

Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest

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Abstract

To address the central question of how climate change influences tree growth within the context of global warming, we used dendroclimatological analysis to understand the reactions of four major boreal tree species – *Populus tremuloides*, *Betula papyrifera*, *Picea mariana*, and *Pinus banksiana* – to climatic variations along a broad latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest. Tree-ring chronologies from 34 forested stands distributed at a 1° interval were built, transformed into principal components (PCs), and analyzed through bootstrapped correlation analysis over the period 1950–2003 to identify climate factors limiting the radial growth and the detailed radial growth–climate association along the gradient. All species taken together, previous summer temperature (negative influences), and current January and March–April temperatures (positive influences) showed the most consistent relationships with radial growth across the gradient. Combined with the identified species/site-specific climate factors, our study suggested that moisture conditions during the year before radial growth played a dominant role in positively regulating *P. tremuloides* growth, whereas January temperature and growing season moisture conditions positively impacted growth of *B. papyrifera*. Both *P. mariana* and *P. banksiana* were positively affected by the current-year winter and spring or whole growing season temperatures over the entire range of our corridor. Owing to the impacts of different climate factors on growth, these boreal species showed inconsistent responsiveness to recent warming at the transition zone, where *B. papyrifera*, *P. mariana*, and *P. banksiana* would be the most responsive species, whereas *P. tremuloides* might be the least. Under continued warming, *B. papyrifera* stands located north of 49°N, *P. tremuloides* at northern latitudes, and *P. mariana* and *P. banksiana* stands located north of 47°N might benefit from warming winter and spring temperatures to enhance their radial growth in the coming decades, whereas other southern stands might be decreasing in radial growth.

Keywords: *Betula papyrifera*, boreal forest, Canada, climate warming, latitudinal gradient, *Picea mariana*, *Pinus banksiana*, *Populus tremuloides*, tree rings

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Introduction

The human-induced build-up of atmospheric CO₂ concentrations from 280 ppm in 1850 to 380 ppm in 2005 and of other greenhouse gases has resulted in an increase of 0.74 °C in global mean surface temperature from 1906 to

2005 (IPCC, 2007). In the Northern Hemisphere, the greatest warming was observed during winter (December–February) and spring (March–May). Atmospheric CO₂ concentration is also expected to rise to 700 ppm by the end of the current century. Consequently, this may lead to an additional 1.1–6.4 °C increase in global mean surface temperature by 2100, with rapid warming at mid to high northern latitudes (IPCC, 2007). In Canada, south of 60°N, mean annual temperature and annual total precipitation from 1900 to 1998 have increased between 0.5 and 1.5 °C, and from 5% to 35%, respectively (Zhang *et al.*, 2000). By 2100, it is expected that mean annual temperature in the eastern Canadian boreal forests (Quebec province) may be about 3.5 °C higher than today, even 5 °C higher during winter, and accompanied by increased precipitation by 10–25% (Plummer *et al.*, 2006).

Climate warming could have profound impacts on the temperature and nutrient-limited circumboreal forests at mid to high latitudes in the Northern Hemisphere (Oechel *et al.*, 1993). Long-term surface phenological observations from Europe (Menzel & Fabian, 1999) and recent satellite remote sensing measurements from North America (Zhou *et al.*, 2001) have respectively indicated approximately an 11-day lengthening of the growing season from 1959 to 1993 and 12 ± 5 days extension from 1981 to 1999 as a consequence of recent warming. Correspondingly, plant phenological observations demonstrated early leafing, flowering, and fruiting in spring/summer, as well as late leaf coloring in autumn recorded across Europe (Menzel *et al.*, 2006) and North America (Chuine & Beaubien, 2001). Rapid warming in surface air temperature at mid to high northern latitudes has also led to increased soil temperature and soil freeze-thaw in both permafrost and nonpermafrost regions (Osterkamp & Romanovsky, 1999). As a result, the decomposition rates of soil organic matter are accelerated (Davidson *et al.*, 2000), thereby resulting in more readily mineralized nutrients available to plants, particularly of the most common limiting nutrient, nitrogen (Luo *et al.*, 2004). In addition, the rising atmospheric CO₂ might have a positive effect on the above/belowground biomass by enhancing plant photosynthesis and water use efficiency in a CO₂-enriched world (Körner, 2006), i.e., the direct CO₂ fertilization effect (Huang *et al.*, 2007). All these impacts together might be leading to a shift in species composition and community structure (Weltzin *et al.*, 2003), and ultimately causing substantial change that varies with vegetation type in the boreal biome (Goetz *et al.*, 2005). Within the context of sustainable forest development, it is critical to better understand the responses of boreal tree species to climate variability and change, and increase our capacity to predict potential changes in forest composition and structure in this biome.

Ecological gradient analysis is often used to identify the interactions between plant species and their spatial distributions in relation to eco-environmental factors (Ohmann & Spies, 1998). The landscape-scale species distribution and abundance patterns are generally believed to be controlled by climate, i.e. temperature and soil moisture (Gosz, 1992) and to be influenced by the spatial and temporal patterns of natural or human-caused disturbances (Bekker & Taylor, 2001). In western Quebec, under the shift in air mass dominance as well as the impacts of natural or human-induced disturbances such as forest fires (Bergeron, 2000) and insect outbreaks (Volney & Fleming, 2000), forest composition gradually changes from the deciduous-dominated temperate forest in the south to the coniferous-dominated boreal forest in the north (ESWG, 1996). A vegetation transition zone between the mixedwood and the coniferous-dominated boreal forest occurs at approximately 49°N (Gauthier *et al.*, 2000).

A recent study has revealed that the current forest situation and the limits of the vegetation zone in the mixedwood boreal forest of Quebec may not have reached a balance with the present climate conditions (Bergeron *et al.*, 2004). A warming climate and a possible decreasing abundance of fires due to climate change and fire suppression (Bergeron, 2000) may favor an extension of the mixedwood into the coniferous forest. Bergeron (2000) reported an increased abundance of northern white cedar (*Thuja occidentalis* L.) in the landscape since 1850 as a consequence of a decrease in fire frequency. Tardif & Bergeron (1999) observed a movement of black ash (*Fraxinus nigra* Marsh.) populations from low flood plain sites to more elevated sites along the flooding gradient in the southeastern Quebec boreal forest. They attributed this movement to an increase in frequency and height of spring water levels associated with increasing snow fall and warmer spring temperatures.

Stem radial growth for any given year often integrates the effects of the previous and current year's climate (Fritts, 1976). Hence, tree rings have long been used as a valid tool to explore the long-term growth reactions to the historical climate variations and to further assess the impacts of future climate warming on tree growth and forest ecosystems. In the eastern Canadian boreal forest, a dendroclimatic investigation on black spruce [*Picea mariana* (Mill.) BSP] and jack pine (*Pinus banksiana* Lamb.) along a latitudinal gradient (48–50°N) indicated that the present vegetation situation was not in equilibrium and that detailed knowledge of species-specific growth responses to changes in a wide range of climate variables was needed (Hofgaard *et al.*, 1999). In this study, we conducted a dendroclimatic investigation on four major boreal tree

species along a broad latitudinal gradient spanning from 46°N and covering the vegetation transition zone in the eastern Canadian boreal forest. These species were: trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh.), black spruce, and jack pine. The objectives of our study were to (1) explore growth responses of the common boreal tree species to a wide range of climate variables along the latitudinal gradient from 46°N in western Quebec, (2) investigate changes in their radial growth-climate associations along the gradient, and (3) assess future potential changes in tree growth in the eastern boreal forest of Canada. We hypothesized that with increasing latitude, temperature may play a more important role in affecting the radial growth of the studied species, whereas synergistic factors (temperature, precipitation, drought) regulating the radial growth could be significant in the south.

Materials and methods

Study area

Our study area is located at the Quebec–Ontario border along a latitudinal gradient ranging south from Petawawa (approximately 46°N) to Radisson (approximately 54°N) in the north (Fig. 1), including the southern Laurentians, the Abitibi Plains, the James Bay area, and the Radisson Plains (ESWG, 1996). The topography along the gradient is generally flat and uniform with low-elevation hills and rock outcrops (300–400 m a.s.l.).

The climate of the region is dominated by dry polar and moderate polar air masses during the winter, and by moist maritime and moist tropical air masses during the summer (Fig. 1). Dry moderate air masses also often occur after an air mass has been advected far from its

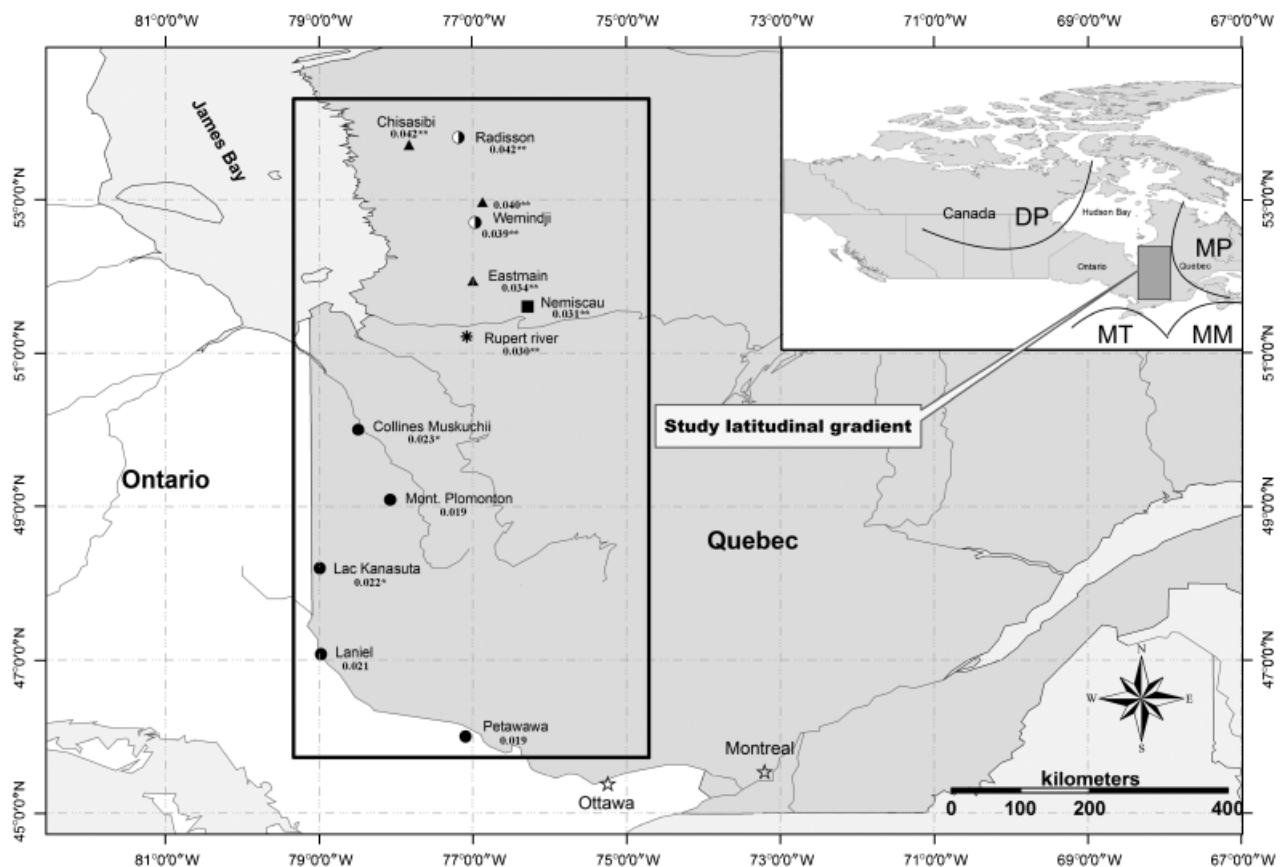


Fig. 1 Map showing the sampling sites for trembling aspen, paper birch, black spruce, and jack pine and the climate data sites in the eastern Canadian boreal forest. Five solid circles indicate that all four species were sampled per site; Three triangles indicate that only two conifers were sampled per site; Two half-solid circles indicate that only two deciduous species were sampled per site; An asterisk indicates that trembling aspen, black spruce, and jack pine were sampled at the site; A square indicates the paper birch sampling site at 51°N; In total, 12 sets of the climate data were used in the current study. The number associated with each site refers to the slope ($^{\circ}\text{C yr}^{-1}$) of the regression line conducted on the growing season average temperature (April–September) for the period 1950–2003; 95% (*) and 99.99% (**) significant levels are indicated. The origins of major air mass types affecting the climate of the region are also indicated: dry polar (DP), moist polar (MP), moderate moist (MM), and moist tropical (MT) (based on Sheridan, 2002).

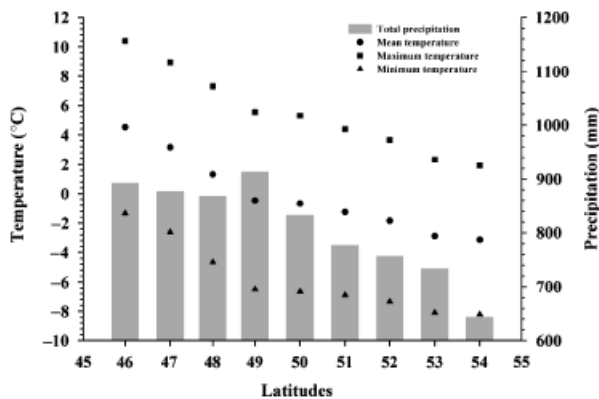


Fig. 2 Annual maximum, mean, and minimum temperatures, and mean annual total precipitation from 1950 to 2003 along the latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest.

source region and has thus been modified considerably (Sheridan, 2002). A climate gradient is also enclosed within the studied latitudinal gradient. Averaged climate data generated from the ANUSPLIN model (see 'Climate data') for the reference period 1950–2003 showed a linear decrease in mean annual maximum temperature ($R_{\text{adj}}^2 = 0.96$, $P < 0.0001$), mean annual temperature ($R_{\text{adj}}^2 = 0.91$, $P < 0.0001$), mean annual minimum temperature ($R_{\text{adj}}^2 = 0.85$, $P = 0.0002$), and mean annual total precipitation ($R_{\text{adj}}^2 = 0.82$, $P = 0.0005$) against the latitude from south to north, i.e. from 10.39, 4.52, -1.35 °C, and 893 mm at 46° N to 1.93, -2.84 , -8.20 °C, and 644 mm at 54°N, respectively (Fig. 2). The growing degree days ($>5^\circ$) also declined from 1 868 °C at 46°N to 862 °C at 54°N across the latitude ($R_{\text{adj}}^2 = 0.90$, $P < 0.0001$). In the study area, a significant warming trend in growing seasonal average temperatures (April–September) from 1950 to 2003 was observed at each site (Fig. 1). Similar trends were also found in climatic data sets of the Climate Research Unit (CRU 2.1 data; Mitchell & Jones, 2005).

Three bioclimatic zones encompass the study area from south to north, including (1) sugar maple-yellow birch domain, which is dominated by sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) with some other species such as paper birch and trembling aspen; (2) balsam fir-yellow birch, and balsam fir-paper birch climax zone, which is dominated by balsam fir [*Abies balsamea* (L.) Mill.], yellow birch, paper birch with postfire stands of jack pine and trembling aspen on the driest sites; and (3) black spruce-lichen, and black spruce-moss climax zone, which is characterized by the dominant black spruce stands with postfire stands such as trembling aspen, paper birch, and jack pine (ESWG, 1996). Along the south–north gradient, common boreal tree species including trembling aspen, paper birch, black spruce, and jack pine

occur but their abundance changes from south to north (Gauthier *et al.*, 2000). The studied gradient crosses the southern boreal forest region where both black spruce and jack pine approach their southern distributional limit of regional dominance (Burns & Honkala, 1990) and where trembling aspen approximately approaches its northern distributional limit, i.e. in the Hudson Bay region (Little, 1971).

Field sampling and laboratory chronology construction

Thirty-four forested stands were sampled in 2005 for the purposes of this study. To minimize the site effect on tree growth and to be representative of the majority of the forests, all stands were chosen from typical mesic or submesic conditions along the gradient (see Supporting information Appendix S1). Tree-ring samples were collected from two deciduous species (trembling aspen and paper birch), as well as from two coniferous species (black spruce and jack pine) along the latitudinal gradient ranging from 46 to 54°N. Sampling was conducted at approximately 1° intervals (Fig. 1). At 48°N, tree-ring increment cores were collected to update the existing black spruce chronology developed by Hofgaard *et al.* (1999). Toward the northern end of the gradient, available old trembling aspen and paper birch stands were fairly rare and only two stands were sampled for each species between 52 and 54°N. Given the numerous incomplete rings or missing rings in some hardwood boreal species like paper birch (Tardif *et al.*, 2001b), tree cross-sections were collected for exact cross-dating when tree cutting was permitted. In each stand, at least 20 old and healthy trees were cored or cut transversely at 1.3 m height (see Appendix S1). In total, 668 trees (340 cross-sections and 655 cores) were sampled from south to north.

In the laboratory, all tree-ring samples were dried and carefully polished with successively finer grits of sandpaper. Visual cross-dating for each sample was conducted under a binocular microscope. The dated samples were carefully measured using a Velmex measuring system interfaced with the 'Time Series Analysis Program' (TSAP; Frank Rinntech, Heidelberg, Germany) to a precision of 0.001 mm. Some black spruce and jack pine disks were scanned using WinDENDRO (Regent Instruments Inc., QC, Canada) to obtain ring-width values. Visual cross-dating was verified using COFECHA (Holmes, 1983) in which the Spearman rank correlation option was selected to diminish the influence of sharp growth reductions caused by insect outbreaks. In addition, the white/narrow rings that were associated with insect outbreaks and observed in trembling aspen and paper birch stands were validated by an independent and experienced technician at the University of Winnipeg.

Standardization was carried out to remove the age- and size-related trends in tree growth and to make the younger, faster growing portion of the tree more comparable with the older, slower growing portion of the tree (Fritts, 1976). This was done using a 60-year cubic spline with a 50% frequency response, which preserved approximately 99% of the variation within individual series at a wavelength of 19 years (Cook & Peters, 1981). When the first standardization did not perform well, the stiffness of the spline was modified to more flexible spline functions. Standardization involved transforming the ring-width measurements into dimensionless indices by dividing the observed ring-width measurements by those estimated using the spline function (Fritts, 1976). These growth indices contained a relatively stable mean and variance over time. This procedure retained high-frequency variations (interannual to decadal) and filtered out medium- to low-frequency trends such as trends in growth due to age/size, biological persistence and long-term stand dynamics (Cook, 1990). Because the standardized tree-ring indices are auto-correlated over time, the autoregressive model (AR) was also performed on each standardized series to remove temporal autocorrelation and enhance the common signal. The minimum Akaike Information Criterion (AIC) (Akaike, 1974) was used to choose the best AR models. The first-order AR model was found to well describe the autocorrelation structure. The residual tree-ring series were then averaged using residuals from AR modeling of the standardized measurement series (Cook, 1985). This procedure provided time-series with first-order autocorrelation values (AR1) approximating values (zero) observed in climate data over our region. To further eliminate the effect of endogenous stand disturbances and enhance the common signal, all residual series were averaged by site using a biweight robust mean, which reduced the effect of outlier values. Chronology construction was carried out using ARSTAN (version 4.0a) (Cook, 1985). In total, 34 residual ring-width chronologies were constructed for four species at nine latitudes.

In western Quebec, studies have shown that both trembling aspen and paper birch stands undergo defoliation by insects such as the forest tent caterpillar (*Malacosoma disstria* Hubner) and (or) large aspen tortrix (*Choristoneura conflictana* Walker) (Bergeron & Charron, 1994; Huang *et al.*, 2008). In the study area, Huang *et al.* (2008) have identified severe insect outbreaks in the host species based on the occurrence of white/narrow rings as well as the host (trembling aspen) and nonhost (black spruce or jack pine) species comparison using OUTBREAK (Swetnam *et al.*, 1985) (For more method details, please see Huang *et al.*, 2008). To maximally eliminate the nonclimatic noise associated with insect

outbreaks in trembling aspen chronologies and, to a certain degree, in paper birch chronologies and at each latitude, the years identified as severe insect outbreak ones in Huang *et al.* (2008) were first removed from the residual chronologies of host species. Second, corrected chronology indices for the removed years were estimated through regressing the host residual chronology against the corresponding nonhost residual chronology at each latitude. The final corrected trembling aspen and paper birch residual chronologies were used in all subsequent dendroclimatological analyses presented in this study.

Climate data

Owing to limited climate observational data in northwestern Quebec, the climate data that were used in our dendroclimatic analyses were generated from ANUSPLIN (version 4.3) (Hutchinson, 2004) by the Great Lakes Forestry Centre of the Canadian Forest Service. ANUSPLIN employs thin plate-smoothing splines to develop elevation-dependent spatially continuous climate surfaces from sparse weather station data (McKenney *et al.*, 2006). Based on the existing climate station data, it has the potential to generate monthly climate data for the period 1901–2003 (Hutchinson, 2004). However, given the lower reliability of the climate data in the north due to fewer climate observations available before 1950 and also to the short time span of some chronologies, only the climate data generated for the period 1950–2003 were used. In addition, at each latitude when the distance between sampling sites was <30 km, the same set of climate data was used for all study sites nearby. Otherwise, another independent set of climate data was generated from ANUSPLIN and used for dendroclimatic analysis. According to this criterion, in total 12 climate data sets were used for the dendroclimatological analyses involving four tree species and nine latitudes (Fig. 1). The climate variables included monthly maximum temperature (T_{\max}), monthly mean temperature (T), monthly minimum temperature (T_{\min}), monthly total precipitation, start date of the growing season (daily mean temperature $\geq 5^\circ\text{C}$ for 5 consecutive days after March 1), end date of the growing season (daily minimum temperature reached -2°C or less after August 1), growing season length (GSL), and growing degree-days (GDD, $>5^\circ$) (McKenney *et al.*, 2006). In addition, the Monthly Drought Code (MDC) from May to October was also calculated as described by Girardin & Wotton (2009) from monthly T_{\max} and precipitation data generated by ANUSPLIN, and it was used to investigate if soil moisture variability had any impact on tree growth in the region. The MDC is a numerical parameter representing the average moisture content of deep and compact organic layers (Turner, 1972) and

was previously shown to correlate well with growth in boreal tree species (Girardin *et al.*, 2006).

Comparison of chronologies and their relationships to climate

To quantify the common variance among species and site residual chronologies along the gradient and to better synthesize changes in the radial growth–climate associations across the latitude, a Principal Components Analysis (PCA) was used. All the data were standardized to have zero mean and unit standard deviation before using PCA. The PCA was performed on all residual chronologies from the four species and for the common interval 1950–2003. Through standard PCA techniques in CANOCO (version 4.52; ter Braak & Smilauer, 2003), the 34 residual chronologies were transformed into principal components (PCs). A correlation matrix where the 34 site chronologies were considered as variables and the years as observations was used. The loadings of the PCs were utilized for analysis of common and species-specific patterns over the latitude. The eigenvalue-one criterion (Kaiser, 1960) and the criterion that any PC accounts for at least 5% of the total variance were used to determine the meaningful PCs to be retained for interpretation (Legendre & Legendre, 1998).

Given that our less reliable precipitation data predicted from ANUSPLIN could influence the results of growth–climate associations calculated by response function, the bootstrapped correlation analysis was used in our study. To identify the common climate factors limiting the radial growth of all four species along the gradient, bootstrapped correlations between the retained meaningful PCs and monthly climate data (variables described above) were calculated using DENDROCLIM2002 (Biondi & Waikul, 2004). This program uses a bootstrapping method to test the significance of correlation coefficients at the 0.05 level. The bootstrap method provides a test of significance of the stability of the correlation coefficients within a specific time period by repeated, random sampling of the data (Guiot, 1992). All correlations were calculated on a 16-month basis from May of the year before ring formation to August of the year of ring formation and for the period 1950–2003. Correlations between the residual ring-width chronologies and climate variables over various multimonth periods were also explored.

To assess potential changes in the radial growth–climate associations across the gradient, a PCA was conducted on bootstrapped correlation coefficients obtained from the radial growth–climate analysis for each species along the gradient (Tardif *et al.*, 2003). This could allow us to constrain the PCA on tree growth responses to climate only and thus extract the common

variance among the radial growth–climate associations of a given species along the gradient. In this procedure, the correlation coefficients that were calculated between the climatic variables and residual chronologies using the bootstrap method were screened and climate variables showing a significant correlation at least once were retained. Through standard PCA techniques in CANOCO (version 4.52; ter Braak & Smilauer, 2003), correlation coefficients of the radial growth–climate associations of each species at nine latitudes were then transformed into new sets of orthogonal variables (Tardif *et al.*, 2003). The loadings of the PCs were utilized for analysis of common and site-specific growth response to climate over the latitude. The first two PCs were retained for further interpretation since they account for a high proportion of the total variance (at least 15%). The equilibrium circle of descriptors in the biplot was displayed to help us judge whether the contribution of each climate variable to the reduced space is greater or smaller. The climate variables located outside the circle account for more of the explained variation than those located inside the circle (Legendre & Legendre, 1998).

Results

Chronologies and general statistics

The length of the trembling aspen chronologies varied from 78 to 143 years, with the longest chronology dating back to 1862 at 53°N (Table 1). The paper birch chronologies spanned from 76 to 176 years in length. Besides the black spruce chronology at 48°N from Hofgaard *et al.* (1999), black spruce and jack pine chronologies developed in our study ranged from 63 to 248 years and from 69 to 179 years, respectively (Table 2). As listed in Table 2, chronological statistics of both conifers were in general similar along the gradient, suggesting that these two species contained a similar number of the common signals from south to north. The similar characteristic was also observed for both hardwoods (Table 1). Of the four species, trembling aspen showed the fastest radial growth whereas black spruce had the slowest radial growth. Both deciduous species had greater mean sensitivity and standard deviations than the two conifers. High EPS (Wigley *et al.*, 1984) and all series correlation within a population, which are the primary tools in evaluating tree-ring chronology quality, indicated a strong common signal in uneven-aged populations along the gradient (Tables 1 and 2).

Both deciduous species also showed higher interannual fluctuations in ring-width indices in the residual chronologies than the two conifers (Fig. 3), indicating

Table 1 Statistical characteristics of the trembling aspen and paper birch residual chronologies along the latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest

Species	Paper birch*															
	Trembling aspen*															
Sites	46°N	47°N	48°N	49°N	50°N	51°N	53°N	54°N	46°N	47°N	48°N	49°N	50°N	51°N	53°N	54°N
Chronology length	1911–2004	1894–2004	1908–2004	1864–2004	1870–2004	1925–2004	1862–2004	1927–2004	1903–2004	1829–2004	1899–2004	1911–2004	1893–2004	1907–2004	1879–2004	1929–2004
Number of trees (radii)	20 (38)	20 (40)	19 (34)	20 (40)	21 (40)	20 (40)	20 (40)	20 (38)	18 (36)	18 (36)	21 (38)	20 (39)	20 (40)	20 (38)	20 (38)	17 (33)
Mean ring width (mm)	2.37	1.83	2.91	1.86	1.48	1.77	1.61	1.60	1.27	0.96	1.92	0.92	1.56	0.78	1.23	1.44
Mean sensitivity	0.19	0.29	0.20	0.24	0.25	0.19	0.31	0.33	0.20	0.30	0.22	0.31	0.23	0.24	0.21	0.22
Standard deviation (mm)	0.19	0.24	0.17	0.22	0.22	0.18	0.26	0.29	0.17	0.24	0.21	0.27	0.19	0.22	0.20	0.21
1st order autocorrelation†	0.36	0.66	0.34	0.44	0.33	0.51	0.36	0.60	0.54	0.59	0.46	0.27	0.46	0.52	0.47	0.69
<i>Common interval analysis for the period 1950–2004</i>																
Number of trees (radii)	18 (35)	19 (36)	18 (32)	18 (35)	21 (38)	20 (39)	20 (40)	19 (36)	15 (27)	10 (16)	18 (27)	13 (16)	19 (38)	15 (27)	20 (36)	11 (20)
Variance in PCI (%)	41.45	51.04	40.34	41.77	51.78	44.09	63.77	60.06	31.32	47.75	36.18	52.00	27.84	25.46	47.99	49.91
EPS	0.92	0.95	0.91	0.92	0.95	0.95	0.97	0.96	0.84	0.88	0.86	0.89	0.86	0.85	0.94	0.90
All series correlation	0.39	0.49	0.38	0.39	0.50	0.42	0.63	0.58	0.27	0.43	0.33	0.48	0.25	0.21	0.46	0.46

*All chronological statistics were obtained before removal of insect outbreak years; EPS, expressed population signal; Common interval analysis for paper birch at 51°N from 1951 to 2000.

†Calculated from standard chronology.

Table 2 Statistical characteristics of black spruce and jack pine residual chronologies along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest

Species	Black spruce												Jack pine											
	46°N	47°N	48°N	49°N	50°N	51°N	52°N	53°N	54°N	46°N	47°N	48°N	49°N	50°N	51°N	52°N	53°N	54°N						
Sites	1942-2004	1889-2004	1690-2004	1917-2004	1831-2004	1761-2004	1822-2004	1757-2004	1869-2004	1925-2004	1883-2004	1915-2004	1910-2004	1915-2004	1921-2004	1936-2004	1826-2004	1916-2004						
Chronology length	19 (38)	19 (37)	36 (72)	19 (38)	20 (39)	20 (39)	20 (38)	20 (40)	20 (40)	19 (37)	18 (36)	20 (39)	20 (39)	20 (40)	17 (29)	20 (40)	18 (31)	20 (40)						
Number of trees (radii)	1.38	1.02	0.68	1.20	0.67	0.41	0.55	0.93	0.84	1.88	1.26	1.62	1.21	1.59	1.63	1.49	0.62	1.13						
Mean ring width (mm)	0.17	0.17	0.15	0.16	0.19	0.16	0.14	0.13	0.12	0.14	0.18	0.17	0.21	0.15	0.15	0.13	0.16	0.16						
Mean sensitivity	0.15	0.15	0.15	0.13	0.15	0.14	0.13	0.11	0.11	0.13	0.15	0.14	0.18	0.12	0.14	0.12	0.15	0.15						
Standard deviation	0.63	0.50	0.76	0.24	0.27	0.47	0.59	0.54	0.50	0.67	0.36	0.52	0.52	0.58	0.71	0.81	0.68	0.72						
1 st order autocorrelation*																								
<i>Common interval analysis for the period 1950-2004</i>																								
Number of trees (radii)	17 (32)	17 (32)	23 (46)	19 (38)	20 (38)	20 (39)	20 (38)	18 (36)	20 (40)	17 (32)	17 (30)	18 (35)	19 (33)	18 (36)	17 (29)	19 (38)	14 (23)	16 (32)						
Variance in	49.78	35.91	40.67	38.14	41.39	32.93	39.72	42.81	32.85	35.95	33.54	47.96	48.71	42.58	42.03	38.76	32.87	40.43						
PCI (%)	0.94	0.88	0.90	0.92	0.92	0.90	0.92	0.90	0.90	0.89	0.88	0.94	0.92	0.92	0.91	0.91	0.85	0.90						
All series correlation	0.48	0.31	0.38	0.35	0.38	0.30	0.37	0.40	0.30	0.33	0.31	0.46	0.46	0.40	0.39	0.36	0.29	0.37						

*Calculated from standard chronology; EPS, expressed population signal.

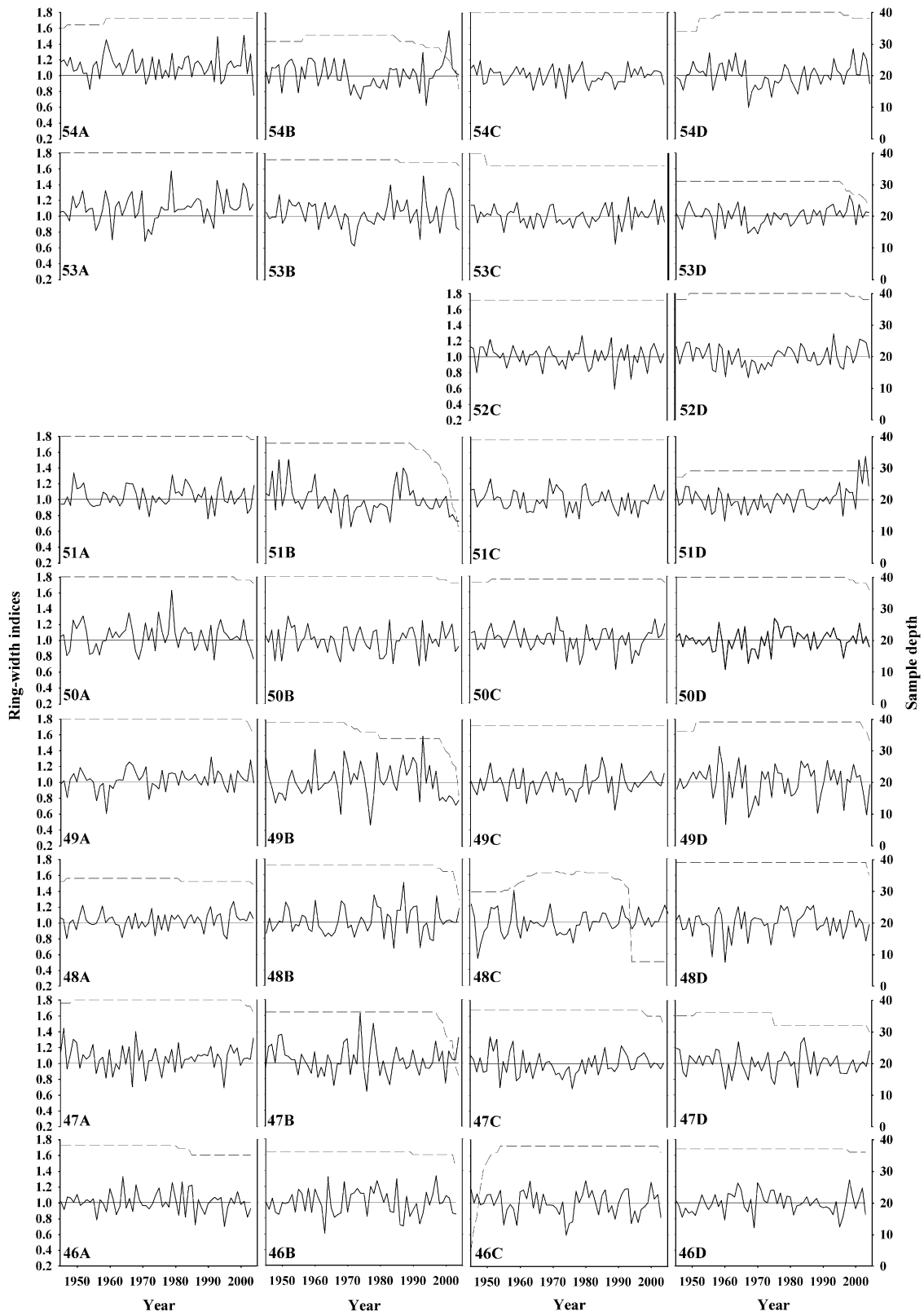


Fig. 3 Ring-width residual chronologies for the period 1945–2004 constructed for trembling aspen (A), paper birch (B), black spruce, (C) and jack pine (D) along the latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest. The dashed lines indicate the number of tree-ring series.

that hardwood species may be more sensitive to inter-annual variations in climate than coniferous species. The residual chronologies for a given species in general demonstrated similar interannual growth variations between nearby sites (Fig. 3).

Growth variations among sites/species and their relation to the common climate

As shown in Fig. 4, PCA conducted on all the residual chronologies showed that the first four PCs (PCI, PCII,

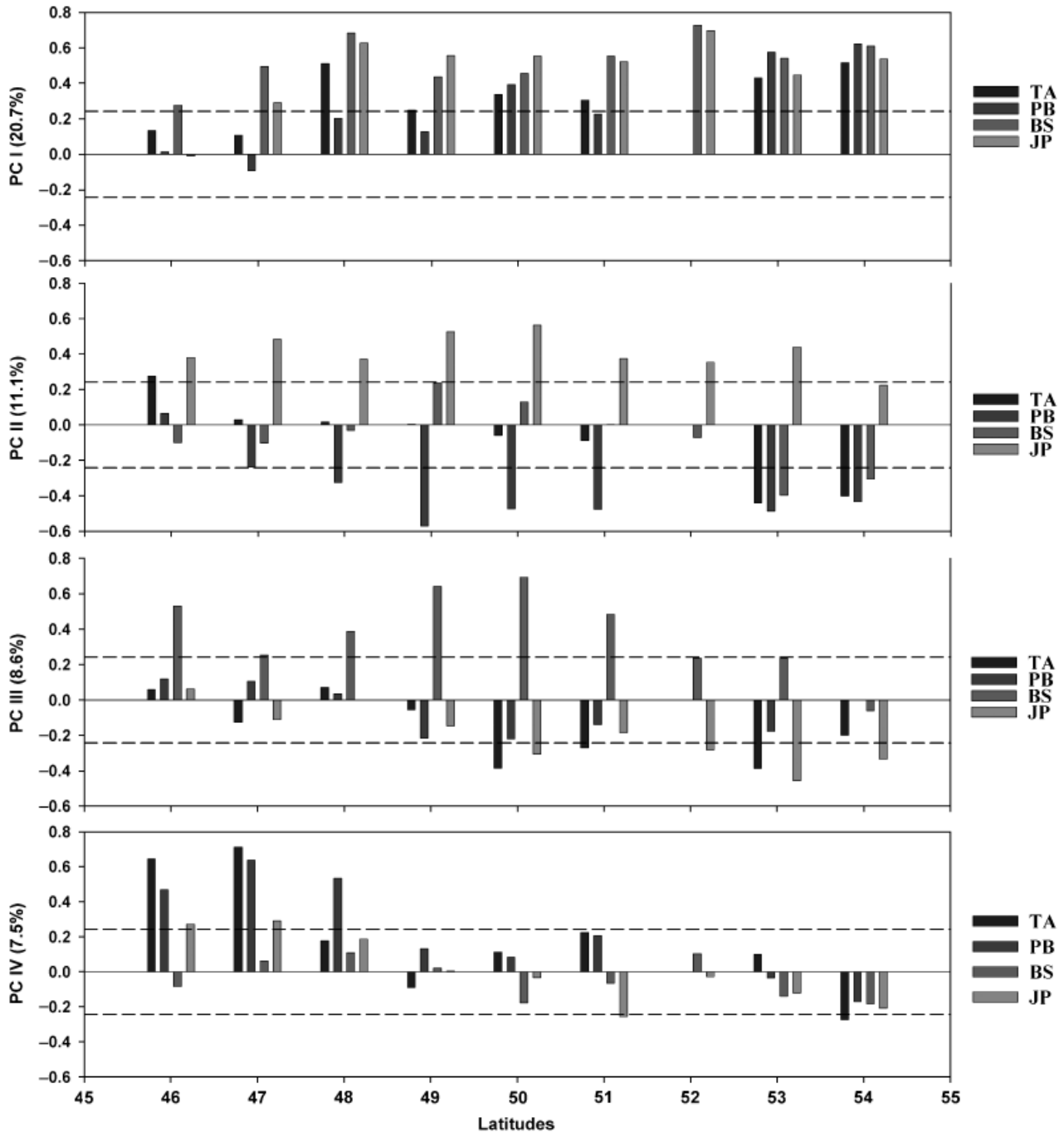


Fig. 4 Principal component analysis of the residual chronologies of trembling aspen (TA), paper birch (PB), black spruce (BS), and jack pine (JP) for the period 1950–2003. The dashed line represents the equilibrium circle of the biplot that enables us to judge whether the contribution of each residual chronology to the reduced space is greater or smaller than expected under the hypothesis of an equal contribution to all principal components (Legendre & Legendre, 1998). The residual chronologies that are clearly shorter than the value of their respective equilibrium contributions contribute little to the formation of the reduced space.

PCIII, and PCIV) were meaningful according to the criteria used in the study, and they in turn accounted for 20.7%, 11.1%, 8.6%, and 7.5% of the total variance of all the chronologies. The PCI describes the environmental signals (e.g. climate) that were held in common by all sites and species. Along the gradient, trembling aspen at 48–54°N, paper birch at 50–54°N, black spruce at 46–54°N, and jack pine at 47–54°N had significant contributions to the PCI, as indicated by their significant higher loadings than the expected values provided by the dashed line. Linear regression of the loadings of each species on the PCI against the latitude demonstrated a significant increasing linear trend for trembling aspen and paper birch toward northern latitudes ($R_{\text{adj}}^2 = 0.41$, $P = 0.05$, and $R_{\text{adj}}^2 = 0.83$, $P = 0.001$, respectively), yet an insignificant linear trend for both conifers. This less significant linear trend in trembling aspen indicated that trembling aspen at most latitudes may contain a similar number of environmental signals. Among the four species, both conifers had more contributions to the PCI than the hardwoods along the gradient. The contribution of both hardwoods to the PCI at 50–54°N and that of both conifers at 48–54°N were in general similar, respectively. In contrast, trembling aspen at 46–47°N, paper birch at 46–49°N, and jack pine at 46°N had low contributions to the PCI, as shown by their lower actual loadings than the ones shown by the dashed line in Fig. 4. The PCII, PCIII, and PCIV encompass variables specific to differences among species. The PCII is mainly a jack pine–paper birch related axis with a few trembling aspen and black spruce northern sites, in which jack pine had high positive loadings, whereas the other three species had negative loadings. The PCIII is mainly a black spruce–other three species related axis, in which black spruce had high positive loadings, yet others had negative ones. Both PCII and PCIII together clearly separated these four species into different groups. The PCIV mostly reflects variables for trembling aspen at 46–47°N and paper birch at 46–48°N, as suggested by their high loadings compared with low loadings of other stands.

Correlation conducted between the PCI and the climate variables (Supporting information Appendix S2) showed that all four species or most of the species were correlated negatively with previous summer temperatures (June–August), positively with January and March–April temperatures and previous June precipitation. Since positive PCII and PCIII implied positive conifer growth and negative hardwood growth (refer to Fig. 4), correlation for PCII suggested that jack pine was reacting positively to November temperatures and current March precipitation, and negatively to October precipitation, whereas an inverse relationship was found for paper birch. Correlation for the PCIII indicated that black spruce was responding negatively to

the current June–July temperatures and current May precipitation, yet an adverse relationship occurred for trembling aspen at northern latitudes. Since PCIV only highlighted trembling aspen and paper birch stands at 46–48°N, correlation for the PCIV reflected that these southern hardwoods were positively responding to current June precipitation, and negatively to current summer MDC (June–August). These common climate factors observed among species/sites were consistent with the ones shown in Figs 5 and 6.

Detailed radial growth–climate associations at different latitudes

In addition to a common growth response to climate along a broad spatial scale in the eastern boreal forest of Canada described above, the species/site-specific growth responses to climate were also found, as illustrated by both Figs 5 and 6. Trembling aspen's radial growth north of 47°N was negatively influenced by autumn temperatures of the previous year (September–November), with most significantly negative correlations to previous autumn T_{max} . Especially for northern latitudes, this negative effect was confirmed by significantly negative correlations between residual chronologies and the previous summer and early autumn MDC (Figs 5 and 6). Trembling aspen radial growth, as a whole, was also positively correlated with the growing season temperatures, with a weak change in significant correlations from March–April at southern latitudes to June–July at northern latitudes. In contrast, only a few positive correlations were found between trembling aspen growth and precipitation along the gradient, such as positive correlations between previous June precipitation and the radial growth of stands at 49–51°N. Trembling aspen radial growth was also found to be positively correlated with the GSL along the south–north gradient, with most significant correlations at 48–51°N. However, a few significant correlations were found for stands at 46°N.

Paper birch radial growth was positively correlated with the January temperature at most of our sites along the gradient, with significant correlations for T_{max} and T at 49–54°N (Fig. 5). In particular, its radial growth at 53–54°N was positively correlated to whole winter temperatures (Fig. 5). In addition, paper birch radial growth was also negatively correlated with previous summer and autumn temperatures in the south, with most significant correlations for T_{max} at 47–50°N (Figs 5 and 6). Compared with trembling aspen, paper birch was found to be positively correlated with precipitation during the current May–July along the gradient, particularly for the latitudes 47–51°N where significant positive correlations were found. This positive

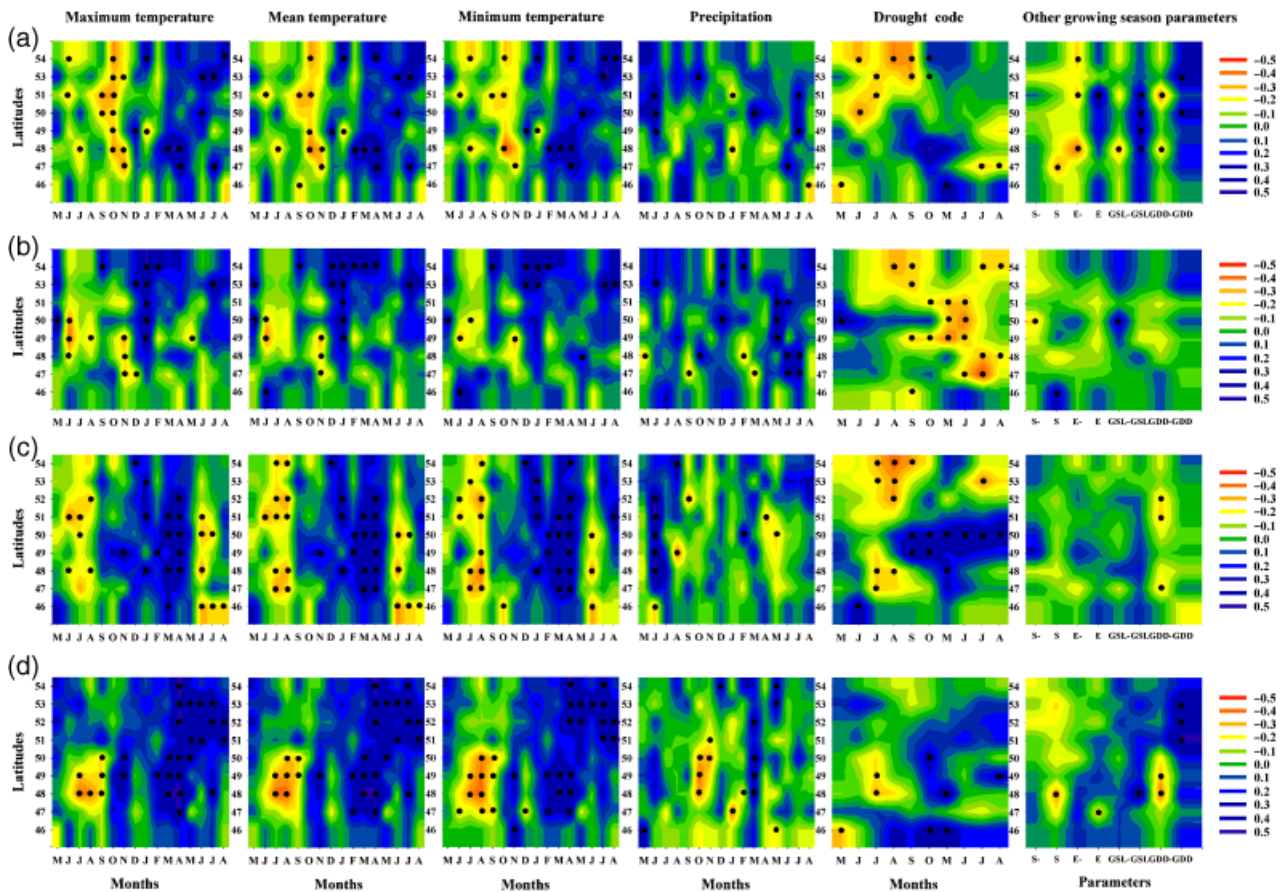


Fig. 5 Bootstrapped correlation coefficients between trembling aspen (A), paper birch (B), black spruce (C), and jack pine (D) residual tree-ring chronologies and the monthly climate variables (monthly maximum, mean, and minimum temperatures, monthly total precipitation, monthly drought code, and other growing season parameters) for the period 1950–2003 along the latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest. Other growing season parameters include the start date of the growing season in the previous year (S–) and the current year (S), end date of the growing season in the previous year (E–) and the current year (E), growing season length in the previous year (GSL–) and the current year (GSL), as well as growing degree-days in the previous year (GDD–) and the current year (GDD). The black dots indicate significant correlations at $P \leq 0.05$ level.

precipitation effect was also reflected by its high sensitivity to MDC, where significantly negative correlations between radial growth and the current May–August MDC were observed at most of our sites. Paper birch growth did not show significant associations with other growing season parameters. Like trembling aspen at 46°N, a few significant correlations were found for paper birch at 46°N.

The radial growth–climate associations of black spruce indicated that the previous summer temperature (June–August) and the current June temperature were negatively associated with their radial growth at most of the latitudes, with most significant variables found for T and T_{\min} (Figs 5 and 6). This negative effect was also confirmed by negative correlations between radial growth and the previous summer MDC. In addition, temperatures during the winter and early-growing

season (December–April) showed positive correlations with black spruce growth along the gradient. In particular, these positive effects were more significant for T and T_{\min} for the stands at 47–52°N. Stands at 46°N were found to be different from the others and showed significant negative correlations with T_{\max} and T of the current June–August. Precipitation and other growing season parameters did not show any systematic associations with radial growth along the gradient, with the exception of positive correlations with the previous June precipitation. In addition, responses of black spruce at individual sites to MDC were also found. For example, black spruce stands at 46°N were positively correlated with the previous June MDC, and those at 49 and 50°N were positively associated with the previous autumn (September–October) and the current May–August MDC.

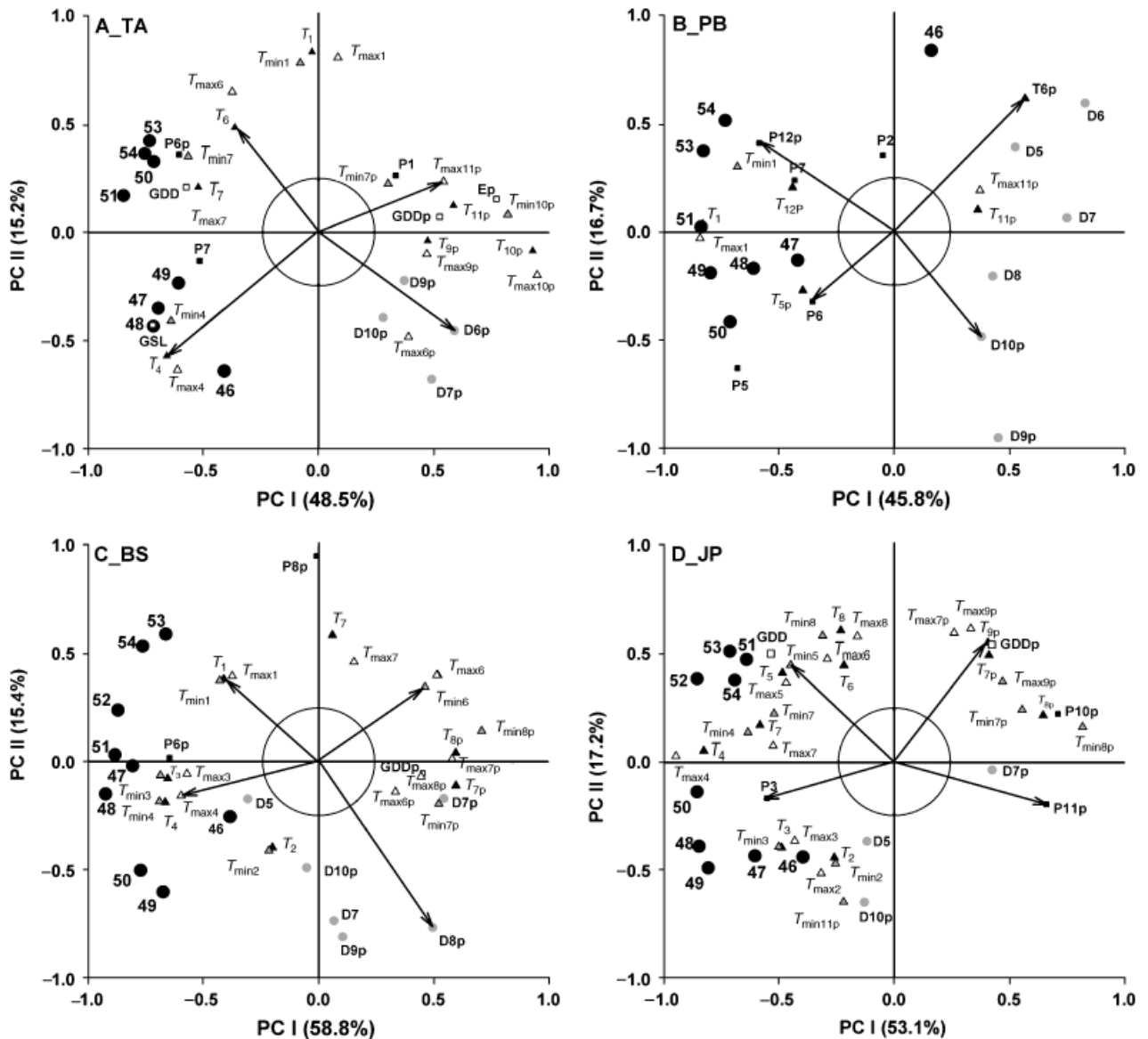


Fig. 6 Principal component analysis of correlation coefficients of the radial growth–climate associations of each of the four species, trembling aspen (A_TA), paper birch (B_PB), black spruce (C_BS), and jack pine (D_JP), along the latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest. Black dots represent our study sites at different latitudes. The equilibrium circle of the biplot enables us to judge whether the contribution of each climate variable to the reduced space is greater or smaller than expected under the hypothesis of an equal contribution to all principal components (Legendre & Legendre, 1998). Climate variables that are clearly shorter than the value of their respective equilibrium contributions were not shown in the biplot. For clarity, arrows pointing from the origin to the climate variables were only, as an example, selectively drawn with black arrows. The climate variables are positioned in the biplot based on their correlations with the canonical axes. In addition, the biplot also approximates the correlation coefficient among descriptors and climate variables. Climate variables and latitudes at sharp angles are positively correlated ($\cos 0^\circ = 1.0$, i.e. perfect correlation). Conversely, obtuse angles indicate negative correlation ($\cos 180^\circ = -1.0$, i.e. perfect correlation). Climate variable abbreviations are for monthly maximum temperature (T_{max} , white \blacktriangle), monthly mean temperature (T , black \blacktriangle), monthly minimum temperature (T_{min} , gray \blacktriangle), monthly total precipitation (P, black \blacksquare), monthly drought code (D, gray \bullet), and other growing season parameters (white \blacksquare) including start (S) and end (E) date of the growing season, growing season length (GSL), as well as growing degree-days (GDD). Climate variables in the previous year are indicated with a ‘p’. For example, monthly maximum, mean, and minimum temperature in the previous August and current August were indicated by $T_{max\ 8p}$, T_8p , $T_{min\ 8p}$, and $T_{max\ 8}$, T_8 , and $T_{min\ 8}$, respectively; Monthly drought code in the previous May and current May were indicated by D_{5p} , and D_5 , respectively.

Correlation functions for jack pine showed that growing season temperatures were positively correlated with their radial growth from south to north, with a seasonal shift from February–April south of 50°N to April–August north of 50°N (Figs 5 and 6). T_{\max} and T showed more significant climate variables than T_{\min} . In addition, previous July–September temperature (T_{\min}) was found to be more negatively correlated to radial growth of jack pine at 47–50°N. In contrast, stands at 46°N seemed to be different from others, as suggested by a few significant correlations with climate variables. Precipitation and other growing season parameters generally did not exhibit any systematic impacts on the radial growth along the gradient, except for some individual sites.

Changes in the radial growth–climate associations along the gradient

As shown in Fig. 6, PCA conducted on the bootstrapped correlation coefficients of the radial growth–climate associations for each of the four species along the gradient showed that the PCI accounted for 48.5%, 45.8%, 58.8%, and 53.1% of the variance for trembling aspen, paper birch, black spruce, and jack pine, respectively. Subsequently, the PCII explained respectively 15.2%, 16.7%, 15.4%, and 17.2% of the variance. Along the south–north gradient, the PCA well separated the radial growth–climate associations of each species into two parts on a broad spatial scale. All trembling aspen stands were separated into the southern latitudes (46–49°N) and northern latitudes (50–54°N) along the latitude 49°N whereas the other three species were set in the southern part (46–50°N, except for paper birch at 46°N) and the northern part (51–54°N) along the latitude 50°N. In addition, the PCA results also showed that stands at closer sites/latitudes in general had similar radial growth–climate associations.

Discussion

The partitioning of the variance in the PCA indicated that all species responded to some common environmental signals. The PCI reflected that there were common climate signals across four species from south to north. Higher loadings at northern latitudes suggested that all species in the north were reacting to the same climate factors, whereas low loadings in the south reflected that either all species were reacting to different climate factors or that they were less climate-sensitive in the south. Of the four species, both black spruce and jack pine contained a similar number of common climate signals across most of the latitudes, suggesting that these species responded to climate similarly from south to north. This is consistent with previous large-

spatial-scale studies of tree species across their distributional range. For example, Cook & Cole (1991) reported that eastern hemlock (*Tsuga canadensis* L.) was positively correlated to March temperatures throughout its range in eastern Northern America. Frank & Esper (2005) also reported that *Picea abies* (L.) H. Karst., *Larix decidua* Mill., and *Pinus cembra* L. tend to show most similar responses to climate across their wide distribution in the European Alps. However, the reactions of both trembling aspen and paper birch to climate were more similar to the conifers in the north than in the south, as indicated by significant increasing loadings of their site chronologies on the PCI toward northern latitudes. This is inconsistent with the above-cited studies that reported similar growth response to climate across a large-spatial scale for the studied species. The inconsistency might be due to the following reasons: (1) these southern deciduous stands were less sensitive to climate, (2) insect outbreaks might reduce or affect their sensitivity to climate, (3) insect outbreak noise might still remain in the residual chronologies of these deciduous stands, and (4) these stands were influenced by the local climate and/or other factors such as species competition. In addition to common climate signals shared by all four species along the broad gradient, the variance explained by the PCII–IV suggested some other common climate signals shared within certain species and/or certain studied sites.

Common climate factors with consistent growth limiting effect among species

All our PCA and bootstrapped correlation analysis results together indicated that the previous summer temperature and moisture budget as well as current March–April temperatures were the common factors affecting radial growth of all four species though these factors were not found at all the sites. For example, previous summer temperatures were shown to negatively affect radial growth of trembling aspen at most latitudes, of paper birch at 48–50°N, of black spruce at almost all the latitudes, and of jack pine at 47–50°N. Hot previous summer temperatures could enhance stand respiration and evapotranspiration, thereby resulting in increased water deficits. This water-stress effect was also confirmed by positive correlation to previous June precipitation and negative correlation to previous summer MDC at many latitudes. Climate conditions in late summer generally influence the size of the buds and the number of leaf primordials produced within them for the growth of predetermined boreal conifers in the previous year (Kozłowski *et al.*, 1991). The size of the dormant bud then affects the amount of leaf area for the most photosynthetically efficient class of leaves and

needles produced in the current year of bud expansion and ring formation. On the other hand, a proper moisture budget allows optimal tree growth and assimilation of the carbohydrates for the next year's growth if soil moisture is sufficient to maintain foliage water potential and minimize vapor pressure deficits (Dang *et al.*, 1998). Trembling aspen as a typical upper canopy species has been widely shown to be moisture limited due to summer drought in the aspen parkland of western Canada (Brandt *et al.*, 2003; Hogg *et al.*, 2005) as well as in the United States (Worrall *et al.*, 2008). Using a conceptual model, Frey *et al.* (2004) demonstrated how drought can either operate directly to cause rapid trembling aspen dieback through xylem cavitation or indirectly in combination with pathogens and other factors to cause long-term growth decline through decreased photosynthesis and a gradual exhaustion of carbohydrate reserves. In contrast, paper birch is a more shade-tolerant, subcanopy species (Strong & La Roi, 1983) and thus exhibits moderate previous summer water-stress effect. Negative summer temperature effect observed only for paper birch at middle latitudes might be attributed to regional strong evapotranspiration during hot summers in those latitudes compared with the others. The summer water deficits were also reported in other hardwood species in the mixed boreal forest of Canada such as black ash (*F. nigra* Marsh.) (Tardif & Bergeron, 1993), sugar maple (*A. saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) (Tardif *et al.*, 2001a) as well as white oak (*Quercus alba* L.) and red oak (*Quercus rubra* L.) (Tardif *et al.*, 2006).

Our black spruce showed strong previous summer moisture stress along the gradient. This trend agreed with previous black spruce studies such as Dang & Lieffers (1989) and Hofgaard *et al.* (1999) who also observed negative summer temperature effects on radial growth in the boreal forest. Negative correlation with previous summer temperature and positive correlation with previous June precipitation might also be explained by a climatic driven floral induction in mast-ing trees like spruce, because these climatic factors were found to be critical for predicting seed production of Norway spruce [*Picea abies* (L.) Karst.] in southern Norway (Selås *et al.*, 2002). In contrast to black spruce, this previous summer water-stress effect was only observed for jack pine stands in the south. The discrepancy observed for both conifers might be ascribed to differences in species/sites. Jack pine is one of the least shade-tolerant evergreen species and usually grows on the sandy soils in the boreal forest, hence demonstrating better drought resistance than black spruce. However, during hot summers in the south, stands growing at high elevations or on slopes such as our jack pine stands at 48–50°N would show certain water deficits due to

high evapotranspiration but low soil water reserves. Hofgaard *et al.* (1999) also documented a negative effect of previous summer temperature on radial growth of jack pine between 48 and 50°N in the mixed boreal forest of western Quebec. Chhin *et al.* (2008) found negative effects of previous summer temperatures on the growth of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) in the Rocky Mountains of western Canada as well. Our multispecies results were consistent with Girardin & Tardif (2005) who also documented negative previous summer temperature effects on radial growth of several hardwoods and conifers in Manitoba.

Current March–April temperatures were found to positively influence radial growth of trembling aspen at southern latitudes, of paper birch at 54°N, and of both black spruce and jack pine at almost all the latitudes. Warmer spring temperatures could favor leaf emergence or budburst earlier, thus resulting in better growth in a prolonged growing season. Graumlich (1993) observed that warm temperatures in April may favor conifer species owing to their evergreen foliage, which allows them to take advantage of early growing season warmth. Suni *et al.* (2003) revealed the significance of air temperature triggering the onset of photosynthesis of boreal conifers in spring. Based on field investigations on photosynthesis in balsam fir in New Brunswick, Canada, Goodine *et al.* (2008) further pointed out that spring air temperature might be particularly important for tree species whose root systems extend below the frost line to trigger the onset of photosynthesis. As for tree species whose root systems grow in frozen soils, the onset of photosynthesis may be triggered by soil thawing (Goodine *et al.* 2008). Warm spring air temperature might accelerate soil thawing, resulting in the availability of unfrozen soil water that is necessary for the photosynthetic onset. Subsequent recovery of full photosynthetic capacity (i.e. the photosynthetic rate of well-watered foliage at a reference temperature and saturating irradiance) may be also favored by warm air temperature (Goodine *et al.*, 2008). Our results were also supported by many previous studies that observed positive spring temperature effect on radial growth of both hardwoods and conifers in the eastern Canadian boreal forest (Tardif *et al.*, 2001b; Girardin *et al.*, 2006).

In addition, our results indicated that January temperature was the common factor for positively affecting radial growth of trembling aspen at 54°N, paper birch at most of the latitudes, and black spruce at northern latitudes. Warmer winter temperatures would protect tree tissues (e.g. buds and roots) from being damaged by severe winter freezing (Miller-Rushing & Primack, 2008). Adversely, a cold winter could cause root damage

of shallow-rooted species when there is no snow pack (Cox & Zhu, 2003), which in turn results in low root pressure and low ability to transport water to buds. Wind and snow abrasion during cold winters can also damage tree crowns, leading to foliage loss (Grier, 1988). In addition, a cold winter could cause freezing-induced cavitation, which may delay flowering or leaf out by delaying the flow of water to buds in the spring (Wang *et al.*, 1992). Our results agreed with the findings of winter temperature effect on radial growth in previous studies (e.g. Tardif *et al.*, 2001b; Pederson *et al.*, 2004). For instance, Pederson *et al.* (2004) observed that January temperature was the most limiting factor for radial growth of six northern range margin tree species in the Hudson River Valley. Additionally, we also found that current summer precipitation or ample moisture was the major common factor influencing radial growth of both hardwoods in the south. With leaf expansion during a hot summer, sufficient precipitation may mitigate water stress for favoring radial growth of the southern hardwoods.

Common climate factors with inverse growth limiting effect among species

In addition to the common climate factors with consistent growth limiting effect found among species as discussed above, the common climate factors with inverse limiting effects on radial growth of our studied species were also observed. For instance, jack pine/paper birch and trembling aspen stands at some southern latitudes were mainly responding positively/negatively to November temperatures and current March precipitation, and negatively/positively to October precipitation, respectively. This is an indication of a regional climate signal. In autumn, paper birch might be damaged by the combination of dry (snow-free) conditions in October followed by severe cold in November, which may lead to deep soil frost. In contrast, jack pine might be favored by warm, dry (sunny) conditions to continue photosynthesis. Sufficient March snow may meet the water demands of jack pine stands during an early growing season, but it could postpone the start of the growing season for hardwood stands in the south. Our results were consistent with the previous studies. For example, Hofgaard *et al.* (1999) also observed a positive November temperature effect on jack pine growth in western Quebec. Savva *et al.* (2008) found significantly positive growth responses of jack pine to precipitation during March in the nearby province of Ontario.

Our results also indicated that current hot summer (June–July) temperatures may increase water stress for limiting radial growth of black spruce south of 51°N,

but provide sufficient warmth for favoring radial growth of the other three species at northern latitudes. Levaniè & Eggertsson (2008) also documented positive relations between paper birch radial growth and the current summer temperatures in northern Iceland. In addition, during the growing season ample May precipitation may provide the required water supply for enhancing radial growth of paper birch at 49–51°N and of jack pine at 53–54°N, yet limit radial growth of black spruce at middle latitudes. Compared with the positive growing season precipitation effect on radial growth of both black spruce and jack pine reported by Tardif *et al.* (2001b), a few positive precipitation effects on their radial growth revealed in our study might be ascribed to less accuracy of the modeled precipitation data from the ANUSPLIN model (McKenney *et al.*, 2006). Other growing season parameters such as start and end date of the growing season, GSL, and GDD were found to play a minor role in regulating radial growth of all four species except for some individual sites.

Species/site-specific climate response

Our results revealed that previous autumn temperature (mostly October T_{\max}) was also a critical factor that negatively affected the radial growth of trembling aspen across the latitudes. Hot autumn temperatures might enhance stand respiration, thus increasing consumption of the carbohydrates that are reserved for the current year's growth. In addition, trembling aspen may be able to benefit from a prolonged GSL to enhance growth, as reflected by its positive correlation to GSL. Taking both common and specific climate responses together, our results suggested that the previous year's moisture condition was the most important factor affecting trembling aspen growth in the current year. Similar findings were also reported in other studies (e.g. Hogg *et al.*, 2005; Leonelli *et al.*, 2008). A recent wood anatomical study conducted in western Quebec found that trembling aspen could produce 3–5% new xylem cells before leaf emergence during the early growing season (L. Zhai, unpublished data), indicating that the carbohydrate reserves in the previous year might play a critical role in producing some new xylem cells.

Paper birch at most of the latitudes was demonstrated to be strongly water limited during the growing season, as suggested by positive correlation to summer precipitation and negative correlation to current summer MDC. This agreed with Tardif *et al.* (2001b) who also observed a positive relationship between paper birch and June precipitation and a negative one with current summer MDC in western Quebec. Ample precipitation would result in improved water conditions and thus favor the formation of carbohydrates during the grow-

ing season (Tardif *et al.*, 2001b). Stands at 46°N showed different climate responses from the others and appeared to be able to enhance growth through warm previous early summer temperatures and an early start of the growing season. Combined with the common limiting factor January temperature, our study as a whole indicated that the current year's climate conditions would play a more important role in controlling paper birch radial growth than the previous year's conditions across the latitudes. A recent wood anatomical study conducted in western Quebec also found that new cells of the xylem were not observed when paper birch leaves unfolded after 1 week (L. Zhai, unpublished data).

In addition to the common climate factors shared with other species, black spruce stands at 49–50°N demonstrated significantly positive correlation to the current summer MDC. This might be ascribed to the effect of local climate on radial growth or an unknown reason. Jack pine stands north of 50°N were also found to be significantly positively correlated to the current GDD. In addition, jack pine response to the growing season temperatures along the gradient showed a seasonal shift from February–April in the south to April–August in the north, suggesting that trees in the south could react to early spring temperatures earlier than those in the north. This corresponds to empirical and modeling phenology observations (Girardin *et al.*, 2008). Altogether, our study suggested that the current-year winter and spring or whole growing season temperatures were particularly important factors for positively affecting radial growth of both conifers across our broad gradient.

Changes in growth–climate associations from south to north

Common variances in the radial growth–climate associations across the latitudes explained by the first two PCs were similar among the four species (ranging from 62.5% to 74.2%), suggesting that the radial growth–climate associations of these four species changed in a similar manner across the latitudes. High variance represented by the PCI indicated that stands from south to north shared similar radial growth–climate associations except for stands at 46°N that contained less common but more local climate effects. Along the broad gradient, PCII clearly separated the radial growth–climate associations of each species into two parts, i.e. southern and northern, indicating that these stands were influenced by different air masses in the south and in the north, respectively. In western Quebec, on the regional scale, the southern area is affected by warm, moist air originating from the south during summer, whereas the northern area is influenced by cold, dry

polar air during winter (Fig. 1) (Sheridan, 2002). The balance between, and the position of, these main air masses undulates over the landscape between years and throughout all seasons. This large-scale climate pattern has given the boreal forest and its ecotones their positions and shapes through time (Bryson, 1966). Although stands are influenced by different air masses in the south and north across the gradient, no sharp climate boundary existing between south and north was revealed (Sheridan, 2002). Rather, the climate transition gradually changes from south to north between 48 and 50°N, as indirectly evidenced by previous studies (Hofgaard *et al.*, 1999; Bergeron *et al.*, 2004). In addition, similar radial growth–climate associations within nearby sites/latitudes indicated a regional climate effect.

Along the vegetation transition zone (approximately 49°N) (Bergeron *et al.*, 2004), it is generally believed that the forests south of 49°N are mostly controlled by warm, moist air masses from the south, and forests north of 49°N are mainly shaped by cold, dry polar air. However, paper birch, black spruce and jack pine stands at 50°N were set in the south, as revealed by the PCA, indicating that they were also influenced by the southern climate, not by the northern climate. This could provide evidence to support the previous speculation that the warm, moist air masses and the cold, dry polar air masses might have been advancing and retreating northwards, respectively, due to recent warming at the transition zone (Hofgaard *et al.*, 1999; Girardin *et al.*, 2006). In contrast, PCA suggested that trembling aspen at 50°N was affected by the northern climate. This contrasting result might suggest that at the transition zone these boreal species have been responding to recent climate warming in different ways. Schulze & Mooney (1994) pointed out that species would respond to climate change individually rather than as a cohesive biome. Based on our analyses, paper birch, black spruce, and jack pine would be more likely to respond positively to climate warming, whereas trembling aspen might be less responsive to warming. The positive responsiveness of paper birch, black spruce and jack pine to warming could be explained by the warming winter and growing season temperatures observed in the study region from 1950 to 2003, because these climate factors were the most important factors for positively affecting their radial growth across the latitudes, but less important for trembling aspen.

Potential changes in tree growth along the gradient

Because climate warming has been resulting in a warmer winter and spring in the Northern Hemisphere (IPCC, 2007), our study may allow us to assess future potential changes in tree growth along the gradient

based on the above understanding of their growth responses to climate. Over broad spatial scale, both black spruce and jack pine north of 47°N, paper birch north of 49°N as well as trembling aspen at northern latitudes (e.g. 53 and 54°N) might be able to benefit from warming winter and spring temperatures to enhance their radial growth in the coming decades. Several jack pine provenance tests in Canada and Europe also reported that the northern seed sources were currently growing at temperatures below the optimum and would benefit from future increased temperatures (Savva *et al.*, 2007). Reich & Oleksyn (2008) observed that warming might alleviate the limited effects of cold temperatures on tree growth such as cold conditions and effects of cold on soil resource supply, hence leading to enhanced growth and survival of Scots pine (*Pinus sylvestris* L.) in the far north across Europe. Our mixed modeling analysis also showed moderate growth increases in trembling aspen at northern sites in the coming decades (M.-P. Lapointe-Garant, unpublished data). In contrast, paper birch and trembling aspen along most of the southern latitudes might be decreasing in radial growth owing to high evapotranspiration and moisture stress in hot summer and autumn seasons as well as increased insect outbreaks (Volney & Fleming, 2000) and other factors such as species competition (Bergeron *et al.*, 2004). Through investigations from two contrasting deciduous forest ecosystems in the boreal and temperate regions of central Canada, Barr *et al.* (2002) reported that the warm spring of 1998 caused early leaf out and increased photosynthesis but had little effect on respiration in the boreal forest ecosystem, whereas in the temperate ecosystem the same warming spring not only caused early leaf out but also enhanced respiration and drought stress. However, our analysis may not be sensitive to longer-term processes associated with climatic variation, e.g., lags in growth responses caused by (1) slow, climate-related changes in soil nutrient regimes, (2) depletion of stored carbohydrates in the roots, (3) depletion of soil water in the rooting zone; and lags in growth responses induced by climate-related increases in damage by insects and disease, or species-specific ecophysiological processes such as leaf longevity, flowering, cone production, and seed development. In addition, future impacts of climate change on tree growth would be strongly influenced by future changes in damage by insects and diseases and by the stand-level dynamics (e.g. mortality and subsequent growth releases of survivors) that are not easy to determine from tree-ring analysis of living trees. Despite this, taken together, our results support the general concern that with climate warming, deciduous species might be able to enhance their growth in the north and then gradually develop into a pure coniferous boreal forest in the future.

Conclusions

To examine the potential impact of climate change on forest growth, our study investigated radial growth response of four dominant tree species to climate along the broad latitudinal gradient from 46 to 54°N in the eastern Canadian boreal forest. We found that the moisture conditions in the previous year played a dominant role in positively affecting radial growth of trembling aspen over the gradient, whereas January temperature and growing season moisture conditions were major factors for positively affecting radial growth of paper birch. Both black spruce and jack pine were primarily positively impacted by the current-year winter and spring or whole growing season temperatures along the gradient. Since different climate factors limited radial growth, the growth responsiveness of these four species to recent warming was inconsistent at the vegetation transition zone, where paper birch, black spruce and jack pine would be the most positively responsive species, whereas trembling aspen might be the least. With continued warming, both black spruce and jack pine north of 47°N might be able to benefit from warming winter and spring temperatures to enhance radial growth. Paper birch north of 49°N and trembling aspen at northern latitudes such as 53 and 54°N could also increase their growth during favorable growing season conditions, whereas paper birch and trembling aspen stands at most of the southern latitudes might be decreasing in radial growth. Foresters should take into account that the northern hardwoods might be favored by the future climate and thus they could make more room for hardwood and mixedwood management in the eastern Canadian boreal forest. In addition, these potential growth changes in different boreal species might also cause substantial changes in carbon sinks in the boreal forest. Hence, it is of great importance to take our multiple species and broad spatial-scale study as a template for exploring the effects of climate warming on growth of different tree species in other boreal regions of the Northern Hemisphere. This could aid us to quantitatively assess potential changes in tree growth and forest composition across the mid-high latitudes of the Northern Hemisphere, which in turn may be used in the long-term planning of sustainable forest management and the assessment of the role of boreal forests in global carbon equilibrium.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characteristics of sampling sites and sampled stands (trembling aspen TA, paper birch PB, black spruce BS, and jack pine JP) along the latitudinal gradient from 46°N to 54°N in the eastern Canadian boreal forest. I: Sugar maple-yellow birch bioclimatic zone; II: Yellow birch-balsam fir, and paper birch-balsam fir climax zone; III: Black spruce-lichen, and black spruce-moss climax zone. The mean distance between sites pertaining to the same species is 1.11° latitude for TA, 1.11° latitude for PB, 0.85° latitude for BS, and 0.96° latitude for JP, respectively.

Appendix S2. Bootstrapped correlation between the PCs (PCI to PCIV) and the climate data (monthly mean temperature, total precipitation, and drought code) from 46°N to 54°N. Only significant climate variables in the previous year (e.g., Jun) and current year (e.g., Jan) at different latitudes were listed in the table. Significant positive and negative correlation ($P \leq 0.05$) was indicated by 'p' and 'n', respectively. The abbreviations 51PB, 53BF, 53CON, 54BF, and 54CON represent the climate data for the paper birch site at 51°N, both deciduous sites at 53°N, both coniferous sites at 53°N, both deciduous sites at 54°N, and both coniferous sites at 54°N, respectively.

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