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1. INTRODUCTION

The natural boreal forest of Quebec constitutes a reservoir of trees with high ecological importance and economic potential that extends from the shoreline to Labrador and northwards to the 55th parallel. This ecosystem has 74% of its territory covered by conifers and the remaining area is either composed of regenerating stands (10%) or occupied by mixed (13%) or hardwood (3%) stands (Gauthier, 2009).

Black spruce (*Picea mariana* (Mill.) B.S.P.) largely dominates the other species of conifers and plays an important role in the boreal forest ecosystem (Parent and Fortin, 2008; Zhang and Koubba, 2008). The other main species are jack pine (*Pinus banksiana* Lamb), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss) and American larch (*Larix laricina* (Du Roi) K. Koch), which can be found in most of the boreal forest distribution (Laird Farrar, 1997). Black spruce is the most abundant species of Quebec and can be found in many different soil types, wet or dry, which demonstrates the high adaptability of this species. Individual trees can reach a height of 20 meters and their life expectancy is around 200 years, although some specimens can reach an age of 280 years (Burns and Honkala, 1990). In the Saguenay-Lac-Saint-Jean region, black spruce represents nearly 80% of softwood and best characterizes the region (Fillion, 2004). Its abundance and properties make it a very popular species for the forest industry (Burns and Honkala, 1990; Vincent *et al.*, 2009). It was used mainly for pulp, but today it is more often used for structural purposes, in addition to being used in recent years in value-added products (Alteyrac, 2005). The high economic values the forest industry attributes to black spruce are associated to the particular wood anatomy of the tree species, which changes indirectly due to environmental variations (Fritts, 1976). As wood quality is closely related to wood anatomy, it is very important to assess their related parameters (Mäkinen et al., 2002). As long as the growth and productivity of high-latitude altitude forests remain unknown, no strategy based on an economically advantageous exploitation of the remote areas can be evaluated or considered.

Conifer tree rings can be divided into two parts: earlywood and latewood. The diameters in earlywood tracheids are two to three times larger than in latewood tracheids (Cuny *et al.*, 2013). The environment (e.g. temperature, water availability, soil fertility, disturbances such as insects or fungi) directly and indirectly affect tree growth by influencing physiological processes such as photosynthesis, respiration, carbon assimilation, hormones, absorption of water and minerals, translocation of sugars and activity of the meristems (Fritts, 1976; Kozlowski and Pallardy, 1997). Xylem phenology is mainly controlled by the temperatures occurring at the boundaries of the growing period by activating or stopping growth. Moreover, the length of the thermally favorable period decreases with altitude and latitude, and increases with a warming scenario, thus influencing the length of the growing season (Rossi *et al.*, 2011) However, the scientific observers are not unanimous about the response of trees along a geographical gradient, and there is a lack of information how the environment parameters affect the different anatomical properties.

The properties and products of wood are related to their anatomical structure (Panshin and De Zeeuw, 1970). The dimensions and adjustments of the tracheids only partly determine the properties of pulp, paper and sawn wood (Dinwoodie, 1965). The morphology of tracheids influences its flexibility, plasticity and resistance and also plays an important role in the physical properties of the wood and paper (Panshin and De Zeeuw, 1970). Density is also recognized as one of the most important properties of wood in regard to mechanical resistance and varies according to the structure of the tracheids (Lindstrom, 1997). The changes in the conifer tree-ring density integrate the variation in the anatomy of the rings; in particular in the thickness of the cell wall, cell diameter and lumen diameter, but also in the proportion of the ring occupied by latewood (Biermann, 1996; Lindstrom, 1997; Vaganov, 1996; Vaganov and Sviderskaya, 1990)

Cambial age has an influence on the quality of wood (Antal and Micko, 1994; Forest Products Laboratory, 2010; Haygreen and Bowyer, 1989; Panshin and De Zeeuw, 1970; Schneider *et al.*, 2008; Spicer and Gartner, 2001; Yang and Hazenberg, 1994). Cambial maturation describes a developmental process that results in a change of dimensions of cambial initials over time, which in turn affects the dimensions of xylem cells produced by the cambium (Barnett and Jeronimidis, 2003). For example, longer initials are known to produce longer tracheids in conifers (Larson, 1994). This rapid changes in the cambium occurs for the first 5-25 years, depending on the species (Barnett and Jeronimidis, 2003). During this period the xylem production is called "juvenile wood" and characterized by lower wood density associated with larger tracheid diameters and larger lumen to ensure appropriate sap flow. During the first few years, mechanical support is not required because the cells produced in the juvenile phase act more in transporting water, carbon and nutrients than in supporting the stem (Schneider *et al.*, 2008). In contrast, xylem produced by a mature cambium is referred to "mature wood" and characterized by relatively uniform anatomical properties (Cown, 1992; Panshin and De Zeeuw, 1970; Senft *et al.*, 1985; Spicer and Gartner, 2001; Zobel and Buijtenen, 1989). Thus, the age is a parameter that has a great to moderate influence on the relative density of wood (Ikonen *et al.*, 2008; Yang and Hazenberg, 1994). Bending properties, modulus of elasticity and modulus of rupture (MOE and MOR) are linearly dependant of the sample age, which is consistent with the fact that mature wood has higher mechanical properties than juvenile wood (Forest Products Laboratory, 2010; Haygreen and Bowyer, 1989). Tracheid lumen diameter, ring density and width, are all factors known to vary with cambial age. Lumen diameter increases with cambial age. In Douglas fir, lumen diameter increased from the pith for about the first 10 years, and then remained constant, whereas the growth ring density increase after an initial decrease in the first years (Panshin and De Zeeuw, 1970; Spicer and Gartner, 2001).

In Norway spruce, tracheid length was found to be dependant on cambial age and growth ring width; a gradual transition in tracheid size taking place from the pith outwards. These differences can be due to genetic and environmental factors close to the pith. Wood formation is probably still under genetic influence and with time, other factors controlling growth will have a guiding effect on the final tracheid structure (Lindstrom, 1996).

Several European researchers have found that a growth increase can lead to a decrease of wood quality (Mäkinen *et al.*, 2002; Shmulsky and Jones, 2011), but the relationship between this behavior and specially in black spruce is not described for North America. The knowledge of how wood quality and growth rate are related in this species will lead to optimization of the final products depending on geographical location.

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1.1. Hypothesis and Objectives

We studied the wood quality through the evaluation of growth and wood characteristics along an alti-latitudinal gradient in a natural forest. We tested the hypothesis that with increasing altitude or latitude, due to lower temperature, the growth rate decreased as shown by narrower tree-rings and lower volume growth, also, longer, thicker and smaller radial diameter of tracheid. These changes in wood characteristics should lead to different wood quality according to age trends improving the wood quality at the northern sites.

The objectives of this study were to quantify the anatomical properties (tracheid analysis) and mechanical strength (elasticity and rupture modulus) at different ages and in different locations in order to identify the relationship between wood properties, age and alti-latitudinal climatic variation. The specific objectives of the study were to:

1. - Evaluate wood quality according to several attributes (e.g. density, mechanical strength, tracheid length) as a function of tree age and radial growth;

2. - Define the relationship between growth, wood quality and climatic variations along an alti-latitudinal gradient.

2. MATERIALS AND METHODS

2.1. Study area

The investigation was carried out in five permanent plots of pure black spruce stands located between the 48th and 53th parallels (Figure 1). All plots were located in the boreal zone of Quebec (Canada) in a south-north oriented transect at different altitudes forming an alti-latitudinal gradient (Table 1).

Figure 1 - Location of the five sites.

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SIM and BER were located in the balsam fir (*Abies balsamea* (L.) Mill.) – white birch (*Betula papyrifera* Marsh.) bioclimatic domain, dominated by balsam fir and white spruce stands mixed with white birch on mesic sites. MIS and DAN were located in the spruce-moss bioclimatic domain, where forest landscapes are fairly uniform, since the canopy is dominated extensively by the black spruce, often growing in pure stands but also by other species, such as balsam fir. The undergrowth is composed of hypnaceous mosses and ericaceous shrubs. MIR was located in the spruce-lichen domain that extends over the entire taiga subzone, which stretches from the 52nd parallel. The main difference from the spruce-moss forest is its low-density forest cover. The lichen mat is dotted with black spruce trees, whose propagation is favored by the harsh climate and low precipitation (Table 1). Each plot is composed of an even-aged, mature, closed and pure black spruce stand.

Table 1. Location of the sites from south to north, climate variables and characteristics of the five black spruce analyzed (DBH – Diameter at breast height, H – Tree height) (Climate stations property of UQAC covering a 10 years period).

SITE	Geographic coordinates	Altitude (m.a.s.l.)	Temperature (°C)	Precipitation annual (mm)	DBH (cm)	H (m)	Age (years)
SIM	48°13' 46.4" N 71°15' 08.5" W	338	1.81	677.9	17.2 ± 0.8	20.9 ± 1.4	80.6 ± 1.5
BER	48°51' 57.3" N 70°20' 29.8" W	611	0.79	699.6	16.8 ± 0.8	20.4 ± 1.8	133.4 ± 2.7
MIS	49°43' 54.6" N 71°56' 52.6" W	342	0.1	807.4	18.2 ± 0.8	20.3 ± 1.6	113.0 ± 4.0
DAN	50°41' 45.7" N 72°11' 00.3" W	487	-1.22	776.5	18.3 ± 1.3	22.0 ± 1.7	134.2 ± 2.5
MIR	53°47' 58.8'' N 72°52' 00.9'' W	441	-6.99	328.4	12.6 ± 0.7	20.5 ± 1.1	110.6 ± 4.3

2.2. Tree selection

Five dominant trees per site were selected to measure each of the properties required in this study. Trees were chosen according to the largest diameter at breast height (DBH), presenting a straight and healthy stem, and with no fungus attack (Table 1).

2.3. Growth estimation

Discs were collected at the heights 0, 0.5, 1, 1.3 and 2 m from the root collar, above 2 m, discs were collected at intervals of 1 m for the remaining length of the stem. Discs were air-dried and sanded with progressively finer grade sandpaper. Tree-ring widths were measured with an accuracy of 0.01 mm using a WinDendro measuring system (Regent Instruments, 2005) along four paths (four cardinal directions) in the sections from zero to 2 meters and two paths in the sections above 2 meters, according to the uniformity of the tree rings on the disc. All ring width series were corrected by cross-dating performed both visually and using the COFECHA computer program (Holmes, 1983). Measurements were averaged for each disc and tree ring.

The tree height (H_{ij}) at age t_{ij} was estimated for the 5 dominant trees using the Carmean method (Carmean, 1972). After having designated the growth rings at the ith cross section with the subscript j varying from 1 to r_i for each tree of age n, the assumptions are expressed mathematically by:

$$H_{ij} = h_i + \left[\frac{h_i+1-h_i}{2(r_i-r_i+1)}\right] + (j-1)\left[\frac{h_i+1-h_i}{r_i-r_i+1}\right] \tag{1}$$

and

$$t_{ij} = n - ri + j \tag{2}$$

where h_i is the height at the ith cross section, t_{ij} the tree age associated with the jth inner ring at the ith cross section and r_i the number of growth rings at the ith cross section. Stem volume was calculated by adding the volume of all tree sections envisaged as truncated cones with the volume V being obtained by the formula:

$$V = \frac{\pi l}{3}(a^2 + ab + b^2) \quad (3)$$

where l is the height of the truncated cone and a and b the minor and major radius (Van Laar and Akca, 2007).

2.4. Anatomical features

Anatomical features were evaluated for each tree at 1 m stem height and each third tree ring, starting from the pith, was selected for measurements (Figure 2 and 3). Samples were embedded in paraffin (Leica TP1020 Automatic Tissue Processor) and cut with a rotary microtome into sections of 7μm (microtome Leitz 1512 and Leica RM2145) and stained with an aqueous solution of 1% safranin and fixed on slides with a histological mounting medium (Deslauriers, 1999). A camera mounted on an optical microscope was used to record the numerical images and to measure the xylem features with WinCELL™ (Regent Instruments, 2011), an image analysis system specifically designed for wood cells. Cell features (cell lumen area, diameter and wall thickness) were measured along the tree rings at 400x magnification along the entire tree ring (Figure 3).

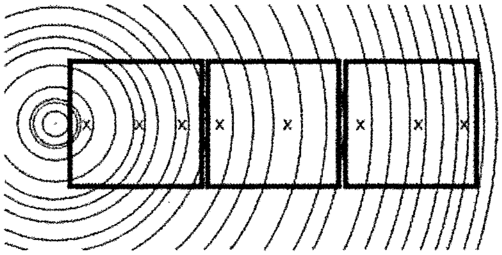

Figure 2 - Schema of a transversal section at 1 m stem height, each tree ring, x – tree-ring selection for anatomical and tracheid measurement, square – localization of the samples of the mechanical tests.

The hydraulic diameter (Dh) of xylem conduits was calculated by selecting all the N cells with a diameter of more than half the diameter of the largest one (Mencuccini et al., 1997 in (Anfodillo *et al.*, 2012)) according to the following equation:

$$\mathrm{Dh} = \frac{\sum_{n=1}^{N} d_n^5}{\sum_{n=1}^{N} d_n^4} \tag{4}$$

where d_n is the diameter of the n cell which weights the hydraulic diameters of single cells according to hydraulic conductance (Sperry et al., 1994 in (Anfodillo *et al.*, 2012)).

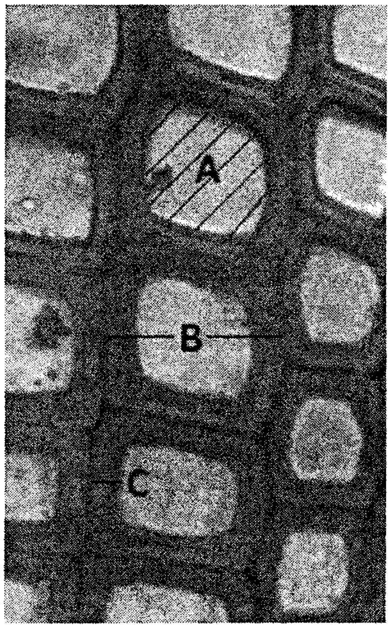

Figure 3 - Example of a microscopical transversal wood section representing the three measured parameters. A – Lumen area, B – Cell diameter, C – Cell wall thickness in every growth ring analyzed.

2.5. Tracheid features

Tracheid dimensions were measured at 1 m tree height for each third tree ring starting from the pith (Figure 2 and 4). Samples were placed in hot water to soften them and separation of the selected year was done under a stereomicroscope using a razor blade. Each individual ring was macerated until whitening in a solution (1:1) of glacial acetic acid and hydrogen peroxide and heated at 60 °C for 1 or 2 days (Franklin, 1945). The obtained tracheids were hydrated and mechanically shaken in a mixer mill MM 200 at a frequency of 300 Hz for 30 seconds for a homogenous separation of the tracheid. The samples were then analyzed by a Fiber Tester

(Lorentzen-Wettre, 2011), based on image analysis. Based on the number of tracheid measured by paper industry, we measured 5000 tracheids par sample in a time of 3600 seconds. Tracheids length under 0.5 mm, by using arithmetic average values, were considered as fine particles and excluded from the analysis. The principle with two plates allows the tracheids to move freely in two dimensions but not in the third and a very small measurement gap between the plates secures a good alignment of the tracheids. The whole tracheid can then be seen by the camera. The instrument measures several different tracheid properties like length and diameter.

2.6. Wood density

The samples were analyzed to obtain the density of wood to see its variation according to the cambial age at 1.3 m stem height. An X-ray densitometer QTRS-01X Tree Ring Scanner was used. The samples were cut so that each one had a final dimension of 25 mm in length and 1.6 to 2 mm thick covering all the tree rings from pith to bark (Figure 4).

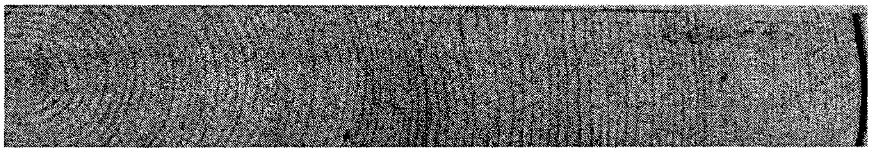

Figure 4 – Example of a densitometric sample taken at DBH including tree rings from pith to bark.

The samples spent about a month in a conditioning chamber at 20 °C and 65% of relative humidity so that the wood remain stable. The approximate density (calculated as the result of the division of the mass over the volume) of the each sample was used as initial data for the densitometer as a density per sample allowing to establish a basis for the calculation of density of each growth ring . The demarcation zone between annual rings was automatically set up for each sample with a sample density and checked manually for every scanned tree-ring profile. The sample was analyzed with an x-ray densitometer, where x-rays traverse the growth rings, at intervals of 0.004 mm starting from the bark towards the pith. An average value of density for each tree-ring is thus obtained. The analysis of wood density using the x-ray densitometer made it possible to obtain, for each analyzed sample, an average density of each growth ring (Figure 5).

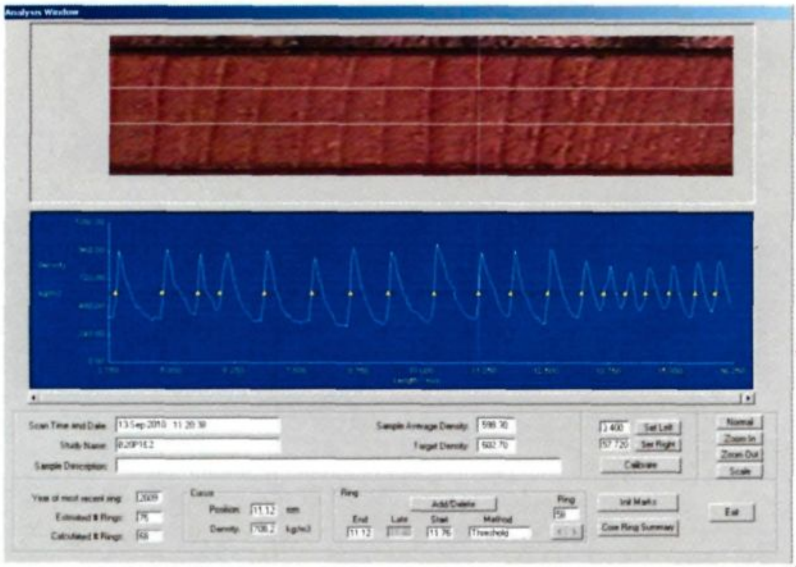

Figure 5 – Example of a density profile for each tree ring using x-ray densitometer.

2.7. Mechanical strength

The modulus of rupture (MOR) is a widely used measure of flexural strength (Bodig and Jayne, 1993) and is expressed as the applied stress at breaking divided by the unit area. This parameter is calculated as the maximum stress of the tracheids of the upper and lower side. MOR values are used to assess, for example, the potential of a material for use as beams and joists (Wangaard, 1950).

The modulus of elasticity (MOE) according Wangaard (1950), expresses the stiffness of the timber, i.e., the ability to resist deformation induced by a load applied only to the proportional limit. This parameter is obtained from the ratio of stress/strain and by the derivation of the values obtained in a static bending test. MOE is used to calculate the deformation of beams and joists and also to calculate secure loads and allowable stresses for timber and columns (Passarini, 2011).

Samples were taken from the area between 0.5-1 m of each tree evaluated. The specimens were tested on a bench in three-point bending according to the ASTM D143-09 standard for small specimens in a conditioning chamber. Samples of 25 per 25 per 410 mm were taken in each tree from the pith to the bark in the north and south directions (Figure 6). For each sample, the number of tree rings and their position from the pith was noted and they were then placed in a conditioning chamber for 30 days (20 °C and 65% RH) to arrive at 12% equilibrium moisture content afterwards the three-point test were applied.

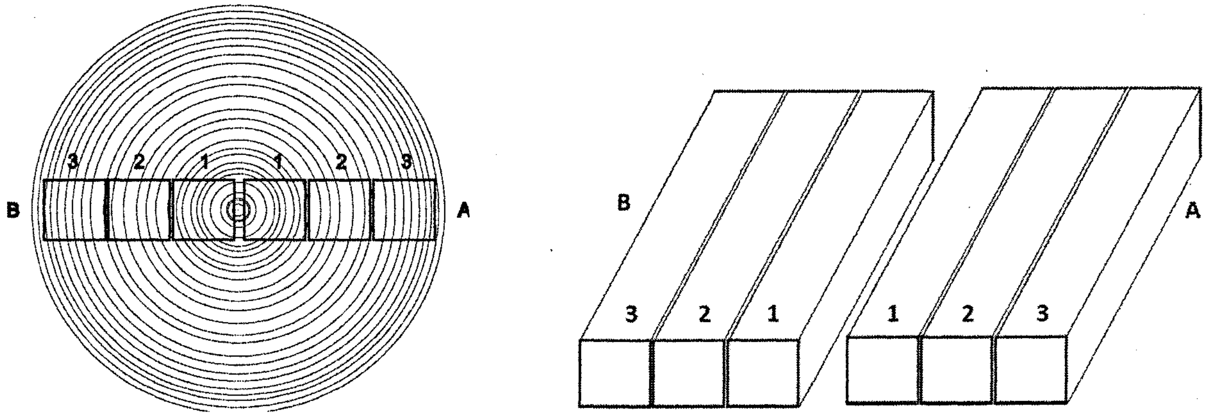

Figure 6 - Samples taken from the 0.5-1 m area in A (north) and B (south) directions from pith to bark.

The MOE and MOR were evaluated on an MTS-Alliance RT/100 machine. For the apparent MOE in static bending and the MOR, the formulas were (Bowyer *et al.*, 2007; Poncsak *et al.*, 2006):

$$MOE = \frac{P_1 L^3}{4bd^3y} \tag{5}$$

and

$$MOR = \frac{3PL}{2bd^2} \tag{6}$$

where:

- P_1 = Maximum load of the elastic domain
- P = Maximum load
- L = Span between two supports
- b = Sample width
- d = Sample thickness
- y = Abscissa of the center of the load-deflection proportional limit (mm)

2.8. Curves fittings

Several functions were used to model the changes in time of the different measured parameters (Table 2). All fittings were analyzed according to cambial age for better observation of variations by age and site. Growths in height, radial and volume were fitted with a sigmoid function using the NLIN procedure (NonLINear regression) and Gauss iterative method in SAS (SAS Institute, 2007) according to Rossi (Rossi *et al.*, 2009). For each variable, curve fitting was performed on the observations for the northern and southern stands. The sigmoid function is defined as:

$$y = ae^{-e^{[-b(x-c)]}} \quad (7)$$

Where y represents stem height or volume and x the tree age. Several possible starting values were specified for each parameter, the NLIN procedure evaluated each combination of initial values using the interactions producing the smallest residual sums of squares. Evaluation of the nonlinear regressions was based on statistics for goodness of fit, fitting behavior and examination of the residuals.

Lumen area and cell diameter were fitted with a quadratic regression in SAS (SAS Institute, 2007)

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$$y = \mathrm{a} + \mathrm{b}x + cx^2 \tag{8}$$

Where y represents lumen area or cell length and x the tree age.

Density, cell wall, MOE and MOR were fitted with a linear regression in SAS (SAS Institute, 2007)

$$y = a + bx \tag{9}$$

Where y represents density, cell wall, MOE or MOR and x the tree age.

Tracheid length, tracheid diameter and hydraulic diameter were fitted with a spherical semi variance function in SAS (SAS Institute, 2007)

$$y = a\left[1 - e^{-\left(\frac{x}{b}\right)}\right] \tag{10}$$

Where *y* represents tracheid length, tracheid diameter and hydraulic diameter and *x* the tree age. The three or two parameters for the formulas are the upper asymptote *a*, the rate of change of the shape *b* and the x-axis placement of the inflection point *c* if there is one. The residuals were regressed onto the partial derivatives with respect to the parameters until the estimates converged.

Table 2. Variables and fitted curves.

Variable	Fitted curve
DBH	Sigmoid function
Tree height	Sigmoid function
Stem volume	Sigmoid function
Lumen area	Quadratic regression
Cell diameter (radial)	Quadratic regression
Cell wall thickness	Linear regression
Hydraulic diameter	Spherical semi variance function
Tracheid length	Spherical semi variance function
Tracheid diameter	Spherical semi variance function
Wood density	Linear regression
MOE	Linear regression
MOR	Linear regression

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3. RESULTS

3.1. Growth

Annual radial growth of the five sites was characterized by an initial increase, a maximum peak and a decrease following a negative exponential curve (Figure 7). The maximum values of radial growth were registered at 20 – 30 years, except for the northern site MIR where the peak was observed only at the age of 40 years. A comparison between the mean radial growths at the age of 80 revealed that the highest growth was registered at SIM whereas BER presents the lowest growth (Figure 7).

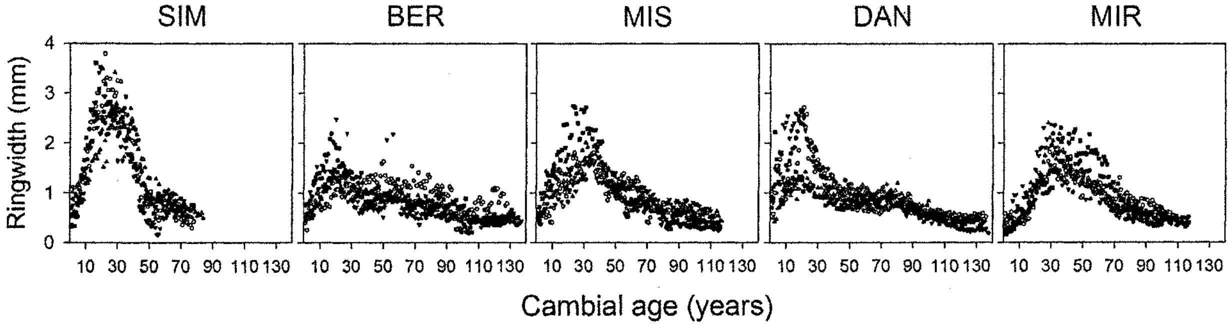

Figure 7 - Ring width variation according to cambial age and site.

Diameter growth in the five sites follows a sigmoid function and the fastest increase was obtained for SIM with an inflection point at the age of 50 years, whereas for the other sites this point was found later at the age of 90 years (Figure 8). MIS and DAN show greater variation between individual trees.

Height growth followed the same sigmoid curve as diameter growth, with the lowest height growth of 10 m at site MIR and stem height of 19 m in site DAN after 130 years (Figure 8 and Table 1). Stem heights of more than 18 m were already measured after 80 years in site SIM. MIR had a lower height than the other sites, DAN reached greater heights but with more variation and SIM reached greater heights in fewer years.

Annual cumulated volume growth shows that SIM has the largest volume at an earlier age, BER, MIS and DAN show similar behavior with high variation between the individual trees and MIR shows the lowest volume with less variation (Figure 8).

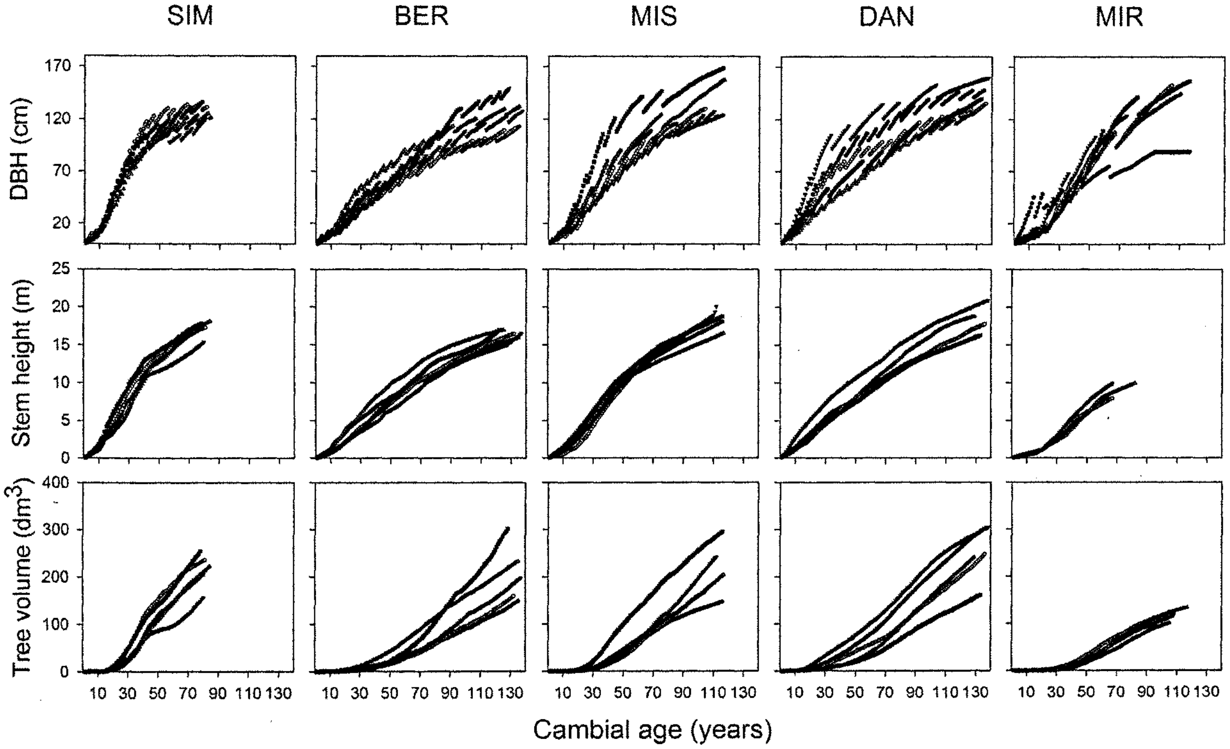

Figure 8 - Annual cumulated values for DBH, height and volume of the five black spruce per site.

3.2. Anatomical features

Lumen area, cell diameter and hydraulic diameter in the five sites followed a quadratic function and cell wall thickness a linear function (Figure 9). Lumen area and hydraulic diameter were characterized by an initial increase and stabilized between the cambial ages of 30 to 60 years. These parameters stabilized very quickly at SIM, at cambial age 30, but much later at MIR (cambial age 60). High variation was found in sites BER and MIS.

Cell diameter was characterized by an initial increase and stabilized between cambial age 20 to 40 years, with a quick increase at sites DAN and SIM and slower at MIR (Figure 9). This parameter shows less variation between trees per site compared to lumen area and cell wall thickness.

Cell wall thickness in the five sites shows an increase with age, with no stabilization and high variability between trees per site, especially for site BER (Figure 9). The cell wall thickness started with values below 2 μm and reached more than 3 μm at the cambial age of 60 years.

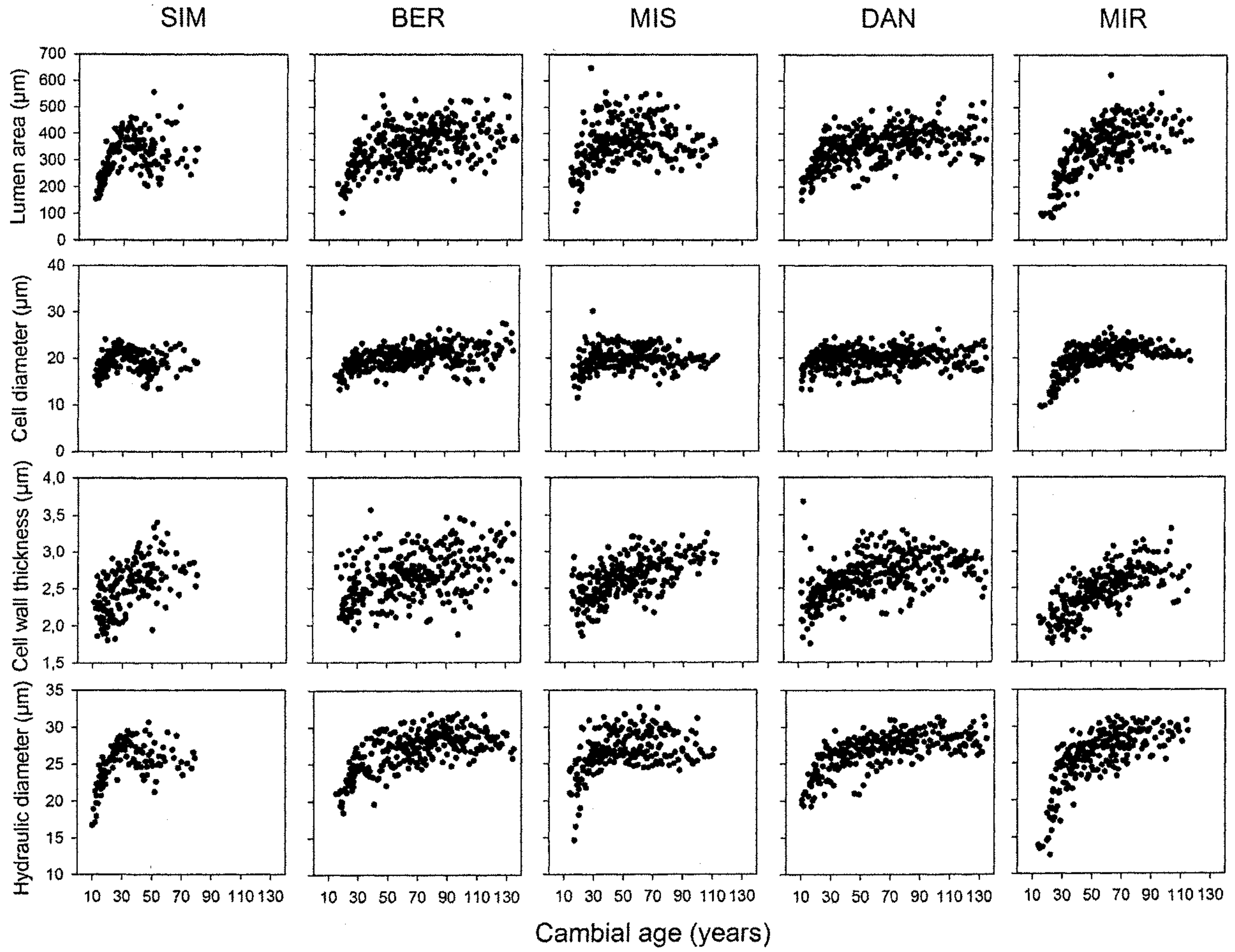

Figure 9 - Annual measurements of lumen area, cell diameter, cell wall thickness and hydraulic diameter for the five black spruce per site.

3.3. Wood Density

Wood density showed similar trends over the years among the trees and sites (Figure 10). In all sites, the first 20 years showed a great variation starting with low values and rising rapidly to high ones before stabilizing. Density values varied between 400 and 600 (kg/m^3). BER and MIS showed greater variation than the other sites while MIR showed less.

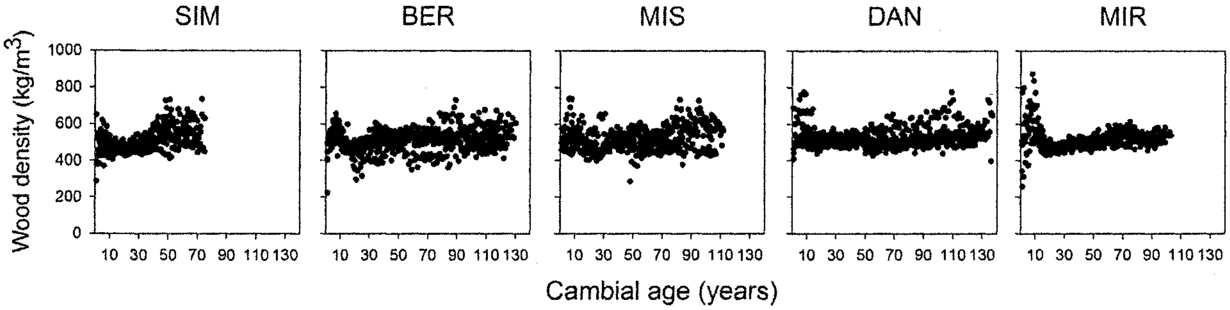

Figure 10 - Average density among the five black spruce trees per site.

3.4. Tracheid features

Tracheid length and tracheid diameter follow a spherical semi variance function, increasing quickly during the first years then continuing to increase at a lower rate until the end (Figure 11).

Tracheid length at SIM and MIR presents lower values compared to the other three sites (Figure 11). Little variation between the five trees was obtained for site MIR and a lot of variation between trees in site SIM. Tracheid length at 80 years of age reached over 3 mm.

Tracheid diameter at SIM had the lowest value at its maximum and stabilized at an earlier age than the other sites (Figure 11). MIR and MIS showed higher diameter values with age than the other sites. Little variation was measured between the five trees per site, except for MIS.

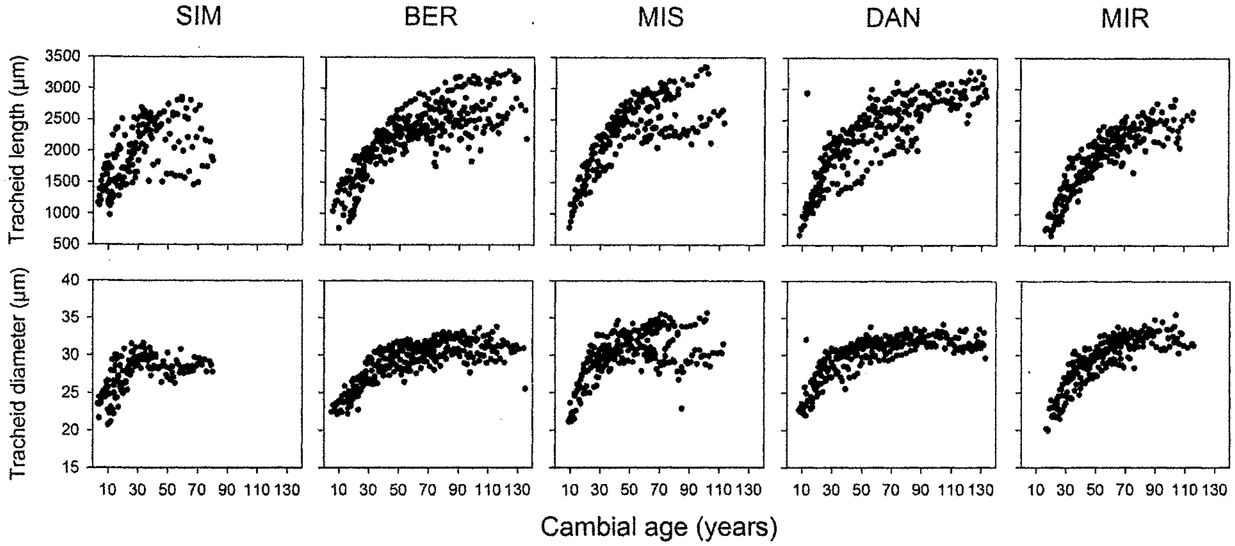

Figure 11 - Tracheid length and diameter among the five black spruce trees per site.

3.5. Mechanical strength

Figure 12 illustrates the MOE and MOR expressed for the average age of each analyzed section. Mechanical strength showed great variation within sites.

Mechanical strength follows a linear function according to age, but not in all sites. Trees at SIM have the best performance in MOE and MOR, with high values at early ages. SIM, MIS and DAN exhibited a clear trend, with lower values of MOE and MOR at early age and higher values later on. However, BER and MIR showed greater variation among the trees with no evident trend with age (Figure 13).

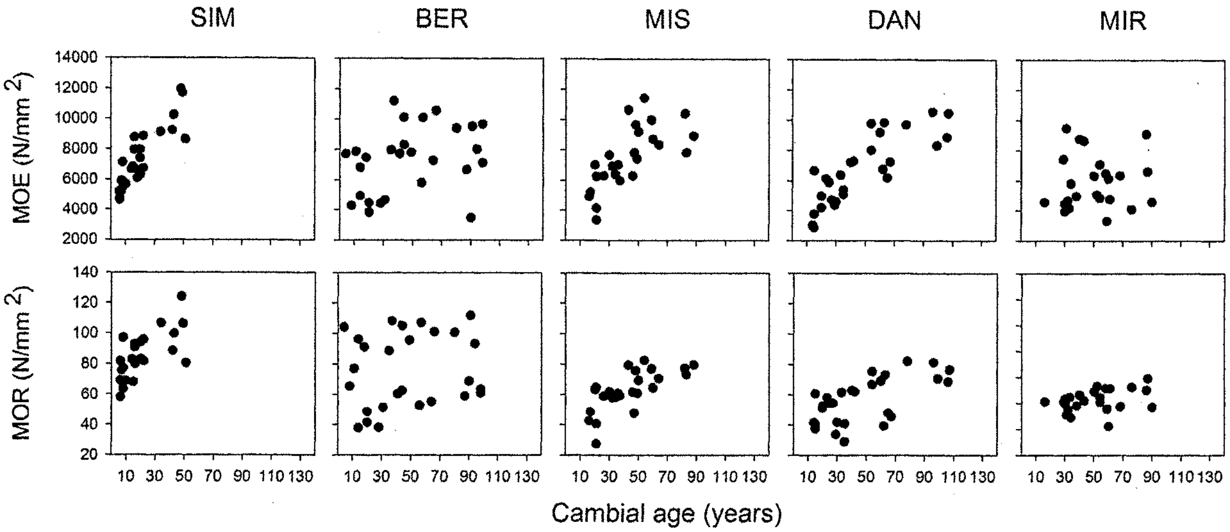

Figure 12 - MOE and MOR measurements for the five black spruce trees per site.

3.6. Comparison between sites

To facilitate the comparison among the sites, mathematical functions were applied to the measurements.

For dendrometric measurements (DBH, tree height, stem volume), high values of coefficients of determination were obtained with R^2 values between 0.82 to 0.98 (Table 3). The growth of DBH had almost arrived at its maximum in SIM at age 40, while only half of their maximum values were found for the other sites at the same age. BER showed a lower DBH increase compared with the other sites (Figure 13). MIR showed a lower growth in height and cumulative volume than the other three sites. MIS and DAN showed similar results for DBH, tree height and stem volume keeping intermediate values of all sites for the analyzed period.

For anatomical measurements, (lumen area, cell diameter, cell wall thickness and hydraulic diameter) lower R^2 values ranging between 0.09 to 0.83 were found (Table 3). Lumen area and cell diameter at site SIM showed increasing values up to approximately 40 years of age before decreasing to values below the other sites (Figure 13). On the contrary, the lumen area and cell diameter at site MIR presented lower values at low cambial age, but the measurement reached higher values than the other sites with increasing cambial age. BER, DAN and MIS presented similar trends, in between the two other sites. Cell wall thickness at site SIM started with the lowest values, but surpassed all sites at 30 years of age. On the contrary, MIR presented the lowest values, whereas the cell wall thickness showed values between the other two sites starting at the cambial age of 30 years. For hydraulic diameter, all sites showed a similar behavior and high values of coefficient of determination varying between 0.42 and 0.83 (Figure 13, Table 3).

Wood density showed low values of coefficients of determination, especially for BER and DAN, because of the high variation in the measurements (Table 3). All sites showed an increase in wood density according to cambial age. SIM and MIS began with lower wood densities but at the age of approximately 44 years, the values began to be higher than the other three sites (Figure 13). At the other sites wood density slowly increased with cambial age and had low values compared to SIM and MIS even at more than 100 years of age.

The tracheid variables (length, diameter) showed high values of coefficients of determination varying between 0.50 to 0.83 except for lower R^2 values in site SIM (Table 3). SIM presented a rapid increase of tracheid length that had already stabilized at 40 years of age. MIR presented a slow increase rate for the tracheid length and formed longer tracheids than SIM only at 80 years of age. The tracheid length evolution of the other three sites was similar, with measurements in between SIM and MIS. The same pattern as tracheid length was obtained for tracheid diameter, except that the diameter at site MIR surpassed the other sites at 70 years of age.

For the mechanical strength variables (MOE, MOR), the coefficients of determination were variable with R^2 values varying between 0.00 to 0.79 (Table 3). The mathematical functions applied represent only the measurements well for sites SIM, MIS and DAN. These sites presented a steady increase in MOE values with the highest rate according to age, SIM having the highest values at an early age and DAN having the lowest values of the three sites. BER and MIR presented the lowest increase rate of MOE, being almost a parallel to one another with MIR having the lowest values of all sites. All sites showed a similar trend for MOR, with BER and MIR having a lower increase of values and SIM, MIS and DAN having a higher and steady increase according to age. The reduced residuals of all curves fitted showed a normal distribution (Annex 1) indicating a good fitting of the models.

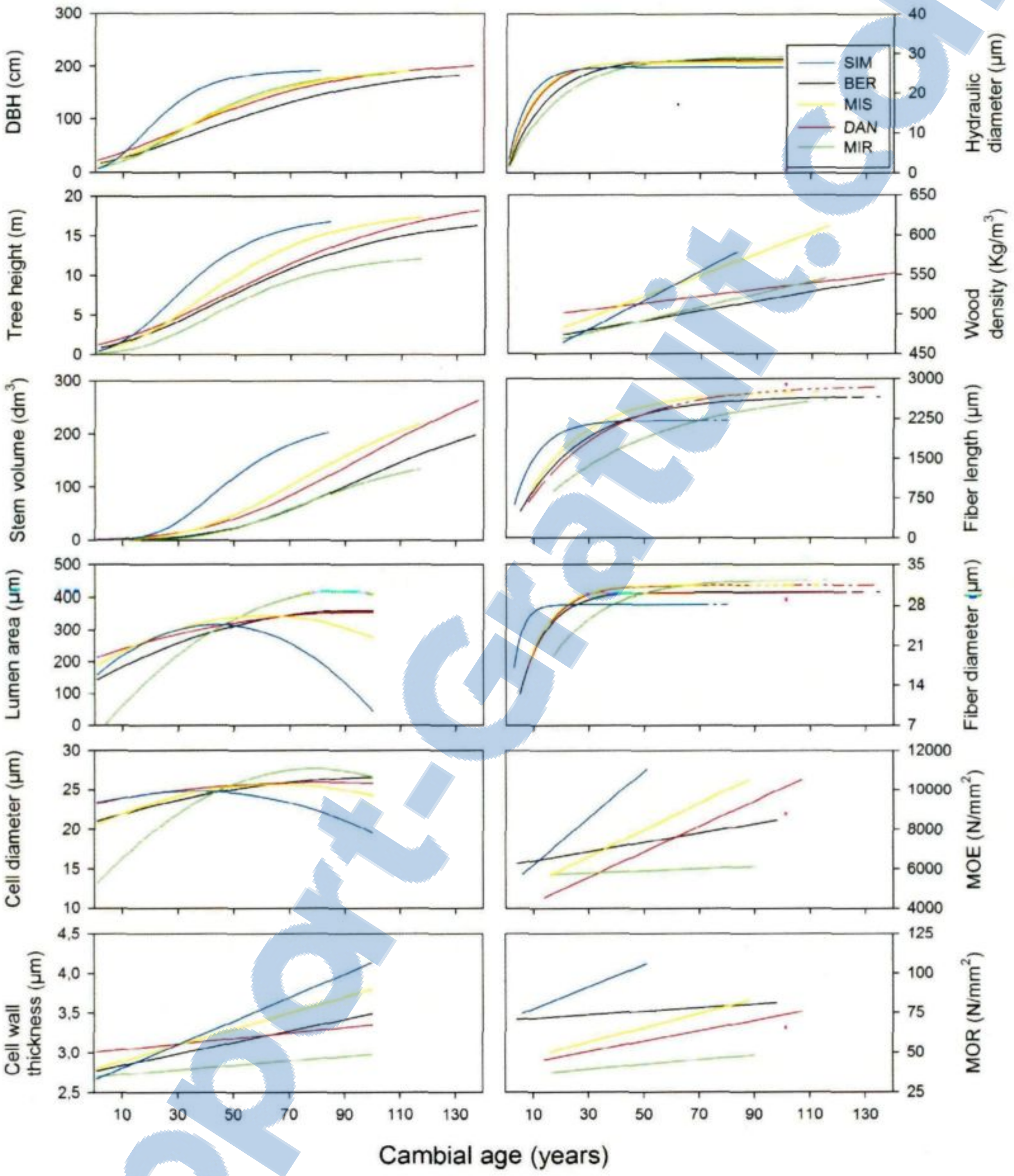

Figure 13 – Variation of growth and wood characteristics of black spruce from five sites in function of cambial age.

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Table 3. Statistics resulting from the regressions fitted. Growth variables (DBH, stem height, tree volume), anatomical variables (Lumen area, cell diameter, CWT and diameter hydraulic) and quality variables (wood density, tracheid length, tracheid width, MOE and MOR) representing growth and wood characteristics of black spruce in five sites. The regression variables were: *a* , the upper asymptote; *b* the rate of change of the shape; *c* the x-axis placement. R^2 and *F* values estimates the quality and validity of the models respectively and *P* values to show the significance level (p<0,05).

		COEFFICIENTS					
VARIABLE	SITE	a	b	c	F	P	R^2
DBH (cm)	SIM	192,6	$7.69\ 10^{-6}$	16,993	$137.714\ 10^{2}$	<.0001	0,95
	BER	200	$2.59\ 10^{-6}$	36,4136	$131.894\ 10^{2}$	<.0001	0,91
	MIS	200,5	$3.61\ 10^{-6}$	28,5584	984.908 10	<.0001	0,91
	DAN	210,6	$2.82\ 10^{-6}$	29,2935	723.694 10	<.0001	0,83
	MIR	191,9	$4.42\ 10^{-6}$	28,2067	$173.799\ 10^{2}$	<.0001	0,95
Stem height (m)	SIM	17,5763	$5.25\ 10^{-6}$	25,9898	$184.624\ 10^{2}$	<.0001	0,97
	BER	17,6773	$2.68\ 10^{-6}$	42,8068	$252.893\ 10^{2}$	<.0001	0,96
	MIS	18,2205	$3.72\ 10^{-6}$	36,2964	$433.502\ 10^{2}$	<.0001	0,98
	DAN	20,624	$2.28\ 10^{-6}$	46,4036	$189.748\ 10^{2}$	<.0001	0,94
	MIR	12,6828	$3.97\ 10^{-6}$	40,1522	$245.164\ 10^{2}$	<.0001	0,97
Tree volume (dm^3)	SIM	225,6	$5.21\ 10^{-6}$	41,8113	327.420 10	<.0001	0,90
	BER	284,5	$2.22\ 10^{-6}$	91,3654	242.418 10	<.0001	0,83
	MIS	296,1	$2.68\ 10^{-6}$	72,3627	212.357 10	<.0001	0,82
	DAN	410,1	$1.87\ 10^{-6}$	94,6774	382.747 10	<.0001	0,87
	MIR	167,5	$3.26\ 10^{-6}$	71,6381	810.638 10	<.0001	0,95
Lumen area (µm)	SIM	150,42087	$7.59\ 10^{-4}$	-0,0866	$956\ 10^{-2}$	0,0003	0,25
	BER	138,87584	$4.75\ 10^{-4}$	-0,02562	$515.2\ 10^{-1}$	<.0001	0,47
	MIS	182,94019	$5.31\ 10^{-4}$	-0,04376	$188.8\ 10^{-1}$	<.0001	0,32
	DAN	210,1355	$3.03\ 10^{-4}$	-0,01589	$414.1\ 10^{-1}$	<.0001	0,44
	MIR	-35,92351	$1.03\ 10^{-3}$	-0,05909	203,78	<.0001	0,82
Cell diameter (µm)	SIM	23,08698	$9.34\ 10^{-6}$	-0,00129	$271\ 10^{-2}$	0,0754	0,09
	BER	20,91682	$1.07\ 10^{-5}$	-0,0005	$384.2\ 10^{-1}$	<.0001	0,40
	MIS	20,46215	$1.59\ 10^{-5}$	-0,00123	$151.3\ 10^{-1}$	<.0001	0,27
	DAN	23,32554	$6.32\ 10^{-6}$	-0,0003817	$996\ 10^{-2}$	0,0001	0,16
	MIR	12,72294	$3.79\ 10^{-5}$	-0,0024	215,66	<.0001	0,83
Cell wall thickness (µm)	SIM	2,655	$1.48\ 10^{-6}$		$464.1\ 10^{-1}$	<.0001	0,44
	BER	2,76691	$7.23\ 10^{-7}$		$787.1\ 10^{-1}$	<.0001	0,41
	MIS	2,79133	$10.08\ 10^{-7}$		$712.6\ 10^{-1}$	<.0001	0,47
	DAN	3,00743	$3.45\ 10^{-7}$		$280.6\ 10^{-1}$	<.0001	0,21
	MIR	2,69768	$2.79\ 10^{-7}$		$122.7\ 10^{-1}$	0,0007	0,12
Diameter hydraulic (µm)	SIM	26,5613	$6.72\ 10^{-4}$		637.164 10	<.0001	0,42
	BER	28,6071	$1.41\ 10^{-3}$		$289.30\ 10^{2}$	<.0001	0,73
	MIS	27,9241	$9.37\ 10^{-4}$		947.706 10	<.0001	0,35
	DAN	28,1243	$1.01\ 10^{-3}$		$291.325\ 10^{2}$	<.0001	0,68
	MIR	29,3536	$1.86\ 10^{-3}$		$147.639\ 10^{2}$	<.0001	0,83
Wood density (kg/m^3)	SIM	427,62494	$1.81\ 10^{-4}$		$950.2\ 10^{-1}$	<.0001	0,24
	BER	461,86117	$6.06\ 10^{-5}$		$669.4\ 10^{-1}$	<.0001	0,11
	MIS	455,95363	$1.33\ 10^{-4}$		412,11	<.0001	0,47
	DAN	492,54517	$4.27\ 10^{-5}$		$543.1\ 10^{-1}$	<.0001	0,09
	MIR	452,2833	$8.12\ 10^{-5}$		225,36	<.0001	0,34
Tracheid length (µm)	SIM	2212,8	$8.87\ 10^{-4}$		239.194 10	<.0001	0,36
	BER	2661,9	$2.39\ 10^{-3}$		$103.714\ 10^{2}$	<.0001	0,71
	MIS	2763,3	$2.22\ 10^{-3}$		725.106 10	<.0001	0,71
	DAN	2867,8	$2.97\ 10^{-3}$		856.437 10	<.0001	0,76
	MIR	2824,4	$4.57\ 10^{-3}$		$106.40\ 10^{2}$	<.0001	0,83
Tracheid diameter (µm)	SIM	28,1728	$3.18\ 10^{-4}$		$152.835\ 10^{2}$	<.0001	0,25
	BER	30,226	$9.44\ 10^{-4}$		$370.066\ 10^{2}$	<.0001	0,50
	MIS	31,4269	$9.66\ 10^{-4}$		$253.175\ 10^{2}$	<.0001	0,56
	DAN	31,3615	$9.94\ 10^{-4}$		$547.674\ 10^{2}$	<.0001	0,67
	MIR	32,4151	$19.09\ 10^{-4}$		$516.895\ 10^{2}$	<.0001	0,81
MOE (N/mm^2)	SIM	5013,39252	$11.86\ 10^{-3}$		$825.700\ 10^{-1}$	<.0001	0,79
	BER	6175,06095	$2.33\ 10^{-3}$		$296\ 10^{-2}$	0,0978	0,11
	MIS	4567,28255	$6.77\ 10^{-3}$		$208.7\ 10^{-1}$	0,0001	0,48
	DAN	3624,4864	$6.45\ 10^{-3}$		$556.7\ 10^{-1}$	<.0001	0,68
	MIR	5640,91769	$5.27\ 10^{-4}$		$8\ 10^{-2}$	0,7776	0,00
MOR (N/mm^2)	SIM	70,40103	$6.95\ 10^{-5}$		$188.8\ 10^{-1}$	0,0003	0,46
	BER	70,3578	$1.11\ 10^{-5}$		$51\ 10^{-2}$	0,4816	0,02
	MIS	42,98589	$4.49\ 10^{-5}$		$216.9\ 10^{-1}$	0,0001	0,49
	DAN	40,94998	$3.25\ 10^{-5}$		$171.4\ 10^{-1}$	0,0003	0,40
	MIR	35,01257	$1.48\ 10^{-5}$		$315\ 10^{-2}$	0,0899	0,13

3.7. Comparison between ages

Principal components analysis was realized at ages of 20, 40, 60 and 80 years for a better understanding of the differences of all parameters shown at these ages (Figure 14). Component 1 accounts for the largest amount of the total variation in the data and varies from 63 to 71%. Component 2 accounts for the maximum amount of the remaining total variation and varies from 28 to 36%.

The importance of components 1 and 2 for the five study sites changes little with cambial age. SIM and MIR are opposite in regard to the two components and BER, MIS and DAN are grouped together for cambial age 40, 60 and 80 (Figure 14).

At 20 years, SIM showed high values for mechanical strength, DBH and tracheid length (Figure 14). MIR presented low values for anatomical measurements, tracheid diameter, tree volume and stem height. MIS and DAN presented highest values of wood density. Component 1 and 2 accounted for 69% and 31%, respectively.

At 40 years, BER, MIS and DAN showed higher values of tracheid diameter and hydraulic diameter. SIM showed highest values of mechanical strength, stem height, tree volume and DBH. MIR showed low values for anatomical measurements. Component 1 and 2 accounted for 63% and 37%, respectively.

At 60 years, BER, MIS and DAN showed highest values of tracheid length and mechanical strength (Figure 14). SIM presented higher values of wood density, DBH, tree volume and stem height and low values for tracheid diameter and diameter hydraulic. MIR presented low values for mechanical strength, tracheid length and cell wall thickness. Component 1 and 2 accounted for 68% and 32%, respectively.

At 80 years, once again, BER, MIS and DAN showed highest values of tracheid length and mechanical strength and low values of DBH. SIM presented higher values of wood density, tree volume and DBH and low values for tracheid diameter. MIR showed low values for mechanical resistance, tracheid length and cell wall thickness. Component 1 and 2 accounted for 72% and 28%, respectively.

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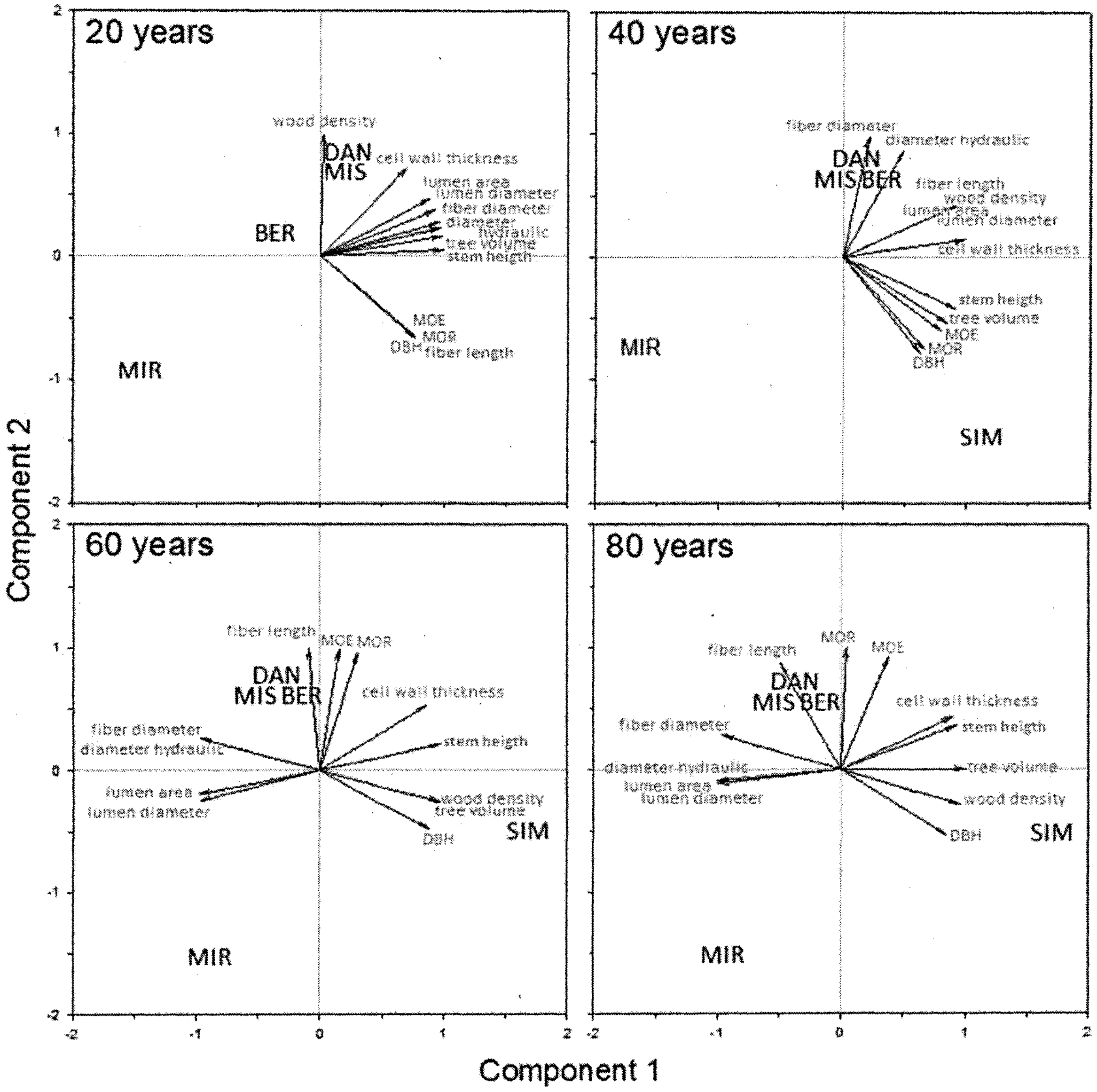

Figure 14 - Multidimensional preference analysis of the ages 20, 40, 60 and 80 years for the five sites including each analyzed parameter.

4. DISCUSSION

4.1. Age

All measured wood properties change with tree age and follow distinct trends. At the initial stage the tree produces a wood called "juvenile wood" characterized by lower density, shorter tracheids, thinner cell walls, smaller tangential cell dimensions, larger fibril angles, larger cell lumen and lower strength properties (Walker, 2013; Yang and Hazenberg, 1994). The formation of "mature wood" follows that of juvenile, with little variation in the anatomical properties (Cown, 1992; Panshin and De Zeeuw, 1970). These two phases were clearly visible in most of the analyzed data set. In between juvenile and mature wood is the transition that occurs between the ages of 11 and 21 for black spruce (Alteyrac *et al.*, 2005; Yang and Hazenberg, 1994).

Almost all properties started with lower values closer to pith before increasing and only lumen area and cell length showed a different behavior (Figure 13). Tracheid length and diameter increase rapidly in a non-linear way during the juvenile phase and afterwards more gradually in mature wood. Wood density results were consistent with previous observations in conifers increasing with the cambial age linking this pattern to the thickness of the cell wall as the tree becomes older (Guller *et al.*, 2012)

In our case, the southern site follows the theoretical pattern (low values at the beginning of life and growing until stable values), meanwhile, a delay in the time of wood maturation seems to occur further north showing the longest period in the juvenile stage and a late change to mature wood especially for tracheid diameter (Figure 13). This observation along the altitudinal gradient may be due to temperature associated with soil depth and genetic differences due to natural selection (Grossnickle, 2000). This theoretical pattern in *Picea mariana* develops closer to optimal growing conditions like temperature, competition, nutrients, status and several other factors found in the southernmost site. The annual growth development under less favorable environmental conditions (5 °C less during the growing season) at the most northern site showed reducing growth and cell wall thickness but increasing lumen area measurements and consequently increasing hydraulic diameter. This leads to increase volume and decrease cell wall mass in each growth ring. Consequently wood density and mechanical properties are decreased demonstrating the adaptability for survival to unfavourable environmental conditions at the northern sites of black spruce. These adaptations may explain the wide distribution of this species in North America (Burns and Honkala, 1990; Laird Farrar, 1997).

4.2. Growth and latitudinal gradient

Xylem production decreased from south to north, SIM and MIR being the sites having the highest and lowest production of xylem respectively and BER, MIS and DAN having a similar development, this trend is due to the reduction in temperature. The length of the growing season is a determinant of xylem production; temperature and precipitation normally influence the annual growth of boreal conifers (Brooks *et al.*, 1998; Kozlowski *et al.*, 1991) because trees are active only from late spring to summer and become dormant in autumn in order to harden for winter (Rossi *et al.*, 2008). However it has been observed that precipitation has no effect on the wood features in black spruce in the Saguenay-Lac-Saint-Jean area (Krause *et al.*, 2010), the main factor affecting xylem production in the northern area was the temperature, as demonstrated by several authors (Deslauriers and Morin, 2005; Gričar *et al.*, 2006a; Gričar *et al.*, 2006b; Oribe and Kubo, 1997; Rossi *et al.*, 2008). Inferring the results of Lupi, warmer spring temperatures lead to earlier cambial reactivation; increasing cell production and delaying cell maturation in autumn (Lupi *et al.*, 2010). It was also verified in Europe that elevation influenced the developmental phases, which were earlier at lower elevations and growth tended to decrease with increased elevation (Moser *et al.*, 2009).

For our sites, xylem production lasted between 80 and 133 days, with SIM having the longest duration (Belien *et al.*, 2012), and reducing further north and with increasing altitude. Depending of the year, the onset of xylem growth occurred from mid-May to mid-June, covering a range of approximately 1 month. Later onsets of xylogenesis were detected in BER and MIR. The ending of xylem growth differed by more than 1 month between the end of August in BER, MIS and DAN, and the beginning of October in SIM (Boulouf Lugo *et al.*, 2012). The last cells in cell wall lignification, which corresponded to the ending of xylem differentiation, were observed at mid-August in MIR (Girard, unpublished data).

The growing season for our sites normally covered the period from June to September (except SIM) with temperatures between 13.3 and 8.8 °C (Table 4). It is clearly visible that SIM presents the longest duration and the highest average temperature during the growing season and MIR is the coldest site with the shortest growth duration.

Xylem production followed the bioclimatic domains and was linked to the temperature decreasing productivity going north. The only exception was BER from the balsam fir – white birch domain, where the growing parameters are similar to the stands from the spruce – moss domain, and this is linked to altitude, BER being the higher site (Figure 15).

In the boreal forest, plant growth is limited by low temperatures and, indirectly, by availability of nutrients, especially nitrogen (Lupi *et al.*, 2012). Soil temperatures affect the decomposition of soil organic matter and nutrient cycles and the duration of snow cover. It is known that the soil temperatures are directly influenced by air temperature, but also by the depth of the different soil layers. For example, Grossnickle (2000) mentioned that in areas with organic soils the frost frequency is higher than in mineral soil and this is caused by the lower capacity of organic soils to store and transmit heat.

Thus, the variation of soil temperature is related to air temperature, depth of the organic layer and, in combination with availability of nutrients, both influencing cambial activity (onset, rate and ending) that is directly correlated to xylem production. A difference of the organic layer was measured, with values between 10-20 cm for stand SIM and deeper organic layers of between 20-40 cm for the other stands. In stand SIM, the soil depth is limited by shallow bedrock that also limits the maximum rooting depth.

Another factor that can explain the different growing pattern between stand SIM and BER is the altitude. Altitude determines how rapidly site temperatures decline because radiative cooling is greater at higher elevations at the same latitude (Grossnickle, 2000) as well as the availability of nutrients (Stottlemyer *et al.*, 2001). Even if sites SIM and BER were only 93 km apart and in the same bioclimatic domain, the elevation difference between these two stands was 273 m (Table 4). This elevation difference causes lower temperatures at one site, lower temperatures are related to slower N mineralization rates (Stottlemyer *et al.*, 2001) making nutrients absorption more difficult for a tree making grown the organic soil layer (Table 4). SIM, with the warmest temperature and shallowest soil depth, probably had the higher xylem production due to better availability of minerals.

The growth differences obtained between the five stands followed the general north - south trend described in the literature, with productivity decreasing towards the north. Temperatures seem to be the main factor influencing cambial activity (Deslauriers *et al.*, 2008). Altitude, the organic soil layer and soil minerals nutrients seem to be important for tree productivity.

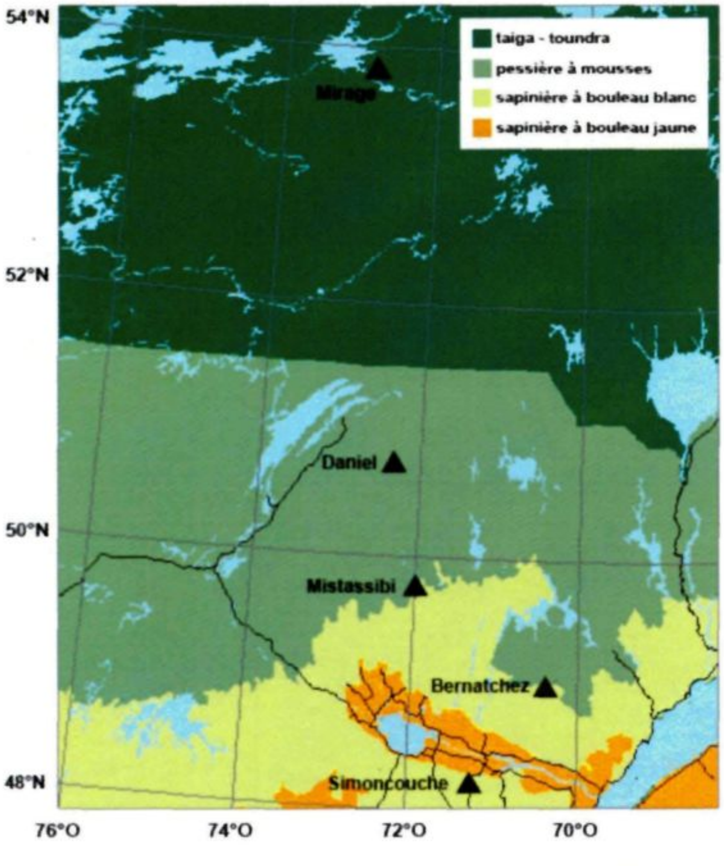

Figure 15 - Bioclimatic domains of the five sites.

Table 4. Cambial activity, temperature, altitude and humus layer of the evaluated sites (Belien *et al.*, 2012; Boulouf Lugo *et al.*, 2012; Rossi *et al.*, 2011) (Girard, unpublished data).

Site	Onset of cambial activity (DOY)	Ending of cambial activity (DOY)	Duration of cambial activity (Days)	Mean temperature May-Sept (°C)	Humus Layer (cm)
SIM	151	269	118	13.3	10-20
BER	156	260	104	11.4	20-40
MIS	155	257	101	12.7	20-40
DAN	171	256	99	11	20-40
MIR	162	240	78	8.8	

4.3. Wood quality

Wood quality for structural purposes had the highest values in the southern site and decreased northwards. Mechanical strength was closely linked to the relationship between cell wall thickness and wood density. Density is one of the most important physical properties of wood (Bowyer *et al.*, 2007; Desch and Dinwoodie, 1996), defined by the relation between its mass (cell wall) and volume (cell wall plus air) at a given moisture content. Thus the cell wall thickness is an excellent indicator of wood density which is influenced by the environment (proportional to temperature in Norway spruce (Franceschini *et al.*, 2013)) determining the rate of growth (Treacy *et al.*, 2000), as well as the type and size of cells and the amount of latewood versus earlywood (Barnett and Jeronimidis, 2003). The linear and strong relationship between wood density and mechanical strength has been also demonstrated by many studies (British Standard EN 384R, 2000; Forest Products Laboratory, 2010; O'Sullivan, 1976; Panshin and De Zeeuw, 1970).

As already discussed, the growing season determined by temperature, influences the amount of wood production, and also the wood quality. Latewood formation is strongly influenced by an increase in the duration of the cell wall thickening phase (Deslauriers and Morin, 2005; Rossi *et* *al.*, 2006). The duration for the latewood formation is shorter in the northern site, which results in reduced cell wall thickness of the latewood and negatively influences the mechanical strength.

Reduced mechanical properties have been associated to wood of rapidly growing red pine (*Pinus resinosa* Ait) in plantations (Kraemer, 1950). Also Barnett (2003) reviewed similar findings linking fast-growing trees with unstable wood. However, the information about the relationship of growth rate and cell wall thickness is contradictory. Koga et al. (1992) found that there was no significant correlation between basic density and annual ring width in Japanese cypress. Koizumi et al. (1992) came to similar conclusion in Japanese larch, and Tsoumis and Passialis (1977) also found that there is no relationship between growth rate and density. On the other hand, Yao (1970) showed that there is a inverse relationship between ring width and density in *Pinus taeda* and similar results were found by Zhang and Oliva in several species and in *Pinus nigra* respectively (Oliva *et al.*, 2006; Zhang, 1995).

The causes of the observed apparent contradictions in ring width, density and rate growth, may be that many studies have not granted sufficient importance to the effect of some fundamental factors on the variation of wood, like genotype, tree age, provenance, site quality, and forest management affecting the correlations between density and ring-width (Zhang *et al.*, 1996). It has also already been proved that the rate of growth had less influence on the mechanical strength than the quality of site where the trees developed (Fernandez-Golfin and Diez, 1996; Fernandez-Golfin Seco *et al.*, 2004; Oliva *et al.*, 2006)

In our case, the rate of growth reduced northwards. Many authors mentioned that a growth increase might lead to a decrease of wood quality, especially in regard to mechanical properties, those being necessary for wood products used for structural applications (Shmulsky and Jones, 2011). A growth increase can lead to a decrease in wood density (Mäkinen *et al.*, 2002), particularly due to an increase in the number of earlywood cells with nearly no change within the latewood cells (Wang *et al.*, 2002; Zhang, 1998). However, our results showed a direct relationship between the rate of growth and wood quality for *Picea mariana*.

Our results are in accordance with the findings of Tsoumis and Passialis (Tsoumis and Passialis, 1977) showing that the density of *Pinus nigra* wood of co-dominant trees was higher in southern locations, with high or intermediate site qualities. Cown also concluded in the same species that wood density decreased when altitude and latitude increased (Oliva *et al.*, 2006). This higher value of wood density at the southern sites also corresponded to higher values of mechanical strength.

In terms of tracheid length, the southern site had the lowest value and this wood parameter increased with latitude. The reduction observed in the mechanical strength northwards is linked to the reduction in cell wall thickness and not because of the tracheid length or the trees being about 50% shorter in the north. This reduction in tree height had an influence on the need to develop a strong resistance to wind to avoid rupture or fall, because, the safety factor against failure decreases as a tree gets taller (Niklas and Spatz, 1999).

In our case, black spruce showed a negative relationship between the rate of growth and tracheid length (the higher growth rate at the southern site corresponded to shorter tracheid length). These results were similar to those of Adamopoulos who founded that of fast tree growth was linked to short tracheids in *Pinus brutia* (Adamopoulos *et al.*, 2012). However, St-Germain found no relationship between growth rate and tracheid length in black spruce (St-Germain and Krause, 2008). Bannan's investigations (1954, 1957) showed that an increase in the rate of periclinal division will encourage earlier pseudotransverse division and the production of shorter tracheids. Also the earlier the fusiform initials are transversely divided in their cycle of elongation and division, the shorter the mean length of the derived tracheid will be. It is therefore possible that variation within a species is also related to differences in genotype, however there is a little information available regarding the variation in tracheid length within a species in the comparison of individuals, species, provenances, or forms (Dinwoodie, 1961). Also our results are contradictory to the results of Dinwoodie, who said that cell length decreased with increasing latitude (Dinwoodie, 1960).

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5. CONCLUSIONS

This study has provided information on the effect of latitudinal and altitudinal gradients on wood productivity and quality; our work hypothesis was partially confirmed. In fact, the latitudinal and altitudinal gradient influenced wood productivity, density and mechanical resistance, achieving lower values at higher gradients. Age also influences the growth and wood quality. All the parameters associated to tree growth increase with the cambial age. In the case of measured parameters associated to wood quality, lower values were obtained during the first stages of the tree life, followed by an increase with age before stabilisation of the wood quality values.

Limitations in this study were basically in the order of accessibility, time and budged regarding the northern sites and the quantity of samples to be analysed. Further studies on the influence of latitudinal and altitudinal gradients, site quality, stem form and microfibril angle would be necessary regarding growth and quality of black spruce. Adding sample sites in the northern part to be able to identify the limit where harvesting is cost-effective and one plot per site to estimate the error at site level. Factors influencing the tracheid length at a physiological level must be analyzed.

From a forestry point of view, the results suggest that the southern sites should be privileged for wood production. If wood quality is the most important factor to consider, the area starting from the southern black spruce distribution up to the 50° parallel should be harvested. In the case that wood supply is needed, forestry companies do not really need to go further north, because wood productivity and quality will decrease generating a reduction in profits.

The knowledge of the age of the black spruce stands, as well as the information of location inside the boreal forest and the final use of the wood should be achieved to optimise the use of the wood. The value of the final product will be linked to higher values of mechanical resistance and density for structural purposes. In the case of paper or derivate, longer tracheid are searched. The volume par each tree has to be considered regarding the end use in combination with economical values. All this evaluated according to the amount of wood found in different populations of black spruce. This investigation is also one step forward towards knowing the point of equilibrium between age, quantity and quality for economically profitable exploitation in a natural forest of black spruce.

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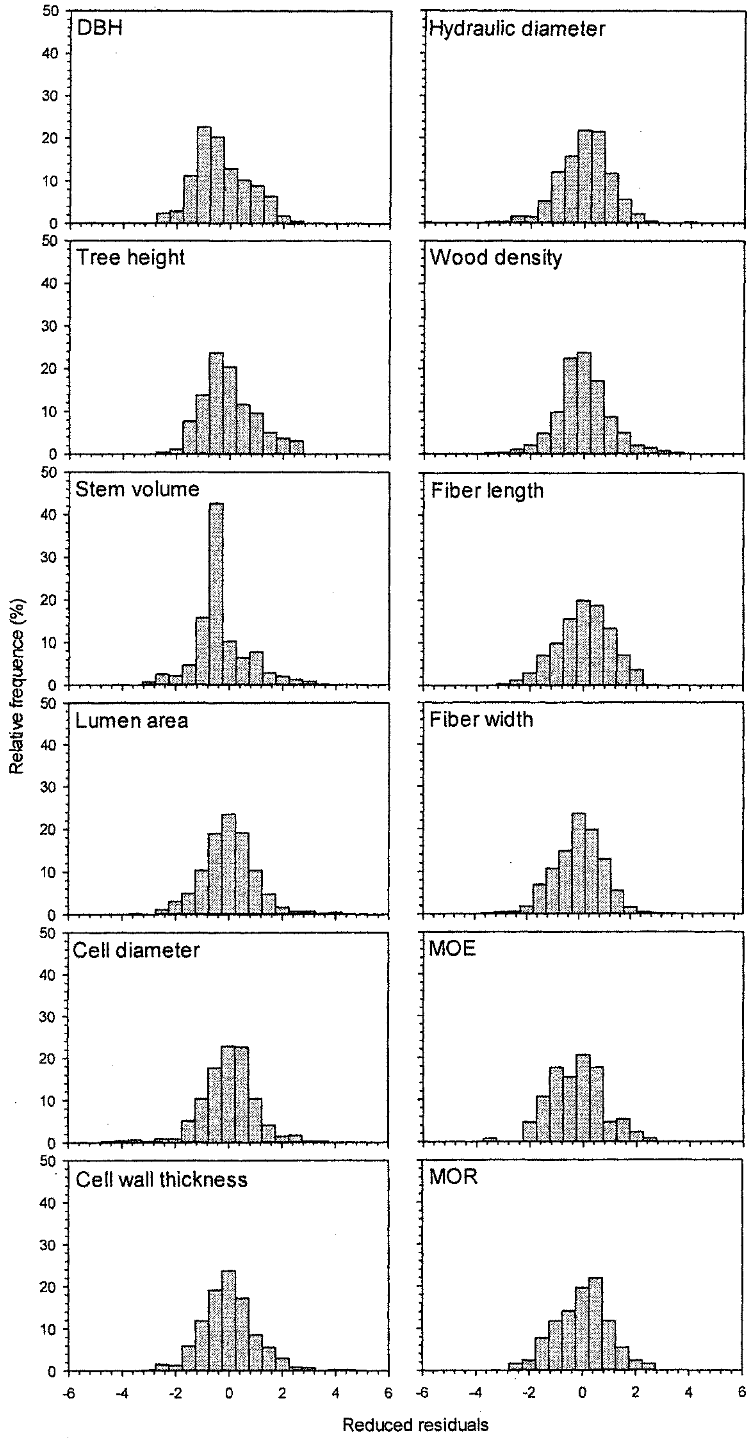
7. ANNEX



Annex 1. Reduced residuals distributions.