

COMPARATIVE ANALYSIS OF THE CLIMATIC RESPONSE OF SEVEN BOREAL TREE SPECIES FROM NORTHWESTERN QUÉBEC, CANADA

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ABSTRACT

We analyzed the radial growth response of seven boreal tree species growing on an island of Lake Duparquet, northwestern Québec. The species investigated were *Betula papyrifera*, *Abies balsamea*, *Thuja occidentalis*, *Picea glauca*, *Picea mariana*, *Pinus banksiana* and *Pinus resinosa*. Seven species chronologies were developed as well as seventy individual tree chronologies. Coniferous species were positively correlated to warm April and to cool-wet July. This indicates that early spring and positive water balance during the growth season favor radial growth. In contrast, the radial growth of *B. papyrifera* was mainly correlated to June precipitation. The response of individual trees to climate was variable but the differences between *B. papyrifera* and the coniferous species were maintained. No microsite factors or tree characteristics were associated with this variability. Except for *B. papyrifera*, it is speculated that climate change could have a similar qualitative physiological consequence on the growth of coniferous species found on homogeneous insular landscapes.

Keywords: boreal tree species, individual tree chronology, response function, correlation, canonical correspondence analysis, insular landscape, Lake Duparquet.

RÉSUMÉ

La réponse climatique de sept espèces arborescentes de la forêt boréale croissant sur une île du Lac Duparquet, nord-ouest du Québec, fut analysée. Les sept espèces étudiées furent le *Betula papyrifera*, le *Abies balsamea*, le *Thuja occidentalis*, le *Picea glauca*, le *Picea mariana*, le *Pinus banksiana* et le *Pinus resinosa*. Une chronologie fut développée pour chacune des espèces de même que pour chacun de 70 arbres inclus dans l'étude. Toutes les espèces, sauf le *B. papyrifera*, ont démontré une commune influence du climat. L'accroissement radial du *B. papyrifera* fut significativement relié aux précipitations de Juin. La réponse climatique des six espèces de conifères fut principalement associée à l'effet positif des températures chaudes d'avril et aux conditions fraîches et humides de juillet. Bien que plus variable, l'analyse des 70 chronologies a démontré que les différences entre le *B. papyrifera* et les conifères étaient maintenues. Aucun facteur du microsite ou caractérisant les arbres (age ou diamètre) ne fut associé à la réponse climatique des arbres. Encore une fois, les arbres des six espèces de conifères ont démontré une réponse climatique très semblable. Sauf pour le *B. papyrifera*, il est spéculé que l'effet des changements climatiques aura un impact physiologique qualitativement similaire pour les espèces de conifère croissant dans des milieux insulaires homogènes.

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RESUMEN

La respuesta climática de siete especies de árboles del bosque boreal situado en una isla del Lac Duparquet, noroeste del Quebec, fue analizada. Los siete especies fueron al *Betula papyrifera*, el *Abies balsamea*, el *Thuja occidentalis*, el *Picea glauca*, el *Picea mariana*, el *Pinus banksiana* et el *Pinus resinosa*. Una cronología fue desarrollada por cada especie y también por cada uno de los setenta árboles. Todas las especies, con la excepción de *B. papyrifera*, presentaron una función respuesta muy similar. El crecimiento radial de *B. papyrifera* mostró una correlación significativa con la precipitación de Junio. Las especies de coníferos correlacionaron positivamente con el clima caluroso de Abril et fresco-húmedo de Julio. El análisis de las setenta cronologías demostró extensa variabilidad en la respuesta climática, pero las diferencias entre *B. papyrifera* y los coníferos fueron mantenidas. Ningún factor del micrositio o de las características de los árboles (edad o diámetro) pudo ser correlacionado con la variabilidad de la función de respuesta de los árboles. Los coníferos de las seis especies también mostraron una respuesta climática muy similar. Con la excepción de *B. papyrifera*, especulamos que el efecto del cambio climático tendrá un impacto fisiológico cualitativamente similar sobre el crecimiento de los coníferos que crecen en sitios insulares muy homogéneos.

INTRODUCTION

Forest stand simulation models suggest that future climatic change caused by increasing concentrations of atmospheric greenhouse gas may cause substantial changes in the range limit of species, in stand composition and in stand biomass (Solomon 1986; Overpeck *et al.* 1990). Many authors have suggested that it is becoming increasingly important that modelers better understand the seasonal behavior of trees under elevated CO₂ concentration (Graumlich 1989, 1993; Cook and Cole 1991).

Loehle and LeBlanc (1996) reported that the structure of the models used to predict the response of forest to climate change may cause them to overemphasize the role of climate in controlling tree growth and mortality. The authors have argued that the growth-climate functions used in most models (*i.e.* JABOWA in Botkin *et al.* 1972; FORET in Shugart 1984; FORENA in Solomon 1986; FORSKA2 in Price and Apps 1996) have little basis in plant physiology and often do not relate to actual tree responses to climate. The simple annual growing degree-day and drought-day sum used in many simulation models may not be adequate to assess the response of vegetation to future climatic change. The assumptions made about the geographic range limits of species being controlled by climatic variables, such as summer and winter temperature, also appear to be invalid. Loehle and LeBlanc (1996) argued that forest simulation models should be based on the fundamen-

tal niche rather than the realized niche of tree species. As a result, dendroclimatic analyses which relate historical fluctuations in tree growth to climate, may thus provide information that may be used in determining parameters and validating forest simulation models (Shugart 1984; Graumlich 1989, 1993; Loehle and LeBlanc 1996). Dendroclimatic analysis could also be used to test the hypotheses made by modelers (Cook and Cole 1991).

Little data have been published on the climatic response of tree species in the Eastern Canadian boreal forest, although the importance of climate as a limiting factor to tree growth has long been recognized (*e.g.* Fritts 1976; Kramer and Kozłowski 1979). In eastern North America, historical climate analyses have reported an increase in both temperature and precipitation (*e.g.* Bradley *et al.* 1987; Folland *et al.* 1990; Karl *et al.* 1993; Jones 1994; Houghton *et al.* 1996) since the end of the Little Ice Age (circa A.D. 1850; Lamb 1982). At the southwestern limit of Québec's boreal forest, proxy records have also provided evidence of climatic change in the last one hundred years. A dendrochronological reconstruction of fire and climate history showed a natural decrease in forest fire frequency related to a decrease in drought frequency since the end of the Little Ice Age (Bergeron 1991; Bergeron and Archambault 1993). Results from a simulation of the Canadian Fire Index under a 2 × CO₂ concentration scenario and General Circulation Model suggested that this decrease in fire frequency will probably continue in the future

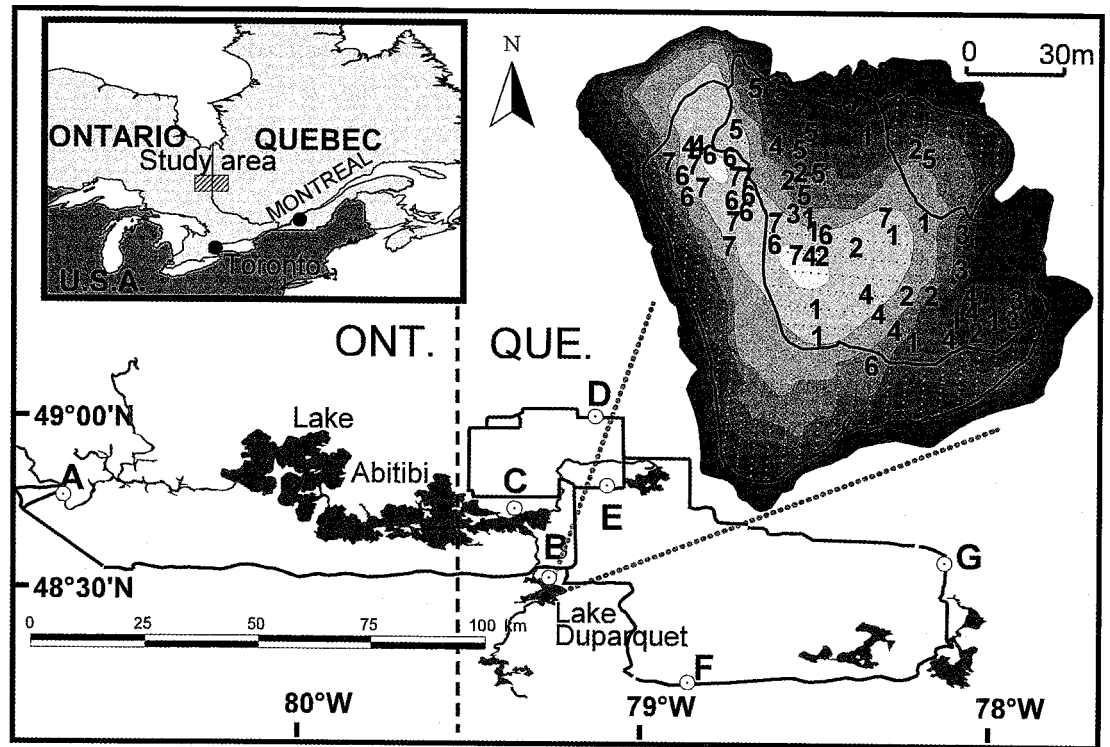


Figure 1. Map of the study area showing the location of Lake Duparquet and of the ecological preserve “des Vieux arbres.” The location of all meteorological stations is indicated as well as the position of the 70 trees on the island. A: Iroquois Falls, B: Lake Duparquet, C: Abitibi Post, D: Val St-Gilles, E: LaSarre, F: Rivière Kinojevis, G: Amos, 1: *Betula papyrifera*; 2: *Abies balsamea*; 3: *Thuja occidentalis*; 4: *Picea glauca*; 5: *Picea mariana*; 6: *Pinus banksiana* and 7: *Pinus resinosa*.

(Bergeron and Flannigan 1995). Furthermore, Tardif and Bergeron (1997) have presented dendrochronological evidence showing that ice damage and water level at spring breakup have increased in the past 150 yr on Lake Duparquet.

The aim of this study is to understand how the radial growth increment of seven of the major tree species of the Eastern Canadian boreal forest—white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white cedar (*Thuja occidentalis*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*) and red pine (*Pinus resinosa*)—is controlled by climate variations. Of these species, *P. resinosa* reached its northern limit of distribution in Lake Duparquet area (Bergeron and Brisson 1990). We will determine which climatic factors are responsible for most of the year to year variations in radial growth, both at the species and the tree level. The

analysis at the species level will be used to assess the importance of regional climate in controlling radial growth, whereas the analysis at the tree level will aid in determining the influence of microsite conditions on tree growth.

METHODS

Study Area

The study area is located about 700 km north of Montréal near Lake Duparquet (48°28'N, 79°17'W), northwestern Québec (Figure 1). Lake Duparquet is a large uncontrolled body of water with an area of about 25 km². About 170 islands are distributed on the lake ranging in size from a few square meters to about 0.7 km². This region is part of the Northern Clay Belt of Québec and Ontario located in the Canadian Shield (Wiken

Table 1. Mean and standard deviation for given characteristics of the seven tree species. BEpa: *Betula papyrifera*; ABb: *Abies balsamea*; THo: *Thuja occidentalis*; PIg: *Picea glauca*; PIm: *Picea mariana*; PNb: *Pinus banksiana* and PNr: *Pinus resinosa*.

| Species | Establishment | | Height (m) | Sapwood (mm) | DBH (cm) ² | Distance (m) ² | Slope (°) |
|---------|---------------|-------------|------------|--------------|-----------------------|---------------------------|------------|
| | Date at 1.3 m | DBH (cm) | | | | | |
| BEpa | 1889 ± 31 | 17.4 ± 4.9 | 14.6 ± 3.8 | 64.6 ± 16.1 | 13.1 ± 6.6 | 2.9 ± 2.2 | 10.5 ± 4.8 |
| ABb | 1954 ± 15 | 15.0 ± 1.2 | 12.6 ± 1.4 | 43.4 ± 23.3 | 11.9 ± 4.6 | 2.9 ± 1.8 | 11.4 ± 5.5 |
| THo | 1906 ± 25 | 21.6 ± 7.9 | 9.5 ± 1.8 | 14.2 ± 4.1 | 15.3 ± 8.7 | 3.6 ± 2.2 | 16.5 ± 7.0 |
| PIg | 1928 ± 27 | 22.3 ± 3.5 | 13.6 ± 3.4 | 39.9 ± 13.9 | 14.5 ± 8.7 | 3.1 ± 1.9 | 9.0 ± 3.0 |
| PIm | 1949 ± 29 | 13.5 ± 2.9 | 11.1 ± 2.1 | 13.1 ± 4.3 | 10.9 ± 3.4 | 1.9 ± 1.0 | 15.2 ± 3.7 |
| PNb | 1921 ± 47 | 22.4 ± 9.2 | 12.1 ± 5.8 | 32.1 ± 15.3 | 12.1 ± 5.0 | 3.4 ± 2.7 | 12.0 ± 5.7 |
| PNr | 1895 ± 59 | 28.5 ± 12.2 | 14.3 ± 6.9 | 56.2 ± 25.1 | 13.9 ± 7.1 | 4.0 ± 2.7 | 14.4 ± 6.8 |

²DBH and distance refer to the mean of the closest trees surrounding each sampled tree in four aspects.

1986) and resulted from the maximum extension of postglacial Lakes Barlow and Ojibway (Veillette 1994).

The climate of the region is continental with cold winters and warm summers. The 1961–1990 mean annual temperature at LaSarre meteorological station, about 42 km north of the study site, is 0.8°C (Environment Canada 1993 and Figure 1) Cold arctic air dominates the area during the winter with a mean January temperature of –17.9°C. Mean July temperature for the region is 16.8°C. Mean annual precipitation is 856.6 mm, with ~25% of the total annual precipitation falling as snow (Environment Canada 1993).

Lake Duparquet is at the southwestern limit of Québec's boreal forest (Rowe 1972) where late successional stands are dominated by *A. balsamea* and *B. papyrifera* (Bergeron and Bouchard 1984). This study site is located on an island of Lake Duparquet, the ecological preserve "des Vieux arbres" (Figure 1). This site was selected because i) all seven species grow on the island, and ii) the disturbance history of the island is well documented. The island covers about 1.4 ha and has an undulating topography with a maximum elevation of 14m above the summer water level of the lake (Figure 1). Two soil moisture conditions can be distinguished. Xeric portions are characterized by exposed bedrock and thin organic deposit in depressions whereas mesic portions of the island are characterized by moraine deposits underlying an organic layer (Bergeron and Brisson 1990). While open areas are mainly colonized by *P. banksiana* and *P. resinosa*, *B. papyrifera*, *Picea* spp. and *A.*

balsamea dominate the close canopy part of the island. Dendroecological evidence indicated that, since ca. A.D. 1800, fire occurred on the island in 1799, 1849, 1881, 1901, and 1914, although the severity of fires differed and several patches were left unburned (Bergeron and Brisson 1990).

Sampling and Data Processing

Seventy trees (10 trees/species) were sampled in August 1998 for tree-ring analysis. For each tree, two cores were extracted at a height of about 1.3 m and one core was extracted at the base for age determination. However, four cores were extracted from all *B. papyrifera* trees because this species produces numerous incomplete (partial) rings (J. Tardif, personal observation). The majority of the trees were established between 1889 and 1949, with both *A. balsamea* and *P. mariana* trees being among the youngest. Mean diameter at breast height (DBH) ranged from 13.5 to 28.5 cm and mean tree height from 9.5 to 14.6 m (Table 1).

Each chronology was constructed following standard methods in dendrochronology (Stokes and Smiley 1968). All the cores were mounted, sanded and visually crossdated using pointer years. Each series was measured to a precision of 0.01 using a Velmex measuring system. To maximize replication in time, cores collected for age determination were also measured if older or better preserved than those from DBH. In many cases, two radii were measured from these cores *i.e.* when they extended to the other side of the tree. The accuracy of the crossdating and data quality were

further validated using program COFECHA (Holmes 1983).

Chronology Development

Each measured series was standardized to remove individual and stand-wide variations not related to climate fluctuations (Fritts 1976; Cook and Kairiukstis 1990). The most important source of these variations are trends in growth due to age-size, biological persistence and long-term stand dynamics (Fritts 1976; Cook and Kairiukstis 1990). To remove these low-frequency trends, all the series were standardized using a 40-yr cubic spline with a 50% frequency response (Cook and Peters 1981). By dividing the observed value by the predicted values, ring-width measures were transformed into relative growth indices that had a relatively stable mean and variance through time (Cook and Kairiukstis 1990). To produce seven species chronologies, indices from individual cores were averaged using a biweight robust mean estimation (Cook and Kairiukstis 1990). All tree-ring series were also prewhitened by autoregressive modeling. This procedure resulted in a transformed residual series without temporal autocorrelation. A residual chronology was also constructed for each species using a robust mean estimation.

Because our second objective was to study the inter-tree variability, a chronology was also produced for each of the 70 sampled trees. To generate these chronologies the following procedures were followed. In ARSTAN (Cook 1985), the tree summaries (chronologies) option was selected. At this stage, ARSTAN uses an arithmetic mean to average the standardized series from the same tree and to compute a standard tree chronology. Autoregressive modeling was also performed on each tree chronology using the FMT program from the Dendrochronology Program Library (Holmes 1992).

Dendroclimatic Analysis

In dendroecology, the relationships between tree-ring indices and individual climate variables are usually calculated in the form of response

function or correlation coefficients (Fritts 1976; Cook and Kairiukstis 1990). In this study, two complementary strategies were followed. The first examined similarities and differences in the climatic response among species, whereas the second approach looked at how microsite characteristics influenced individual tree response to climate.

(a) Species Response to Climate

To analyze the common variation among the 7 chronologies, the structure of their variance was analyzed using principal component analysis (PCA) (Peters *et al.* 1981; Arquillière *et al.* 1990; Graumlich 1993; Holfgaard *et al.* 1999). A PCA was calculated for the common period 1938–1997 using a covariance matrix. This approach was considered appropriate as our descriptors (residual chronologies) were of the same kind, shared the same order of magnitude, and were measured in the same units (Legendre and Legendre 1998). Each year was considered as a sample and each tree growth index as a descriptor (Mode Q, see Legendre and Legendre 1998). The PCA was computed using CANOCO (Ver 4.0; ter Braak and Smilauer 1998). To determine which components were meaningful, the broken stick model (Frontier 1976) was used and the sum of eigenvalues in our analysis was compared with those of the predicted model (Legendre and Legendre 1998). To assess the climatic response of the species, both Pearson's correlation and bootstrap response functions were calculated between the principal component scores and the climatic variables. Bootstrap response functions were calculated using 999 bootstrap iterations with program PRECON (Ver 5.16; Fritts *et al.* 1991). Pearson's correlations were also computed between the climatic variables and with each residual chronology as a comparison.

Data from 7 meteorological stations within a radius of ~105 km of Lake Duparquet were used to compute regional monthly mean temperature and total precipitation (Figure 1 and Table 2). Because LaSarre has been relocated several times throughout the record, each period was treated as an individual station. Program MET from the Dendrochronology Program Library software package was used to estimate missing data and to construct

Table 2. Characteristics of the seven meteorological stations used to compute regional climate for the Lake Duparquet region.

| Station | Location | Distance from Duparquet Station (km) | Elevation (m asl) | Period of Records | Missing Data (%) | ¹ Mean Annual Temperature (°C) | ¹ Mean Annual Precipitation (mm) |
|-----------------|--------------------|--------------------------------------|-------------------|-------------------|------------------|---|---|
| Abitibi Post | 48°23'N 79°22'W | 16.6 | 259 | 1896–1936 | 7.3 | n.a. | n.a. |
| Amos | 48°34'N 78°07'W | 84.9 | 305 | 1913–1997 | 5.7 | 1.56 | 806.7 |
| Duparquet | 48°31'N 78°16'W | 0 | 290 | 1981–1994 | 11.9 | 1.45 | 855.1 |
| Iroquois Falls | 48°45'N 80°40'W | 106.2 | 259 | 1913–1997 | 2 | 1.06 | 653.7 |
| Kinojevis | 48°13'N 78°52'W | 44.6 | 290 | 1974–1994 | 12.8 | 2.01 | 748 |
| LaSarre | 48°48'N 79°12'W | 31.9 | 274 | 1951–1977 | 5.6 | n.a. | n.a. |
| | 48°47'N 79°06'W | 32.1 | 290 | 1978–1983 | 18.8 | n.a. | n.a. |
| | 48°47'N 79°13'W | 29.9 | 244 | 1983–1997 | 11.1 | ² 0.70 | ² 795.3 |
| Val St-Gilles | 48°59'N 78°07'W | 99.1 | 290 | 1973–1997 | 11.8 | 0.22 | 722.4 |
| Harricana River | 48°34'N 78°07'W | 84.9 | ³ 3680 | 1915–1933 | 0 | n.a. | n.a. |
| | 48°36'N 78°06'W | 86.5 | ³ 3680 | 1933–1997 | | n.a. | n.a. |

¹Both annual mean temperature and total precipitation are from the reference period 1981–1990.

²1983–1990.

³Watershed area (km²).

the regional climatic series (Holmes 1992). The regional climatic series were highly correlated with both Duparquet (1981–1994) and LaSarre (1951–1977 and 1983–1997) data with a respective mean correlation (r) for temperature of 0.99, 0.96 and 0.99 and a respective mean correlation (r) for precipitation of 0.84, 0.89, and 0.92. A period of 17 months, from May of the previous growing season to August of the current growing season, was used in all analyses.

(b) Tree-Climate Response to Environment

To analyze the homogeneity of the climatic responses at the tree level and their relations to environmental factors, canonical correspondence analysis (CCA) was used (ter Braak and Smilauer 1998). CCA is the canonical form of correspondence analysis (CA) and allows the simultaneous

analysis and direct comparison of the two data matrices (Legendre and Legendre 1998). CCA is a combination of ordination and multiple regression with external (environmental) variables (ter Braak and Smilauer (1998). In canonical ordination, the regression model is inserted in the ordination model. To establish our first data matrix, Pearson's correlations were calculated between each of the 70 individual trees residual chronologies and the climatic variables (see previous section). All correlations significant at $p < 0.1$ were transformed into four categories using their significance level ($p < 0.1 = 1$, $p < 0.05 = 2$, $p < 0.01 = 3$ and $p < 0.001 = 4$). This procedure was needed because there was no common interval of sufficient length among the 70 chronologies. When inverse coefficient signs were observed for the same variable, the variable was duplicated (e.g. November temperature: negative and positive effect on growth).

Table 3. General statistics for each of the seven tree-ring chronologies. BEpa: *Betula papyrifera*; ABb: *Abies balsamea*; THo: *Thuja occidentalis*; PIg: *Picea glauca*; PIm: *Picea mariana*; PNb: *Pinus banksiana* and PNr: *Pinus resinosa*.

| | BEpa | ABb | THo | PIg | PIm | PNb | PNr |
|--------------------------------------|-----------|-----------|-----------|-----------|-----------|-----------|-----------|
| Chronology Length | 1851–1997 | 1878–1997 | 1865–1997 | 1869–1997 | 1897–1997 | 1824–1997 | 1828–1997 |
| Number of trees | 10 | 10 | 10 | 10 | 10 | 10 | 10 |
| Number of radii | 38 | 27 | 20 | 30 | 36 | 28 | 26 |
| Mean ring width (mm) | 0.78 | 1.44 | 0.89 | 1.52 | 1.11 | 1.4 | 1.4 |
| Means sensitivity | 0.34 | 0.28 | 0.18 | 0.17 | 0.22 | 0.18 | 0.22 |
| Standard deviation | 0.31 | 0.27 | 0.17 | 0.16 | 0.2 | 0.16 | 0.19 |
| Variance due to auto-regression (%) | 27.1 | 26.3 | 19 | 3.9 | 14.9 | 6 | 18.6 |
| ARMA model (AR) | 3 | 1 | 1 | 1 | 1 | 1 | 1 |
| Common interval analysis (1955–1997) | | | | | | | |
| Number of trees | 9 | 9* | 10 | 9 | 10 | 10 | 9 |
| Number of radii | 33 | 21 | 20 | 21 | 18 | 23 | 17 |
| Signal to noise ratio | 5.73 | 4.02 | 4.11 | 3.47 | 4.38 | 6.6 | 5.37 |
| Variance in PC1 (%) | 44.95 | 39.97 | 35.41 | 36.07 | 38.02 | 44.66 | 43.92 |
| Expressed population signal | 0.85 | 0.8 | 0.8 | 0.78 | 0.81 | 0.87 | 0.84 |
| Intercore correlation | 0.41 | 0.34 | 0.3 | 0.31 | 0.31 | 0.41 | 0.39 |
| Intertree correlation | 0.39 | 0.31 | 0.29 | 0.28 | 0.3 | 0.4 | 0.37 |
| Intratree correlation | 0.64 | 0.71 | 0.52 | 0.64 | 0.44 | 0.6 | 0.68 |

*Common interval 1965–1997.

Only variables having at least three occurrences were kept for the analysis. In addition to regional climate, mean monthly discharge data from the Harricana River was used in the analysis (Table 2). The Drought Code of the Canadian Forest Fire Behavior System (Turner 1972) was also calculated using daily data from the Iroquois Falls meteorological station. Compared to the Palmer drought severity index, the Drought Code is a daily parameter and represents the water content of the deep humus layers and is particularly well adapted to the conditions found in the boreal forest of Canada. Many days of heavy rains are necessary to reduce the Drought Code to zero, while its exponential drying constant is 52 days (Turner 1972). The daily drought indices from May to September were averaged to produce monthly mean drought indices.

In this analysis, we considered as environmental variables (second data matrix) both abiotic and biotic factors that we assumed could be related to the tree's response to climate. The environmental variables used were tree species (seven classes), genus *Pinus* and *Picea* (2 classes), tree age, tree DBH, tree height, mean sapwood width, mean distance and DBH of the nearest tree in four quad-

rants (two variables), understory species cover, mean length of the lowest four living branches, slope, slope aspect, xeric-mesic (one class) and spatial coordinates (third-degree spatial polynomial of X and Y coordinates; see Legendre and Legendre 1998). In the matrix, all classes of the qualitative environmental variables were transformed into dummy binary variables (ter Braak and Smilauer 1998). A forward selection of environmental variables and a Monte Carlo permutation test of significance (999 iterations) were used to select only significant environmental variables ($p < 0.05$). In this analysis, each tree was considered as a sample and each correlation to climate as a descriptor (Mode R; see Legendre and Legendre 1998).

RESULTS

Chronology Statistics

The general statistics calculated for each species chronology revealed that all species, except *B. papyrifera*, shared similar characteristics (Table 3). The mean sensitivity and standard deviation of the *B. papyrifera* residual chronology were highest

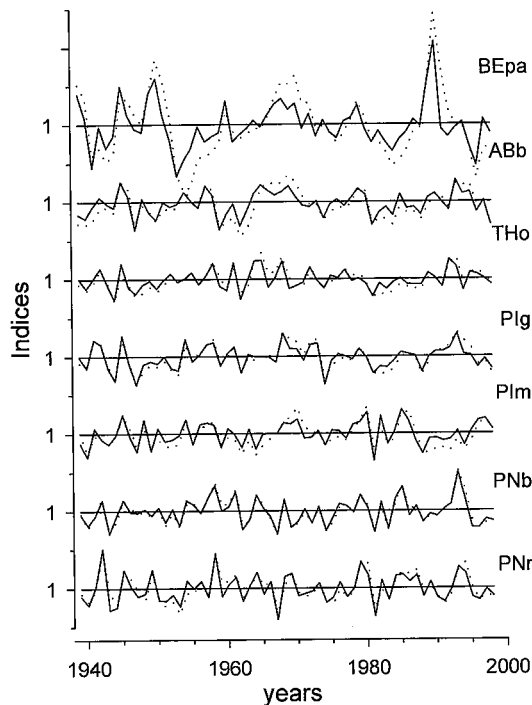


Figure 2. The seven species tree-ring chronologies for the period 1938–1997. The standard chronologies are represented by dotted lines and the residual chronologies by solid lines. BEpa: *Betula papyrifera*; ABb: *Abies balsamea*; THo: *Thuja occidentalis*; Plg: *Picea glauca*; Plm: *Picea mariana*; PNb: *Pinus banksiana* and PNR: *Pinus resinosa*.

compared to the other chronologies. Comparison for the common period 1955–1997 revealed comparable statistics among species (Table 3). Tree-ring indices from different cores within trees were similarly correlated except for *P. mariana* which showed more variability. Chronologies with the highest percentage of variance held in common were from *B. papyrifera*, *P. banksiana* and *P. resinosa*. The similarities among the coniferous species is further emphasized by the numerous shared years with high and low growth indices (Figure 2).

Species Response to Climate

The first four eigenvalues of the PCA explained respectively 49.8, 14.7, 12.0 and 10.5% of the total variance in the original data set. These four components were determined to be meaningful after comparing the sum of their eigenvalue with that

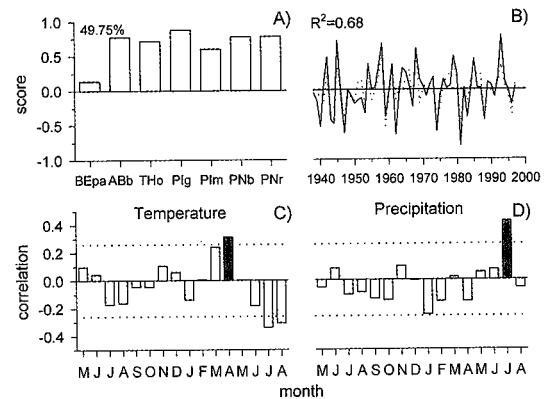


Figure 3. Species (A) and years (B) scores from the first component of the principal component analysis. The dark dotted line represents the estimated scores derived from the bootstrapped response function model. The model r -squared value is indicated. Correlation coefficients between radial growth indices and mean monthly temperature (C) and total monthly precipitation (D). The dotted lines indicate the $p < 0.05$ level of significance and the filled bars indicate significant climatic variable selected by the bootstrapped response function.

of the broken stick model. Only the first two components however will be presented here. The loadings for PC-1 were all positive, indicating that the growth patterns were correlated among the seven species chronologies (Figure 3a). However, *B. papyrifera* has a lower correlation with PC-1, whereas all the conifer species presented large and positive loadings. The radial growth-climate model derived from the bootstrapped response function was highly significant (Figure 3b). Scores from PC-1 were negatively correlated with July–August temperature of the current growing season (Figure 3c,d). April temperature and July precipitation of the current year were positively correlated to growth. These results indicate that the growth of conifer species was best during years with warmer springs and cooler-wetter July.

The second component revealed that *B. papyrifera* had a large positive loading compared to the other species (Figure 4a). Again, the radial growth-climate model derived from the bootstrapped response function was highly significant (Figure 4b). The scores from PC-2 were positively correlated to June precipitation of the current year (Figure 4d). This suggests that *B. papyrifera* growth was higher when early growing seasons

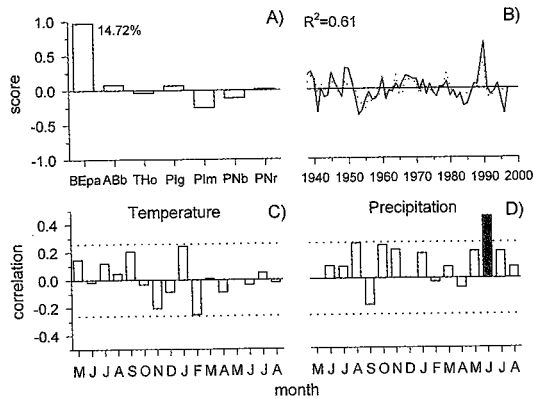


Figure 4. Species (A) and years (B) scores from the second component of the principal component analysis. The dark dotted line represents the estimated scores derived from the bootstrapped response function model. The model r-squared value is indicated. Correlation coefficients between radial growth indices and mean monthly temperature (C) and total monthly precipitation (D). The dotted lines indicate the $p < 0.05$ level of significance and the filled bars indicate significant climatic variable selected by the bootstrapped response function.

were wetter than normal. The similarities among the coniferous species was further highlighted by the correlation functions calculated for the seven residual chronologies (not presented). Again, the importance of warm early spring and wet July was stressed. Among the coniferous species, *P. glauca*, *P. banksiana* and *P. resinosa* showed the strongest relation with temperature in early spring. The climatic response of *B. papyrifera* was also shown to be different from conifers; both June and July precipitation was significantly correlated to radial growth.

Individual Tree Response to Climate

The correlation functions calculated between the 70 individual tree residual chronologies and the climatic variables showed that July precipitation of the current year was the variable most often correlated with radial growth indices (Figure 5). About 45% of all trees had a positive relationship with July precipitation, with both *A. balsamea* and *P. mariana* trees having the highest relative frequency (90%). In only 21 cases did 50% or more of the trees show the same response to a climate variable. In only one case were all 10 trees from

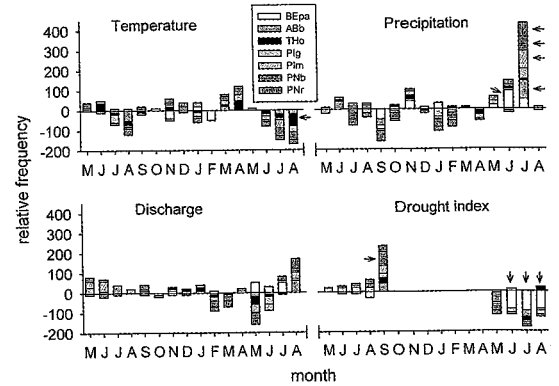


Figure 5. Stacked bar representing the relative frequency of trees/species showing significant Pearson's correlation coefficients ($p < 0.1$) with selected climatic variables. The arrows indicate when 60% or more of the trees in a species had a significant correlation with a given climatic variable. BEpa: *Betula papyrifera*; ABb: *Abies balsamea*; THo: *Thuja occidentalis*; Plg: *Picea glauca*; Plm: *Picea mariana*; PNb: *Pinus banksiana* and PNr: *Pinus resinosa*.

a single species significantly correlated with a given climatic factor. This was observed in *B. papyrifera*, with 100% of the trees showing a negative correlation with the July drought index (Figure 5). A positive correlation with June precipitation and negative correlation with June and August drought index were also observed in 90% of the *B. papyrifera* trees.

To assess if the observed variability in the cli-

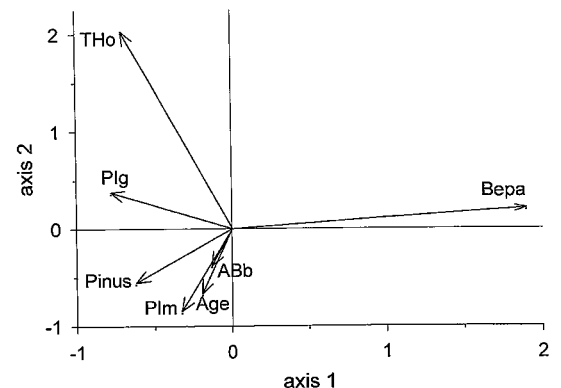


Figure 6. Biplot scores of environmental variables for the first and second axes of the CCA ordination. Length of the vectors indicates the strength of the correlation with the ordination axes and shows the maximum change for a variable. See Figure 5 to compare the variation among individual trees and species.

matic response of trees could be related to the environment of the tree, a canonical correspondence analysis (CCA) was conducted. The CCA was calculated using the matrix of correlations presented in Figure 5 and an environmental matrix (see methods). The CCA showed that a low percentage of variance was accounted for by the first two axes of the ordination which explained, respectively, 8.4% and 4.9% of the variance. Surprisingly, no ecological factors other than the species were related to variability in the climatic response of the trees (Figure 6). For example, the first canonical component was clearly related to *B. papyrifera*, emphasizing a negative correlation with temperature in November and February, a positive correlation with June precipitation and river discharge in May–June–July, and a negative correlation with high drought indices in June–July–August (see Figure 5). The CCA also revealed that both species in the genus *Picea* differed in their response to climate in contrast to the two *Pinus* species (Figure 5 and Figure 6). To better assess the variation among conifers, a second CCA was calculated after elimination of *B. papyrifera* (not presented). Again no variables other than the species were related to variation in the climatic response. The strong similarity between the climatic response of coniferous species was maintained.

DISCUSSION AND CONCLUSIONS

Species Responses to Climate

Our results indicate that climatic variation is important in controlling the radial growth of the seven tree species. About 50% of the variance was held in common by all species (58% when *B. papyrifera* was excluded) and much of it can be explained by variation in the regional climate. Species-to-species differences were unexpectedly minor except for *B. papyrifera*, the only deciduous species. The same pattern was true for the individual trees. Despite high variability in their response to climate, individual trees had responses that were generally similar to other individuals of the same species. Strong similarities among the species, with the exception of *B. papyrifera*, was also reported by Tardif *et al.* (2001) using band dendro-

meters installed on 40 of the 70 trees from present study.

B. papyrifera

B. papyrifera, a diffuse-porous species, responded strongly to precipitation in the early summer. The positive relation of *B. papyrifera* to June precipitation could relate to leaf expansion, which precedes radial growth in diffuse porous species. Tardif and Bergeron (1993) showed that black ash (*Fraxinus nigra*), a ring-porous species, is also strongly dependant on precipitation in June. Abundant precipitation in June is believed to result in greater photosynthesis and improved water conditions during the growing season. Similar findings have also been reported for more southern hardwood species such as sugar maple and American beech (Tardif *et al.* 2001). Radial growth indices of these species are also strongly correlated with precipitation in June. In contrast to these species, *B. papyrifera* may have, to a certain degree, indeterminate growth in which relatively few leaves emerge early in the growing season. This leaf growth is followed by a series of individual late leaves produced by gradually elongating shoot through the summer (Kramer and Kozlowski 1979; Lechowicz 1984). This may help explain why 90% of the *B. papyrifera* trees were negatively impacted by high drought indices during the growing season summer months (June–July–August).

Coniferous Species

In our study, the six coniferous species had a very similar response to climate, even though *P. resinosa* reaches its northern limit of distribution in Lake Duparquet area (Bergeron and Brisson 1990). The weak differences between the two *Pinus* species may indicate that this limit may not be due to a qualitative effect of climate on growth. The main climatic signal for all coniferous species came from July precipitation. Warm temperatures in early spring are also related to better radial growth. Holfgaard *et al.* (1999) also observed that early spring temperatures (March–April) are important for *P. banksiana* and *P. mariana* radial

growth. However, in our study *P. mariana* did not show a strong response to spring temperature. Our results illustrate that coniferous species are in better position to take advantage of an early growing season start. As observed by Graumlich (1993), warm temperatures in April may favor conifer species because their evergreen foliage allows them to take advantage of early growing season warmth.

The similar response to climate of the six conifer species is of particular interest for dendrochronological reconstructions of insect outbreaks, especially where species are compared that respond differently to climate (Swetnam *et al.* 1985). Our results showed that in an insular environment, the assumption of the similarity of the climatic response may hold true. The observed homogeneity of the climatic response may reflect the relatively uniform conditions occurring on the island.

These results are useful to attempt to predict the response of boreal tree species to climatic change. At this site, the coexistence of the seven species, except for *B. papyrifera*, was apparently not mediated by different response to climate. This was stressed by the highly significant correlations among the species and among tree chronologies produced from trees of different size and age. The similar growth pattern was also not due to a common disturbance, and microsite conditions are insignificant in controlling the species response to climate. Each species/tree occupies a given niche believed to be created or maintained by a given disturbance regime. On the island, traces of past forest fires (Bergeron and Brisson 1990) and insect outbreaks (personal observation) were reported. Bergeron *et al.* (1997) also showed that all seven species were potentially growing on all xeric islands of Lake Duparquet, their absence or presence being mainly related to a complex process of colonisation.

We speculated that any future change in climate may have a similar qualitative physiological effect on the growth of the coniferous species of our study site. For example, an increase in July temperature may affect all coniferous species in a similar way. However, the influence of climate on tree-ring chronologies appears to be mediated through the influence of a small number of years with extreme climate, rather than by changes in

mean conditions (Graumlich 1993). The absence of a strong quantitative effect of climate on radial growth makes it difficult to predict which coniferous species could gain or lose competitive advantage and how this may affect future stand composition. Only in *B. papyrifera*, because of its qualitatively different response to climate, could better predictions be made.

Widely used models predicting forest response to climatic change utilize relatively simple growing season temperature variables (*e.g.* growing degree-days, Shugart 1984; Pastor and Post 1988; Overpeck *et al.* 1990). Our results and those of Graumlich (1993) indicate that a finer differentiation with respect to the seasonal timing of warmth and precipitation is needed to better model species behavior. Both the qualitative and quantitative effect of climate on tree growth, disturbance regimes and the colonization processes may be needed to better simulate the impact of future climatic changes on forest dynamics.

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