cuttings of *Picea abies* (L.) KARST. Scand. J. For. Res. **1**: 293–302 (1986). — SAMUEL, C. J. A. and JOHNSTONE, R. C. B.: A study of population variation and inheritance in sitka spruce. I. Results of glasshouse, nursery and early forest progeny tests. Silvae Genetica **28**(1): 26–32 (1979). — SKRØPPA, T. and DIETRICHSSON, J.: Genetic variation and ortet/ramet relationships in a clonal test with *Picea abies.* Scand. J. For. Res. **1**: 323–332 (1986). — ST. CLAIR, J. B. and KLEINSCHMIT, J.: Genotype-environment interaction and stability in ten-year height growth of Norway spruce clones (*Picea abies* KARST.). Silvae Genetica **35**: 177–186 (1986). — UNUNGER, J. and EKBERG, I.: Rejuvenation of Juvenile Growth Characters in *Picea abies.* Scand. J. For. Res. **2**: 441–453 (1987).

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

By B. HANNRUP[1][4], L. WILHELMSSON[2] and Ö. DANELL[3]

(Received 17th March 1998)

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 (CV_A), the environmental coefficient of variation (CV_E), and the phenotypic coefficient of variation (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 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 CV_A, CV_E and 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, branch characteristics and to some extent wood density. Wood properties significantly affect the properties of wood- and fiber-based 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

---

[1] Department of Forest Yield Research, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden.

[2] The Forestry Research Institute of Sweden, S-751 83 Uppsala, Sweden.

[3] Department of Animal Breeding and Genetics, Swedish University of Agricultural Sciences, S-750 07 Uppsala, Sweden.

[4] Corresponding author: BJÖRN HANNRUP
Phone: +46 18 67 31 58
Fax: +46 18 67 27 18
e-mail: bjorn.hannrup@sprod.slu.se

competition on genetic parameters of wood density is less studied and depends partly on the strength of the correlation with diameter growth.

The aims of this study were to estimate genetic parameters of wood density for different time intervals, which are assumed to reflect different competitive environments, and to compare the estimates with corresponding estimates for height and diameter growth. These aims are part of the general goal of a larger project, aiming to describe the possibilities of integrating selection for wood properties into the *Pinus sylvestris* breeding program.

Materials and Methods

Plant material

Wood samples were collected in a 33 year old (tree age) *Pinus sylvestris* progeny trial, Norra Kvill, located in south-eastern Sweden, lat. 57°44', long. 15°33'. The progenies originate from controlled matings between grafted plus trees, carried out around 1960 in a seed orchard in southern Sweden (JOHNSSON, 1973). Plus trees were selected in natural stands for vigour, height, diameter, straightness and branches with low diameter and straight angle. Wood density was not considered in this selection. The progeny trial included 106 full-sib families from controlled matings between 30 female parent trees and 4 male parent trees (*Fig. 1*). The males were randomly sampled among the trees used as females. Selfings were excluded.

Males

FEMALES	5	22	27	11
1	x	x	x	
2	x	x	x	x
3	x	x	x	x
4	x	x	x	x
5		x	x	x
6	x	x	x	x
7	x	x	x	x
8	x	x	x	x
9	x	x	x	x
10		x	x	x
11	x	x	x	
12	x	x	x	x
13	x	x	x	x
14	x	x	x	x
15	x	x	x	x
16	x	x	x	x
17	x	x	x	x
18	x	x	x	x
19	x	x	x	x
20	x	x	x	
21	x	x		
22			x	x
23	x	x	x	x
24			x	
25	x	x	x	x
26	x	x	x	x
27	x	x		x
28	x	x	x	x
29	x	x	x	x
30	x	x	x	

Fig. 1. — Schematic diagram of the mating design. The four trees that were designated both as female and male trees are underlined.

Design of the progeny trial

A randomized block design with non-contiguos single-tree plots was used. There are 10 blocks with 4 randomly planted trees of each family in each block. The original spacing was 1.4 m x 1.4 m and the trial has been thinned in 1990, performed as a low thinning with a certain demand for the remaining stems to be evenly distributed. The arithmetic means of breast height diameter and tree height were at the time of sampling (June 1995) 105 mm and 10.8 m, respectively. Further details of the progeny trial can be found in WERNER and ERICSSON (1980).

Sample size

Wood density is an expensive trait to measure and within the frame of the present study totally about 1 000 trees were possible to measure. When sample size decreases, the standard error of the heritability increases. However, the precision of the estimate can be maximized for a given total sample size by balancing the number of families against the number of individuals per family (ROBERTSON, 1959). This requires prior knowledge of the magnitude of the heritability. Within a total effort of about 1 000 trees measured and heritability assumed to be in the range of 0.1 to 0.5, a near optimal design was expected to be 8 trees sampled per family or conversely 32 trees per female tree. Missing matings due to empty entries in the mating design were compensated for by sampling more trees from matings with males among the same female. This was not fully achieved, but totally 948 trees from 106 families in 10 blocks were sampled.

Traits assessed and sample methods

All traits included in the study are presented in *table 1.* Total height and diameter at breast height over bark were measured on all the sample trees. Earlier height measurements at ages 9, 12 and 22 years from seed were also included in the study. To measure wood density, a 10 mm thick knot-free increment core was taken from the interwhorl closest to 1.3 m above ground level. The cores were sampled from northwest i.e. 90° against the prevailing wind direction to avoid reaction wood. Increment cores from leaning trees were taken at 90° angle to the lean of the tree, but such cases were rare.

The increment cores were cut into 4 segments:

1. Juvenile wood where heartwood formation may be initiated. Year ring 1 to 4 from the pith.
2. Juvenile wood without heartwood formation. Year ring 5 to 8 from the pith.
3. Transition wood, containing approximately 12 year rings.
4. Mature wood. Year ring 1 to 6 from the bark.

This partitioning of the wood cores was made assuming that the relative impact of cambial age is largest in the wood closest to the pith and the effect of the year-of-ring formation is largest in the older wood. The wood in the two segments closest to the pith is formed by a cambium of the same age, while all wood samples from the segments closest to the bark have been formed during the same chronological year.

The green volume of the segments was measured by the water displacement method (SMITH, 1954; OLESEN, 1971) and length of the segments was recorded with a micrometer. Oven-dry weight was measured after 24 hours in 106 °C and the wood density was estimated as the ratio of oven-dry weight to green volume.

Among the increment cores sampled, some did not hit the pith. To adjust the length of these increment cores a method was applied where the distance from the innermost part of the core and the pith was estimated by the use of a transparent template with concentric rings. The adjusted length of the segments were then calculated by use of the Pythagorean theorem.

Computed variables

Wood density and length of the segments express traits of wood produced during different periods of time. The total height data represent cumulative values and to enable comparisons between the two types of traits, the four height increments corresponding to the four increment core segments were calculated as the differences between the total height

Table 1. – Number of observations and mean values of the included traits.

Trait	Tree age 1)	Annual rings from pith	n	Mean
Wood density (kg/m^3)				
Segment 1	8-11	1-4	834	369
Segment 2	12-15	5-8	834	395
Segment 3	16-27	9-20	944	433
Segment 4	28-33	21-26	944	491
Increment core segment length (mm)				
Segment 1	8-11	1-4	834	14.1
Segment 2	12-15	5-8	834	8.5
Segment 3	16-27	9-20	944	14.7
Segment 4	28-33	21-26	944	4.5
Tree height increments (m)				
Increment 1	1-9		944	1.9
Increment 2	10-12		944	1.2
Increment 3	13-22		944	3.8
Increment 4	23-32		944	3.9
Area-weighted wood density (kg/m^3)	8-33	1-26	834	431
Diameter over bark at breast height (mm)	33		944	105
Total height (m)	32		944	10.8

1) For wood density and segment length, annual rings from pith were converted to tree age by adding 7 years. For further details see text.

measurements. To further facilitate comparisons the cambial breast height age of wood density and segment length was converted to tree age by adding 7 years, which was the average time interval for the trees to reach breast height. To enable comparisons between wood density and total height and diameter at the time of sampling, the area-weighted density (AWD) was calculated as:

$$AWD = \frac{\sum_{i=1}^{4} a_i * wd_i}{\sum_{i=1}^{4} a_i} \qquad [1]$$

where a_i is the cross-sectional area represented by segment i and wd_i is the wood density of segment i.

Statistical analysis

Increment cores, that were found to contain reaction wood when visually examined were excluded resulting in 944 cores available in the statistical analysis. For wood density of segment 1 and 2 and area-weighted density, only the increment cores where the pith was hit or missed by less than 4 mm were used (n = 834). Genetic and environmental variance components were estimated by an EM algorithm for Restricted Maximum Likelihood (REML) derived from HENDERSON's Mixed Model Equations (MME), (e.g. HENDERSON, 1984) as performed in the VDIAL software designed for diallel and factorial mating designs (DANELL, 1989).

The fitted mixed diallel model was

$$Y_{ijj'k} = b_i + p_j + p_{j'} + f_{jj'} + e_{ijj'k} \qquad [2]$$

where $Y_{ijj'k}$ is an observation of each trait of the $ijj'k^{th}$ tree, b_i is the fixed effect of the i^{th} block, p_j and $p_{j'}$ are the random genetic effects of the first (j) and the second (j') parent respectively belonging to the same set of parents, $f_{jj'}$ the random genetic interaction effect between the parents and $e_{ijj'k}$ is the random residual.

The model assumes that the random factors are normally distributed with expectation 0 and consequently $E(y_{ijj'k}) = b_i$. Furthermore

$$\mathrm{Var}\begin{bmatrix} \mathbf{p} \\ \mathbf{f} \\ \mathbf{e} \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma^2_p & 0 & 0 \\ 0 & \mathbf{I}\sigma^2_f & 0 \\ 0 & 0 & \mathbf{I}\sigma^2_e \end{bmatrix}. \qquad [3]$$

where σ^2_p is the parental variance, assuming that no maternal effects were present at the ages studied, σ^2_f is the family variance and σ^2_e is the residual variance. Estimates of model effects and variances were attained by iteration on the following MME system

$$\begin{bmatrix} \mathbf{X'X} & \mathbf{X'Z_1} & \mathbf{X'Z_2} \\ \mathbf{Z_1'X} & \mathbf{Z_1'Z_1} + \mathbf{I}\lambda_1 & \mathbf{Z_1'Z_2} \\ \mathbf{Z_2'X} & \mathbf{Z_2'Z_1} & \mathbf{Z_2'Z_2} + \mathbf{I}\lambda_2 \end{bmatrix} \begin{bmatrix} \hat{\mathbf{b}} \\ \hat{\mathbf{p}} \\ \hat{\mathbf{f}} \end{bmatrix} = \begin{bmatrix} \mathbf{X'Y} \\ \mathbf{Z_1'Y} \\ \mathbf{Z_2'Y} \end{bmatrix} \qquad [4]$$

where **Y** is the observation vector, **X**, $\mathbf{Z}_1$ and $\mathbf{Z}_2$ are incidence matrices for blocks, parents and families respectively and $\hat{\mathbf{b}}$, $\hat{\mathbf{p}}$ and $\hat{\mathbf{f}}$ are solutions for block, parent and family effects, respectively. The λ_1 and λ_2 are variance ratios $\frac{\hat{\sigma}_e^2}{\hat{\sigma}_p^2}$ and $\frac{\hat{\sigma}_e^2}{\hat{\sigma}_f^2}$, respectively, where the variance components were computed from the EM-algorithm at each round of the iteration (first values were guessed). The solutions were considered to have converged when the differences between two successive estimates were less than 0.01% for all variance components.

Additive genetic variance was found as

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

and dominance variance as

$$\hat{\sigma}_D^2 = 4\hat{\sigma}_f^2. \qquad [6]$$

Individual tree heritabilities were obtained as

$$\hat{h}^2 = \frac{4\hat{\sigma}_p^2}{2\hat{\sigma}_p^2 + \hat{\sigma}_f^2 + \hat{\sigma}_e^2} = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_P^2} \qquad [7]$$

and the coefficients of variation as

$$CV_i = 100\sqrt{\sigma_i^2}/\bar{X} \qquad [8]$$

where i is the considered variance and $\bar{X}$ the phenotypic mean of the trait. In a breeding context these standardized measures express the precision in the detection of genetic differences from phenotypes and degree of utilizable variation, respectively.

Standard errors of the heritabilities (lower boundary estimates) were calculated as in BECKER (1984).

Results

The mean values of all age intervals used are shown in *table 1*. Wood density increased with the age of the wood.

Estimates of heritabilities and coefficients of variation for area-weighted density, breast height diameter and total height are given in *table 2*. Area-weighted density shows tendencies towards higher heritability but lower additive genetic coefficient of variation than the growth traits. Consequently, the phenotypic coefficient of variation is lower for area-weighted density than for the growth traits.

Table 2. – Estimated heritabilities with standard errors, additive genetic (CV_A) and phenotypic (CV_P) coefficients of variation for area-weighted wood density at age 33 (AWD33), breast height diameter at age 33 (DBH33) and total height at age 32 (HT32).

	Estimated genetic parameters			
Trait	h^2	S.E. (h^2)	CV_A (%)	CV_P (%)
AWD33	0.50	0.14	3.9	5.5
DBH33	0.27	0.09	9.8	18.8
HT32	0.32	0.10	5.7	10.2

The time trends of heritabilites and coefficients of variation for wood density, segment length and height increment showed different trend patterns (*Fig. 2*). For wood density the phenotypic coefficient of variation (CV_P), the environmental coefficient of variation (CV_E) and the additive genetic coefficient of variation (CV_A) all showed a similar stable trend over time with the exception of the most juvenile wood which showed higher values. The dominance genetic coefficient of variation (CV_D) fluctuated. The heritability showed stable values over time with a slight increase in the third measurement owing to a corresponding increase for the CV_A. CV_P, CV_E and CV_A of segment length showed similar trends with monotonically increasing values. The CV_D started with high values in the first two measurements but then decreased to zero. The heritability varied with the highest values in the later measurements. For height increment, CV_P and CV_E fluctuated with a pronounced peak in the second measurement but CV_A showed stable values. The heritability decreased during the second measurement where CV_E peaked but the other values were quite stable. The CV_D showed high values in the first two measurements followed by a decrease to a lower level for the later measurements.

Discussion

Mean values of wood density

Wood density means increased with age of the wood (*Table 1*) and no stabilization was observed in the mature wood as has been showed in other studies of *Pinus sylvestris* (ATMER and THÖRNQVIST, 1982; PERSSON et al., 1995). However, the partitioning of the increment cores was not done with the purpose of a closer examination of the radial wood density variation. Especially in segment 3 there were too many year rings (12) to enable an observation of a possible stabilization of the wood density.

Effect of the thinning

A potential source of error is the weak low-thinning carried out at age 28 as sampling was made only among remaining stems. As regards height measured at age 22 and diameter at age 27, mean values increased with 4% and 10% respectively compared to the unthinned population. Both the additive genetic variance and the phenotypic variance decreased in the thinned population resulting in a marginal increase and decrease of the heritabilities of height and diameter respectively (data not shown). This indicates that the thinning caused a change in all parameter estimates of height and diameter. The effect on wood density should be lower as the correlations found in the same material between this trait and height and diameter respectively in general were weak (B. HANNRUP et al., unpublished).

Time trends of the estimated genetic parameters

The coefficients of variation of the traits showed different time trends (*Fig. 2*). As for wood density and height increment, CV_E and CV_A were stable with the exception of the peaks in the first and the second measurements, respectively. A trend of increasing values was observed for segment length. No clear trend could be observed for the CV_D of any trait. However, the dominance variance in this study is estimated with a large standard error and a fluctuating pattern could just be an effect of sampling.

A plausible explanation for the peaks observed for wood density and height increment is initiation of heartwood formation and measurement error, respectively. The use of a chemical reagent (sulfanilic acid + sodium nitrite) on a number of test cores showed that some trees had heartwood in the first annual rings. The heartwood has a higher wood density in pines (GOGGANS, 1961). If the start of the heartwood formation is genetically determined, this would be reflected in a varying content of heartwood among families, which could be the reason for the higher coefficients of variation. Height increment being the difference between two subsequent total height measurements, will inevitably be associated with a measurement error. The period between the first and the second meas-

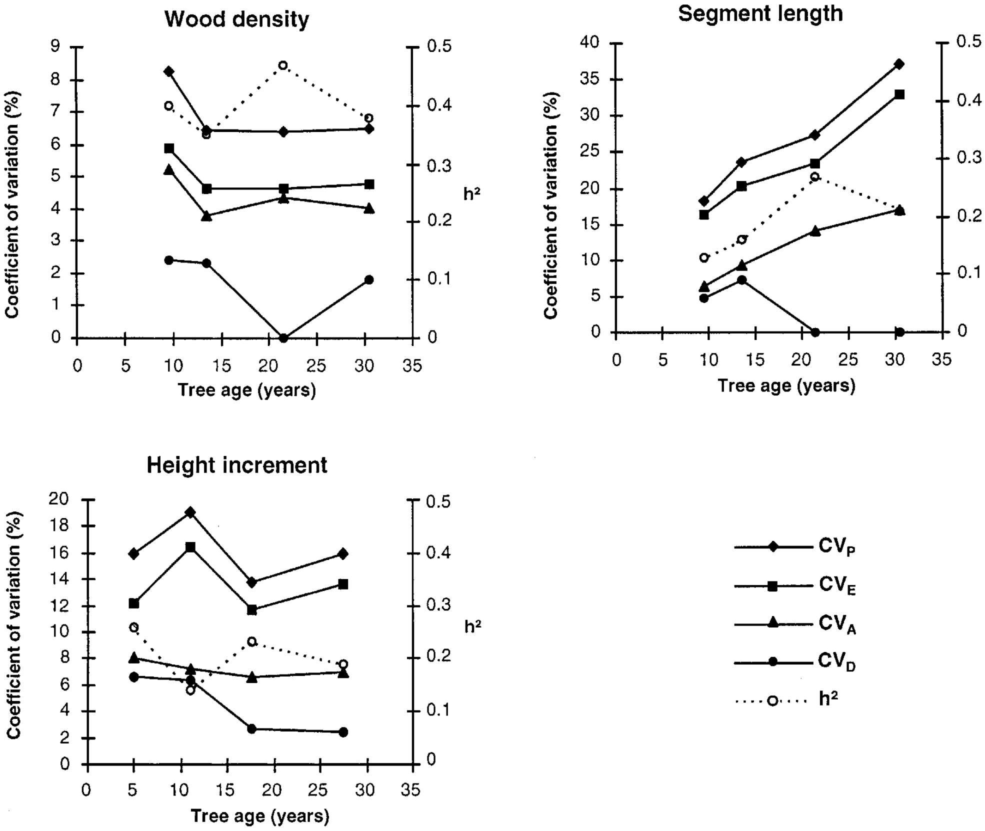

Fig. 2. — Time trends of the phenotypic (CV_P), environmental (CV_E), additive genetic (CV_A) and dominance genetic (CV_D) coefficients of variation and heritability (right axis) for wood density, segment length, and height increments. Symbols indicate the middle of each age interval.

urement was only three years (*Table 1*) giving a large relative impact of this error. The error contributes to the environmental variation and it is this component of the variance that is causing the peak at the second measurement of height increment.

If the peak values for wood density and height increment are ignored for the reasons given above, these traits show stable trends for CV_E and CV_A, in contrast to the pattern of increasing values for segment length. We consider this as a difference between the traits in their response to increasing competition, the parameters of segment length being sensitive to competition whereas the opposite is true for wood density and height increment. The implications of this are that diameter has to be measured early to avoid distortion of the estimated parameters, whereas wood density and height parameters can be validly estimated during a longer period. For wood density we suggest that a heritability of 0.45 and a CV_A of 4% could be regarded as values undistorted by competition. Corresponding values for height increment would be 0.2 and 7% respectively and for segment length 0.15 and 6% respectively.

Comparisons with other studies

Our estimated heritability of wood density corresponds well with other studies in *Pinus sylvestris* (PERSSON, 1972; HALUPÁNÉ-GROSZ and MÁTYÁS, 1975) as is also true of the generally found moderate to high heritability for juvenile wood density in pines (WISELOGEL and TAUER, 1982; TALBERT et al., 1983; FRIES, 1986; HARDING et al., 1991; BURDON and LOW, 1992; HODGE and PURNELL, 1993). Our estimated CV_A for wood density agrees fairly well with average results in a review by CORNELIUS (1994) who found a median CV_A of 5.1% for this trait. The estimated values for height increment and segment length show good agreement with the results in a compilation of 32 Swedish *Pinus sylvestris* progeny trials (L. WILHELMSSON, unpublished). The average heritability at an age of 11.6 years was 0.18 and 0.14 for height and diameter, respectively, whereas CVA for the corresponding traits were 7.6% and 8%, respectively.

Comparisons between traits

The results found here agree also with expectations based on these traits' possible roles in an evolutionary context. The undistorted values suggested above as well as the whole tree values (*Table 2*) imply that wood density possesses higher heritability but lower CVA than height and diameter traits. Wood density is a morphological trait with probably little or no influence on fitness, whereas the height and diameter traits are likely to have a higher association with fitness. It has been shown clearly from compilations of more than 1000 studies that morphological traits possess higher heritabilities than life history traits which are more closely related to fitness (ROFF and MOUSSEAU, 1987; MOUSSEAU and ROFF, 1987). Our results agree with this. The lower CV_A and CV_E observed for wood density than for height and diameter traits agrees with HOULE (1992) who in a compilation of studies found that traits closely related to fitness had higher CV_A and CV_E than traits with low fitness association. Like fitness traits, height and diameter may be of a more complex quantitative nature than wood density and could then be expected to be influenced by a higher number of genes and environmental variables.

Possible gain from selection

In a simplified situation where equal information on each candidate is available, the relative genetic response of selection for one specific trait may be predicted as $\frac{\Delta G}{\bar{X}} = iCV_A r_{TI}$ where i is the selection intensity, CV_A the additive genetic coefficient of variation, and r_{TI} the correlation between the true genetic value of the goal trait and the predicted value of the assessed trait. The latter is determined by the heritability, the genetic relationship between candidates and evaluated individuals and the number of replicates (e.g. FALCONER and MACKAY, 1996, p. 243).

Applied to wood density parameters from this study ($h^2 = 0.45$ and $CV_A = 4\%$), a selection intensity of unity and assessments made on the candidates themselves ($r_{TI} = 0.67$) is expected to give a response in wood density of 2.7%. Progeny testing with 30 halfsib progenies ($r_{TI} = 0.89$) will only slightly improve the response to 3.6%. Similarly, single trait selection for height increment with parameters from this study [$h^2 = 0.2$, $CV_A = 7\%$ and $i = 1$; $r_{TI} = 0.44$ (own phenotype), $r_{TI} = 0.78$ (30 halfsib progenies)] is expected to give responses of 3.1% and 5.5%, respectively. These examples illustrate that selection for wood density may well be based on phenotypic selection, while there is more to gain by progeny testing for height increment.

The relatively high heritability for wood density in all segments (1 to 4) indicates that it may be effective to assess wood density at an early tree age provided that the correlation between the juvenile wood assessed and the considered total wood production is high. Data from this study (HANNRUP and EKBERG, submitted) and other *Pinus* species (e.g COWN et al., 1992; WILLIAMS and MEGRAW, 1994) indicate high age-age correlations for wood density. If phenotypic selections for wood density (high or low) can be accomplished at a very low tree age a screening for this and possible other traits with sufficiently high heritabilities (WILHELMSSON and ANDERSSON, 1993) may be effective to improve gain without extensive progeny testing. Selected progenies from such screening may then be crossed and progeny tested for economically important traits with considerable genetic variation but with possibly lower heritabilities. However, further studies of early evaluations of wood density and nondestructive sampling are needed, before such strategies can be outlined in detail.

References

ARMSTRONG, J. P., SKAAR, C. and DE ZEEUW, C.: The effect of specific gravity on several mechanical properties of some world woods. Wood Sci. Technol. **18**: 137–146 (1984). — ATMER, B. and THÖRNQVIST, T.: The properties of tracheids in spruce (*Picea abies* KARST.) and Pine (*Pinus silvestris* L.). Swed. Univ. Agric. Sci., Dept. For. Prod. Rep. **134**: 1–59 (1982). — BECKER, W.: Manual of quantitative genetics. Academic Enterprises, Pullman, WA. 195 pp. (1984). — BURDON, R. D. and LOW, C. B.: Genetic survey of *Pinus radiata*. 6: Wood properties: variation, heritabilities and interrelationships with other traits. N. Z. J. For. Sci. **22**: 228–245 (1992). — CORNELIUS, J.: Heritabilities and additiva genetic coefficient of variation in forest trees. Can. J. For. Res. **24**: 372–379 (1994). — COWN, D. J. and KIBBLEWHITE, R. P.: Effects of wood quality variation in New Zealand radiata pine on kraft paper properties. N. Z. J. For. Sci. **10**: 521–532 (1980). — COWN, D. J., YOUNG, G. D. and BURDON, R. D.: Variation in wood characteristics of 20-year-old half-sib families of *Pinus radiata*. N. Z. J. For. Sci. **22**: 63–76 (1992). — DANELL, Ö.: User-manual of VDIAL. The Institute for Forest Improvement, Uppsala. 5 pp. (1989). — DUCHESNE, I., WILHELMSSON, L. and SPÅNGBERG, K.: Effects of in-forest sorting of Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* L. KARST.) on wood fibre properties. Can. J. For. Res. **27**: 790–795 (1997). — ERICSON, B., JOHNSON, T. and PERSSON, A.: Wood and sulphate pulp of Scots Pine from virgin stands. Royal College of Forestry, Dept. For. Yield. Research Notes **25**, 143 pp. (1973). — FALCONER, D. S. and MACKAY, T. F. C.: Introduction to quantitative genetics. 4th ed. Longman Group Ltd., Essex. 464 pp. (1996). — FOSTER, G. S.: Inter-genotypic competition in forest trees. *In:* Proceedings 20th southern forest tree improvement conference 1989 June 26.30. United States Dept. of Agric. 21–35 (1989). — FRIES, A.: Volume growth and wood density of plus tree progenies of *Pinus contorta* in two Swedish field trials. Scand. J. For. Res. **1**: 403–419 (1986). — GOGGANS, J. F.: The interplay of environment and heredity as factors controlling wood properties in conifers with special emphasis on their effects on specific gravity. North Carolina State Univ. Tech. Rep. **11**: 56 pp. (1961). — HALUPÁNÉ-GROSZ, Z. and MÁTYÁS, C.: Major observations in examination of characteristics of wood of graft clones of Scots pine. Erdészeti Kutatások **71**: 149–161 (1975). — HANNRUP, B. and EKBERG, I.: Age-age correlations for tracheid length and wood density in *Pinus sylvestris* (L.). Can. J. For. Res., Submitted. — HARDING, K. J., KANOWSKI, P. J. and WOOLASTON, R. R.: Preliminary genetic parameters estimates for some wood quality traits of *Pinus cariabea* var. *hondurensis* in Queensland, Australia. Silvae Genet. **40**: 152–156 (1991). — HENDERSON, C. R.: Application of linear models in animal breeding. Univ. Guelph, Guelph. 462 pp. (1984). — HODGE, G. R. and PURNELL, R. C.: Genetic parameter estimates for wood density, transition age, and radial growth in slash pine. Can. J. For. Res. **23**: 1881–1891 (1993). — HOULE, D.: Comparing evolvability and variability of quantitative traits.
Genetics **130**: 195–204 (1992). — JOHNSSON, H.: Progeny test of a pine seed orchard, based on ten years old test families. Annual Report, Inst. For. Improv. Uppsala: 140–159 (1973). — KIBBLEWHITE, R. P.: Radiata pine corewood and slabwood, and their interrelations with pulp and handsheet properties basic densities and tracheid lengths. N. Z. J. For. Sci. Forest Research Institute. **10**: 533–550 (1980). — KIBBLEWHITE, R. P., EVANS, R. and RIDDEL, M. J. C.: Handsheet property prediction from Kraft-fibre and wood-tracheid properties in eleven radiata pine clones. Appita Journal **50**: 131–138 (1997). — MAGNUSSEN, S.: Effects and adjustments of competition bias in progeny trials with single-tree plots. For. Sci. **35**: 532–547 (1989). — MISHIRO, A., COWN, D. J. and WALFORD, G. B.: A further examination of the clearwood properties of radiata pine grown in New Zealand. FRI-Bulletin No. 104, For. Res. Inst. New Zealand. 23 pp. (1986). — MOUSSEAU, T. A. and ROFF, D. A.: Natural selection and the heritability of fitness components. Heredity **59**: 181–197 (1987). — OLESEN, P. O.: The water displacement method a fast and accurate method of determining the green volume of wood samples. For. Tree Improv. **3**: 1–23 (1971). — PERSSON, A.: Studies on the basic density in mother trees and progenies of pine. Studia For. Suec. **96**: 1–37 (1972). — PERSSON, B., PERSSON, A., STÅHL, E. G. and KARLMATS, U.: Wood quality of *Pinus sylvestris* progenies at various spacings. For. Ecol. Managem. **76**: 127–138 (1995). — ROBERTSON, A.: The sampling variance of the genetic correlation coefficient. Biometrics **15**: 219–226 (1959). — ROFF, D. A. and MOUSSEAU, T. A.: Quantitative genetics and fitness: lessons from *Drosophila*. Heredity **58**: 103–118 (1987). — SAKAI, K.-I. and MUKAIDE, H.: Estimation of genetic, environmental and competitional variances in standing forests. Silvae Genet. **16**: 149–152 (1967). — SMITH, D. M.: Maximum moisture content method for determining specific gravity of small wood samples. U.S. For. Prod. Lab. Rep. No. 2014 (1954). — ST. CLAIR, J. B. and ADAMS, W. T.: Relative family performance and variance structure of open-pollinated Douglas-fir seedlings grown in three competetive environments. Theor. Appl. Genet. **81**: 541–550 (1991). — TALBERT, J. T., JETT, J. B. and BRYANT, R. L.: Inheritance of wood specific gravity in an unimproved loblolly pine population: 20 years of results. Silvae Genet. **32**: 33–37 (1983). — WERNER, M. and ERICSSON, T.: Wood quality and studies in progenies from a Scots pine seed orchard. Annual Report, Inst. For. Improv., Uppsala: 40–69 (1980). — WILHELMSSON, L. and ANDERSSON, B.: Breeding programmes in Sweden – Scots pine and Lodgepole pine. *In:* LEE, S. J. (ed.): Proceedings of "Progeny testing and breeding strategies". Meeting of the Nordic Group for Tree Breeding, Edinburgh, October 6 to 10 (1993). — WILLIAMS, C. and MEGRAW, R. A.: Juvenile-mature relationship for wood density in *Pinus taeda*. Can. J. For. Res. **24**: 714–722 (1994). — WILLIAMS, M. F.: Matching wood fiber characteristics to pulp and paper processes and products. TAPPI **77**: 227–233 (1994). — WISELOGEL, A. E. and TAUER, C. G.: Genetic variation of specific gravity and tracheid length in shortleaf pine. TAPPI Research and Development Division Conference Asheville, NC. 169–178 (1982). — ZHANG, S. Y. and MORGENSTERN, E. K.: Genetic variation and inheritance of wood density in black spruce (*Picea marina*) and its relationship with growth: implations for tree breeding. Wood Sci. Technol. **30**: 63–75 (1995). — ZOBEL, B. J. and JETT, J. B.: Genetics of wood production. Springer-Verlag, Berlin. 326 pp. (1995).