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ANATOMICAL PROPERTIES IN *THUJA OCCIDENTALIS*: VARIATION AND RELATIONSHIP TO BIOLOGICAL PROCESSES

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ABSTRACT

The variability in wood properties of eastern white cedar (*Thuja occidentalis* L.) is relatively poorly known. Here we report the axial and the radial variation in selected anatomical properties, namely, ring width, wood density, and tracheid length and width. Forty-five trees were randomly sampled and felled from three selected sites in the Abitibi-Témiscamingue region, Quebec, Canada. Disks were systematically sampled at 0.5, 1.3, and 3 m stem height and at every 2 meters thereafter up to the tree top. Average ring density at breast height was 355 kg/m^3 with a small difference between earlywood and latewood. The latewood proportion was uniform and constant within the tree at about 32%. The tracheids were fine and long, averaging 25.3 μm in width and 2.07 mm in length. The variation in wood density components between trees was highly significant. The cambial age effect on all measured properties was highly significant. Ring density decreased from a maximum near the pith to a minimum in the juvenile–mature wood transition zone and remained constant or decreased slightly thereafter. Annual ring width decreased from a maximum near the pith to a minimum at the 10th ring and increased thereafter. Tracheid length and width showed typical radial variation characterized by a steady increase from pith to bark. Within-tree axial variation was highly significant, but ring width showed more substantial changes. Changes in wood properties with height depend on cambial age and thus are implied since the proportion of juvenile wood in the stem increases from the base to the top.

Keywords: Within-tree variation, ring density, ring width, tracheid length, tracheid width.

INTRODUCTION AND BACKGROUND

Eastern white cedar (EWC) (*Thuja occidentalis* L.) is common throughout southeastern Canada and the northeastern United States. It ranges from southwestern Nova Scotia, Prince Edward Island, New Brunswick, the Gaspé Peninsula in Quebec, and Anticosti Island in the Gulf of Saint Lawrence; west to northern Ontario and southeastern Manitoba; south to southeastern Minnesota and northern Illinois; and east through extreme northwestern Michigan and the New England states (Fowells 1965; Koubaa & Zhang

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2008). Owing to its low density, high natural durability, and excellent dimensional stability (Taylor *et al.* 2002), this wood produces valuable timber that is highly prized for indoor joinery, outdoor furniture, and decking. EWC wood is also used extensively in niche markets such as shakes, shingles, fence posts, and mulch (Taylor *et al.* 2002; Wan *et al.* 2007). Its dimensional stability increases its value for use in wooden structures subject to moisture fluctuations (Johnston 1990). Therefore, EWC has been used to improve the ability of medium density fiberboard (MDF) (Behr 1972), oriented strandboard (OSB) (Wan *et al.* 2007), and flakeboard to withstand decay and termites (Haataja & Laks 1995). Moreover, the strict new North American standards for the use of treated wood offer new opportunities for this timber. Despite its prized wood, EWC is the least studied commercially valuable tree species in the regions in which it grows.

Wood is a highly variable material owing to its biological origin (Koga & Zhang 2004; Zobel & Van Buijtenen 1989). For a given species, wood shows genetic, inter-site, inter-tree, and intra-tree variation. Intra-tree variation is further subdivided into within-ring variation from pith to bark (radial variation) and along the stem (axial variation) (Zhang *et al.* 1994; Koga & Zhang 2004; Guller *et al.* 2012). The wide variability in wood characteristics makes it difficult to accurately assess wood performance. Therefore, a better understanding of wood variability within a species would be useful for determining its suitability for various uses.

Ring width is related to the produced wood volume as well as end-product uniformity (Koga & Zhang 2004). Wood density is considered a key criterion of quality owing to its high correlation with mechanical strength and end-use performance (Zobel & Van Buijtenen 1989). Intra-ring wood density variation is also relevant: woods with small differences between earlywood and latewood densities are uniform, whereas woods with large differences between earlywood and latewood densities are not uniform. Intra-ring wood density variation also determines the suitability of a wood for specific end-uses, especially for high-value-added applications (Zobel & Van Buijtenen 1989; Zhang *et al.* 1994; Koubaa *et al.* 2002). For instance, uniform wood density is recommended for slicing and veneer peeling.

Intra-ring wood density variation also provides information on wood formation and physiological processes (Keunecke *et al.* 2009; Lachenbruch *et al.* 2011). Physiological variation of wood density is related to cambial activity and varies with age (characteristics of juvenile and mature wood), and is dependent on crown location in the tree (Spicer & Gartner 2001; Gartner *et al.* 2002). Thus, the physiological variation is the main cause of within-a-tree variations which include axial, radial, and within-a-ring (intra-ring) variations (Plomion *et al.* 2001; Gartner *et al.* 2002). The X-ray densitometry profile of a single growth ring provides considerable information on how the ring was formed and how physiological processes changed during the growing season (Koubaa *et al.* 2002).

Juvenile wood is one of the most important sources of inter-tree wood variation, particularly in conifers (Zobel & Van Buijtenen 1989; Larson *et al.* 2001). The proportion of juvenile wood is highly influenced by silvicultural treatments (Clark III & Saucier 1989). It is important to assess juvenile wood properties because of their impact on end-product quality. Juvenile wood forms a central core around the pith from tree base to top, following the crown as it grows (Clark III & Saucier 1989; Zobel & Van Buijtenen 1989). Typically, the properties of juvenile wood make a gradual transition toward those of mature wood (Zobel & Sprague 1998; Gryc *et al*. 2011). However, the properties of juvenile and mature wood in EWC have not been investigated to date.

Few studies have investigated axial variation in wood density in conifers, and the results are contradictory (Spicer & Gartner 2001; Burdon *et al*. 2004). For example, in *Pinus radiata* (Burdon *et al*. 2004), ring density decreased with stem height in even-aged trees. The same conclusion was found for Laricio pine (*Pinus nigra* subsp. *salzmannii*) (Oliva *et al*. 2006) and jack pine (*Pinus banksiana*, Park *et al*. 2009), whereas ring density remained constant along Douglas-fir (*Pseudotsuga menziesii*) stems (Spicer & Gartner 2001). The transition from juvenile to mature wood is abrupt in these species, where the typical radial pattern is characterized by a high wood density in mature wood compared to juvenile wood. However, EWC is a gradual transition species (Koubaa & Zhang 2008). According to Zobel and Van Buijtenen (1989), the standard pattern of gradual transition species is characterized by a higher wood density in the juvenile wood than in mature wood.

EWC is known to have low and uniform density, which results in high dimensional stability but low strength. The trees can reach a considerable age (Archambault & Bergeron 1992), which helps researchers understand the relationships between wood properties and cambial age. Few studies have investigated radial variation in ring density of EWC (Koubaa & Zhang 2008). However, no study to date has investigated the variation between earlywood and latewood or the variation between juvenile wood and mature wood in EWC. The radial variation in tracheid morphological characteristics (tracheid length and tracheid width) is also unknown. Furthermore, axial variation in wood density and tracheid morphological properties in this species have not been studied to date.

The main objective of this study was therefore to investigate within-tree variation in ring width, ring density, and tracheid morphological properties in *Thuja occidentalis* grown at three different sites in the Abitibi-Témiscamingue, Québec, Canada. The specific objectives were to (1) investigate radial patterns of ring density components (annual ring density, earlywood density, latewood density, and transition density), growth traits (ring width, earlywood width, latewood width, and latewood proportion), and tracheid morphological characteristics (fiber length and width) from pith to bark within trees and (2) determine the variation in wood density components and tracheid morphological characteristics along stem height. Such information is essential to assess the wood quality of this species and for wood processors in predicting end-product quality.

MATERIALS AND METHODS

Study material

Trees for this study were sampled from three mature EWC stands in the Abitibi-Témiscamingue region in the province of Quebec, Canada: [Abitibi (48° 28' N, 79° 27' W); Lac Duparquet (48° 25' N, 79° 24' W), and Témiscamingue (47° 25' N, 78° 40' W)]. All stands were dominated by balsam fir and EWC. Soil characteristics of the studied stands were described in a previous report (Bouslimi *et al*. 2013). Stand and

Table 1. Stand and tree characteristics of *Thuja occidentalis* grown in the Abitibi-Témiscamingue region, Quebec, Canada.

Stand	Abitibi (A)	Lac Duparquet (L)	Témiscamingue (T)
Latitude	48°, 28' N	48°, 25' N	47°, 25' N
Longitude	79°, 27' W	79°, 24' W	78°, 40' W
Altitude	314 m	272 m	333 m
Average temperature [a]	1.65 °C	1.64 °C	2.33 °C
Average maximum temperature	7.45 °C	7.55 °C	8.23 °C
Annual precipitation [a]	854 mm	841mm	933 mm
Tree age (years)	96 (58–134) [b]	121 (73–198)	93 (75–127)
Total height (m)	11.6 (8.5–14.3)	11.0 (7.0–13.8)	11.2 (8–13.4)
Diameter at breast height (cm)	29.7 (22–41)	29.7 (19–41)	26.9 (16–37)
Crown proportion (%)	65 (41–74)	64 (53–75)	59 (48–70)

[a] Values were calculated from weather data reported from 1930 to 2007 (Régnière & St-Amant 2007).
[b] Data range is given in parentheses.

tree characteristics are summarized in Table 1. The age of sampled trees ranged from 60 to 198 years, with an average of 93, 121, and 93 years for the Abitibi, Lac Duparquet, and Témiscamingue sites, respectively.

In all, 45 trees (15 per site) were randomly sampled from the selected sites. The sampled trees were felled, and total height, crown height, and diameter at breast height (DBH) were measured using a steel tape (Table 1). The crown proportion was calculated as the ratio of crown height to total tree height (Table 1). The trees had similar heights and DHBs at the three stands, averaging 11 to 12 m height and 30 cm DBH at the Abitibi and Lac Duparquet sites and 27 cm DBH at the Témiscamingue site (Table 1). From each felled tree, 10-cm-thick disks were sampled at 0.5, 1.3, and 3 m stem height and at every 2 meters thereafter up to the tree top. Disks were placed on pallets and air-dried with fans for several months in order to avoid decomposition until sample preparation and measurement.

Ring width and wood density measurement

To determine wood density, thin strips (20 mm wide and 1.57 mm thick) were sawn from each disk (bark to bark passing through the pith). The strips were then extracted with cyclohexane/ethanol solution 2 : 1 (v/v) for 24 h and with distilled water for another 24 h to remove resinous substances and water-soluble carbohydrates. Extractives can account for 1 to 20 % of the oven-dry weight of wood of various tree species, and can appreciably influence wood density (Grabner *et al*. 2005). Samples were then conditioned to 8 % equilibrium moisture content (EMC) before measurement.

Ring and wood density components were measured using a QTRS-01X Tree-Ring X-Ray Scanner (QMC, Knoxville, Tennessee). A linear resolution step size of 20 μm was used for X-ray densitometry. The mass attenuation coefficient ($cm^2\ g^{-1}$) required to calculate the density was determined on a set of 20 radial strips from cores with previously determined densities, using the maximum moisture content method (Smith

1954). After conditioning, rings from pith to bark were scanned in air-dry condition. During scanning, precautions were taken to eliminate incomplete or false rings and rings with compression wood or branch traces.

From the wood density profiles, average (RD), earlywood (EWD), and latewood (LWD) density were calculated for each annual ring. Demarcation between earlywood and latewood was determined for each annual ring by the maximum derivative method using a six-degree polynomial (Koubaa *et al.* 2002). The density at the demarcation point on the polynomial curve was defined as the transition density (TD). From the same density profiles, annual (RW), earlywood (EWW), and latewood (LWW) ring width were determined. Latewood proportion (LP) was calculated as the ratio of latewood width to annual ring width. False and missing rings were detected by cross-dating ring width chronologies. Cross-dating was numerically verified using COFECHA software (Holmes 1983). Because some strips had decay, several strips were discarded. Accordingly, a total of 261 strips were analyzed by X-ray densitometry.

Measurement of tracheid properties

A total of ten decay-free trees were randomly selected for morphological data analysis. In all, 47 disks were analyzed: 10 disks at 0.5, 1.3, 3, and 5 m stem height and 7 disks at 7 m. Disks at higher heights were not considered. A 1 cm long and 1 cm deep pith-to-bark plank was then sawn from each disk and prepared for fiber quality analysis (FQA). Whole ring thin longitudinal specimens were extracted from each disk at systematic cambial ages (5, 10, 12, 15, 20, and every 10^{th} annual ring up to the bark). Specimens were then macerated using Franklin's (1945) method.

Tracheid length and width were measured automatically using a Fiber Quality Analyzer (FQA, OPTEST, Canada). Based on image analysis (Robertson *et al.* 1999), the FQA allows rapid determination of tracheid length, tracheid width, and several other morphological properties. The FQA measures the true contour length and not the projected length. A total of 5,000 fibers were measured for each sample. To determine the length, the FQA computes three parameters: mean length, length-weighted mean, and weight-weighted mean fiber length (Robertson *et al.* 1999). The last parameter was used in this study because it gives more weight to the fibers and reduces the potential impact of fines on length determination. Individual tracheid length and width are reported to a precision of 0.01 mm and 1 μm, respectively (Robertson *et al.* 1999).

The pith-to-bark variation in wood traits is frequently described in terms of juvenile and mature wood zones and is used to estimate the transition age. The radial variation profile of tracheid length increased steadily with ring number from pith outwards to stabilize at cambial age 30. Considering the pattern of variation (Fig. 3) and that of other traits (Fig. 1 and 2), the wood produced from the pith up to the 30th ring is considered to be juvenile and the remaining wood mature.

Statistical analysis

Wood density components and ring widths were subjected to variance analyses (ANOVA) using a mixed-model approach, with cambial age as the repeated measure (Littell *et al.* 2006). The factors site, cambial age, and stem height were considered as fixed effects and tree was considered as a random effect. Only significant interactions were retained in the model. The hierarchical effects of individual tree and site were accounted for using two nested levels, with the tree effect nested within the site effect, as follows:

$$Y_{ijkl} = \mu + \alpha_i + \beta_j + \gamma_k + \delta_l + (\alpha\,\beta)_{ij} + \varepsilon \qquad \text{(Eq. 1)}$$

where Y is the dependent variable, μ is the grand mean, α_i is the fixed effect of stem height, β_j is the fixed effect of cambial age, $(\alpha\,\beta)_{ij}$ is the interaction between stem height and cambial age, γ_k is the fixed site effect, δ_l is the random tree effect, and ε is the residual error. Because of small site replication (3 sites), results of the Z-tests must be considered indicative only in this analysis (Littell *et al.* 2006). Although all trees had at least 58 annual rings, data beyond the 50^{th} annual ring were not considered. Because the first annual ring was not included in the analysis, data included 49 repeated measures (rings 2–50). Five systematic heights (0.5, 1.3, 3, 5, and 7 m) were retained for the analysis.

The SAS mixed-model procedure (PROC MIXED) was used to fit the models using restricted maximum likelihood (REML) (SAS 2008). Instead of assuming independent errors, we imposed a first-order autoregressive correlation structure AR (1). Degrees of freedom were determined using the Kenward–Roger method (Littell *et al.* 2006). All data were log-transformed to achieve model assumptions such as homoscedasticity and residual normality. The statistical significance of fixed effects was determined using *F*-tests at $P \leq 0.05$. Z-tests were conducted to determine whether the random effect significantly differed from zero (Littell *et al.* 2006).

The mean and standard deviation for each wood property were calculated for each annual ring and then plotted against cambial age (from pith to bark). Radial patterns were characterized quantitatively using pattern descriptors (Guller *et al.* 2012). Stem heights were compared for cambial age 2, 10, 20, 30, 40, and 50 using the least squares means procedure with the following equation:

$$Y_{ijkl} = \mu + \alpha_i + \gamma_k + \delta_l + \varepsilon \qquad \text{(Eq. 2)}$$

where ε is an error term with a correlation between the i^{th} stem height in the l^{th} tree at the k^{th} site. Tukey's multiple range method was used to test significant statistical differences in wood density properties between stem heights at selected cambial ages. Differences were considered statistically significant at $P \leq 0.05$.

Tracheid morphological characteristics (tracheid length and width) were also subjected to variance analyses (ANOVA) using a mixed-model approach according to the model in equation 1. Because heights were unequally distributed, a parametric power transformation was applied to model the autocorrelation effects using the Tukey–Kramer adjustment (Littell *et al.* 2006).

RESULTS AND DISCUSSION

Characteristics of eastern white cedar wood

Means and variations of ring width, wood density and tracheid morphological properties between juvenile and mature wood and with tree at breast height in

Table 2. Means and coefficients of variation (CV) [in parentheses (%)] in ring width, ring density components, and tracheid morphological properties for whole tree and juvenile (rings 2–15) and mature wood (rings 31–90) at breast height in *Thuja occidentalis* trees[a] grown in the Abitibi-Témiscamingue region, Quebec, Canada.

	Ring density components (kg m^{-3})			
	Ring density	Earlywood density	Latewood density	Transition density
Whole tree	355 (15.5)	302 (19.0)	516 (16.7)	455 (16.6)
Juvenile wood	397.5 (25.3)	355.3 (30)	475.3 (24)	441.7 (25)
Mature wood	345 (10.3)	289 (11.1)	524 (14.8)	456 (14.6)
	Ring widths (mm)			
	Ring width	Earlywood width	Latewood width	Latewood proportion (%)
Whole tree	1.0 (52.3)	0.77 (59.7)	0.27 (62.0)	28.7 (47.9)
Juvenile wood	0.95 (68.8)	0.62 (81.2)	0.33 (74.9)	37.5 (41.1)
Mature wood	1.06 (49.5)	0.8 (56.2)	0.26 (62.4)	31.8 (43.0)
	Tracheid properties			
		Width (μm)	Length (mm)	Length/Width
Whole tree		25.3 (9.2)	2.07 (17.4)	81.8 (29.6)
Juvenile wood		23.2 (8.4)	1.61 (15.9)	69.4 (20.3)
Mature wood		28.7 (7.2)	2.74 (7.5)	95.5 (7.2)

[a] Tree number was 44 for ring width and ring density components, and 10 for tracheid morphological characteristics.

Thuja occidentalis are presented in Table 2. Average annual ring width (RW) was one mm in this species and showed a small variation between juvenile wood (0.95 mm) and mature wood (1.06 mm) (Table 2).

Annual ring density (RD) was 355 kg m^{-3}, which is higher than that reported previously (281–324 kg m^{-3}) for this species in Wisconsin (Maeglin 1973). Latewood density (LWD) was 41% higher than earlywood density (EWD) (Table 2). However, this difference is low (214 kg m^{-3}) compared to that reported in jack pine (383 kg m^{-3}) (Park *et al*. 2009), and black spruce (243–383 kg m^{-3}) (Koubaa *et al*. 2000). In addition, the variation in average RD between juvenile and mature wood was minor (Table 2). The difference was only 52 kg m^{-3} (Table 2), which is low compared to other species such as spruce (*Picea abies* (L.) Karst.) (105 kg m^{-3}) and Scots pine (*Pinus sylvestris* L.) (162 kg m^{-3}) (Gryc *et al*. 2011). The within-tree distribution of latewood (LP) in EWC was also relatively uniform, accounting for over 32% of the wood (Table 2). Thus, the EWC wood is more uniform than that of abrupt-transition species, which may make the wood easier to machine and produce a more uniform veneer which would be an advantage for applications that require wood uniformity (Fritts & Swetnam 1989). For example, veneer peeling and slicing are an excellent end-use where a high degree of uniformity is very beneficial and where EWC can be valued.

EWC tracheids are long and fine, with whole tree average length of 2.07 mm and average width of 25.3 μm at breast height (Table 2). These values are higher in mature wood compared to juvenile wood (Table 2). Both tracheid length and width showed small across-tree variation (CV = 9–17 %).

Radial variation in ring density, ring width, and tracheid size

The radial variation in ring density components and ring width for 44 *Thuja occidentalis* trees are shown in Figures 1 and 2, respectively. The variation in tracheid length and width with cambial age for 10 *Thuja occidentalis* trees is shown in Figure 3. The pith-to-bark variation in studied wood traits revealed that the transition from juvenile to mature wood is gradual in EWC (change in wood properties is prolonged and gentle). The RD of juvenile wood was high near the pith (Fig. 1A) and decreased slowly to reach a minimum in the juvenile–mature wood transition zone (at about age 30). In mature wood, RD remained constant or increased slowly and steadily thereafter.

This variation pattern is similar to that reported by Koubaa and Zhang (2008), and appears to be comparable to the general pattern reported for members of the Cupressaceae and other gradual transition conifers species, such as western hemlock (*Tsuga heterophylla*) (Zobel & Van Buijtenen 1989), yew (*Taxus baccata*) (Keunecke *et al*. 2009), subalpine fir *(Abies lasiocarpa)* and western red cedar (*Thuja plicata)* (Zobel & Van Buijtenen 1989). For these species, including EWC, the inner juvenile wood

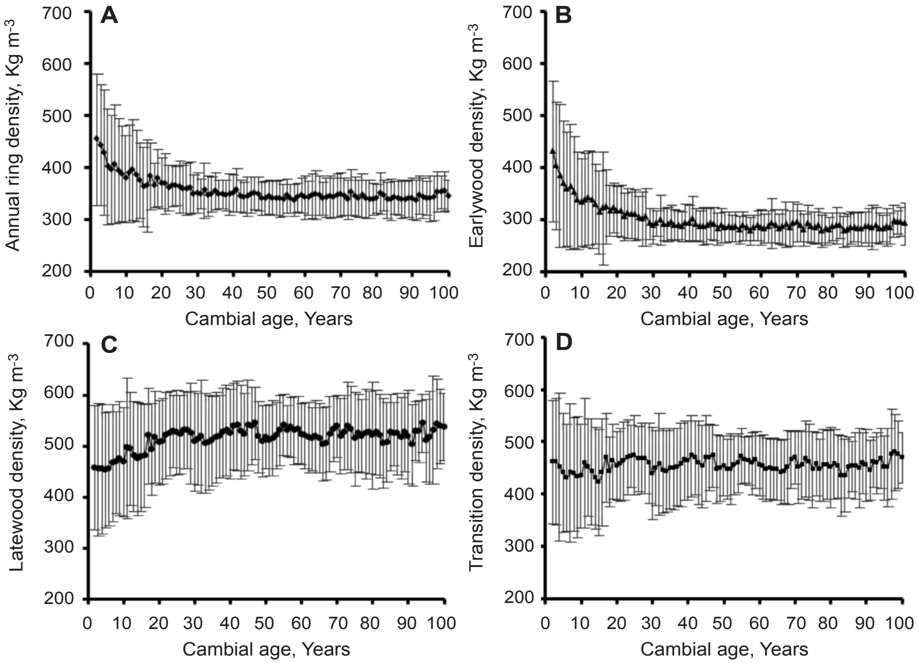

Figure 1. Patterns of radial variation and standard deviation of annual ring density (RD, kg m^{-3}), earlywood density (EWD, kg m^{-3}), latewood density (LWD, kg m^{-3}), and transition density (TD, kg m^{-3}) with cambial age (from the pith) at breast height in 44 *Thuja occidentalis* trees growing in Abitibi-Témiscamingue, Quebec, Canada.

has comparatively higher density than the outer mature wood (Keunecke *et al*. 2009; Lachenbruch *et al*. 2011). There are several causes for the radial pattern, such as the relationship to the age of the cambium or to the proximity to the crown (Zobel & Van Buijtenen 1989). According to Lachenbruch *et al*. (2011), the radial variation in wood structure in woody plants is due to age-related changes in tree structure and function. According to Anfodillo *et al*. (2013), the wood structure variation within trees is particularly useful in terms of both hydraulic safety and efficiency. For example, the phase of the cell expansion differs downwards in the stem, and is one key factor in controlling the rate of progressive lumen widening from the stem apex to the base, which is the typical axial conduit pattern (Anfodillo *et al*. 2012). Transversally in the stem, conduits are smaller close to the pith and larger in the outermost rings (Anfodillo *et al*. 2012).

The standard deviation was larger from the pith up to age 30, at which point the variation lessened (Fig. 1A). The larger standard deviation observed within the first 30 rings is linked to the juvenile wood characteristics (Zobel & Van Buijtenen 1989; Larson *et al*. 2001; Lachenbruch *et al*. 2011). EWD followed a similar pattern to that of RD (Fig. 1B), decreasing slowly from a maximum near the pith to a minimum in the transition zone, and remaining relatively constant with age thereafter. In contrast, LWD showed a completely different radial pattern (Fig. 1C): low and almost constant near the pith up to the 10^{th} ring and increasing thereafter to a maximum in the juvenile–mature wood transition zone and remained constant thereafter. The between-tree variation, as related to cambial age, was greater in latewood (Fig. 1C) than in earlywood (Fig. 1B). The transition density (TD) showed a similar pattern to that of LWD (Fig. 1D), increasing from a minimum near the pith to a maximum in the transition zone to mature wood and remaining constant thereafter.

RW decreased from a maximum near the pith to a minimum at the 10^{th} ring, increasing gradually thereafter to reach a maximum in the transition zone and remaining constant or decreasing slightly thereafter (Fig. 2A). This pattern differs from the typical growth pattern reported previously for most conifers, such as western hemlock, jack pine and black spruce (Zobel & Van Buijtenen 1989; Koubaa *et al*. 2005), where decreasing RW during the first years of growth was not observed. For these species, RW increased from the pith to a maximum in the transition zone and then decreased outward. The standard deviation for RW (Fig. 2A) is very high, indicating large tree-to-tree variation.

The intra-annual dynamics of RW increase differed between years and depend to the responses of cambium phenology to many environmental and physiological factors (Briand *et al*. 1993; Deslauriers *et al*. 2008, Rathgeber *et al*. 2011). According to Fabris (2000) and Larson *et al*. (2001), the underlying cause of within- and between-tree RW variation is the relationship of crown size to the length of stem devoid of branches. As presented in Table 1, the crown proportion showed significant inter-tree variation in EWC (ranging from 41–75%).

In our stands EWC was associated with balsam fir, spruce, and yellow birch (Bouslimi *et al*. 2013). These species showed a more rapid growth rate than EWC (Tardif & Bergeron 1997; Denneler *et al*. 1999; Bergeron 2000). Thus, during the first years

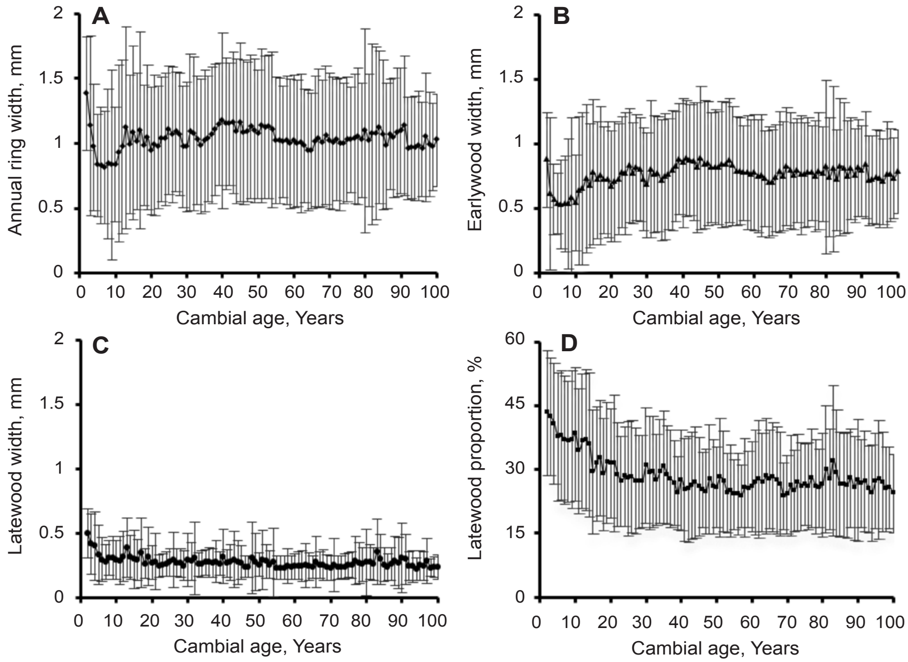

Figure 2. Patterns of radial variation and standard deviation for annual ring width (RW, mm), earlywood width (EWW, mm), latewood width (LWW, mm), and latewood proportion (LP, %) related to cambial age (from the pith) at breast height in 44 *Thuja occidentalis* trees growing in Abitibi Témiscamingue, Quebec, Canada.

of growth, the competition with understory associates could negatively affect cambial activity and consequently tree growth (Fig. 2A), especially when the layering accounts for a considerable amount of EWC reproduction in studied sites (Bergeron 2000; Rooney *et al*. 2002). RW increased sharply after cambial age 10 (Fig. 2A), probably because the competition with undergrowth decreased with increasing years, and tree seedling establishment resumed. The slight decrease observed in mature wood is due to increased tree circumference with increasing age, and not to a decrease in cambial activity (Koubaa *et al*. 2005).

Earlywood width (EWW) (Fig. 2B) showed a similar pattern to that for RW (Fig. 2A), decreasing rapidly from a maximum near the pith to a minimum at age 10, increasing slowly thereafter up to age 30, and then remaining constant or slightly increased in mature wood. The standard error was relatively high (Fig. 2B). In contrast to RW and EWW, latewood width (LWW) was constant over tree age (Fig. 2C). The between-tree variation, as related to cambial age, was lower in LWW than in RW and EWW (Fig. 2). LP showed a similar pattern to that for LWW: high near the pith (>43 %), decreasing gradually to reach a minimum in the transition zone, and remaining constant thereafter (Fig. 2D). The high standard deviation indicate larger tree-to-tree variation (Fig. 2D).

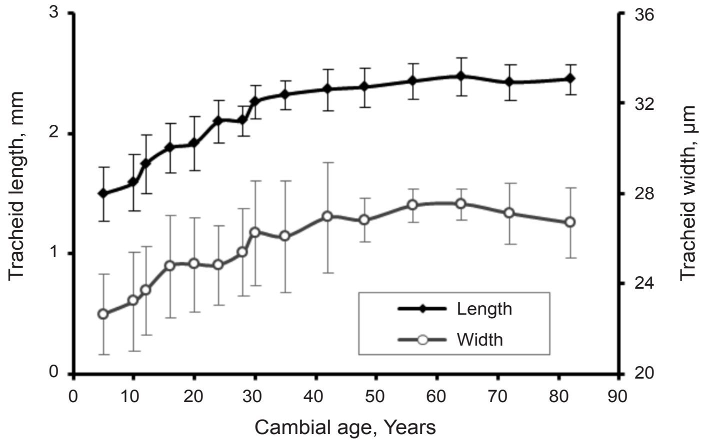

Figure 3. Patterns of radial variation of the whole ring and standard deviation for tracheid length (mm) and tracheid width (µm) with cambial age (from the pith) at breast height in 10 *Thuja occidentalis* trees growing in Abitibi Témiscamingue, Quebec, Canada.

The radial variation in tracheid length (Fig. 3) showed a rapid increase from the pith to the transition zone, increasing more slowly outward thereafter. This variation pattern is similar to the standard pattern in softwoods, except in roots (Zobel & Van Buijtenen 1989; Fujiwara & Yang 2000; Peterson *et al*. 2007). The radial variation in tracheid width showed a steady increase from the pith to the bark. The lower values of tracheid width near the pith are in good agreement with Anfodillo *et al*. 2012 who stated that stem conduits are smaller close to the pith and larger in the outermost rings, as a function of the distance of the conduits to the stem apex during their formation. The standard errors for ring width were relatively high (Fig. 3). This is probably due to the natural between-tree variation in crown volume, which influences tracheid width, and to the site quality effect on crown growth efficiency (DeRose & Seymour 2009).

The radial RD pattern (Fig. 1A) can be explained by the variation in EWD (Fig. 1B) and LP (Fig. 2D). For each annual ring, earlywood was the predominant ring component, accounting for over 57 % (up to 73 %) of the total ring width (Fig. 2D). The variation pattern for EWD in the juvenile phase (Fig. 1B) was similar to that for RD (Fig. 1A). LWD (Fig. 1C) was significantly higher than EWD (Fig. 1B), indicating that a slow increase in the LP within an annual ring directly affects RD. This could partly explain the steady increase in RD in the last 20 years (Fig. 1A).

A slow increase in RW could also negatively affect RD (Koga & Zhang 2002). The percentage of earlywood and latewood in a growth ring determines the overall density of the ring, and in EWC the LWW is relatively constant (Fig. 2C). Therefore, the RW (Fig. 2A) is closely related to the EWW (Fig. 2B). As the RW in EWC increases, the width of the earlywood increases without a corresponding increase in the amount of latewood, causing lower RD (Fig. 1A). In juvenile wood, earlywood cells have a thin wall layer, which is one of the reasons for lower density (Zobel & Van Buijtenen 1989). According to Zhang *et al*. (1996), the decrease in RD combined with the increase in RW in conifers was more pronounced in species that showed a gradual transition from earlywood to latewood (such as *Thuja occidentalis*) than in species that made an abrupt transition.

Factors other than vegetative competition among trees, tree age (Spicer & Gartner 2001) and climatic and ecological conditions (Ackermann 1995; Larocque 1997; Bergès *et al*. 2008) could explain RD and RW variation. In the first years of growth, RW decreases owing to increased competition from other undergrowth in the same stand (Fig. 2A). Consequently, the LP is high near the pith (Fig. 2D). When subsequent growth conditions are good, RW increases, which increases the earlywood proportion but decreases the latewood proportion (Fig. 2D). According to Zobel and Van Buijtenen (1989), the initial decreases in RD components and LP are usually attributed to the presence of live branches that remain photosynthetically active during growth, which prolongs earlywood production, such that the transition from juvenile to mature wood is more gradual.

EWC has a low growth rate (Fig. 2A). In fact, this species is associated with late successional stages (nondominant tree) (Johnston 1990; Bergeron 2000). Thus, it grows more slowly owing to more limited resource acquisition compared to dominant trees (Binkley *et al*. 2002). According to Hofmeyer *et al*. (2010), the competition between trees in a same stand, due to differences in crown structure and canopy position, could significantly affect xylem development in EWC. This might explain the larger between-tree variation in tracheid width and ring width in this species (Fig. 2 and 3). Furthermore, the topology of the xylem network could also affect the water transport, and consequently plant survival and growth in EWC (Tyree & Ewers 1991; David *et al*. 2012). Under adverse conditions, EWC tended to sectorize its radial architecture in order to almost completely isolate the hydraulic pathways to different parts of the stem and crown, thereby increasing the odds of survival, but decreasing significantly its growth rate (Larson *et al*. 1993; Larson *et al*. 1994; Matthes-Sears *et al*. 1995; Matthes *et al*. 2002).The hydraulic sectoriality in branches, stem, and taproot may be regarded as an adaptive trait to cope with environmental stress (David *et al*. 2012).

Longitudinal variation in ring density, ring width, and tracheid size

The variation in wood density and ring width along selected stem heights with cambial age is shown in Figures 4 and 5. The analysis of variance (Table 3) showed that stem height as well as cambial age and tree significantly affected traits. However, the site effect was not significant on RD and EWD. This result is surprising, but could be partially explained by the significant effect of tree nested within site (Table 3). Despite the variation in site properties (Bouslimi *et al*. 2013), the site effect could be masked by the tree-to-tree variation (Table 3). The tree effect on RD was highly significant ($p<0.001$). The significant effect of stem height could also mask the site effect (Table 4). The effect of stem height on RD was highly significant ($p<0.001$) (Table 3). Furthermore, for most properties, the F-value for stem height increased from juvenile to mature wood (Table 3). This suggests that the magnitude of the longitudinal variation depends on wood type.

The axial variation is related to different sources, such as cambial age and ring width (Zobel & Van Buijtenen 1989). Hence, the cambial age effect was highly significant

Table 3. Linear Mixed Model Analysis of Variance, with F-value for fixed effects, Z-value for random effects, and their significance for each source of variation for wood density components and ring widths in *Thuja occidentalis*.

	Fixed effects				Random effects	
Source of variation	Site	Cambial age	Height	Cambial age X height[a]	Tree nested within site	Residuals
	F-value	F-value	F-value	F-value	Z-value	Z-value
Characteristics — All data: Rings 2–50						
Ring density	1.1 ns	20.3***	45.4***	1.3**	3.4**	39.8***
Earlywood density	1.4 ns	28.5***	16.4***	1.1 ns	3.7**	39.6***
Latewood density	3.8 ns	2.2***	14.4***	1.3**	3.2**	33.2***
Transition density	3.4*	1.5**	15.2***	1.3**	3.2**	36.2***
Ring width	9.0**	0.9 ns	4.7**	1.4***	3.8***	31.1***
Earlywood width	9.0**	0.9 ns	11.7***	1.4***	3.8***	32.5***
Latewood width	5.1*	4.5***	7.0***	1.3**	3.7**	39.4***
Latewood proportion	6.3**	4.3***	31.5***	1.2*	3.5**	40.3***
Tracheid length	0.05 ns	63.4***	24.2***	1.7***	1.3*	15.9***
Tracheid width	0.3 ns	6.4***	31.3***	0.4 ns	1.2 ns	15.9***
Characteristics — Juvenile wood: Rings 2–30						
Ring density	0.6 ns	19.1***	18.8***	1.1 ns	3.4**	31.1***
Earlywood density	1.0 ns	26.9**	5.2***	1.0 ns	4.2**	47.2***
Latewood density	5.2*	3.2***	5.6**	1.3**	2.6**	26.5***
Transition density	4.1*	1.6*	6.4***	1.3*	2.6**	28.8***
Ring width	9.3**	0.9 ns	15.7***	1.3*	3.6**	25.9***
Earlywood width	9.2**	1.0 ns	22.2***	1.3*	3.5**	27.1***
Latewood width	3.7*	5.2***	2.61 ns	1.3*	3.5**	32.5***
Latewood proportion	5.4**	5.1***	23.0***	1.2*	3.4**	33.1***
Tracheid length	0.4 ns	54.5***	3.9**	0.7 ns	1.0 ns	11.6***
Tracheid width	0.7 ns	8.1***	21.2***	0.3 ns	0.4 ns	11.7***
Characteristics — Mature wood: Rings 31–50						
Ring density	1.1 ns	2.9***	40.7***	1.4*	3.0**	26.5***
Earlywood density	1.6 ns	2.3**	20.9***	1.3*	3.1**	27.7***
Latewood density	1.8 ns	1.1 ns	14.5***	1.0 ns	3.0**	21.6***
Transition density	2.0 ns	1.0 ns	13.7***	1.1 ns	3.1**	23.2***
Ring width	7.9**	0.8 ns	15.6	1.3*	3.7***	19.9***
Earlywood width	7.1**	0.7 ns	11.7	1.4*	3.8***	20.5***
Latewood width	7.7**	0.9 ns	17.2***	0.9 ns	3.1**	23.5***
Latewood proportion	3.5*	0.8 ns	20.6***	1.0 ns	3.6**	24.3***
Tracheid length	0.2 ns	4.4***	33.4***	0.4 ns	1.3**	10.8***
Tracheid width	0.1 ns	0.8 ns	12.9***	0.5 ns	1.2 ns	10.8***

[a] Interaction between cambial age and height. F-value is the ratio of the between-group to within-group variation. The F-statistic increases with increasing between-group difference. Significance level: * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$, and ns = not significant.

for most properties except for RW and EWW (Table 3). The variation due to cambial age was greater in juvenile than in mature wood, as indicated by the lower F-value for mature than for juvenile wood (Table 3). The high variation in juvenile wood (Table 3) is attributed to the juvenile variation in these traits (Zobel & Van Buijtenen 1989). Juvenile wood is characterized by wider variation in terms of cell dimensions and cell wall formation compared to mature wood (Larson *et al*. 2001; Lachenbruch *et al*. 2011).

The longitudinal variation in RD (Fig. 4A), EWD (Fig. 4B), and LWD (Fig. 4C) near the pith (rings 1 to 10) is minimal, and the density values follow almost the same curve for each density component. However, beyond the 10th ring from the pith, RD and EWD decreased steadily with increasing tree height. On the other hand, LWD showed a different variation pattern: it increased at the tree bottom, remained constant at mid-height, and decreased at the tree top (Fig. 4C). At constant cambial age (Table 4), the variation in RD, EWD, and LWD was minimal, although a consistently slight decrease in these properties is observed with increasing tree height. Similar findings were reported for jack pine, where RD started to decrease from the tree base upward after age 10 (Park *et al*. 2009). RW longitudinal variation decreases steadily from the tree base upward (Table 4). However, at constant cambial age, the RW longitudinal

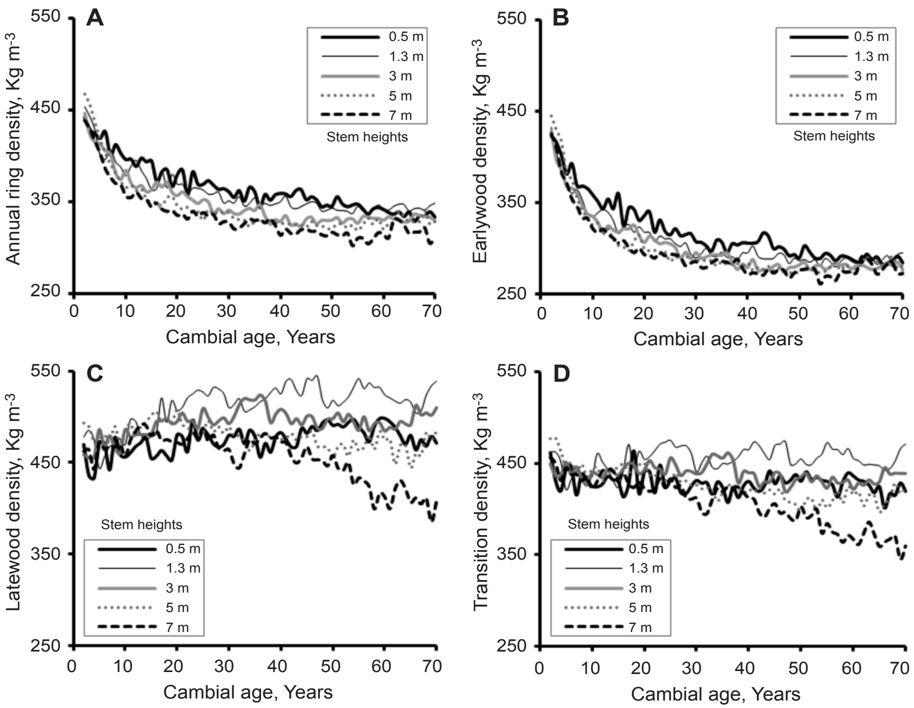

Figure 4. Variation in annual ring density (A), earlywood density (B), latewood density (C), and maximum density (D) with cambial age at 5 selected stem heights along the stem of 44 *Thuja occidentalis* trees.

Table 4. Longitudinal variation in wood ring, earlywood and latewood densities at selected cambial ages.

	Means of ring density components					Means of ring width components				
Stem height[1]	0.5 m	1.3 m	3 m	5 m	7 m	0.5 m	1.3 m	3 m	5 m	7 m
Cambial age	Annual ring density (kg m^{-3})					Annual ring width (mm)				
2	442[a]	453[a]	447[a]	467[b]	439[a]	1.12[a]	1.07[a]	1.30[b]	1.37[bc]	1.52[bd]
10	396[a]	379[bc]	384[ac]	366[bd]	356[bd]	0.86[a]	0.84[a]	1.00[b]	1.30[bc]	1.32[bd]
20	380[a]	369[a]	357[b]	346[bc]	336[bd]	0.94[a]	0.95[a]	1.11[a]	1.16[b]	1.13[b]
30	361[a]	351[bc]	342[bd]	339[bd]	328[be]	0.95[a]	0.98[a]	1.08[a]	0.98[a]	1.01[a]
40	359[a]	350[bc]	329[bd]	327[bd]	324[bd]	1.13[a]	1.18[a]	1.02[a]	1.05[a]	0.81[b]
50	346[a]	344[ac]	331[bd]	322[be]	317[b]	1.27[a]	1.07[a]	0.91[b]	0.84[b]	0.85[b]
Cambial age	Earlywood density (kg m^{-3})					Earlywood width (mm)				
2	423[a]	433[bc]	429[ac]	445[bd]	425[ac]	0.74[a]	0.67[a]	0.78[ac]	0.85[bc]	1.0[bd]
10	359[a]	335[bc]	335[b]	326[b]	322[bd]	0.54[a]	0.55[a]	0.64[a]	0.96[b]	0.94[b]
20	336[a]	318[bc]	307[b]	300[bd]	294[bd]	0.67[a]	0.68[a]	0.77[a]	0.90[b]	0.86[b]
30	308[a]	290[a]	296[a]	289[a]	286[b]	0.65[a]	0.69[a]	0.81[a]	0.73[a]	0.75[a]
40	306[a]	295[a]	280[b]	284[b]	272[b]	0.80[a]	0.86[a]	0.79[a]	0.78[a]	0.63[a]
50	290[a]	287[a]	282[a]	274[b]	276[b]	0.84[a]	0.82[a]	0.70[a]	0.60[b]	0.64[b]
Cambial age	Latewood density (kg m^{-3})					Latewood proportion (%)				
2	470[a]	479[a]	459[a]	493[b]	462[a]	36.7[a]	39.4[a]	40.7[a]	40.4[a]	35.9[a]
10	456[a]	469[a]	486[b]	485[b]	456[a]	39.5[a]	38.4[a]	37.0[a]	28.2[b]	31.0[b]
20	480[a]	507[bc]	495[ac]	508[b]	472[a]	33.8[a]	31.5[a]	30.8[a]	25.3[b]	26.3[b]
30	480[a]	510[b]	492[ac]	489[ad]	464[ad]	34.7[ae]	31.0[b]	27.3[b]	29.3[b]	27.0[b]
40	483[a]	525[b]	508[b]	475[a]	473[a]	34.8[a]	27.6[b]	24.9[b]	26.0[b]	24.2[b]
50	491[a]	518[bc]	498[ac]	455[bd]	458[bd]	33.0[a]	25.9[b]	27.0[bc]	31.0[ac]	25.7[bc]

[1]Multiple comparison tests of different stem heights for each selected cambial age were performed with Tukey–Kramer adjustment. Averages followed by the same letter indicate no significant difference between stem heights at $p < 0.05$.

variation showed substantial changes (Table 4; Fig. 5A). Near the pith, RW increased from the tree base upward. However, at higher cambial ages, RW showed the reverse variation pattern, decreasing with increasing tree height (Fig. 5A).

In the juvenile phase, RW significantly increased with stem height (Fig. 5A). This means that at the same cambial age, the cambium will produce narrower rings at the tree base than at higher heights. The variation in the RW change rate at different stem heights and with cambial age (Table 4) explains the highly significant effect of the interaction between stem height and cambial age on RW (Table 3). The same trend was observed for the longitudinal variation in EWW with cambial age (Fig. 5B, Table 4). This reflects the fact that EWW is strongly correlated with RW in this species. LWW also showed a similar pattern of variation with stem height, but the magnitude of this variation was lower compared to RW and EWW (Fig. 5C). In mature wood, LWW was significantly higher at 0.5 m height, but variation between other stem heights was not significant (Fig. 5C). This could explain the non-significant effect of the interaction between stem height and cambial age on LWW (Table 3). The longitudinal variation in LP (Fig. 5D) with cambial age was similar to that of RD and EWD (Fig 4A and B).

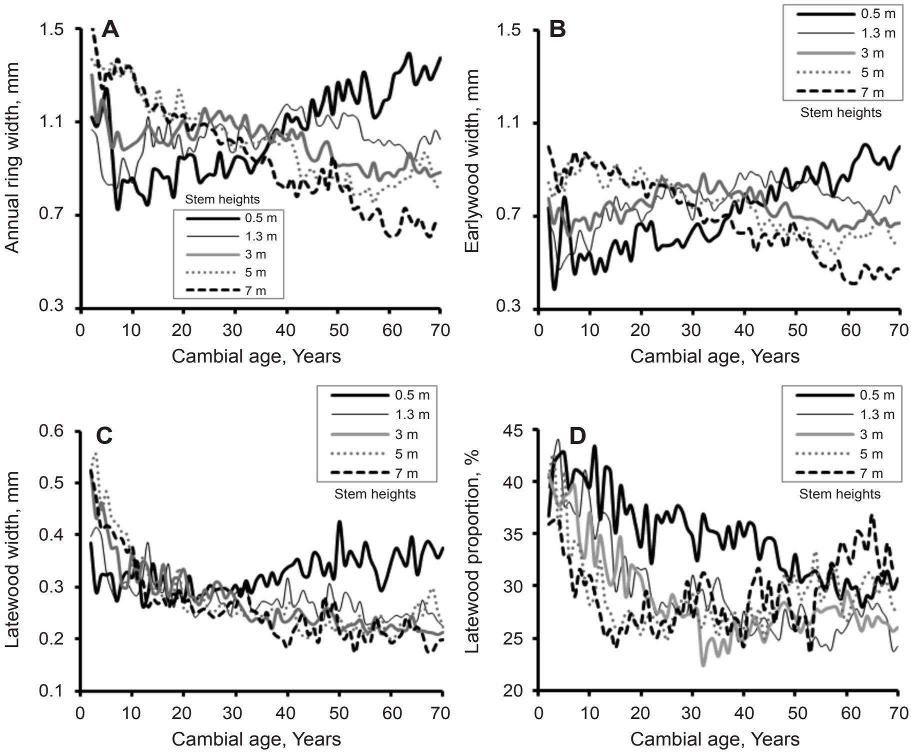

Figure 5. Variation in annual ring width (A), earlywood width (B), latewood width (C), and latewood proportion (D) with cambial age at 5 stem heights along the stem of 44 *Thuja occidentalis* trees.

The analysis of variance (Table 3) showed that stem height and cambial age significantly affected tracheid length and width. However, the site and tree effects on tracheid length and width were nonsignificant. The variation in tracheid length and width along selected stem heights with cambial age is shown in Figure 6.

Tracheid length increased from tree base upward to 5 m height and decreased thereafter. Tracheid width also increased from tree base upward to 3 m height and decreased thereafter. These results are in good agreement with the findings of Anfodillo *et al.* (2012) who investigated the variation of xylem anatomy with stem height for Norway spruce (*Picea abies*). They reported that the lumen area of the cells varied along the stem with the smallest values observed at 9 m height. Increasing values were measured towards the base up to 3–4 m height, but at heights of 1–2 m, lumen area decreased again slightly. According to Anfodillo *et al.* (2012, 2013) this pattern of variation could be explained by the axial conduit pattern commonly referred to as 'conduit tapering'. Wider cells are those staying longer in the distension phase during xylogenesis, because plants adopt a mechanism to modulate the time for cell enlargement to precisely design xylem conduits optimally widened from the stem apex downwards for hydraulic purposes.

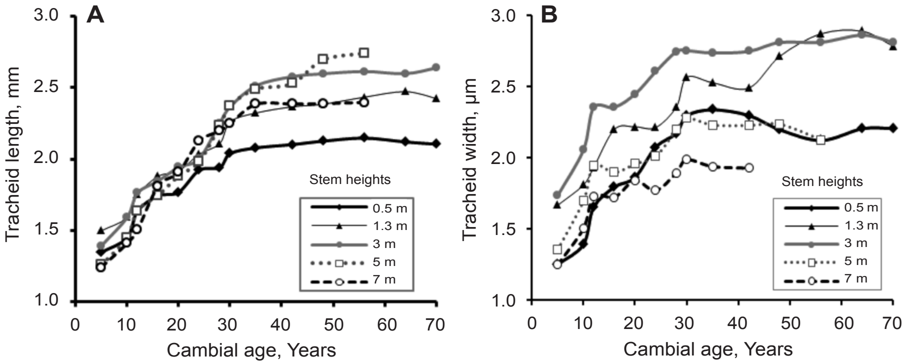

Figure 6. Variation in tracheid length and width with cambial age at 5 selected stem heights in 10 *Thuja occidentalis* trees.

Many studies suggest that the location of the crown is the key to understanding the variability in wood quality along the stem in conifers (Hillis 1972; Fabris 2000; Gartner *et al*. 2002; Gartner *et al*. 2005; Masaki & Okamoto 2007). For many species in which juvenile wood greatly differs from mature wood, a change in wood properties with height is automatic since the proportion of juvenile wood in the stem increases extensively from the base to the top (Zobel & Van Buijtenen 1989; Gartner *et al*. 2002). Therefore, the wood structure is dependent on cambial age (Larson *et al*. 2001; Passialis & Kiriazakos 2004). Trees produce only juvenile wood under the effect of the live crown. Thereafter, with increasing cambial age, the cambium stops producing juvenile wood and starts to produce mature wood at the tree base (Zobel & Sprague 1998; Gartner *et al*. 2002). This could explain the decrease in RD and LP with stem height observed in this study (Fig. 4A and Fig. 5D): at the tree top, there is only juvenile wood, which is characterized by lower density and lower latewood proportion than mature wood (Zobel & Van Buijtenen 1989; Larson 2001; Passialis & Kiriazakos 2004).

In addition to cambial age effect, the wood structure is dependent on the hormonal and nutritional gradients generated by the active crown (Larson *et al*. 2001; Plomion *et al*. 2001; Schowalter & Morrell 2002). Auxin is the primary hormonal signal that controls wood formation. It is produced mainly in young leaves, moves downward through the cambium, and controls earlywood and latewood width, cell wall thickness, and cell expansion (Plomion *et al*. 2001). Along the tree axis, gradients of decreasing auxin concentration from leaves to roots generate gradients of cell width, cell expansion, wall composition, and density in the wood (Plomion *et al*. 2001; Schowalter & Morrell 2002). Hence, near the crown, the plant growth regulators stimulate the annual ring width, earlywood width, and consequently the tracheid width. These plant growth regulators have less effect at the tree base, and this is where high quality adult wood is produced. However, the tree produces juvenile wood within the crown (Fabris 2000; Plomion *et al*. 2001).

According to Anfodillo *et al*. (2013), high concentrations of auxin would accelerate the cellular differentiation, but reduce the cell expansion. Accordingly, the diameter of xylem conduits increases towards the stem base. This axial profile provides the distal regions of the xylem pathways with the conduits most resistant to cavitation (Rosner 2013), and it confines the greater part of total hydraulic resistance towards the downstream ends of the flow path (Petit & Anfodillo 2009; Anfodillo *et al*. 2012). Thus, it seems to be useful in terms of both hydraulic safety and efficiency (Rosner 2013). According to Rosner (2013), high wood density is supposed to be a common strategy to guarantee low vulnerability to cavitation. These could explain the observed increase in ring width, tracheid length, and width and the decrease in ring density along stem height (Fig. 3, 5, 6).

According to Spicer and Gartner (2001), the variation in RD with tree height is also related to the variation in tracheid width. As shown in Figure 6, ring tracheid width increased with stem height. Consequently, the increase in tracheid width from tree base to top induced an increase in earlywood width (Fig. 5B) and a corresponding decrease in both the proportion of latewood (Fig. 5D) and ring density (Fig. 4A) along the stem height.

The effect of cambial age and plant growth regulators on wood structure cannot explain the decline in growth observed after age 40 (Fig. 5A). Instead, the increasing dimension of the tree itself may be the main driving force for age-related changes (Day *et al*. 2001; Binkley *et al*. 2002). The same conclusion was reached with jack pine (Park *et al*. 2009). Other factors, including reduced crown volume with tree aging, and therefore an attenuation of the growth rate due to cambium aging, or weak activity in the lower branches as the stand canopy closes, could explain the observed decrease in growth with tree height (Day *et al*. 2001; Binkley *et al*. 2002). Growth accelerates as canopies develop in young forests, and declines substantially soon after the maximum leaf area is attained (Day *et al*. 2001).

CONCLUSIONS

Within-tree variation in growth, wood density, and tracheid morphological characteristics were investigated in eastern white cedar (*Thuja occidentalis*). The following conclusions can be drawn:

The wood of *Thuja occidentalis* is relatively uniform. The average ring density in trees grown at Abitibi-Témiscamingue was 355 kg m^{-3}. The tracheids were fine and long but slightly shorter than those found in other softwoods.

Cambial age significantly affected ring width, ring density, and tracheid morphological properties. Ring density decreased gradually from the pith to the juvenile–mature transition zone and remained constant thereafter. This decrease was due more to earlywood density variation than to the variation in latewood proportion or density. However, tracheid length and width increased from a minimum near the pith to a maximum in the transition zone and remained steady afterward. The highly significant effect of cambial age on wood density components in juvenile wood is attributed to the juvenile variation in these traits.

Axial variation in growth, wood density and tracheid morphological properties was determined. Stem height significantly affected wood properties. The variation in RD, near the pith is minimal. However, beyond the cambial age of 10 years, RD decreased steadily with increasing tree height. The RW longitudinal variation was greater than the RD variation. Near the pith, RW increased from the base of the stem to the tree top, but the longitudinal variation showed the reverse trend at higher cambial ages. In mature wood, the ring parameters decreased from the tree base upward. A change in wood properties with height is automatic since the proportion of juvenile wood in the stem increases extensively from the base to the top.

The between-tree variation in wood density components was highly significant. Compared to ring width, ring density showed considerably smaller within-tree variation.

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