Influence of climate on tree rings and vessel features in red oak and white oak growing near their northern distribution limit, southwestern Quebec, Canada

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Abstract: Little is known about environmental controls on vessel features in ring-porous tree species. Our objectives were to assess (*i*) the association between tree-ring descriptors (vessels and width) and climate in two oak species, white oak, *Quercus alba* L., and red oak, *Quercus rubra* L., and (*ii*) the utility of vessel series in climate reconstruction. The study was conducted in southern Quebec and 10 trees of each species were analyzed. For each species, 11 chronologies (vessel and ring width) were developed and compared. Few differences were observed between the oak species. All vessel chronologies were associated with those of ring dimension and none revealed a unique climate signal. Current growing season conditions were mainly associated with latewood features, whereas those of the year prior to ring formation were mainly associated with earlywood features. The best climate variable to reconstruct was the July Canadian Drought Code and the best reconstruction model was derived from earlywood, latewood, and ring-width chronologies. We conclude that vessel chronologies for *Q. alba* and *Q. rubra* have limited use in dendroclimatology. Vessel features are best used to identify event years recorded during the life of a tree. Vessel series could prove useful, however, in calibrating physiologically based models of tree growth.

Résumé : On sait peu de choses de l'influence de l'environnement sur les caractéristiques des vaisseaux chez les espèces à zone poreuse. Nos objectifs consistaient à évaluer (*i*) l'association entre les paramètres des cernes annuels (vaisseaux et largeur) et le climat chez *Quercus alba* L. et *Quercus rubra* L. et (*ii*) l'utilité des séries chronologiques basées sur les vaisseaux pour reconstituer le climat. L'étude a été réalisée dans le sud du Québec et 10 arbres de chaque espèce ont été analysés. Pour chaque espèce, 11 chronologies (vaisseaux et largeur des cernes) ont été développées et comparées. Peu de différences ont été observées entre les espèces de chêne. Toutes les chronologies de vaisseaux étaient reliées à celles de la dimension des cernes annuels et aucune n'a révélé de signal climatique particulier. Les conditions de la saison de croissance en cours étaient surtout associées aux caractéristiques du bois final tandis que celles de l'année précédant la formation du cerne annuel étaient principalement associées aux caractéristiques du bois initial. La meilleure variable climatique à reconstituer était le code canadien de la sécheresse en juillet et le meilleur modèle pour la reconstitution était dérivé des chronologies des largeurs du bois initial, du bois final et des cernes annuels. Nous concluons que les chronologies des vaisseaux chez *Q. alba* et *Q. rubra* ont peu d'utilité en dendroclimatologie. Les caractéristiques des vaisseaux sont surtout utiles pour identifier les années où des événements ont été enregistrés durant la vie d'un arbre. Les séries de vaisseaux pourraient cependant s'avérer utiles pour calibrer les modèles de croissance des arbres basés sur la physiologie.

[Traduit par la Rédaction]

Introduction

In dendrochronology, ring width has constituted the main parameter used in retrospective studies, and conifers have also traditionally received much more attention than hardwoods. In ring-porous species, earlywood and latewood width has been used to infer climatic signal (Fritts 1962; Phipps 1982; Tardif 1996; Lebourgeois et al. 2004). Until recently, anatomical features in ring-porous species have mainly been used to reconstruct discrete events recorded during the life of a tree. Baillie (1982) documented some of the difficulties in cross-dating due to vessel anomalies in oak. Fletcher (1975) stressed the utility of rings with abnormally small earlywood vessels in cross-dating oak panels and speculated that these were formed in years with an exceptionally severe winter and a cold spring. García Gonzáles and Eckstein (2003) reported that in the English oak, *Quercus robur* L., abnormally narrow earlywood vessels could develop after severe winter–spring drought. In ring-porous species, insect defoliation has also been associated

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with reduced latewood width (Huber 1982; Asshoff et al. 1998–1999) and the production of fewer earlywood vessels in the year following defoliation (Huber 1993; Asshoff et al. 1998–1999). It is in dendrogeomorphology that anatomical markers in ring-porous species have yielded the most success. Vessel anomalies in ring-porous species were successfully used to identify past flooding (Yanosky 1983; Astrade and Bégin 1997; St. George and Nielsen 2003) and floodplain deposition events (Sigafoos 1964; Cournoyer and Bégin 1992).

Numerous researchers have suggested that the development of continuous vessel chronologies for ring-porous species could prove valuable in dendroclimatological reconstruction (Eckstein and Frisse 1982; Woodcock 1989*a*; Fonti and García Gonzáles 2004). In North America, Woodcock (1987, 1989*a*) was the first to assess the relationship between climate variables and vessel features in tree rings of the bur oak, *Quercus macrocarpa* Michx. Using few data and a non-exhaustive approach, Woodcock (1989*a*) concluded that latewood vessel diameter could be successfully used to reconstruct past precipitation, but that more research into the climatic sensitivity of anatomical variables was needed. More recently, García Gonzáles and Eckstein (2003) reported that mean earlywood vessel lumen area could be used as a proxy to reconstruct spring precipitation. Fonti and García Gonzáles (2004) reported that mean vessel lumen area in the European sweet chestnut, *Castanea sativa* Mill., could also be used as a climate proxy.

The white oak, *Quercus alba* L., reaches the northern limit of its distribution range in southern Quebec, Canada, and is listed as rare in the province (Labrecque and Lavoie 2002). Populations are found in only five distinct localities, all in the Ottawa valley, where it forms mixed stands with the northern red oak, *Quercus rubra* L., on subxeric to xeric sites with south- to southwest-facing slopes (Gagnon and Bouchard 1981; Gauthier and Gagnon 1990). Both oak species have ring-porous wood with larger vessels produced in the earlywood accompanied by a transition to smaller latewood vessels (Panshin and De Zeeuw 1970). The presence of these two co-occurring species made it possible to compare their radial growth and vessel features in a site located at the northern limit of the distribution range of *Q. alba* in southern Quebec.

The objectives of this study were (*i*) to compare ring dimension and vessel features in both *Q. rubra* and *Q. alba*, (*ii*) to determine the degree of association of these variables with interannual variations in climate, and (*iii*) to quantify the usefulness of developing continuous vessel series in dendroclimatology. Neither oak species has been previously used in this type of analysis and no study has formally evaluated the potential of using ring-porous vessel chronologies in addition to the more easily obtainable ring-width chronologies. We present sufficiently long time series (dendrochronology and climate) to effectively calibrate and verify regression models over independent periods. We hypothesized that year-to-year variation in ring-vessel features is greater in *Q. alba* than in *Q. rubra* because it is growing at its northern limit of distribution, and that the addition of vessel variables to ring-width chronologies should improve climate reconstructions.

Materials and methods

Study area

The study area is located in southwestern Quebec, in the locality of Belvédère Huron in the Eardley region (45°29′N, 75°54′W). The area is about 18 km northwest of Ottawa, the national capital. The oak forest sampled has developed on a xeric south-facing slope of the Precambrian Shield. The slope ranged from 39% to 80% and trees were growing on acidic sandy loams derived from rocky tills (Nantel 1995). More complete descriptions of the oak forests of this region can be found in Gagnon and Bouchard (1981) and Tardif et al. (2006).

The meteorological station with the longest record (1896 to the present) in the area is Ottawa CDA (45°23′N, 75°43′W, 79 m a.s.l.). The mean annual temperature and total precipitation for the reference period 1971–2000 are 6.3 °C and 914.2 mm, respectively (Environment Canada 2003). The average maximum temperature reached is 26.4 °C in July and an average minimum of –14.8 °C is reached in January. About 80% of total annual precipitation occurs as rainl, with about 48% falling from May to September.

Data collection and chronology development

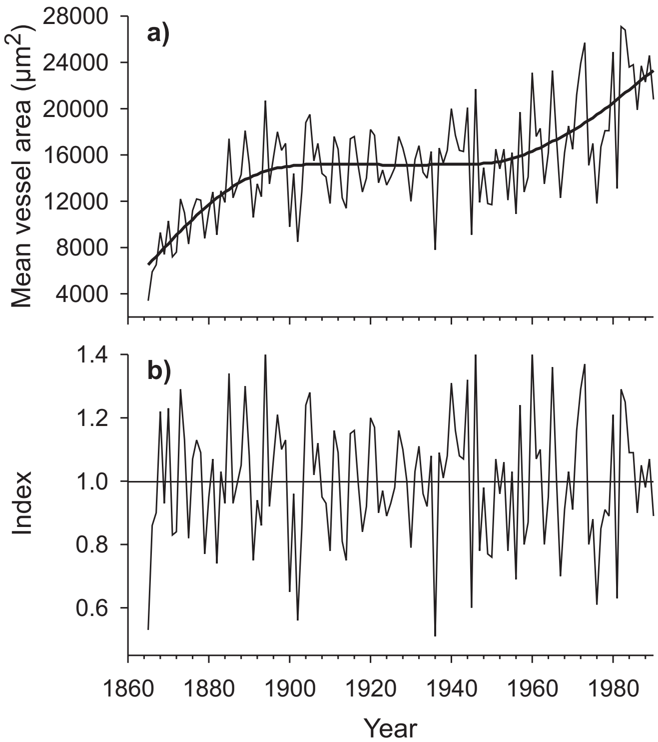
Ten living trees each of *Q. alba* and *Q. rubra* were selected and each tree was cored at its base with a 5 mm diameter borer. *Quercus alba* trees had a diameter at breast height of 19.6 ± 4.6 cm (mean ± standard deviation), height of 8 ± 2m, and date of origin of 1888 ± 19 years. *Quercus rubra* trees were comparable, with a diameter at breast height of 21.7 ± 6.7 cm, height of 8 ± 2 m, and date of origin of 1899 ± 31 years. All wood samples were dated and visually crossdated, then their ring widths were measured using a Velmex measuring system. Data quality was further validated with the COFECHA program (Holmes 1999).

Prior to image acquisition, each core/ring was cleaned with pressurized air and rubbed with white chalk to fill the vessels. A Nikon SMZ800 stereomicroscope equipped with a Polaroid DMC digital camera was used to capture images at 1200 × 1600 resolution and 20× magnification. In *Q. alba* and *Q. rubra*, 1034 and 923 tree rings were captured, respectively. Each image was analyzed using the WinCELL Pro (version 2001a) program (Régent Instruments Inc. 2001). Colour analysis was performed and the minimum vessel lumen area for both *Quercus* species was set at 450 μm^2. It was assumed that the few vessels under this size had a negligible impact on the conductive capacity of the ring (Gasson 1985).

The parameters measured for each tree ring included the number of entire vessels and their respective cross-sectional lumen length, width, and area. The earlywood and latewood width for each ring was measured along two radial files (upper and lower portions of the image) and averaged. The sum of the two yielded the ring width. The boundaries between earlywood and latewood were determined qualitatively using vessel distribution and size (Fonti and García Gonzáles 2004; Lebourgeois et al. 2004). In *Q. rubra* the bimodal distribution in vessel size is indicative of the transition between earlywood and latewood (Woodcock 1989*b*). The transition from earlywood to latewood is also generally more abrupt in *Q. alba* than in *Q. rubra* (Panshin and De Zeeuw 1970). From these parameters, nine variables per ring were generated: earlywood width (EW), latewood width (LW), ring width (RW), percent latewood (%LW), maximum vessel area (MAX), mean vessel area of those above the 3rd quartile (A3Q); mean vessel area (MVA), total vessel area (TVA), and number of vessels (NV). As in Woodcock (1989*a*), the area of the largest earlywood vessel (MAX) was included as an approximation of conductivity. Further, two variables were also divided by ring width (NV* = NV/RW and TVA* = TVA/RW) to provide an estimate of vessel density as well as a more uniform measure of conductivity for each ring (Gasson 1985). Eleven tree-ring features were thus analyzed. All cores were about 5 mm wide and no attempt was made to eliminate ray area from the calculation.

Each time series produced was standardized using a spline function with a 50% frequency response of 50 years (Fig. 1*a*; Cook and Kairiukstis 1990). Standardization involved transforming the measurement into a dimensionless index by dividing the observed value by the expected value given by the spline function (Fig. 1*b*). This procedure retains high-frequency variation and filters out medium- to low-frequency trends associated with age–size and stand dynamics (Cook and Kairiukstis 1990). Many vessel features in ring-porous species are known to vary with age or from the pith to the bark (Phelps and Workman 1994; Corcuera et al. 2004; Fonti and García Gonzáles 2004). Autoregressive modeling was also performed on each standardized series to remove temporal autocorrelation, thus creating residual series. Autocorrelation reduces the effective number of independent observations and thus reduces the degrees of freedom used to determine confidence in statistical tests (Legendre and Legendre 1998). This was also justified because the climate variable to be reconstructed (see below) was not serially autocorrelated (Meko and Graybill 1995). To further diminish the effect of endogenous disturbances and enhance the common signal, all residual series were averaged using a biweight robust mean. All procedures were conducted using the ARSTAN program (Holmes 1999) and resulted in 11 residual chronologies per species.

Fig. 1. Standardization procedure for *Quercus alba* tree 994. (*a*) Mean vessel area (thin line) and 50-year spline curve (thick line). (*b*) Indices obtained by dividing each observed mean vessel area value by the value predicted by the spline curve.



Chronologies and relationship to climate

Principal components analysis (PCA) and redundancy analysis (RDA) were used (*i*) to compare the structure of correlation among the 22 chronologies and (*ii*) to assess their association with climate (Girardin et al. 2004*a*). In dendroecology, the associations between growth indices and climate variables are usually calculated in the form of a correlation or a response function (Cook and Kairiukstis 1990). RDA is also effective in quantifying the relationship between growth indices and climatic factors (Girardin et al. 2004*a*; Tardif et al. 2006). RDA is the canonical form of PCA and the direct extension of multiple regression applied to multivariate data (Legendre and Legendre 1998). In RDA, the ordination axes are constrained to be linear combinations of supplied environmental (climate) variables (ter Braak 1994). Significant ($p < 0.05$) climate variables were selected after a forward selection using a Monte Carlo permutation test based on 999 random permutations. All ordination analyses were computed, using the CANOCO program (version 4.52), from a correlation matrix, and scaling of ordination scores was done using a correlation biplot (ter Braak 1994). For cross-verification, Pearson's correlation coefficients were calculated between the 11 chronologies/species and climate variables.

For all climate analyses, mean monthly temperature and total monthly precipitation from May of the year before ring formation ($t - 1$) to August of the year the annual ring formed (t) were used.

Climate data for the period 1895–1999 were obtained from the Ottawa CDA meteorological station, which is included in the Canadian historical monthly rehabilitated precipitation and homogenized temperature database (Mekis and Hogg 1999; Vincent and Gullett 1999). In addition, the Canadian Drought Code (CDC) component of the Canadian Forest Fire Behaviour System (Van Wagner 1987; Girardin et al. 2004*b*) was used. The CDC is a daily indicator of summertime moisture in deep organic layers in boreal conifer stands (Van Wagner 1987). Daily CDC indices were computed using daily maximum temperature and daily precipitation data from the Ottawa CDA weather station (Meteorological Service of Canada 2000). The computation was conducted following the procedure of Van Wagner (1987) and mean monthly average CDC indices were produced.

Climate reconstruction and ring features

We evaluated the potential for using vessel features in climate reconstruction by comparing four regression models resulting from different combinations of variables: (1) ring width (1 variable per species), (2) earlywood, latewood, and ring width (3 variables per species), (3) vessel variables (5 variables per species), and (4) all chronologies (11 variables per species). Based on preliminary analyses of temperature, precipitation, and CDC (not presented), the variable offering the greatest potential for reconstruction was the mean July CDC. Eighty percent of the variance in the July CDC for the period 1896–1990 can be explained by both May–July mean temperature (T_{MJJ}, $p = 0.038$) and May–July total precipitation (P_{MJJ}, $p < 0.0001$; July CDC = $(74.500 \times T_{MJJ}) + (-0.915 \times P_{MJJ}) + 3114.038$; adjusted $r^2 = 0.795$, $n = 95$, $p < 0.0001$, standard error of the estimate = 30.864), making this variable representative of weather conditions in the early growing season. The drought signal in the July CDC also persists until August and September, making this variable also representative of overall growing season conditions (Girardin et al. 2004*b*).

Each July CDC model was developed following standard procedures (Cook and Kairiukstis 1990; Fritts 1991). The residual chronologies were transformed into orthogonal eigenvectors using PCA to remove multicollinearity among variables. Vessel features are usually highly intercorrelated (Corcuera et al. 2004; Fonti and García Gonzáles 2004). The first four principal components (PCs) (except model I, which used only two) were lagged –1, 0, and +1 years from the year of the July CDC and used in subsequent calculations. First, a full-period model was calibrated using data for the period 1900–1989. Each of the four full models was estimated by a stepwise multiple regression calculated using the July CDC as predictand and the subset of PCs as predictors. The ability of each model to predict the July CDC was then tested using a split-sample procedure (Meko and Graybill 1995). The procedure consisted in calibrating the model over the first half of the data (1900–1944) and verifying it on the second half (1945–1989) and then inverting the procedure. The verification is conducted on the period withheld from the calibration and the predicted July CDC values are then compared with the instrumental ones. The accuracy of the verification was measured using the reduction of error, product means test, Spearman's rank correlation, and the sign test (Cook and Kairiukstis 1990; Fritts 1991; Meko and Graybill 1995). The reduction of error and product means test verification statistics were calculated using the VFY program (Holmes 1999).

Results

Series and chronology comparisons

The general statistics showed that the 11 chronologies developed for each species shared many statistical properties (Fig. 2, Table 1). The latewood-width and ring-width chronologies for *Q. alba* and *Q. rubra* exhibited greater interannual variation than earlywood width and vessel variables (Fig. 2), as is also indicated by their highest mean sensitivity values and standard deviations (Table 1). The statistics obtained from the common-interval analysis showed that the former chronologies also had the highest expressed population signal, variance in PC1, and mean correlation among series, indicating a stronger common signal (Table 1). This stronger signal is also observed in derived variables: percent latewood, vessel conductivity (total vessel area / ring width), and vessel density (number of vessels / ring width). Of all variables, earlywood width exhibited the lowest common signal, indicating greater variability among trees (Table 1). Vessel chronologies occupied an intermediate position between earlywood and latewood width (Fig. 2, Table 1). Among the oak vessel chronologies, mean vessel area, maximum vessel area, and mean vessel area of those above the 3rd quartile had no significant autocorrelation (Table 1).

Correlation structure among chronologies

The structure of the correlation matrix among the 22 oak chronologies (Fig. 2) indicated a bipolar mode with latewood width on the positive side of PC1 and maximum vessel area on the negative side of PC2; Fig. 3*a*). Few differences were observed between the two oak species, as indicated by the acute angle between the vectors of each pair of variables (Fig. 3*a*). PC1, representing 45.3% of the variance, was most strongly associated with variables correlated with latewood dimensions. Latewood width, ring width, percent latewood, and number of vessels were highly correlated with PC1 and positively intercorrelated, as illustrated by the acute angle between their vectors (Fig. 3*a*). This was also corroborated by Pearson's correlation coefficients between latewood width (ring width) and the remaining variables (Table 2). Conductivity (total vessel area / ring width), and to a lesser extent vessel density (number of vessels / ring width) and mean vessel area, were negatively correlated with PC1, indicating that larger rings tend to have a lower proportion of their area occupied by vessels.

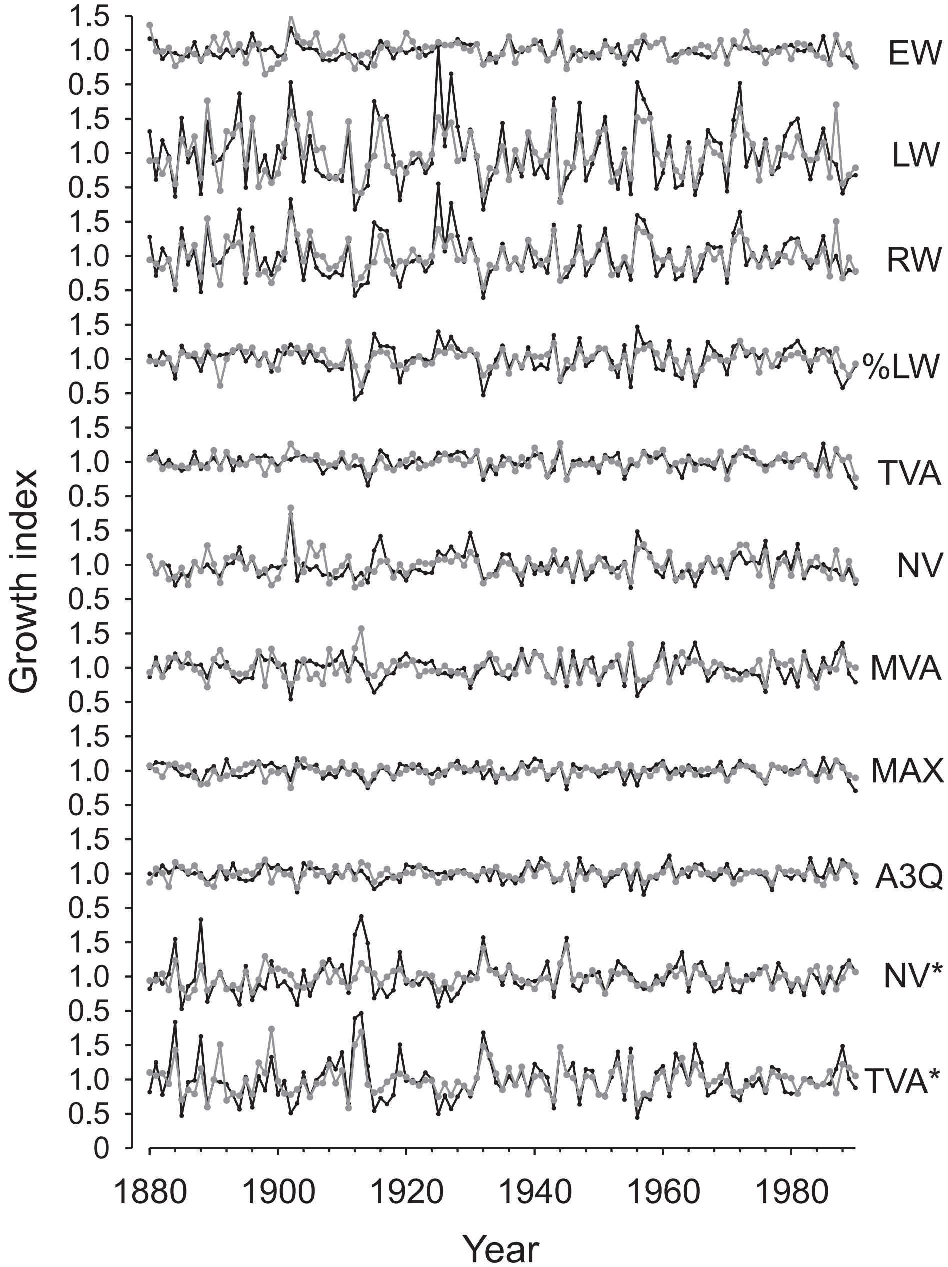
PC2 represented 26.3% of the variance and was mainly associated with variables fluctuating with maximum vessel area (Fig. 3*a*). Total vessel area, maximum vessel area, mean vessel area of those above the 3rd quartile, and, to a lesser extent, earlywood width and mean vessel area all shared a negative loading on this axis. This suggests that in years when earlywood is wider, vessels and total vessel area tend to be larger. This is also corroborated by Pearson's correlation coefficients between earlywood width and the remaining variables (Table 2). Compared with earlywood width, the earlywood vessel features (mean vessel area of those above the 3rd quartile, maximum vessel area, and total vessel area) were, however, almost independent from PC1 and latewood features, as indicated by the near 45° angle between respective vectors (Fig. 3*a*).

A positive correlation was also observed between latewood width in one year and earlywood width (total vessel area and maximum vessel area) in the following year (Table 2). Earlywood width showed no significant association with vessel features and dimension of the ring produced in the following year (Table 2). Earlywood width and latewood width were most strongly correlated with total vessel area and number of vessels, respectively (Fig. 3*a*, Table 2).

Association between tree-ring features and climate

The radial growth – climate association showed few differences between the two oak species despite *Q. alba* being at its northern distribution limit (Figs. 3*b* and 4). The climate variables most strongly associated with earlywood features were July temperature (negative association) and June–August precipitation (positive association) in the year

Fig. 2. The 11 residual chronologies for *Quercus alba* (black line) and *Quercus rubra* (grey line) for the reference period 1880–1990. Variables are as follows: EW, earlywood width; LW, latewood width; RW, ring width; %LW, percent latewood; TVA, total vessel area; NV, number of vessels; A3Q, mean vessel area of those above the 3rd quartile; MVA, mean vessel area; MAX, maximum vessel area; NV*, number of vessels / ring width; TVA*, total vessel area / ring width.



prior to ring formation. The importance of previous-year conditions was also emphasized by the strong negative correlation of earlywood features with the CDC index in the year prior to ring formation (Figs. 3*b* and 4). May temperature and June precipitation in the year of ring formation were also positively associated with some earlywood vessel features. The effect of May temperature on ring development was somewhat ambiguous, being positively associated with the formation of larger vessels (mean vessel area) and negatively associated with latewood width (number of vessels). In contrast to earlywood variables, the climatic factor most strongly associated with latewood features was June precipitation (positive association) during the year of ring formation. The impact of water stress on radial growth was further emphasized by the strong negative correlation with the July CDC index (Figs. 3*b* and 4).

Dendroclimatic reconstruction

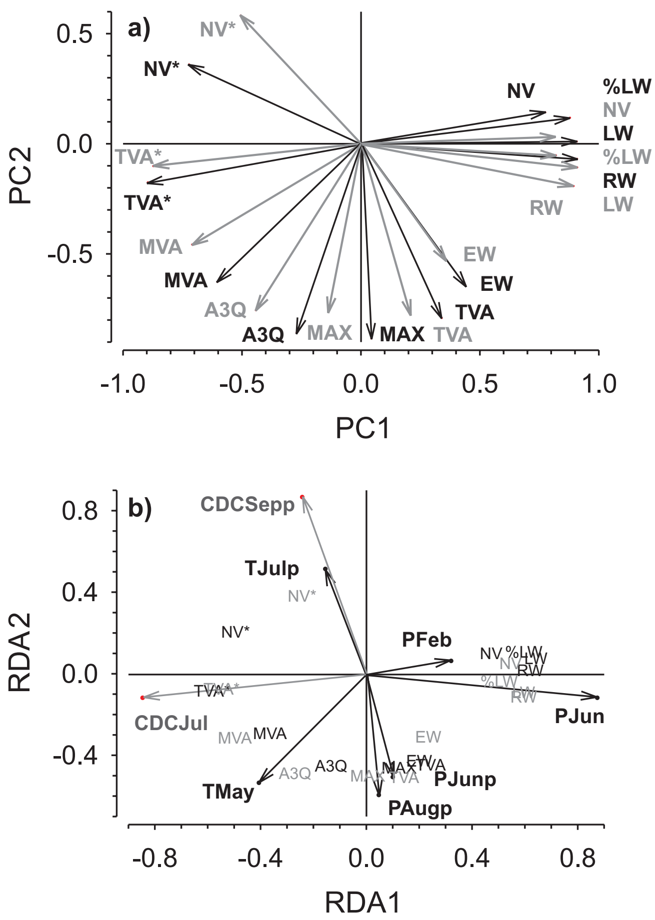
Four regression models were developed to reconstruct the mean July CDC and test the usefulness of developing long vessel chronologies for dendroclimatic purposes. The first model included only ring width as a predictor, whereas the subsequent models included more ring dimensions and (or) vessel variables. All models were highly significant and

Table 1. Descriptive statistics for residual chronologies for *Quercus alba* and *Quercus rubra* derived for each tree-ring feature.

	Mean[a]		Mean sensitivity[b]		SD		Autocorrelation[c]		Variance in PC1 (%)[d]		EPS signal[d,e]		Intercore correlation[d]	
Variable	*Q. alba*	*Q. rubra*	*Q. alba*	*Q. rubra*	*Q. alba*	*Q. rubra*	*Q. alba*	*Q. rubra*	*Q. alba*	*Q. rubra*	*Q. alba*	*Q. rubra*	*Q. alba*	*Q. rubra*
Ring width (mm)	0.818	1.063	0.367	0.297	0.324	0.252	0.293	0.277	65.360	58.960	0.940	0.920	0.612	0.536
Earlywood width (mm)	0.271	0.387	0.123	0.167	0.116	0.156	0.196	0.181	31.950	33.490	0.740	0.704	0.222	0.192
Latewood width (mm)	0.547	0.676	0.541	0.441	0.462	0.364	0.310	0.191	67.060	55.530	0.944	0.907	0.629	0.493
Percent latewood	58.10	58.81	0.208	0.169	0.192	0.159	0.317	0.116	63.220	42.940	0.934	0.844	0.587	0.350
Number of vessels	25.76	31.45	0.188	0.202	0.177	0.179	0.243	0.218	38.540	41.540	0.813	0.834	0.304	0.335
Total vessel area (10^4 µm^2)	35.36	48.70	0.126	0.141	0.113	0.126	0.081	0.228	46.360	46.300	0.865	0.863	0.390	0.386
Mean vessel area (10^4 µm^2)	1.71	1.69	0.195	0.190	0.173	0.163	0.001	–0.114	42.700	46.530	0.845	0.870	0.353	0.402
Max. vessel area (10^4 µm^2)	4.47	4.30	0.121	0.103	0.111	0.091	0.059	0.049	46.120	26.180	0.866	0.641	0.392	0.151
Mean vessel area 3rd quartile (10^4 µm^2)	3.59	3.61	0.143	0.109	0.126	0.090	–0.005	–0.109	50.700	39.540	0.887	0.822	0.440	0.315
Total vessel area/mm	54.99	53.52	0.343	0.275	0.301	0.256	0.187	0.144	61.510	52.850	0.928	0.897	0.565	0.465
Number of vessels/mm	34.58	33.36	0.265	0.179	0.245	0.176	0.234	0.311	43.980	40.460	0.813	0.803	0.303	0.290

Note: The chronologies for *Q. alba* and *Q. rubra* cover the periods 1865–1990 and 1840–1990, respectively. The common period was held constant for each species with a total of 10 trees.
[a]Calculated from the measurement series.
[b]Mean sensitivity is an index ranging from 0 (no differences between successive ring widths) to 2 (every second ring missing); larger values indicate the presence of considerable high-frequency variance (Cook and Kairiukstis 1990).
[c]Calculated from standard chronologies.
[d]Calculated from the common period 1932–1990 (10 trees).
[e]The expressed population signal (EPS) is an indicator of chronology reliability and is based on the mean correlation between all series. It measures how well the chronology compares with a theoretical chronology based on an infinite number of trees. The statistic ranges from 0.0 to 1.0, i.e., from no agreement to perfect agreement, and a value of 0.85 has often been suggested as a threshold to determine the quality of tree-ring chronologies (Wigley et al. 1984; Cook and Kairiukstis 1990).

Fig. 3. Principal components analysis (PCA) (*a*) and redundancy analysis (RDA) (*b*) calculated from the 22 residual chronologies. See Fig. 2 for a list of abbreviations of variables. Black labels and vectors refer to *Q. alba* and grey labels and vectors to *Q. rubra*. In the RDA, significant ($p < 0.05$) climatic factors are indicated by a vector with a black line; variables that were made passive are indicated by a vector with a grey line. In *b*, other abbreviations are as follows: T, temperature; P, precipitation; CDC, Canadian Drought Code; p, year prior to ring formation. Note that in both PCA and RDA biplots, the length of the vectors indicates the strength of the correlation with the ordination axes. The correlation between variables is approximated by the cosine of the angle between two vectors (arrows). Vectors pointing in roughly the same direction indicate a high positive correlation, vectors crossing at right angles correspond to a near-zero correlation, and vectors pointing in opposite directions show a high negative correlation (ter Braak 1994). In RDA, climatic variables with long vectors are the most important in the analysis. For visual clarity the vectors (arrows) related to the 22 chronologies are not shown in the RDA.



showed some predictive ability with adjusted r^2 values ranging from 0.33 to 0.47 (Fig. 5, Table 3). Spearman's correlation coefficients and values for sign tests, reduction of error, and product means test calculated over the verification periods indicated significant predictive capacity of the calibration models (Table 3). Estimation of the mean July CDC in all models appears to track year-to-year and decadal fluctuation (Fig. 5). Our results indicated that the model using only ring width was the weakest, while the model utilizing earlywood width, latewood width, and ring width was the best (Fig. 5, Table 3). It should be noted that models using earlywood width or vessel features showed that both positively and negatively lagged PCs entered the regression model. This occurred because PC2 loadings were positively correlated with PC1 loadings at lag $t - 1$, reflecting the fact that earlywood width is correlated with latewood width in the preceding year (Table 2).

Discussion

Chronology comparisons and correlation structure

The positive association between latewood width in one year and earlywood width in the following year, the lack of year-to-year variability observed in earlywood width compared with latewood (ring) width, and the greater contribution of latewood width to ring width compared with earlywood width have been reported for numerous ring-porous species (e.g., Phipps 1982; Tardif 1996; Lebourgeois et al. 2004). The lower autocorrelation observed in vessel features than in ring width (Eckstein and Frisse 1982; Woodcock 1989*a*; García Gonzáles and Eckstein 2003), as well as the lower mean sensitivity in vessel area chronologies than in ring width and vessel density (Woodcock 1989*a*; Fonti and García Gonzáles 2004), have also been previously noted. In our study, mean sensitivity values for vessel features were generally higher than those reported elsewhere (Corcuera et al. 2004; Fonti and García Gonzáles 2004), suggesting greater climatic sensitivity of *Q. rubra* and *Q. alba*.

The structure of the correlations among the 22 oak chronologies was also similar to that reported in other studies, indicating that both earlywood and latewood vessel descriptors loaded on separate components (Woodcock 1987; Corcuera et al. 2004). Our PCA results were very similar to those of Fonti and García Gonzáles (2004), except that earlywood variables contributed more to the formation of their factor-1. This may reflect the filtering approach used by Fonti and García Gonzáles (2004), which led to rejection of small vessels from their analysis. Nonetheless, the results of both studies suggest that rings with larger earlywood have greater total vessel area (maximum vessel area) and that rings with larger latewood have reduced mean vessel area, indicating that latewood vessels contribute little to total vessel area. In larger rings, the density of the vessel decreases and the proportion of smaller vessels increases, thus reducing the mean vessel area (Woodcock 1987; Fonti and García Gonzáles 2004).

Tree-ring features and climate

Few differences were observed between the two oak species despite *Q. alba* being at its northern distribution limit. The two species had comparable ring-width chronologies and their growth–climate association was similar. This was also noted by Tardif et al. (2006) in a study of 12 *Q. alba* stands (including the one in this study) distributed along the species' northern distribution limit in southern Quebec. Our results indicated that earlywood- and latewood-related variables were generally driven by different climatic conditions.

Table 2. Pearson's correlation coefficients between ring dimensions and vessel features for *Quercus alba* and *Quercus rubra* in both the year of ring formation (*t*) and the subsequent year (*t* + 1).

	Q. alba			*Q. rubra*		
Variable	Earlywood	Latewood	Ring width	Earlywood	Latewood	Ring width
EW	1.00	0.33	0.43	1.00	0.30	0.47
LW	0.33	1.00	0.99	0.30	1.00	0.96
RW	0.43	0.99	1.00	0.47	0.96	1.00
%LW	0.19	0.89	0.84	0.05 ns	0.86	0.75
TVA	0.81	0.30	0.36	0.72	0.25	0.37
NV	0.42	0.72	0.72	0.49	0.76	0.79
MVA	0.04 ns	–0.58	–0.54	0.01 ns	–0.61	–0.54
MAX	0.56	0.04 ns	0.09 ns	0.24	–0.03 ns	–0.02 ns
A3Q	0.38	–0.25	–0.19	0.17 ns	–0.29	–0.26
NV*	–0.45	–0.72	–0.76	–0.42	–0.60	–0.62
TVA*	–0.23	–0.86	–0.85	–0.21	–0.85	–0.82
EW (*t* + 1)	0.02 ns	0.35	0.31	0.07 ns	0.37	0.33
LW (*t* + 1)	–0.04 ns	0.02 ns	0.02 ns	0.10 ns	0.01 ns	0.02 ns
RW (*t* + 1)	–0.08 ns	0.02 ns	0.01 ns	0.02 ns	–0.01 ns	–0.02 ns
%LW (*t* + 1)	0.07 ns	0.07 ns	0.08 ns	0.20	0.17 ns	0.20
TVA (*t* + 1)	0.06 ns	0.42	0.39	–0.01 ns	0.43	0.37
NV (*t* + 1)	0.03 ns	0.09 ns	0.08 ns	0.17 ns	0.08 ns	0.09 ns
MVA (*t* + 1)	0.00 ns	0.02 ns	0.01 ns	–0.26	0.10 ns	0.04 ns
MAX (*t* + 1)	0.11 ns	0.30	0.28	–0.04 ns	0.30	0.24
A3Q (*t* + 1)	0.02 ns	0.17 ns	0.14 ns	–0.13 ns	0.27	0.21
NV* (t + 1)	0.01 ns	–0.18 ns	–0.17 ns	0.04 ns	–0.26	–0.23
TVA* (*t* + 1)	–0.07 ns	–0.04 ns	–0.05 ns	–0.15 ns	0.03 ns	0.00 ns

Note: The analysis was conducted using the reference period 1880–1990. Variables are as follows: EW, earlywood width; LW, latewood width; RW, ring width: %LW, percent latewood; MAX, maximum vessel area; A3Q, mean vessel area of those above the 3rd quartile; MVA, mean vessel area; TVA, total vessel area; NV, number of vessels; NV*, number of vessels / ring width; TVA*, total vessel area / ring width; ns denotes a nonsignificant correlation ($p > 0.05$).

Similar observations were reported for numerous ring-porous species (e.g., Tardif 1996; García Gonzáles and Eckstein 2003; Fonti and García Gonzáles 2004; Lebourgeois et al. 2004). Our results are also consistent with those from studies of *Q. alba* and *Q. rubra* across their distribution range (e.g., Fritts 1962; Foster and LeBlanc 1993; LeBlanc and Terrel 2001; Terrell and LeBlanc 2002). The results of these studies suggested that water stress in the early growing season is the most important factor controlling radial growth. Our results indicated that the absence of water stress in the year of ring formation leads to a thicker latewood zone, a wider ring, and the formation of more vessels.

Like those of Fonti and Garcia Gonzales (2004), our results indicated that earlywood vessel variables generally provide a record of conditions during two physiologically distinct periods of vessel growth: (1) storage of reserves in the previous summer and (2) the onset of cambial activity in the current year. First, reduced water stress in the growing season prior to ring formation was positively associated with the formation of thicker earlywood, larger earlywood vessels, and rings with a greater total vessel area. This dependence of earlywood features on conditions during the year prior to ring formation has been frequently described and associated with the importance of carbohydrate reserves for earlywood formation in ring-porous species (e.g., Tardif 1996; Fonti and García Gonzáles 2004; Lebourgeois et al. 2004). Zasada and Zahner (1969) observed that in *Q. rubra,* maturation of the first earlywood vessels occurred before bud opening, that no earlywood vessel elements were initiated once leaf expansion was completed, and that earlywood formation from initiation of vessel elements to complete maturation lasted about 10 weeks. Earlywood formation thus strongly relies on carbohydrates stored during the previous year, and presumably on the accumulation of auxin precursors during the growing season prior to ring formation (Aloni 1991).

Second, conditions at the onset of cambial activity also influence earlywood features. The effect of May temperature on ring development was somewhat ambiguous, being positively associated with the formation of larger vessels (mean vessel area) and negatively associated with latewood width (number of vessels). This negative association between May temperature and variables related to latewood (ring) width was higher in *Q. alba* (Fig. 4), and was consistently observed in all 12 stands studied by Tardif et al. (2006). In contrast to our results, Woodcock (1987) observed that May temperature was negatively associated with the size of earlywood vessels in *Q. macrocarpa*. A positive correlation with May precipitation was also observed (Woodcock 1989*a*), suggesting that reduced water stress at the time of earlywood vessel expansion favours the production of larger earlywood vessels. Similar observations were also made in European ring-porous species (García Gonzáles and Eckstein 2003; Corcuera et al. 2004; Fonti and García Gonzáles 2004). These contrasting results suggest that drought stress (high temperature) in the early growing season may play a more important role in regions where lower soil moisture replen-

Fig. 4. Pearson's correlation coefficients between *Q. alba* and *Q. rubra* chronologies and the monthly climatic variables for the period 1896–1990. See Fig. 2 for a list of abbreviations. From top to bottom, the panels illustrate correlations with mean monthly temperature, mean monthly Canadian Drought Code, and total monthly precipitation. Darker blue indicates a positive correlation and darker red indicates a negative correlation. Significant (p < 0.05) correlations are also denoted by black circles.

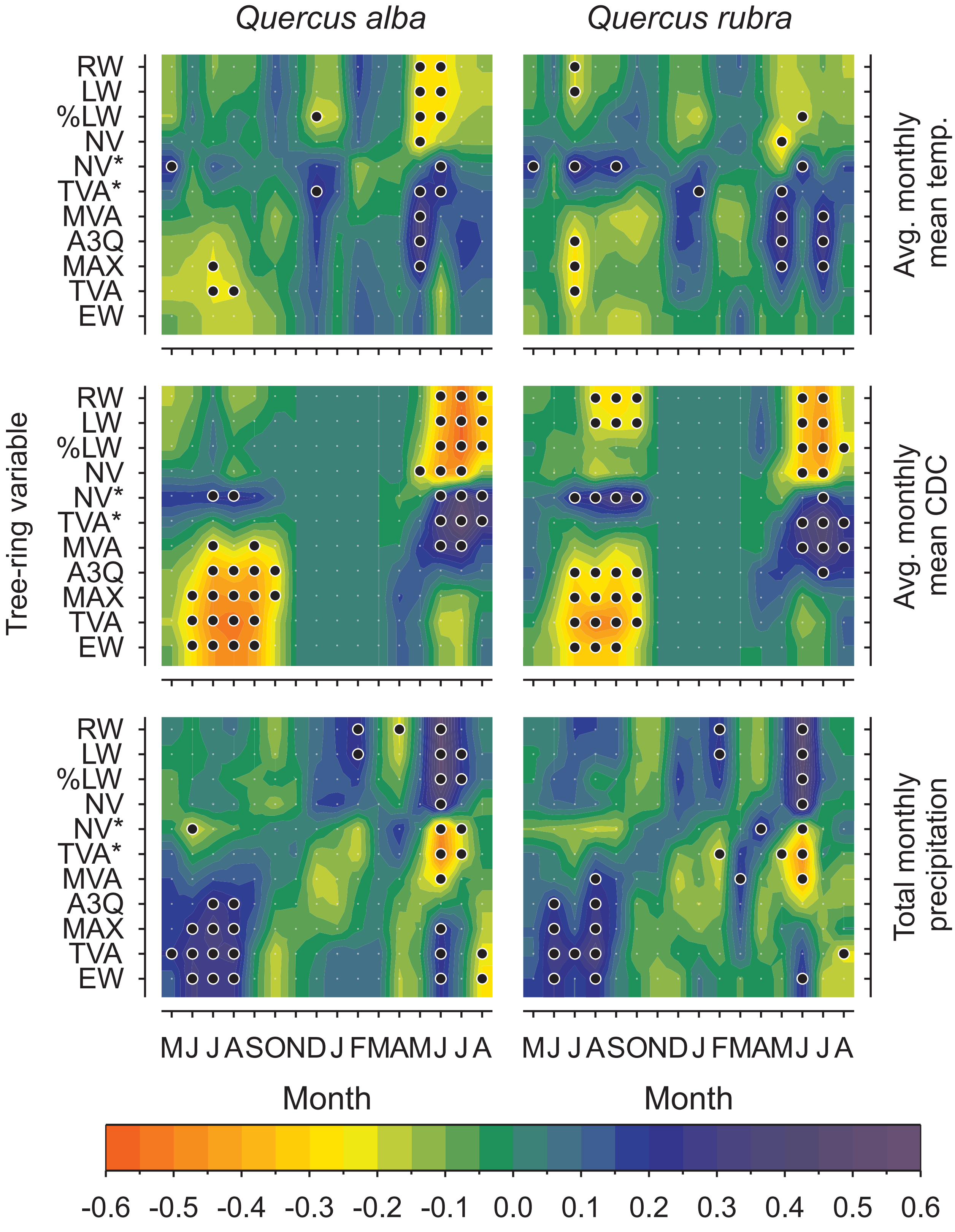
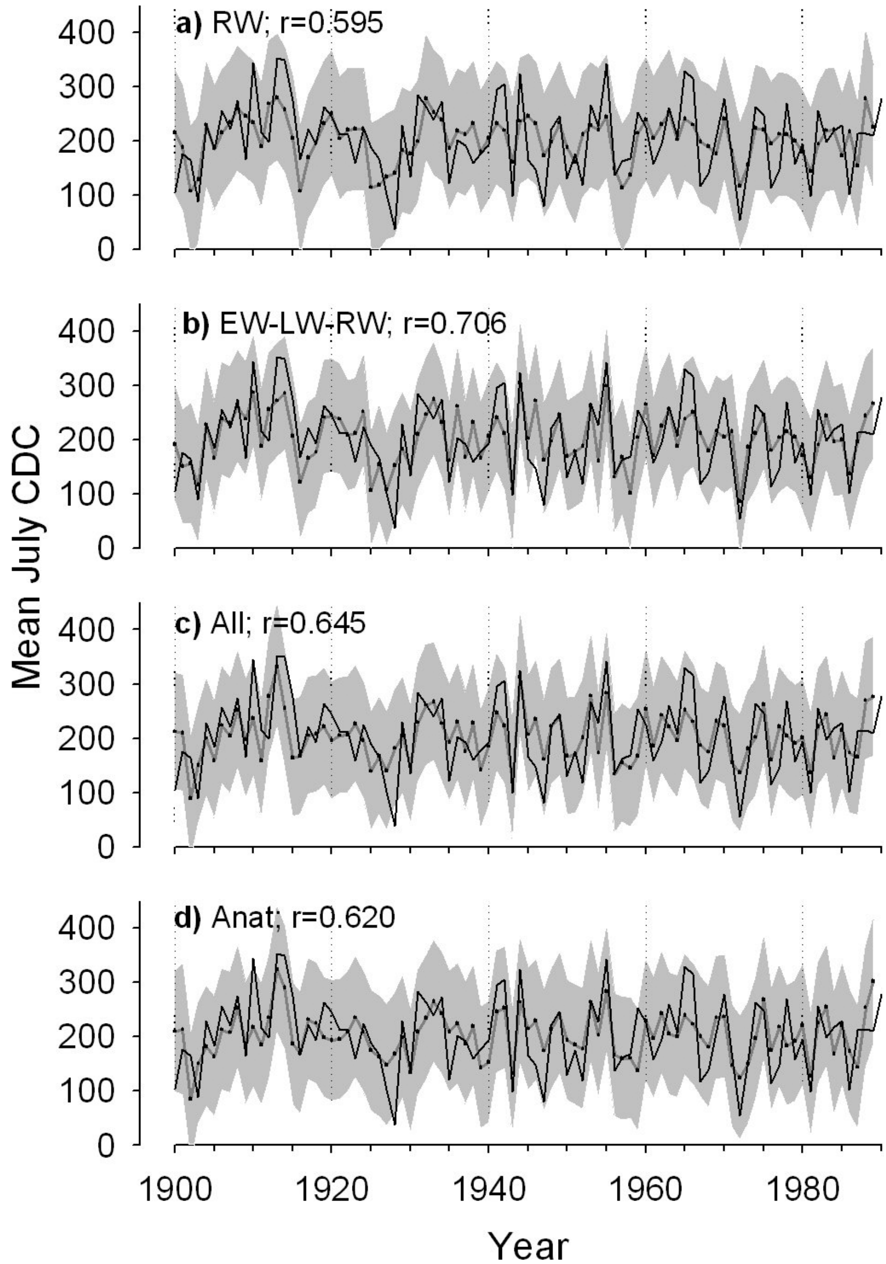


Fig. 5. Predicted mean July Canadian Drought Code (CDC) for each of the four regression models: ring width only (RW) (*a*), earlywood, latewood, and ring width (EW-LW-RW) (*b*), all variables (*c*), and vessel features only (anat.) (*d*). The CDC scale ranges from soil saturation (0) to extreme drought (>300). The black line shows the instrumental mean July CDC (1900–1989) and the shaded areas represent the 95% confidence intervals. The correlation coefficient between the instrumental mean July CDC and its predicted value is indicated for each model.



ishment by winter precipitation (rain or snowmelt) predominates. We speculate that in southern Quebec, a high May temperature could favour resumption of xylem growth at a time when water is not limiting, thus leading to the production of larger earlywood vessels and an overall increase in the conductive capacity of the tree rings. Zasada and Zahner (1969) presented evidence that maximum tangential enlargement of *Q. rubra* vessels was attained within a week after initiation, whereas radial enlargement was slower, being limited by the overall rate of xylem growth and thus requiring more time to reach a maximum. A high May temperature could play a role in accelerating early earlywood production (cell division), thus promoting radial vessel expansion and resulting in larger vessels.

Precipitation in June was also positively correlated with earlywood features, and this is consistent with Fritts (1962), who also observed that earlywood width in *Q. alba* increased in years with abundant moisture in June. Zasada and Zahner (1969) observed that shoot extension and leaf expansion in *Q. rubra* started in about the middle of earlywood formation and lasted for 2 weeks. This supports the importance of water availability at the time of shoot, late-earlywood, and latewood growth. An earlier start to the growing season (a warm May) could also increase the proba-

Table 3. Calibration and verification statistics for each of the four multiple regression models developed to predict mean July Canadian Drought Code (Cook and Kairiukstis 1990; Fritts 1991).

	Model I (RW ONLY)			Model II (EW-LW-RW)			Model III (anatomical features)			Model IV (all)		
Calibration period:	1900–1944	1945–1989	1900–1989	1900–1944	1945–1989	1900–1989	1900–1944	1945–1989	1900–1989	1900–1944	1945–1989	1900–1989
Verification period:	1945–1989	1900–1944	—	1945–1989	1900–1944	—	1945–1989	1900–1944	—	1945–1989	1900–1944	—
Calibration												
PCs	PC1, PC1 (t + 1), PC2 (t + 1)			PC1, PC2 (t – 1), PC3 (t + 1), PC2, PC1 (t + 1)			PC1 (t – 1), PC2, PC2 (t – 1)			PC1, PC2 (t – 1)		
Multiple r	0.63	0.56	0.60	0.80	0.73	0.71	0.69	0.57	0.62	0.66	0.65	0.65
r^2	0.40	0.31	0.35	0.64	0.53	0.50	0.47	0.33	0.39	0.44	0.43	0.42
Adjusted r^2	0.36	0.26	0.33	0.59	0.47	0.47	0.43	0.28	0.36	0.41	0.40	0.40
SE of the estimate	57.64	56.69	56.37	46.18	48.08	50.26	54.05	55.99	55.01	55.20	51.11	53.27
p	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.001	0.000	0.000	0.000	0.000
Verification												
Reduction of error (RE)[a]	0.29	0.10	—	0.31	0.32	—	0.16	0.12	—	0.29	0.11	—
Product means test[b]	3.08	2.82	—	2.71	3.90	—	2.71	3.22	—	3.05	3.15	—
Spearman's correlation coefficient	0.56	0.49	0.61	0.55	0.61	0.68	0.37	0.45	0.59	0.55	0.44	0.63
Sign tests[c]												
Agreements	34	28	68	29	34	70	30	26	69	31	30	67
Disagreements	13	20	27	18	14	25	17	22	26	16	18	28
p	<0.05	ns	<0.05	ns	<0.05	<0.05	ns	ns	<0.05	<0.05	ns	<0.05

[a]Considered satisfactory if RE is greater than 0; when RE is greater than zero, the reconstruction is considered to be a better estimate than the calibration-period mean.
[b]A significant product means test result indicates that the magnitude and direction of these changes are statistically significant.
[c]A significant sign test result indicates good fidelity in the direction of year-to-year changes in the real and reconstructed data.

bility of water stress during the growing season, thus leading to a reduction in latewood width (number of vessels) and therefore an increase in mean vessel area. The negative correlation between mean vessel area and latewood width (number of vessels) and the inverse correlation of each variable with May temperature support this interpretation. Further, Shumway et al. (1991) observed that inducing drought stress at the time of bud swell in 2-year-old red ash, *Fraxinus pennsylvanica* Marsh., seedlings significantly reduced latewood width, with a mitigated effect on earlywood width. The authors found that the mean diameter of vessels in both earlywood and latewood was not affected by drought; however, drought-stressed seedlings produced significantly fewer earlywood and latewood vessels (27% and 69%, respectively). The response of *F. pennsylvanica* to drought during the early growing season was to produce less foliage, less latewood, and fewer vessels.

Dendroclimatic assessment of tree-ring features

Our results indicated that all four models developed to reconstruct the mean July CDC showed good predictive ability. Spearman's correlation coefficients, sign tests, reduction of errorand product means test calculated over the verification periods indicated significant predictive capacity of the calibration models (Cook and Kairiukstis 1990; Fritts 1991). Our results also indicated that utilizing earlywood, latewood, and total ring width yielded the best model and that models using vessel variables did not improve estimation of the instrumental mean July CDC. Contrary to Phipps' (1982) suggestion, the results indicate that the extra effort of separating earlywood from latewood width can yield better reconstruction of long-term water availability because of the specificity of each variable to climatic influences.

A number of studies (Woodcock 1989*a*; García Gonzáles and Eckstein 2003; Fonti and García Gonzáles 2004) suggested that earlywood or latewood vessel chronologies in ring-porous species contained a strong climatic signal that could prove valuable in dendroclimatological reconstructions. While we do not deny the strength of the correlations with climate that we observed, our results showed that vessel variables yield little new climatic information compared with the more easily derived earlywood and latewood widths. Compared with ring dimensions, the lower common signal in vessel features is also of concern and adds to the time-consuming task of generating well-replicated vessel-measurement series. In contrast to Fonti and García Gonzáles (2004), who suggested that mean vessel area bears a unique signal associated with conditions in the early growing season, our results indicate that it strongly reflects year-to-year variation in latewood width (number of vessels). Mean vessel area is, however, affected by the vessel-selection (filtering) procedure. García-González and Fonti (2006) report that the definition and selection of earlywood vessels affect the identification of climate–growth relationships because vessels are formed at different times: early spring for the largest earlywood vessels and later in spring for the smallest earlywood vessels. Compared with earlywood- and latewood-width measurements, more uniform procedures in selecting vessels may be needed to allow better comparison among species and studies.

The lack of an unequivocal signal in vessel chronologies and the conflicting interpretations reported above may also be due, in part, to our longer vessel chronologies (climate series), the use of species growing at (*Q. alba*) or close to (*Q. rubra*) their northern distribution limit, and the different climate system that characterizes southwestern Quebec. Our chronologies were also derived from only one site and 10 trees per species, and a methodological bias cannot be totally excluded. However, the similarity of the ring width – climate association with that of 11 other oak stands distributed along a 200- km corridor in southwestern Quebec (Tardif et al. 2006), the similarity in vessel chronologies between the two oak species, and the strength of the common signal in the vessel chronologies suggest that a strong methodological bias due to the size of the data set is improbable. The common signal strength statistics of our vessel chronologies were also very similar to those reported from a single site with 8 trees (García Gonzáles and Eckstein 2003) and from three sites, each with 15–19 trees (Fonti and García-Gonzáles (2004). Despite the apparent weakness of vessel chronologies for use in dendroclimatic reconstructions, the development of these series could prove useful in calibrating physiologically based models of tree growth, which are oriented towards identifying causal biological relationships (Fritts et al. 1991; Foster and LeBlanc 1993; Misson et al. 2004). Our study was limited to two ring-porous species, and the utility of continuous vessel chronologies in diffuse-porous species for climate reconstruction (Eckstein and Frisse 1982; Saas and Eckstein 1995) needs to be further assessed.

Conclusion

All vessel features studied in both *Q. alba* and *Q. rubra* from southern Quebec were intrinsically linked to ring dimension. Earlywood width and respective vessel features were mainly influenced by the weather conditions prior to ring formation, whereas latewood width and respective vessel features were mainly associated with weather conditions during the year of ring formation. The potential impact of late-spring temperature was better reflected in maximum vessel area. However, none of the vessel variables were found to be independent of ring dimensions and none provided distinct climatic information, which brings into question the utility of developing long, continuous vessel chronologies for use in dendroclimatic reconstructions, given the time involved in preparing samples and generating measurements. The common signal exhibited by vessel features was also generally lower than the ring dimensions, indicating that more trees would need to be analyzed to adequately reconstruct climate variables. The vessel features measured in the two *Quercus* species growing at the distribution limit of *Q. alba* did not increase the climatic information that could be obtained from earlywood–latewood width. The best climate-reconstruction model of water availability was obtained from the earlywood, latewood, and ring-width chronologies and was superior to those that used solely ring width or a combination of vessel features.

We concur with Hughes (2002), who stated, regarding the use of stable isotopes in dendroclimatology, that if vessel features provide no new information beyond that obtained from the much easier and cheaper measurement of ring width, they should not be used as a continuous paleoclimatic record. In a recent review, Wimmer (2002) concluded that only a few anatomical features of tree rings have proved useful in climate study, and that these are often intercorrelated with more easily obtainable variables, thus providing little new environmental information. It should be noted that numerous anatomical variables that may prove useful were not investigated in this study. Vessel variations in ring-porous species have proved to be successful in identifying discrete events (ring anomalies) related to geomorphic or ecological processes occurring during the lifetime of a tree without requiring the development of continuous vessel chronologies. Vessel features in ring-porous species may thus be best used to decipher discontinuous signal related to tree growth and, in particular, to understand tree physiology.

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