Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec

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Abstract: Tracheid cell number, cell diameter, and cell-wall thickness of black spruce (*Picea mariana* (Mill.) BSP) tree rings at the tree line (northern Quebec, Canada) were measured using image analysis. The densitometric data from the same samples were used to evaluate the features of image analysis. The anatomical data were correlated with summer temperature variables, including: means of pentad temperature (five consecutive days), growing season (May–September), sum of degree-days, and number of frost-free days. Our results suggest that the main cause of the pale appearance of light rings is thinner latewood cell-wall thickness. Some latewood variables are strongly correlated with corresponding indices for ring cell number and diameter, and ring cell wall thickness. Anatomical ring cell number and the sum of cell diameters (ring widths) were correlated to tree-ring width parameters derived from densitometry. Ring cell number and annual sum of cell diameter also showed very similar trends with both chronologies, suggesting that ring-width length may depend on the number of cells within a ring. Ratio diagram of double cell-wall thickness to cell radial diameter showed similar trend to wood density profile. There is a statistically significant correlation between maximum density and the highest annual ratio between cell wall thickness and lumen diameter. Cell-wall thickness was significantly correlated to maximum density, and both were significantly correlated with summer temperature variables. Our results suggest that wood anatomy may be used as a substitute to densitometry for climate reconstruction as densitometric data require expensive equipments. Also the anatomical method allows the recording of intra-annual information for dendroecological purposes.

Résumé : Le nombre de trachéides, le diamètre des cellules et l’épaisseur des parois cellulaires des cernes annuels de l’épinette noire (*Picea mariana* (Mill.) BSP) située à la limite des arbres (nord du Québec, Canada) ont été mesurés par analyse d’images. Les données densitométriques provenant des mêmes échantillons ont servi à déterminer les caractéristiques pour l’analyse d’images. Les données anatomiques ont été corrélées aux températures estivales (moyenne des températures pour 5 jours consécutifs, saison de croissance (mai à septembre), somme des degrés-jours et nombre de jours sans gel). Nos résultats suggèrent que les cernes pâles sont causés par un faible épaississement de la paroi des cellules de bois final. Certaines variables du bois final sont fortement corrélées avec les indices correspondants du nombre de cellules, de la largeur et de l’épaisseur des parois cellulaires du cerne entier. Le nombre de cellules et la somme du diamètre des cellules (largeur des cernes) sont étroitement liés aux paramètres de la largeur des cernes obtenus par densitométrie. Le nombre de cellules et la largeur des cernes montrent aussi des tendances analogues dans les deux chronologies utilisées, ce qui suggère que l’épaisseur d’un cerne varie en fonction du nombre de cellules qu’il contient. Le diagramme du rapport entre la double épaisseur des parois cellulaires et le diamètre radial des cellules montre un profil similaire à celui des données densitométriques. La corrélation entre la densité maximale et le plus haut rapport annuel entre l’épaisseur de la paroi cellulaire et le diamètre du lumen est significative. L’épaisseur de la paroi cellulaire est significativement corrélée à la densité maximale qui concordent toutes deux avec les variables des températures estivales. Nos données montrent que l’anatomie du bois peut remplacer la densitométrie lors de reconstitutions climatiques, cette dernière technique n’étant pas toujours disponible à cause des coûts élevés de l’équipement. La méthode anatomique est particulièrement intéressante en dendroécologie, lorsqu’il s’agit d’analyser les variations intra-annuelles des cernes de croissance.

Introduction

Tree-ring width data are used as proxy data to assess past patterns of seasonal to century-scale climate variability (Garfinkel and Brubaker 1980; Bradley 1985; Bradley and Jones 1992; Colenutt and Luckman 1995). In recent decades, tree-ring densitometric data from boreal and subalpine conifers have been shown to be sensitive to summer

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conditions (Polge 1963; Parker and Henoch 1971; Schweingruber et al. 1978; Conkey 1986; Schweingruber 1988; Briffa et al. 1990, 1992, 1995; Luckman et al. 1997). Densitometry allows insights into intra-annual development of tree rings providing more information than could be obtained from annual ring width. Maximum latewood density has been used as a supplementary variable to ring-width data for dendroclimatic purposes (Schweingruber et al. 1978, 1988, 1991; Conkey 1979; Hughes et al. 1984; Cleaveland 1986; Briffa et al. 1988, 1990; Jacoby et al. 1988; D'Arrigo et al. 1992), mostly for the reconstruction of summer temperatures. Combined densitometric and ring-width data have produced better climate reconstructions than either variable alone (Hughes et al. 1984; Conkey 1986; Hughes and Diaz 1994).

However, correlations between climate and tree-ring development can be studied with higher intra-annual resolution than is possible with densitometric data by using variation in wood anatomical structure within radial tracheid files (Jacoby and Telewski 1989). Tracheidograms represent profiles of cell size and cell-wall thickness in relation to time and may provide more information than density profiles (Zobel and van Buijtenen 1989). The use of tracheidograms as accurate indicators of climate variability on a yearly or even intra-annual basis has recently been increasing (Jacoby and Telewski 1989; Park and Telewski 1993; Munro et al. 1996; Gindl 1999). Since tracheidograms represent cellwise development throughout the growing season, it is possible to track cambial activity with precise temperature intervals to find out the period of the growing season that affects tracheid development and how temperatures are distributed throughout the growing season. In conifers, changes in tree-ring density may be defined by the ratio of tracheid cell-wall thickness to cell lumen diameter within an annual ring (Vaganov 1990). The correlation between morphometric and X-ray density measurements is typically high (mean r = 0.93) (Ivkovich and Koshy 1997).

Wood anatomical variables derived from image analysis have not been used for the reconstruction of climate. Different types of climatic information may be reconstructed from anatomical, densitometric, and ring-width variables. However, the physiological processes that link variation in these tree-ring characteristics to variation in climate are not well understood.

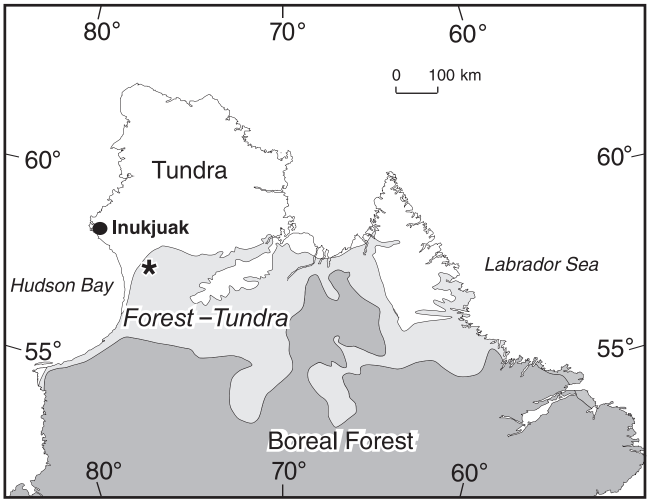
The objectives of this study were (*i*) to investigate the inter-correlations among wood cell characteristics, tree ring-width variables, and densitometric variables for black spruce (*Picea mariana* (Mill.) BSP) and (*ii*) to document the correlations between these various aspects of black spruce tree rings and variables that reflect growing season temperature at a tree-line site in northern Quebec.

Material and methods

Sample selection

The sample discs were collected in the Boniface River area at tree line (57°44′05″N, 76°07′30″W), in northern Quebec, 30 km east of Hudson Bay (see study site description in Arseneault (1996) and Arseneault and Payette (1997)) (Fig. 1). Spruce trees were collected for this study in three different conditions, i.e., living trees (17 radii of 13 samples), exposed dead trees (upright or those lying on the ground) (17 radii of 15 samples), and subfossil trees buried in peat (69 radii of 45 samples). For some stems, we took two radii from different radial directions of the disc, because one radius was only partly available because of the poor quality of the stems (e.g., reaction wood, scars, and cracks). All the sampled trees were growing in sites with well-drained soil conditions (Arseneault and Payette 1997). The samples were naturally dried and then finely sanded. The samples were cross-dated based on the occurrence of light rings (rings with exceptionally few latewood cell layers) using the techniques of Filion et al. (1986), Delwaide et al. (1991), and Arseneault and Payette (1998). These three types of spruce were used to build a millennial-long chronology (Wang et al. 2001).

Fig. 1. Study site (*, Boniface River) and the location of the weather station (Inukjuak).



Temperature data selection

Continuous air temperatures have been recorded at an automated weather station since 1988 in the Boniface area. Because records from the Boniface area are too short for long-term climate reconstruction, we used the climatic data (AD 1940–1992) from the Inukjuak weather station located 125 km northwest of the study site as a representative substitute of weather conditions at Boniface. The correlation of daily and monthly temperatures between the two stations from 1988 to 1998 was very high (r = 0.96 (daily), 0.99 (monthly), P < 0.0001).

Previous dendroclimatic studies done in this region have demonstrated that mean growing season temperature (May–September) is more strongly correlated with tree ring mean and maximum density than other climate variables (Yamaguchi et al. 1993; Wang et al. 2000). Therefore, we performed growth–climate correlation analyses using temperature variables for these months. Intra-annual variation in wood cell anatomy and density were also correlated with pentad temperatures (means of non-overlapping 5-day periods, beginning May 1 and ending September 28) (Vaganov et al. 1999).

Densitometric measurements

Radii were measured with a mean of 89.15 years per radius. The longest series had 207 years and the shortest 18 years, since only a part of the rings in some cross-dated samples were available for densitometric and anatomical measurements. Some curves were discontinuous because of cracks along the ring margin of light rings.

The radii were selected for measurements using disc sections free of cracks and reaction wood (one or two radii from each disc; three to six measurements for each year). Each radius was split into two parts along radial directions: the first part was used for density analysis, and the second part was used for anatomical image analysis. For each radius, thin laths (1 ± 0.045 mm; mean ± SD) were cut using a twin-blade saw (Dendro cut, Walesch Electronics) with careful adjustment to reach a 90° angle to the axis of longitudinal tracheids. Resins were extracted from the laths in a Soxhlet extractor with 96% alcohol for 48 h (Park et al. 1992). The laths were exposed to an X-ray source for 50 min (20°C, 50% relative humidity), 11 kV, 20 mA over a double-sided emulsion film (Kodak RP/M). An automatic processor (X-O-Mat) was used to develop the film for 90 s. The optical darkness on the film, expressing the wood density, was calibrated with a standard cellulose acetate wedge, and then measured by an X-ray densitometer (Dendro-2003, Walesch Electronics). Measurements were recorded at 12-μm intervals along the radial direction from the pith to the outermost ring. These data were used to make continuous profile curves of annual ring density. Maximum density, minimum density, earlywood mean density, latewood mean density, earlywood width, latewood width, and annual ring width were the parameters used in this study.

Image analysis of wood anatomy

Thin wood sections (one to three for each radii depending on the length of radii) about 20 μm thick were processed using a microtome (AO 860) along the second part of each radius used for densitometry. The sections were stained with safranin and permanently mounted on microscope slides. A black and white CCD digitizing video camera used on an optical microscope and connected to a Macintosh IICX was used for numerical image analysis. National Institutes of Health IMAGE (NIH image) version 1.57 software was used for measurements (Rasband 1990). The pixel size was 1.04 μm. Lumen radial diameter and cell-wall thickness of the tracheids were measured along each of three radial files of each growth ring. Mean values for anatomical variables were computed for each annual ring based on data from three to six measurements. However, some years had a high frequency of cracks, and means for anatomical variables were computed for only a few radii. The radii measured had a mean of 89 annual rings, with a maximum of 207 rings and a minimum of 18 rings. Short radii were the consequence of discontinuities in densitometric and anatomical series resulting from cracks along the margins of light rings. The mean ring cell-wall and latewood cell-wall thickness (RCWT, LCWT), ring and latewood cell number (RCN, LCN), ring width and latewood width derived from the sum of cellulose widths (RCW, LRW), and ratio of double cell-wall to cell diameter in the radial direction (WALL/CELL) were compared with X-ray density measurements. The earlywood and latewood cells were clearly defined on the ratio profile of image analysis (Mork 1928; Denne 1988). Representative samples were selected for the characteristics of light rings and normal rings (Wang et al. 2000). Narrow, medium, and large ring groups were derived from the mean – standard deviation, mean, and mean + standard deviation in all data. For each group, 14–18 samples were selected among the samples that had mean cell number in the group.

Statistical analyses

Index chronologies for ring width, cell numbers, and ring width derived from the sum of cell diameters were constructed by fitting a polynomial curve to the annual values to remove age-related trends. The density and cell-wall thickness series only show very small tendency for low-frequency variation over time. Therefore, the density and anatomical series were standardized using straight lines ((value – mean)/mean) (Conkey 1986) then indexing the radii by year to construct a mean chronology (Fritts 1976).

The validity of combining the different types of trees together to build a long-term chronology was tested (Wang et al. 2001). The relationships between anatomical and densitometric parameters and between tree-ring variables and summer temperatures were tested by Pearson's correlations. Partial correlations were used to test the correlations between one set of tree-ring data (anatomy or densitometry) and temperatures when another set of tree-ring data is fixed.

Results

Anatomical characteristics of black spruce tree rings

There were minimal differences in profile patterns among rings of different size (Fig. 2). However, the proportion of latewood cells within a narrow ring was larger than that in medium and large rings because of yearly differences in the number of earlywood cell layers. The percentage of latewood cells within a ring was negatively correlated to ring cell number ($r = -0.255$, $p < 0.0001$, $n = 18774$). Latewood cell number was always lower in light rings than in normal rings for all ring sizes (Fig. 2A). The cell-wall thickness of light rings showed lower value than that of normal rings (Fig. 2B). The profiles for tracheid cell radial diameters were almost the same for light rings and normal rings (Fig. 2C).

Correlation among anatomical and densitometric profiles

Maximum density and latewood mean density were significantly correlated to all anatomical variables, whereas earlywood density and earlywood, latewood, and annual ring widths were correlated in part to anatomical variables (Table 1). These results clearly indicate that latewood density, instead of earlywood characteristics, are the best expression of the anatomical structure of tree rings.

Annual ring cell number (RCN) and width (RCW) were correlated to all densitometric variables except earlywood density. Latewood cell number and width significantly correlated to all three densitometric variables (Table 1).

Fig. 2. Anatomic ring profile of normal and light rings: (A) ratio of cell wall to cell lumen; (B) cell-wall thickness; and (C) cell radial length (tracheid diameter). The solid lines show normal rings, and the broken lines show light rings. The horizontal line in Fig. 2A corresponds to the boundary of latewood and earlywood cells.

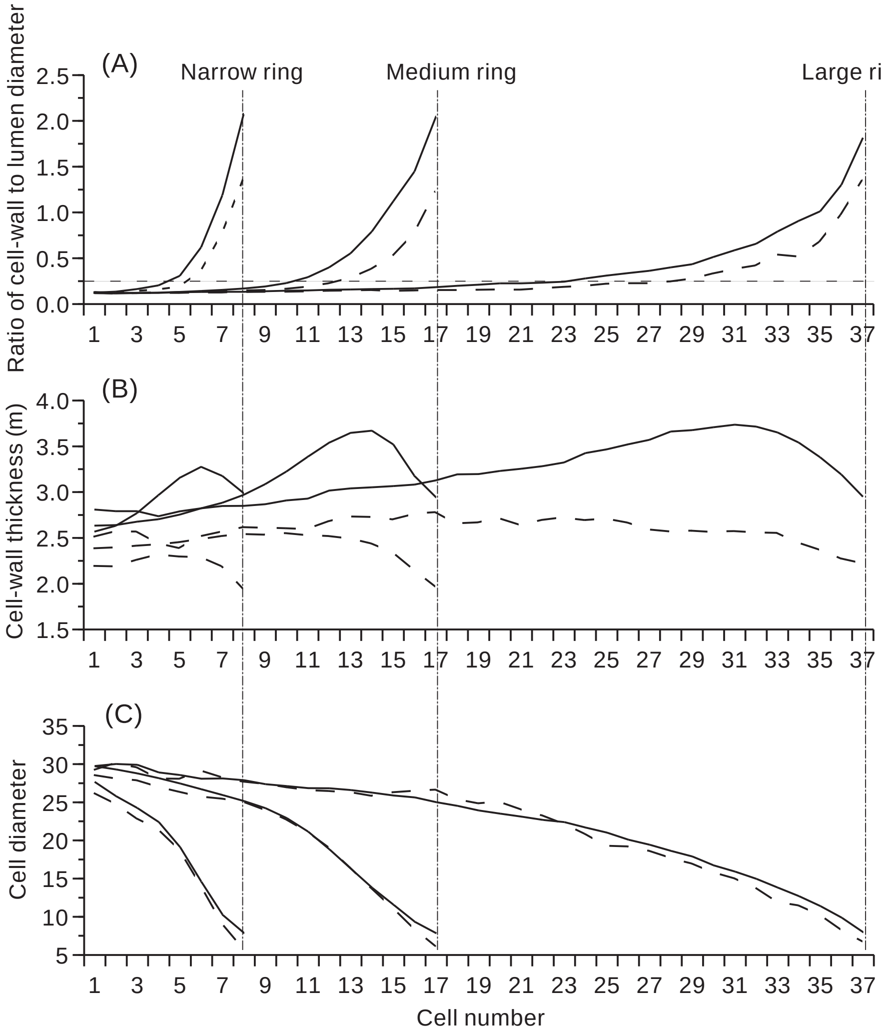


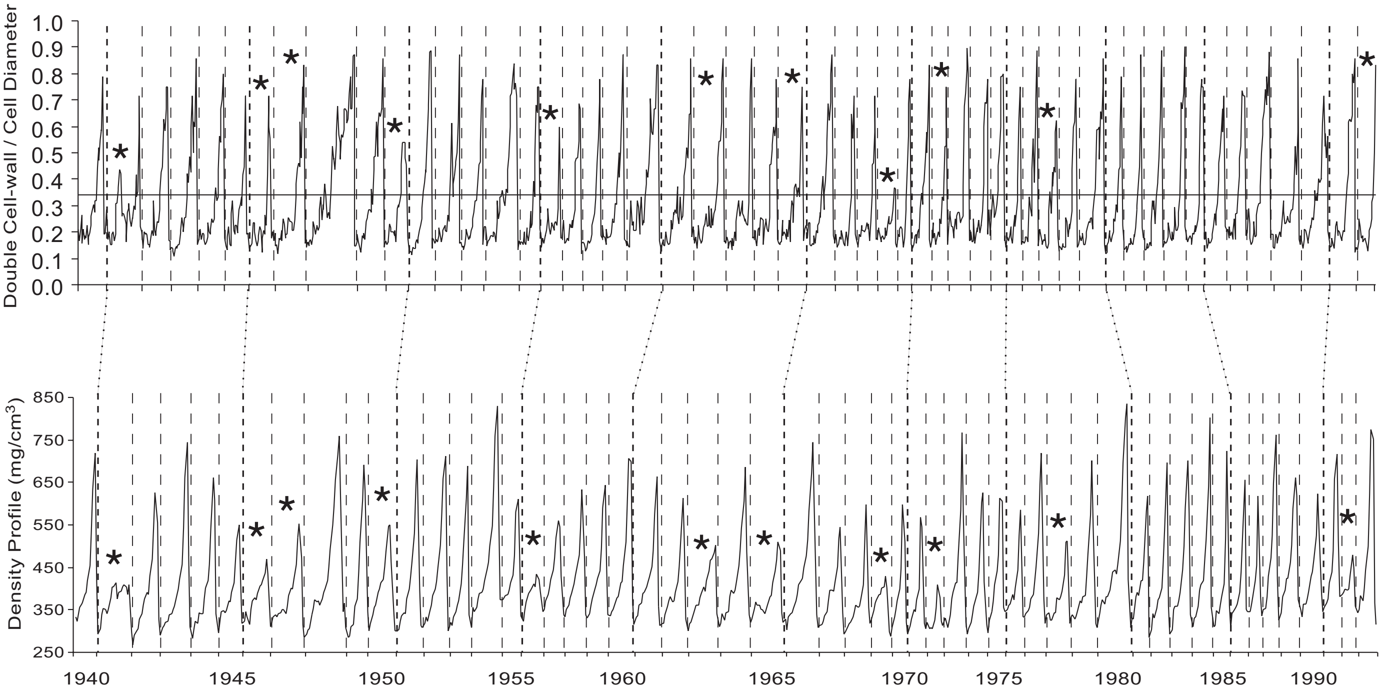
Table 1. Correlation between anatomic parameters and densitometric variables ($N = 53$).

	MAXD	EWD	LWD	EWW	LWW	ARW
RCN	0.317*	0.14	0.306*	0.459**	0.368**	0.498**
LCN	0.549**	0.350*	0.558**	0.235	0.013	0.203
RCW	0.297*	0.063	0.274*	0.493**	0.388**	0.529**
LCW	0.555**	0.348*	0.560**	0.267	0.071	0.251
RCWT	0.570**	0.402**	0.578**	0.172	–0.186	0.072
LCWT	0.793**	0.460**	0.792**	0.321*	–0.208	0.185
WALL/CELL	0.594**	0.203	0.586**	0.087	–0.352**	–0.047

Note: Variables are defined as follows: RCN, ring cell number; LCN, latewood cell number; RCW, sum of cell radial diameter of ring; LCW, sum of cell radial diameter of latewood; RCWT, mean cell-wall thickness; LCWT, mean latewood cell-wall thickness; WALL/CELL, ratio of double cell-wall thickness to total cell diameter; MAXD, maximum density; EWD, earlywood mean density; LWD, latewood mean density; EWW, earlywood width; LWW, latewood width; ARW, annual ring width. *, $P < 0.05$; **, $P < 0.01$.

The ratio of double cell-wall thickness to cell diameter along the radial files appeared to be similar in shape with the density profile (Fig. 3). The annual ring widths derived from the densitometric profile (*Y* axis) did not match the *Y* axis on the anatomical profile that was produced by cell radial files on this figure because of the different measuring units (distances vs. number of cells). Slight differences may also be caused by varying tissue elasticity according to different sample preparation procedures between densitometry and wood anatomical analysis. However, the highest ratio within

Fig. 3. Anatomic profile (ratio of double cell-wall to cell diameter) and densitometric profile in one sample. Stars are light-ring years.



a yearly cell radial file was significantly correlated to maximum density ($r = 0.66$, $p < 0.0001$) within an annual ring for the period 1940–1992 (one must take into account that both measurements cannot be applied to the same cell, although analysing the same tree ring). The densitometric profile indicated low values for light-ring years much clearer than the anatomical diagram. Density is known to be very sensitive to the densest wood component, i.e., lignin, although cell-wall thickness applies to overall wood components.

Correlations between summer temperature and tree-ring growth

Pearson correlation

Mean cell-wall thickness for the entire ring, latewood cell-wall thickness and ratio of cell-wall to lumen diameter were significantly correlated to all the summer temperature variables ($p < 0.01$) (Table 2). These results are similar to densitometric data corresponding to summer temperatures (Table 2). Maximum and latewood densities were significantly correlated to all summer temperature parameters. Earlywood and annual ring widths were positively correlated to mean temperature from May to September, sum of degree-days and early sum of degree-days. The highest correlations between tree rings and climate variables were between maximum density (MAXD) and latewood cell-wall thickness (LCWT) and mean growing season (May–September) temperature (Table 2, Fig. 4).

Partial correlation between tree-ring variables and temperature

Only the ratio of cell-wall to cell diameter on anatomical variables was significantly correlated with three summer temperature parameters (MAY–SEPT, SUMDEGREE, and EARLYSUM), while all densitometric variables were significantly correlated to at least one of the four summer temperature parameters (Table 3).

Correlation between tree-ring variables and pentad temperatures during the growing season

Tracheid production (number of cataclinal cell divisions indicated by the number of cell layers forming the ring) expresses the mean temperature during the growing season (May–September) (Fig. 5). All anatomical variables were correlated with pentad temperatures at the end of August and the beginning of September, while LCN and LCWT showed five continuous pentads correlated to temperature in this period. Latewood cell-wall thickness (LCWT) was correlated to 8 of 15 pentads in the early part of the growing season.

Maximum and latewood densities correlated to pentad temperatures from the end of May to July and late August to early September (Fig. 6), similar to latewood cell-wall thickness. Earlywood width was correlated with pentad temperatures during the first half of the growing season. Latewood width and annual ring width were positively correlated with pentad temperatures during July but negatively correlated with pentad temperatures in September.

Discussion

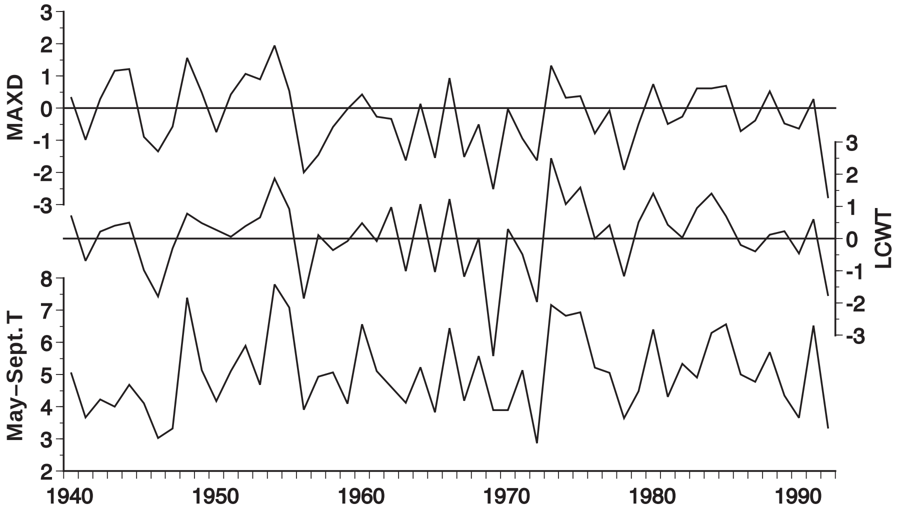
The synchronous variations between cell number and ring width indicate that a favorable year for tree growth can increase the number of cells, hence producing a larger ring. As a result, a larger ring is formed by a greater number of tracheid layers rather than by larger cells (Fig. 2). Moreover, earlywood is developing much more tracheid layers than latewood in a larger ring. Hence, the percentage of latewood decreased when ring cell number increased. This observation emphasizes that earlywood width could be a sensitive indi-

Table 2. Correlation between anatomical and densitometric variables and summer temperatures.

	MAY–SEPT	SUMDEGREE	EARLYSUM	LATESUM	FROSTFREE
RCN	ns	ns	ns	ns	ns
LCN	ns	ns	ns	ns	ns
RCW	ns	ns	ns	ns	ns
LCW	ns	ns	ns	ns	ns
RCWT	0.504**	0.429**	0.322*	0.494**	0.477**
LCWT	0.665**	0.503**	0.498**	0.535**	0.64**
WALL/CELL	0.606**	0.591**	0.46**	0.51**	0.543**
MAXD	0.718**	0.504**	0.519**	0.641**	0.691**
EWD	0.421**	0.341*	ns	0.446**	0.367**
LWD	0.725**	0.507**	0.509**	0.663**	0.692**
EWW	0.416**	0.328*	0.546**	ns	0.348*
LWW	ns	ns	ns	ns	ns
ARW	0.333*	0.278*	0.515**	ns	ns

Note: Tree-ring variables are as in Table 1. MAY–SEPT, mean temperature from May to September; SUMDEGREE, sum of degree-days from May to September; EARLYSUM, sum of degree-days in early summer (May–July); LATESUM, sum of degree-days in late summer (August–September); FROSTFREE, number of frostfree days (>0°C) from May to September. ns, no significant correlation. *, $P < 0.05$; **, $P < 0.01$.

Fig. 4. The synchronous variations of maximum density (MAXD) and latewood cell-wall thickness (LCWT) to summer temperature (1940–1992).



cator for yearly variations of heat sum availaible for tree production in the first half of the growing season. However, latewood density (especially maximum density) expresses more clearly the mean summer temperatures.

Latewood cell number and diameter did not respond to any densitometric data (Table 1). This may be attributable to different definitions of earlywood–latewood boundary. Since the earlywood–latewood boundary is clearly defined at the cell wall–lumen level (Mork 1928; Denne 1988), this borderline would not be biased by extremely low latewood density as in light rings (Wang et al. 2000). This could be supported by correlations between annual ring cell number and diameter and densitometric variables. For density variables, mean latewood density showed higher correlation and partial correlation to summer temperatures than maximum density. This is probably because mean latewood density is more integrative of the conditions that occurred after the complete development of annual foliage until the end of the growing season. Although the earlywood–latewood boundary is difficult to define when maximum density values are extremely low on typical light rings (Wang et al. 2000), latewood density still has a stronger correlation with summer temperatures than maximum density and, therefore, is a better indicator of climate variability.

The annual highest WALL/CELL seemed not to indicate the occurrence of light-ring years at tree line as apparently as MAXD (Fig. 3). One reason is probably that the thinner cell wall in light rings would not present much difference with that in normal rings when divided by tracheid cell diameter that is almost the same to normal rings (Fig. 2). However, the lower value of LWCT and WALL/CELL in light rings than in normal rings may express detailed information about subseasonal variations of xylem development in radial growth.

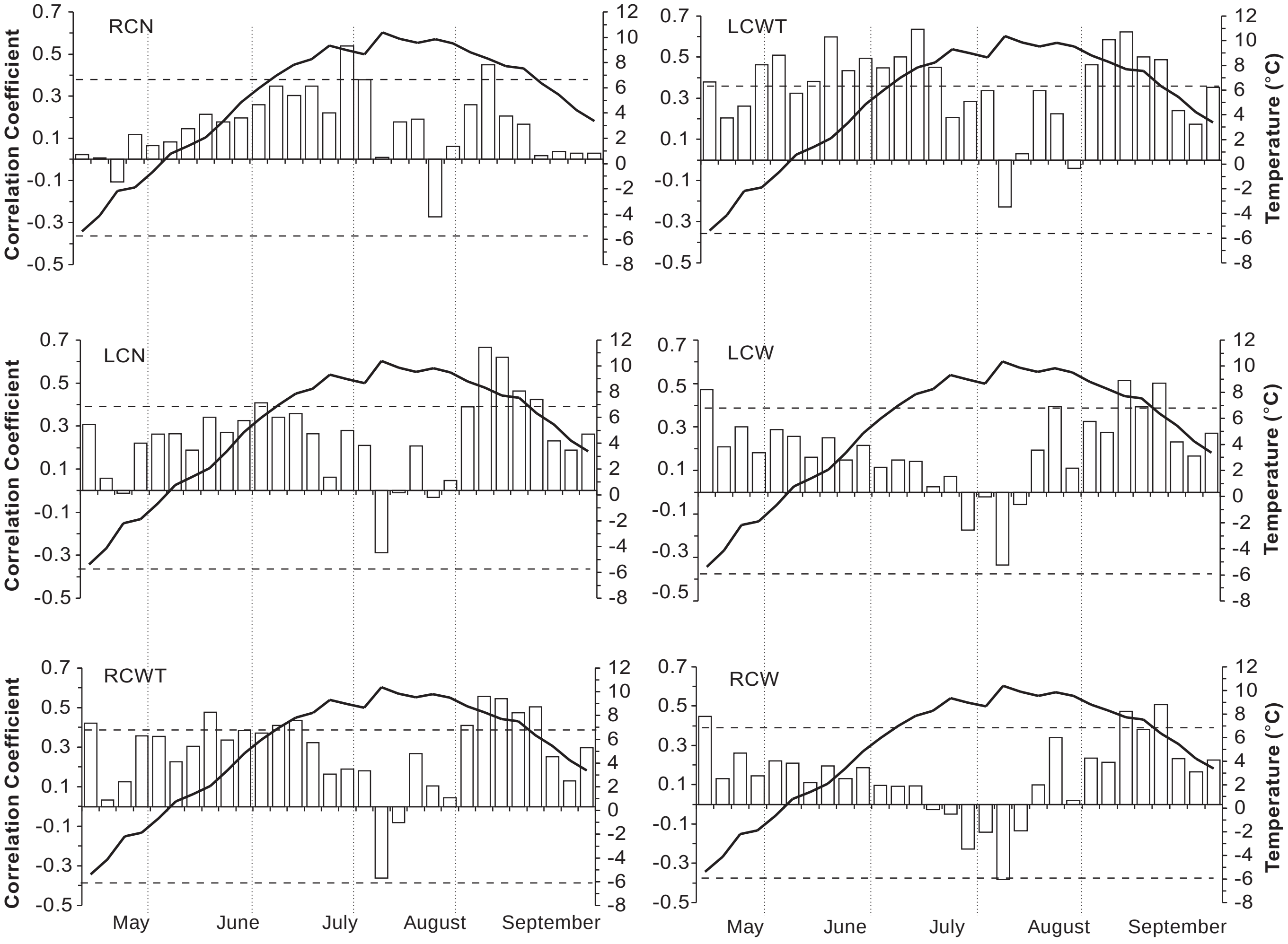
Our anatomical data indicated that only cell-wall variables (RCWT, LCWT, and WALL/CELL) showed correlations to summer temperatures (Table 2). Cell number and diameter parameters seem not suitable to record large-scale tempera-

Table 3. Patial correlation coefficients between densitometric and anatomical variables and summer temperatures.

	MAY–SEPT	SUMDEGREE	EARLYSUM	LATESUM	FROSTFRE
Anatomical variables					
RCWT	0.17	0.20	0.07	0.18	0.14
LCWT	0.23	0.19	0.19	0.04	0.20
WALL/CELL	0.47**	0.56**	0.42**	0.23	0.27
Densitometric variables					
MAXD	0.34*	0.11	0.15	0.41**	0.33*
EWD	0.22	0.19		0.30*	0.13
LWD	0.37**	0.12	0.13	0.46**	0.33*
EWW	0.36**	0.32*	0.51**		0.24
ARW	0.40**	0.38**	0.56**		

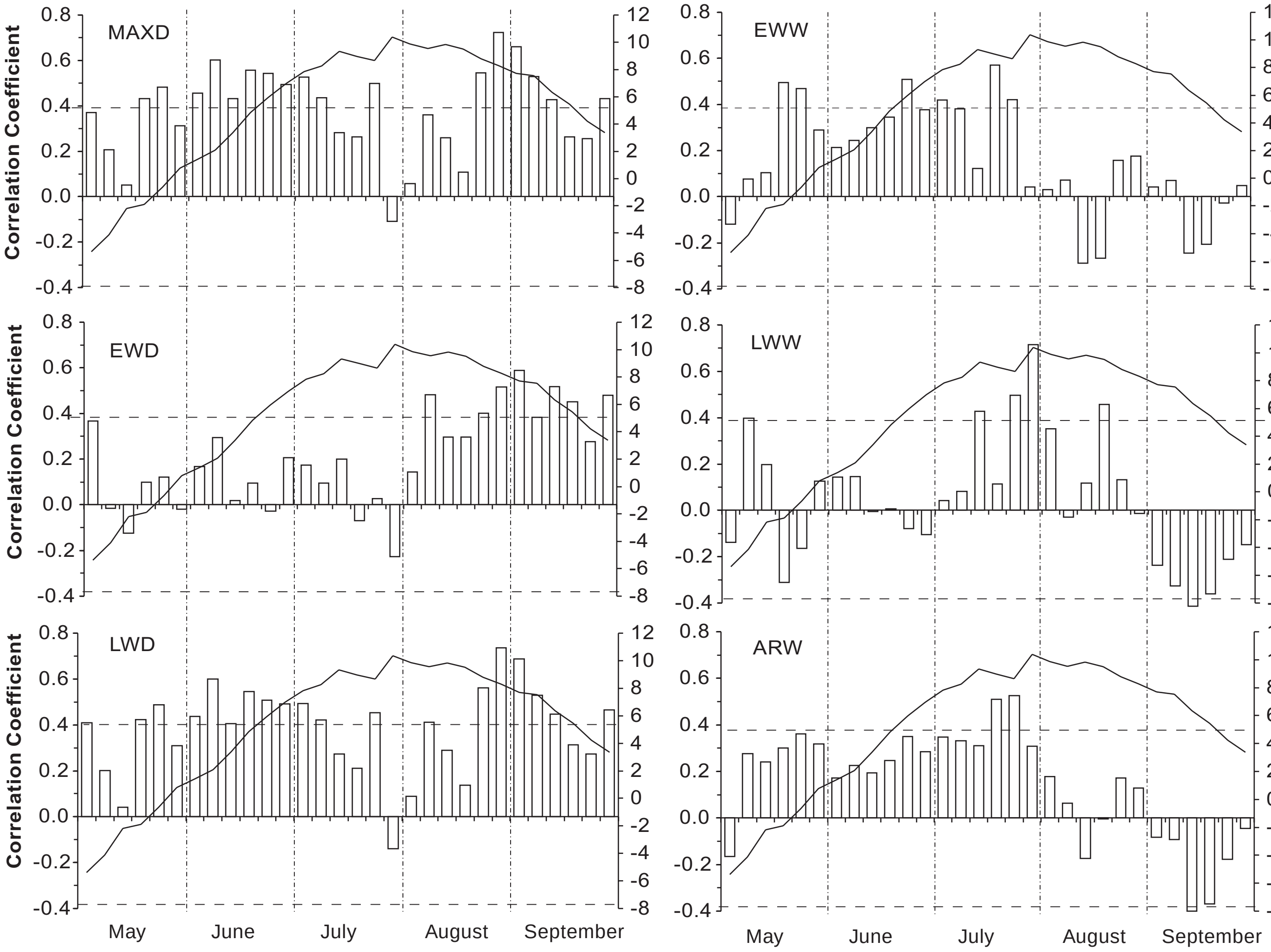
Note: Tree-ring and temperature variables are the same as in Tables 1 and 2. The significant tree-ring variables that correlated with temperatures in Tables 1 and 2 are calculated. Each densitometric variable is calculated to temperature while controlling for all computed anatomical variables and vice versa. *, $P < 0.05$; **, $P < 0.01$.

Fig. 5. Correlation of anatomical variables to pentad temperatures. The solid line is the mean temperature of five continuous daily mean air temperature records for 53 years (1940–1992). The bars are the correlation coefficients, and the horizontal broken lines show the limits of significant correlations at $P < 0.05$. The vertical broken lines delimit the months.



ture changes (annual or seasonal), since the development of wood tracheids is often disturbed by short or abrupt environmental changes. One can notice the differences between LCWT and MAXD for May–September and late summer temperatures in Table 2, as well as in the following R^2 value: MAXD accounts for 52 and 41% of the variation in May–September and late summer temperature, compared with 44 and 29% accounted for by LCWT (based on correla-

Fig. 6. Correlation of densitometric variables to pentad temperatures (format as in Fig. 5).



tion values in Table 2). This extra ~10% of explained variation supports the use of densitometric data for dendroclimatic modeling and climate reconstruction. Therefore, density data may better correlate with larger-scale temperature variations.

Tree-ring chronologies in the study area contain a strong climatic signal. However, climatic inferences for black spruce may not necessarily apply to other tree species because of different climate–growth relationships. Different climate-dependent growth patterns of tree rings were observed for radial cell size and cell-wall thickness (Shiyatov et al. 1996). The initiation and cessation of tree growth vary along with temperature in the early and late parts of summer. The length of summer appeared to be a controlling factor of cell-wall thickening (Mikola 1962). A shortened growing season may cause incomplete cell-wall thickening (Denne 1976). For radial cell enlargements, June and July temperatures were the major variables that affected radial growth (Figs. 5 and 6), also shown in other studies (Jacoby et al. 1985; Kalela-Brundin 1998). This may be because tracheids are mostly dividing and enlarging during the warmest period of the growing season. Late July – early August was the period during the growing season when temperature was least related to either cell size or cell-wall thickening (Parker 1976). It is likely because water supply may become a limiting factor during the warmest part of the summer (Yasue et al. 1997).

Ivkovich and Koshy (1997) suggest that the anatomical method can be used as an adequate substitute to X-ray densitometry if properly calibrated. The similarity between our anatomical and densitometric data suggests that the inter-annual characteristics of tree rings and densitometric measurements can be explained by wood anatomical data. Partial correlations in this study indicated the differential responses to growing season temperatures could lead to the use of these two methods for extracting the maximum possible information for different research purposes. Researchers who use black spruce for climate reconstruction need to obtain either anatomical or densitometric data, not both. However, our anatomical analysis was appropriate to record xylem details of intra-ring variations in signal years rather than to compute a large data set for the construction of long chronologies considering the time allowed to gather such data. Anatomical information can be obtained with a microtome and camera-computer system in a general biological laboratory, whereas the densitometer is an expensive and uncommon instrument in most laboratories.

Because the measurements for densitometry (densitometer sensor steps) and image analysis (number and size of tracheid cells) are not measured in the same units (Fig. 3), intra-annual variations in the two curves cannot be compared directly. Although the result in Fig. 3 is derived from only a single sample, it may raise the possibility of using the anatomical method to replace densitometry when focussing on the retrieval of intra-annual information for dendroecological purposes. Thus, better computing methods are needed to convert both types of measurements into dimensionless index series for further comparisons. Also physiological studies of tree growth at treeline are needed to better understand the causal mechanisms producing changing radial growth in trees.

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