TRANSITION FROM JUVENILE TO MATURE WOOD IN BLACK SPRUCE (*PICEA MARIANA* (MILL.) B.S.P.)

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ABSTRACT

The radial patterns of several intra-ring traits in increment cores of black spruce (*Picea mariana* (Mill.) B.S.P.) plantation trees were modeled with polynomials to characterize their trends and to estimate the transition age from juvenile to mature wood. Wood density, ring width, latewood density, and latewood proportion were obtained by X-ray densitometry. Average radial trends were similar to those reported earlier in *Picea* species. For all traits measured, significant differences were found among diameter classes. Thus, the juvenile wood production period varies with growth rate. In addition, transition age for a given diameter class varies, depending on trait. Hence, transition age needs to be defined more precisely, basing it on biological processes.

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

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INTRODUCTION

Black spruce (*Picea mariana* (Mill.) B.S.P.) is widely distributed across North America. Its natural range extends from Newfoundland and northern Quebec, west across northern Canada to the west coast of Alaska, south to central British Columbia, south and east to central Minnesota, and east to Rhode Island and Massachusetts (Little 1979). Its wood is valuable as both lumber and pulpwood. The species is therefore of vital economic importance. In eastern Canada, important artificial regeneration programs and tree improvement research and breeding activities have been devoted to this species in recent years. Large-scale reforestation with fast-growing genotypes is likely to shorten rotations in the near future. This may lead to an increase in the amount of juvenile wood. This portion of the tree stem surrounding the pith is characterized by a progressive change in cell features and wood properties (Panshin and de Zeeuw 1980). In comparison with mature wood, juvenile wood is made of smaller and shorter tracheids with thinner walls and larger microfibril angles, higher spiral grain angles, lower holocellulose and alpha cellulose contents, higher lignin and hemicellulose contents, and lower strength properties (Di Lucca 1987; Yang and Benson 1997; Zobel and Sprague 1998).

Juvenile wood is not substandard for products such as newsprint and quality printing paper (Zobel 1984). However, it may cause serious problems for quality products, especially solid wood products. This is due to its low bending strength and dimensional instability upon drying (Bendtsen 1978; Bendtsen and Senft 1986; Zobel and Sprague 1998; Zobel and van Buijtenen 1989). One possible means to reduce the negative impact of juvenile wood is to select for an earlier transition age from juvenile to mature wood. Duration of the juvenile wood production period varies among families in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Abdel-Gadir and Krahmer 1993b; Vargas-Hernandez and Adams 1992) as well as among families (Loo et al. 1985) and provenances (Syzmanski and Tauer 1991) of loblolly pine (*Pinus taeda* L.). Environmental conditions and site quality have also been reported to affect transition age (Kennedy 1961; Larson 1962, 1969). Silvicultural practices such as initial spacing and pruning might also influence transition age, but reports on these matters are contradictory. Closer spacing increases natural pruning (Larson 1962). This results in less uniform wood in which the within-ring proportion of high density latewood increases rapidly with age. In contrast, crown recession is delayed in open-grown trees; this may extend the juvenile period and cause a more gradual transition from juvenile to mature wood. However, initial spacing was also reported not to affect the juvenile wood period in black spruce (Yang 1994) and Norway spruce (Kucéra 1994). In Douglas-fir, similar conclusions were reported since no evidence was found to support the concept that tree spacing and live-branch pruning have significant effects on the cambial age of transition from juvenile to mature wood (Gartner et al. 2002).

The pith-to-bark variation in wood traits such as density, fiber length, fibril angle, longitudinal shrinkage, ring width and latewood proportion is frequently described in terms of juvenile and mature wood zones and is used to estimate the transition age. This method of estimation of transition age is time consuming and wood destructive for most of the above traits. In addition, transition ages obtained from different wood traits may vary (Loo et al. 1985; Hodge and Purnell 1993; Yang and Benson 1997).

Several methods have been proposed to estimate transition age (Zobel and Sprague 1998). These include visual examination of pith-to-bark profiles over tree age (e.g., Clark and Saucier 1989), mathematical approaches such as the Gompertz function (Hodge and Purnell 1993), or segmented regression techniques (Abdel-Gadir and Krahmer 1993a; Loo et al. 1985; Sauter et al. 1999; Szymanski and Tauer 1991; Tasissa and Burkhart 1998). Other methods used curve-fitting routines that produce a unique polynomial model from each pith-to-bark profile (e.g., Olesen 1982). Iterative and constrained solutions were also used to determine the juvenile-mature wood demarcation in loblolly pine trees

(Tasissa and Burkhart 1998). However, few studies have tested for autocorrelation among the errors between successive rings within a core sample (Sauter et al. 1999). When regression analysis is applied to repeated measurements, the error terms cannot, in general, be assumed to be independent (Herman et al. 1998). If they are correlated, ordinary least squares yield unbiased but inconsistent estimates of the regression parameters, which leads to invalid inferences about the parameters (Johnston 1984). Since radial variation of wood properties is based on repeated tree ring measurements, it appears essential to model temporal autocorrelation. The objectives of this work were: 1) to characterize the average trend in growth and wood density of black spruce (*Picea mariana* (Mill) B.S.P.) as a function of age; and 2) to obtain consistent estimates of transition age from juvenile to mature wood.

MATERIALS AND METHODS

A total of 934 trees from a 50-year-old black spruce commercial plantation established at Victoriaville (lat. 46°01′N, long. 72°33′W, elev. 90 m) were sampled from five diameter classes (10, 12.5, 15, 17.5, and 20 cm). Spacing in this plantation was 2 m × 2 m. Average annual precipitation in the plantation site is 1000 mm and average annual temperature is 4.5°C. The length of the growing season varies from 180 to 190 days.

From a constant compass direction, increment cores 6 mm in diameter were taken at breast height from the sampled trees. Coring was done in the south section of the sampled stems. Each increment core was wrapped in a plastic bag and kept frozen until preparation. After air-drying, cores were sawn to 1.57 mm in thickness, extracted with a cyclohexane/ethanol solution 2:1 (v/v) for 24 h, and then in distilled water for another 24 h. Rings were scanned from pith to bark by X-ray densitometry in air-dry conditions. Earlywood (EWD), latewood (LWD) and ring (RD) densities, earlywood (EWW), latewood (LWW), and ring (RW) widths were computed from intra-ring microdensitometric profiles. Ring area was calculated from ring width and circumference data. The boundaries between earlywood and latewood (540 kg/m^3) within each ring and between rings (450 kg/m^3) were determined experimentally from preliminary analyses of several ring density profiles of a subsample of cores according to the procedure described by Parker et al. (1980). Incomplete or false rings as well as rings with compression wood or branch tracers were eliminated from the analysis. The X-ray source had sufficient resolution to measure annual rings 1 mm thick or more (Josza et al. 1987). A limited number (less than 0.5%) of annual rings were less than 1 mm thick. In such cases, the X-ray densitometer reading program could not identify the transition zone from earlywood to latewood or the end of the ring. In these cases, characteristics were measured from a computer screen image, and only data on whole-ring width and density were used in the analyses; the corresponding data on earlywood and latewood widths and densities were considered to be missing.

Radial patterns of wood density, ring width, and latewood density and latewood proportion were modeled using third- or fourth-order polynomials, depending on trait. Transition ages from juvenile to mature wood were estimated from each trait as the age at which the fitted functions reached either a minimum or a maximum, depending on the property studied. This involved setting the derivative of the third- or fourth-degree function equal to zero and solving for age. For third-degree polynomials, two solutions were obtained in each case but only one was of biological interest and retained. For fourth-degree polynomials, three solutions can be obtained and again in each case only one was of biological interest and was retained. Higher polynomial degrees (up to six) were tested. However, except for ring width, no differences were detected between the transition ages as estimated from the minimum or the maximum of interest derived from the various degrees of the polynomial models. Correlation among the errors from successive rings on the same core was incorporated into the model. Since the first and second annual rings from the pith could not be scanned from many samples during X-ray measurements, data from these rings were excluded from the analyses. All trees had at least 25 annual rings, and data beyond the twenty-fifth annual ring were eliminated from the analyses. Data therefore included 23 repeated measurements from each tree in each diameter class.

Using the third-degree polynomial model, the mean of each trait, as a function of cambial age, was modeled as follows:

$$T_{ij} = \mu + \rho_i + \beta_j A_{ij} + \gamma_j A_{ij}^2 + \delta_j A_{ij}^3 + e_{ij} \qquad (1)$$

Using the fourth-degree polynomial model, the mean of each trait, as a function of cambial age, was modeled as follows:

$$T_{ij} = \mu + \rho_i + \beta_j A_{ij} + \gamma_j A_{ij}^2 + \delta_j A_{ij}^3 + \lambda_j A_{ij}^4 + e_{ij} \qquad (2)$$

where T_{ij} is the mean of the trait in the j^{th} ring from the core samples of the trees within diameter class i (i = 1, . . . , 5; and j = 1, . . . , 23); μ is an overall effect; ρ_i is the effect of the i^{th} diameter class; A_{ij} is age of the j^{th} ring from the trees of diameter class i; β_j, γ_j , δ_j, and λ_j are parameters to be estimated; e_{ij} is the random error term associated with the j^{th} ring from the trees of diameter class i, and it is assumed that $\mathbf{e}_i \sim N(0, \Sigma)$, where the bold character for $\mathbf{e}_i$ denotes the 23 × 1 vector of $\{e_{ij}\}$ specific to diameter class i, and Σ is a 23 × 23 symmetric positive definite matrix with variances on its main diagonal and covariances elsewhere.

The model was fitted using the MIXED procedure of SAS/STAT® (SAS Institute, Inc. 1997; Littell et al. 1996). The model was reduced to its most parsimonious form. The structure was investigated through a hierarchical series of variance-covariance structures. Each structure in the hierarchy was compared with the previous one through a likelihood-ratio test. First, it was assumed that it had no special structure except for symmetry. This involved the estimation of (23)(22)/2 = 253 variance-covariance parameters. This structure was then simplified to a Toeplitz structure with 22 parameters (Littell et al. 1996). The Toeplitz covariance structure is such that the variances of errors in models (1) or (2) are assumed constant over cambial ages, the covariance between the errors on adjacent rings is assumed constant, the covariance between the errors for two rings apart is also assumed constant, but distinct from that for adjacent pairs, and so on. This means that the variances and covariances in each matrix (Σ) are assumed constant along any diagonal or subdiagonal, distinct from one diagonal or subdiagonal to another, and not constrained to be larger for adjacent rings than for more remote ones. Reduction of the Toeplitz to even simpler structures such as AR(1) (Littell et al. 1996) was attempted, until, ultimately, complete independence among errors and homogeneity would be assumed, and would be specified as a diagonal matrix with constant variance for all rings and zero covariance for all pairs of rings. This last structure is equivalent to the current practice that ignores autocorrelation among the errors on successive rings. The reduction process was stopped whenever the likelihood-ratio test for goodness of fit of the model with the most constrained covariance structure between the two being compared was significant. The variance-covariance matrix from the previous step was then selected (α = 0.05).

The jackknife procedure was used to determine the standard deviation and the interval of confidence for the transition age in each diameter class. In this procedure, one tree or a group of trees from each diameter class is eliminated one by one and the new data set submitted to the same procedure described above in order to estimate the transition ages. When this sequential process is completed, the average transition age as well as its standard deviation and interval of confidence are computed.

RESULTS AND DISCUSSION

Radial variations of intra-ring properties

The average profiles of each intra-ring trait over all sampled trees are shown in Figs. 1 to 4. The ring density of juvenile wood is high near the pith and decreases rapidly to reach a minimum in the transition zone leading into mature wood, where a slow but steady increase is observed (Fig. 1). This pattern of variation is of type II (Panshin and de Zeeuw 1980) and is similar to those previously reported for black

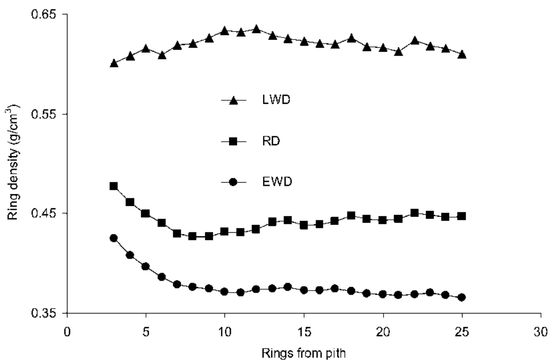

FIG. 1. Mean black spruce ring density (RD, g/cm^3), earlywood density (EWD, g/cm^3), and latewood density (LWD, g/cm^3) by ring number (from pith). Standard errors of the means vary from 0.003 to 0.008 for RD, from 0.002 to 0.006 for EWD, and from 0.003 to 0.011 for LWD.

spruce (Villeneuve et al. 1987), white spruce (*Picea glauca* (Moench) Voss) (Corriveau et al. 1990), and Norway spruce (*Picea abies* (L.) Karst.) (Blouin et al. 1994; Kucéra 1994). Earlywood density (Fig. 1) also decreases rapidly from its maximum near the pith to a low value in the transition zone, but this density slowly decreases with age thereafter. Latewood density (Fig. 1) increases to a maximum at about ring 12 and then decreases slowly through the outer rings. Ring and earlywood widths (Fig. 2) increase rapidly in the initial rings, reach their maximums at about the seventh ring, and then decrease rapidly. Mean latewood width decreases slowly but constantly between the third and fifteenth rings, and is almost constant in the last ten rings. These patterns of variation are similar to those reported for white spruce (Corriveau et al. 1990).

Ring area is low near the pith, increases steadily to reach a maximum at about ring 10, and then decreases steadily outwards (Fig. 3). This pattern of variation is similar to that of ring width except that the maximum width is reached later. This is due to the fact that the decrease in the ring width beyond the maximum is not due to a decrease in cambial activities but to an increase in tree circumference with increasing age.

The radial density pattern can be explained by variations in earlywood density (Fig. 1) and latewood proportion (Fig. 4). Earlywood is the predominant ring component. The pattern of variation of its density in the juvenile phase is similar to that of ring density (Fig. 1). As with ring density, the latewood proportion of tree rings (Fig. 4) is high near the pith (more than 30%), decreases to a minimum at the seventh ring, and then increases outward from the pith. Since latewood density is very high compared with that of earlywood (Fig. 1), an increase of its proportion within an annual ring directly affects ring density. This could partially explain the steady increase of wood density in mature wood. Several factors have been proposed to explain the patterns of variation in ring density, earlywood den-

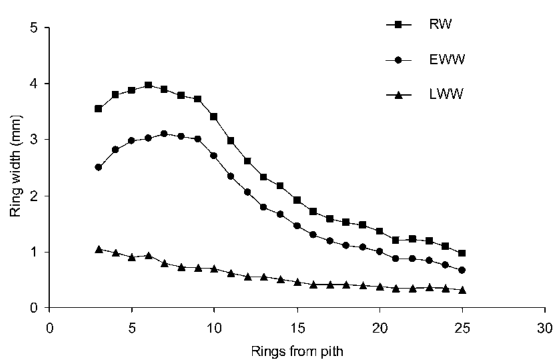

FIG. 2. Mean black spruce ring width (RW, mm), earlywood width (EWW, mm), and latewood width (LWW, mm) by ring number (from pith). Standard errors of the means vary from 0.040 to 0.117 for RW, from 0.032 to 0.115 for EWW, and from 0.012 to 0.049 for LWD.

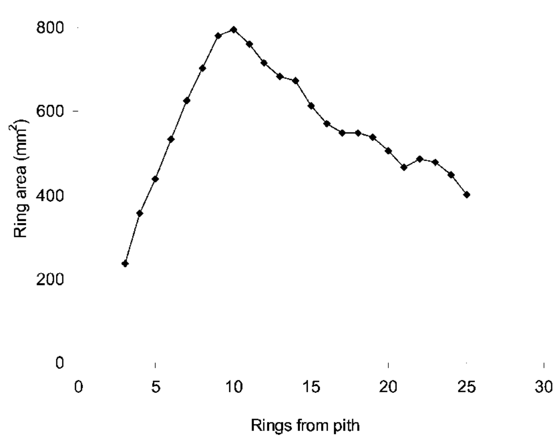

FIG. 3. Mean black spruce ring areas (mm^2) by ring number (from pith).

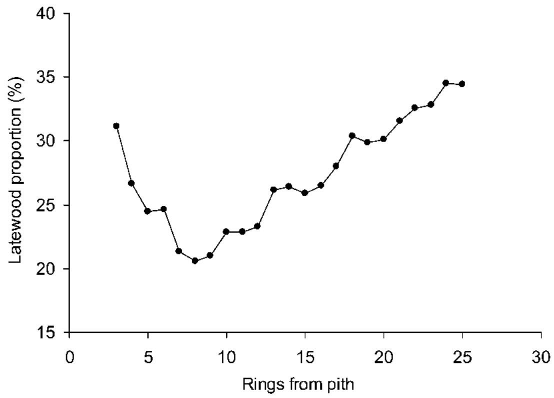

FIG. 4. Mean black spruce latewood proportion (LWP, %) by ring number (from pith).

sity, latewood proportion and ring width variations, including vegetative competition among trees of the same stand (Larson 1962, 1969), aging of the cambium (Larson 1962; Panshin and de Zeeuw 1980; Olesen 1982), and climatic conditions (Kennedy 1961; Larson 1962; Olesen 1977). Competition for space among trees of the same stand results in natural pruning of the lower part of the crown and establishment of a hormonal differential which affects xylem development (Larson 1962, 1969). To a large extent, crown size and structure govern the patterns of variation in latewood proportion, ring density, and width of the wood in the bole (Larson 1962). Initial decreases in both latewood proportion and ring densities are associated with the presence of live branches that remain photosynthetically active for a few years. As a result, earlywood production is prolonged, transition from juvenile to mature wood is more gradual, and the latewood proportion is smaller. In mature, unthinned plantations, however, trees are generally grown in conditions favorable to natural pruning. A rapid increase in latewood proportion with increasing age then characterizes wood production (Larson 1962). This phenomenon was observed in the studied plantation where latewood proportion increased rapidly with cambial age in mature wood (Fig. 4).

Aging of the cambium also plays an important role in the radial variations of wood density, latewood proportion, and ring width (Larson 1962; Panshin and de Zeeuw 1980). It results in systematic variation in the secondary tissues, which affects both the anatomical and physico-mechanical properties of wood. At early ages, more earlywood tracheids are produced. These cells are large in diameter and thin-walled (Larson 1960, 1962). This explains the initial increases of ring width, earlywood width, and ring area and the decreases in earlywood and total ring densities. As cambium ages, cell diameter decreases and cell-wall thickness increases (Larson 1960). These result in a decrease in ring width and ring area. Such effects also explain the steady increase in wood density observed in mature wood (Fig. 1).

Radial variation in growth and density showed opposite trends. This is because conditions favorable to fast growth usually lead to lower wood densities. When expressed as a ratio (density/width), these two traits follow a quadratic curve (Fig. 5). In good agreement with previous studies on white spruce (Wang and Micko 1983; Corriveau et al. 1990), this curve is characterized by a rapid decrease followed by a period of stabilization and then by a rapid constant increase. The initial decrease in the density/width ratio is characteristic of the juvenile wood period, the ensuing stabilization is related to the transition period, and the following rapid increase, to the formation of mature wood (Corriveau et al. 1990).

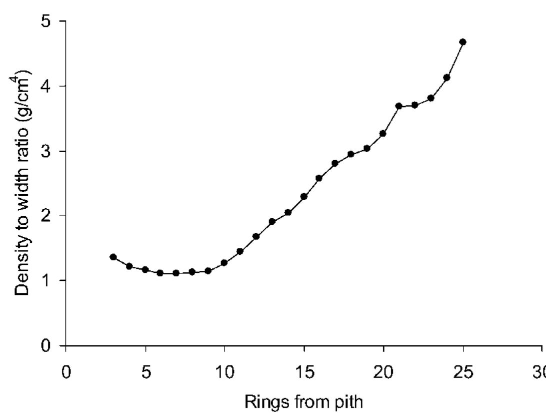

FIG. 5. Mean black spruce ring density to ring width ratios (g/cm^4) by ring number (from pith).

TABLE 1. *Analysis of covariance of black spruce wood density, latewood density, latewood proportion, and ring width (Model (1) or (2)).*

	Ring density			Latewood density			Latewood proportion			Ring width		
Source	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value	df	F-value	p-value
Diameter class	928	34,619.8	0.0001	925	104,212.3	0.0001	928	243.1	0.0001	927	6,434.5	0.0001
Age within class	926	149.8	0.0001	908	4.87	0.0002	913	162.2	0.0001	927	1,642.8	0.0001
Age^2 within class	924	9.1	0.0001	915	195.6	0.0001	912	163.4	0.0001	914	15.7	0.0001
Age^3 within class	914	341.7	0.0001	900	34.10	0.0001	906	112.3	0.0001	913	73.3	0.0001
Age^4 within class	922	101.1	0.0001	—	—	—	—	—	—	—	—	—

Diameter class effect, linear age effect within class, quadratic age effect (Age^2) within class, cubic age effect (Age^3) within class and quartic age effect (Age^4) within class corrrespond respectively, to ρ_i, $\beta_j A_{ij}$, $\gamma_j A_{ij}^2$, $\delta_j A_{ij}^3$, and $\lambda_j A_{ij}^4$ in model (1) or (2).

Transition from juvenile to mature wood

The radial profiles of ring density, ring width, latewood density, and latewood proportion were used to estimate transition age according to either model (1) or (2). The variance-covariance structure of the error vector could not be reduced at all, and models had to be fitted with the unstructured version of $\mathbf{\Sigma}$. This means that it is important to account not only for autocorrelation among errors on successive rings from the same core sample, but also for variance heterogeneity. Otherwise, estimates of the variances of any parameter estimate are biased. Thus, analyses of covariance are based on model (1) or (2), with an unstructured variance-covariance matrix for the error vectors. The effect of diameter class on ring density, latewood density, latewood proportion and ring width was significant (Table 1). The significance of the linear, quadratic, and cubic effects of age was also tested for all traits. Significance of the quartic effect of age was tested for ring density only. The linear, quadratic, and cubic effects were significant for all traits, and the quartic effect was significant for ring density.

Typical patterns of variation estimated from (2) for ring density and (1) for latewood proportion are shown in Figs. 6 and 7, respectively. From ring density (Table 2), fast-growing trees tend to produce wood with both low density and high transition ages. For example, using ring density, the transition age for trees belonging to the 10-cm-diameter class was 7.5 years (6.9 to 8.2 years) compared to 9.1 years (8.6 to 9.5 years) for trees belonging to the 20-cm-diameter class (Table 2). The differentials between juvenile and mature ring densities and latewood proportions are higher in fast-growing trees (Table 3). On the other hand, slow-growing trees have denser and more uniform wood with low differentials between juvenile and mature wood densities. The juvenile to mature wood transition age is lower in slow-growing trees than in fast-growing ones. Within the groups of fast-growing trees (diameter classes 17.5 and 20 cm), transition age did not vary much (Table 3).

Transition ages estimated from ring density (Fig. 6) and latewood proportion (Fig. 7) profiles are congruent (Table 2). This might be explained by the fact that these two traits are closely related (Koubaa et al. 2000, 2003). Latewood density generally gave higher transition age estimates than those from latewood proportion and ring density (Table 2).

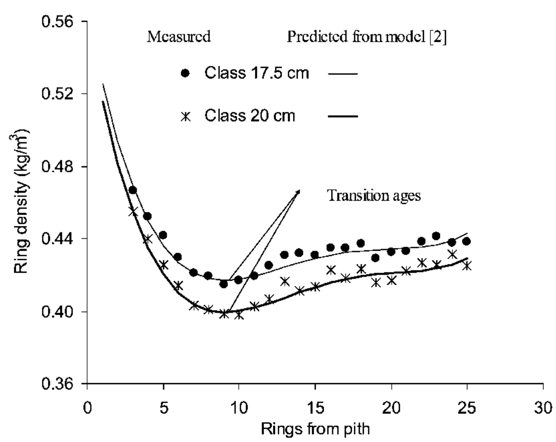

FIG. 6. Mean black spruce ring density (g/cm³) by ring number (from pith) as estimated from model (2) for the two diameter classes and the estimated average over these diameter classes.

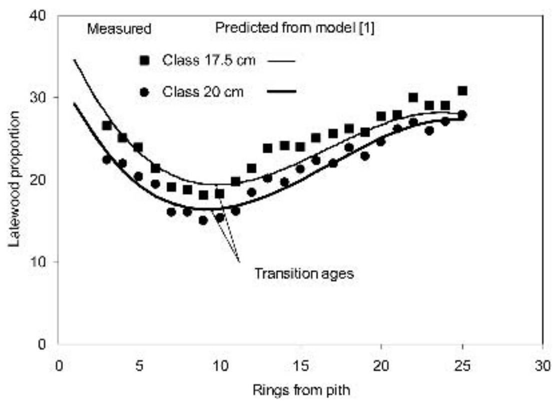

FIG. 7. Mean black spruce latewood proportion (%) by ring number (from pith) as estimated from model (1) for two diameter classes of the Victoriaville plantation, and the estimated averages of these diameter classes.

Transition ages estimated using latewood proportion and latewood density profiles were generally lower for slow-growing trees than for fast-growing trees. Thus, fast growth appears to be associated with a longer period of juvenile wood proportion. In mature wood, the weighted average latewood density does not seem to vary with growth rate (Table 3). However, in juvenile wood and transition phases, latewood density showed a slight decrease with increasing growth rate. The latewood proportion decreased with growth rate in both juvenile wood and mature wood. This trend is similar to that of ring density.

These results suggest on one hand that fast growth in black spruce is generally associated with low density, low latewood proportion, non-uniform wood, and high juvenile wood proportion. On the other hand, slow-growing trees have generally high density, high latewood proportions, uniform wood, and low juvenile wood proportion.

Transition ages estimated from ring width models are not congruent with those estimated from any of the other traits measured. Both the third and the fourth degree polynomial models showed a lack of fit in the initial portion of the curve (data from 3 to 10 rings from pith), and the solution for the initial maximum was outside the age domain (Table 2). Thus, it seems that polynomial models of the third degree might not be a good approach for estimating the transition age from ring width data. Higher polynomial models

TABLE 2. *Transition ages estimated from model (1) or (2) and 95% confidence intervals (in parentheses) as computed using the Jackknife procedures.*

Transition age	Diameter class (cm) 10	12.5	15	17.5	20
			Ring density		
Model (2)	7.5	8.2	8.4	9.0	9.1
Jackknife procedure	7.5 (6.9–8.2)	8.2 (7.6–8.7)	8.4 (8.2–8.7)	9.0 (8.6–9.4)	9.1 (8.6–9.5)
			Latewood proportion		
Model (1)	6.0	8.2	8.7	9.3	9.2
Jackknife procedure	6.4 (3.4–9.4)	8.1 (7.5–8.8)	8.7 (8.4–8.9)	9.3 (8.9–9.6)	9.2 (8.6–9.8)
			Latewood density		
Model (1)	11.2	12.2	12.8	12.1	—‡
Jackknife procedure	11.1 (10.1–12.1)	12.2 (11.1–13.2)	12.8 (12.1–13.4)	12.1 (10.9–13.2)	—‡
			Ring width		
Model (1)	−10.6	−1.8	0.1	−0.9	0.9
Jackknife procedure	−8.3 (−22.2–5.6)	−1.6 (−5.0–1.7)	0.2 (−1.6–2.1)	−0.6 (−4.3–3.2)	1.4 (−2.8–5.6)
			Ring width		
Model (1)	24.3	24.0	23.6	23.7	24.2
Jackknife procedure	24.3 (23.2–25.4)	24.0 (23.4–24.6)	23.6 (23.3–23.8)	23.6 (23.1–24.2)	24.2 (23.3–25.0)

‡ No solution was found from the model.

TABLE 3. *Average ring density, ring width, latewood proportion, and latewood density for juvenile and mature wood zones.*

Property	Diameter class (cm)				
	10	12.5	15	17.5	20
	Juvenile wood (rings 3 to 6)				
Ring density (g/cm^3)	0.462	0.461	0.452	0.445	0.434
Latewood density (g/cm^3)	0.613	0.607	0.609	0.602	0.599
Latewood proportion (%)	26.5	27.1	25.4	23.7	20.8
Ring width (mm)	3.42	3.82	4.22	4.61	4.95
	Mature wood (rings 14 to 25)				
Ring density	0.461	0.452	0.444	0.433	0.418
Latewood density	0.622	0.624	0.626	0.623	0.622
Latewood proportion	34.1	31.5	28.9	25.4	22.7
Ring width	1.15	1.40	1.65	1.94	2.26

were tested and the lack of fit persisted. The intervals of confidence for the minima estimated from ring width profiles were also very large compared to the intervals of confidence estimated from other traits (Table 2). Thus, all these observations suggest that ring width is not a good criterion to define the juvenile-mature wood transition as discussed above. This conclusion, however, contrasts with a previous recommendation by Yang and Benson (1997). Indeed, these authors suggested that for plantation-grown trees, ring width was a better characteristic than wood density on which to base the estimation of transition age from juvenile to mature wood. The use of other growth alternatives such as ring area might give better estimates. In this study, however, ring area was tested and the problems of autocorrelations were persistent and could not be resolved with any of the tested statistical procedures.

The first solution of the derivatives of the fitted third-degree polynomial within the domain of age corresponds to the point at which minimum ring width is reached. For all diameter classes, this corresponds to about age 24 (Table 2). However, estimating transition age as this minimum ring width is not very promising. Indeed, ring width is not likely to increase or remain constant but will continue to decrease in this phase of tree growth, because tree circumference increases, competition among tree crowns starts to operate, and cambium ages (Panshin and de Zeeuw 1980). The combination of the increasing circumference and aging of the cambium will be translated in a continuing decrease in ring width. Thus, the use of older material with more annual rings might result in higher transition ages. Estimating transition age as the point at which two sections of segmented regression lines intersect yields estimates with very large variances unless the intersection point is very sharply defined (Abdel-Gadir and Krahmer 1993a; Loo et al. 1985; Szymanski and Tauer 1991).

For all studied traits, the jackknife procedure was used to estimate the confidence intervals of the estimated transition ages. Compared to other techniques, such as the segmented regression procedures (Sauter et al. 1999), the polynomial models and the jackknife procedure gave smaller confidence intervals.

Implications of the results

In contrast to previous studies, this work presented estimates of the juvenile to mature transition ages from various wood traits, taking into account the possible correlation between successive readings on the same core samples. Since the estimate of the transition age is not independent of the trait examined, it is more appropriate to estimate transition age on the basis of traits having a direct impact on wood properties and processing behavior. Wood density is a character related to most wood physical, mechanical, and even processing properties. Thus, from the end user's point of view, estimating the juvenile to mature wood transition age from wood density profiles seems more appropriate than using any other trait to do so. Furthermore, wood density and related traits are known to be under strong genetic control (Zobel and van Buijtenen 1989) and are amenable to selection and breeding. Results of this study also provide some useful information for breeding strategies. Breeding for growth or wood quality is a controversial matter, and many approaches have been suggested (Zobel and van Buijtenen 1989). Among the most valid approaches is the one proposed by Beaulieu and Corriveau (1985), and Corriveau et al. (1990) for white spruce, which consists of selecting for high wood density within populations, families or provenances with high growth rate. If valid, this approach (Zobel 1997) should help maximize wood production with acceptable, or even superior, wood density. However, this strategy could result in the production of nonuniform wood, or wood with a high proportion of juvenile wood. Thus, integrating other criteria into this approach would be beneficial for wood quality. Using the radial profiles of wood density, it would be possible to identify black spruce individuals, families, or provenances with high growth rate, high density, low juvenile wood proportion, and uniform wood. A selection index integrating all these traits would certainly help develop black spruce varieties possessing all the desired traits. This approach would be particularly useful to improve wood properties of fast-grown plantation trees known to have a high proportion of juvenile wood, low wood density, and poor mechanical and processing properties compared with trees from natural forests (Bendtsen and Senft 1986; Zobel and Sprague 1998).

CONCLUSIONS

The radial profiles of wood density and growth components of black spruce are typical of those reported previously for *Picea* species. Using these profiles, estimates of the juvenile to mature wood transition ages were obtained from various traits taking into account the correlation between successive readings on the same sample. The estimated transition age depended on the trait examined and among diameter classes. From end-users' perspective, wood density is an appropriate trait to determine the transition from juvenile to mature wood. This study further indicated that selection for a single trait such wood density or growth rate might result in wood with characteristics not desirable by some end-users. Using a selection index integrating more than a single trait would be beneficial for the forest industry.

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