

# Relationships Between Wood Density Components and Juvenile Height Growth and Growth Rhythm Traits for Norway Spruce Provenances and Families

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## Abstract

Measurements of heights at ages 2, 4 and 7 years and of flushing, early shoot elongation and lammas growth at age 7 years were made in nurseries and in a short-term trial with seedlings from provenances and open pollinated families of *Picea abies*. Fifteen of the provenances and 45 of the families were planted in a long-term field trial. At age 29 years from seed, basic wood density and its components: earlywood and latewood density and latewood percentage from increment cores were measured by X-ray analysis. The trees of the northern provenances, which were the shortest ones, had the earliest growth start and the lowest proportion of trees with lammas growth, and had also the highest wood density and proportion of latewood. Moderate to strong negative relationships were found between the wood density traits and early height growth and growth rhythm traits, suggesting that the latter ones could be good predictors of provenance differences in wood density. For the families, much weaker and in most cases non-significant phenotypic correlations were found between the two groups of traits. The genetic correlation coefficients were in most cases negative and had low absolute values. The possible causes of the differences in relationship patterns between provenances and families are discussed.

*Key words:* *Picea abies*, provenances, families, basic wood density, flushing, lammas growth.

## Introduction

Wood density of conifer tree species shows substantial genetic, environmental and age-related variation, see ZOBEL and VAN BULJTENEN (1989) for reviews. In studies of Norway spruce (*Picea abies* (L.) KARST.), genetic variation has been demonstrated among provenances which often have been transferred different distances (e.g. MERGEN *et al.*, 1964; VELLING, 1980; HYLEN, 1996; PERSSON and PERSSON, 1997), and also among families and clones (e.g. KENNEDY, 1966; WORRALL, 1975; BIROT and NEPVEU, 1979; LEWARK, 1982; HYLEN, 1997). The expression of genetic variation may depend on the environmental conditions, and therefore variability may be expressed in some environments, but not in others (WORRALL, 1975; HYLEN, 1996).

Wood density is strongly influenced by the relative proportions of earlywood and latewood (ZOBEL and VAN BULJTENEN, 1989). Earlywood is formed in the first part of the growth season and has low density, while latewood is produced later and has higher density. The relative proportions of the two types of wood may depend on the cambial growth rhythm, in particular the timing of growth initiation, the transition from earlywood to latewood and the cessation of growth (MERGEN *et al.*, 1964; DIETRICHSON, 1964; WORRALL, 1970). Genetic variation among provenances and families in the relative propor-

tions of earlywood and latewood has been demonstrated in Douglas fir (VARGAS-HERNANDEZ and ADAMS, 1994), in loblolly pine (JAYAWICKRAMA *et al.*, 1997) and in Norway spruce (WORRALL, 1975; HYLEN, 1997). Because latewood is formed after cessation of leader growth (LARSSON, 1969), a provenance or a family that ceases shoot growth early may have available a longer period for latewood formation (WORRALL, 1970; JAYAWICKRAMA *et al.*, 1997). Associations should consequently be present between the annual shoot growth rhythm and wood density and its components.

In Norway spruce, the timing and duration of shoot growth vary both among provenances, families and clones (e.g. DIETRICHSON, 1969; WORRALL, 1975; SKRØPPA, 1982; EKBERG *et al.*, 1985; SKRØPPA and MAGNUSSEN, 1993). HYLEN (1997) studied the genetic variability in wood density in a combined provenance and family trial in western Norway. Measurements of height growth and growth rhythm had earlier been made when these provenances and families were grown in nurseries and in a short-term trial in eastern Norway (DIETRICHSON, 1967, 1969). The aim of the present study was to relate the results from these early tests to the variation in wood density for both provenances and families.

## Materials and Methods

### *Trials and measurements*

In 1962, seeds from open pollinated trees in natural stands of Norway spruce located in different parts of southern Norway and from selected provenance were sown in a nursery in the southernmost part of Norway (DIETRICHSON, 1967). The Norwegian material comprised 45 families from 10 stands, originating between latitudes 58°40'N and 60°40'N and altitudes 45 m to 410 m. Fifteen provenances are included: 6 from Finland, 5 from Poland, 1 from Germany and 3 from Denmark. The Danish seed samples were collected in stands planted with seedlings most likely of German origin (ROULUND, pers. inf.). The Finnish provenances originated from latitudes between 60°24'N and 63°40'N, and the Polish ones between 49°20'N and 54°12'N.

After two growth seasons the seedlings were transplanted in the nursery at the experimental farm Hoxmark, Ås, latitude 59°40'. In 1966, a short-term trial was planted at Hoxmark, and a long-term trial was planted at Håheim, Etne, latitude 59°40', in western Norway. The long-term trial contained a subset of the families and provenances. The experimental designs were randomised blocks with 4 replicates in the nursery and 16 replicates of 4-tree plots both in the short- and long-term trial.

Measurements made in the nurseries and in the short-term trial were described by DIETRICHSON (1967, 1969). Seedling heights were measured after 2 and 4 growth seasons (years) in the nurseries and after the end of growth season 7 in the short-term trial at Hoxmark. Assessment of flushing was made at

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the beginning of the seventh growth season (May 13 and 14) according to the method by LANGLET (1960), using scores from 1: «bud slightly swollen» to 4: «needles elongating to double bud length» (KRUTZSCH, 1973). The same year, the shoot growth attained on June 11 and 12 and total shoot lengths were measured, and in September each tree was individually assessed for lammass growth.

In the long-term trial at Håheim, increment cores were taken at breast height from all trees in 6 replicates in 1990, when the trees were 29 years from seed. The basic wood density (overall density), earlywood and latewood density and the percentage of latewood were determined by X-ray analyses as described by HYLEN (1997). Tree heights were measured in this experiment in 1984 at age 23 years.

#### Statistical analyses

The percentage of trees with lammass growth was determined per plot and the overall means for the different entries were calculated. For each tree the relative shoot elongation by June 12 to 13 in percentage of total shoot growth was calculated. Plot means and family means were calculated for this percentage and for the flushing scores. Percentage values were also transformed by the arcsine transformation. All statistical analyses were performed both for the percentages and for the transformed values. As minor differences were present, only results for the percentages will be presented. Provenance and family means were similarly calculated for overall density and its components.

Analyses of variance were made of the provenance measurements regarding provenance as fixed and blocks as random factors. In addition, separate analyses were performed with the provenances pooled into three provenance groups: Finland, Denmark and Poland, regarding the country as fixed and provenance within country as random.

DIETRICHSON (1967, 1969) made analyses of variance of the juvenile height growth and growth rhythm traits for families, while HYLEN (1997) did the same for the wood density traits. Estimates of heritabilities were taken from these analyses or were calculated if not available.

PEARSON correlation coefficients between pairs of wood density and juvenile traits were calculated both for provenance and family means. For the families such correlation coefficients were also calculated based on deviations of each respective family from its stand mean.

The family correlation coefficients between pairs of traits were based on measurements of different individuals from the

same families, planted in different environments. Under such conditions the type B genetic correlation between two traits  $x$  and  $y$  can be estimated as

$$r_{gxy} = \frac{r_{xy}}{h_x h_y}$$

where  $r_{xy}$  is the phenotypic correlation coefficient between the family means, and  $h_x$  and  $h_y$  are the square roots of their family mean heritability estimates (BURDON, 1977). The genetic correlations were estimated by this formula. The sampling errors of these estimates are not easily available (BURDON, 1977). However, a test was made of the hypothesis that the genetic correlation equals zero by testing the significance of  $r_{xy}$ .

#### Results

The range of variation among provenance means and family means for each of the traits reported are shown in *table 1*. The range of variation among families and among provenances was rather similar for most traits.

#### Provenances

The variation among provenances was significant at the 1% level for all heights and for the growth rhythm traits. The trees of the provenances from Finland were at all ages shorter than the more southern ones from Denmark and Poland. They started their growth earlier and had on June 12 1968 on average completed 57% of their shoot growth for that year compared to 32% for the Polish provenances. On average, 18% of trees of the Finnish provenances showed lammass growth, compared to 82% for the Polish and 89% for the Danish ones. The variation among provenances was significant for overall density ( $p=0.02$ ), earlywood density ( $p=0.05$ ), latewood density ( $p=0.04$ ) and latewood percentage ( $p=0.004$ ).

When 14 of the provenances were pooled into three groups, defined by the countries Finland, Denmark and Poland, the variation among countries was significant for most traits, but not among provenances within country. The mean overall density for the three countries Finland, Denmark and Poland were 0.300 g/cm<sup>3</sup>, 0.279 g/cm<sup>3</sup> and 0.284 g/cm<sup>3</sup>, respectively.

The phenotypic correlation coefficients between height and diameter growth at different ages and the wood density traits were generally negative (*Table 2*). They were not significant for earlywood density and had the highest absolute values for the latewood percentage and overall density. The strongest relationships were observed between these two density traits and

*Table 1.* – Range of variation of provenance and family means of the reported traits. The wood density traits were measured on increment cores collected at age 29 in the long-term trial. All ages referred are growth seasons from germination.

Traits	Provenances	Families
<i>Nursery or short-term trial:</i>		
Height year 2 (cm)	7.7 – 13.8	6.8 – 11.8
Height year 4 (cm)	19.4 – 28.8	17.6 – 26.5
Height year 7 (cm)	46.1 – 79.9	51.3 – 76.3
Flushing year 7	1.4 – 2.7	1.3 – 3.3
Early shoot elongation year 7 (%)	26.5 – 67.8	22.2 – 54.7
Lammass growth year 7 (%)	0.0 – 89.4	3.1 – 92.2
<i>Long-term trial:</i>		
Overall density (g/cm <sup>3</sup> )	0.274 – 0.304	0.265 – 0.320
Earlywood density (g/cm <sup>3</sup> )	0.259 – 0.279	0.259 – 0.289
Latewood density (g/cm <sup>3</sup> )	0.449 – 0.472	0.440 – 0.489
Latewood percentage (%)	8.0 – 23.3	4.3 – 28.0
Height year 23 (cm)	467 – 726	465 – 648

Table 2. – Phenotypic correlation coefficients among provenance means for wood density components and growth and growth rhythm traits. Significance levels: 5% (\*), 1% (\*\*) and 0.1% (\*\*\*) for  $|r| = 0.52, 0.64$  and  $0.76$ , respectively.

Traits	Overall density	Earlywood density	Latewood density	Latewood percentage
<i>Nursery or short-term trial :</i>				
Height year 2	- 0.62*	- 0.34	- 0.51	- 0.63*
Height year 4	- 0.41	- 0.11	- 0.43	- 0.51
Height year 7	- 0.80***	- 0.43	- 0.70**	- 0.83***
Flushing year 7	0.62*	0.36	0.60*	0.59*
Early shoot elongation year 7	0.79***	0.47	0.65**	0.78***
Lammas growth year 7	- 0.88***	- 0.51	- 0.73**	- 0.89***
<i>Long-term trial:</i>				
Height year 23	- 0.75**	- 0.38	- 0.67**	- 0.84***

the percentage of trees with lammas growth. Provenances with a high proportion of trees with lammas growth had the lowest latewood percentage and the lowest overall density. A similar, but somewhat weaker relationship was observed for the flushing and shoot elongation percentages. The provenances with the earliest growth start, which had completed the highest proportion of growth on June 11 to 12, had the highest latewood percentage and highest overall density.

A geographic pattern of regional provenance variation and relationships therefore emerged. The provenances from Finland, which had the earliest growth start, the lowest proportion of trees with lammas growth and were the shortest ones, also had the highest overall density and the highest percentage of latewood.

The phenotypic correlation coefficient between the provenance mean heights after growth season 7 in the short term test and after growth season 23 in the long-term trial was 0.72 ( $p < 0.003$ ).

#### Families

A non-significant variation among stands, but significant variation among families has earlier been presented by HYLEN (1997) for the wood density traits. For the height growth and growth rhythm traits in the nursery and short-term trial DIETRICHSON (1967, 1969) demonstrated significant variation both among stands and families. In the long-term trial, significant variation was found for height at age 23 years among families ( $p = 0.005$ ), but not among stands (HYLEN, 1997).

Phenotypic correlation coefficients among family means for the two sets of traits are presented in table 3. Only minor

differences in the values of the correlation coefficients were found when the calculations were based on deviations from the stand means. All correlation coefficients had low absolute values and only three were significant at the 1% level. The estimates of the genetic correlation coefficients have slightly higher values than the corresponding phenotypic correlation coefficients (Table 4).

The phenotypic correlation coefficient between the family mean heights after 7 years in the short term test and 23 years in the long-term trial was  $-0.03$  ( $p = 0.85$ ).

#### Discussion

Phenotypic correlations are here used to study the relationship between two sets of traits, measured on different individuals of the same genetic units (provenances, families) grown in two different environments. Environmental effects common to members of the same genetic unit should not bias these correlations as the traits are measured at different locations, but non-genetic effects arisen in the nursery prior to planting may be one source of bias (BURDON, 1977). The phenotypic correlations will generally underestimate the corresponding genetic correlations since family means will be inflated by contributions from measurement error and environmental variance (LYNCH and WALSH, 1998). The presence of genotype x site interactions will lower the phenotypic correlation. A low correlation, however, should not be taken as a conclusion that an interaction is present (LYNCH and WALSH, 1998).

The high overall density of the Finnish compared to the Central European provenances and the negative relationships between growth and density are in agreement with earlier results

Table 3. – Phenotypic correlation coefficients among family means for wood density components and growth and growth rhythm traits. Significance levels: 5% (\*), 1% (\*\*) and 0.1% (\*\*\*) for  $|r| = 0.30, 0.39$  and  $0.49$ , respectively.

Traits	Overall density	Earlywood density	Latewood density	Latewood percentage
<i>Nursery or Short-term trial :</i>				
Height year 2	- 0.26	- 0.06	- 0.40**	- 0.37*
Height year 4	- 0.33*	- 0.23	- 0.36*	- 0.33*
Height year 7	- 0.27	- 0.17	- 0.27	- 0.28
Flushing year 7	- 0.23	0.16	- 0.40**	- 0.47**
Early shoot elongation year 7	- 0.09	0.18	- 0.24	- 0.27
Lammas growth year 7	- 0.22	0.01	- 0.32*	- 0.37*
<i>Long-term trial:</i>				
Height year 23	- 0.34*	- 0.29	- 0.19	- 0.28

Table 4. – Genetic correlation coefficients between wood density components and growth and growth rhythm traits. The values for height year 23 are taken from HYLEN (1997). Significance levels: 5% (\*), 1% (\*\*) and 0.1% (\*\*\*) for  $|r| = 0.30, 0.39$  and  $0.49$ , respectively.

Traits	Overall density	Earlywood density	Latewood Density	Latewood percentage
<i>Nursery or</i>				
<i>Short-term trial :</i>				
Height year 4	- 0.45**	- 0.33*	- 0.46**	- 0.44**
Height year 7	- 0.34*	- 0.23	- 0.32*	- 0.35*
Flushing year 7	- 0.27	0.20	- 0.44**	- 0.53***
Early shoot elongation year 7	- 0.11	0.23	- 0.27	- 0.32*
Lammas growth year 7	- 0.27	0.01	- 0.37*	- 0.44**
<i>Long-term trial:</i>				
Height year 23	- 0.68***	- 0.58***	- 0.51***	- 0.58***

(e.g. PERSSON and PERSSON, 1997). For the provenances, rather strong relationships were found between the density and the juvenile heights and growth rhythm measured in the short-term test. The correlations were in particular high between overall density and latewood percentage on one side and height year 7, shoot elongation percentage and lammas growth on the other side. These data confirm earlier results that have demonstrated associations between shoot growth rhythm and wood density for Norway spruce provenances (DIETRICHSON, 1964; WORRALL, 1970). The higher density of the Finnish compared to the Polish provenances obtained in this trial is most likely due to their earlier cessation of shoot growth and longer period available for latewood production on this test site.

Cessation of height growth, which has been found to determine the date of transition between earlywood and latewood (WORRALL, 1970; JAYACKRAMA *et al.*, 1997), was not directly measured in the short-term trial. However, the different points in time describing the start, development and cessation of the shoot growth period are interrelated. They are components of an annual sequence of developmental events, which describes the annual growth rhythm of the tree (REHFELDT, 1986; SKRØPPA and MAGNUSSEN, 1993) and may therefore all to some degree be related to the density variations. The total height growth of Norway spruce provenances grown under southern Scandinavian conditions is also strongly determined by the shoot growth rhythm, and provenances with a long shoot elongation period and a late cessation of growth have been shown to have the best height growth (SKRØPPA and MAGNUSSEN, 1993). This may explain the negative relationships between height growth and the density traits, as such provenances may not have been able to produce substantial amounts of latewood before temperature becomes a limiting factor. Relationships between wood density and growth traits may vary with age (CHALUPKA *et al.*, 1977), but due to the young age of the long-term experiment, such changes in relationships could not be studied with this material.

The presented results confirm that the annual shoot growth rhythm is an important determinant of the variation in wood density traits for provenances. Latewood production largely depends on the growing conditions after the termination of shoot growth, particularly moisture and temperature (WORRALL, 1970). Variation in latewood percentage will therefore also depend on the site conditions. The fact that strong relationships were obtained from measurements at different ages in trials growing under very different environmental conditions strengthens the conclusion. The results also depend to a large extent on the geographic range of the provenances tested. If only the provenances of Polish or Finnish origin had been ana-

lysed, then no strong relationships between the two groups of traits would have been obtained. It is also likely that the distance of latitudinal provenance transfer is important, so that the results obtained here may not be directly applicable if the same provenances are transferred to a different latitude (PERSSON and PERSSON, 1997).

For the families, no similar relationships were found between the density traits and heights and growth rhythm traits. In some cases, correlations that were positive at the provenance level, were even negative for families, i.e. between flushing and latewood percentage. Family x site interactions and low juvenile-mature correlations may be explanatory factors. The lack of significant correlations between the family mean heights in the short- and long-term trial indicates the presence of such interactions, which may be caused by the differences in climatic conditions between the test sites. The trial at Etne in western Norway is located in a more humid and milder climate than the nursery and short-term test site in eastern Norway.

Another explanation could be that relationships among traits are different for families and provenances. EKBERG *et al.* (1994) found weak correlations between growth rhythm and growth capacity in Norway spruce within populations, but strong correlations among populations. Similar observations were made by SKRØPPA and MAGNUSSEN (1993) and SKRØPPA (unpublished). In the long-term experiment, low and non-significant phenotypic correlations were found between density and heights, while the genetic correlations were significant (HYLEN, 1997). The relationships found here for families are in accordance with JAYACKRAMA *et al.* (1997) who found weak or no relationships between wood density and growth rhythm and growth for families within the same provenance of loblolly pine (*Pinus taeda*).

The variability in adaptive traits at provenance and family level may be affected by different factors (JOHNSEN and SKRØPPA, 1996). For provenances, a common influence of the climatic conditions during reproduction on the offspring could be important for the relationships observed. For families from the same geographic region this influence is most likely reduced. Such influences could explain the differences in trait relationships at the provenance and family level.

The strong relationships obtained between wood density and growth rhythm for provenances suggest that the latter traits could be good predictors of provenance differences in wood density. However, as the latewood production depends on environmental conditions after shoot growth cessation, environmental modifications, and also effects of age, may be expected (ZOBEL and VAN BULJTENEN, 1989). This is particular the case if the

growth rhythm traits are measured under photoperiodic and temperature conditions different from those in the production stand.

Similar strong relationships between wood density and growth rhythm do not generally seem to be present for families. Indirect selection for wood density based on such traits may therefore not be efficient and it will be necessary to measure the density directly. This will delay the selection until reliable wood density predictions can be made (HYLEN, 1999). However, this offers opportunities to select for different combinations of growth, growth rhythm and wood density.

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# The Effect of Pedigree Error by Misidentification of Individual Trees on Genetic Evaluation of a Full-sib Experiment

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## Abstract

A simulation based on real data shows how increasing rates of individual tree misidentification result in increasing underestimation of additive genetic variance and narrow-sense heritability as well as increasing overestimation of the dominance variance. The data used came from a *Pinus sylvestris* L. progeny trial with 202 full-sib families from 52 unrelated parents at about one-third of the rotation. When 1% of 4970 individual

trees were misidentified, the estimates of additive variance and heritability decreased by an order of magnitude that corresponded to the standard errors. The estimate of dominance variance approached that of additive variance when the error rate increased to 2%, after which further misidentification made the estimates diverge beyond the expected parameter space of the genetic model. The error effect was less pronounced when selecting the best parents using approximate best linear unbiased predictors, but their predicted performance was increasingly underestimated as the error rate increased.

*Key words:* additive variance, BLUP, breeding value, dominance variance, genetic parameter, heritability, pedigree error, mixed model equations, *Pinus sylvestris*, REML.

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