Genetic Variation in Juvenile Wood Basic Density at Different Stages of Development in Norway Spruce

DARIUS DANUSEVIČIUS AND RIMVYDAS GABRILAVIČIUS

Lithuanian Forest Research Institute,
Girionys Liepų 1, LT-4312 Kaunas reg., Lithuania

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Variation in juvenile wood basic density and tree diameter between 31 open-pollinated Norway spruce families from seven Lithuanian provenances grown in a progeny trial were assessed at age 23. Wood basic density of increment cores which were partitioned into segments of three year rings was estimated by the water displacement method. Family variance components, genetic and environmental correlations between wood density and tree diameter were estimated separately for the inner, central and outer parts of the increment cores. The results showed that within provenance variation in basic density was greater than the among provenance variation. Additive heritability for wood density was higher (h_a^2=0.55) than for tree diameter (h_a^2=0.21). The highest individual tree heritability for wood density was obtained in the wood which was formed during the period of intensive radial increment at age 9 to 14 years. Genetic variation in wood density was highly negatively correlated with genetic variation in tree diameter (r_G =-0.71). However, there were families with positive breeding values for both wood density and tree diameter. Such families, presumably, terminated growth late and, thus, grew thicker and were able to form relatively more latewood while efficiently utilising favourable climatic conditions at the end of the growth period. Such genotypes may be given a priority when selecting material for the subsequent breeding circles.

Key words: genetic correlation, growth rhythm, heritability, *Picea abies*, tree diameter, wood quality

Introduction

Wood strength and pulp yield are the key determinants of wood quality. Wood strength and pulp yield are dependent on wood density, which is a complex trait mainly depended on cell diameter, cell wall thickness and amount of extractives (Zobel & van Buitenen 1989). These properties are controlled by genetic, physiological and environmental factors. Silvicultural practices are influencing tree growth which in turn affects wood density (Zobel & van Buitenen 1989).

An annual ring contains earlywood and latewood. Earlywood cells are formed during the period of intensive growth at the beginning of growth period. Therefore, earlywood cells are large with thin walls resulting in low wood density. Whereas, latewood cells are formed at the later part of summer when tree growth is less intensive. Such cells have a low radial diameter and high cell wall thickness giving high wood density. The greater the amount of the latewood in an annual ring the higher is the overall wood density (Zobel & van Buitenen 1989).

Wood density varies in the radial direction. In coniferous species there are two basic sources of this variation. The first is the difference in annual ring width in cross-section from the pith to the bark. Wood density is negatively correlated with ring width in Norway spruce (e.g. Klem 1934, Hakkila 1966). This negative correlation is due to a decrease in latewood with increasing ring width (Bernhart 1964). In conifers, thick trees possess less latewood and consequently are of softer wood than thin trees (e.g. Danusevicius 1994). The second reason is the variation in cell radial diameter when moving towards the pith. The wood cells close to the pith are of low diameter leading to a greater amount of cell walls, which means higher wood density than at the outer wood sections (Olesen 1977).

External factors which promote intensive tree growth are usually delaying latewood formation. For instance, access of moisture during the period of intensive growth would result in relatively large proportion of earlywood (Zobel & van Buitenen 1989). Another example is stand spacing where wood density is higher in a stand at narrow spacing than in a stand at wide spacing (Persson 1975). Narrow spacing favours formation of latewood (Larson 1969).

In Lithuania, Norway spruce stands are mainly established artificially. Wood quality of artificially established Norway spruce stands may be improved through breeding towards high wood density. Incorporation of wood density into a selection index requires information on degree of genetic control on

wood density and genetic relationships with growth traits. In coniferous species, thick trees possess softer wood than thin trees (e.g. Ericson 1960). The correlation coefficient, however, may not always be equal to one. If possible, the genotypes which are able to form relatively more and hardier wood should be preferred by tree breeders. Studies on genetic parameters of wood density of Lithuanian Norway spruce populations are limited.

The objectives of this study were to study the genetic variation in juvenile wood basic density among Norway spruce families from seven populations in Lithuania and to assess the genetic relationship between wood basic density and stem diameter.

Material and methods

Open-pollinated seeds were collected from 31 trees in seven natural Norway spruce stands (provenances) in north-eastern, central and eastern parts of Lithuania (Fig. 1). In 1974, a progeny trial was established on an abandoned agricultural land in Vaisvydava forest district near Kaunas in Lithuania (54°53' N, 24°00' E, 70 m a.s.l.). Four to six families per provenance with 90 seedlings per family were planted with spacing of 1.5 m x 1.5 m. Families of certain provenance were planted consequently in rows with 30 seedlings in each row making up 3 rows per family. No blocking was used. However, to have an estimate of environmental variation within a provenance, the plot occupied by certain provenance was subdivided into three sections

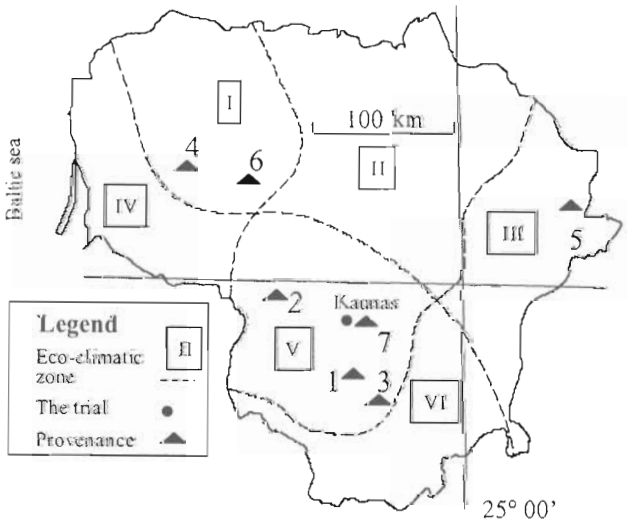

Figure 1. Location of the trial and origin of the provenances. Basically, the eco-climatic zones reflect continentality of the climate and are partitioning the country into the southern and northern parts. Zones I, III and VI delineate highlands, whereas zones IV, II, V delineate lowlands.

("replications"). The first 10 trees in each row within a provenance plot were assigned to "replication" No. 1, the following 10 trees to "replication" No. 2 and the last 10 trees to "replication" No. 3. This progeny trial being of sufficient age to assess wood basic density contained provenances from a broader range in Lithuania than the other Lithuanian Norway spruce provenance-progeny trials suitable for wood studies. Neither fertilization nor thinning were applied.

In 1995, increment cores were sampled at breast height (1.3 m) from the southern side of a tree from 20 trees per family. The sample trees were selected systematically by choosing approximately each forth tree in a row. Trees in the edge rows of the trial or the trees markedly suppressed by competition or having symptoms of a disease were not sampled. Diameter of the trees from which the increment cores had been sampled was measured at breast height across and along to the drilling direction.

The increment cores were cut into segments of 3 annual rings each. The increment cores on average contained 21 annual rings. Wood basic density which indicates the amount of dry matter per unit green volume was measured by using the water displacement method (Olesen 1971). The increment cores with defects were excluded from the analysis. We have assumed that the trees in our experiment contain juvenile wood only. According to Olesen (1973), transition from juvenile to mature wood in Norway spruce occurs between 9th and 20th annual rings from the tree pith.

Statistical analysis

To compare wood basic density and the genetic parameters between the inner, central and outer parts of an increment core, it was subdivided into three sections (RCLAS, Fig.6). The first six annual rings from the bark were ascribed to section No.1 (RCLAS=1), the next six to section No.2 (RCLAS=2) and the rest to section No.3 being closest to the pith (RCLAS=3).

The analysis of variance (ANOVA), estimation of variance components and genetic parameters for basic density were made on two levels: total increment core level and separately by each section (RCLAS). In the analysis on the total increment core level, the unit of observation was the mean basic density of an increment core, and in the analysis by RCLAS, the unit of observation was mean basic density of a corresponding RCLAS. The ANOVAs, variance components, family breeding values and the associated standard errors were calculated by using the procedures GLM and MIXED in SAS statistical package (SAS Institute Inc. 1989). The variables were LOG transformed to

normalise the residuals and to homogenise the variances.

The ANOVAs were performed according to the following model:

$$y_{ijkl} = P_i + F_{j(i)} + R_{k(i)} + e_{ijkl}$$

where y_{ijkl} is the unit of observation, P_i is fixed effect of i-th provenance, $F_{j(i)}$ is random effect of j-th family within i-th provenance, $R_{k(i)}$ is fixed effect of k-th "replication" within i-th provenance, and e_{ijkl} refers to random error.

Variance component for family was estimated by the following model:

$$y_{ik} = F_i + e_{ik}$$

where y_{ik} is the unit of observation, F_i is random effect of i-th family, e_{ik} is random error.

The half-sib family additive variance was estimated as:

$$s_a^2 = 4\, s_f^2$$

where s_f^2 is the family variance component.

Individual tree (additive) heritability was estimated as:

$$h_a = s_a^2 / s_{ph}^2$$

where s_{ph}^2 is the total phenotypic variance estimated as the sum of the variance component for family and the variance component for error.

Standard error for the individual tree heritability was calculated according to Becker (1984).

Half-sib family heritability was estimated as suggested by Fins *et al.* (1992):

$$h_f^2 = s_f^2 / (s_f^2 + s_e^2 / k)$$

where k is the harmonic mean of number of observations per family:

The correlation between the predicted and true breeding values was calculated by Fins *et al.* (1992)

$$r_{g,\hat{g}} = \sqrt{\frac{\sigma_{\hat{g}}^2}{\sigma_g^2}} \qquad \text{where} \quad \sigma_{\hat{g}}^2 = \frac{(1/2\sigma_e^2)^2}{\sigma_{phf}^2}, \quad \sigma_g^2 = \sigma_a^2$$

s_{phf}^2 is the phenotypic variation among the families, $s_{ijkl.f}^2 = s_f^2 + s_e^2 / k$.

Genetic (r_G), environmental (r_E) and phenotypic (r_P) correlation coefficients were calculated by the following formulas:

$$r_G = \frac{4\sigma_{f(xy)}}{\sqrt{4\sigma_{f(x)}^2 4\sigma_{f(y)}^2}} \qquad r_E = \frac{\sigma_{e(xy)} - 3\sigma_{f(xy)}}{\sqrt{(\sigma_{e(x)}^2 - 3\sigma_{f(x)}^2)(\sigma_{e(y)}^2 - 3\sigma_{f(y)}^2)}}$$

$$r_P = \frac{\sigma_{e(xy)} + \sigma_{f(xy)}}{\sqrt{(\sigma_{e(x)}^2 + \sigma_{f(x)}^2)(\sigma_{e(y)}^2 + \sigma_{f(y)}^2)}}$$

where $s_{f(xy)}$ is genetic covariance between two variables, $s^2_{f(x)}$ and $s^2_{f(y)}$ are family variance components, $s_{e(xy)}$ is environmental covariance, $s^2_{e(x)}$ and $s^2_{e(y)}$ variance components for error.

The genetic covariance was calculated by using the algebraic relationship of the variance of a sum of two variables:

$$\sigma_{f(x+y)}^2 = \sigma_{f(x)}^2 + 2\sigma_{f(xy)} + \sigma_{f(y)}^2$$
$$\sigma_{f(xy)} = (\sigma_{f(x+y)}^2 - \sigma_{f(x)}^2 - \sigma_{f(y)}^2)/2$$

Before calculation of the variance components for the sum of the two variables, these variables were standardized to zero mean and unit variance. Standard errors of the genetic correlation coefficients were estimated according to Falconer (1989).

Results

Variation in wood basic density and tree diameter within the provenances was greater than the corresponding variation among the provenances (Fig. 2). The main cause of the significance of the provenance effect in the ANOVA on wood basic density was that provenance No.6, which originated from the highland in north-western Lithuania, had the highest estimate of wood basic density (Table 1, Fig. 2). Provenances No.4 and No.6 from the highland in north-western Lithuania possessed relatively lower diameter, which resulted in one star significance of provenance effect on tree diameter (Table 1, Fig. 2). Within provenance variation in tree diameter was less than within provenance variation in wood basic density, for which the effect of family nested within provenance was of three star significance for all the core sections (RCLAS) (Table 1). Effect of "replication" nested with a provenance was not significant for both variables.

Table 1. Results from ANOVAs on basic density and tree diameter. ANOVAs on basic density were made on total increment core level (TOTAL) and separately by the segments (RCLAS), where RCLAS=1 is the outer segment. Significance levels of F statistics are given. In the row for Error the numbers show the degrees of freedom for error.

Source		Basic density				Diameter
	DF	RCLAS=1 Pr>F	RCLAS=2 Pr>F	RCLAS=3 Pr>F	TOTAL Pr>F	Pr>F
PROV	6	0.0001	0.0001	0.0001	0.0001	0.0236
FAM(PROV)	24	0.0001	0.0001	0.0001	0.0001	0.0041
REPL(PROV)	10	0.0359	0.9279	0.1118	0.4758	0.1238
Error	509		d.f. 511	d.f. 496	d.f. 512	d.f. 512
R^2	0.23		0.21	0.22	0.22	0.14

predicted family breeding values was greater within provenances than among provenances (Fig.5). Correlations between true and the predicted breeding values were high: 0.86 for wood basic density and 0.71 for tree diameter, what shows that the prediction was reliable. Basically, the higher the breeding value for basic density the lower was the breeding value for tree diameter (Fig. 5). However, families No.7, 12, 14, 19, 21, 29 showed positive breeding values both for the diameter and basic density (Fig. 5). The families No.5, 8, 20, 26 had positive breeding values for diameter and negative but close-to-zero breeding values for basic density (Fig 5).

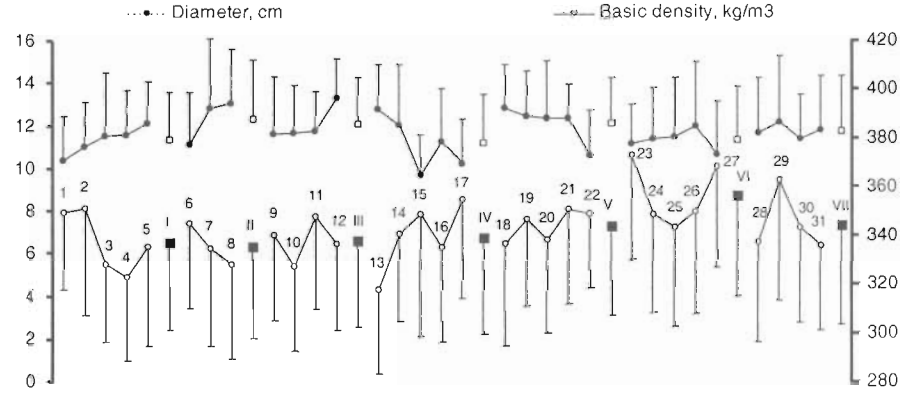

Figure 2. Values of wood basic density (right axis) and tree diameter (left axis). The dots show family mean values and the squares show provenance mean values. Families of the same provenance are joined by a line. Provenances are labelled in roman numbers. The error bars show standard deviation. The values are not transformed.

Variation in wood basic density from the pith to the bark averaged over all the increment cores is shown in Fig.3. The wood closest to the pith being formed during the age of 1 to 6 years (RCLAS=3) was of the highest basic density. Moving towards the bark, basic density gradually decreased and reached the minimum value at approximately age 11 years (RCLAS=2), followed by gradual increase of wood density at age 18 to 20 years (RCLAS=1) up to similar values as of the inner section. Annual rings were widest during the period of intensive radial increment at the age 9 to 16 years (RCLAS=2). Therefore, basic density of the wood formed during the former period was lowest. Later on, in the crown closure phase, increased competition among the trees resulted in a decrease of the radial increment and, consequently, in high basic density of the wood formed in the outer section (RCLAS=1), (Fig. 3).

Family variance component for basic density was greater than family variance component for tree diameter (Fig. 4). Consequently, the additive heritability was significantly higher for total core basic density than for tree diameter (Table 2). The highest heritabilities for wood basic density were obtained in the middle section of the increment cores (RCLAS=2), where wood basic density was lowest (Table 2). Variation in the

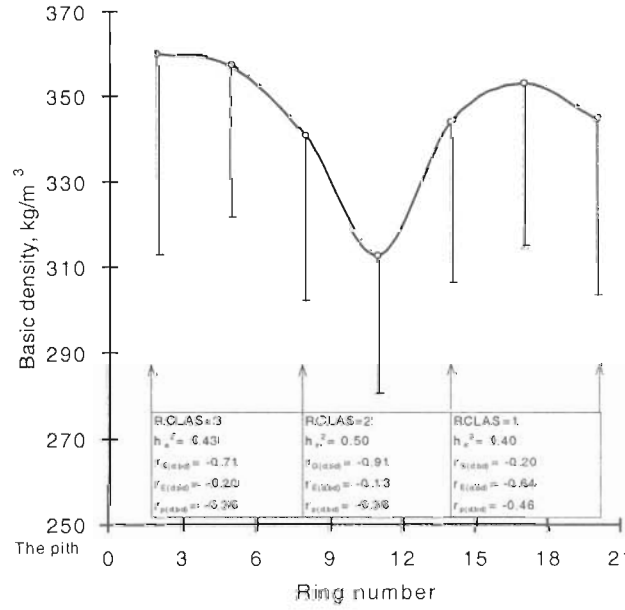

Figure 3. Variation of wood basic density along the increment core from the pith to the bark. The figure is averaging estimates of all the increment cores sampled. The error bars show standard deviation. In the lower box, correlation (genetic, environmental and phenotypic) between basic density and tree diameter as well as additive heritability for basic density are given separately for each of the increment core sections (RCLAS).

Table 2. Additive (h_a^2) and family (h_f^2) heritabilities for basic density and tree diameter. The heritabilities for basic density are presented by the increment core sections (RCLAS) and total increment core (TOTAL). Standard error of the additive heritability is given in the brackets.

Parameter	Basic density				Diameter
	TOTAL	RCLAS=1	RCLAS=2	RCLAS=3	
h_a^2	0.55 (0.17)	0.40 (0.16)	0.50 (0.16)	0.43 (0.15)	0.21 (0.11)
h_f^2	0.74	0.66	0.72	0.67	0.50

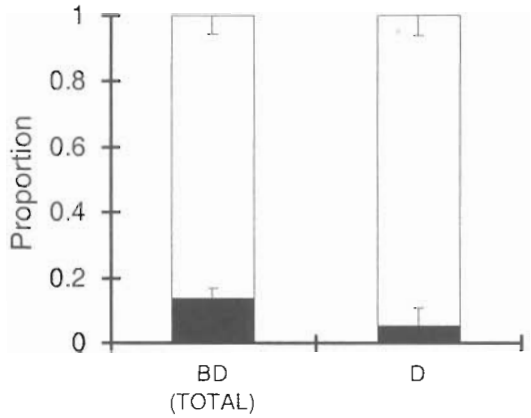

Figure 4. Variance components for family and error for wood basic density of total increment core (BD) and tree diameter (D) expressed as proportion from the total variance.

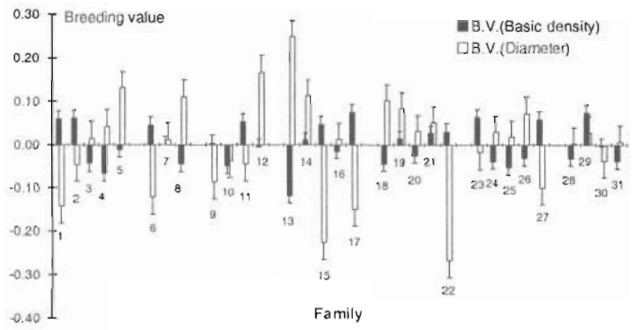

Figure 5. Predicted family breeding values (B.V.) for tree diameter and wood basic density. Family group representing a provenance is separated by a blank space. The families are ordered according to the provenance No. from I to VII.

Genetic, environmental and phenotypic correlation coefficients between tree diameter and wood basic density are presented in Table 3. The genetic relationships are illustrated in scatter plots between the family breeding values for wood basic density and tree diameter (Figs. 6 and 7). Note, that owing to the large standard errors of the family predicted breeding values the correlation among the breeding values usually is an underestimate of the genetic correlation. The genetic relationship between tree diameter and total core basic density was strong and negative (Table 3, Fig. 7). The genetic correlation between tree diameter and wood basic density in the outer segment of the core was not significant (Table 3, Fig 6), whereas, the environmental correlation between wood basic density of the outer segment and tree diameter was highest (Table 3). The highest genetic correlation and the lowest environmental correlation between tree diameter and wood basic density was obtained in the middle section of the increment cores, which possessed the softest wood (Table 3).

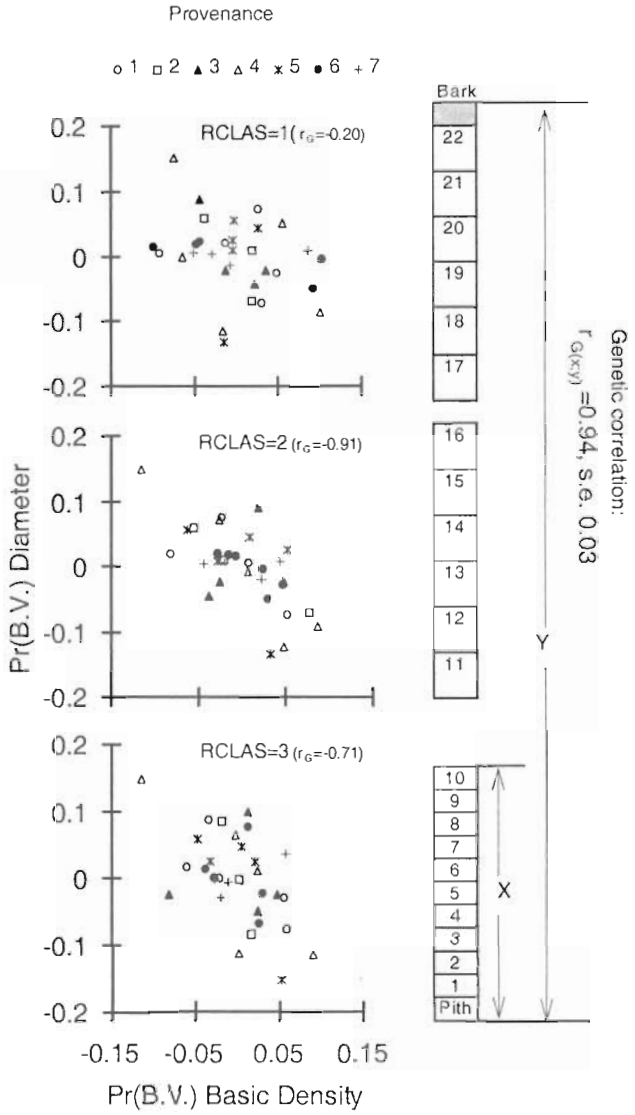

Figure 6. Relationship between family predicted breeding values (B.V.) for tree diameter and wood basic density by increment core sections (RCLAS). At the right side of the figure, genetic correlation between basic density of the inner segment (near the pith) and basic density of total increment core is given.

Correlation coefficient	Between D and BD, which is averaging estimate of				Between BD of RCLAS=3 and TOTAL
	TOTAL	Outer segment		Inner segment	
	incr. core	RCLAS=1	RCLAS=2	RCLAS=3	
r_G	-0.71 (0.14)	-0.20 (0.28)	-0.91 (0.05)	-0.71 (0.14)	0.94 (0.03)
r_E	-0.43	-0.64	-0.13	-0.20	0.53
r_P	-0.50***	-0.46***	-0.38***	-0.36***	0.72***
No. obs.	N=553	N=550	N=552	N=537	N=537

Table 3. Genetic (r_G), environmental (r_E) and phenotypic (r_P) correlation between tree diameter (D) and basic density (BD), which is averaging estimates of total increment core (TOTAL) and separate core sections (RCLAS). Correlations between basic density of the inner core section (RCLAS=3) and basic density of total increment core are presented in the last column. Standard error of genetic correlation is given in the brackets. The total number of observations is given in the last row.

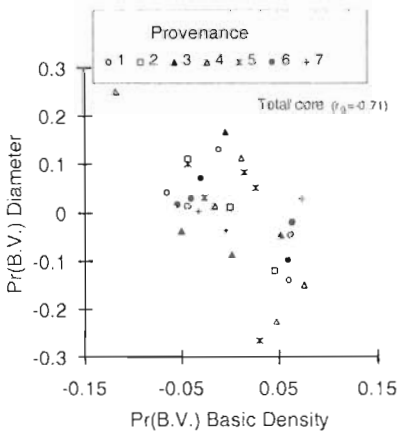

Figure 7. Relationship between family predicted breeding values (B.V.) for tree diameter and wood basic density of total increment core.

Discussion

Provenances No. 4 and No. 6, which were moved for approximately 1° of latitude southwards and to a 100 m lower altitude, had somewhat lower diameter than the other provenances (Fig. 2). When transferred southwards or to a relatively lower altitude, Norway spruce provenances cease growth earlier and, thus, produce less volume than local provenances (e.g. Hannerz 1998). High wood density of provenance No. 6 may be attributable to relatively earlier growth cessation, which may be associated with production of comparably less early wood than of the other provenances in this experiment (cf. Persson and Persson 1992, 1997). However, the former pattern was not as clearly expressed as regards wood density of provenances No. 4 and No. 5, for which the transfer distance southwards and to a lower elevation was similar as the transfer distance for provenance No. 6. Presumably, the provenances originated from too small geographical range to capture a pronounced pattern of geographical variation with the number of families within a provenance in our experiment. This would especially be true if considering large within population variation in growth rhythm and the associated traits including wood density. Nanson *et al.* (1975) did not find significant differences among Norway spruce provenances in Belgium in latewood content.

The annual rings from 9 to 15 in the middle section of the increment cores were formed during the period of intensive tree growth and, therefore, were larger and of lower wood density than the rings close to the pith (No. 1-9). A similar pattern of the radial variation in wood density in Norway spruce was observed by Hylen (1997), Noren (1996), Brolin *et al.* (1995) and Pape (1999). During the subsequent development stages (rings No. 15- 21), radial growth intensity decreased owing to a strong competition, which has resulted in formation of narrow rings of relatively higher wood basic density. We suggest to adjust currently existing silvicultural management in Lithuanian Norway spruce stands to avoid wide spacing during the period of intensive radial increment.

The family mean and additive heritabilities for wood basic density of the total increment core obtained in our study were close to those estimated by Hylen (1997) in the study of the 28-year-old open-pollinated Norway spruce families. Comparably low heritability for tree diameter was reported in many studies with forest trees (e.g. Karlsson and Danell 1989). Heritability of wood density was highest during the period of intensive, competition-free growth of the trees at the age of 9-16 years (RCLAS=2), i.e. after the establishment phase. This also was reflected by the highest negative genotypic and the lowest environmental correlation coefficients between basic density of the wood in the middle core section (RCLAS=2) and tree diameter (Table 3). The heritabilities for basic density of the wood formed during the juvenile stage (until 8-years-old, RCLAS=3) were relatively lower. This may

be explained by the fact that young trees in the phase of establishment are more sensitive to the environment than trees at the subsequent development stages. Presumably, the tree spacing at the age of 9-16 years allowed the genetic properties to be expressed to a higher degree than later on, when different genotypes had reacted differently to a strong competition at the given spacing. Consequently, the genotypic correlation between wood density of the outer section of the increment cores (RCLAS=1) and tree diameter was not significant, whereas the environmental correlation was highest (Table 3). Thus, the genetic variation in wood basic density is to a large extent determined by the genotypic control of growth capacity, which, in turn, is associated with growth rhythm in Norway spruce. High negative correlation coefficients between wood basic density and tree diameter as well as other traits directly or indirectly associated with growth rhythm were reported in many studies on Norway spruce (e.g. Ericson 1960, Olesen 1976 and Hylen 1997). Within population variation in growth rhythm is large in Norway spruce (Dietrichson 1969 and Ekberg *et al.* 1985 and Hannerz 1998). Given this association, significant differences among families within one population in wood density may be expected (Table 1, Nilsson 1963, Worrall 1975 and Hylen 1997).

Late flushing Norway spruce origins usually possess higher growth capacity (Persson and Persson 1992) and should, thus, produce wood of lower basic density than early flushing origins, unless being controlled by the spacing (Dietrichson 1964, Stairs and Adapa 1969, Worrall 1970 and Persson and Persson 1997). However, ability of late flushing origins while growing for a longer period to produce relatively more latewood than early flushing origins may be considered (Klem 1957). In the later case, climatic conditions in the region of interest may be of importance, since presence of abundant moisture at the end of growth period favours formation of latewood (Larson 1969). However, late-flushing genotypes usually are of high growth capacity and may form wood of too low density if spaced too wide during the period of intensive radial increment. The silvicultural practices should thus consider not only the site type but also origin of the trees and climatic conditions in a breeding zone.

The families with positive breeding values for tree diameter and with positive or negative close-to-zero breeding values for wood basic density would be the most desirable in tree breeding. Such families would genotypically be able to produce relatively more and relatively harder wood. As discussed above, such families, presumably, terminated growth late and, thus, grew thicker and were able to form relatively more latewood while efficiently utilising favourable climatic conditions at the end of the growth period. In our study, we have found 10 of such families, which being included in a breeding population would contribute to improvement of wood quality of the new generations. In contrast, the families which are genotypically determined to produce relatively less and soft wood and are thus having negative breeding values for diameter and negative or low positive breeding values for basic density should be rejected by the breeders.

In conclusion, results of our study have indicated that wood basic density is under strong genetic control, which may to a certain extent be influenced by the environment and silvicultural treatments. This extent is influenced by the reaction norm of different genotypes being adopted to different climatic conditions. Within provenance variation in basic density is greater than among provenance variation. The highest individual tree heritability for wood basic density was obtained in the wood formed during the period of intensive radial increment. Silvicultural practices may be adjusted according to a climatic zone and site type to secure a proper spacing during the period of intensive radial increment to fulfil wood density requirements for sawn or pulp wood. Genetic variation in wood basic density was highly negatively correlated with genetic variation in tree diameter. However, there are genotypes which are able to produce relatively more and hardier wood. These genotypes should be included in breeding programmes. Wood density may be included in multi-trait selection indexes.

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ГЕНЕТИЧЕСКИЕ РАЗЛИЧИЯ БАЗОВОЙ ПЛОТНОСТИ ДРЕВЕСИНЫ МЕЖДУ СЕМЕЙ ЕЛИ ОБЫКНОВЕННОЙ В РАЗЛИЧНЫХ СТАДИЯХ РОСТА ДЕРЕВЬЕВ

Д. Данусявичюс, Р. Габрилавичюс

Резюме

Устоновленны различия базовой плотности древесины между 31-ой семьей от свободного опыления (23 – летнего возроста) из 7 популяций ели обыкновенной Литвы. Базовая плотность древесины изучена для каждой части образцов, взятых возростным буровом, трех годичных кольцев методом вытеснения воды. Компоненты изменчивости, генетические коэффициенты корреляции и окружающей среды между плотностью древесины и диаметром дерева вычисленны отдельно для наружной , центральной и внутренней части образца. Полученные результаты показали, что внутрипопуляционная изменчивость плотности древесины больше, чем межпопуляционная. Адитивный коэффициент наследуемости базовой плотности древесины ($h_a^2 = 0,55$) больше, чем диаметра ($h_a^2 = 0,21$). Найвысший адитивный коэффициент наследуемости установлен в древесине, которая сформировалась во время интенсивного радиального прироста (9-14-летнего возроста). Корреляционные связи плотности древесины и диаметра отрицательны (r_G=-0,71). Имеются продуктивные семьи с плотной древесиной. По всей вероятности, такие семьи оканчивают рост позже (поэтому у них больший диаметр) и в тоже время используют блогоприятные климатические условия для формирования относительно больше поздней древесины. Такие генотипы имеют приоритет для включения их при создании селекционных популяций.

Ключевые слова: генетическая корреляция, ритм роста, наследуемость, *Picea abies*, диаметр дерева, качество древесины.