

# Dendroclimatic analysis of *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* from an old-growth forest, southwestern Quebec

Jacques Tardif, Jacques Brisson, and Yves Bergeron

**Abstract:** Radial growth of three tree species (eastern hemlock, *Tsuga canadensis* (L.) Carrière; sugar maple, *Acer saccharum* Marsh.; and American beech, *Fagus grandifolia* Ehrh.) from an old-growth forest, in southwestern Quebec was compared using a dendroclimatic approach. The beech and maple tree-ring chronologies were significantly correlated, whereas the hemlock chronology was correlated only to that of beech. Radial growth of all three species was positively correlated with precipitation and negatively correlated with temperatures during the early summer months of the year the annual ring was formed. This suggests early summer water balance limits the growth of these species on this site. Radial growth of the three species was also negatively correlated with temperatures during the late summer months of the year prior to ring formation. Only hemlock and sugar maple showed a positive correlation with precipitation during the year prior to ring formation. Of the three species, hemlock was most influenced by temperature and showed a positive correlation with winter temperatures. Our results also showed that, since the mid-19th century, certain climatic variables temporarily dominated the growth–climate association of the species. Hemlock showed the most stable growth–climate association, whereas in sugar maple, negative correlations with late winter temperature showed up during the second half of the 20th century.

**Résumé :** L'accroissement radial de trois espèces arborescentes (pruche de l'est, *Tsuga canadensis* (L.) Carrière; érable à sucre, *Acer saccharum* Marsh.; et hêtre, *Fagus grandifolia* Ehrh.) d'une vieille forêt du sud-ouest du Québec a été comparé à l'aide de l'approche dendroclimatique. Une corrélation significative a été observée entre les chronologies du hêtre et de l'érable alors que celle de la pruche était faiblement corrélée à celle du hêtre. La croissance des trois espèces est positivement corrélée avec les précipitations et négativement corrélée avec les températures du début de l'été. Cela suggère que pendant l'année de formation des cerne, le bilan hydrique limite l'accroissement sur ce site. La croissance des trois espèces est aussi négativement corrélée aux températures de la fin de l'été précédant la formation du cerne. Seul l'érable et la pruche montrent une corrélation positive avec les précipitations de l'année précédente. Des trois espèces, la pruche est la plus fortement reliée aux températures et une corrélation positive avec les mois d'hiver fut observée. Nos résultats démontrent aussi que depuis la milieu du 19<sup>e</sup> siècle, la réponse climatique des espèces a été temporairement dominée par certaines variables climatiques. La pruche montre une grande stabilité des relations cerne-climat alors que chez l'érable à sucre, la deuxième moitié du 20<sup>e</sup> siècle est caractérisée par l'apparition de corrélations négatives avec les températures de la fin de l'hiver.

## Introduction

One objective of dendroclimatology focuses on the use of tree-ring width to gain information about long-term variation in climate. To be successful, old trees that are sensitive to

climatic factors are needed. In the deciduous forests of northeastern America, relatively few sensitive tree-ring chronologies of reasonable length have been developed (Cook 1982; Phipps 1982; Cook and Sheppard 1988; Delwaide and Fillion 1999). The impact of forest disturbances since settlement has been so great that forest stands older than 150 years are exceptional.

In northeastern North America, radial growth of trees has been reported to be less sensitive to climate, because climate is believed to be less limiting to growth than in southwestern North America (Fritts 1976; Phipps 1982). Factors like nutrient availability and stand competition are thought to obscure the climatic response of trees compared with the more arid southwestern United States. However, Graumlich (1993) found that climate was an important factor influencing the radial growth of 11 northeastern tree species growing at sites not traditionally perceived to be highly limited by climate. In northeastern North America, eastern hemlock (*Tsuga canadensis* (L.) Carrière) is considered an important tree species for dendroclimatic studies. The species has proved to

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**J. Tardif<sup>1,2</sup> and Y. Bergeron.** Groupe de recherche en écologie forestière interuniversitaire (GREFI), Université du Québec à Montréal, C.P. 8888, succursale Centre-Ville, Montréal, QC H3C 3P8, Canada.

**J. Brisson.** Institut de recherche en biologie végétale, 4101 rue Sherbrooke est, Montréal, QC H1X 2B2, Canada.

<sup>1</sup>Corresponding author.

<sup>2</sup>Present address: Centre for Forest Interdisciplinary Research (C-FIR), University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada (e-mail: [j.tardif@uwinnipeg.ca](mailto:j.tardif@uwinnipeg.ca)).

be sensitive to climate and suitable for climatic reconstruction (Lyon 1943; Avery et al. 1940; Cook 1982; Cook and Cole 1991) and can also live up to 800 years (Godman and Lancaster 1990). Sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) were also observed to be sensitive to climate (Diller 1935; Friesner and Friesner 1942; Fritts 1958, 1959, 1962; Graumlich 1993; Yin et al. 1994; Payette et al. 1996). Both species are characteristic of the northeastern hardwood forest and can live to more than 300 years (Godman et al. 1990; Tubbs and Houston 1990).

In southern Quebec, few old tree ring chronologies have been developed. The discovery of an old-growth beech–maple forest of presettlement origin, the Bois -des-Muir forest (Brisson et al. 1992), makes it possible to evaluate how the major tree species of the northern hardwood forest responded to climate fluctuations over the past 150 years. The goals of this study were twofold. The first objective focussed on the identification of the principal climatic factors influencing the radial growth of three major tree species of the northern hardwood forest near the northern limit of their ranges. Of the three species, American beech and eastern hemlock are closest to their northern distribution limit; beech has the most southern one, whereas sugar maple has the northernmost range. Thus, we hypothesized that temperature may be more limiting to radial growth of beech and hemlock than in sugar maple. Our second objective was to assess the temporal stability of the climatic response of the three species. It was hypothesized that each species would respond individually to periods in which extreme climatic conditions may have occurred since the end of the mid-19th century. To assess the stability of the radial growth – climate association will allow (i) better characterization the climatic response of each species and (ii) evaluation of the importance of this constraint in future climatic reconstruction (Tessier 1989; Nola and Bracco 1991; Briffa et al. 1998; Biondi 2000).

## Methods

### Study area

The Bois -des-Muir forest is an 11-ha old-growth forest located 70 km southwest of Montr al (45°28'N, 74°17'W) in the Haut-Saint-Laurent region of Quebec (Fig. 1). This region is characterized by extensive lowlands covered by clays deposited in Champlain Sea between 12 000 and 10 000 years BP. These lowlands are interrupted by moraines, glacial depressions, and zones of marine alteration. The clay plain has been entirely deforested for agricultural uses, while morainic deposits still support forest communities. These forests, generally of small area, have suffered anthropogenic disturbances of varied intensity and nature since European settlement, some 200 years ago (Brisson et al. 1988; Bouchard et al. 1989). Forests of the uplands, mostly of second- or third-growth origin, are dominated by sugar maple accompanied by bitternut hickory (*Carya cordiformis* (Wang.) K. Koch), basswood (*Tilia americana* L.), ironwood (*Ostrya virginiana* (Mill.) K. Koch), black cherry (*Prunus serotina* Ehrh.), white ash (*Fraxinus americana* L.), and others (Brisson et al. 1992). The Bois -des-Muir is the only forest of presettlement origin recognized so far in the region. It is located on a morainic ridge, with mostly mesic site conditions but with a few wet depressions. It is dominated by sugar maple and American beech, accompanied by ironwood, basswood,

and hemlock. The understory is typical of a beech–maple forest, with a low percentage of ground cover, and the presence of acidophilic species such as *Polystichum acrostichoides* (Michx.) Schott. and *Maianthemum canadense* Desf.

The forest has been exceptionally well protected from major human disturbance since the time of settlement; only very restricted partial cuts have occurred, especially between 1820 and 1830 (Brisson et al. 1992). The Bois -des-Muir forest is now an Ecological Reserve, a status that provides maximum legal protection, only allowing research or education activities with permission of the minist re de l'Environnement du Qu bec (1983). Before 1990, there were no signs of recent large-scale natural disturbances, like major windthrow, fire, maple dieback, or beech bark disease. However, high mortality of American elms (*Ulmus americana* L.) because of the Dutch elm disease was observed in few wet depressions of the forest (Brisson et al. 1994). The larger canopy trees range in age from 150 to more than 300 years. Many of the larger trees, especially beech, had rotten heartwood and consequently could not be aged. Large dead trees were scattered throughout the forest as snags or fallen logs with intact or highly decomposed wood. In 1990, the first signs of beech bark disease were noted, and since then, the disease has progressed. In January 1998, a severe ice storm caused major damage, the majority of the maples and beeches lost more than 25% of their canopies, while hemlock was little affected.

The nearest meteorological station is at Huntingdon, about 5 km to the west (Fig. 1). The mean annual temperature and total precipitation are, respectively, 6.5°C and 1006.9 mm for the years 1961–1990. The mean temperature reaches a high of 21°C in July and a minimum of –9.5°C in January. About 78% of the precipitation occurs as rainfall. The mean frost-free period at Huntingdon is 140 days (Environment Canada 1993).

### Data collection and dendroclimatic analyses

The Bois -des-Muir forest was sampled in both 1987 and 1994. One to four cores were collected per tree with a Haglof increment borer. All the samples were prepared following the standard method in dendrochronology (Stokes and Smiley 1968). Cores from the same tree were dated and visually cross-dated using pointer years to identify either false or incomplete rings. Only in hemlock were incomplete rings observed. Cross dating is performed to insure accuracy in the assignment of annual growth rings to the year each was formed. Ring widths were then measured to 0.01 mm with a VELMEX measuring system. Tree-ring width values for each core were graphed, periods of anomalous suppression or release from growth were eliminated, and the series was split (Blasing et al. 1983). The few missing rings that had originated from broken cores during the 1987 sampling were estimated using the measurements made from another core from the same tree. Using a 10-year window (5 years before and 5 after a core break), each annual value from the dependent series was divided by the corresponding value of the reference series. After calculating the mean ratio, the missing value was estimated by multiplying this ratio with the measurement value of the reference series. Data quality was further validated with program COFECHA, which calculates cross correlations between individual series and an average chronology (Holmes 1992). The cores that were poorly correlated with the mean chronology, or had higher correlations when the dating of the core chronology was shifted, were rechecked and either corrected or eliminated.

To extract the age-related trend and the nonclimatic signal, each measurement series was standardized using a spline function with a 50% frequency response of 50 years (Cook and Peters 1981). Standardization involved transforming ring-width values into dimensionless index values by dividing the observed ring-width values by the expected values (Fritts 1976) given by the spline

function. This procedure retained high-frequency variations (interannual to decadal), whereas other low-frequency trends were eliminated. Autoregressive modelling was also performed on each standardized series to remove temporal autocorrelation and make the observations independent, a condition necessary for most statistical analyses (Legendre and Legendre 1998). To diminish the effect of endogenous stand disturbances and to enhance the common signal, all residual series were averaged by species using a biweight robust mean. These procedures were conducted using program ARSTAN (Cook 1985) and resulted in the production of one residual tree-ring chronology for each species. The maple residual chronology covered the period 1768–1993 and was composed of 37 trees and 67 radii. The beech residual chronology covered the period 1771–1994 and was composed of 17 trees and 32 radii. The hemlock residual chronology spanned from 1693 to 1994 and was composed of 23 trees and 49 radii.

Climatic responses in each of the three species was investigated with both bootstrapped response function and correlation analyses (Fritts 1976; Guiot 1993; Briffa and Cook 1990). Calculations were done with the empirical model PRECON (version 5.16), which included a bootstrap method to estimate the standard error of the response function weight (Fritts et al. 1991). The bootstrapped response function provided an alternative approach to test the significance and stability of the regression coefficients within a specific time period. Mean regression coefficients were considered significant if they were at least twice their standard deviation after 999 bootstrapped iterations. Pearson correlations between climate variables and the tree-ring chronologies were also computed for comparison. Because of the limitations inherent in PRECON (i.e., a maximum 100 years of data), the climatic analysis was conducted for the period 1888–1987.

To assess the temporal variability in the radial growth – climate associations, correlations for each species were calculated and compared for successive 50-year segments shifted by 10 years. The purpose of this analysis was to determine if the species registered any temporal changes in their climate response and to address any patterns that may appear. Temporal variation in the climatic response could be related to short-term effects of a few extreme climate events or to longer term changes related to climate change or to stand dynamics.

Meteorological data from 19 stations were used to compute the regional mean monthly temperature and total monthly precipitation for the period 1841–1994 (Fig. 1). These stations were the closest ones and were located within 5–66 km from our site (i.e., Huntingdon and McGill stations, respectively) with a mean of 33 km. Program MET from the PROGLIB library (Holmes 1992) was used to compute the regional climatic series. For each station, monthly variables were transformed into normalized standard deviation (departure) to give each station the same weight in calculating the regional mean value for each month and year. When station relocation or a recording interruption occurred, the station was split and considered as different stations. The McGill station located in the city of Montréal was also split in 1939 to minimize the effect of warming caused by increasing urbanization in the second half of the 20th century. The association between the regional mean temperature and the Huntingdon data is illustrated in Fig. 2. Huntingdon data showed a strong warming trend compared with the regional climatic series. Both data sets also showed a decrease in the interannual variation of mean annual temperature after the 1940s. To further assess the validity of the monthly regional series, cross correlations were computed with the Huntingdon station using all available monthly data from the periods 1870–1891, 1913–1918, and 1951–1991 (mean  $r$  for temperature = 0.92, all  $p$  = 0.0001, mean  $r$  for precipitation = 0.85, all  $p$  = 0.0001). Monthly data from May of the preceding growing season ( $t - 1$ ) to August of the current growing season ( $t$ ) were used as predictands. When

missing data occurred in the regional series, these were estimated using the mean of that month.

## Results

### Chronologies and descriptive statistics

The residual chronology of all three species showed that interannual variation of radial growth has decreased since the late 1800s (Figs. 3 and 4A). Mean sensitivity is the average difference between successive ring index values. There is a tendency for mean sensitivity to decrease with age. However, the mean sensitivity of all three species increased synchronously during the mid-1800s and then decreased synchronously after the 1871–1920 peak (Fig. 4A). The hemlock residual chronology exhibited greater interannual variation in ring width (mean sensitivity and standard deviation) and more common variation among individual trees (VFE, and intertree correlation) than the hardwood species (Table 1). These comparisons suggest that, in hemlock, radial growth may have been more influenced by climate than in the other two species.

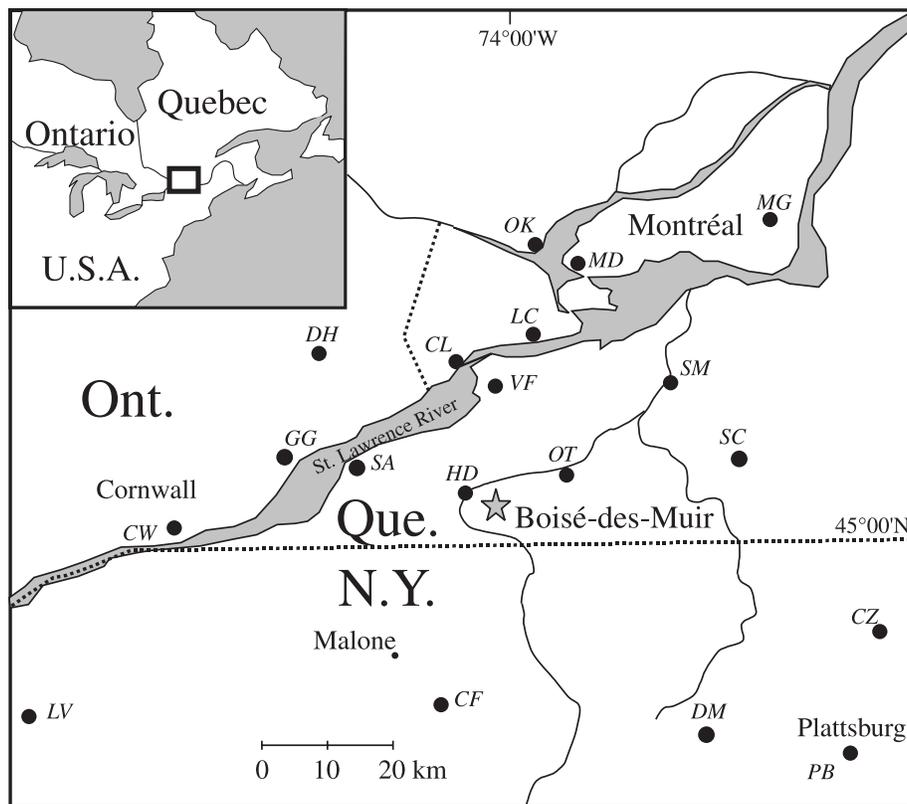
The Pearson correlations calculated for the entire 1888–1987 period showed that mean chronologies for the three species were significantly correlated (maple–beech:  $r$  = 0.644,  $p$  = 0.0001; maple–hemlock:  $r$  = 0.239,  $p$  = 0.017; and beech–hemlock:  $r$  = 0.452,  $p$  = 0.0001). Maple and beech chronologies were also significantly correlated for most 50-year periods during this time span (Fig. 4B). Correlations between maple and hemlock chronologies were rarely significant for these 50-year periods. Correlations between beech and hemlock continuously increased over the period of record and were significant after 1860. All correlations with the sugar maple chronology also showed a pronounced decrease around the 1921–1970 segment (Fig. 4B). Before 1825, the low number of cores included in the hardwood chronologies precluded any interpretation.

### Radial growth – climate relationship

The bootstrapped response function calculated for the period 1888–1987 explained close to 54% of the variance in the species residual chronologies (Fig. 5). The good fit of the models was further illustrated in Fig. 6, which shows the species' residual chronologies and the estimated series developed from their response to climate. During the 1888–1987 period, all three species shared a common negative correlation with the July–August temperature of the year prior to ring formation and with the June temperature of the year the growth ring was formed (Fig. 5). The significant positive relationship with the current June precipitation was observed in both response and correlation functions (Fig. 5).

Certain aspects of the growth–climate association differed among the species. Hemlock showed a positive association with July precipitation of the year prior to ring formation (Fig. 5C). Hemlock was also characterized by a positive correlation with warm winters (January–March). The species also showed a negative relationship with December and March snowfall ( $r$  = -0.207,  $p$  = 0.021,  $n$  = 124 and  $r$  = -0.196,  $p$  = 0.026,  $n$  = 128, respectively). At the Huntingdon meteorological station for the reference period 1961–1990, snowfalls represented 60.5 and 49.6%, respectively, of the

**Fig. 1.** Location of the Bois -des-Muir forest and the 19 meteorological stations. The star is the study site, and the solid circles are the meteorological stations. LC, Les C dres; CF, Chasm Fall; CZ, Chazy; CW, Cornwall; CL, Coteau-du-Lac; DH, Dalhousie; DM, Dannemora; GG, Glen Gordon; HD, Huntingdon; LV, Lawrenceville; MD, MacDonald; MG, Montr al (McGill); OK, Oka; OT, Ormstown; PB, Plattsburg; SA, St. Anicet; SC, St. Clothilde; SM, Ste. Martine; VF, Valleyfield.



**Table 1.** General statistics characterizing the *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* chronologies.

	<i>Acer</i>	<i>Fagus</i>	<i>Tsuga</i>
<b>Species-specific interval analyses</b>			
Time span	1768–1993	1771–1994	1693–1994
No. of trees (radii)	37 (67)	17 (32)	23 (49)
Mean ring width	1.66	1.51	0.9
Mean sensitivity	0.25	0.19	0.32
SD	0.21	0.17	0.27
VA (%)	24.4	4.6	13.5
AR model	1	1	1
<b>Common interval analysis (1900–1984)</b>			
No. of trees (radii)	22 (34)	8 (16)	14 (23)
VFE (%)	36.02	43.15	47.81
APC	0.914	0.818	0.916
Intertree correlation	0.326	0.36	0.437

**Note:** Mean correlation between trees of the same species is also presented. VA, variance resulting from autocorrelation; AR, order of the autoregressive model; VFE, variance in first eigenvector; APC, agreement with population chronology.

total precipitation. Warm temperature in May was also negatively correlated with radial growth, whereas July precipitation was positively correlated (Fig. 5C). Beech had the lowest number of significant correlations with climate. This species was characterized by a unique positive correlation

with April temperature (Fig. 5B). Maple had a unique positive association with August precipitation during the year prior to ring formation (Fig. 5A). Radial growth of maple also presented a negative correlation with wet April–May and cold May periods.

#### Stability of the growth–climate correlations

The correlation functions calculated for each 50-year period indicated for all three species that the early summer conditions (June–July) of the year the annual ring was formed as well as the late summer conditions (July–August) of the year prior to ring formation were frequently correlated to radial growth (Fig. 7). The positive correlations between radial growth in hemlock and temperature from early to late winter (December to March) were also significant for many periods. Despite these similarities, results indicated that the species' growth–climate association was not fully stable. Few significant correlations were constantly observed since the mid-19th century (Fig. 7). In maple, the correlation with temperature in July prior to ring formation and precipitation in May and June of the year the annual ring was formed were observed in 62, 46, and 62%, respectively, of the periods (Fig. 7A). The climatic response of beech showed less consistency with the correlation with June precipitation of the current year occurring in 46% of the periods (Fig. 7B). The growth–climate association of hemlock was more consistent with temperature in July of the preceding year and March and May of the current year being correlated in 54,

92, and 54% of the periods, respectively. The relationship with July precipitation of the current year also showed in 54% of the periods (Fig. 7C).

To examine the temporal variation of the growth–climate association, the full set of significant correlations from Fig. 6 was subjected to a correspondence analysis (CA). When inverse correlations occurred for a given monthly variable (see March temperature), two variables were created (March positive and negative). A “temporal walk” was then constructed by joining the period in chronological order in the plan supported by the two first axis of the CA (Fig. 8). This allows comparison of the temporal evolution of the radial growth – climate association within and among species. The results showed that the climate response of the three species varied since the mid-19th century. The first axis of the CA was related to sugar maple response and clearly separated the periods prior to 1911–1960 from the later ones. Radial growth in sugar maple presented an increasing negative correlation with warm late winter temperatures beginning in the second half of the 20th century (Fig. 7A). A shift was also observed from March to February temperature being negatively associated with radial growth. The negative correlation with precipitation in May became stronger in later periods, while the strength of the positive correlation with July precipitation decreased over time (Fig. 7A).

The results indicated that, until the period 1891–1941, both maple and beech had similar responses to climate. This was illustrated by the proximity of these species on the CA ordination (Fig. 8). During these intervals, the current June temperatures and July precipitation were more highly correlated to growth (Figs. 7A and 7B). In the last half of the 20th century, it was observed that June precipitation became more limiting to beech growth. In contrast to the hardwood species, the climate response of hemlock was less variable (Figs. 7C and 8). However, it was observed that temperature in the previous year (July–August) had stronger correlation beginning in the 1921–1970 period. During the same intervals, the strength of the positive correlation with January temperatures and the negative correlation with February precipitation increased (Fig. 7C).

## Discussion

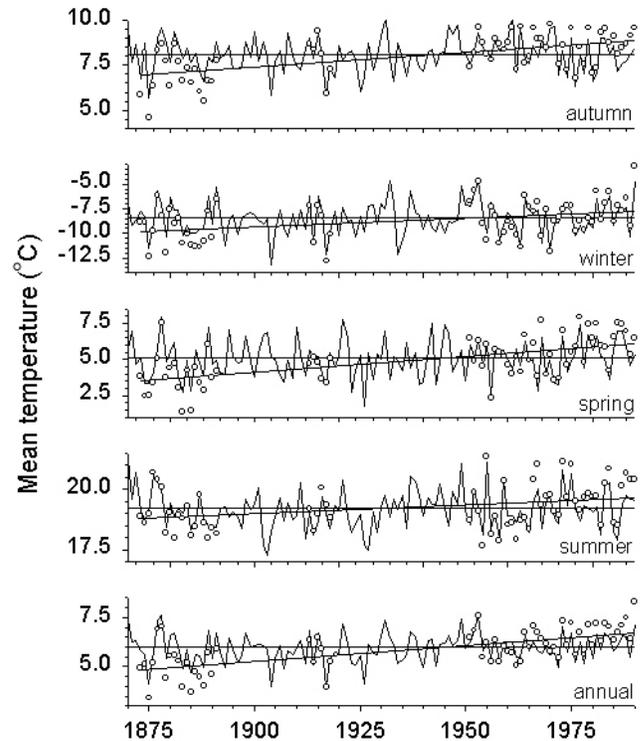
The chronology statistics calculated for the three species were comparable with those published for eastern North America (e.g., Phipps 1982; Graumlich 1993; Payette et al. 1996; Tardif and Bergeron 1997). However, in this study, mean sensitivity in hemlock was slightly higher than those reported by other researchers (Cook 1976; Delwaide and Fillion 1999). Our results also supported those of Graumlich (1993) who found that beech and maple shared a similar response to climate compared with hemlock, which occupied a unique position between the mesic hardwoods and the xeric conifers.

### Radial growth – climate associations

#### *Eastern hemlock*

At the Bois -des-Muir, hemlock radial growth was significantly correlated with temperature. Winter temperature may also become limiting near the northern range of the species.

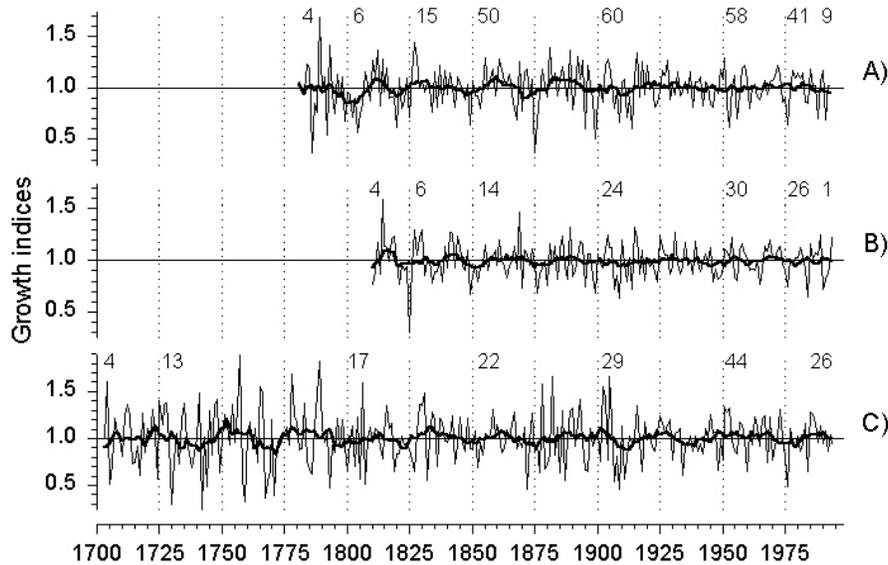
**Fig. 2.** Mean temperature calculated using data from 19 meteorological stations (solid line) and the Huntingdon meteorological station (open circles). Standard meteorological seasons were used: winter is December to February dated by the year of January. The regression was calculated using Huntingdon data and showed an increase in temperature from 1870 to 1990.



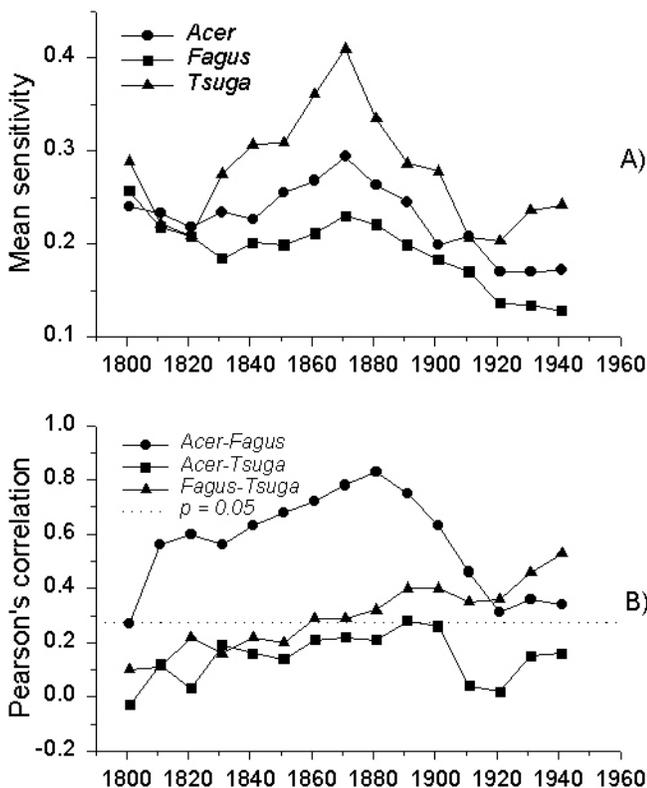
This contrasts with findings of Kavanagh and Kellman (1986) who suggested that hemlock may not be limited by temperature near its northern edge in central Ontario because of a preference for westerly and northerly facing slopes. Our results indicated that radial growth was limited by warmth during the previous year summer (July–August), by cold temperature during winter – early spring (January–March) and by warm May temperatures. Gove and Fairweather (1987) also observed a similar relationship with January–March temperatures. Hemlock responded positively to the previous July precipitation and the current June–July precipitation, which could reflect the evapotranspiration demands during the growing season. Many studies reported negative relationships with moisture deficiency during the previous and current growing seasons (Lyon 1935; Cook and Jacoby 1977; Gove and Fairweather 1987; Abrams et al. 2000).

Cook and Cole (1991) in a dendroclimatic study conducted throughout most of hemlock geographic range reported that the species responded negatively to prior July temperatures and positively to March temperatures of the current year. These correlations were notably apparent in the northern portion of the species range. Above-average March temperatures could improve the thermal conditions by quickly removing snow cover and by allowing for an earlier-than-normal resumption of photosynthesis (Cook and Cole 1991). Our results showed that March snow precipitation was also negatively correlated to hemlock growth. In our re-

**Fig. 3.** Residual tree-ring chronologies for *Acer saccharum* (A), *Fagus grandifolia* (B), and *Tsuga canadensis* (C). The number of cores included is shown above the chronologies. The bold lines represent a 5-year weighted running mean to highlight the short-term fluctuations in the radial growth indices.



**Fig. 4.** Mean sensitivity for *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* (A) and cross correlation among the three species residual chronologies (B). Both mean sensitivity and Pearson correlations were calculated using 50-year segments lagged by 10 years. The mean sensitivity constitutes a measure of the relative change in ring index variation from year to year and is calculated as the absolute difference between adjacent indices divided by the mean of the two indices (Fritts 1976).

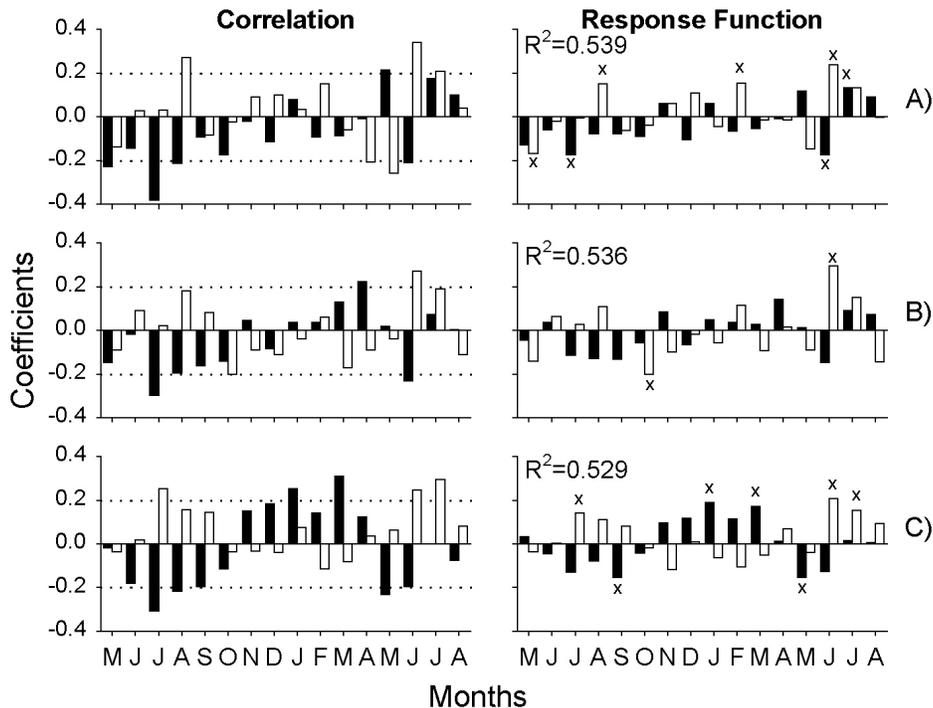


gion, about half of the precipitation in March may occur in the form of snow, and warmer March temperature may control the late accumulation of snow on the ground. According to Fraser (1956), the initiation of growth in hemlock appeared to be controlled by late winter and early spring temperatures, which controlled the spring warm-up of the soil. However, no relationship with winter temperatures was reported by Cook and Cole (1991), and this may reflect the absence of northern sites from their study.

*Sugar maple*

Our results strongly contrasted with those of Houle (1990) who reported no significant correlations between radial growth and climatic variables in sugar maple. Other studies, however, supported our results (Lane et al. 1993; Yin et al. 1994; Payette et al. 1996). At the Bois -des-Muir, a cool July and a wet August in the year prior to ring formation had a positive impact on radial growth. Reduced water stress in late summer could allow for supplementary accumulation of carbohydrate reserve (Lane et al. 1993). Our results also suggested that too much water in May would be detrimental to maple growth. The negative correlation with May precipitation was also reported by Payette et al. (1996) in numerous stands distributed throughout southern Quebec. Abundant precipitation during this period could lead to an excessive soil water content and, thus, lower growth. In the current year, the negative correlation with June temperature and positive correlation with June precipitation indicates that water stress influences growth during the early growing season. These results are consistent with those of Friesner and Friesner (1942) and Miller (1951) who observed that radial growth in sugar maples in Indiana had the highest correlation with June–July precipitation likely because of the much warmer and drier environment. Payette et al. (1996) also reported that July precipitation was most strongly related to sugar maple growth.

**Fig. 5.** Correlation and bootstrapped response function coefficients computed between the species residual chronologies and the climatic variables for (A) *Acer saccharum*, (B) *Fagus grandifolia*, and (C) *Tsuga canadensis*. Both analyses were calculated using data for 1888–1987. The dotted lines show significant correlations coefficients ( $p < 0.05$ ), and the bold X shows significant response function coefficients after 999 bootstrapped iterations. Solid bars are temperature, and open bars are precipitation.



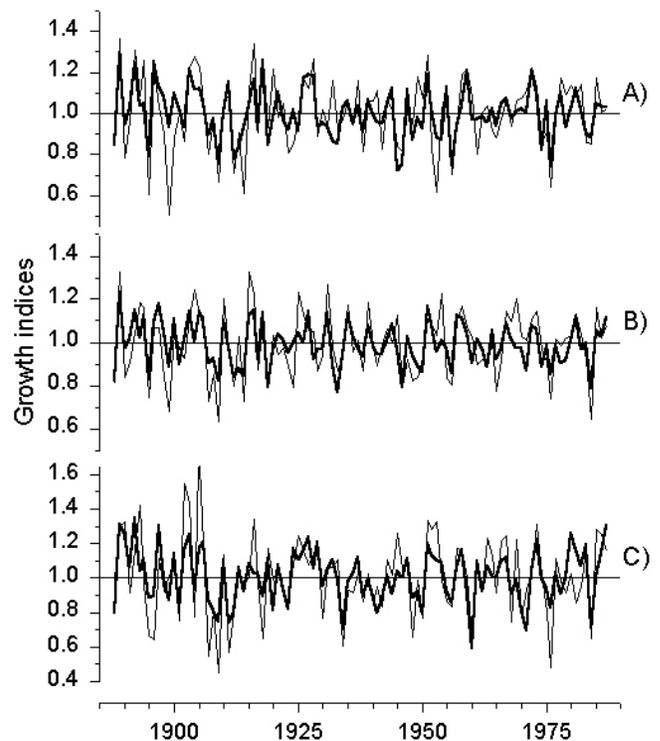
#### American beech

Unlike hemlock and maple, beech has determinate apical growth, and we expected that climate conditions at the time of bud formation during the prior year would have stronger influence on the amount of foliage, and therefore wood, produced the following year (Kozłowski and Pallardy 1997).

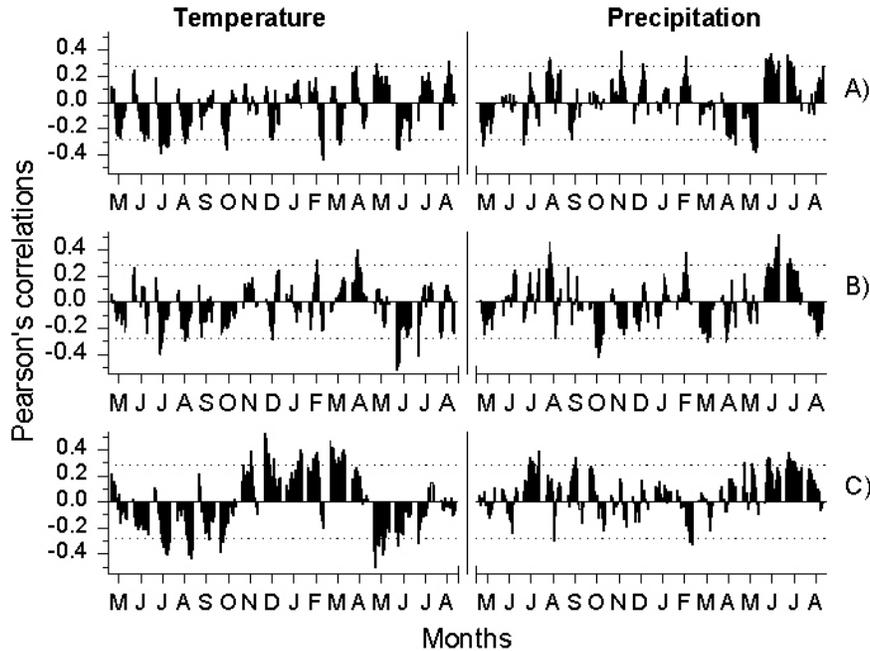
Unexpectedly, radial growth in beech was less strongly related to conditions of the preceding growing season compared with hemlock and maple. Only July temperatures showed a significant negative correlation. However, it was reported that drought years had strong effects on beech growth during the following season (Diller 1935; Fritts 1962).

Even though beech at the Boisé-des-Muir site is closer to its northern range limit than the other two species, radial growth was not significantly correlated with winter temperature. This contrast with Webb (1986) who suggested that beech range limit was determined by winter temperature. At our site, radial growth in beech appeared to be mainly controlled by June conditions. High June temperatures increased transpiration and, thus, have the same effect as a reduction in water supply (Diller 1935; Fritts 1958). Because of its determinate growth habit, beech achieves maximum leaf area early in the growing season (Kozłowski and Pallardy 1997). Beech also uses twice as much water annually for transpiration and growth processes compared with more drought-resistant species (Tubbs and Houston 1990). In years of insufficient water supply, the reduced turgidity may limit both the total leaf area and the total amount of sugar synthesized, thus affecting radial growth.

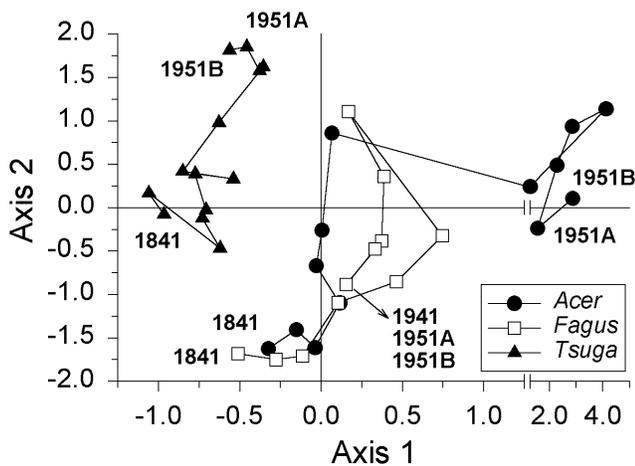
**Fig. 6.** Relationship between the growth indices from the residual chronologies (thin line) and the reconstructed growth indices (thick line) following the bootstrapped response function analysis for 1888–1987 (see Fig. 5) for (A) *Acer saccharum*, (B) *Fagus grandifolia*, and (C) *Tsuga canadensis*.



**Fig. 7.** Correlation coefficients calculated between the residual chronologies and the climate data for (A) *Acer saccharum*, (B) *Fagus grandifolia*, and (C) *Tsuga canadensis*. Correlations were calculated using 50-year segments moved by 10 years. The coefficient calculated for the last interval for each month was obtained using data from the Huntingdon meteorological station (1951–1991). This station located about 5 km away from our sampling site was used as a comparison with the regional climate series.



**Fig. 8.** Temporal walk displaying the evolution of the species correlation with climatic variables after a correspondence analysis of the significant correlation coefficients for the 13 time intervals illustrated in Fig. 7. The plot symbol labelled 1841 corresponds to the 1841–1890 interval, and subsequent symbols are for 10-year intervals up to 1951. The symbol labelled 1951A refers to results obtained using the regional climatic data, whereas the symbol 1951B refers to those obtained using the Huntingdon climatic data. Only correlations that were significant in more than one interval were kept in the analysis.



**Stability of the radial growth – climate correlations**

Since the mid-19th century, the radial growth of all three species was mainly limited by temperature in the previous year summer and by the early summer water balance during

the year of ring formation. Despite these similarities, it was observed that the radial growth – climate association of the species varied through time. This may have fundamental implications for climatic reconstruction but also adds to the difficulty of comparing growth–climate association reported in studies using different time intervals (Biondi 2000). Many factors may account for this instability. First, it could be related to the quality of our climatic data as well as the different spatiotemporal coverage of the region. However, the highly significant correlations observed between the regional data and the Huntingdon data (5 km from our site) suggested that this may constitute a minor problem. Furthermore, the changes observed in mean sensitivity and in cross correlations indicated some temporal change in growing conditions.

Second, it may be argued that the species’ response to climate may be age dependant. Szeicz and MacDonald (1994) speculated that physiological changes related to aging may affect the stability of the tree response to climate. However, this question has only been recently addressed by dendrochronologists (Colenutt and Luckman 1991; Szeicz and MacDonald 1994; Parish et al. 1999). However, the changes observed in the growth–climate association did not appear to be gradual as could be expected if they were due to aging. Third, disturbance episodes in the Bois -des-Muir may have affected the climate response of the species. During these episodes, the climate signal contained in high-frequency variation may be temporarily offset by new limiting factors. However, a study of the disturbance history by Brisson et al. (1992) showed that the three species only experienced significant radial growth releases during the 1825s. Our data does not support the hypothesis that the synchronous increase in mean sensitivity observed in the late 19th century was related to increased stand disturbances.

Fourth, the observed changes in the climatic response may reflect subtle and complex fluctuations in the climatic signal since the mid-19th century. Graumlich (1993) showed that correlations between climate and radial growth can be strongly influenced by years of extreme climatic conditions. From a biological point of view, extreme values in certain climate variables may dominate growth in given periods but may be absent in others (Visser and Molenaar 1988). It is speculated that episodes of climatic fluctuations in the 20th century have had an impact on the radial growth – climate association of the three species. The Huntingdon data showed that mean seasonal and annual temperatures have warmed since the end of the 19th century. However, it is not clear how much of this trend may be due to urbanization. This trend was stronger in the Montréal McGill data (not presented) and almost absent from the regional climatic series. In addition, our data showed that year-to-year variability in the annual mean temperature (regional and Huntingdon series) has decreased in the 20th century and especially after the 1940s. Coincidentally, it also corresponded to the beginning of a decrease in mean sensitivity for all species and to an increase in correlations between beech and hemlock chronologies. At the same time, a decrease in correlations between sugar maple and the others species started.

An unexpected result of our study concerns sugar maple and the increasingly negative correlation with mild late winter in the late 20th century. Yin et al. (1994) and Payette et al. (1996) also reported a negative correlation with warm February using climatic data mainly covering the second half of the 20th century. Our results supported the hypothesis that anomalous mild late winters (February–March) are associated with reduced sugar maple radial growth and could be connected to dieback episodes observed in the late 20th century. Auclair et al. (1996) reported that, for Quebec, the onset of the major episodes of dieback in the 20th century coincided with unusually prolonged thaws in winter and early spring followed by sudden, severe freezing. Internal frost injury related to early sap flow (Yin et al. 1994) and severe bud mortality (Auclair et al. 1996) may occur following sub-freezing temperatures in February.

Auclair et al. (1996) also observed that, prior to the 1940s, no prolonged severe dieback episodes were reported despite the occurrence of a high frequency of thaw–freeze events. The authors argued that the susceptibility to climatic injury by sugar maple is related to aging and that mature trees are more susceptible to freezing stresses. Our results substantiated their hypothesis that episodes of major climatic injury and dieback in Quebec may have occurred in preconditioned older sugar maple forests at times when freezing stresses were significantly correlated with warming annual temperature (Auclair et al. 1996). In our study, the significant correlation with February–March temperature was not observed prior to the 1921–1970 period.

In contrast to sugar maple, the growth–climate profile of beech became dominated by June precipitation in the second half of the 20th century. Both the increased sensitivity of maple to warm winters and of beech to June precipitation may explain the divergence between the species tree–climate profiles and the decreased correlation between their chronologies. Furthermore, Payette et al. (1996) have stressed the

importance of the forest tent caterpillar (*Mallacosoma disstria* Hbn.) outbreaks as a factor contributing to radial growth divergence between sugar maple and beech.

The tree–climate associations of hemlock were more stable than for the other species. Visser (1986) also reported that radial growth in hemlock was best fitted by a constant rather than by a time-dependent response function model. Since the 1920s, however, the preceding year July–August conditions may have become more limiting to growth than the current-year conditions. Cook and Cole (1991) speculated that a persistent increase in July temperatures coupled with decrease in June precipitation could have a negative effect on hemlock and could lead to an eastern contraction of the species range.

## Conclusion

This study has documented the climatic response of eastern hemlock, American beech, and sugar maple growing near the northern limit of the eastern deciduous forest. It has demonstrated the potential of trees in old-growth forest as proxy climate indicators. This was especially true of hemlock, which had more stable growth–climate associations than the hardwood species. Many factors may influence the temporal stability of the growth–climate relationship. The climate data, the climatic fluctuations, tree age, and stand dynamics may relate to this instability. Our results stressed that an increase in climate instability or climatic warming resulting from warmer winters or summers could affect the three species in different ways. The chronologies reported here were unusually long for the region. The finding of remnants of old-growth forest in the southern portion of Quebec opened the door to a further understanding of past and future climates and how species could be affected by them. The discovery of other old-growth forests near to the Bois-des-Muir with trees of the same quality would help to better differentiate the regional climatic signature from that of local disturbances of either natural or anthropogenic origins.

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