Original article

Relationships of climate and cell features in stems and roots of black spruce and balsam fir

Cornelia KRAUSE*, Sergio ROSSI, Maxime THIBEAULT-MARTEL, Pierre-Y. PLOURDE

Université du Québec à Chicoutimi, Département des Sciences Fondamentales, 555, boulevard de l'Université, Chicoutimi (Qc) G7H 2B1, Canada

Abstract

• The anatomical differences of mature black spruces and balsam firs were examined at stem and root level in order to characterize their wood properties at cellular level and link these differences to climate.

• Anatomical variability of these species was evaluated in relation to climate data gathered from 2001 to 2004 during the cell enlargement (CE) and wall thickening and lignification (WTL) phases. Lumen area, single cell wall thickness and total tracheid radial diameter were analyzed and regrouped into earlywood and latewood.

• Results from a principal component analysis (PCA) indicated that both first eigenvectors account for 82% and 90% of total variance for CE and WTL respectively. These component factors revealed that precipitation, humidity and number of days with precipitation significantly influence the lumen area ($p = 0.0168$) and radial cell diameter ($p = 0.0222$) in earlywood. Significant differences were registered between species and tree parts (stem and root) for the lumen area, radial cell diameter and cell wall thickness in both earlywood and latewood.

• In our study, black spruce exhibited smaller tracheid size in both stem and roots compared to balsam fir. Furthermore, the lower amount of tracheids produced during the growing season and higher proportion of latewood ensure a higher wood density of black spruce. The influence of temperature on earlywood formation is significant, whereas no influence was observed on latewood.

Résumé – Relations entre climat et caractéristiques cellulaires dans la tige et les racines de l'épinette noire et du sapin baumier.

• Les différences anatomiques au niveau de la tige et du système racinaire d'épinettes noires et de pins gris matures ont été examinées afin de caractériser la qualité de leur bois au niveau cellulaire et de le relier aux conditions climatiques.

• Les propriétés anatomiques de ces espèces ont été évaluées en relation avec des variables climatiques compilées au cours des années 2001 à 2004 durant la phase d'élargissement des cellules (CE) et celle de l'épaississement et de la lignification des parois (WTL). L'aire du lumen, l'épaisseur des parois ainsi que le nombre total de trachéides au niveau du diamètre radial des cellules ont été analysés et regroupés selon le bois final et le bois initial.

• Les résultats issus d'une analyse en composantes principales (PCA) ont révélé que les deux premiers facteurs (eigenvector) représentent 82 % et 90 % de la variance totale de CE et de WTL respectivement. Ces composantes ont indiqué que la précipitation, l'humidité et le nombre de jours avec pluie influencent significativement la formation de l'aire du lumen ($p = 0.0168$) et le diamètre radial des cellules ($p = 0.0222$) dans le bois initial. Des différences significatives ont aussi été enregistrées entre les espèces et les parties de l'arbre pour l'aire du lumen, le diamètre radial des cellules et l'épaisseur des parois dans le bois initial comme dans le bois final.

• Dans notre étude, l'épinette noire a présenté dans les tiges et les racines des trachéides de plus petite dimension contrairement au sapin baumier. De plus, la faible quantité de trachéides produite durant la saison de croissance combinée à une proportion plus grande de bois final confère à l'épinette noire une densité de bois plus élevée. Une influence significative de la température a été enregistrée sur la formation du bois initial.

* Corresponding author: ckrause@uqac.ca

1. INTRODUCTION

It is well known that climate influences tree-ring formation and wood characteristics, as demonstrated by numerous dendroclimatological studies worldwide (Hughes, 2002). These studies focussed on the relationships between climatological data and ring width in the stems of several tree species. However, the commercial species of the Canadian boreal zone have only occasionally been examined and roots rarely considered (Krause and Morin, 1995; 1999). In the last decade, some innovative approaches have been developed to investigate climate-growth relationships at both high temporal and spatial resolution, such as dendrometers, microsampling and pinning (Rossi et al., 2008; Turcotte et al., 2009). Deslauriers et al. (2003) and Deslauriers and Morin (2005) provided interesting information on cambial activity and its relation to climate by examining tracheid formation and xylogenesis of balsam fir in the boreal forest of Quebec. The authors showed that this species needs an adequate water availability and sufficiently high night-time temperatures to produce tracheids. A relationship between the onset of cambial activity and low temperatures has been also evidenced by Thibeault-Martel (2007) in black spruce. However these analyses were possible only after repetitive sampling of growing tissues, with the impossibility of a retrospective examination. Moreover, to our knowledge, no long-term monitoring of tree-ring formation has been done.

The scarcity of research at root level is obviously explained by the lack of commercial interest in these organs. However, roots play an essential role in the physiology and stability of trees, so investigations on their structure and growth can allow mechanisms of development of the tree as a whole to be understood. It is already known that roots may contain xylem with higher contents of parenchyma and fewer cells than the stem (Fayle, 1968). In addition, cells produced in the roots are usually wider and longer, with thinner and less lignified walls (Trendelenburg and Mayer-Wegelin, 1955). Such information is almost non-existent for the boreal species in Canada, even for stems. However, the wood and paper industries prefer black spruce to balsam fir because the former exhibits higher wood stiffness (Alteyrac et al., 2006). This parameter is directly linked to wood density, as well as microfiber angles (Cown, 2005; Downes et al., 2002; Wimmer et al., 2008). From an anatomical point of view, the major contributing factor to wood density is the proportion of latewood and, specifically, cell wall thickness (Antal and Micko, 1994; Ivkovich et al., 2002). This suggests that an increase in cell wall thickness, as well as the percentage of latewood, should translate into better mechanical properties. This knowledge is currently unavailable for roots.

Genetic traits play a role in regard to wood density and cell anatomy, interacting with climatic parameters to influence the xylogenesis. Climate-growth relationship has seldom been examined at root system level despite its potential for dendroclimatological studies having been shown by Schulman (1945). In four tree species from northern Germany, different climatic signals are found in roots and stem. The highest temperature signal is registered within the stem, whereas the highest precipitation signal occurs within the roots (Krause and Eckstein, 1993). The increasing interest in the influence of climate on wood features is still limited to few species and locations around the world (Drew and Downes 2009; Fritts et al., 1999). By examining tree-ring development, a longer period of cambial activity is assumed to occur in roots (Stevens, 1931). Thibeault-Martel et al. (2008) showed that cell production in roots and stem occurred at the same time, although significant differences in cell maturation were observed between the two tree parts. Compared to the stem, lignification of cell walls started later in roots and lasted for a longer period. Thus, climatic parameters do affect the anatomical features of wood, but the influences are expected to occur at different intensities in the tree parts because of the different time window available for tracheid formation in roots and stem.

This paper aims to assess the anatomical differences between stem and roots in black spruce and balsam fir and to link these differences to climate. We tested the hypothesis that, given the higher wood stiffness, black spruce exhibits wood with a higher amount of latewood and greater cell wall thickness compared to balsam fir.

2. MATERIALS AND METHODS

Two study plots were selected in the southern part of the boreal forest in the Lac-Saint-Jean region (Quebec, Canada), at the Simoncouche research station (48° 12' N, 71° 14' W). The plots were 250 m apart and located within monospecific stands of black spruce and balsam fir originating from a forest fire in 1922 (Gagnon, 1989). The average annual temperature, recorded at the closest weather station, 1.5 km away, was 1.5 °C in the period from 2001 to 2004. The average summer temperature was 14.7 °C and annual precipitation was 667 mm.

2.1. Sampling

Ten dominant or co-dominant adult trees with upright stem and similar radial growth, as well as similar number of tracheids formed per tree ring, were selected for each species (Tab. I). Trees with polycormic stems, partially dead crowns, reaction wood (by checking increment cores), or evident damage due to parasites were excluded. On each tree, microcores were collected on the stem at breast height, and on two horizontally-oriented roots at an approximate distance of 80 cm from the stump beneath a 1–5 cm layer of soil and mosses. Samplings in the stem were oriented parallel to the slope and, in roots, were taken on the upper part in order to avoid compression wood or discontinuous rings, which are frequently noted on the underside of roots (Fayle, 1968). Anatomical measurements were performed on the tree rings produced during the period 2001–2004.

Table I. Characteristics of the sampled trees.

	Balsam fir	Black spruce
Age (cm)	50	70
Tree height (m)	14.4 (1.7)	17.8 (1.7)
DBH (cm)	18.4 (1.3)	21.1 (2.5)

Table II. Anatomical parameter statistics of trees sampled by species and tree part.

Balsam fir		Stem			Root	
Parameters	RW	EW	LW	RW	EW	LW
Tracheid count	33.7 (8.1)	26.8 (7.1)	6.9 (1.9)	39.7 (23.4)	33.2 (22.1)	6.5 (3.1)
Tracheid count (%)		80	20		84	16
Lumen area		982.7 (255.1)	166.0 (122.2)		981.1 (301.7)	211.8 (128.9)
Cell wall thickness		2.5 (0.7)	4.2 (0.9)		2.9 (0.8)	4.5 (0.8)
Cell radial diameter		37.0 (5.4)	16.0 (6.0)		38.4 (6.2)	18.8 (6.0)
Cell wall/lumen ratio		0.09 (0.04)	0.82 (0.52)		0.10 (0.05)	0.7 (0.4)
Black spruce		Stem			Root	
Parameters	RW	EW	LW	RW	EW	LW
Tracheid count	20.7 (6.2)	13.0 (4.1)	7.7 (2.9)	35.5 (23.6)	23.9 (19.3)	11.6 (6.7)
Tracheid count (%)		63	37		67	33
Lumen area		724.2 (187.7)	124.4 (95.9)		649.3 (200.3)	193.4 (111.5)
Cell wall thickness		2.5 (0.6)	4.5 (1.1)		3.5 (0.8)	5.4 (1.1)
Cell radial diameter		31.4 (5.2)	16.0 (5.3)		33.8 (4.9)	22.1 (6.5)
Cell wall/lumen ratio		0.10 (0.05)	0.95 (0.51)		0.15 (0.11)	0.67 (0.43)

RW: Ring-width; EW: earlywood; LW: latewood.

Microcores were dehydrated by successive immersions in ethanol and D-limonene, embedded in paraffin, then transverse sections of 8–10-μm thickness were cut with a rotary microtome (Rossi et al., 2006a). The sections were stained with aqueous 1% safranin and fixed on slides with the Eukitt® histological mounting medium. A camera mounted on an optical microscope was used to record numerical images and measure xylem features with an image analysis system specifically designed for wood cells (WinCELL™). Anatomical features of xylem (cell lumen area, cell radial diameter and cell wall thickness) were measured along three radial paths of each tree ring at magnifications of 200×, standardized and averaged for each tree (Deslauriers et al., 2003; Vaganov et al., 1990).Tracheids were classified as belonging to earlywood or latewood according to Mork's formula, which classifies all cells with lumen areas of less than twice the thickness of a double cell wall as latewood (Denne, 1988).

2.2. Climate data

A standard weather station was installed in an artificial gap close to the sites to measure temperature at a height of 3 m (T_{mean}, T_{min}, T_{max}, °C) and under cover (T_{cov}, °C), soil water content (SWC, m^3/m^3), precipitation (P, mm), relative humidity (H, %), and radiation (R, Wm^2). Soil water content was measured with a Campbell Scientific CS615 (water content reflectometer), which measures the volumetric water content of porous media using time-domain measurement methods. Data were recorded every 5 min and stored as hourly means or sums in a CR10X datalogger (Campbell Scientific Corporation). The number of days with precipitation (DP) was also calculated for each growing season.

2.3. Statistical analyses

The climatic variables (air and under cover temperatures, precipitation, relative humidity, radiation and soil water content) were separated in two groups and averaged according to the periods of (i) cell enlargement and (ii) wall thickness and lignification, as defined by Deslauriers et al. (2003). The timings of xylogenesis were assessed for this study area by Thibeault-Martel et al. (2008). In both species,

the first enlarging cells were observed at the end of May, while cell wall thickness and lignification occurred until August and September in stem and roots, respectively. These observations were made over a three-year period and small annual variations were registered. Principal component analyses (PCA) were then performed on the averages of the climatic variables calculated for the four sampling years and during earlywood and latewood formation. PCA removed the effects of common factors between the variables producing unique factors uncorrelated with each other. The principal components (PC) extracted using the FACTOR procedure with VARIMAX orthogonal factor rotation (SAS, 2003) were used to project data onto the new reduced space, and were compared with cell lumen area, radial diameter and wall thickness through analysis of covariance (ANCOVA).

3. RESULTS

3.1. Anatomical features of xylem

The samples revealed that balsam fir stems produced 40% more tracheids than those of black spruce at the ring-width level (33.7 versus 20.7) and even 50% within earlywood. The difference was less marked in roots (Fig. 1, 39.7 versus 37.9). Root systems registered higher tracheid counts than the stems in black spruce, with a significant increase of 40% (35.5 versus 20.7). The number of tracheids produced over a four year timespan showed no clear increasing or decreasing tendency.

The proportions of latewood measured within the stem and root tree-rings of balsam fir were low; 20% and 14% respectively. These proportions increased to 37% in black spruce stems and 31% in root tree-rings (Tab. II). The number of latewood tracheids in stems and roots of black spruce was significantly higher than in balsam fir (Fig. 1).

3.2. Cell wall/lumen ratio

Black spruce exhibited a higher cell wall/lumen ratio than balsam fir, especially in the stem latewood, with a value of 0.95
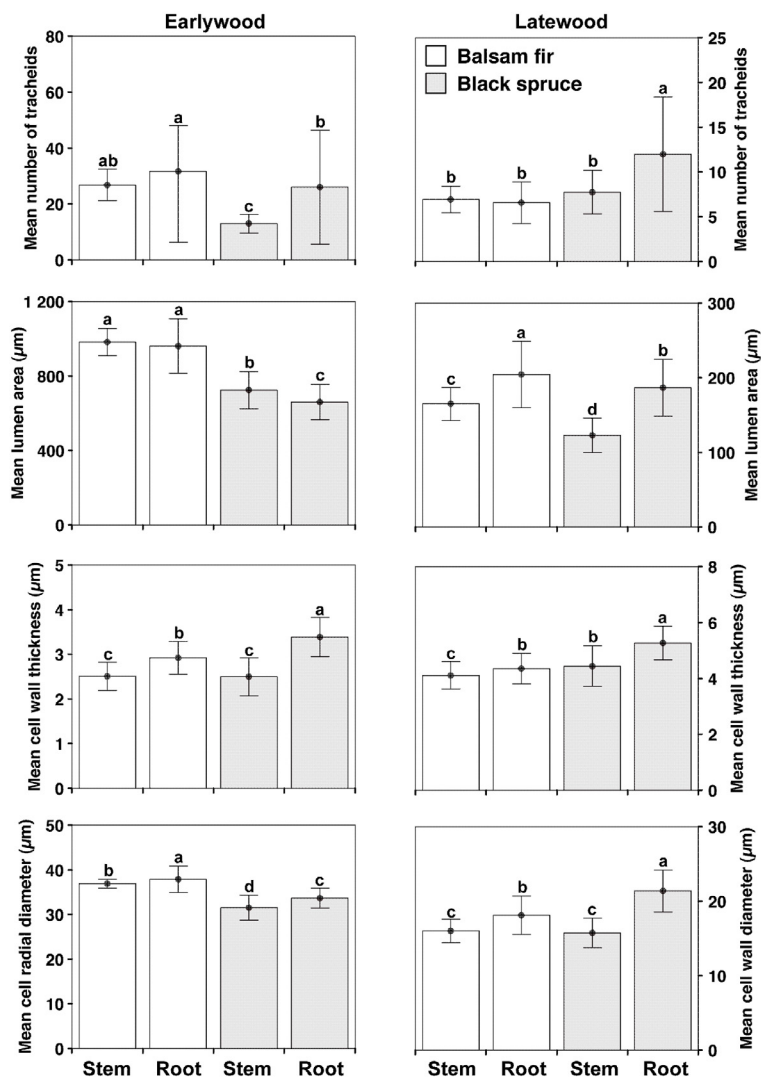
Figure 1. Mean comparisons of anatomical parameters between stem and root within the earlywood and latewood for black spruce and balsam fir. Vertical bars refer to the standard deviation. Same letters are not significantly different ($p < 0.05$).

(Tab. II). This parameter was also higher in the root systems but only in earlywood.

The inter-annual pattern of cell wall thickness within the stems and roots of balsam fir and black spruce was characterized by low values at the start of tree-ring formation (earlywood), followed by a gradual increase toward the end of earlywood development. This trend continued during the early phase of latewood formation, but was replaced by a decrease in cell wall thickness at the end of tree-ring formation. The cell wall thickness was similar (2.5 μm) within the stem of both species in the earlywood. In the latewood, the cell wall thickness was higher in black spruce (Fig. 1). At root level, black spruce registered significantly higher cell wall thickness values in earlywood and latewood compared to balsam fir.

The average values of lumen area in the stems of balsam fir were 1250 μm² at the start of tree ring development and gradually decreased to reach values below 500 μm² towards the end of earlywood development. By dividing the tree-ring, the tracheid lumen area within the earlywood averaged 983 μm², whereas it decreased to 166 μm² in the latewood (Fig. 1). A similar trend was observed along the root tree rings, where smaller lumen area values were measured in the latewood.

The tracheid lumen area in black spruce was significantly smaller than in balsam fir in both the earlywood (724 μm²) and latewood (124 μm²) (Fig. 1). Lower lumen area values were also measured in black spruce roots in the earlywood (649 μm²), but significantly higher in the latewood (193 μm²).

3.3. Cell radial diameter

In balsam fir, the tracheid radial diameters were almost similar in stems and roots in the earlywood, whereas they were larger in the latewood of roots (Tab. II).
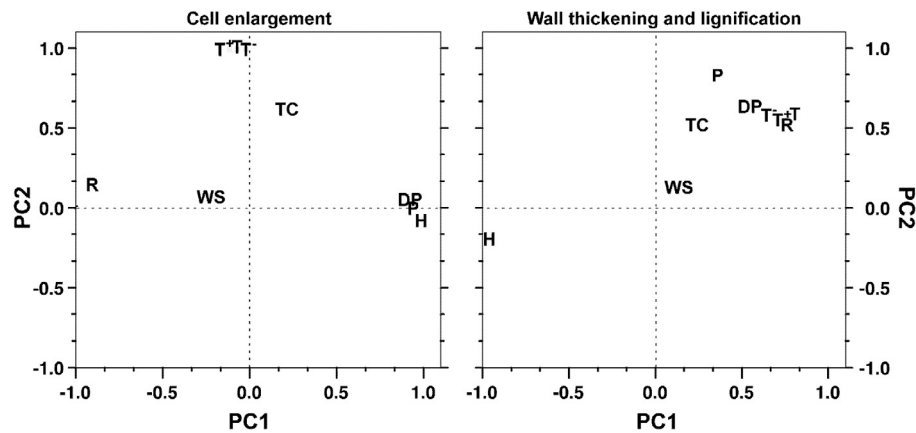
Figure 2. Principal components (PC1 and PC2) calculated on the climatic variables measured during cell enlargement and wall thickening and lignification in xylem of black spruce and balsam fir. The climatic variables included in the analysis are precipitation (*P*), humidity (*H*), number of days with precipitation (DP), mean air temperature (*T*), maximum air temperature (*T*+), minimum air temperature (*T*−), temperature under cover (TC), global radiation (*R*), water in soil (WS).

Table III. Eigenvalues and proportion and cumulative variance explained by the first three principal components (PCs) based on the analysis of climatic variables measured during cell enlargement and wall thickening and lignification in xylem of black spruce and balsam fir.

	Cell enlargement			Wall thickening and lignification		
	Eigenvalue	Proportion (%)	Cumulative (%)	Eigenvalue	Proportion (%)	Cumulative (%)
PC1	4.09	45.51	45.51	7.01	77.87	77.87
PC2	3.29	36.58	82.09	1.12	12.47	90.34
PC3	1.26	14.02	96.12	0.38	4.23	94.57

Table IV. Results of analysis of covariance including principal component factors (PC1 and PC2), species (black spruce and balsam fir) and tree part (stem and roots).

	Earlywood			Latewood		
	Lumen area	Cell diameter	Wall thickness	Lumen area	Cell diameter	Wall thickness
PC1	0.63	1.97	0.07	0.34	0.07	2.29
PC2	7.92*	7.07*	0.00	0.08	0.48	0.68
Species	231.96****	159.41****	4.86*	12.15**	2.33	15.69**
Tree part	3.92	22.72***	30.37***	39.75****	24.23***	12.60**

Asterisks indicate significant differences where * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$ and **** = $p < 0.0001$.

3.4. Relationship between anatomical measurements and climate data

Cell radial diameters were smaller in the earlywood of black spruce stems compared to balsam fir. Small differences were found in the latewood of both species (Tab. II). Average cell radial diameter in the earlywood of black spruce roots was smaller than balsam fir, but larger in the latewood (Tab. II).

The first two principal components (PC1 and PC2) accounted for 82.1 and 90.3% of the total variation. By adding PC3, the variance explained reached 96.1 and 94.6% during cell enlargement and wall thickening and lignification, respectively, although the increase in the variance explained was only 4.2% for wall thickening and lignification (Tab. III). During cell enlargement, PC1 explained 45.5% of the variation and was a measure of water availability, with the higher positive loadings represented by relative humidity, number of days with precipitation and amount of precipitation (Fig. 2). Radiation, as expected, was negatively correlated with water availability and showed highly negative loadings. PC2 represented mainly the air temperature and, to a lesser extent, that under cover. For cell wall thickening and lignification, PC1 explained 77.9% of the variance and measured mainly air temperature and relative humidity, but with opposite effects. Precipitation showed the higher loadings along PC2, although the separation between water availability and temperature was less evident (Fig. 2).

ANCOVA performed between the anatomical features of xylem and PCs produced significant models in both differentiation phases, with *F*-values ranging between 7 and 61 and probabilities lower than 0.01 (Tab. IV), although no influence of PC1 was observed either during earlywood or latewood formation ($p > 0.05$). For PC2, significant results were observed

on lumen area and cell diameter of earlywood, with *p*-values lower than 0.05, but not on wall thickness. No relationship was detected between PC2 and lumen area and cell diameter of latewood. Differences between species and tree part were always significant with p lower than 0.001, except for lumen area between stem and roots and for cell diameter between black spruce and balsam fir ($p > 0.05$).

4. DISCUSSION

4.1. Climate and cell features

The PCA performed between climate data and cell features was based on the period of cambial activity and tree-ring formation observed for the two species in the same sites, and the growing season was subdivided into two growing phases: (a) cell enlargement and (b) cell wall thickening and lignification (Thibeault-Martel et al., 2008). The climatic parameters explained more than 80% and 90% of the total variation within cell enlargement and cell wall thickness and lignification, respectively (Tab. III). Despite the significant differences between species and tree parts, only temperature appeared to be an important factor affecting cell features in earlywood. Cambium activity culminates during June and July (Rossi et al., 2006c), but temperatures can still be cold, even below 0 °C (data not shown). Low temperatures are known to affect cell division, but this study demonstrated their important influence on the processes of cell maturation, so affecting the size of cells and walls. Studies by Richardson and Dinwoodie (1964) and Farrar and Barnfield (1969) revealed that cell enlargement of earlywood occurs essentially at night, when temperatures are low in the boreal forest and so can significantly affect growth. On the contrary, latewood formation occurs during August-September (Deslauriers et al., 2003), when the temperatures are warmer and freezing events infrequent. Moreover, at the end of the growing season, trees set up mechanisms that concentrate the cell sap and lower the freezing point of vegetal tissues, thus improving their frost resistance (Wisniewki and Ashoworth, 1986). Consequently, most latewood is produced during a period of the year with more favourable thermal conditions, thus explaining the lack of influence of the temperature on cell features (Tab. IV). The lower amount of latewood cells (only 6–11 cells along a tree ring) might also explain the weak relationships between climatic parameters and anatomical features. Furthermore, compared to earlywood, longer periods are required for completing maturation in latewood (Rossi et al., 2006b), so extreme weather conditions are expected to influence tracheid formation of earlywood more strongly, because of the shorter time for differentiation. In latewood, unfavourable conditions would have to occur over several consecutive days to be able to significantly influence its anatomical features.

To our knowledge, only one study has correlated anatomical properties to climatic parameters in the Canadian boreal forest. St-Germain and Krause (2008) found no relationship between anatomical measurements along a north-south gradient of temperature and precipitation. The absence of weather stations near the studied stands might explain the results of that work. Although based on two species and two tree parts, our investigation concerns only a 4-year period (tree-ring growth of 2001–2004). Further studies over longer periods are necessary to improve our understanding of the impact of climate on cell and wall formation in boreal conifers.

4.2. Cell features

In our study, the proportion of latewood in balsam fir stems was only 20% of the total ring-width, whereas in black spruce it was 37%. Moreover, the cell wall/lumen ratio was higher in black spruce stems than in balsam fir. These findings confirmed the hypothesis in regard to different anatomical features in black spruce and balsam fir. The proportion of latewood in tree rings is one of the best known parameters used to quantify wood density (Ivkovich et al., 2002). Since latewood and wood density, expressed by cell wall/lumen ratio as well as microfiber angle, are the most important contributors to the mechanical properties of a tree (Downes and Drew, 2008), our findings confirm the higher wood density of black spruce compared with balsam fir, which should result in higher mechanical stiffness.

The high proportion of latewood recorded in black spruce in our research is generally higher than previously published results for other *Picea* species. For example, proportions of latewood in *Picea abies* were around 20% within a tree ring (Bosshard, 1961), whereas this percentage reached 30% in *Picea glauca* and *Picea engelmanni* (Ivkovich et al., 2002). A comparable proportion of latewood (35%) to that measured in black spruce has only been reported in *Picea sitchensis* (Mitchell and Denne, 1997). Our findings indicate that the anatomical features of black spruce explain why this species exhibits better mechanical properties compared to other *Picea* species.

Investigations in roots showed that black spruce exhibits smaller tracheid sizes than balsam fir, which results in higher cell wall/lumen ratios (Tab. II). These anatomical differences are related not only to environmental conditions but also to mechanical forces affecting the root system (Gartner, 1997; Riedl, 1937). By considering only the mechanical stiffness, the cell wall/lumen ratio in balsam fir roots is lower than in the stems (Tab. II). The results are different for roots of black spruce, where the ratio is higher in earlywood but lower in latewood compared to the stem (Tab. II). It is expected that black spruce, as a slow-growing species, requires a smaller lumen area for supporting water transport than the more demanding balsam fir. Compared with balsam fir, the longer needle retention combined with the smaller photosynthetic surface of black spruce might explain the anatomical difference observed between the xylem tissues of the two species. The broad distribution of black spruce within the boreal forest could be attributed to a better anatomical adaptation to the cold climate of high latitudes, with the production of smaller and abundant latewood cells aiming to improve the tissue protection and mechanical stability.

REFERENCES

Alteyrac J., Cloutier A., and Zhang S.Y., 2006. Characterization of juvenile wood to mature wood transition age in black spruce (*Picea mariana* (Mill.) B.S.P.) at different stand densities and sampling heights. Wood Sci. Technol. 40: 124–138.

Antal M. and Micko M.M., 1994. Variation and field estimation of wood quality parameters for black spruce. Holzforsch. Holzverw. 46: 70–72.

Bosshard H.H., 1961. The structure of spruce wood from different sites. Schweizer Zeitung für Forstwesen 112: 317–332.

Cown D., 2005. Understanding and managing wood quality for improving product value in New Zealand. N. Z. J. For. Sci. 35: 205–220.

Denne M.P., 1988. Definition of latewood according to Mork (1928). IAWA Bull. 10: 59–62.

Deslauriers A. and Morin H., 2005. Intra-annual tracheid production in balsam fir stems and the effect of meteorological variables. Trees 19: 402–408.

Deslauriers A., Morin H., and Begin Y., 2003. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). Can. J. For. Res. 33: 190–200.

Downes G.M. and Drew D.M., 2008. Climate and growth influences on wood formation and utilisation. Southern Forests 70: 155–167.

Downes G.M., Wimmer R., and Evans R., 2002. Understanding wood formation: gains to commercial forestry through tree-ring research. Dendrochronologia 20: 37–51.

Drew D.M. and Downes G.M., 2009. The use of precision dendrometers in research on daily stem size and wood property variation: a review. Dendrochronologia 27: 159–172.

Farrar J.L. and Barnfield C.R., 1969. Localized heating and cooling effects on wood development of White Spruce (*Picea glauca* (Moench) Voss., Extr. From Rep. Res. For. Bot. Glendon Hall Fac. For. Univ., Toronto.

Fayle D.C.F., 1968. Radial growth in tree roots-distribution, timing, anatomy. Faculty of Forestry, Technical Report No. 9, Toronto, 183 p.

Fritts H.C., Shashkin S., and Downes G.M., 1999. A simulation model of conifer ring growth and cell structure. In: Wimmer R., Vetter R.E. (Eds.), Tree-ring analysis: biological, methodological and environmental aspects, CABI Publishing, New York.

Gagnon R., 1989. Maintien après feu de limites abruptes entre des peuplements d'épinettes noires (*Picea mariana*) et des formations de feuillus intolérants (*Populus tremuloides* et *Betula papyrifera*) dans la région du Saguenay-Lac St-Jean (Québec). Nat. Can. 116: 117–124.

Gartner B.L., 1997. Trees have higher longitudinal growth strains in their stems than in their roots. Int. J. Plant Sci. 158: 418–423.

Hughes M.K., 2002. Dendrochronology in climatology – the state of the art. Dendrochronologia 20: 95–116.

Ivkovich M., Namkoong G., and Koshy M., 2002. Genetic variation in wood properties of interior spruce. II. Tracheid characteristics. Can. J. For. Res. 32: 2128–2139.

Krause C. and Eckstein D., 1993. Dendrochronology of roots. Dendrochronologia 11.

Krause C. and Morin H., 1995. Impact of spruce budworm defoliation on the number of latewood tracheids in balsam fir and black spruce. Can. J. For. Res. 25: 2029–2034.

Krause C. and Morin H., 1999. Tree-ring patterns in stems and root systems of black spruce (*Picea mariana*) caused by spruce budworms. Can. J. For. Res. 29: 1583–1591.

Mitchell M.D. and Denne M.P., 1997. Variation in density of *Picea sitchensis* in relation to within-tree trends in tracheid diameter and wall thickness. Forestry 70: 47–60.

Richardson S.D. and Dinwoodie J.M., 1964. Studies on the physiology of xylem development. I. The effect of night temperature on tracheid size and wood density in conifers. J. I. Wood Sci. 6: 3–13.

Riedl H., 1937. Bau und Leistung des Wurzelholzes. Jahrbücher für wissenschaftliche Botanik 85: 1–75.

Rossi S., Anfodillo T., and Menardi R., 2006a. Trephor: a new tool for sampling microcores from tree stems. IAWA J. 27: 89–97.

Rossi S., Deslauriers A., and Anfodillo T., 2006b. Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the Alpine timberline. IAWA J. 27: 383–394.

Rossi S., Deslauriers A., Anfodillo T., Morin H., Saracino A., Motta R., and Borghetti M., 2006c. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. New Phytol. 170: 301–310.

Rossi S., Deslauriers A., Gričar J., Seo J.-W., Rathgeber C.B.K., Anfodillo T., Morin H., Levanic T., Oven P., and Jalkanen R., 2008. Critical temperatures for xylogenesis in conifers of cold climates. Glob. Ecol. Biogeogr. 17: 696–707.

SAS, 2003. SAS System, version 9.1.3. SAS Institute Inc., Cary, N.C.

Schulman E., 1945. Root growth-ring and chronology. Tree-Ring Bull. 12: 2–5.

Stevens C.L., 1931. Root growth of white pine (*Pinus strobus* L.). Yale University School Forest Bull. 32: 1–32.

St-Germain J.L. and Krause C., 2008. Latitudinal variation in tree-ring and wood cell characteristics of *Picea mariana* across the continuous boreal forest in Quebec. Can. J. For. Res. 38: 1397–1405.

Thibeault-Martel M., 2007. L'activité cambiale et la xylogenèse entre les tiges et les racines de l'épinette noire (*Picea mariana* (Mill.) BSP) et du sapin baumier (*Abies balsamea* (L.) Mill.). M.S. thesis, Université du Québec à Chicoutimi, 83 p.

Thibeault-Martel M., Krause C., Morin H., and Rossi S., 2008. Cambial activity and intra-annual xylem formation in roots and stems of *Abies balsamea* and *Picea mariana*. Ann. Bot. 102: 667–674.

Trendelenburg R. and Mayer-Wegelin H., 1955. Das Holz als Rohstoff [Wood as a raw material], 2nd ed. Carlttanser Verlag, München, 541 p.

Turcotte A., Morin H., Krause C., Deslauriers A., and Thibeault-Martel M., 2009. The timing of spring rehydration and its relation with the onset of wood formation in black spruce. Agric. For. Meteorol. 149: 1403–1409.

Vaganov E.A., Sviderskaya I.V., and Kondratyeva E.N., 1990. Weather conditions and structure of the annual rings of tree: simulation model of tracheidogram. Lesovedenie 2: 37–45.

Wimmer R., Downes G.M., and Evans R., 2008. Effects of site on fibre, kraft pulp and handsheet properties of *Eucalyptus globulus*. Ann. For. Sci. 65: 602.

Wisniewki M. and Ashowarth E.N., 1986. A comparison of seasonal ultrastructural changes in stem tissue of peach (*Prunus persica*) that exhibit contrasting mechanisms of cold hardiness. Bot. Gaz. 147: 407–417.