection of clones among all families for H5 in nursery (—) and after selection for weighted BLUP-values (INC) (----).

the field test is very large. There are also remarkable differences between families in response for selection (Fig. 3).

## 5. Discussion

The results from this study indicate that significant interactions at different levels create severe obstacles for early clone selection and later mass propagation for forest regeneration. The interactions dealt with in this study can be divided into two parts; 1. ortet in nursery x ramet in field test interaction, and 2. clone x site interaction at field testing.

## 5.1 Nursery (ortet)-field (ramet) correlation

Skrøppa and Dietrichson (1986) found significant correlation estimates between 8-year old ortets from 52 families in a full-sib family progeny test of *Picea abies* and their 348 clones tested in a field trial 7 years after propagation. In their study, the progeny test for selection and the clone test were growing at the same location, and another difference was that their ortets were older. The nursery – field issue is focused in Skrøppa and Dietrichson's study by the family mean correla-

Table 8. – Results from the complete series analysis. % = percentage of random variance.

					Source	of variat	ion				
Clone Clone						one×site Error		r			
Trait	$\sigma^2_{c(f)}$	se	Pr> Z	%	$\sigma^2_{c \times s}$	se	Pr> Z	%	$\sigma_{e}^{2}$	se	$H^2$
SURV	2038	2756	0.4596	0.7	24597	4303	0.0001	7.4	306705	60696	0.00
H8	1.84	0.39	0.0001	13.6	1.94	0.26	0.0001	14.4	9.66	0.20	0.14
H11	6.30	1.46	0.0001	11.6	8.37	1.11	0.0001	15.5	39.45	0.83	0.12
INC	1.31	0.38	0.0006	7.4	2.67	0.36	0.0001	15.0	13.8	0.29	0.07

tion estimates between 4-year old nursery measurements and the 8-year progeny field test being only 0.49 and 0.55, respectively in two sets of families.

In a study by Mullin and Park (1994), field height at age 10 years was related to 25-week old greenhouse results in a material of clonally replicated full-sib families of *Picea mariana*. Poor correlation was found for families on half-sib level, even weaker on full-sib level and low, non-significant between clone means.

MULLIN et al. (1995) report high correlation between 3-year nursery height and field trial height after 10 years in one experimental series with open pollinated families of *Picea mariana*,

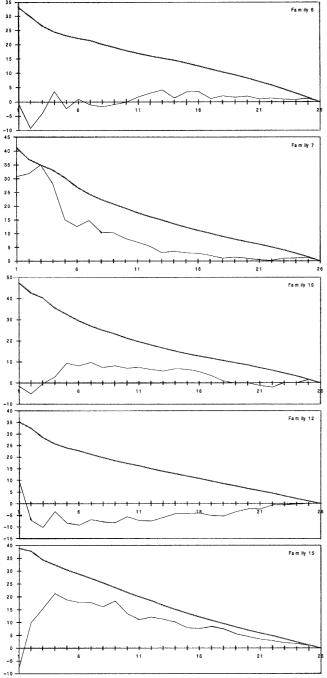


Figure 3. – Comparison between relative gain (%) for within-family selection in weighted BLUP-values for INC (Y-axis) when selecting for H5 in nursery (—) and after selection for weighted BLUP-values (INC) (—). X-axis = number of selected clones.

but lower in another. They concluded that nursery tests may be good enough for culling the worst families but not to intensively select the very best. Their result is in agreement with Samuel and Johnstone (1979) who report poor agreement between nursery tests and forest tests up to 6 years of age in a study of 116 open pollinated plus tree families of *Picea sitchensis*. Li et al. (1993) showed for *Picea glauca* that strong genetic correlation between 3-year nursery height and 8-year old plants in field tests resulted in considerable genetic gain after selection for nursery height. They concluded that at least culling of material with poor nursery growth would be efficient.

## 5.2 Effects of clone and family selection

ROULUND et al. (1986) showed 17% gain in height after 10 years in a field test after selection of the better third among 4-year old seedlings of Norway spruce before vegetative propagation. The corresponding effect in our study at the same selection ratio was 5.6% (Fig. 2) on height increment. Their result is equal to the effect of selection among the clones in the best responding family (15) in our study (Fig. 3). In the study by ROULUND et al. (1986) the tested clones were first cycle cuttings, while our study consisted of second cycle cuttings. That probably means that the C-effects due to the ortet's physiological status were smaller in our study. The fact that the study by ROULUND et al. includes only one field test site makes the result less reliable.

KLEINSCHMIT and SVOLBA (1991) reported a 5.4% gain in height at age 17 when performing a 20% selection at age 4 in a cutting-propagated clone material of Norway spruce. That is 60% of the total gain that would have been achieved at selection at age 17, which would be high enough to justify early selection of individual clones. In our study, the loss when selecting ortets among all clones compared with selection after field testing was 85% of the possible gain which, in our opinion, is too much to omit field tests.

Högberg and Karlsson (1997) showed selection effects between  $2.4\,\%$  and  $3.4\,\%$  in field trial height when selecting the top  $20\,\%$  after ranking by nursery height after the first propagation cycle in cutting-propagated clones of Norway spruce. The material in their study had no replications in the nursery, which makes comparisons with the results in our study relevant, where a selection gain of gain in INC of ca  $5.5\,\%$  was achieved.

Looking at table 7, families 7 and 15 show significant positive nursery-field correlation and are also stable over sites, while the coefficients for families 6 and 10 were positive but not significant and vary more over sites. It is obvious that family 12 is an extreme, with negative correlation estimates at all sites. Both that family and family 6 have continental fathers, Neufchateau 25 and Westerhof 2 of Belgium and German origin, respectively. It seems as if these families are responsible for a large part of the poor nursery - field-test correlation. Are these two families too poorly adapted to the Central Swedish forestry conditions? The fact that they perform well as families in field tests (Figure 1) means that they probably are good enough as families, but not suited for early clone selection. The question then remains why tall plants in the nursery do not perform well in field trials. Ununger et al. (1987) studied the difference between six yearold ortets and their cuttings at age two for shoot elongation time and time of growth cessation. They found that a large part of the variation was due to genetic origin. It is very likely that a trait such as free growth varies widely in our plant material with such a wide range of parent origin and probably varying levels of adaptation to the climate. Families 6 and 12 have the highest values for D90W (Table 4), indicating that they have a later growth cessation. A significant positive correlation estimate between D90W and WINC indicates that a late growth cessation is beneficial for the plants. However, this measure of growth cessation might not be exact enough for origins with a very long transfer like the paternal side of family 12.

It is very hard to draw any general conclusions about family selection in our study since the number of families is too limited. The question why family 7, which performed the best in the nursery, does not grow well in the field tests is hard to answer conclusively. The variation for H5W was larger for this family, which could indicate individual plants with more "optimistic" behaviour in the nursery that might be beneficial in a rather protected environment such as the nursery, but not in the harsher environment in the field trials.

The trend goes towards stronger significance for family differences with time both at Hall and at Röskär. It seems somewhat surprising that the significant family differences obtained in the nursery at Röskär did not continue in the field trial, which is less than 2 kilometres away and with almost identical climatic conditions.

## 5.3 Clone x site interaction

In our study there are significant clone x site variance components for growth traits (Table 8). For all traits the interaction component was found to be larger than the clone component, and for INC it was 15% of the random variation which is twice as large as the clone component. Bentzer et al. (1988) reported 5-year height correlation estimates between 6 trials ranging from 0.59 to 0.71 in one field trial series including 490 clones of Picea abies, and 0.82 to 0.99 in a second with 423 clones. The G x E variance components in the two series were 39% and 18% of the clone components, respectively. In another study, with 75 clones of Picea abies, Bentzer et al. (1989) found the interaction component to be below 20% of the clone component for different growth traits up to 10 years. St. Clair and Kleinschmit (1986) report strongly significant clone x site interaction for 10-year height in a 7-site series with 40 clones of Picea abies, with an interaction component of 40% of the clone component. Another analysis of the same clone test series resulted in clone x site components below 35% of the clone component for all traits from age 3 to age 17 (ISIK et al., 1995). KARLSSON and HÖGBERG (1997) report clone x site components of almost the same magnitude as the clone components in a test series with 14-years old cuttings from 310 clones of Picea abies. In relation to cited studies, our findings are remarkably high. At assessment, the trials were still rather young and have suffered from frost damage, game browsing and also to a certain extent competition from weeds and self seeded broadleaves. All these factors could have been partially responsible for the large interaction effects. If so, this is an indication that too early assessments may be unreliable. It is also important to

Table 9. – Correlation estimates between BLUP-values for total height (H11) and height increment (INC) in field trials.

		Vitmos	sen	Hall	
		H11	INC	H11	INC
Vitmossen	H11			0.38	
	p<			0.0001	
	INC				0.28
	p<				0.0015
Röskär	H11	0.48		0.47	
	p<	0.0001		0.0001	
	INC		0.45		0.41
	p<		0.0001		0.0002

be aware of the limited number of families in this study. However  $H^2$ -values (*Table 5*) are rather high and agree well with results from other reports of clone tests with Norway spruce (Karlsson and Högberg, 1997; Roulund et al., 1986).

#### 6. Conclusions

Skrøppa and Dietrichsson (1986) suggested propagation of cuttings from juvenile seedlings in tested full-sib families and testing of the clones in clone tests. They also stress the importance of evaluating that strategy against bulk propagation without clone testing. Our conclusion agrees well with that since selection of clones in the nursery seem to be unreliable unless the family has been tested before and has shown good selection response. It is also important to remember that, even if refined methods to predict field performance are developed, they must be applicable in practical use. As long as no reliable and practically applicable method of predicting field performance of single clones exist, we claim that clone testing in field trials is necessary. It is important, though, to carefully consider the number and status of test sites.

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# Time Trends for Genetic Parameters of Wood Density and Growth Traits in *Pinus sylvestris* L.

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#### Abstract

Genetic parameters of wood density in *Pinus sylvestris* were estimated and compared with corresponding parameters for height and diameter increment. Measurements were made on 10 mm increment cores from a 33-year old non-contiguos single-tree plot progeny trial. Totally 944 trees from 106 full-sib families were included in the study. REML-estimates of the variance components were obtained by iteration on a mixed model equation system and time trends for the calculated parameters were plotted.

With the exception of the most juvenile wood, which showed higher values, the additive genetic coefficient of variation  $(\mathrm{CV}_A)$ , the environmental coefficient of variation  $(\mathrm{CV}_E)$ , and the phenotypic coefficient of variation  $(\mathrm{CV}_P)$  for wood density, all showed stable values over time. The heritability was high, fluctuating around 0.4 and with no tendency to differ between juvenile and mature wood. Wood density showed lower  $\mathrm{CV}_A$  but higher heritability than height increment. The effect of competition on the estimated genetic parameters was discussed and the effect seemed moderate for wood density and height increment but strong for diameter increment where  $\mathrm{CV}_A$ ,  $\mathrm{CV}_E$  and  $\mathrm{CV}_P$  increased monotonically over time.

Key words: REML, heritability, coefficient of variation, competition, progeny test.

 $FDC:\ 165.3;\ 165.6;\ 232.1;\ 561;\ 812.31;\ 174.7\ Pinus\ sylvestris;\ (485).$ 

## Introduction

The general breeding goal for Swedish *Pinus sylvestris* breeding is to attain higher total net value of the forest production (Wilhelmsson and Andersson, 1993). So far, operational breeding goals have been concentrated on combined improvement of volume growth, hardiness, vigour, stem straightness,

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branch characteristics and to some extent wood density. Wood properties significantly affect the properties of wood- and fiberbased products as well as production processes (WILLIAMS, 1994; Kibblewhite et al., 1997; Duchesne et al., 1997) and in Sweden (WILHELMSSON and ANDERSSON, 1993) and other parts of the world (ZHANG and MORGENSTERN, 1995; ZOBEL and JETT, 1995) efforts are under way to incorporate wood properties in current breeding programs. To do this efficiently, it is necessary to estimate genetic parameters such as genetic variation and heritability of wood properties. This study provides such estimates for wood density. Wood density affects the strength of solid wood products (Armstrong et al., 1984; Mishiro et al., 1986), pulp yield (ERICSON et al., 1973), and in conjunction with tracheid length the strength properties of kraft-pulp (Cown and Kibblewhite, 1980; Kibblewhite, 1980; Kibblewhite et al., 1997).

For *Pinus sylvestris*, wood density increases rapidly in the juvenile phase up to a cambial age of about 15 years and then stabilizes in the mature phase (e.g. Persson et al., 1995). Estimates of genetic parameters of the wood of both these phases are of interest but competition in the mature stands may make the estimates less accurate. Consequently, it is important to study time trends for genetic parameters of wood density and how they are influenced by competition. Most studies of wood density in pines are performed on juvenile wood. The few available time trends for wood density indicate that there are no major difference in the heritability between juvenile and mature wood (WISELOGEL and TAUER, 1982; Talbert et al., 1983; Hodge and Purnell, 1993).

Estimates of genetic parameters are often obtained on the assumption that there is no interaction between neighbouring trees, i.e. that they are not affected by environmental covariance. In the presence of competition this assumption is likely not to be fulfilled, because taller trees will tend to suppress their neighbours and shorter trees leave expansion space for their neighbours. When single-tree plots are used, competition will increase between family variance, which will lead to greater estimates of heritability than in the case of no competition (Magnussen, 1989; Foster, 1989; St. Clair and Adams, 1991). Different traits, however, respond differently to competition. For instance, height appears to be less sensitive to competition whereas diameter is very much affected by it (e.g. Sakai and Mukaide, 1967; Magnussen, 1989). The effect of

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