Genetic Variation of Wood Density and its Relationship with Growth Traits in Young Norway Spruce

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Abstract

Juvenile wood density from increment cores was measured by direct X-ray analysis. 47 open-pollinated families of Norway spruce from a 28-year-old progeny test, located at Håheim in Hordaland County, Norway, were examined to assess the magnitude of family differences of overall wood density and its components, and to calculate the phenotypic and genetic correlations among traits. The overall wood density and its components varied significantly among the families, as indicated by the high individual (h² ≥ 0.34) and family mean heritabilities (h² ≥ 0.69). Density components had strong genetic correlations with overall wood density (r ≥ 0.78) but were moderate to strongly related among themselves (0.28 ≤ r ≤ 0.99). Overall density and its components were negatively correlated with height growth (−0.51 ≤ r ≤ −0.68). Selection based solely on height growth would lower overall density with 3.7%.

Key words: Picea abies, heritability, genetic correlation, progeny test, earlywood, latwood, wood density.

FDC: 165.3; 165.51; 232.11; 812.3; 811.4; 174.7 Picea abies.

Introduction

Density is considered the most important wood property because of its effect on nearly all final products of wood (Zobel and Bulliten, 1989). Fast growing trees with short rotation have a higher proportion of low-density juvenile wood which is undesirable for both wood strength and pulp yield (Schiabl and Gawn, 1989; Shvynaraine and Smith, 1990; Brodin et al., 1995; Klig et al., 1995). This raises concerns about the wood density in timber from intensively managed forests as compared to slower growing and more mature natural stands. One alternative for improving wood quality from intensively managed forests could be breeding for high density. This might also increase the uniformity of wood density across the stem (Zobel and Bulliten, 1989).

Development of a breeding program for wood density or incorporation of wood density into an existing tree breeding program requires information about the genetic variation of wood density and its genetic relationships with growth traits. Such information is generally lacking for Norway spruce (Picea abies). There are some reports about broad sense heritabilities for Norway spruce, but these vary widely (Kenne-
Wood density is a complex trait being the result of various combinations of the proportions of earlywood and latewood and the relative density of each (Vargas-Hernandez and Adams, 1991). Knowledge of genetic control of these components and their interrelationships may help understand the genetics of overall wood density in Norway spruce.

The objectives of the present study were to characterize the genetic variation of overall wood density and its components in Norway spruce, and to study the interrelationship of these components with overall density and growth traits.

**Material and Methods**

*Plant material*

Families included in this study originated from open pollinated seed collected from natural stands of Norway spruce located in different parts of southern Norway (Fig. 1). The progeny test was established in 1967 with 6 years old seedlings at Håheim in Hordaland County, Norway. The families were planted in 4-tree plots at 2 m x 2 m spacing according to a randomized complete block experimental design with 16 replicates. The number of trees per family varied. The wood samples used here were taken from all surviving trees in 6 blocks comprising 47 families from 10 stands.

**Measurements and calculations**

After growth cessation in the fall of 1990, 1 pith to bark (4 mm) increment core sample was taken at breast height (1.3 m) at the south side of each tree. The cores were dried to an equilibrium moisture content of about 9% and then sawn to a uniform thickness of 1.5 mm in cross section. The cores were extracted for resin with a solution of toluene-ethanol (2:1) for 24 hours. Thereafter the cores were dried to the initial equilibrium moisture contents (9%) and kept in this condition throughout the remaining analyses.

Intraring wood density components for each core were obtained by using direct X-ray analysis conducted at Weyerhaeuser Technology Center, Tacoma, Washington, USA. The first 2 annual rings closest to the pith were discarded because they were too dense for reliable separation. For each of the remaining rings average density values and total ringwidth were obtained. Further, average densities for earlywood and latewood were determined, as well as the latewood percentage. The transition point between earlywood and latewood was preset to the point where basic density in each ring became greater than 0.42 (g/cm³). Density records higher than this limit were regarded as latewood, and records lower than this limit were regarded as earlywood. This point was based on a detailed comparison of the results obtained by X-ray analyses and the definition of latewood given by Mork (1928).

Areal weighted averages from pith to bark were calculated for all the individual wood density components. The areal weighting are done as follow:

\[
D = \sum_{i=1}^{n} d_i \frac{a_i}{\sum_{i=1}^{n} a_i}
\]

where \(D\) is weighted wood density for average density, and for its components, \(d_i\) is average individual ring density output by the X-ray computer program, and \(a_i\) is individual ring area calculated as \(\pi (r_{i+1}^2 - r_i^2)\) where \(r_i\) is the distance from pith through ring \(i\) and \(r_{i+1}\) is the distance from the pith through ring \(i+1\).

The diameter growth was calculated from the X-ray output, and height measurements were done when the progeny test was 23-year-old from seed.

**Statistical model and analyses**

Analysis of variance for all the observed traits was performed according to the complete random effects model for individual tree data, equation (2), using the General Linear Model (GLM) procedure of the Statistical Analysis System (SAS Institute Inc., 1989b):

\[
Y_{ijkl} = \mu + S_i + F_{j(i)} + B_k + SB_{ij} + FB_{j(i)k} + \epsilon_{ijkl}
\]

where \(Y_{ijkl}\) is the measured value of trait \(l\) from block \(k\) from family \(j\) within stand \(i\), \(\mu\) is the general mean, \(S_i\) is the effect of stand \(i\), \(F_{j(i)}\) is the effect of family \(j\) within stand \(i\), \(B_k\) is the effect of block \(k\), \(SB_{ij}\) is the interaction of stand \(i\) with block \(k\), \(FB_{j(i)k}\) is the plot effect, and \(\epsilon_{ijkl}\) is the within plot error.

The significance of the variance components was tested by synthetic F-tests. The linear combination of mean squares of family within stand and the interactions between stand and block was used for testing the stand component. Family within stand and the interactions between stand and block were tested against the mean square of the interaction between family within stand and block. The plot effect was tested against the residual.

In order to study the variation between families regardless of stand, a reduced random effects model, equation (3), was used,

\[
Y_{jkl} = \mu + F_j + B_k + FB_{jk} + \epsilon_{jkl}
\]
where $Y_{ijl}$ is the measured value of tree $l$ from block $k$ from family $j$, $\mu$ is the general mean, $F_i$ is the effect of family $i$, $B_j$ is the effect of block $j$, $FB_{ij}$ is interaction between family $i$ and block $k$, and $e_{ijkl}$ is the plot error. The family and block components were tested against the mean square of the interaction between family and block. The interaction component was tested against the error term.

Estimates of variances and the covariances were obtained from Type III sums of squares from the GLM procedure, and Interactive Matrix Language (SAS Institute Inc., 1989b) was used for further calculations. The standard errors on variance components were calculated as in SCHEINBERG (1966). Covariances were calculated for traits with significant genetic variation.

**Genetic parameters**

The estimate of phenotypic variance ($\hat{\sigma}_{ph}^2$) was calculated as the sum of all linear variance components, excluding that of block ($\hat{\sigma}_b^2$) as this effect would normally be adjusted prior to any selection (COTTERILL, 1987).

Genetic relationships among open pollinated progeny from a natural stand are expected to be somewhat larger than half-sib correlations, and will estimate a larger proportion of the additive variance (SQUILLACE, 1974). Although the degree of inbreeding is unknown, the family variance was estimated more conservatively than recommended by FALCONER (1989). Supposing the families are mixtures of half-sibs and full-sibs the additive variance ($\hat{\sigma}_A^2$) was estimated by

$$(4) \quad \hat{\sigma}_A^2 = 3\hat{\sigma}_f^2$$

where $\hat{\sigma}_f^2$ is the family variance component.

Individual tree heritability ($h^2$) was calculated as

$$(5) \quad h^2 = \frac{\hat{\sigma}_A^2}{\hat{\sigma}_{ph}^2}$$

where $\hat{\sigma}_{ph}^2$ is the phenotypic variance.

The heritability of open pollinated family means $h^2_p$ was estimated by

$$(6) \quad h^2_p = \frac{\hat{\sigma}_f^2}{\hat{\sigma}_A^2 + \frac{\hat{\sigma}_A^2}{n_s} + \frac{\hat{\sigma}_f^2}{n_h n_s}}$$

where $n_s$ is number of blocks and $n_h$ is the harmonic mean of the number of trees per plot.

Approximate standard errors for phenotypic and additive variance, individual and family heritabilities were calculated by formulas for the variance of the quotient of two random variables given in MOOD et al. (1974) page 181.

Phenotypic correlation coefficients ($r_{xy}$) between traits were estimated as PEARSON correlation coefficient using the SAS correlation procedure (SAS Institute Inc., 1989b). The genetic correlation ($r_g$) between 2 traits $X$ and $Y$ was calculated by

$$(7) \quad r_g = \frac{\text{Cov}_{xy}}{\sqrt{\hat{\sigma}_{x}^2 \times \hat{\sigma}_{y}^2}}$$

where $\text{Cov}_{xy}$ is the estimated genotypic covariance of 2 traits with significant genetic variation, and $\hat{\sigma}_x^2$ and $\hat{\sigma}_y^2$ are the genotypic variance components.

Approximate standard errors on the genetic correlations ($s.e.r_g$) were calculated by generalizing the formulas in SCHEINBERG (1966), and correcting the degrees of freedom as indicated in BECKER (1985).

**Results**

The descriptive statistics of the wood density components and growth traits are summarized in Table 1. Even though the ranges for the overall density, earlywood and latewood density were wide, the coefficients of variation (cv) were relatively low. Latewood percentage had a wide range and the coefficient of variation was close to 50%. Diameter growth was more variable than height growth.

![Table 1](image)

Analyses of variance for the complete model in equation (2) showed no significant differences among stands and no significant interaction between stand and block in average values for any of the traits considered ($p > 0.09$). The analysis of variance for the reduced model in equation (3) gave the same conclusions as the full model for the effect of family, block and family x block. Therefore, only results from the reduced model are presented.

The family variance component contributed significantly to the variation in overall density and its components, and accounted for a relatively high proportion of the phenotypic variance ($11.5 \leq \text{Var}\% \leq 25.9$) (Table 2). Compared with the density traits, the family differences accounted for less of the phenotypic variance for height ($\text{Var}\% = 9.6$) and diameter ($\text{Var}\% = 1.4$) (Table 3).

No interaction between family and block was present for overall density and its components (Table 2), while both growth traits had such interactions (Table 3). The interaction accounted for a relatively high portion of the phenotypic variance for height growth ($\text{Var}\% = 25.8$). Such contribution was less for diameter growth ($\text{Var}\% = 9.6$) (Table 3).

None of the individual wood density components had estimates of heritability greater than that found for latewood density ($h^2 = 0.78$) (Table 4). Earlywood density had the lowest heritability ($h^2 = 0.34$). The heritability of overall density was equal to 0.47. Heritability for height growth was equal to 0.29. The heritability of diameter ($h^2 = 0.04$) is included for comparison, even if this trait did not show any significant genetic variation. The family heritabilities varied between 0.17 and 0.86 for all the considered traits (Table 4).

All the phenotypic correlation coefficients were statistically significant (Table 5). The wood density components were strongly correlated with overall wood density, and were moderately to strongly interrelated among themselves. The wood density components were weakly to moderately negatively correlated with both growth traits. Compared with height, the diameter had higher negative correlation coefficients with the density components (Table 5).

The genetic correlation coefficients were of the same magnitude and directions as the phenotypic correlations for all the density traits (Table 5). The genetic relationships between height growth and wood density components were negative with generally high standard errors (Table 5).
Table 2. – Results from F-tests (df, F and p-values) from analyses of variance of wood density components, and its proportion of total phenotypic variance (Var%). The remaining proportion of the total variance is the within-plot error.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Overall density</th>
<th>Earlywood density</th>
<th>Latewood density</th>
<th>Latewood percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
<td>Var %</td>
<td>F</td>
</tr>
<tr>
<td>Family</td>
<td>2.99</td>
<td>0.0001</td>
<td>15.6</td>
<td>2.34</td>
</tr>
<tr>
<td>Block</td>
<td>13.47</td>
<td>0.0001</td>
<td>-</td>
<td>6.82</td>
</tr>
<tr>
<td>Family×block</td>
<td>0.94</td>
<td>0.67</td>
<td>0</td>
<td>0.98</td>
</tr>
</tbody>
</table>

Table 3. – Results from F-tests (df, F and p-values) from analyses of variance of growth traits, and its proportion of total phenotypic variance (Var%). The remaining proportion of the total variance is the within-plot error.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Diameter (age 28)</th>
<th>Height (age 23)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
</tr>
<tr>
<td>Family</td>
<td>1.13</td>
<td>0.28</td>
</tr>
<tr>
<td>Block</td>
<td>6.96</td>
<td>0.0001</td>
</tr>
<tr>
<td>Family×block</td>
<td>1.27</td>
<td>0.03</td>
</tr>
</tbody>
</table>

Table 4. – Estimates of phenotypic (\(\sigma^2\)) and additive (\(\sigma^2_a\)) variances and individual tree (\(\sigma^2_h\)) and family (\(\sigma^2_A\)) heritabilities and the standard error (s.e.) of the genetic parameters for wood density components and growth traits. The variances for overall density and its components are multiplied by 1000.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Overall density</th>
<th>Earlywood density</th>
<th>Latewood density</th>
<th>Latewood percentage</th>
<th>Diameter</th>
<th>Height</th>
</tr>
</thead>
<tbody>
<tr>
<td>(\sigma^2_h)</td>
<td>0.573</td>
<td>0.127</td>
<td>0.387</td>
<td>9.337</td>
<td>869.031</td>
<td>136.630</td>
</tr>
<tr>
<td>(\sigma^2_A)</td>
<td>0.268</td>
<td>0.078</td>
<td>0.301</td>
<td>5.577</td>
<td>37.752</td>
<td>39.363</td>
</tr>
<tr>
<td>(h^2)</td>
<td>0.47</td>
<td>0.34</td>
<td>0.78</td>
<td>0.60</td>
<td>0.04</td>
<td>0.29</td>
</tr>
<tr>
<td>(h^2_A)</td>
<td>0.15</td>
<td>0.13</td>
<td>0.21</td>
<td>0.18</td>
<td>0.08</td>
<td>0.14</td>
</tr>
<tr>
<td>(h^2)</td>
<td>0.77</td>
<td>0.69</td>
<td>0.86</td>
<td>0.80</td>
<td>0.17</td>
<td>0.52</td>
</tr>
<tr>
<td>s.e. (\sigma^2_h)</td>
<td>(0.30)</td>
<td>(0.31)</td>
<td>(0.30)</td>
<td>(0.20)</td>
<td>(0.23)</td>
<td>(0.29)</td>
</tr>
<tr>
<td>s.e. (\sigma^2_A)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>s.e. (h^2)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>s.e. (h^2_A)</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

Table 5. – Estimates of genetic correlations (\(r_g\), below the diagonal) and individual tree phenotypic correlations (\(r_{ph}\), above the diagonal) between overall density and its components and growth traits.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Overall density</th>
<th>Earlywood density</th>
<th>Latewood density</th>
<th>Latewood percentage</th>
<th>Diameter</th>
<th>Height</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>p</td>
<td>Var %</td>
<td>F</td>
<td>p</td>
<td>Var %</td>
</tr>
<tr>
<td>Family</td>
<td>0.84</td>
<td>0.75</td>
<td>0.86</td>
<td>-0.19</td>
<td>-0.45</td>
<td></td>
</tr>
<tr>
<td>Earlywood</td>
<td>0.78</td>
<td>0.24</td>
<td>0.45</td>
<td>-0.13</td>
<td>-0.34</td>
<td></td>
</tr>
<tr>
<td>Latewood</td>
<td>0.81</td>
<td>0.28</td>
<td>1</td>
<td>-0.17</td>
<td>-0.36</td>
<td></td>
</tr>
<tr>
<td>Latewood percentage</td>
<td>0.88</td>
<td>0.39</td>
<td>0.99</td>
<td>1</td>
<td>-0.18</td>
<td>-0.43</td>
</tr>
<tr>
<td>Height</td>
<td>-0.68</td>
<td>-0.58</td>
<td>-0.51</td>
<td>-0.58</td>
<td>1</td>
<td>0.60</td>
</tr>
</tbody>
</table>

All calculations of wood density traits are based on area weighted averages. As rings further away from the pith contribute more to the volume and typically have lower density than rings closer to the pith, the area weighted average will be lower than a simple or length weighted average.

All increment cores were taken from the south side of the trees. This may be misleading with respect to absolute density level as there can be systematic variation in wood density, as a result of systematic variation in ringwidth between directions around the stem (Olesen, 1973).

Genetic variation

The negligible effect of stand for all considered traits may be a result of small genetic differences between the sampled stands. There are reports about no significant difference in density among seed sources of Norway spruce when grown in the same climate, even when they are transferred from Central and Eastern Europe to Norway (Worrall, 1975; Hylen, 1996). The small number of families from each stand may also have influenced the result. The results indicate a large genetic variation among families.

The results indicate that families, independent from origin, have different potential to produce juvenile wood density.
higher than 0.42 g/cm³ when grown under the same climatic condition. DIETRICHSON (1969) found large variation in growth rhythm for families within stand. The families he used were from the same stands as those in the present study, but they were grown in Eastern Norway. The difference in flushing time between the families may explain some of the variation found in wood density traits. Late flushing trees and populations of Norway spruce are found to have lower wood density than those flushing early (DIETRICHSON, 1964; LACAZE and POLGE, 1970; THIERCELIN, 1970; WORALL, 1970). Late flushing trees enhance the production of earlywood formation and delay the initiation of latewood (ZOBEL and BULJTENEN, 1989).

The family contribution to height growth was moderate, while there was no significant family effect for diameter growth. This is due to the significant interaction between families and blocks and large experimental error. Similar patterns were revealed in work on the related white spruce grown in British Columbia (YANCHUK and KISS, 1993). It seems that growth traits are more affected by variation in growth conditions at the planting site than the density traits, since there in particular were significant plot effect for both growth traits.

Heritability

The heritability estimates for overall density are in the range found for 10-year-old trees grown in Norway and are also comparable to those reported for other conifers (e.g. ZOBEL and BULJTENEN, 1989). The moderate inheritance of height growth and the lack of inheritance for diameter growth are comparable to results reported for open-pollinated families of Norway spruce grown in Eastern Norway (KLEM, 1934, 1957; NYLINDER, 1951, 1953; ERICSON, 1960, 1966; HAKKILA, 1966, 1968; OLESEN, 1976). The family contribution to height growth was moderate, while selection for density only reduces height growth by 6.5% using the formulas given in FALCONER (1989) when the first generation, while selection for density only reduces height growth with 1%. This negative correlation between overall density and height growth complicates the breeding task. An alternative might be to use multitrait selection with restricted selection indices. Such a strategy limits the undesirable change in one trait while optimizing the improvement in the other.

Implied genetic correlation between wood density and height, which is different from the significant correlation coefficient found in the present study. In this material an increase in height growth affect overall density and its components in a undesirable way.

With increasing diameter overall density and latewood percentage will decrease. This is in full agreement with previously conducted investigations (KLEM, 1934, 1957; NYLINDER, 1951, 1953; ERICSON, 1960, 1966; HAKKILA, 1966, 1968; OLESEN, 1976).

Diameter and height growth are found to have positive phenotypic relationship which correspond with results found in earlier studies of Norway spruce (WERNER et al., 1984; NIEMAN and BOYLE, 1989).

Implications for breeding

The results from this study indicate that for Norway spruce wood density and its components are under sufficiently genetic control to respond well to selection in a tree breeding program. Direct selection for overall density gave an increase in density by 6.5% using the formulas given in FALCONER (1989) when the top 20% of the families were selected (selection intensity i = 1.393). Expected correlated response in density from indirect selection based on latewood percent gave an increase in overall density by 6.0%. Indirect selection on the other density components gave less response than selection on latewood percent. Combining these highly positively correlated density components in a multitrait index might not prove more efficient than direct selection for wood density, since adding two or more highly correlated traits in an index have little benefit (BAKER, 1986).

Most tree breeding programs for Norway spruce place exclusive or major emphasize on improving growth rate. Based on the genetic parameters estimated in the present material, selection based solely on height growth is expected to lower wood density with 3.7% relative to the original population in the first generation, while selection for density only reduces height growth with 1%. This negative correlation between overall density and height growth complicates the breeding task. An alternative might be to use multitrait selection with restricted selection indices. Such a strategy limits the undesirable change in one trait while optimizing the improvement in the other.

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References