Variation of Brown Rot Decay in Eastern White Cedar (*Thuja occidentalis* L.)

Besma Bouslimi, Ahmed Koubaa,* and Yves Bergeron

Variations in brown rot decay and proportions of heartwood and sapwood were investigated in eastern white cedar (*Thuja occidentalis* L.). This experiment tested the hypothesis that the incidence of brown rot decay depends on the site, tree age, tree height, and heartwood/ sapwood ratio. Forty-five trees were sampled and felled from three mature stands in the Abitibi-Témiscamingue region, Quebec, Canada. From each tree, disks were systematically sampled along the entire stem, and the heartwood, sapwood, and decay proportions and volumes were determined for each disk. Scanning electron microscopy showed that growth of fungi causing brown rot decay was limited and slower in latewood than in earlywood due to the narrow cell lumen, thick wall, and limited number of bordered pits in latewood tracheids. Site, tree height, and tree age had significant effects on the proportions of sapwood, heartwood, and decay. Heartwood and brown rot decay proportions decreased from the base of the tree upward, while the sapwood proportion increased. There was more decay in older trees and in those growing on moist versus dry sites; however, decay was not serious in trees younger than 80 years. In addition, brown rot decay proportion correlated strongly and positively with heartwood proportion and tree volume, but negatively with sapwood proportion.

Keywords: Brown rot decay; Wood structure; Site effect; Within-tree variation; Heartwood; Sapwood

*Contact information: Institut de recherche sur les forêts, Université du Québec en Abitibi-Témiscamingue, Québec, J9X 5E4, Canada; *Corresponding author: ahmed.koubaa@uqat.ca;Phone: 819 762-0971 Ext 2579; Fax: 819 797-4727.*

INTRODUCTION

Eastern white cedar (EWC) (*Thuja occidentalis* L.), one of only two arborvitae species native to North America, is distributed over a vast territory extending from the Gulf of St. Lawrence in the east to southeastern Manitoba in the west and from southern James Bay in the north to the Lake States in the south (Burns and Honkala 1990; Little 1979). It grows in a wide variety of soils and on both uplands and lowlands, including swamps, stream banks, lake shores, and even dry rocky cliffs (De Blois and Bouchard 1995; Johnston 1990; Koubaa and Zhang 2008; Matthes-Sears *et al.* 1991).

EWC has outstanding commercial and ecological value (Archambault and Bergeron 1992; Denneler *et al.* 2008; Taylor *et al.* 2002). The timber of this species, especially the heartwood component, has a natural durability that enhances its utility in wooden structures exposed to constant moisture (Taylor *et al.* 2002). For example, the average service life of an untreated EWC heartwood post is 27 years, compared to just 5 years for an untreated, black spruce post (Koubaa and Zhang 2008). Hence, products such as shakes, shingles, fence posts, and mulch made from EWC have considerable potential market value (Behr 1976; Haataja and Laks 1995). The resistance of EWC to microbial attack and decay is attributed to toxic extractives present mainly in the tree's heartwood tissues (DeBell *et al.* 1997; Gripenberg 1949; MacLean and Gardner 1956; Rudloff and Nair 1964; Taylor *et al.* 2002). Even the most decay-resistant woods, however, are susceptible to rot under some combined moisture and temperature conditions.

Stems of maturing coniferous trees typically consist of cylinders of living wood, or sapwood, protected on the outside by bark, and surrounding a central core of physiologically dead wood, or heartwood. The living sapwood is generally resistant to decay as long as it remains alive, which helps protect the heartwood from invasion of decay fungi; however, this protective layer does not remain intact indefinitely. With age, various openings due to wounds, for example, are formed, through which heart-rot fungi may enter (Wagener and Davidson 1954). Additionally, minor discontinuities through which fungi may enter include sapsucker and woodpecker wounds, leaf and twig scars, lenticels and minor fissures, and dead or abscising twigs (Boddy and Rayner 1983).

Heartwood and sapwood proportions vary between and within species and have been related to growth rates, stand and individual tree characteristics, site conditions, and genetic control (Pinto *et al.* 2004). Both woods show several differences other than wood colour, such as wood moisture content, extractives content, and wood permeability (USDA 1999). These differences are critical factors in solid wood and fiber processing and in wood drying (Jozsa and Middleton 1994). For pulping, heartwood is at a disadvantage as its extractives can affect the process and product properties. For solid wood applications the different properties of heartwood and sapwood influence drying, durability, and aesthetic values for the consumer.

Sapwood and heartwood proportions within the stem have a significant effect on the rational utilization of timber (Nawrot *et al.* 2008). Although a few studies have examined sapwood and heartwood distribution in EWC and the effects on wood processing and in-service performance (USDA 1999; Jozsa and Middleton 1994), little information is available on within-tree distribution or site variation. In addition, the relationship between the relative proportion of sapwood and heartwood and tree growth is not known.

Fungal decay is a serious microbiological deterioration that can cause rapid structural failure (Downes *et al.* 2009). It is a very complex process, depending on the type of decay, the wood species, the environment, the wood structure, and the interactive competition between the fungi and the environment (Blanchette 2000; Clausen and Kartal 2003; Fabiyi *et al.* 2011; Green III and Highley 1997; Harju *et al.* 2003; Oliveira *et al.* 2010). In a natural environment, decay colonization is usually initiated by a limited number of spores or hyphal fragments. Thus, wood species containing high quantities of extractives can inhibit fungal colonization (Gripenberg 1949; Kim *et al.* 2009; Rudloff and Nair 1964; Taylor *et al.* 2002), thereby providing resistance to decay.

Any decay that becomes progressive in the central dead wood of a living tree may be termed a heart rot (Wagener and Davidson 1954). EWC is highly susceptible to heart rot, which can cause significant losses and predispose infected trees to windthrow (Hofmeyer *et al.* 2009; Johnston 1990). The most common type of heart rot in EWC is brown cubical rot caused by *Postia balsamea* and *Phaeolus schweinitzii* (Fowells 1965; Koubaa and Zhang 2008). It is widespread in old and damaged trees (Hofmeyer *et al.* 2009). In this respect, EWC presents a particularly interesting opportunity for study because this species is highly susceptible to brown cubical rot.

Heartwood contamination progresses from the pith outward (Amusant *et al.* 2004; Downes *et al.* 2009). Although it varies with wood species, the decay generally occurs in a sequential process of incipient, intermediate, and advanced decay, inducing different physical, chemical, and morphological changes in the wood. Little attention has been paid to the effects of growing conditions on decay occurrence in EWC. Among the few studies, Hofmeyer *et al*. (2009) found decay across all drainage upland sites (well, moderate, and low drained), with the most severe decay (88 % to 97%) in well drained sites.

EWC is considered one of the most decay-resistant wood species of North America (Johnston 1990; Koubaa and Zhang 2008). The trees can attain considerable age, which helps researchers better understand the relationship between age and decay. No study to date, however, has investigated environmental or within-tree variation in decay in this species. The main objective of this study was therefore to investigate site and within-tree variation in heartwood subjected to brown rot decay in eastern white cedar wood.

MATERIAL AND METHODS

Three EWC stands in the Abitibi-Témiscamingue region in the province of Quebec (Témiscamingue, Abitibi, Lac Duparquet), Canada were selected to cover a wide range of soil moisture content conditions (dry, moderate, and moist sites). All stands were dominated by balsam fir and EWC; however, the Témiscamingue site also contained some spruce and yellow birch. The Abitibi site naturally regenerated from fires that occurred from 1760 to 1944 (Archambault and Bergeron 1992; Dansereau and Bergeron 1993). Climatic data for each site were obtained from weather data, from 1930 up to 2007 (Régnière and St-Amant 2007), and stand density was also calculated for each site (Paul 2011). Site location and tree characteristics are summarized in Table 1.

To assess site characteristics, five quadrats (4 m^2) were systematically established at each site. Understory species and organic layer depth were measured at every 1 m^2 quadrat. Five samples of organic horizon soil (organic layer) were collected from each site and analyzed for the following soil properties: pH, moisture and texture, and carbon (C), nitrogen (N), and phosphorus contents (Table 2). Samples were air-dried at 30°C for 48 h and ground to pass through 6-mm sieves. Substrate pH was analyzed in distilled water (Lafleur *et al.* 2011). The carbon and nitrogen contents were determined from dry combustion using a LECO CNS 2000 analyzer (LECO Corporation, St. Joseph, Michigan). The phosphorus content was determined by the Bray II method (Lafleur *et al.* 2011).

A total of 45 trees (15 per site) were randomly sampled from each site. The sampled trees were felled, and total height and diameter at breast height were measured using a steel tape (Table 1). From each felled tree, 10 cm-thick disks were sampled at 0.5, 1.3, and 3 m stem heights and at every 2 meters thereafter up to the top of the tree. In order to determine the age of the studied trees, a total of 90 cores (2 per tree) were taken from these trees at approximately 50 cm above the ground. This height represents a loss of about 3 to 5 years of growth in relation to total tree age (Savva *et al*. 2010). Ring number and density were determined on increment cores sampled at breast height using a QTRS-01X, a Tree-Ring X-Ray Scanner (QMC, Knoxville, Tennessee) according to the procedure described in Koubaa *et al.* (2002).

Heartwood diameter and sapwood thickness were determined visually for all sampled disks. The total diameter (TD) inside the bark and heartwood diameter (HD) were measured for each disk, along and perpendicular to the longest axis based on an established measurement rule. Sapwood thickness (ST) was computed from the half-difference between the total disk diameter and the heartwood diameter (ST=(TD-HD)/2) (DeBell and Lachenbruch 2009). When present, decay diameter (DD) was calculated in the same way at each sampling height to the nearest millimeter.

In stem cross section, the heartwood area decreased from the base to the top, following the stem shape. In the sampled discs, the shape of decay approximates a circle, as do tree sections; therefore, decay, sapwood, and heartwood areas were estimated assuming a circular shape, according to Alteyrac *et al.* (2006). Heartwood, sapwood, and decay volumes in the tree were estimated using a truncated cone formula (Alteyrac *et al.* 2006; Wernsdörfer *et al.* 2006).

Table 1. Stand and Tree Characteristics of Eastern White Cedar Grown in the Abitibi-Témiscamingue Region, Quebec, Canada

Stands	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	314m	272m	333m
Ecological type	Cedar-fir stand	Cedar-fir stand	Cedar-fir stand
Average Temperature [a]	1.65 °C	1.64 °C	2.33 °C
Annual precipitation [a]	854.1mm	840.7mm	932.8 mm
Tree age (years)	96(58–134)	121(73–198)	93(75-127)
Stand density (%)	72.97	84.31	69.81
Age of decay incipient	90 (77–101)	80 (73–105)	73 (70–122)
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)
Wood density (kg/m^3)	360 (260-526)	360 (262-525)	354 (266-532)

[a] Values were calculated from weather data, from 1930 up to 2007 (Régnière and St-Amant, 2007);
Data range is given in parentheses.

Table 2. Soil Properties of the Sampled Stands

Stands	Abitibi (A)	Lac Duparquet (L)	Témiscamingue (T)
Organic layer depth (cm)	7.6	45	350
pH (CaCl2)	6.99	6.32	4.65
Moisture (%)	26.13	29	37.16
Clay (%)	40.35	54.7	5.6
Silt (%)	27.95	28.75	43.75
Sand (%)	16.7	16.55	50.65
Texture	Clay	Clay	Sandy loam
C (%)	31.76	32.28	43.02
N (%)	1.30	1.30	1.39
C/N	24.43	24.83	30.95
P (mg/g)	0.075	0.070	0.064

Disks were air-dried for up to 9 months until sample preparation for scanning electron microscopy (SEM) analysis and other property measurement. SEM analysis was conducted on selected sound and decayed heartwood samples for comparison. Two small samples from each class of wood (sound wood, and initial and advanced stages of decay) were cut and prepared for scanning electron microscopy (SEM). Samples were first soaked in water overnight for softening. They were then oven-dried for 2 h at 100 °C. The area of interest was cut out with a razor and deposits of platinum followed by carbon were applied to the surface. The observations were performed using a scanning electron microscope (model JSM-840A).

Data were analyzed using Statistical Analysis System (Littell *et al.* 2006; SAS 2008). Sapwood, heartwood, and decay proportions were subjected to variance analysis using a mixed-model approach with cambial age as repeated measures (Littell *et al.* 2006), where the factors tree height, site, and cambial age (within each height) were considered as fixed effects and tree as a random effect. 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 (Eq. 1):

$$Y_{\mathrm{ijk}} = \mu + S_{\mathrm{i}} + T_{\mathrm{j(i)}} + \alpha_{\mathrm{k(j)}} + A_{\mathrm{l(kj)}+}\varepsilon_{\mathrm{ijkl}} \quad (1)$$

Where Y_{ijk} is the mean of the response variable for the k^{th} height of the j^{th} tree at the i^{th} site, μ is the overall mean of the response variable of the k^{th} height of the j^{th} tree at the i^{th} site, S_i is the fixed effect associated with the i^{th} site, $T_{(j)i}$ is the random effect associated with the j^{th} tree at the i^{th} site, $\alpha_{k(j)}$ is the fixed effect associated with the k^{th} height of the j^{th} tree, $A_{l(kj)}$ is the fixed effect associated with the l^{th} age at the k^{th} height of the j^{th} tree, and ε_{ijkl} is the residual error. Because heights were not equally distributed, a parametric power transformation was applied to model autocorrelation effects using the Tukey–Kramer adjustment (Littell *et al.* 2006).

The MIXED procedure in SAS (Littell *et al.* 2006; SAS 2008) was used to fit models using restricted maximum likelihood (REML). Degrees of freedom were determined using the Kenward–Roger method. 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. Due to small site replication, results of the Z-tests must be considered indicative only (Littell *et al.* 2006). Tukey's multiple range test was performed to estimate the statistical significance of tree height differences. Variance components were estimated as a percentage of the total variation (VAR) of all effects, using the VARCOMP procedure. Correlation analyses were also conducted using the CORR procedure to establish relationships between decay volumes, tree volume, tree age, heartwood volume, and sapwood volume.

RESULTS AND DISCUSSION

Macroscopic Structure of Sound and Brown Rot Decayed Wood

Figure 1 illustrates the macroscopic structure of sound wood (Fig. 1a), early stages of decayed wood (Fig. 1b), and advanced stages of decayed wood (Fig. 1c and 1d). Figure 1a shows the variations in shape and color between heartwood and sapwood. The heartwood of eastern cedar has a dark red color that distinguishes it from the sapwood due to the higher extractives content in the heartwood (Amusant *et al.* 2008; Freitag and Morrell 2001; Taylor *et al.* 2002).

The decay in sampled trees was limited to the heartwood (Fig. 1b), and was generally characterized by brown discoloration and a friable, cubically cracked texture when dry (Fig. 1b-d). Similar observations were reported by Eriksson *et al.* (1990). In advanced decay, cracks appeared in the decayed wood (Fig. 1c). In late stages of advanced decay, the wood was completely degraded, resulting in the appearance of a cavity in the center of the log (Fig. 1d). Merchantable losses due to brown rot decay can be extensive in older trees, because the most valuable part of the tree, the butt log, is the most seriously affected.

Fig. 1. Macroscopic structure of heartwood, sapwood, and decay in *Thuja occidentalis* L.:
a. Cross-section of eastern white cedar showing shape and color variations between heartwood and sapwood.
b. Cross-section of eastern white cedar showing shape and color variations in the early stage of decay.
c. Cross-section of eastern white cedar showing brown cubical rot and the appearance of cracks.
d. Cross-section of eastern white cedar showing an advanced stage of decay where the wood is completely rotten.

Microscopic Structure of Sound and Decayed Heartwood

Sound heartwood in *Thuja occidentalis* is relatively homogeneous and simple in structure, consisting primarily of overlapping tracheids, uniseriate xylem rays, and parenchyma cells (Fig. 2a and b). The tracheid cell walls are organized in layers of different thicknesses: thick latewood cell walls and thin earlywood cell walls (Fig. 2b). The cell walls surround the lumen, and the walls of adjacent cells are bonded together by the middle lamella (Fig. 2b). The tracheid cells are connected by bordered pits, which are visible and abundant on the radial face (Fig. 2c and d). Latewood tracheids are characterized by a narrow cell lumina (Fig. 2b) and a limited number of sparse bordered pits (Fig. 2c).

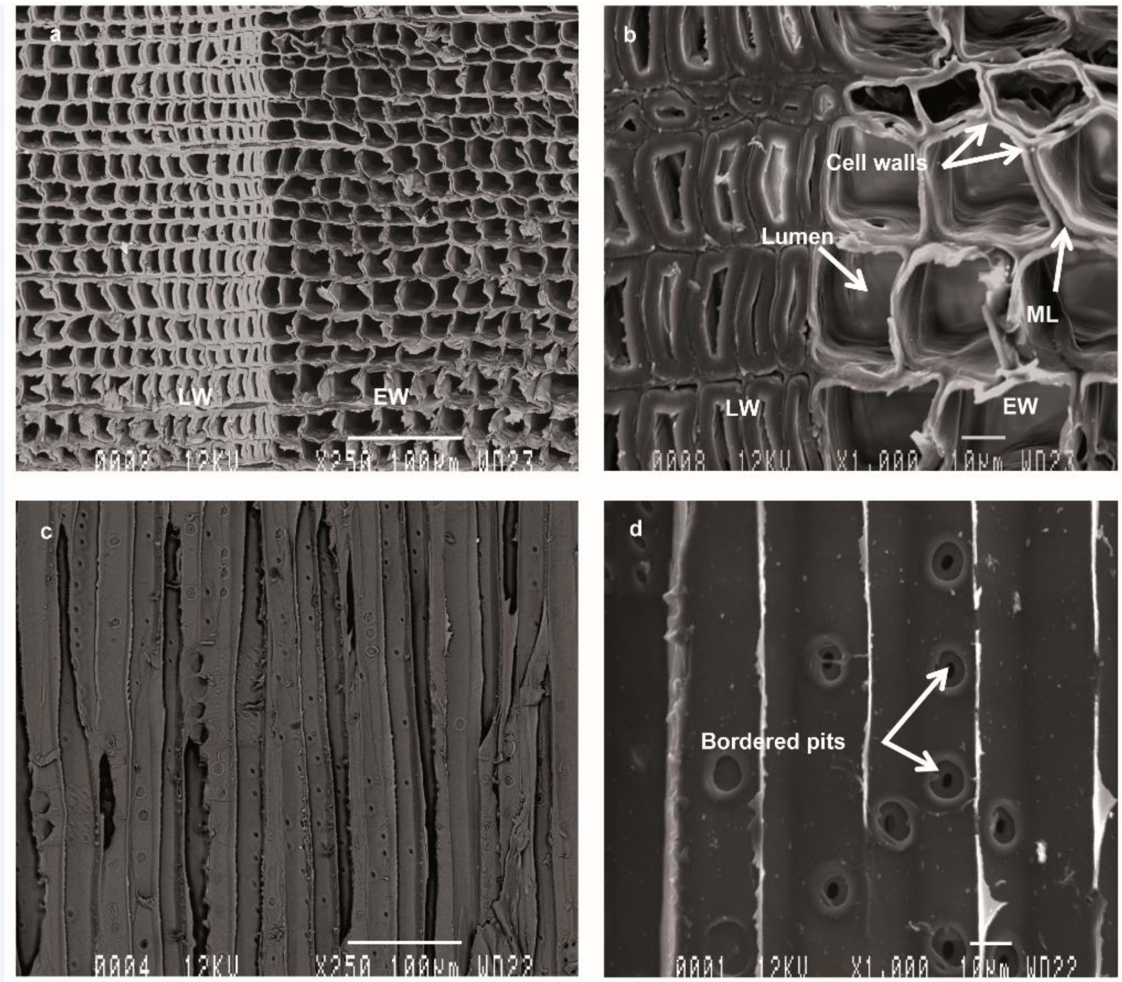

Fig. 2. Cell structure of sound *Thuja occidentalis* L. heartwood:

a. Transverse section showing earlywood (EW) and latewood (LW) tracheids and a ray cell (R)
b. Transverse section showing cell walls, middle lamella (ML), and lumen in earlywood (EW) and latewood (LW) tracheids
c. Radial section showing bordered pits in earlywood and latewood tracheids
d. Radial section showing intertracheid bordered pits in earlywood

The structure of decayed heartwood (Fig. 3) shows the presence of hyphae and a progressive degradation of the wood structure (Fig. 3a). The fungal growth occurred rapidly within the broad cell lumina of the earlywood tracheids, causing a progressive degradation of lumen (Fig. 3b and 3c). The initial decay was more extensive in earlywood than in latewood (Fig. 3b) due to the narrow cell lumina and the thick cell walls characteristic of latewood compared to earlywood (Fig. 2b). In advanced decay, earlywood cells showed substantial degradation (Fig. 3c), which extended to latewood cells (Fig. 3d). This degradation produced porous zones in the earlywood and latewood tissues in the late decay stage, which typically leads to the development of cracks between adjacent holes in the radial cell walls. Eventually, the holes coalesce and crack (Fig. 3d).

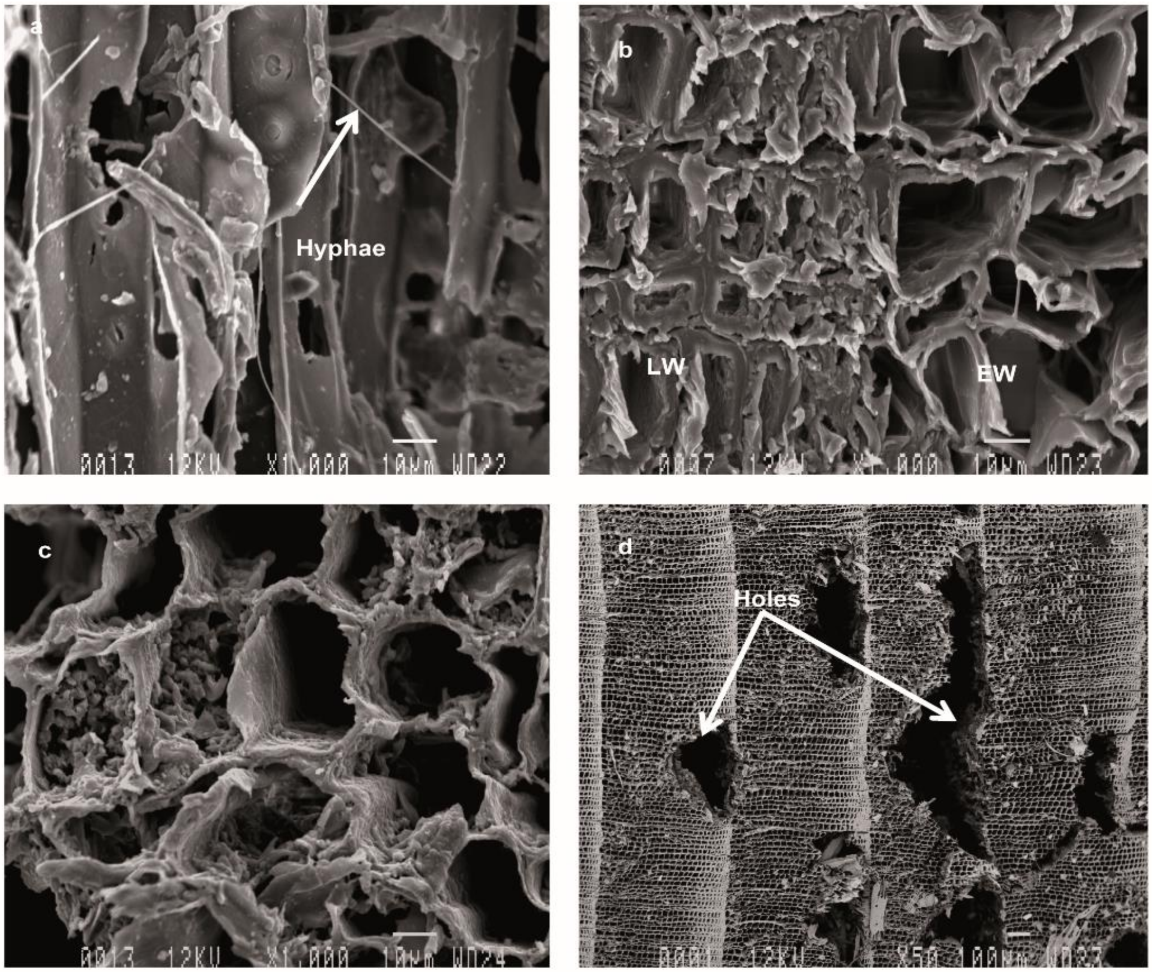

Fig. 3. Cell structure of decayed heartwood in *Thuja occidentalis* L.:

a. Radial section showing initial decay, with hyphal growth in earlywood tracheids
b. Transverse section showing rapid decay growth in the cell lumina of earlywood tracheids (EW) compared to latewood tracheids (LW)
c. Transverse section showing substantial degradation of lumen, cell walls, and middle lamella in earlywood tracheids
d. Transverse section showing porous areas (holes and cracks) in both earlywood and latewood tracheids in advanced decay

In the early stages of brown rot decay, higher degradation was found in early-wood. This result is in good agreement with previous reports of decay in other woods such as oak and Norway spruce (Schwarze 2007; Schwarze and Ferner 2003; Schwarze *et al.* 2004). This early evidence of cell wall degradation in earlywood was attributed to birefringence loss (Schwarze and Ferner (2003). The lower degradation of latewood fibres appears to be related to higher cell wall lignification in the thick walls, which hampers the transfer of the cellulolytic enzyme produced by the fungal hyphae into the cell wall (Schwarze 2007). Blanchette (2000) attributed this lower degradation to the limited number of bordered pits in the latewood cell walls compared to earlywood, delaying the proliferation of decay.

Variations in Sapwood, Heartwood, and Decay

Site and inter-tree variations in sapwood, heartwood, and decay volume are presented in Table 3. For example, average heartwood volume proportion ranged from 31 to 77%, while sapwood proportion ranged from 23 to 69%. Brown rot decay volume ranged from 0 to 23%. Coefficients of variation for sapwood and heartwood volume proportions were 22.3% and 13.7%, respectively; however, decay proportions showed significant inter-tree variation (141.8%). The average decay proportions ranges from 1.9 to 3.6% with site, and goes as high as 23% of the total tree volume (Table 3).

Table 3. Means, Ranges, and Coefficients of Variation (CV %) of Sapwood, Heartwood, and Decay Volume in *Thuja occidentalis* L. from Three Different Sites

Sites	Sapwood volume (%)			Heartwood volume (%)			Decay volume (%)		
	Mean*	Range	CV	Mean*	Range	CV	Mean*	Range	CV
Abitibi	46.4 [a]	23-69	25.6	53.6 [a]	31-77	15.3	1.9 [a]	0-14	157
Lac Duparquet	43.0 [a]	24-57	22.3	57.0 [b]	43-76	13.5	3.2 [b]	0-22	134.5
Témiscamingue	46.3 [a]	28-63	17.9	53.7 [a]	37-72	11.8	3.6 [b]	0-23	133.2
All data	45.3	23-69	22.3	54.7	31-77	13.7	2.9	0-23	141.8

*Average followed by the same letter indicate no significant difference between sites at p=0.05

The analysis of variance (Table 4) showed that tree height as well as tree and cambial age significantly affected sapwood, heartwood, and decay proportions. The site effect, however, was significant on decay proportion only. The variations in sapwood, heartwood, and decay proportions with tree height and site are shown in Fig. 4. The variations in sapwood, heartwood, and decay volume with tree age and tree height are shown in Figs. 5 and 6, respectively.

The sapwood proportion showed a typical longitudinal variation characterized by a steady increase from the base of the tree upward (Fig. 4a); however, sapwood proportion was more variable toward the top than at the base (Fig. 4a). The same observations were reported with Tasmanian bluegum (*Eucalyptus globulus* Labill.), where sapwood thickness remained practically constant in the lower part of the stem, and increased upwards independently of spacing (Gominho and Pereira 2005; Miranda *et al.* 2006).

In general, the Duparquet site showed the lowest sapwood proportion and the Abitibi site the highest, but the difference between sites was not statistically significant (Fig 4a and Table 4). The height effect was the most important source of variation in sapwood proportion (Table 4), accounting for 60.3% of the total variation, followed by tree (7.6%), cambial age (5.9%), and site (0.1%). The same tendency was observed in the variation in sapwood volume with tree height (Fig. 6a). Sapwood volume increased with tree height. The coefficient of determination for the relationship between tree height and sapwood volume was highly significant (R^2=0.87). Tree age (Fig. 5) was also an important source of variation in tree sapwood volume (R^2=0.52), as sapwood volume decreases with increasing tree age.

Height is the main source of the variation in heartwood proportion. It accounts for 62.3% of the total variation (Table 4). The heartwood proportion normally decreases from the base of the tree upward (Fig. 4b). The same tendency was observed for the variation in heartwood volume with tree height (Fig. 6a). Tree height is also a major source of variation in tree heartwood volume (R^2=0.37). In addition, heartwood volume was positively and strongly related to tree age (R^2=0.52) (Fig. 5). These results are in good agreement with previous findings for European larch (*Larix decidua* Mill.) (Nawrot *et al.* 2008) and maritime pine (*Pinus pinaster* Ait.) (Knapic and Pereira 2005). According to Pinto *et al.* (2004), the tree as a whole is composed of sapwood until the age at which the stem exceeds the lifespan of the parenchymal cells. Because cambium age decreases with increasing stem height, the age of the parenchymal cells decreases as well. Hence, the death of these cells initiates the transformation of sapwood into heartwood, and the relative proportion of heartwood decreases from the base of the stem towards the tree top. The same observations were reported with Tasmanian bluegum (*Eucalyptus globulus* Labill.), where heartwood volume decreased from the base upwards and was positively correlated with tree growth (Miranda *et al.* 2006).

Table 4. Linear Mixed Model Analysis of Variance; Showing F Values for Fixed Effects, Z Values for Random Effects, their Significance, and the Variance Component (VAR COMP) of each Source of Variation for Decay, Heartwood, and Sapwood Area in Percent for *Thuja occidentalis* L.

Fixed effects							
Sources	df a	F value	VAR COMP (%)	F value	VAR COMP (%)	F value	VAR COMP (%)
		Sapwood		Heartwood		Decay	
Site	2	0.9^{ns}	0.1	0.8^{ns}	1.2	5.2^{**}	1.3
Height	7	82.7^{***}	60.3	88.9^{***}	62.3	52.8^{***}	35.8
Cambial age	123	1.6^{*}	5.9	1.6^{*}	6.0	2.8^{**}	23.2
Random effects							
Sources	df [a]	Z value	VAR COMP (%)	Z value	VAR COMP (%)	Z value	VAR COMP (%)
Tree	14	2.4^{**}	7.6	2.4^{*}	5.3	1.9^{*}	2.6
Residual	137	6.4^{**}	26.1	6.3^{**}	25,2	6.9^{**}	37.2
[a] Degree of freedom; Significance level: * = p<0.05, ** = p<0.01, ***= p<0.001, and ns = not signif.							

The site effect on heartwood and sapwood proportions was not significant. The significant effect of trees nested within sites could partially explain this result (Table 4). Despite the variation in site properties (Table 1), the site effect could be masked by the tree-to-tree variation. The tree effect on sapwood and heartwood proportions was highly significant (Table 4). It accounted for 7.6% and 5.3% of the sapwood and heartwood proportions, respectively. This effect could be explained by the age difference between the sampled trees. The analysis of variance revealed significant effects of site, tree, tree height, and cambial age on the decay proportion (Table 4).

Tree height was the main source of variation, accounting for 35.8% of the total variation. The larger height variation in decay proportion was associated with a large standard error, which was greater for the Témiscamingue site (Fig. 4c and Table 3). Decay initially increased from tree base upward to about breast height and decreases upward thereafter. The same tendency was observed for the variation in decay volume with tree height (Fig. 6b). The coefficient of determination for the relationship between tree height and decay volume was highly significant (R^2=0.87).

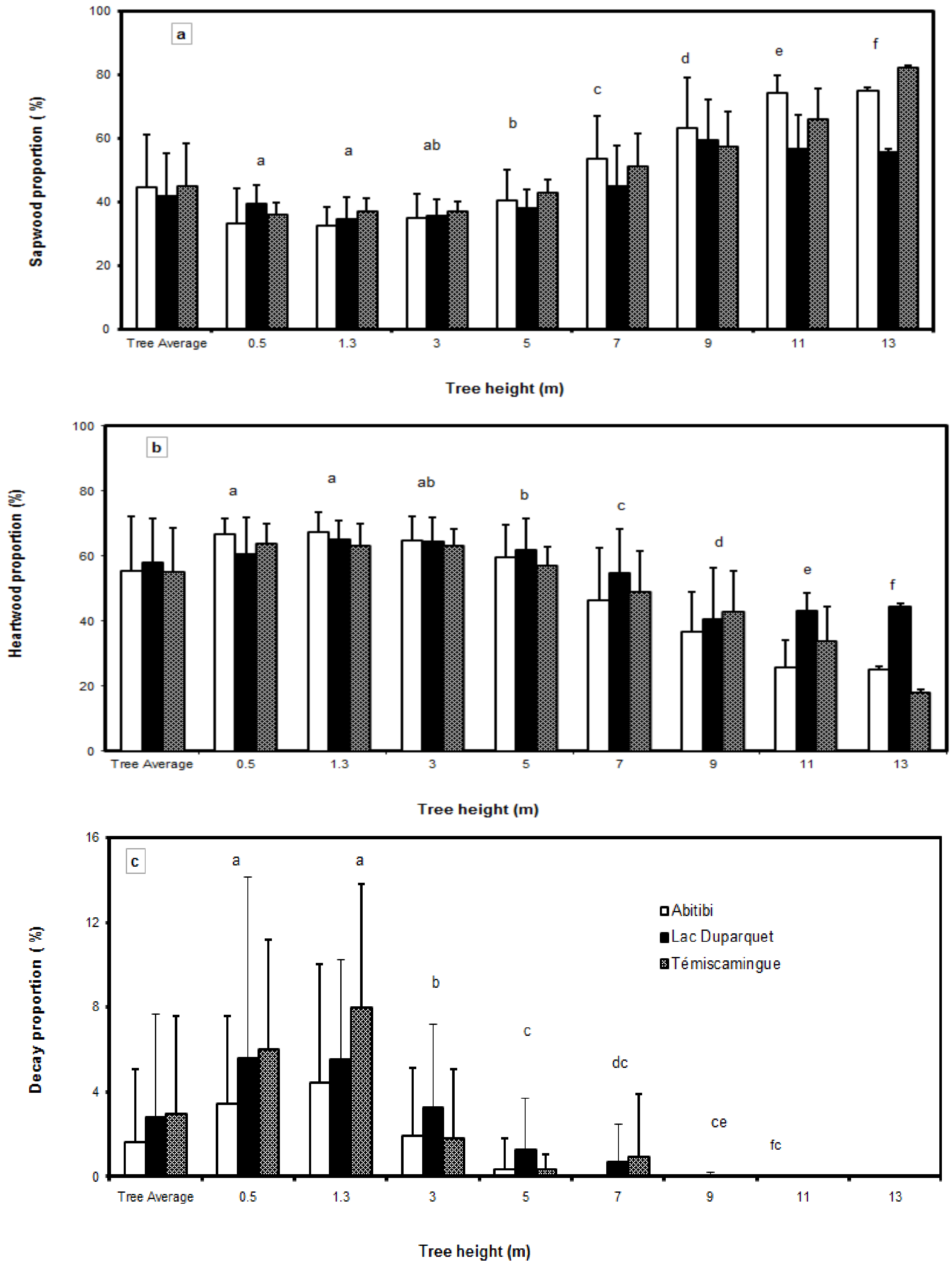

Fig. 4. Tree height variation in a) sapwood, b) heartwood, and c) decay proportion in *Thuja occidentalis* L. from three sites in Abitibi-Témiscamingue, Québec. Bars indicate standard errors. The same letter indicates no significant difference at p=0.05.

The wood is more susceptible to decay in the base than in the top (Fig. 4c). The lower part of tree is more susceptible to fungal infection due to various openings through which heart rot fungi may enter. Wounds from various origins such as fire, weather factors, logging and silvicultural operations, and animal and insect activity are among the causes of entry (Hofmeyer *et al.* 2009; Wagener and Davidson 1954). In addition, studies on a large number of species have reported greater decay resistance in the tree top than in the base (Amusant *et al.* 2004; Debell *et al.* 1999; Gartner *et al.* 1999), which can partially explain the results of this study.

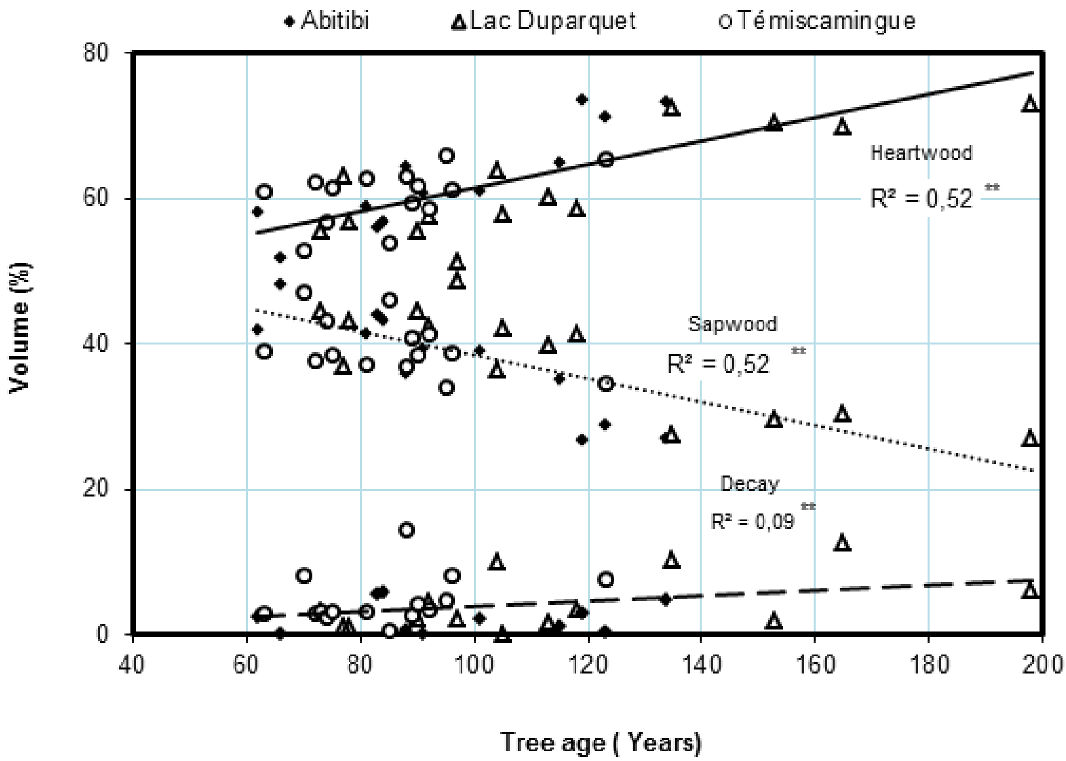

Fig. 5. Variation in sapwood, heartwood, and decay volume with tree age in *Thuja occidentalis* L. Significance level: ** $p<0.01$

Decayed wood was found mainly in the heartwood (Fig. 1). Thus, the heartwood appears to be more susceptible than sapwood to decay development. In the upper parts of the tree, where the heartwood proportion is relatively low, the proportion of decay is consistently lower compared to the base of the tree (Fig. 4b and c). These results are in good agreement with Wagener and Davidson (1954), who reported that the heartwood of practically every tree species is subject to decay in the living tree by one or more rot fungi.

Although the effect of site on decay proportion is highly significant ($p<0.01$), it accounts for only 1.3% of the total variation. This low site variation could be explained by the natural variation in decay resistance between trees within a same stand, masking site differences (Freitag and Morrell 2001). Figure 4c illustrates the variation in decay proportion between the three sites. The lowest incidence of decay was found in wood from the Abitibi site, followed by the Lac Duparquet site. The highest incidence of decay was found in wood from the Témiscamingue site. The site variation in decay proportion could be explained by several factors, including different site conditions.

The incidence of decay is lower in samples from the Abitibi site (Fig. 4c), where the soil is dryer and has less organic content (Table 2). These results are in good agreement with previous studies on decay incidence in wood species (Blanchette 2000; Hofmeyer *et al.* 2009; Little *et al.* 2010). Other potential factors such as nutrient levels (Little *et al.* 2010) and temperature (Trevisan *et al.* 2007) could affect the decay incidence. The average temperature (Table 1) at the Témiscamingue site was higher (2.33 °C) than that of the two other sites (1.64-1.65 °C). This higher temperature could favor decay development and partially explain the higher level of decay in the Témiscamingue site.

The soil at the Témiscamingue site is more acidic (pH=4.65) than that of the two other studied sites (Table 2). Zabel and Morell (1992) suggest that fungi grow at a pH of 4 to 5 and reach a maximum growth rate at a pH of 6. Duncan (1960) reported that a pH of 9 had a retarding effect on fungal growth. These results are also in good agreement with Little *et al.* (2010), who reported that a highly alkaline soil with an initial pH of 9.3 produced little decay, because acidic forest soils statically produce the greatest decay (Arenz and Blanchette 2011); however, due to the limited number (3) of sites investigated in this study, these results should be interpreted with caution.

At the Témiscamingue site, where the incidence of decay is the highest (Fig. 4c), the soil is rich in carbon (C) and nitrogen (N) and has a moisture of 37.2% (Table 2). These soil conditions favour decay proliferation (Arenz and Blanchette 2011; Darrel 1973; Little *et al.* 2010; Smith and Gjovik 1972). According to Smith and Gjovik (1972), the moisture content of the soil could cause a serious increase in the moisture content of the wood, which favours decay. According to Bhat *et al.* (2005), trees growing in wet sites are more vulnerable to decay than trees growing in dry sites. Zabel and Morrell (1992) reported that the ideal moisture content for decay is from 40 to 80%. These findings, however, conflict with those of Anagnost and Smith (1997), who reported that brown rot fungi proliferated better in sites with a low soil moisture content (38%) than in sites with a high moisture content (90%).

The Témiscamingue site has a higher C:N ratio (30.95), which means that the nitrogen was depleted from the soil reserves, influencing site productivity (Brais and Drouin 2012). Fungal abundance is strongly and positively correlated with carbon and nitrogen contents (Arenz and Blanchette 2011). Nitrogen is therefore a limiting factor for the fungal growth required for enzyme production (Schwarze 2007). Gartner *et al.* (1999) reported that trees grown in poor soils produced heartwood that is more susceptible to decay.

The among-tree effect was also significant, but contributed to only 2.6% of the total variation. It is worth noting that the error term accounts for 37.2% of the total variation in decay; therefore, other unconsidered factors could have significantly impacted the decay incidence.

The effect of cambial age on decay was highly significant, accounting for 23.2% of the total variation. The variation in tree age and total decay volume is shown in Fig. 5. Although the coefficient of determination between tree age and tree volume was low, it was highly significant. Decay was present, but not serious (less than 10%), in trees less than 80 years old (Fig. 5), but the difference between sites was very marked. For example, the Témiscamingue site, with an average tree age of 90 years, shows approximately 15% decay, whereas at the Abitibi site, where the trees were 83 years old on average, the decay accounts for only 5.8%.

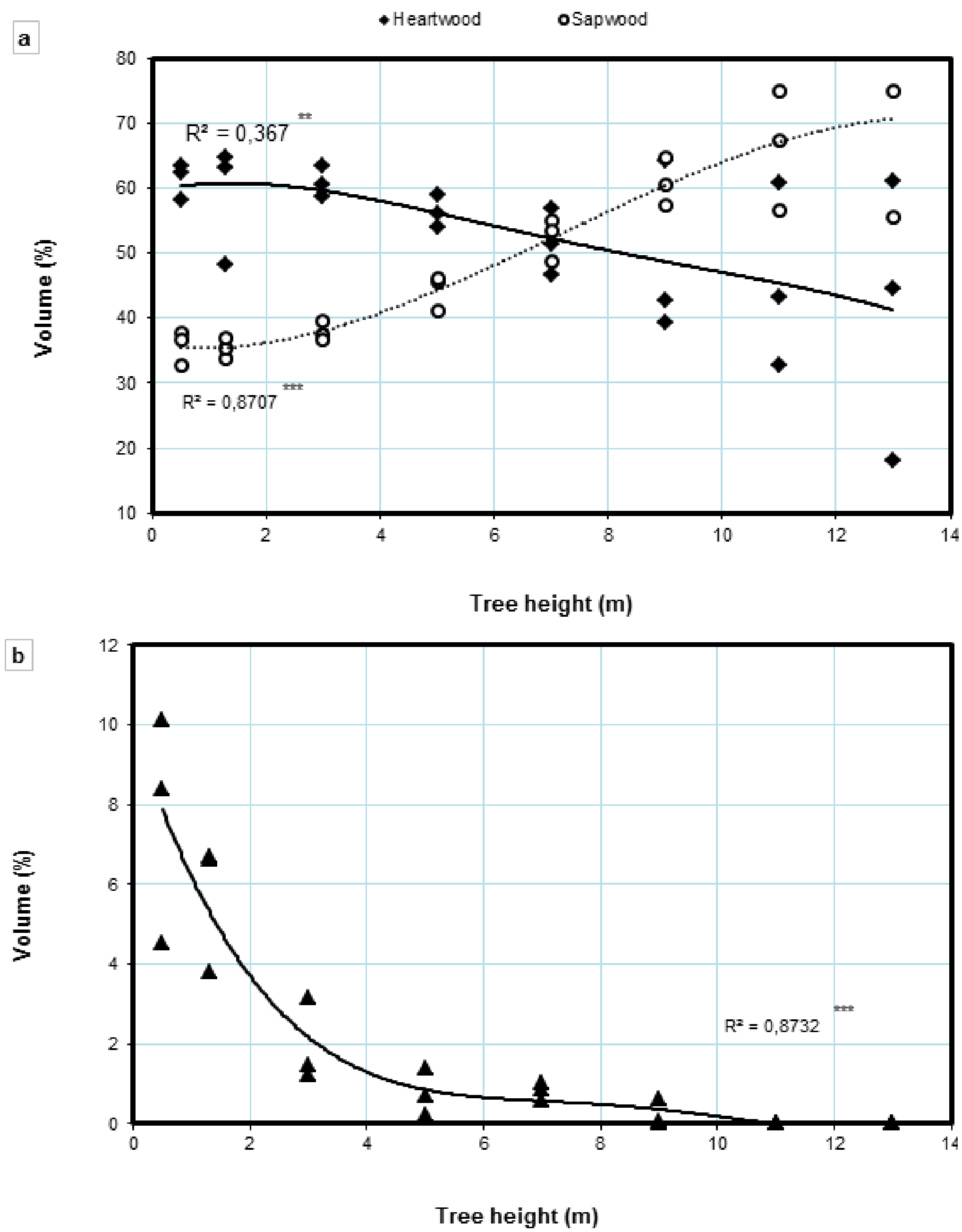

Fig. 6: Tree height variation in a) sapwood and heartwood, and b) decay volume (percentage of volume in discs at the different tree heights) in *Thuja occidentalis* L. Significance level: ** = p<0.01 and *** = p<0.001.

The significant tree effect on decay could be partially explained by the age difference among trees from a same site. This result is in good agreement with previous findings (Guilley *et al.* 2004; Windeisen *et al.* 2002). Moreover, several studies have attributed a significant tree effect on decay to the difference in extractives content between trees, which is age dependent (Anagnost and Smith 1997; Oliveira *et al.* 2010;

Windeisen *et al.* 2002). For example, Gierlinger *et al.* (2004) attributed the variation in heartwood extractives of larch trees to the advanced age of the sampled trees (>150 years). It is well known that aged trees have a significantly higher extractives content compared to young trees.

Heartwood, Sapwood, Age, and Brown Rot Decay Correlations

Decay volume correlated positively with heartwood volume (r=0.40) and tree volume (r=0.37) (Table 5). However, decay volume correlated negatively and strongly with sapwood volume (r=0.40). Thus, decay development correlated with the morphological characteristics of the living tree. These results are in good agreement with Amusant *et al.* (2004), who showed that the mass loss of heartwood correlated negatively with sapwood diameter (r=0.37) and positively with tree diameter (r=0.44). The proportion of heartwood increased with increasing tree diameter downward from the top of the tree, implying that older trees contain a greater proportion of heartwood than younger trees (DeBell and Lachenbruch 2009; Miranda *et al.* 2006). According to Sellin (1994) and Knapic and Pereira (2005), both sapwood and heartwood proportions increased with increasing diameter at the stem base, with the heartwood portion increasing more rapidly.

The negative correlation between decay and sapwood proportions (r=-0.40) suggests that, in functional sapwood, decay colonization might be restricted by either active defense mechanisms or by passive microenvironmental restrictions resulting from the high water content and low availability of oxygen (O2) in living sapwood (Boddy and Rayner 1983; Pearce 1996). According to Boddy and Rayner (1983), the absence of decay in living sapwood is due to the unsuitability of functional sapwood for mycelial establishment, owing to its high moisture content and lack of easy assimilation of nutrients within living cells. Gartner *et al.* (1999) reported that trees with a greater sapwood area could produce more decay-resistant heartwood than trees with a smaller sapwood area, because the tree would have more photosynthates available for the production of carbon-based defense compounds that protect the heartwood; however, sapwood area and decay resistance were closely correlated. This was attributed to the young age of the studied trees, which masked a more marked effect. Consequently, studies in older stands were recommended to further understand the relationships between heartwood decay percent and tree morphological characteristics.

Table 5. Coefficients of Correlation between Decay, Heartwood, and Sapwood Volumes and Tree Age in *Thuja occidentalis* L.

Characteristics	Decay volume	Heartwood volume	Tree volume	Sapwood Volume	Tree age
Decay volume	1				
Heartwood volume	0.40***	1			
Tree volume	0.37***	0.69***	1		
Sapwood volume	-0.40***	-1***	-0.69***	1	
Tree age	0.50***	0.55***	0.46***	-0.55***	1
*** Significant level at p<0.001					

Practical Implications

The occurrence of brown rot decay in *Thuja occidentalis* is site and age dependent (Table 4). The higher decay proportion in the Témiscamingue site was partially explained by the growing conditions characterized by higher temperature, moisture, and pH values. Prevention of decay due to site is not possible except by preventing tree injuries during silvicultural treatments and tree harvesting. Tree injuries are known to favour infection with fungus, and this impact is accentuated with tree age.

Tree aging accentuates the occurrence of brown rot decay in *Thuja occidentalis* (Table 5), especially in the Témiscamingue site (Fig. 5). From a processing point of view, one of the precautions to prevent the degradation of the wood in the standing trees is harvesting in susceptible sites before critical aging. However, the limited number of trees in this study does not allow recommending a harvesting age. Further investigations are needed. Nevertheless, decay is more susceptible in the Témiscamingue site that also showed the highest growth rate. Thus, harvesting at younger age in this site might be a good compromise between wood volume and quality.

Processing *Thuja occidentalis* containing brown rot decay might be critical for yield and quality of the end-products. Brown rot decay at early stages mainly degrades the earlywood cells, the main component of the ring, which will lead to a substantial degradation in the wood strength properties. Thus, wood with brown rot decay, even at early stages, will not be suitable for applications where strength is required. Companies processing *Thuja occidentalis* may consider sorting logs with brown rot decay for use in applications were strength is not an issue such as shakes and shingles. Nevertheless, the yield of such products from rotten logs is seriously affected due to the heartwood degradation. Severely rotten heartwood and residues from shingles and shakes production are generally used for mulch.

In contrast to dead wood, in living tree the decay is limited to the heartwood. The living sapwood is free from decay, due to the unsuitability of functional sapwood for mycelial establishment. Thus, using rotten logs to extract sapwood for applications such shingles and shakes will affect mainly the products yield.

The occurrence of brown rot decay in *Thuja occidentalis* trees was especially critical in the lower part of the tree stem. At higher tree heights, the decay proportion is very low or negligible (Fig. 6). Processing upper tree logs from rotten trees is generally less critical than lower logs. These observations highlight the importance of log sorting in processing operations.

CONCLUSIONS

1. Decay incidence varies with the cell types and within wood. In early stages of decay, degradation is limited to cell lumina of the earlywood tracheids, while in advanced stages of decay, wood degradation is observed in both earlywood and latewood tracheids.
2. Brown rot decay is site and age dependent. Trees growing in a moist site are more susceptible than trees in a dry site to develop decay. Within a same site, older trees are more susceptible to decay than younger trees. In general, decay was not serious in trees younger than 80 years old as the heartwood formation has just started.
3. The within-tree variation in decay as well as in sapwood and heartwood proportions was further established. Both the heartwood and decay proportions decreased from the bottom of the tree upward, whereas the sapwood proportion increased from the bottom of the tree upward.

4. The wood is more susceptible to decay in the base than in the top of the tree. The lower part of tree is more susceptible to fungal infection due to various openings through which rot fungi enter.
5. The correlations between decay and morphological tree characteristics were investigated. Decay volume was positively correlated to heartwood volume and negatively to sapwood volume.
6. In contrast to dead wood, in living tree, the decay was limited to the heartwood. The living sapwood is free from decay, due to the unsuitability of functional sapwood for mycelial establishment.
7. Harvesting at earlier ages in critical sites and log sorting are among the most practical approaches to limit the occurrence and negative impacts of brown rot decay.

ACKNOWLEDGEMENTS

The authors thank the Canada Research Chair Program, the Ministère des ressources naturelles et de la faune, Quebec (MRNF), and the NSERC-UQAT-UQAM Industrial chair on forest sustainable management for funding this project.

REFERENCES CITED

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 Science and Technology* 40(2), 124-138.

Amusant, N., Beauchene, J., Fournier, M., Janin, G., and Thevenon, M. F. (2004). "Decay resistance in *Dicorynia guianensis* Amsh: Analysis of inter-tree and intra-tree variability and relations with wood colour," *Annals of Forest Science* 61(4), 373-380.

Amusant, N., Fournier, M., and Beauchene, J. (2008). "Colour and decay resistance and its relationships in *Eperua grandiflora*," *Annals of Forest Science* 65(8), 806.

Anagnost, S. E., and Smith, W. B. (1997). "Comparative decay of heartwood and sapwood of red maple," *Wood and Fiber Science* 29(2), 189-194.

Archambault, S., and Bergeron, Y. (1992). "An 802-year tree-ring chronology from the Quebec boreal forest," *Canadian Journal of Forest Research* 22(5), 674-682.

Arenz, B. E., and Blanchette, R. A. (2011). "Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula, Ross Sea Region and McMurdo Dry Valleys," *Soil Biology and Biochemistry* 43(2), 308-315.

Behr, E. A. (1976). "Special physical and chemical properties of northern white cedar," Proceedings of the National Northern White Cedar Conference. Michigan State University Publication. No. 3-76:11-15.

Bhat, K., Thulasidas, P., Maria Florence, E., and Jayaraman, K. (2005). "Wood durability of home-garden teak against brown-rot and white-rot fungi," *Trees - Structure and Function* 19(6), 654-660.

Blanchette, R. A. (2000). "A review of microbial deterioration found in archaeological wood from different environments," *International Biodeterioration and Biodegradation* 46(3), 189-204.

Boddy, L., and Rayner, A. D. M. (1983). "Origins of decay in living deciduous trees: the role of moisture content and a re-appraisal of the expanded concept of tree decay," *New Phytologist* 94(4), 623-641.

Brais, S., and Drouin, P. (2012). "Interactions between deadwood and soil characteristics in a natural boreal trembling aspen - jack pine stand," *Canadian Journal of Forest Research* 42(8), 1456-1466.

Burns, R. M., and Honkala, B. H. (1990). "Silvics of North America," in: *Conifers. Agriculture Handbook*, Forest Service, United States Departement of Agriculture, Washington, D. C., Vol. 1, 654 pp.

Clausen, C. A., and Kartal, S. N. (2003). "Accelerated detection of brown-rot decay: Comparison of soil block test, chemical analysis, mechanical properties, and immunodetection," *Forest Products Journal* 53(11-12), 90-94.

Dansereau, P. R., and Bergeron, Y. (1993). "Fire history in the southern boreal forest of northwestern Quebec," *Canadian Journal of Forest Research* 23(1), 25-32.

Darrel, D. N. (1973). "Wood deterioration and its prevention by preservative treatments. Volume II: Preservatives and Preservatives Systems," Syracuse University Press. Syracuse wood science series 5. University press, New York.

De Blois, S., and Bouchard, A. (1995). "Dynamics of *Thuja occidentalis* in an agricultural landscape of southern Quebec," *Journal of Vegetation Science* 6(4), 531-542.

DeBell, J. D., and Lachenbruch, B. (2009). "Heartwood/sapwood variation of western redcedar as influenced by cultural treatments and position in tree," *Forest Ecology and Management* 258(9), 2026-2032.

DeBell, J. D., Morrell, J. J., and Gartner, B. L. (1997). "Tropolone content of increment cores as an indicator of decay resistance in western redcedar," *Wood and Fiber Science* 29(4), 364-369.

Debell, J. D., Morrell, J. J., and Gartner, B. L. (1999). "Within-stem variation in tropolone content and decay resistance of second-growth Western redcedar," *Forest Science* 45(1), 101-107.

Denneler, B., Bergeron, Y., Bégin, Y., and Asselin, H. (2008). "Growth responses of riparian *Thuja occidentalis* to the damming of a large boreal lake," *Botany*, 86(1), 53-62.

Downes, G. M., Drew, D., Battaglia, M., and Schulze, D. (2009). "Measuring and modelling stem growth and wood formation: An overview," *Dendrochronologia* 27(2), 147-157.

Duncan, C. G. (1960). "Soft rot in wood and toxicity studies on causal fungi," *Proc. Am. Wood-Preservers' Assoc*. 56, 27-35.

Eriksson, K. E. L., Blanchette, R. A., and Ander, P. (1990). *Microbial and Enzymatic Degradation of Wood and Wood Components*, Springer, Tokyo, 407 pp.

Fabiyi, J. S., McDonald, A. G., Morrell, J. J., and Freitag, C. (2011). "Effects of wood species on durability and chemical changes of fungal decayed wood plastic composites," *Composites Part A: Applied Science and Manufacturing* 42(5), 501-510.

Fowells, H. A. (1965). "Silvics of Forest Trees of the United States," In: *Agriculture Handbook*, United States, 271 pp.

Freitag, C. M., and Morrell, J. J. (2001). "Durability of a changing western redcedar resource," *Wood and Fiber Science* 33(1), 69-75.

Gartner, B. L., Morrell, J. J., Freitag, C. M., and Spicer, R. (1999). "Heartwood decay resistance by vertical and radial position in Douglas-fir trees from a young stand," *Canadian Journal of Forest Research* 29(12), 1993-1996.

Gierlinger, N., Jacques, D., Grabner, M., Wimmer, R., Schwanninger, M., Rozenberg, P., and Pâques, L. E. (2004). "Colour of larch heartwood and relationships to extractives and brown-rot decay resistance," *Trees - Structure and Function* 18(1), 102-108.

Gominho, J., and Pereira, H. (2005). "The influence of tree spacing in heartwood content in *Eucalyptus globulus* Labill," *Wood and Fiber Science* 37(4), 582-590.

Green III, F., and Highley, T. L. (1997). "Mechanism of brown-rot decay: Paradigm or paradox," *International Biodeterioration and Biodegradation* 39(2-3), 113-124.

Gripenberg, J. (1949). "The constituents of the wood of *Thuja occidentalis* L.," *Acta Chemica Scandinavica* 3(7), 782.

Guilley, E., Charpentier, J. P., Ayadi, N., Snakkers, G., Nepveu, G., and Charrier, B. (2004). "Decay resistance against *Coriolus versicolor* in sessile oak [*Quercus petraea* Liebl.: Analysis of the between-tree variability and correlations with extractives, tree growth and other basic wood properties," *Wood Science and Technology* 38(7), 539-554.

Haataja, B. A., and Laks, P. E. (1995). "Properties of flakeboard made from northern white cedar," *Forest Products Journal* 45(1), 68-70.

Harju, A. M., Venäläinen, M., Anttonen, S., Viitanen, H., Kainulainen, P., Saranpää, P., and Vapaavuori, E. (2003). "Chemical factors affecting the brown-rot decay resistance of Scots pine heartwood," *Trees - Structure and Function* 17(3), 263-268.

Hofmeyer, P. V., Seymour, R. S., and Kenefic, L. S. (2009). "Influence of soil site class on growth and decay of northern white-cedar and two associates in maine," *Northern Journal of Applied Forestry* 26(2), 68-75.

Johnston, W. F. (1990). "*Thuja occidentalis* L. Northern white-cedar," in: *Silvics of North America. 1: Conifers*, Burns, R. M., and Honkala, B. H. (tech. coords.), *Agricultural Handbook* 654, USA, pp. 1189-1209.

Jozsa, L. A., and Middleton, G. R. (1994). "A discussion of wood quality attributes and their practical implications," Forintek Canada Corp. No. SP-34. 42 pp.

Kim, J. W., Harper, D. P., and Taylor, A. M. (2009). "Effect of extractives on water sorption and durability of wood-plastic composites," *Wood and Fiber Science* 41(3), 279-290.

Knapic, S., and Pereira, H. (2005). "Within-tree variation of heartwood and ring width in maritime pine (*Pinus pinaster* Ait.)," *Forest Ecology and Management* 210(1-3), 81-89.

Koubaa, A., Tony Zhang, S. Y., and Makni, S. (2002). "Defining the transition from earlywood to latewood in black spruce based on intra-ring wood density profiles from X-ray densitometry," *Annals of Forest Science* 59(5-6), 511-518.

Koubaa, A., and Zhang, S. Y. (2008). "White cedar *Thuya occidentalis*," in Zhang andt Koubaa, 2008, *Softwood of Eastern Canada*. *Their Silvics, Characteristics, Manufacturing and End-uses*, SP-526E FPInnovations, Chapter 11.

Lafleur, B., Paré, D., Fenton, N. J., and Bergeron, Y. (2011). "Growth and nutrition of black spruce seedlings in response to disruption of *Pleurozium* and *Sphagnum* moss carpets in boreal forested peatlands," *Plant and Soil* 345(1), 141-153.

Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D., and Schabenberber, O. (2006). *SAS for Mixed Models Second Edition*, SAS Institute, Inc, Cary, NC. 814 pp.

Little, E. L., Jr. . (1979). "Checklist of United States trees (native and naturalized). Agriculture Handbook. N°. 541." Forest Service, United States Departement of Agriculture, Washington, D. C, 375 pp.

Little, N. S., Schultz, T. P., and Nicholas, D. D. (2010). "Effect of different soils and pH amendments on brown-rot decay activity in a soil block test." *Holzforschung* 64(5), 667-671.

MacLean, H., and Gardner, J. A. F. (1956). "Distribution of fungicidal extractives (thujaplicin and water-soluble phenols) in western red cedar heartwood," *Forest. Products. Journal* 6(12), 510-516.

Matthes-Sears, U., Stewart, S. C., and Larson, D. W. (1991). "Sources of allozymic variation in *Thuja occidentalis* in southern Ontario, Canada," *Silvae Genet* 40(3-4), 100-105.

Miranda, I., Gominho, J., Lourenço, A., and Pereira, H. (2006). "The influence of irrigation and fertilization on heartwood and sapwood contents in 18-year-old *Eucalyptus globulus* trees," *Canadian Journal of Forest Research* 36(10), 2675-2683.

Nawrot, M., Pazdrowski, W., and Szymański, M. (2008). "Dynamics of heartwood formation and axial and radial distribution of sapwood and heartwood in stems of European larch (*Larix decidua* Mill.)," *Journal of Forest Science* 54(9), 409-417.

Oliveira, L. S., Santana, A. L. B. D., Maranhão, C. A., de Miranda, R. D. C. M., Galvão de Lima, V. L. A., da Silva, S. I., Nascimento, M. S., and Bieber, L. (2010). "Natural resistance of five woods to *Phanerochaete chrysosporium* degradation," *International Biodeterioration and Biodegradation* 64(8), 711-715.

Paul, V. (2011). "Les facteurs écologiques limitant la répartition nordique du thuja de l'est (*Thuja occidentalis* L.)," Master in Biology Master's thesis, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec, Canada, 84 pp.

Pearce, R. B. (1996). "Tansley review No. 87. Antimicrobial defences in the wood of living trees," *New Phytologist* 132(2), 203-233.

Pinto, I., Pereira, H., and Usenius, A. (2004). "Heartwood and sapwood development within maritime pine (*Pinus pinaster* Ait.) stems," *Trees - Structure and Function*, 18(3) 284-294.

Régnière, J., and St-Amant, R. (2007). "Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico," *International Journal of Biometeorology* 51(5), 415-430.

Rudloff, E. V., and Nair, G. V. (1964). "The sesquiterpene alcohols of the heartwood of *Thuja occidentalis* L.," *Canadian Journal of Chemistry* 42(7691).

SAS. (2008). "SAS Institute Inc, Cary, NC."

Savva, Y., Koubaa, A., Tremblay, F., and Bergeron, Y. (2010). "Effects of radial growth, tree age, climate, and seed origin on wood density of diverse jack pine populations," *Trees - Structure and Function* 24(1), 53-65.

Schwarze, F. W. M. R. (2007). "Wood decay under the microscope," *Fungal Biology Reviews* 21(4), 133-170.

Schwarze, F. W. M. R., and Ferner, D. (2003). "Ganoderma on trees - Differentiation of species and studies of invasiveness," *Arboricultural* 27, 59-77.

Schwarze, F. W. M. R., Mattheck, C., and Engels, J. (2004). *Fungal Strategies of Wood Decay in Trees*, Springer, Heidelberg,163 pp.

Sellin, A. (1994). "Sapwood-heartwood proportion related to tree diameter, age, and growth rate in *Picea abies*," *Canadian Journal of Forest Research* 24(5), 1022-1028.

Smith, R. S., and Gjovik, L. R. (1972). "Interlaboratory testing of wood preservatives using ASTM D1413-61," *Wood and Fiber Science* 4(3), 170-178.

Taylor, A. M., Gartner, B. L., and Morrell, J. J. (2002). "Heartwood formation and natural durability - A review," *Wood and Fiber Science* 34(4), 587-611.

Trevisan, H., Tieppo, F. M. M., De Carvalho, A. G., and Lelis, R. C. C. (2007). "Evaluation of physical and mechanical properties of wood from five species as a function of deterioration in two environments," *Revista Arvore* 31(1), 93-101.

Wagener, W. W., and Davidson, R. W. (1954). "Heart rots in living trees," *The Botanical Review* 20(2), 61-134.

Wernsdörfer, H., Le Moguédec, G., Constant, T., Mothe, F., Nepveu, G., and Seeling, U. (2006). "Modelling of the shape of red heartwood in beech trees (*Fagus sylvatica* L.) based on external tree characteristics," *Annals of Forest Science* 63(8), 905-913.

Windeisen, E., Wegener, G., Lesnino, G., and Schumacher, P. (2002). "Investigation of the correlation between extractives content an natural durability in 20 cultivated larch trees," *Holz als Roh - und Werkstoff* 60(5), 373-374.

Zabel, R. A., and Morrell, J. J. (1992). "Wood microbiology: Decay and its prevention," *Academic Press,* San Diego, 476 pp.

Article submitted: March 10, 2013; Peer review completed: May 10, 2013; Revised version received: July 28, 2013; Accepted: July 29, 2013; Published: July 30, 2013.