EFFECTS OF CAMBIAL AGE AND STEM HEIGHT ON WOOD DENSITY AND GROWTH OF JACK PINE GROWN IN BOREAL STANDS

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Abstract. Jack pine specimens were examined for longitudinal and radial variations in selected wood quality parameters. Wood density and ring width of cross-sections were measured systematically from pith to bark along the merchantable stem using X-ray densitometry. Effects of cambial age and stem height were analyzed using a linear mixed model with two levels of nesting. A strong interaction between the two factors was found in corewood. Tree individual variation increased with cambial age for all studied wood properties and was larger in earlywood than in latewood. Radial patterns in the studied parameters closely approximated published ones in the lower stem but lessened considerably with increasing stem height. By contrast, longitudinal patterns reversed with cambial age in earlywood. High coordination was found between longitudinal patterns in corewood and radial patterns in the stem base, indicating a similar maturation pattern in the apical meristem and cambia. However, with increasing cambial age, this high coordination disappeared rapidly.

Keywords: Jack pine, wood density, ring width, longitudinal variation, radial variation.

INTRODUCTION

Jack pine (*Pinus banksiana* Lamb.) is the most widely distributed pine species in the North American boreal forest, attaining 21-m height and 20 – 30 cm diameter at maturity. Economically and ecologically, it is one of the most important tree species in eastern North America.

In recent decades, wood demands have increased, whereas available land bases for wood production have decreased. Consequently, the forest industry must improve its productivity (Kennedy 1995). Intensive plantation management combined with the use of fast-growing species is one possible solution. Maximizing the value of harvested wood stems is another. The large variation in within-stem wood properties may provide opportunities to improve the value of each piece of wood produced through appropriate categorization for specific end use (Burdon et al 2004; Xu and Walker 2004). Wood density and ring width are the most commonly used indicators of wood material quantity

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and quality. Wood density is considered the best single index for overall wood quality as well as pulp yield and quality (Bendtsen 1978), whereas ring width is related to the volume of wood produced as well as end product uniformity.

In North America, detailed radial variations in wood density are known for most commercial tree species (e.g., Panshin and de Zeuuw 1980; Jozsa and Middleton 1994; Kennedy 1995). For hard pines such as jack pine, wood density increases rapidly to an asymptote from the pith outward (Zobel and van Buijetenen 1989). Most of these measures were performed at breast height. There are relatively few data available on radial variation in wood density at different stem heights. Furthermore, previous results have often been contradictory, even for a same species. Spicer and Gartner (2001) found that wood density and ring width patterns were essentially the same along the stems of 35-yr-old Douglas-fir trees [*Pseudotsuga menziesii* var. menziesii (Mirb.) Franco], whereas Jozsa and Brix (1989) reported that radial patterns generally lessened with stem height for similar-aged trees.

The best known longitudinal variation is a decreasing tendency in whole disk density with stem height (Singh 1984, 1986). However, this is mainly attributable to the increasing proportion of juvenile wood stem upward (Zobel and Sprague 1998). Megraw (1985) found that longitudinal wood density patterns in loblolly pine (*Pinus taeda* L.) were dependent on radial position or cambial age. Recent studies have shown clear longitudinal patterns in mean annual ring density (AD) and annual ring width (AW), although patterns can vary considerably. For example, in Norway spruce [*Picea abies* (L.) Karst.], Mäkinen et al (2007) found no significant height effect on AD, although an increasing trend was reported by Molteberg and Høibø (2007) and Jyske et al (2008). Alteyrac et al (2005) also reached the same conclusion for black spruce [*Picea mariana* (Mill.) B.S.P.].

All these studies showed that wood properties vary systematically with stem position. However, the patterns are highly variable and sometimes contradictory, even for a same species. Therefore, to effectively categorize wood, detailed information on the within-stem position of the wood and the growth history of trees is needed. Accordingly, intensive studies on within-stem wood property changes have been conducted on major commercial conifer species in eastern Canada (e.g., Koga and Zhang 2004; Alteyrac et al 2005). Nevertheless, information on detailed within-tree variation in jack pine is still lacking (Schneider et al 2008).

The specific objectives of this study were to (1) examine the radial patterns of specific wood properties along stem height; (2) examine vertical patterns with cambial age; and (3) determine variation dependencies between earlywood and latewood.

MATERIALS AND METHODS

Sample trees were collected from five mature jack pine stands along an east–west transect in the Abitibi region in the province of Quebec, Canada (Table 1): Castagnier-nord, Duprat-est, Dollard (DL), Cléricy, and Figuery. The regional climate is continental with a mean annual temperature of 1.2°C and an average total annual precipitation of 918 mm. All stands were established on well-drained coarse-textured glaciolacustrine upland soils. Site productivity, based on the site index at 50 yr, was intermediate for the region (Béland and Bergeron 1996). All sites are pure, even-aged jack pine stands regenerated naturally after fire. No silvicultural treatments were reported on the sites before 1998. Starting in 1999, thinning and fertilization trials were initiated. Data beyond 1998 was not considered in this study.

For each site, 12 trees were randomly selected from the dominant trees in the buffer zones of the plots. One tree (DL 64) from the DL site was excluded from the analysis as a result of the presence of large fire scars. For each sample tree, diameter at breast height, total height, and live crown length were measured (Table 1). The crown base was defined as the lowest

Table 1. *Stands and tree characteristics.*

	Castagnier-nord	Duprat-est	Dollard	Cléricy	Figuery
			Stand characteristics		
Latitude (north)	48°48′	48°23′	48°20′	48°18′	48°26′
Longitude (west)	77°55′	79°07′	77°03′	78°39′	78°12′
Altitude (m.a.s.l.)	346	352	362	324	366
Stand age	41 (40 – 41)[c]	47 (46 – 48)	47 (44 – 49)	64 (61 – 65)	75 (71 – 76)
Site index at age 50[a]	17.3	16	15.9	15.6	15.1
Density of merchantable stems[b]	1654 (1416 – 1892)	1950 (1800 – 2100)	1758 (1584 – 1931)	1758 (1499 – 2018)	1227 (996 – 1458)
			Tree characteristics		
No. of sampled trees	12	12	11	12	12
Tree height (m)	16 (14.5 – 17.0)	16 (15.2 – 17.2)	16 (12.4 – 17.3)	18 (14.7 – 21.6)	19 (17.0 – 21.5)
Diameter at breast height (cm)	18 (14.3 – 21.1)	18 (14.1 – 21.2)	17 (13.5 – 19.2)	20 (16.3 – 24.4)	22 (18.9 – 25.4)
Crown ratio (%)[d]	41 (36.2 – 49.3)	44 (31.4 – 50.7)	45 (35.2 – 63.8)	38 (30.8 – 44.3)	37 (30.7 – 46.8)

[a] Average height of dominant trees at 50 yr.
[b] Number of stems per hectare with diameter greater than 10 cm.
[c] Data range is given in parentheses.
[d] The crown length was defined as the difference between tree top to the lowest whorl of crown that has at least one living branch and is not separated by more than one dead whorl.

whorl of crown with at least one living branch that is separated from other living whorls by no more than one dead whorl. Disks were taken at 0, 0.3, 0.6, 1.0, 1.3, and 2 m stem height and at every meter thereafter up to the tree top. All disks were air-dried for several months. Stem height for each age for each tree was estimated by linear extrapolation according to the procedure described by Carmean (1972) using WinSTEM (Regent Instruments Inc., Quebec, Canada).

Wood density was measured on disks taken at 0.3, 1.3, 3, and every 2 m thereafter up to the 10-cm tree top. Thin sections approximately 20-mm wide and 2-mm thick were sawn from each disk from pith to bark. Wood density from pith to bark was obtained in 40-μm resolution using X-ray densitometry (QTRS-01X Tree Ring Analyzer; QMS Inc., Knoxville, TN). From the wood density profiles, average densities were calculated for each annual ring (AD), earlywood (ED), and latewood (LD). Earlywood and latewood demarcation were determined for each annual ring according to the maximum derivative method using a six-degree polynomial (Koubaa et al 2002). The density of the demarcation point of the polynomial was defined as the transition density (TD). From the same density profiles, annual ring width (AW), earlywood ring width (EW), and latewood ring width (LW) were determined. Latewood percentage (LP) was calculated as the ratio of LW to AW. The presence of false and missing rings was detected from AW chronologies using crossdating. Crossdating quality was numerically verified using COFECHA (Holmes 1983). Tree rings with compression wood or branch traces were eliminated from the analysis. A total of 16,805 tree rings from 455 disks taken from 59 trees were analyzed in this study.

Because wood properties strongly depend on tree age, they were compared across the study sites for a common period only corresponding to the youngest site. The period was a cambial age (CA) of 40, 37, 34, 30, 25, 21, 16, and 11 yr from stem base to the top [0.3, 1.3, 3, 5, 7, 9, 11, and 13 m in stem height (HT), respectively]. This common period was divided into three age periods for variance analysis: corewood (CA 2 – 11, HT 0.3 – 13 m), transition (CA 16 – 25, HT 0.3 – 7 m), and outerwood (CA 30 – 38, HT 0.3 – 1.3 m). For each period, CA and HT samplings were balanced across sites. Effects of CA and HT on the response variables were examined using a mixed-model approach with repeated measures (Littell et al 2006). The hierarchical effects of individual tree (TR) and site (ST) were accounted for using two nested levels, the TR effect being nested within the ST effect as follows:

$$Y_{ijkl} = \mu + a_i + h_j + (a^*h)_{ij} + s_k + t_{(l)k} + e_{ijkl} \quad (1)$$

where μ is the overall mean; a_i, h_j, and $(a{*}h)_{ik}$ are the fixed effects associated with the i^{th} cambial age, j^{th} stem height, and their interactions, respectively; s_k and $t_{(l)k}$ are the random effects associated with the k^{th} site and the l^{th} tree at the k^{th} site; and ε_{ijkl} is an error term. The random effects s_k and $t_{(l)k}$ are assumed to be normally distributed with zero mean and corresponding variances σ^2_k, and $\sigma^2_{(l)k}$, whereas the error term ε_{ijkl} has zero mean. Instead of assuming independent errors, we imposed a first-order autoregressive correlation structure.

We used the MIXED procedure of the SAS software (SAS 2004) to fit the model with a restricted maximum likelihood (REML) method. Degrees of freedom were determined using the Kenward-Roger method. The homogeneity and normality of residuals were checked to ensure that assumptions were met. We determined statistical significance (α=0.05) of fixed effects with the *F*-test. Variance components of random effects and their standard errors were expressed as a percentage of total variation of all random effects. We conducted Z-tests to determine whether the random effect significantly differed from zero. As a result of small site replications, the results of the Z-tests must be considered indicative only (Littell et al 2006).

Radial patterns were characterized quantitatively using pattern descriptors (Burdon et al 2004). Least squares (LS) means were calculated for CA 2, juvenile–mature wood transition age as defined by Koubaa et al (2005) (CA with the maximum or minimum value depending on the wood property), CA 20, and outerwood (>CA 30) using the following equation:

$$Y_{jkl} = \mu + h_j + s_k + t_{(l)k} + e_{jkl} \quad (2)$$

where e_{ijk} is an error term with a correlation between the j^{th} stem height in the l^{th} tree at the k^{th} site. Because heights were not evenly distributed, a spatial power function was used to model autocorrelation effects (Littell et al 2006). The Tukey-Kramer adjustment was used to test the difference between LS means ($p \leq 0.05$). We again used the SAS MIXED procedure to fit the models by REML using the previously described approach.

Some parameters such as TD, LD, and LW in 1.3, 3, 11, and 13 m in HT did not show any juvenile mature wood transition age before reaching the outerwood. For these parameters, LS means were calculated for CA 5.

The radial change was determined using linear regressions for the period from the juvenile–mature wood transition age to cambial age 30. For stem height above 7 m, in which cambial age is lower than 30, all available rings after the juvenile–mature wood transition age were used. If there was no transition age such as for TD and LD, the regression was performed at age 2 – 10 for all stem heights.

The longitudinal change rate was also determined using linear regressions performed over all available heights for each cambial age. This approach permits a direct comparison of overall changes in longitudinal patterns over CA for the given parameters.

RESULTS AND DISCUSSION

Average tree ring width of the sample trees was 1.96 mm and average wood density was 469 kg/m^3, of which 25% was latewood (Table 2). The AD reported here is consistent with the published data on jack pine (e.g., Hatton and Hunt 1990; Kang et al 2004). Average difference between ED and LD was 383 kg/m^3, or

Table 2. *Averages and coefficients of variation [in parentheses (%)] of ring density and width of jack pine trees grown in different boreal stands.*

Site	Ring density components (kg/m^3)				Ring width components (mm)			Latewood proportion (%)
	Annual	Earlywood	Latewood	Transition	Annual	Earlywood	Latewood	
Castanier-nord	470 (14)	379 (12)	768 (13)	645 (12)	2.16 (53)	1.69 (59)	0.47 (45)	24.6 (37)
Duprat-est	478 (13)	381 (11)	781 (14)	655 (12)	1.89 (44)	1.45 (49)	0.45 (40)	25.3 (32)
Dollard	465 (12)	377 (11)	761 (13)	642 (12)	2.01 (45)	1.57 (51)	0.44 (38)	23.9 (32)
Cléricy	465 (14)	374 (12)	754 (14)	633 (13)	1.87 (46)	1.45 (53)	0.42 (35)	24.9 (34)
Figuery	465 (14)	377 (11)	743 (15)	628 (13)	1.86 (46)	1.43 (52)	0.43 (40)	25.2 (34)
Total	469 (13)	378 (11)	761 (14)	640 (12)	1.96 (48)	1.51 (54)	0.44 (40)	24.8 (34)

about a 100% increase from earlywood to latewood within tree rings.

The substantially larger variations in ring width parameters over ring density parameters (Table 2) are in good agreement with earlier studies on conifers, e.g., Douglas-fir (Abdel-Gardir et al 1993), black spruce (Zhang et al 1996; Koubaa et al 2005), and balsam fir [*Abies balsamea* L. (Mill.)] (Koga and Zhang 2004). The 34% variation in LP (Table 2) was relatively low compared with other conifers, e.g., balsam fir (Koga and Zhang 2004). This result could be attributable to different demarcation methods, because we chose the maximum derivative method (Koubaa et al 2002) over the fixed threshold method. Site variation generally accounted for less than 3% of the variation in wood density components and latewood percentage (Table 3) and up to 11% of the variation in ring width components (Table 3). The larger site variation for growth components was associated with a large standard error (Table 3). The low site variability in wood density is not surprising, because the study sites had similar climatic, soil, and topological conditions (Table 1).

Among-tree variation explained 7 – 40% of the total random variation depending on the ring parameter and age period (Table 3). Compared with ring width components, wood density components varied more. For a given parameter, this variation tended to increase with age. In the case of AD, it increased from 18% in the corewood to 40% in the outerwood period. Compared with latewood, earlywood parameters showed greater variance (Table 3).

Radial Variation in Wood Density and Growth with Stem Height

Previous studies on radial variation in wood density were based on a constant tree height, generally at breast height. In this study, variation in wood density at different tree heights was investigated. At breast height, all wood density components increased from the pith outward until reaching a stable period, generally at about 30 yr for AD and ED and 15 yr for TD and LD (Fig 1). AD decreased first from the pith to age 3, at 393 kg/m^3, then increased to around age 30, and stabilized at about 540 kg/m^3 thereafter. This variation pattern is in good agreement with previous reports on jack pine (Villeneuve et al 1987; Barbour et al 1994). ED density followed a similar variation pattern, stabilizing at about 415 kg/m^3, or about 130 kg/m^3 lower than AD (Fig 1; Table 4). These variation patterns indicate that, at breast height, AD and ED did not vary with tree age in outerwood. Analysis of variance confirmed that the effect of cambial age on AD and ED is not significant in outerwood (Table 3).

At breast height, LD increased almost linearly to a maximum density of about 800 kg/m^3 (Fig 1; Table 4). Transition density followed a similar variation pattern as that of latewood density, reaching maximum TD at about 670 kg/m^3, or about 130 kg/m^3 lower than that of latewood density (Fig 1; Table 4). These variation patterns indicate that, at breast height, LD and TD did not vary with tree age in transition wood or outerwood. Analysis of variation confirmed that the effect of cambial age is not

Table 3. *Linear mixed model analysis of variance: F-value (F) for the fixed effects and variance components estimates for the random effects.*

	Fixed effects			Random effects		
	Height	Cambial age	Height × cambial age	Site	Tree nested within site	Residuals
Ring characteristics	F values			Variance components estimate ± SE (%)		
Corewood (age 2 – 11, height 0.3 – 13 m)						
Annual ring density	12.2**	33.4**	2.0**	0.5 ± 1.7	18.3 ± 4.2	81.2 ± 2.5
Earlywood density	19.3**	84.0**	1.7**		18.5 ± 4.1	81.5 ± 2.7
Latewood density	17.7**	181.9**	1.5**	3.0 ± 2.7	6.9 ± 2.0	90.1 ± 2.6
Transition density	15.3**	109.9**	1.7**	2.1 ± 2.2	9.1 ± 2.3	88.8 ± 2.4
Annual ring width	34.1**	46.4**	2.1**	11.0 ± 9.2	20.8 ± 4.7	68.2 ± 2.4
Earlywood width	36.5**	38.8**	2.0**	10.7 ± 8.9	19.0 ± 4.3	70.3 ± 2.4
Latewood width	18.3**	34.9**	1.8**	5.7 ± 4.9	12.9 ± 3.0	81.5 ± 2.2
Latewood percentage	30.0**	15.6**	1.9**	2.9 ± 2.7	8.4 ± 2.1	88.7 ± 2.3
Corewood – middlewood transition zone (age 16 – 25, height 0.3 – 7 m)						
Annual ring density	7.8**	18.7**	1.0 n.s.	2.5 ± 3.6	25.4 ± 5.6	72.1 ± 2.4
Earlywood density	7.7**	10.8**	1.0 n.s.		26.3 ± 5.6	73.7 ± 2.6
Latewood density	3.5**	0.7 n.s.	0.8 n.s.	2.6 ± 3.0	14.6 ± 3.8	82.8 ± 3.2
Transition density	1.9 n.s.	0.6 n.s.	0.8 n.s.	1.7 ± 2.4	16.4 ± 4.0	81.9 ± 2.9
Annual ring width	22.7**	41.9**	1.4 n.s.		23.1 ± 5.4	76.9 ± 3.4
Earlywood width	11.8**	43.4**	1.4 n.s.		21.3 ± 5.1	78.7 ± 3.5
Latewood width	68.2**	9.8**	1.0 n.s.		20.2 ± 4.5	79.8 ± 2.7
Latewood percentage	11.5**	22.6**	0.7 n.s.	1.7 ± 2.3	13.6 ± 3.4	84.8 ± 2.7
Outerwood (age 30 – 38, height 0.3 – 1.3 m)						
Annual ring density	0.1 n.s.	1.9 n.s.	1.9 n.s.	2.0 ± 4.3	39.9 ± 9.0	58.1 ± 3.3
Earlywood density	0.0 n.s.	1.2 n.s.	2.2*	1.6 ± 3.7	32.9 ± 8.2	65.5 ± 4.2
Latewood density	0.6 n.s.	0.9 n.s.	1.7 n.s.		32.2 ± 8.2	67.8 ± 4.9
Transition density	0.6 n.s.	0.6 n.s.	1.2 n.s.		31.9 ± 7.5	68.1 ± 4.1
Annual ring width	29.8**	9.5**	4.8 n.s.	14.8 ± 12.8	31.1 ± 7.6	54.1 ± 3.6
Earlywood width	21.2**	8.4**	4.1 n.s.	11.2 ± 10.4	33.3 ± 8.1	55.5 ± 3.8
Latewood width	27.4**	4.8**	3.0**	9.5 ± 8.7	23.0 ± 6.1	67.5 ± 4.1
Latewood percentage	0.0 n.s.	3.6**	0.6 n.s.	1.2 ± 3.2	28.7 ± 7.4	70.2 ± 4.3

* $p < 0.05$;
** $p < 0.01$;
n.s., nonsignificant.
Note: The F-value is the ratio of the between-group variation to the variation within group (residual or unexplained variance). The value of the F-statistic increases as does the difference between groups.

significant in outerwood and juvenile–mature transition wood for LD and TD (Table 3).

AD and ED also increased near the pith with increasing stem height but at a considerably decreasing growth rate (Fig 1; Table 4). This difference in growth rate explains the highly significant interaction between height and cambial age in the corewood period (Table 3). A similar pattern was reported in 70-yr-old black spruce (Alteyrac et al 2005), loblolly pine (Megraw 1985), radiata pine (*Pinus radiata* D. Don) (Nicholls 1986), and Douglas-fir (Jozsa and Brix 1989). These studies only described this tendency, whereas the present study quantified these changes.

Radial variation in wood density components at different heights followed apparently similar patterns as those shown at breast height (Fig 1). However, close examination of the data showed significant differences in radial variations with stem height. For average density, average radial change rate decreased with stem height (Table 5). The greatest increase rate was shown at 1.3-m height at about 6 times faster (5.8 $kg/m^3/yr$) than at the stem top (1.0 $kg/m^3/yr$). A similar pattern was reported with Douglas-fir (Jozsa and Brix 1989). By contrast, Gartner et al (2002) found no systematic changes with height in similar-aged Douglas-fir as did Koga and Zhang (2004) for balsam fir.

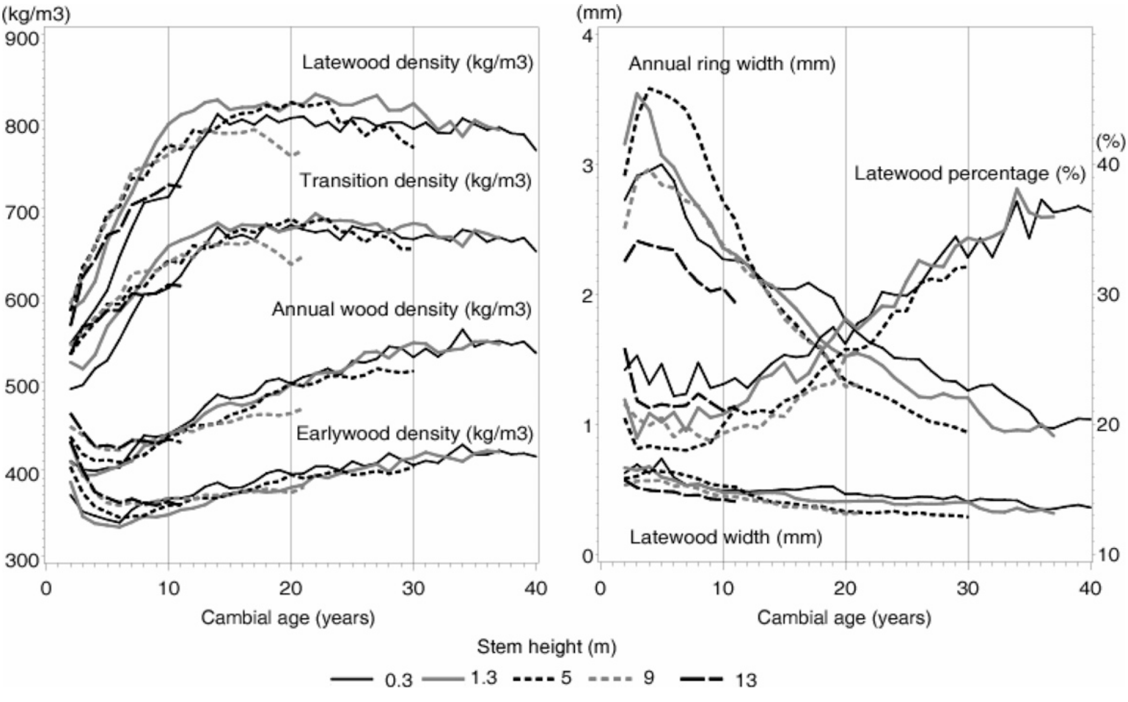

Figure 1. Average radial patterns of wood density and ring width components for selected stem heights with cambial age. For clarity, only 5 of 8 stem heights are presented.

Latewood density and TD differed from AD and ED in two ways. First, LD and TD increased directly from the pith to a maximum at around age 15 and decreased slightly outward from the pith thereafter. Second, this pattern was essentially the same at all stem heights (Fig 1). LD increased almost linearly to a maximum below 3-m height. Above this stem height, the increase follows rather a power function form (Fig 1). This pattern is consistent with the results by Mutz et al (2004), who found that a quadratic fit was better than a linear fit for this increase period in Scots pine (*Pinus sylvestris* L.). This result accounts for the significant interaction between CA and HT (Table 3) despite the similar pattern along the stem (Fig 1). The average change rate of LD was highest at 1.3-m height, at 29.5 kg/m^3/yr, and decreased toward the stem top to 21 kg/m^3/yr at stem top (Table 5). The LD radial pattern did not change substantially with stem height as observed in many other conifers, e.g., black spruce, Douglas-fir (Jozsa and Brix 1989), loblolly pine (Megraw 1985), radiata pine (Nicholls 1986), and balsam fir (Koga and Zhang 2004). TD followed a similar pattern as LD (Fig 1).

The varying change rates at different stem heights largely explain the highly significant interaction between height and cambial age in the corewood period for all studied parameters (Table 3). The slower increase in AD with stem height is comparable to Megraw's (1985) observation on loblolly pine. A similar pattern was also found in other conifers such as radiata pine (*Pinus radiata* D. Don) (Nicholls 1986) and Douglas-fir (Jozsa and Brix 1989). Based on our observations, this systematic variation in the change rate of AD is from the ED variation because LD did not show such a systematic variation with stem height (Fig 1; Table 5). One plausible explanation for this variation with height would be the effect of maturation of the apical meristems, or cyclophysis (Olesen 1978). There is strong evidence of this effect on cambial activity (Mellerowicz et al 1995; Rossi et al 2008), which results in reduced

Table 4. *Least squares mean for selected pattern descriptors for each stem height and multiple comparisons tests.*

	Wood density components				Ring width components			
Height (m)	Cambial age 2	Juvenile–mature wood transition age	Cambial age 20	Outerwood	Cambial age 2	Juvenile–mature wood transition age	Cambial age 20	Outerwood
	Annual ring density (kg/m^3)				Annual ring width (mm)			
0.3	408 c*	399 b	498 a	541 a	2.45 b	2.75 b	1.73 a	1.08 a
1.3	431 bc	393 b	498 a	541 a	2.93 a	3.21 a	1.45 b	0.97 b
3	421 bc	392 b	485 a	516 b	2.84 ab	3.35 a	1.45 b	0.87 c
5	437 abc	407 ab	499 a		2.85 ab	3.50 a	1.29 b	
7	411 ab	415 ab	483 a		2.77 ab	3.27 a	1.35 b	
9	450 ab	422 a	464 b		2.43 b	2.86 ab	1.24 b	
11	451 ab	422 a			2.29 b	2.58 bc		
13	465 a	427 a			2.21 b	2.33 c		
	Earlywood density (kg/m^3)				Earlywood width (mm)			
0.3	369 c	338 c	394 a	415 a	1.85 b	2.01 b	1.28 a	0.71 a
1.3	385 bc	333 c	379 b	416 a	2.32 a	2.60 a	1.03 b	0.62 b
3	383 bc	332 c	376 b	394 b	2.14 ab	2.75 a	1.07 b	0.59 b
5	402 b	344 bc	394 a		2.26 ab	2.85 a	0.95 b	
7	408 ab	356 b	387 ab		2.22 ab	2.71 a	1.01 b	
9	409 ab	358 b	373 b		1.93 ab	2.29 ab	0.93 b	
11	415 ab	357 b			1.67 b	1.98 b		
13	433 a	374 a			1.62 b	1.80 b		
	Latewood density (kg/m^3)†				Latewood width (mm)			
0.3	546 a	604 b	804 a	788 a	0.59 a	0.64 a	0.45 a	0.38 a
1.3	584 a	663 a	821 a	798 a	0.64 a	0.58 a†	0.39 ab	0.33 b
3	567 a	674 a	817 a	799 a	0.64 a	0.58 a†	0.37 bc	0.27 c
5	583 a	694 a	822 a		0.57 a	0.64 a	0.32 cd	
7	586 a	698 a	793 a		0.54 a	0.59 a	0.33 cd	
9	591 a	687 a	761 a		0.52 a	0.54 ab	0.30 d	
11	553 a	657 a			0.56 a	0.55 ab†		
13	567 a	671 a			0.55 a	0.47 b†		
	Transition density (kg/m^3)†				Latewood percentage (%)			
0.3	493 b	524 b	681 a	664 a	23.6 a	21.2 a	25.6 a	37.9 a
1.3	524 ab	565 a	677 a	671 a	21.1 a	18.9 ab	27.1 a	34.5 a
3	518 ab	565 a	682 a	665 a	22.3 a	17.2 b	25.5 a	31.7 b
5	532 a	590 a	688 a		20.0 a	17.8 b	25.2 a	
7	538 a	590 a	669 ab		19.5 a	16.2 b	24.3 a	
9	543 a	586 a	637 b		21.1 a	18.5 ab	24.4 a	
11	515 ab	575 a			24.7 a	19.0 ab		
13	534 a	584 a			24.5 a	20.7 a		

* Multiple comparisons were performed with Tukey-Kramer adjustment. Averages followed by the same letter are not statistically difference at $p = 0.05$.
† LS mean was calculated for cambial age 5 because of the lack of juvenile-mature wood transition ages.

AW (Dodd and Walker 1988; Takemoto and Greenwood 1993). However, its effect on wood density is not well known (Olesen 1982).

Ring width components (AW, EW, and LW) showed asymptotic behavior from the pith outward (Fig 1). AW generally mirrored the radial AD pattern at all stem heights (Fig 1). The significant cambial age effect during the entire period indicates that AW may not reach its asymptote until the age of 40 yr. The nonsignificant interaction with height during the transition period (Table 3) indicates that the strong decrease of up to 74% in AW during this period (Table 4) occurred at all stem heights. A similar tendency of a rapid decrease in ring width at midheight of the stem was also found in radiata pine (Nicholls 1986) and loblolly pine (Tasissa and Burkhart 1997).

The average change rate at stem base was about one-half that at midstem (Table 5) such that AW

Table 5. *Radial and longitudinal average changes for ring density and ring width components for jack pine.*

	AD (kg/m^3)	ED (kg/m^3)	LD (kg/m^3)	TD (kg/m^3)	AW (mm)	EW (mm)	LW (mm)	LP (%)
Height (m)	Radial average change (per year)							
0.3	5.4	2.7	23.3	16.7	−0.06	−0.05	−0.01	0.49
1.3	5.8	3.1	29.5	18.7	−0.08	−0.07	−0.01	0.57
3	5.3	2.7	27.6	16.2	−0.1	−0.09	−0.01	0.63
5	4.7	2.5	25.8	14.2	−0.11	−0.1	−0.01	0.65
7	4	2.2	27.1	15.1	−0.12	−0.1	−0.02	0.48
9	2.9	1.3	24.9	13.4	−0.1	−0.09	−0.02	0.55
11	2.7	1.4	25.9	14.8	−0.08	−0.07	−0.02	0.2
13	1	−1.7	21.2	10.2	−0.06	−0.05	−0.02	0
Age	Longitudinal average change (per meter)							
2	3.6	4.2	0.2	1.8	−0.06	−0.05	−0.01	0.18
5	2.6	2.6	2.6	3.1	−0.06	−0.05	−0.01	−0.02
8	0.5	1	−0.5	0.1	−0.03	−0.03	−0.01	−0.08
10	−0.1	0.7	−1.6	−1.1	−0.02	−0.02	−0.01	−0.11
15	−3.1	−0.6	−4.1	−3.1	−0.03	−0.01	−0.01	−0.39
20	−3.3	−1	−5.2	−4.1	−0.05	−0.03	−0.02	−0.25
25	−5	−1.7	−3.8	−2.8	−0.06	−0.03	−0.02	−0.61
30	−5.9	−1.9	−6.8	−4.1	−0.08	−0.05	−0.03	−0.36

AD, annual ring density (kg/m^3); ED, earlywood density (kg/m^3); LD, latewood density (kg/m^3); TD, transition density (kg/m^3); AW, annual ring width (mm); EW, earlywood width (mm); LW, latewood width (mm); LP, latewood percentage (%).

at the stem base was significantly narrower than in the upper stem (Fig 1; Table 4). EW followed a similar pattern but at a slightly lower level and rate (Tables 4, 5). LW also showed a similar pattern and was consistently largest at the stem base for all ages (Fig 1; Table 4). A similar pattern was reported in loblolly pine (Tasissa and Burkhart 1997).

The LP radial pattern of variation was closer to that of ED and AD (Fig 1). Stem upward, midstem had the lowest LP value, especially at 3 – 9-m height. Once the increase occurred, however, LP increased most rapidly in the upper stem (Table 5). The analysis of variance revealed that LP continued to vary significantly with cambial age in outerwood (Table 3). The jack pine is known to be one of the fastest growing boreal conifers in North America, second only to tamarack [*Larix laricina* (Du Roi) K. Koch] in the first 20-yr growth (Rudolph and Laidly 1990). The long stagnation period is roughly coincident with this period. Moreover, the largest AW was produced during this period (Fig 1). Maintaining low LP may be an efficient strategy for supporting this rapid growth (Schneider et al 2008), because earlywood is about 11 times more efficient than latewood in terms of water conductivity (Domec and Gartner 2002). High conductivity is directly related to the superior growth of jack pine (Pothier et al 1989).

Longitudinal Variations in Wood Density and Growth with Cambial Age

Longitudinal variations are generally considered marginal (Kellison 1981) and have usually been found to have no significant effect on ring width or wood density (Duff and Nolan 1953; Olesen 1982; Mäkinen et al 2007). A similar conclusion was reached for AW (Shea and Armson 1972) and AD (Hatton and Hunt 1990) in jack pine. However, in this study, a clear HT effect was observed for almost all parameters during the study period (Table 3). AD completely reversed the longitudinal patterns with cambial age (Fig 2). Near the pith, AD increased from stem base to top. For instance, at age 2, it increased at 3.6 $kg/m^3/m$ (Table 5), resulting in a 57 kg/m^3 or 17% increase from stem base to top. This pattern closely resembled the radial pattern with a minimum of 1.3 – 3 m and the asymptote at above 9 m (Fig 2). However, AD increased more rapidly in the lower stem (Fig 1; Table 5).

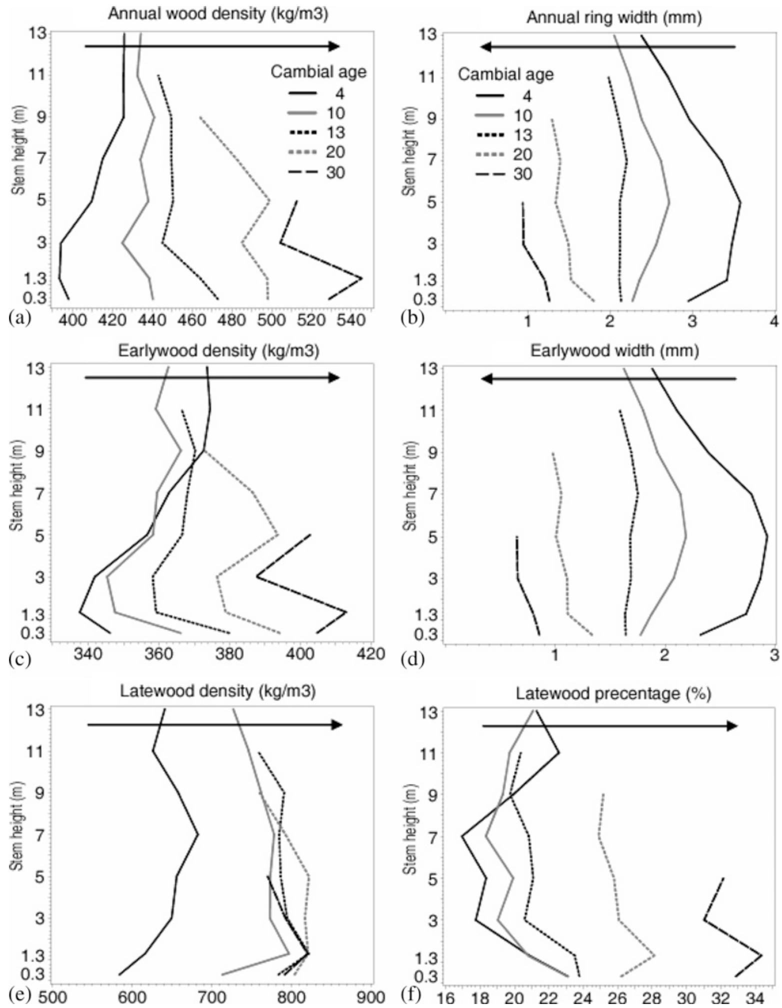

Figure 2. Longitudinal patterns of selected wood density and ring width components for annual ring, earlywood, and latewood for selected cambial ages. The arrow indicates the progress of cambial age.

After age 10, AD constantly decreased almost linearly from stem base to the top (Fig 2; Table 5). Megraw (1985) reported more or less constant AD above 5-m stem height up to 10 yr, whereas AD decreased in all other stem parts, including below the stem, for the same cambial age. In jack pine, Hatton and Hunt (1990) reported no difference in AD between juvenile wood in the lower stem and topwood, although their study was based on similar-aged and -sized jack pine trees as those in the present study and grown in Quebec. This discrepancy can be largely explained by the different analysis methods, because their comparison was based on average ages up to 28 yr.

Like the radial patterns, longitudinal ED patterns closely followed AD patterns. The LD pattern resembled the radial pattern, e.g., with a maximum at 7 m at age 4 (Fig 2). An approximately 94 kg/m^3 difference was found in the longitudinal direction between LD at 7-m height and 0.3 m at age 5 (Table 4). After age 10, however, the maximum point moved rapidly down to 1.3 m and remained farther outward (Fig 2), whereas LD decreased stem upward at, e.g., –6.6 $kg/m^3/m$ at age 30 (Table 5). TD followed a similar pattern.

AW generally decreased from 1.3 m to top (Table 5). However, there was a clear difference both before and after 13 yr. Before age 13, AW increased up to 5-m height and decreased thereafter (Fig 2). Multiple tests determined that AW for heights of 1.3 – 9 m was significantly larger than for stem extremities (Table 4). This initial increase of AW with stem height disappeared rapidly with cambial age such that AW decreased almost linearly from age 13. Up to 33% reduction was found from 5 m to the stem top at the juvenile–mature transition age (Table 4). Unlike AD, AW decreased most rapidly over 0.3 – 3 m, which explains the significant HT effect in the outerwood period (Table 2). A very similar pattern was found in loblolly pine (Tasissa and Burkhart 1997). By contrast, these systematic patterns are contradictory to what Duff and Nolan (1953) observed in red pine (*Pinus resinosa* Ait.) and Shea and Armson (1972) in jack pine. EW longitudinal variation closely followed that of AW, albeit less negatively (Fig 2; Table 5), as did LW but at a much lower rate (Table 5).

Interestingly, LP mirrored the longitudinal LD pattern with a minimum at 7 m at age 5 (Fig 2). With increasing age, LP showed a stronger tendency to decrease stem upward. A difference of 26% was found between 7 and 13 m at age 2 (Table 4).

The widely accepted view is that wood structure dynamics are dependent on cambial age as well as the hormonal and nutritional gradients from the active crown (Lindström 1996). However, this cannot explain the systematic changes found in corewood given that the wood in this region is always produced in the crown, the relative distance to the crown is constant for a given age, and the wood is at the same cambial age. Therefore, this theory is less likely to explain the high similarity between the two patterns, which we suggest is most likely from the intrinsic maturation characteristics of both the apical and lateral meristems. However, this high coordination disappeared rapidly with age. Recent tree physiological studies have indicated that this genetically programmed maturation may not fully explain declining growth with age. Instead, the increasing dimension of the tree itself may be the main driving force for age-related decline as a result of increasing environmental restrictions in water transport, nutrition, and respiration (Binkley et al 2002). Although these physiological studies have gained in popularity, the understanding of the underlying mechanisms is far from complete (Ryan et al 2004). We may speculate here that increasing physiological limitations with increasing tree size, especially hydraulic restrictions, given that jack pine is known to be less sensitive to nutritional supply (Strong and Grigal 1987), could have caused the simultaneous decrease toward the tree top in earlywood.

In conclusion, apex maturity appears to have a strong influence on tree ring formation near the pith. After about 5 yr, however, this influence weakens rapidly as cambial maturation increasingly occurs under the influence of cyclophysis and physiological restrictions. This view is supported by the revised interpretation of Olesen (1982) that "the maturation processes of both the apical and lateral meristem have to be considered as well as the relationship between these." We add here the importance of environmental limitations because of ever-increasing tree size.

CONCLUSIONS

This study showed that the average wood properties of jack pine obtained from the medium-production study sites in the Abitibi region are similar. Comparisons of longitudinal and radial patterns demonstrated that variations were mostly systematic for all studied ring parameters. Differences were shown in longitudinal variations for density parameters. At any given age in the corewood, density parameters generally increased with increasing stem height, but the opposite trend was found in outerwood. However, ring width parameters decreased with increasing stem height in both corewood and outerwood. Variations in earlywood ring parameters were greater than those in latewood.

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