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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 ($h^2 \geq 0.34$) and family mean heritabilities ($h^2_F \geq 0.69$). Density components had strong genetic correlations with overall wood density ($r_g \geq 0.78$) but were moderate to strongly related among themselves ($0.28 \leq r_g \leq 0.99$). Overall density and its components were negatively correlated with height growth ($-0.51 \leq r_g \leq -0.68$). Selection based solely on height growth would lower overall density with 3.7%.

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

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

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Introduction

Density is considered the most important wood property because of its effect on nearly all final products of wood (ZOBEL and BUIJTENEN, 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 (SCHAIBLE and GAWN, 1989; SHIVNARAINE and SMITH, 1990; BROLIN et al., 1995; KLIGER 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 BUIJTENEN, 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* (L.) KARST). There are some reports about broad sense heritabilities for Norway spruce, but these vary widely (KENNE-

DY, 1966; WORRALL, 1975; BIROT and NEPVEU, 1979; LEWARK, 1982).

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.

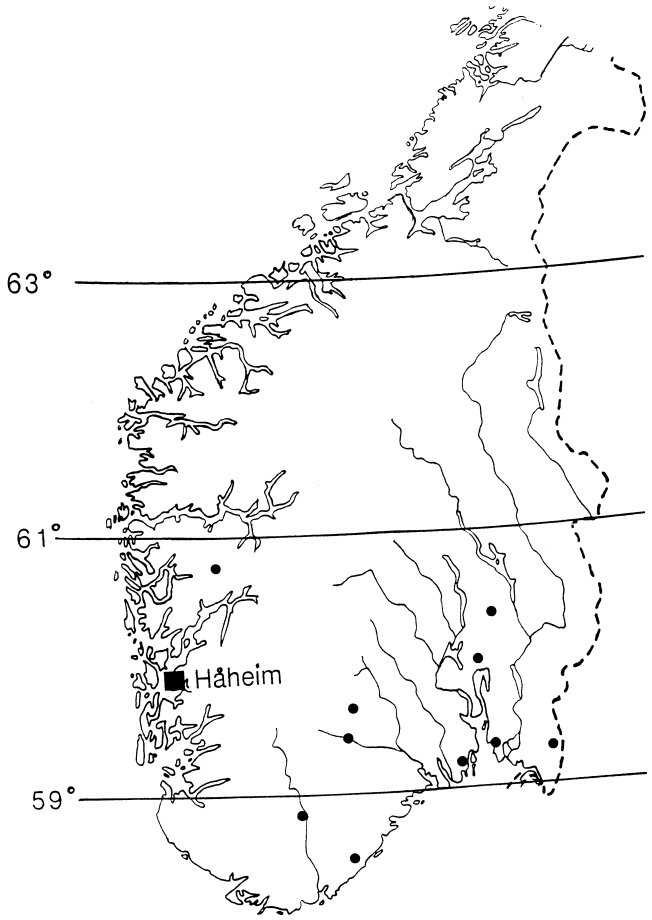

Figure 1. – Location of the experimental site Håheim and the origin of the stands where open pollinated families were collected.

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/cm^3). 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:

$$D = \frac{\sum_{i=3}^{n} d_i a_i}{\sum_{i=3}^{n} a_i} \qquad (1)$$

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 $\pi\ (r_i^2 - r_{i-1}^2)$ 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., 1989*b*):

$$Y_{ijkl} = \mu + S_i + F_{j(i)} + B_k + SB_{ij} + FB_{j(i)k} + \varepsilon_{ijkl} \qquad (2)$$

where Y_{ijkl} is the measured value of tree l from block k from family j within stand i, μ 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, $FB_{j(i)k}$ plot effect, and ε_{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,

$$Y_{jkl} = \mu + F_j + B_k + FB_{jk} + \varepsilon_{jkl} \qquad (3)$$

where Y_{jkl} is the measured value of tree l from block k from family j, μ is the general mean, F_i is the effect of family j, B_k is the effect of block k, FB_{ik} is interaction between family i and block k, and ε_{jkl} 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., 1989*a*) was used for futher 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 ($\hat{\sigma}^2_{ph}$) was calculated as the sum of all linear variance components, excluding that of block ($\hat{\sigma}^2_B$) 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 in breeding is unknown, the family variance was estimated more conservatively than recommended by FALCONER (1989). Supposing the families are mixtures of half-sibs and ful-sibs the additive variance ($\hat{\sigma}^2_A$) was estimated by

$$\hat{\sigma}^2_A = 3\hat{\sigma}^2_f \tag{4}$$

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

Individual tree heritability (h^2) was calculated as

$$h^2 = \frac{\hat{\sigma}^2_A}{\hat{\sigma}^2_{ph}} \tag{5}$$

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

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

$$h^2_F = \frac{\hat{\sigma}^2_f}{\hat{\sigma}^2_f + \frac{\hat{\sigma}^2_{f\times b}}{n_b} + \frac{\hat{\sigma}^2_\varepsilon}{n_b n_h}} \tag{6}$$

where n_b 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_{ph}) between traits were estimated as PEARSON correlation coefficient using the SAS correlation procedure (SAS Institute Inc., 1989*b*). The genetic correlation (r_g) between 2 traits X and Y was calculated by

$$r_g = \frac{Cov_{f_{xy}}}{\sqrt{\hat{\sigma}^2_{f_x} \times \hat{\sigma}^2_{f_y}}} \tag{7}$$

where Cov_{fxy} is the estimated genotypic covariance of 2 traits with significant genetic variation, and $\hat{\sigma}^2_{fx}$ and $\hat{\sigma}^2_{fy}$ 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 relative 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. – Experimental means ($\bar{x}$), coefficient of variation (cv) and individual and family range of wood density components and growth traits.

Trait	$\bar{x}$	cv	Range indiv.	Range fam.
Overall density (g/cm^3)	0.300	7.3	0.231 – 0.379	0.265 – 0.320
Earlywood density (g/cm^3)	0.278	5.6	0.227 – 0.320	0.259 – 0.289
Latewood density (g/cm^3)	0.466	3.6	0.424 – 0.550	0.440 – 0.489
Latewood percentage (%)	17.2	49.9	0.1 – 48.0	5.0 – 28.0
Diameter (mm)	125.3	22.2	47.0 – 209.5	103.5 – 154.3
Height (age 23) (m)	6.62	13.6	1.9 – 10.4	5.7 – 8.1

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 ($p \geq 0.09$). 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 (Var% = 9.6) and diameter (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 (Var% = 30.8). Such contribution was less for diameter growth (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 $0.17 \leq h^2_F \leq 0.86$ 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.

Trait	Overall density			Earlywood density			Latewood density			Latewood percentage		
	F	*p*	Var %	*F*	*p*	Var %	*F*	*p*	Var %	*F*	*p*	Var %
Family	2.99	0.0001	15.6	2.34	0.0001	11.5	4.63	0.0001	25.9	3.48	0.0001	19.9
Block	13.47	0.0001	-	6.82	0.0001	-	11.55	0.0001	-	12.98	0.0001	-
Family×block	0.94	0.67	0	0.98	0.55	0	0.98	0.56	0	1.04	0.37	1.4

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.

Trait	Diameter (age 28)			Height (age 23)		
	F	*p*	Var %	*F*	*p*	Var %
Family	1.13	0.28	1.4	1.76	0.005	9.6
Block	6.96	0.0001	-	29.14	0.0001	-
Family×block	1.27	0.03	9.6	2.29	0.0001	30.8

Table 4. – Estimates of phenotypic ($\hat{\sigma}^2_{ph}$) and additive ($\hat{\sigma}^2_A$) variances and individual tree (h^2) and family (h^2_F) 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.

Trait	Overall density	Earlywood density	Latewood density	Latewood percentage	Diameter	Height
$\hat{\sigma}^{2\,a}_{ph}$	0.573	0.227	0.387	9.337	869.031	136.630
	(0.046)	(0.018)	(0.034)	(0.875)	(80.185)	(12.375)
$\hat{\sigma}^{2\,b}_A$	0.268	0.078	0.301	5.577	37.752	39.363
	(0.083)	(0.029)	(0.079)	(1.613)	(71.267)	(19.328)
h^2	0.47	0.34	0.78	0.60	0.04	0.29
	(0.15)	(0.13)	(0.21)	(0.18)	(0.08)	(0.14)
h^2_F	0.77	0.69	0.86	0.80	0.17	0.52
	(0.30)	(0.31)	(0.30)	(0.30)	(0.33)	(0.29)

[a]) $\hat{\sigma}^2_B$ are not included in $\hat{\sigma}^2_{ph}$
[b]) $s.e._{\hat{\sigma}^2_A}$, $s.e._{h^2}$ and $s.e._{h^2_F}$ are enclosed in parentheses

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.

Trait	Overall density	Earlywood density	Latewood density	Latewood percentage	Height	Diameter
Overall density	1	0.84[a]	0.75	0.86	−0.19	−0.45
Earlywood density	0.78 (0.12)[b]	1	0.34	0.45	−0.13	−0.34
Latewood density	0.81 (0.10)	0.28 (0.21)	1	0.89	−0.17	−0.36
Latewood percentage	0.88 (0.09)	0.39 (0.20)	0.99 (0.04)	1	−0.18	−0.43
Height	-0.68 (0.25)	-0.58 (0.30)	-0.51 (0.23)	-0.58 (0.24)	1	0.60

[a]) All r_{ph} are significant at the 0.001 level
[b]) Standard errors of r_g ($s.e._{r_g}$) are enclosed in parentheses

Discussion

Influencing factors

The mean value for overall density is lower than values reported for juvenile wood in Norway spruce grown in Southwestern Norway (HYLEN, 1996). It is difficult to do a strict comparisons of the levels reported in this study with other investigations, because wood density is greatly influenced by the location of the planting site, age of the trees and the measurement methods employed.

None of the families included in this study are native to the area where the progeny test was established. The families were moved westward to a milder and more humid climate compared to the climate of the native origins of their parents.

The amount of latewood contributes directly to overall wood density (LARSON, 1973*a* and *b*). Latewood formation is controlled by moisture availability, temperature, day length and growth rhythm of the individual trees. Each factor plays a role in determining the length of time a tree produces latewood cells (ZOBEL and BUIJTENEN, 1989). When plentiful moisture content and favorable temperature for growth are present throughout the season, as is almost always the case at Håheim, earlywood formation is enhanced and initiation of latewood formation is delayed (POLGE, 1965; ZOBEL and BUIJTENEN, 1989). This will result in low overall wood density.

The density level is also influenced by the number of growth rings included and their distance from the pith. The average number of growth rings in the present study is 16. It is assumed that all the growth rings in each core belong to juvenile wood, since the juvenile-mature wood transition for Norway spruce take place between the 8th and 20th annual growth ring counting from pith (OLESEN, 1973, 1977; MADSEN et al., 1978; DANBORG, 1994). Annual rings in the juvenile zone have low latewood percentage, which causes low wood density (LARSON, 1973*a* and *b*).

HOAG and KRAHMER (1991) found density of Douglas-fir measured with X-ray technique to be lower than gravimetric densities, because mass and volume were measured on X-ray samples at 9% moisture content, while mass of wood samples were based on ovendry weight, and volume on green moisture content.

The cores in the present study were extracted for resins which may give lower wood density compared with unextracted samples (ZOBEL and BUIJTENEN, 1989).

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/cm^3 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; WORRALL, 1970). Late flushing trees enhance the production of earlywood formation and delay the initiation of latewood (ZOBEL and BUIJTENEN, 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 of 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 TALBERT (1984); YANCHUK and KISS (1993); SKRØPPA, unpublished).

Latewood density and latewood percentage appear to be under stronger genetic control than overall density. This is equal to result reported for *Pinus radiata* but opposite of Douglas-fir (NICHOLLS et al., 1980; VARGAS-HERNANDEZ and ADAMS, 1991). The strong heritability found for latewood percentage corresponds with results for clonal Norway spruce reported by KENNEDY (1966). He found a high broad sense heritability equal to 0.85 for latewood percentage.

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 Ontario, Canada, and to those reported for full-sib families grown in Sweden and Norway (KARLSSON and DANELL (1989); NIEMAN and BOYLE (1989); SKRØPPA, unpublished).

All the estimates of heritability in this study may be somewhat upwardly biased because measurements were restricted to a single test site where family-site interactions are not accounted for.

Relationships among traits

The strong genetic relationship between overall density and each of its components reflects to a large extent the fact overall density is a compound trait resulting from different combinations of the proportion and the relative density of each component.

The low genetic correlation coefficient between earlywood density and latewood density or latewood percentage indicates that these density components may be controlled by different sets of genes. VARGAS-HERNANDEZ and ADAMS (1991) found a strong genetic relationship between density traits in a study of Douglas-fir, and draw a different conclusion: "traits are probably controlled to a large extent by the same set of genes". The difference in conclusion maybe attributed to differences between the VARGAS-HERNANDEZ and ADAMS (1991) study and this study. The 2 species studied are different, they are grown under different climate, and 2 different criteria were employed to demarcate the transition point between earlywood and latewood.

The very high genetic and phenotypic correlation between overall density and latewood percentage indicates that percent latewood is the most important factor affecting overall density. Also earlier investigations for Norway spruce reported a strong phenotypic correlation between overall density and latewood percentage (NYLINDER, 1953; HAKKILA, 1966).

The strong relationship both genetically and phenotypically between latewood density and latewood percentage tells that individuals with large amount latewood also have high density latewood. This is natural since the longer the formation of latewood cells take place the thicker the cell walls of the tracheids get. Further, these components are highly correlated by the way they are constructed.

The genotypic correlation between height and density components tend to be more negative than the phenotypic ones. For very juvenile wood SKRØPPA (unpublished) found a none-significant 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 percent 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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