PHENOTYPIC CORRELATIONS BETWEEN JUVENILE-MATURE WOOD DENSITY AND GROWTH IN BLACK SPRUCE

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ABSTRACT

Phenotypic correlations between juvenile-mature wood density and growth were examined based on increment core samples from two plantations, a provenance test and a commercial plantation, of black spruce [*Picea mariana* (Mill.) B.S.P.]. The ring density components are significantly correlated to their respective ring width components: earlywood and ring densities are negatively correlated to ring and earlywood widths, respectively, while ring and latewood densities are positively correlated to latewood width. These hold true in both juvenile and mature wood. However, the correlation between ring width and ring density decreases with increasing age. This suggests that the correlation between wood density and growth rate tends to lessen as the tree ages. For each character, the correlation between juvenile and mature wood is significant but moderate. Thus, juvenile wood characters are only indicative of mature wood ones. On the other hand, trees with 12 growth rings from the pith were good predictors of wood density and radial growth of the whole tree. Individual growth rings from the juvenile-mature wood transition zone can be used to predict to some extent the wood density of either mature wood or the whole tree.

Keywords: Black spruce, juvenile wood, mature wood, ring density, ring width.

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INTRODUCTION AND BACKGROUND

With the evolution in forest management toward shorter rotations and the use of genetically improved planting stocks for growth and volume, wood quality has become a major concern in the forest products industry (Bendtsen 1978; Kellogg 1989; Vargas-Hernandez and Adams 1992; Zhang 1994; Zhang et al. 1996). Faced with this trend, tree breeders have realized that wood quantity and quality cannot be treated as independent factors and that wood quality traits should be incorporated into any tree breeding programs where wood is to be the end product (Keith and Kellogg 1986; Zobel and van Buijtenen 1989; Magnussen and Keith 1990). To implement this strategy and obtain optimal gains, it is essential to study the relationship between growth traits and wood density and other quality traits.

The relationship between growth rate and wood density has been studied intensively, but is rather controversial. Hence, some researchers have reported that in conifers, there is little relationship between ring width and wood density (Zobel and van Buijtenen 1989; Zobel and Jett 1995). However, others have stated that accelerated growth reduces wood density, especially in conifers other than hard pines (Zobel and van Buijtenen 1989). For spruces, many studies (Keith 1961; Olesen 1976; Beaulieu and Corriveau 1985; Corriveau et al. 1987, 1990, 1991; Rozenberg and Cahalan 1997) have also reported negative relationships between growth rate and wood density. In black spruce, the relationship is still contradictory. On one hand, Risi and Zeller (1960) showed that ring width and wood density of mature trees were not correlated. In Newfoundland mature stands, the relationship between growth rate and wood density was weak and dependent on location and environmental factors (Hall 1984). On the other hand, Boyle et al. (1987) found a negative correlation of wood density with both the tree height and the tree diameter in 15-yr-old trees. In addition, Zhang et al. (1996) reported that wood density was negatively related to growth rate in juvenile wood for a 15-yr-old plantation. Zhang (1995) recently examined the relationship of growth rate to wood density and mechanical properties in 16 mature tree species belonging to 4 distinct wood categories and reported negative correlations for softwoods. For plantation-grown white spruce, mature trees with high ring width led to low density, high juvenile wood content, and low strength properties, while trees with high ring density and moderate or slow growth rate led to satisfactory strength properties (Zhou and Smith 1991). From these results, relationship of growth rate to wood density in black spruce seems to be age-dependent. The negative relationship is statistically significant in young trees (Boyle et al. 1987; Zhang et al. 1996) but not significant in mature trees (Risi and Zeller 1960; Hall 1984). However, there is no information available on the evolution of this relationship with tree age.

Breeding programs usually take many years to complete every cycle. As a result, a selection at an early age would reduce the length of breeding cycle and be cost-effective. In fact, the age of selection, to a large extent, determines the length of breeding cycle and the amount of genetic gain that can be achieved per unit of time (Lambeth 1980; McKeand 1988). To pursue selection at an early age, it is important to understand the relationships between juvenile and mature wood at both genetic and phenotypic levels. Determining the extent of any relationship between juvenile and mature wood properties and between juvenile wood and values for the whole tree is of great interest and utility for breeding purposes (Zobel and Sprague 1998). In white spruce, Corriveau et al. (1987) reported moderately positive correlations (both phenotypic and genetic) between juvenile density and mature wood density. Since genetic correlations were of the same order and sign as the phenotypic correlations, they concluded that mass selection could be made at a younger age for genetic improvement of wood density or wood mass production in the species. In Norway spruce, Nepveu and Birot (1979) reported high simple and canonical correlations of juvenile wood density and growth with mature wood density and growth. Blouin et al. (1994) reported that mature and juvenile wood densities were highly correlated in the same species. The available information on the juvenile-mature wood relationships in pines was summarized by Zobel and Sprague (1998).

The juvenile-mature wood relationships are important not only for tree breeding purposes but also for end-use purposes. For the end users, the relationships between juvenile wood properties and those of whole trees are even more important than juvenile-mature wood relationships. Such relationships are needed for an early assessment of wood available at harvest time (Zobel and Sprague 1998).

This study was initiated to examine the phenotypic relationships between juvenile and mature wood characteristics in black spruce [*Picea mariana* (Mill.) B.S.P.], the most important commercial species in eastern Canada. Specifically, the objectives of this study were to: 1) examine the extent of phenotypic correlations among some intra-ring characteristics within and between juvenile and mature wood zones; 2) determine the age upon which mature wood density and growth rate could be predicted; and 3) evaluate the possibility of predicting total wood density from individual rings. Since there was no family structure for the plantations sampled, this study examined only phenotypic correlations.

MATERIALS AND METHODS

A provenance test was established in 1974 using a randomized complete 6-block design with 16-tree (4 × 4) square plots on 6 different sites distributed throughout the province of Quebec. Each square plot had trees spaced at 2.5 m × 3 m (Beaulieu et al. 1989). At the end of the 1995 growing season, 86 provenances and 12 trees per provenance from 3 blocks were sampled in the test site located at Mont-Laurier (lat. 46°36′N, long. 75°48′W, alt. 300 m). In this location, the average annual precipitation is 910 mm and the average annual temperature is 3.5°C. The length of the growing season varies from 170 to 180 days. The soil is deep alluvial sand. Moreover, at the end of the 1996 growing season, 944 trees were sampled from a 50-yr-old black spruce commercial plantation in Victoriaville (lat. 46°01′N, long. 72°33′W, alt. 90 m). The initial spacing for the plantation was 2 m × 2 m. The average annual precipitation in Victoriaville is 1,000 mm, and the average annual temperature is 4.5°C. The length of the growing season varies from 180 to 190 days.

From a constant compass direction, an increment core (6 mm in diameter) was taken at breast height from each tree selected in both plantations. All increment cores were wrapped in plastic bags and kept frozen until the sample preparation. The core samples were sawn to a 1.57-mm thickness longitudinally. The strips were then extracted with cyclohexane/ethanol solution 2:1 (v/v) for 24 h and with distilled water for another 24 h. X-ray densitometry was used to measure wood density. After conditioning, rings from the pith to the bark were scanned in the air-dry condition. Data on earlywood density (EWD), latewood density (LWD), and ring density (RD) of individual rings were obtained based on the intra-ring microdensitometric profiles. The same profiles served for determining earlywood width (EWW), latewood width (LWW), and ring width (RW) of individual rings. The boundaries delimiting earlywood and latewood (540 kg/m^3) and between the end of the latewood zone of a ring and the beginning of the earlywood of the following ring (450 kg/m^3) were determined experimentally by undertaking preliminary analyses of some ring density profiles of a subsample of cores. During the scanning, precautions were taken to eliminate incomplete or false rings, and rings with compression wood or branch tracers. The averages for each parameter were weighted on the basis of ring area. The latewood percentage (LWP) was calculated as the ratio of latewood width to ring width.

The normality of the experimental data was

TABLE 1. *Descriptive statistics for the Mont-Laurier provenance test and the Victoriaville commercial plantation.*

Plantation	RD (kg/m^3)	EWD (kg/m^3)	LWD (kg/m^3)	RW (mm)	EWW (mm)	LWW (mm)	LWP (%)
Mont-Laurier†							
Average‡	443	396	609	3.36	2.6	0.76	23.1
SD	37	2.7	24	0.63	0.63	0.26	7.9
CV (%)	8.4	6.8	4	18.7	24.2	34.2	34.2
Victoriaville†							
Average‡	441	375	623	2.51	1.9	0.60	27
SD	30	20	25	0.43	0.42	0.13	6.3
CV (%)	6.8	5.3	4	17.1	22.1	21.7	23.3
Victoriaville‖							
Average‡	440	382	625	3.34	2.59	0.75	23.9
SD	30	19	25	0.58	0.59	0.19	6.2
CV (%)	6.8	5	4	17.4	22.3	25.3	25.9

Abbreviations: RD, ring density; EWD, earlywood density; LWD, latewood density; RW, ring width; EWW, earlywood width; LWW, latewood width; LWP, latewood proportion; SD, standard deviation; CV, coefficient of variation.

† Whole disc average.

‡ Averages are weighted on ring area.

‖ Averages of the first 15 rings.

verified using the Wilk-Shapiro test (SAS 1988a). Correlation and regression analyses were conducted on the data using CORR and REG SAS procedures (SAS 1988b). Because of the large sample size, a conservative significance level ($\alpha = 0.01$) was set *a priori* for declaring results significant. Furthermore, a Bonferroni correction was applied to the significance level for taking account of the numerous simultaneous tests (Neter et al. 1985). Another set of analyses based on tree means was conducted to see how well average mature wood density (MWD) could be predicted from juvenile wood characters using stepwise regression analysis (SAS 1988b). The significant level for entry and staying in the model for any juvenile wood property was specified as $\alpha = 0.01$.

RESULTS AND DISCUSSION

The average wood density for the provenance test (443 kg/m^3) was similar to that of the commercial plantation (441 kg/m^3) despite differences in age (Table 1). Trees grown in these plantations had higher average wood density than that reported by Zhang and Morgenstern (1996) for a black spruce family test in New Brunswick (399 kg/m^3). As shown in Table 1, earlywood density for the provenance test was higher than that of the commercial plantation while the latewood density was lower. Even when both plantations were compared at the same age,[2] the weighted averages for earlywood and latewood densities were still statistically different ($P < 0.01$). The average ring, earlywood, and latewood widths for the provenance test were higher than those of the commercial plantation (Table 1). This is likely due to the age differences between both plantations: at the same age, the ring, earlywood, and latewood widths of both plantations were comparable.

Correlation among traits

For both plantations, ring density was positively correlated with earlywood and latewood densities (Table 2) and in both cases, the correlation between ring density and earlywood density was higher than between ring density and latewood density. Trees from the Victoriaville plantation with high earlywood density showed a tendency to exhibit high latewood density in the juvenile wood, whereas this relationship was not observed in mature wood (Table 3). On the other hand, ring den-

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[2] Means for the trees in the Victoriaville plantation were computed for the first 15 annual rings.

TABLE 2. *Correlation coefficients between all possible pairs of intra-ring traits for the two plantations. Upper part, Victoriaville commercial plantation; lower part, Mont-Laurier provenance test.*

	RD	EWD	LWD	RW	EWW	LWW	LWP
Ring density (RD)		0.87**	0.58**	−0.29**	−0.59**	0.73**	0.93**
Earlywood density (EWD)	0.91**		0.28**	−0.18**	−0.46**	0.67**	0.68**
Latewood density (LWD)	0.54**	0.43**		−0.24**	−0.39**	0.37**	0.50**
Ring width (RW)	−0.44**	−0.27**	−0.42**		0.95**	0.14**	−0.53**
Earlywood width (EWW)	−0.66**	−0.43**	−0.37**	0.91**		−0.18**	−0.75**
Latewood width (LWW)	0.69**	0.51**	0.43**	0.19**	−0.21**		0.71**
Latewood proportion (LWP)	0.88**	0.77**	0.48**	−0.35**	−0.68**	0.83**	

** Significant at $\alpha = 0.01$ after a Bonferroni correction. Hence, a P-value must be lower than or equal to 0.01/21 = 0.00048 to be declared significant.

sity was strongly correlated with latewood proportion in both juvenile and mature wood (Table 3). Thus, latewood proportion and earlywood density seem more important in determining overall wood density than latewood density. As shown in Fig. 1, the correlation between ring density and latewood proportion was almost constant (about 0.83) over the tree age. However, the correlation between ring density and earlywood density decreased consistently with age. Thus, latewood proportion seemed more important than earlywood density in determining mature wood density.

This study also disclosed a negative relationship between growth rate and wood density in black spruce at the phenotypic level (Tables 2 and 3). Indeed, the correlation between ring density and ring width was negative and statistically significant. Earlywood density was also negatively correlated with both ring width and earlywood width. But it was different for latewood, as the correlation between latewood density and latewood width is positive. These observations were in agreement with previous results (Zhang et al. 1996; Zhang 1998). Selection for high latewood width might have a positive effect on both wood density and tree growth because latewood width is positively correlated with ring density and ring width. These relationships remain to be confirmed at the genetic level. However, both genetic and phenotypic correlations between wood density and growth in black spruce were reported to be of the same order and sign in another study carried out on different sites (Zhang et al. 1996; Zhang and Morgenstern 1996).

The correlations of ring density with both ring and earlywood widths were weaker in mature wood (Table 3). This suggests that the negative effect of high radial growth on wood density decreases when the wood reaches maturity. The negative correlation was no longer statistically significant after 25 years of age (Fig. 2). These results were similar to those reported by Keith (1961), where a reduction in the correlation between growth rate and

TABLE 3. *Correlation coefficients between the different traits for the juvenile (upper) and mature (lower) wood in the Victoriaville commercial plantation.*

	RD	EWD	LWD	RW	EWW	LWW	LWP
Ring density (RD)		0.86**	0.59**	−0.33**	−0.53**	0.44**	0.91**
Earlywood density (EWD)	0.78**		0.31**	−0.31**	−0.42**	0.25**	0.61**
Latewood density (LWD)	0.47**	−0.01 n.s.		0.15**	0.02 n.s.	0.40**	0.50**
Ring width (RW)	−0.44**	−0.26**	−0.29**		0.95**	0.13**	−0.49**
Earlywood width (EWW)	−0.67**	−0.42**	−0.41**	0.96**		−0.20**	−0.74**
Latewood width (LWW)	0.71**	0.50**	0.39**	0.55**	0.32**		0.77**
Latewood proportion (LWP)	0.86**	0.65**	0.21**	−0.52**	−0.69**	0.34**	

** Significant at $\alpha = 0.01$ after a Bonferroni correction. Hence, a P-value must be lower than or equal to 0.01/21 = 0.00048 to be declared significant.
n.s. = not significant.

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