Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus rubra*) at the northern distribution limit of white oak in Quebec, Canada

J. C. Tardif¹,²*, F. Conciatori¹,², P. Nantel²† and D. Gagnon²

1Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, 515 Portage Avenue, Winnipeg, MB, Canada R3B 2E9 and ²Groupe de recherche en écologie forestière interuniversitaire (GREFI), Université du Québec à Montréal, Case postale 8888, Succursale Centre-ville, Montréal, QC Canada, H3C 3P8

**ABSTRACT**

**Aim** The objectives of this study were: (1) to compare radial growth patterns between white oak (*Quercus alba* L.) and northern red oak (*Quercus rubra* L.) growing at the northern distribution limit of white oak; and (2) to assess if the radial growth of white oak at its northern distribution limit is controlled by cold temperature.

**Location** The study was conducted in three regions of the Ottawa valley in southern Quebec. All stands selected were located at the northern limit of distribution of *Q. alba*.

**Methods** Twelve mixed red and white oak stands were sampled and increment cores were extracted for radial growth analyses. For each oak species, 12 chronologies were derived from tree-ring measurement (residual chronologies). Principal components analysis and redundancy analysis were used to highlight the difference between radial growth in both species and to determine their radial growth–climate association.

**Results** There was little difference between the radial growth of each species; *Q. alba*, however, exhibits more year-to-year variation in growth than *Q. rubra*. More than 65% of the variance in radial growth was shared among sites and species. Both species showed a similar response to climate, which suggested that the limit of distribution of *Q. alba* might not be determined by effects on growth. Both species had a classic response to climate and drought in the early growing season.

**Main conclusions** The northern distribution limit of *Q. alba* does not appear to be directly controlled by effects on growth processes as indicated by the similarities in radial growth and response to climate between the two species. The location of the stands on southern aspects suggested that cold temperature could have been a major factor controlling the distribution limit of *Q. alba*. However, it is speculated that stands growing on southern aspects may be more prone to forest fires or to drought, which would favour the maintenance and establishment of oaks, and of *Q. alba* in particular. Models relating the northern distribution limits of species to broad climate parameters like annual mean temperature will need to be reviewed to incorporate more biologically relevant information. Such assessments will in turn provide better estimates of the effect of climate changes on species distribution.

**Keywords** Dendrochronology, limit of distribution, principal components analysis, *Quercus alba* L., *Quercus rubra* L., growth–climate association, redundancy analysis, tree ring.
INTRODUCTION

Over the last century the climate of eastern Canada has become wetter and warmer. Instrumental climate records show an increase of annual mean temperature by 0.5–1.5 °C in the last 100 years, with a greater warming in minimum than maximum temperature (Vincent & Gullett, 1999; Zhang et al., 2000; Houghton et al., 2001). Mean precipitation has also significantly increased, and particularly the amount of snowfall in spring (Mekis & Hogg, 1999). Simulations of climate by general circulation models (GCMs) also forecast that at current rates of atmospheric CO2 and aerosol emissions the warming will increase by an additional 1.5–4.5 °C by 2050 (Boer et al., 2000). It is believed that climate change will have a major impact on forest ecosystems.

Both static and dynamic models have been used to project potential effects of climate change on forest dynamics. Most models suggest that future climatic change may cause substantial changes in the distribution limits of species, in stand composition and in stand biomass (Bonan & Sirois, 1992; Rizzo & Wiken, 1992; Lenihan, 1993; Loehle & LeBlanc, 1996; Loehle, 1996, 2000; Price & Apps, 1996; Masek, 2001). The use of these models has recently been criticized for the assumption made of a climatic control over the distribution limits of species. The idea that the limit of species distribution is controlled by climatic factors has had a long history. The southern and the northern limit of species distribution have long been thought to be associated with warm temperature (dryness) and cold temperature, respectively (Hart, 1894, 1895; Forrest, 1914). However, it may not be valid to assume that climate variables such as summer or winter temperature control the geographical range limits of tree species (Loehle & LeBlanc, 1996; Loehle, 2000; LeBlanc & Terrell, 2001). The argument is that the structure of the current models used to predict the response of forest to climate change causes them to overemphasize the role of climate in controlling tree growth and mortality. Many authors have suggested that it is becoming increasingly important that modellers better understand the seasonal behaviour of trees so that they can model the response of trees to elevated CO2 concentrations (Graumlich, 1989, 1993; Cook & Cole, 1991; Loehle & LeBlanc, 1996; Loehle, 1996, 2000; Stephenson, 1998; LeBlanc & Terrell, 2001).

White oak (Quercus alba L.) reaches the northern limit of its distribution in southern Québec and is listed as rare in the province (Bouchard et al., 1983; Labrecque & Lavoie, 2002). Populations of the species are found in only five distinct localities, all occurring in the Ottawa valley, where it forms mixed stands with northern red oak (Quercus rubra L.) on subxeric to xeric sites with south- to south-west-facing slopes (Gagnon & Bouchard, 1981; Gagnon, 1985; Gauthier & Gagnon, 1990). Many threatened or vulnerable plant species are found almost exclusively in these dry and open forests in Québec (Gagnon, 1985). Both tree species share a wide overlapping distribution; however, Q. rubra reaches more northern latitudes (Rogers, 1990; Sander, 1990). The occurrence of these two species together made it possible to compare their growth in sites located at the northern distribution limit of Q. alba.

The overall objective of this study was to assess whether climate conditions were related to the northern distribution limit of Q. alba. More specifically, we will: (1) compare radial growth between Q. rubra and Q. alba growing at the northern distribution limit of white oak; and (2) assess how the association between radial growth and climate of both species differs. In a context where the northern limit of distribution of Q. alba is limited by climate, we hypothesized that low temperature will be more limiting to radial growth of Q. alba than to Q. rubra. If temperature controls the northern limit of distribution, positive correlations with temperature are expected. Both species should also show a different response to drought as Q. rubra is reported to be less drought resistant than Q. alba (Abrams, 1990).

METHODS

Study area

The study area is located in south-western Quebec and stretches for approximately 200 km (Fig. 1). Twelve mixed oak stands were sampled in three regions of the Ottawa valley in southern Québec (Fig. 1): the Pointe-au-Chêne region; the Eardley escarpment region in Gatineau Park, near Luskville; and the Waltham region. The most northerly population of Q. alba in North America occurs in the Waltham region (Nantel, 1995).

The oak forests sampled have developed on subxeric to xeric south- to south-west-facing slopes of the Precambrian Shield. Soils were brunisols (Commission canadienne de pédologie, Comité de la classification des sols, 1978), on acidic sandy loams derived from rocky tills of varying thickness, but mostly thin. These oak forests have all developed after a major disturbance. Burned or cut stumps were present in most plots, and many trees with multiple stems indicate that they have grown from stump sprouting. Pieces of charcoal were observed in the superficial layer of the soil in most sampling plots.

Over all sampling plots, Q. alba and Q. rubra represented, respectively, from 12% to 82% and 2% to 75% of the total basal area of the stands, but on average total oak basal area dominated and varied between 75% and 82% of total tree basal area in the three study regions (Nantel, 1995). The other most common tree species were Ostrya virginiana (up to 20% of total basal area), Fraxinus americana (up to 19%), Acer saccharum (up to 11%) and Pinus strobus (up to 39%). These last two species were seldom found in the same plot. More complete descriptions and analyses of these oak communities are found in Gagnon & Bouchard (1981) and Gauthier & Gagnon (1990).

The meteorological station with the longest and most complete record in the area is Ottawa CDA (Fig. 1 & Table 1). The mean annual temperature and total precipitation for the period 1971–2000 are 6.3 °C and 914.2 mm, respectively.
The average maximum temperature in July is 26.4 °C and the average minimum in January is 14.8 °C. Approximately 78% of the total annual precipitation occurs as rainfall, with approximately 49% falling during the growing season. Few climatic differences are observed among the three regions (Table 1). Instrumental data indicate that north-western stations are, however, slightly drier and colder.

### Data collection and chronology development

Twelve paired *Q. alba* and *Q. rubra* tree-ring residual chronologies were developed for the Ottawa valley in southern Québec (Fig. 1). Stand selection was based on the abundance of *Q. alba*. *Quercus alba* cover in Eardley and Pointe-au-Chêne populations had a patchy distribution. There were stands with a high percentage of *Q. alba* trees separated by other types of...
forests in which Q. alba trees were absent or found in low numbers. Therefore, in those two regions, stands were chosen for their high proportion of Q. alba. The Eardley population was divided into seven stands, each containing two sampling plots of 0.1 ha (20 × 50 m). The Pointe-au-Chêne population was divided into four stands, each containing one to four sampling plots of 0.1 ha. The Waltham population was divided into three stands, each containing a 0.1-ha sampling plot. At Waltham, all the samples were, however, pooled because of proximity.

In each stand, 60–100% of the oak stems, depending on the individual plot, were cored at their base. In total, 548 Q. alba and 599 Q. rubra trees were sampled and detailed information on a per site basis is provided in Table 2. All wood samples were prepared following standard methods (Stokes & Smiley, 1968; Fritts, 1976). They were visually cross-dated to identify pointer years using a variant of the list method proposed by Yamaguchi (1991). Cross-dating is done to ensure accuracy in the assignment of annual growth rings to the year each was formed. Ring widths were then measured at a precision of 0.001 mm using a Velmex measuring system (Velmex, Inc., Bloomfield, NY, USA). Data quality was further validated with the COFECHA program, which calculates cross-correlations between individual series and a reference chronology (Holmes, 1983).

Each measured series was standardized using a spline function with a 50% frequency response of 50 years (Cook & Peters, 1981). Standardization involved transforming the value for ring width into a dimensionless index value by dividing the observed ring widths by the expected ring widths (Fritts, 1976) given by the spline function. These new growth indices have a relatively stable mean and variance through time (Cook & Kairiustis, 1990). This procedure retained high-frequency variations (interannual to decadal) and filtered out medium- to low-frequency trends. The most important sources of low-frequency variations are trends in growth due to age–size, biological persistence and long-term stand dynamics (Fritts, 1976; Cook & Kairiustis, 1990). Autoregressive modelling was also performed on each standardized series to remove temporal autocorrelation and to enhance the common signal. To further diminish the effect of endogenous stand disturbances and to enhance the common signal, all residual series were averaged by site/species using a biweight robust mean. This procedure reduces the weight of statistical outliers in the calculation of the mean value for each year of a chronology. All procedures were conducted using the program ARSTAN (Cook, 1985) and resulted in 12 residual chronologies per species, one for each sampled stand.

**Comparison of chronologies and relationship to climate**

Principal components analysis (PCA) and redundancy analysis (RDA) were used (1) to compare all tree-ring chronologies and (2) to assess the association between radial growth and climate in both species. To determine the common variation among all chronologies, the structure of their variance was first analysed using PCA (Peters *et al.*, 1981; Arquillière *et al.*, 1990; Graumlich, 1993; Hofgaard *et al.*, 1999; Girardin & Tardif, 2005). The objective of the PCA is to compress our initial data set (12 residual tree-ring chronologies) into a smaller set of uncorrelated variables that expresses the maximum percentage of variance in the original data set.

In dendroecology, the relationships between tree-ring indices and climate variables are usually calculated in the form of a correlation or a response function (Fritts, 1976; Cook & Kairiustis, 1990). Redundancy analysis is also effective in quantifying the relationship between tree-ring indices and climatic factors (Beeckman, 1992; Tardif *et al.*, 2003; Girardin *et al.*, 2004a). Redundancy analysis is the direct extension of multiple regression applied to multivariate data (Legendre & Legendre, 1998). In RDA, the canonical form of PCA, the ordination axes are constrained to be linear combinations of supplied environmental variables (ter Braak & Prentice, 1988; ter Braak, 1994; ter Braak & Smilauer, 1998). Redundancy analysis is most appropriate when short environmental gradients are covered (ter Braak & Smilauer, 1998; Legendre & Legendre, 1998). This is highlighted here by the excellent cross-dating among trees, sites and species, indicating that a common macroclimatic signal was coherent for all chronologies over the study area.

All PCAs and RDAs were calculated from a covariance matrix since our descriptors (tree-ring chronologies) were of the same kind, shared the same order of magnitude and were measured in the same unit (Legendre & Legendre, 1998). In RDAs, significant climatic variables ($P < 0.05$) were selected after a forward selection using a Monte Carlo permutation test based on 999 random permutations. All ordination analyses were computed using the program CANOCO (version 4.02) and scaling of ordination scores was done using a correlation biplot (ter Braak, 1987, 1994). To compare the RDA results with methods more commonly used in dendroecology, Pearson’s correlations were calculated between each of the 12 residual tree-ring chronologies and climate variables.

For all climate analyses, mean monthly temperature and total monthly precipitation from May of the preceding growing season ($t-1$) to August of the current growing season ($t$) were used as predictands. Meteorological 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 data base (Mekis & Hogg, 1999; Vincent & Gullett, 1999). In addition, the Canadian Drought Code (CDC) component of the Canadian Forest Fire Behaviour System (Turner, 1972; Van Wagner, 1987; Girardin *et al.*, 2004b) was used. Daily CDC indices were computed using daily maximum temperature and daily precipitation data from the Ottawa CDA station (data from the Meteorological Service of Canada, 2000). The computation was conducted following the procedure of Van Wagner (1987) and mean monthly CDC averages were produced. The CDC is a daily parameter representing the average moisture content of deep and
<table>
<thead>
<tr>
<th>Site:</th>
<th>BH</th>
<th>CA</th>
<th>CH</th>
<th>CL</th>
<th>CM</th>
<th>MB</th>
<th>MK</th>
<th>PC</th>
<th>RB</th>
<th>RR</th>
<th>TM</th>
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<tr>
<td>Number of trees</td>
<td>87</td>
<td>55</td>
<td>35</td>
<td>35</td>
<td>16</td>
<td>49</td>
<td>20</td>
<td>51</td>
<td>48</td>
<td>89</td>
<td>21</td>
<td>58</td>
</tr>
<tr>
<td>Number of radii</td>
<td>93</td>
<td>61</td>
<td>39</td>
<td>41</td>
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<td>21</td>
<td>58</td>
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<tr>
<td>Mean ring width (mm)</td>
<td>0.72</td>
<td>0.95</td>
<td>1.27</td>
<td>1.08</td>
<td>2.04</td>
<td>1.41</td>
<td>1.0</td>
<td>0.98</td>
<td>1.06</td>
<td>1.04</td>
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<td>First-order autocorrelation</td>
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<td>0.28</td>
<td>0.32</td>
<td>0.32</td>
<td>0.30</td>
<td>0.35</td>
<td>0.38</td>
<td>0.22</td>
<td>0.26</td>
<td>0.20</td>
<td>0.12</td>
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<tr>
<td>Mean sensitivity*</td>
<td>0.35</td>
<td>0.31</td>
<td>0.25</td>
<td>0.23</td>
<td>0.28</td>
<td>0.25</td>
<td>0.30</td>
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<td>0.25</td>
<td>0.43</td>
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<tr>
<td>Standard deviation</td>
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<td>0.27</td>
<td>0.21</td>
<td>0.20</td>
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<td>0.22</td>
<td>0.26</td>
<td>0.21</td>
<td>0.31</td>
<td>0.21</td>
<td>0.38</td>
<td>0.28</td>
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<tr>
<td>Variance in the first principal component (%)</td>
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<td>0.33</td>
<td>0.25</td>
<td>0.32</td>
<td>0.28</td>
<td>0.30</td>
<td>0.35</td>
<td>0.38</td>
<td>0.22</td>
<td>0.26</td>
<td>0.20</td>
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<td>Mean correlation among all radii</td>
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<td>0.47</td>
<td>0.51</td>
<td>0.49</td>
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<td>0.53</td>
<td>0.50</td>
<td>0.64</td>
<td>0.49</td>
<td>0.66</td>
<td>0.66</td>
</tr>
</tbody>
</table>

*Mean sensitivity is the average difference between successive ring index values. This index ranges from 0 (no differences between successive ring widths) to 2 (every second ring missing) and larger values indicate the presence of considerable high-frequency variance (Fritts, 1976).

†Calculated from the standard chronology.

‡The expressed population signal statistic is an indicator of chronology reliability. It measures how well the chronology compares with the theoretical population chronology based on an infinite number of trees (Cook & Kairiukstis, 1990). The statistic ranges from 0.0 to 1.0, i.e. from no agreement to 1.0 for perfect agreement with the population chronology.
compact organic layers (Turner, 1972). It is a useful indicator of seasonal drought (season approximates April to October) and shows the likelihood of fire involving the deep duff layers and large logs. A CDC rating of 200 is high, and 300 or more is extreme, indicating that fire will involve burning deep subsurface and heavy fuels. For all climate analyses, the reference period was set to 1920–89.

RESULTS AND DISCUSSION

Chronologies and descriptive statistics

The oldest $Q. rubra$ and $Q. alba$ residual chronologies spread over a time span ranging from the 1820s to the 1990s (Table 2 & Fig. 2). The general statistics computed show that all residual chronologies share similar characteristics (Table 2). Only chronology mean sensitivity and standard deviation differed between the two oak species ($P = 0.003$ and 0.004, respectively, as determined by paired $t$-tests). Both oak species shared similar mean ring width, indicating a similar growth rate. $Quercus alba$ residual chronologies, however, had a slightly higher mean sensitivity and standard deviation. Mean sensitivity is the average difference between successive ring index values. This difference is further illustrated by the higher year-to-year fluctuations in radial growth indices observed in the $Q. alba$ chronologies (Fig. 2). At the northern distribution limit of $Q. alba$, both species showed higher mean sensitivity than those reported for more southern sites ($Q. alba$: McIlenahen & Dochinger, 1985; Jacobi & Tainter, 1988; Robertson, 1992; Graumlich, 1993; Rubinio & McCarthy, 2000, and $Q. rubra$: Tainter et al., 1990; Robertson, 1992; Graumlich, 1993). The common interval analysis also showed that all residual chronologies shared a similar signal strength with similar expressed population signal (EPS) values and variance in the first principal component, ranging from 49% to 66% (Table 2). The EPS value represents the variance agreement between a finite and a theoretical infinite sample size (see Cook & Kairiustis, 1990). The PCA analyses conducted for the period 1920–89 on the network of 24 residual chronologies showed that 65.2% of the variance was shared by all oak chronologies (all chronologies had positive loading on axis 1, not presented). Axis 2 represented 9.7% of the variance and mainly separated the three most easterly sites in the proximity of Pointe-au-Chêne (not presented). This difference in variance could reflect the influence of the climate prevailing in the Montreal region (Fig. 1) or other specific signals pertaining to these tree-ring chronologies.

Radial growth–climate association

Redundancy analysis further highlighted the similarities among the 24 oak chronologies as well as the similarity in their association with climatic variables (Fig. 3a). This similarity was also observed in $Q. alba$ and $Q. rubra$ growing in the Great Lakes region (Graumlich, 1993). All chronologies shared a positive loading on axis 1 suggesting that they all contribute to the establishment of that axis (Fig. 3a). This grouping reflected the tendency for growth patterns in oak to be correlated over the entire region. Furthermore, the positive correlation among all oak chronologies is stressed by the acute angle formed between the respective vectors of any two oak chronologies. Vectors pertaining to only a few chronologies were drawn for visual clarity (Fig. 3a); however, the angle formed by vectors pertaining to two chronologies can be easily visualized using their vectors’ apices. A slight separation of the oak species was, however, observed on axis 2. The $Q. rubra$ chronologies showed positive values in comparison to most $Q. alba$ chronologies (Fig. 3a).

The climatic variables most strongly and positively correlated to radial growth in both species were June–July precipitation

Figure 2 The 12 residual tree-ring chronologies for all sites for $Q. alba$ (a) and $Q. rubra$ (b) for the reference period 1820–1989. The sample depth (number of cores) is indicated at the bottom of each graph.
The correlation coefficient between the axis scores and their estimated values is indicated. The black line represents the RDA scores whereas the grey line represents their estimation. The correlation between biotic and abiotic variables is given by the cosine of the angle between two vectors (arrows). Vectors pointing in roughly the same direction (acute angle) indicate a high positive correlation, vectors crossing at right angles correspond to a near-zero correlation and vectors pointing in opposite directions (obtuse angle) show a high negative correlation (ter Braak & Verdonschot, 1995; Legendre & Legendre, 1998). Parts (b) and (c) indicate how well the climatic variables fit the first RDA axis and second RDA axis respectively. The black line represents the RDA scores whereas the grey line represents their estimation. The correlation coefficient between the axis scores and their estimated values is indicated.

Our results are consistent with other studies of *Q. alba* and *Q. rubra*. At the northern limit of distribution of *Q. alba*, May temperature (negative correlation) and June precipitation (positive correlation) were the most strongly correlated variables to radial growth in both species. In *Q. alba*, Jacobi & Tainter (1988) found that cool May and June precipitation were positively associated with growth rate. Rubino & McCarthy (2000) observed that precipitation in June yielded the highest correlation with radial growth. Fritts (1962) also observed that wide earlywood bands were associated with a cool and wet early growing season. In *Q. rubra*, Zasada & Zahner (1969) reported that mature earlywood vessels were first observed about 5 weeks after their initiation, i.e. at the time the first leaves were unfolding. Earlywood formation continued for another 5 weeks, whereas shoot growth lasted 2 weeks. It is thus reasonable to think that favourable May and June conditions would promote earlywood growth, optimum leaf expansion in the early growing season and relatively large rings.

Our results agree with those of LeBlanc & Terrell (2001) who, in an analysis of 128 *Q. alba* sites distributed across the eastern USA, observed that *Q. alba* was particularly sensitive to water balance in the early growing season. The authors noted that June conditions were those that had the most spatially consistent correlation with radial growth. Our results also support those of Terrell & LeBlanc (2002) who, in an analysis of 71 *Q. rubra* sites distributed across the eastern USA, observed that radial growth in *Q. rubra* was particularly sensitive to climatic conditions in the early growing season (May to July). In studies of *Q. alba* and/or *Q. rubra*, water balance in the early growing season was shown to dominate the response to climate (Friesner & Friesner, 1941; Miller, 1950; Fritts, 1962; Estes, 1970; Guyette et al., 1982; Jacobi & Tainter, 1988; Smith & Rennie, 1991; Robertson, 1992; Foster & LeBlanc, 1993; Graumlich, 1993; Rubino & McCarthy, 2000; LeBlanc & Terrell, 2001; Terrell & LeBlanc, 2002).
In our study, weak correlations were observed between conditions in the year prior to ring formation and radial growth of the current year. This weak association is in contrast with the results of Jacobi & Tainter (1988) who found a negative correlation between radial growth and July–August temperature of the year prior to ring formation in *Q. alba*. 

Radial growth of *Q. rubra* was more strongly correlated with climate conditions during the year prior to ring formation, with positive associations with prior July precipitation and negative correlations with prior August CDC. Taken together, correlations with these two variables indicated that *Q. rubra* is more sensitive to drought during the prior year than is *Q. alba*. This observation is consistent with the claim of Abrams (1990) that *Q. rubra* is more sensitive to water stress than *Q. alba*.

**Limit of distribution**

In a context where the northern limit of distribution of *Q. alba* would be determined by climate, we expected to see specific details related to the characteristics of *Q. alba* chronology and radial growth–climate correlations. The radial growth chronologies derived for each species showed no major differences, and both species had comparable ring width. *Quercus alba* chronologies did present higher year-to-year variations (mean sensitivity) when compared with *Q. rubra*, but this difference failed to translate into a specific radial growth–climate association. We initially hypothesized that low temperatures would limit growth processes in *Q. alba* due to this species being at its northern distribution limit. However, our results

**Figure 4** Pearson correlation coefficients between the *Q. alba* and *Q. rubra* residual tree-ring chronologies and the monthly climatic variables for the period 1920–89. From top to bottom, the figures indicate correlations with average monthly minimum, mean and maximum temperature, average monthly Canadian Drought Code, as well as total monthly precipitation. The 12 residual chronologies by species are arranged from easternmost (1) to westernmost (12) sites. Darker blue indicates positive correlation and darker red indicates negative correlations. Significant correlations (*P* < 0.05) are also indicated by either black or white dots.
indicated no positive correlations between growth rate and temperature. The similarity of growth–climate associations for Q. alba and Q. rubra suggests that something other than direct effects of climate on growth processes control the northern range limit of Q. alba. The range of Q. rubra extends several hundred kilometres to the north. If the effects of climate on radial growth controlled the northern limit for Q. alba we would expect a climatic variable to differ between Q. alba and Q. rubra.

Our results suggest that the restriction of Q. alba stands to south to south-west facing slopes is not associated with control on growth processes by cold temperature. Despite its commonness in eastern North America (Rogers, 1990), Q. alba has a much more restricted habitat in southern Quebec than Q. rubra (Sander, 1990), which is found over a large range of soil moisture and soil richness conditions. Quercus alba is also reported to be more tolerant to drought and fire than Q. rubra (Abrams, 2003). Quercus alba is a disturbance-adapted species that regenerates in gaps and post-fire, but is a poor competitor beneath closed canopies (Abrams, 2003). According to Nantel (1995), the natural fire disturbance regime, which originally created conditions for the perpetuation of the oak stands in south-western Quebec, has been permanently altered by fire control. Tree-ring studies have indicated that periodic fire played a crucial role in the development and perpetuation of oak forests before and after European settlement (Shumway et al., 2001; Abrams, 2003). The observed decline in Q. alba’s importance across most of its distribution range and the probable successional replacement of most oak and pine forests to later successional species may be attributable to fire suppression.

The current northern distribution limit of Q. alba could be explained by a combination of changed fire periodicity (anthropogenic and climatic causes) reducing opportunities for the establishment of new populations, as well as low dispersal ability. Recruitment (seedlings and saplings) was observed in all 12 study populations, and the year 1991 corresponded to a mast year in both oak species (Nantel, 1995). The apparently successful recruitment reduces support for interpretations that propose climate as a major limitation to reproduction and seedling survival in Q. alba near its northern distributional limit. Demographic projections by Nantel (1995) showed that under current growing conditions of increasing canopy closure, seedlings of both oak species will take between 228 and 323 years to complete all stages of their life cycle, whereas the current maximum age of oak trees is approximately 150 years. This model suggests there were periods of much faster growth in the past and probably more open canopy conditions. These oak stands will require recurrent disturbances in the future, such as fire, if they are to retain their current structure and composition. Demographic analyses also revealed no significant differences between the dynamics of Q. alba and Q. rubra in the studied stands (Nantel, 1995), supporting the dendrochronological findings of this study.

Empirical studies examining the population dynamics and/or the association between radial growth and climate of tree species growing at or near their northern limit of distribution in Canada have suggested that cold climate might not be the main factor controlling species distribution. As suggested by Meilleur et al. (1997), tree species at the northern limit of their distribution have often been reported to exhibit small stature, slow growth and low reproduction. They may also be restricted to topographical positions that provide favourable microclimate such as south-facing slopes. In their study of the northernmost population of pitch pine (Pinus rigida Mill.), the authors concluded, however, that adverse climatic conditions were not the prime factor related to establishment of the northern limit of the species. This limit appeared to mainly be associated with habitat availability rather than a physiological response to climate. Asselin et al. (2003) have shown that jack pine (Pinus banksiana Lamb.) could grow and develop 300 km north of its present distribution limit, despite producing non-viable seeds, and concluded that low fire frequency and small fire area, and not climate, were the most important factors determining the northern distribution limit of the species.

In north-western Quebec, both ecophysiological (Flannigan & Woodward, 1993) and tree-ring (Tardif et al., 2002) studies have supported the idea that the distribution limit of red pine (Pinus resinosa Ait) was not related to climate. Disturbance regime and habitat availability were the main factors highlighted (Flannigan & Woodward, 1994; Flannigan & Bergeron, 1998). Similar results were obtained in Manitoba where P. resinosa reaches its north-westernmost distribution limit in Canada (Sutton et al., 2002; J.C. Tardif, unpubl. data). In north-western Manitoba, the radial growth of northern white cedar (Thuja occidentalis L.), growing hundreds of kilometres outside its continuous range of distribution, also did not show strong correlation with climate (Tardif & Stevenson, 2002). Only in eastern hemlock (Tsuga canadensis L.), growing near the northern limit of its distribution in southern Quebec, was radial growth significantly and positively correlated with winter temperature (Tardif et al., 2001). The authors suggested that the positive correlation between radial growth and warm winters could indicate that cold winters play a role in the species’ distribution. At Churchill, Manitoba, the positive association observed between radial growth of black spruce (Picea mariana [Mill] BSP), white spruce (Picea glauca [Moench] Voss), eastern larch (Larix laricina (Du Roi) K. Koch.) and June–July temperature (Girardin et al., 2005) could indicate that cold temperature (shortened growing season) is limiting for growth processes at the treeline. For P. mariana, it has also been suggested that other factors such as the inability to reproduce on thick lichen mats may be more important in setting its northern distribution limit (Bonacci & Sirois, 1992).

In conclusion, our findings question the long-accepted idea in biogeography that cold temperatures control the northern limits of distribution of species such as Q. alba. Both Q. alba and Q. rubra had a similar response to climate, and cold temperatures were not affecting radial growth of Q. alba despite the species reaching the northern limit of its distribution. Climate, however, could affect other stages and processes.
in the life cycle of *Q. alba*. For example, extreme events leading to freeze-induced mortality in the dormant season may not leave traces in the subsequent annual tree rings. The establishment of seedlings and saplings could also be more sensitive to temperature controls than mature trees. Further studies of stand dynamics will be needed to address this point. Studies of other tree species will also be needed before across-species generalization can be made. This said, we concur with the criticism made that static and dynamic models used to predict the impact of climate change on tree growth and forest dynamics need to be reviewed to integrate more biologically realistic climate forcing (Graumlich, 1989, 1993; Cook & Cole, 1991; Loehle & LeBlanc, 1996; Loehle, 1996, 2000; Stephenson, 1998; LeBlanc & Terrell, 2001; Terrell & LeBlanc, 2002). The assumption normally made that the northern distribution limit of *Q. alba* may be controlled by a direct negative influence of cold temperature on growth processes is not supported by our analyses. Rather than supporting the cold climate assumption, we speculate that at the northern distribution limit of *Q. alba*, south- to south-west-facing slopes may be more prone to forest fires and/or to severe drought, two factors that would favour the maintenance and establishment of oaks, and of *Q. alba* in particular. In order to produce better models of the impact of future climatic changes on forest dynamics, improved quantifications of the effects of climate on tree growth (seasonal timing of warmth and soil moisture), the disturbance regimes and the colonization processes are needed. Both ecophysiological and dendroecological studies may provide useful information in determining any important effects of climate forcing on the distribution of tree species and in validating results from forest simulation models (Graumlich, 1989, 1993; Cook & Cole, 1991; Bonan & Sirois, 1992; Loehle & LeBlanc, 1996).

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**BIOSKETCHES**

**Jacques C. Tardif** is Canada Research Chair in Dendrochronology and associate professor at the University of Winnipeg. His research focuses primarily on tree growth, forest dynamics and reconstruction of past disturbances and climate using tree-ring analysis.

**France Conciatori** is a technician at the Centre for Forest Interdisciplinary Research. She is involved in teaching dendrochronology, in developing a network of tree-ring chronologies for the major tree species of the Canadian boreal forest and in wood anatomy studies.

**Patrick Nantel** is a population ecologist working at Parks Canada and he is interested in population viability analyses and their applications in planning the recovery of endangered and threatened species.

**Daniel Gagnon** is a professor at the Université du Québec à Montréal. His research interests are mainly on the population dynamics of endangered and threatened plant species, and in developing solutions for their conservation.

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