

Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest

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Abstract: To decipher spatial and temporal tree-growth responses to climate change we used tree-ring data from *Picea mariana* (Mill.) BSP and *Pinus banksiana* Lamb. along a latitudinal transect in western Quebec. The transect encompassed the distinct transition between mixed and coniferous forests at approximately 49°N. Correlation analyses and principal component analyses were used to identify common spatiotemporal growth patterns, and site- and species-specific patterns since 1825. A moist summer in the year $t - 1$ and an early start of the current growing season favored growth of both species. A prolongation of the growing season into fall was the most distinguishing factor between the species. A long and gradual climatic gradient shifted to a short gradient with a clear segregation between the southern and northern parts of the transect. This shift, around 1875, was abrupt and characterized by a turbulent climatic period. The observed pattern was likely related to a large-scale shift in the mean position of the Arctic Front that occurred at the end of the 1800s. No discrete climatic setting explained the present switch from mixedwoods to conifers at 49°N. Awareness of such nonequilibrium relations between climate and species distribution is essential when assessing vegetation responses to future climate change.

Résumé : À l'aide d'une approche dendrochronologique, nous avons étudié les effets spatio-temporels des changements climatiques sur la croissance radiale de *Picea mariana* (Mill.) BSP et *Pinus banksiana* Lamb. selon un gradient latitudinal dans l'ouest du Québec. Le transect inclut, près du 49° de latitude N., une transition abrupte entre la forêt mixte et la forêt coniférienne. Des analyses de corrélations ainsi qu'en composantes principales sont utilisées pour mettre en évidence, depuis 1825, les patrons de croissance spatio-temporels communs, ainsi que les changements plus spécifiques aux sites et aux espèces. La croissance des deux espèces est favorisée par des étés humides à l'année $t - 1$ et par un début hâtif de la saison de croissance durant l'année courante. Un allongement de la période de croissance durant l'automne est le principal facteur qui distingue les deux espèces. Une transition climatique graduelle du sud au nord a fait place à un gradient plus court discriminant les portions sud et nord du transect. Autour de 1875, ce changement fut abrupt et caractérisé par une période de grandes fluctuations climatiques. Une fluctuation importante de la position moyenne du front polaire vers la fin du 19^e siècle serait vraisemblablement la cause des changements observés. La transition entre la forêt mixte et la forêt coniférienne observée au 49° de latitude N. ne s'explique pas par la présence de conditions climatiques distinctes. L'absence d'un équilibre entre les conditions climatiques et la distribution des espèces est un élément important à considérer dans l'étude des effets des changements climatiques futurs sur la végétation.

Introduction

The climate of the North Atlantic region and bordering areas is influenced by shifts in the position of the Arctic frontal system connected with ocean circulation and changes in air mass distribution (Bryson 1966; GRIP members 1993; Hurrell 1995). Consequently, changes in climate have affected boreal areas bordering the North Atlantic throughout

the entire Holocene and have caused marked changes in species distribution and abundance (Bryson 1966; Larsen 1971; Huntley 1990; Richard 1993; Payette and Lavoie 1994). On shorter and more recent time scales these climatic changes have caused changes in community structure, growth, and productivity (Ritchie 1986; Kullman 1996a; Hofgaard 1997; Scott et al. 1997); triggered changes in the disturbance regime on both sides of the North Atlantic (Bergeron and Archambault 1993; Engelman et al. 1994); and caused changes in vitality and physiognomy of forest ecosystems (Kullman 1986; Hofgaard et al. 1991; Lavoie and Payette 1994) and in moisture conditions and availability (Cook and Jacoby 1977; Tardif and Bergeron 1997a).

Climatic prerequisites for forest growth change gradually from south–north throughout the boreal zone. Generally the limiting effect of precipitation decreases and the importance of temperature increases with increasing latitude (cf. Tuhkanen 1984; Woodward 1987). Along such latitudinal gradients, both continuous and abrupt changes in regional vegetation pattern can be observed. In eastern Canada an

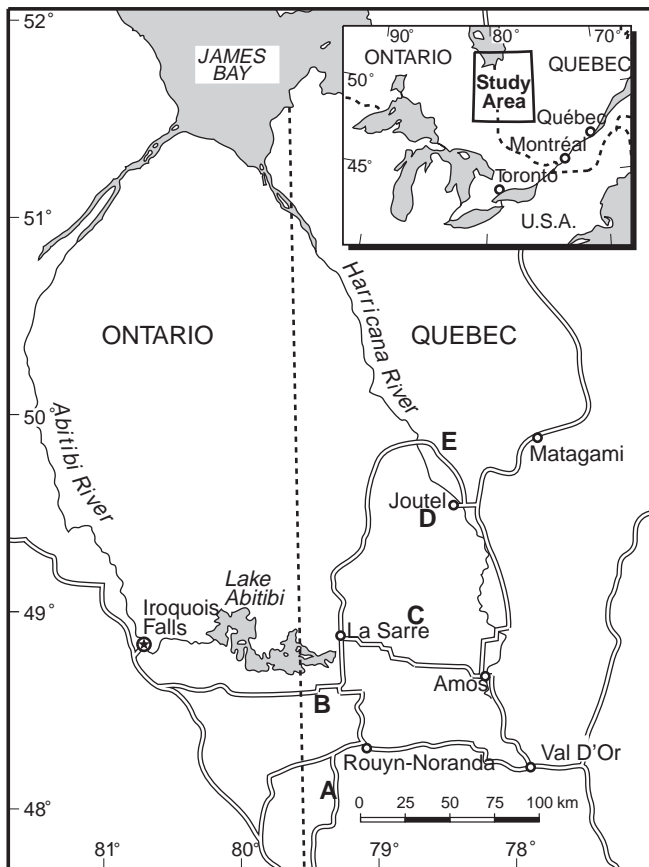
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Fig. 1. Location map of the study area in western Quebec. The inset shows the position of sites (A–E) along the south–north gradient and locations of the meteorological station (*), main water courses, and main roads.



apparent transition from balsam fir (*Abies balsamea* (L.) Mill.) dominated areas into black spruce (*Picea mariana* (Mill.) BSP) dominated areas occurs at approximately latitude 49°N (Grondin et al. 1996). Hypothetically, this shift in regional vegetation pattern may be caused by long-term climate. This would imply that climate to the south of such a spatial position must, at least during some period of time, have been significantly different from climate to the north. Thus, an abrupt climatic change may explain the switch from a mixed forest characterized by late-successional stands of balsam fir to the south and black spruce and jack pine (*Pinus banksiana* Lamb.) forests to the north. This hypothesis is complicated by the fact that all major species are found in both vegetation zones but with strong differences in regional abundance. Alternatively, the transition between these vegetation zones might be explained by spatial differences in disturbance regimes. There is a growing amount of literature documenting the effects of climate change on fire frequency (Clark 1988; Johnson and Larsen 1991; Bergeron and Archambault 1993).

In addition to the spatial climatic gradient from south–north, the climate settings during the last 200 years constitute a temporal climatic gradient. This period covers the termination of the Little Ice Age (LIA), which was a 400- to 500-year long cold period (Grove 1988). The LIA included both warm and cold climatic anomalies; the coldest intervals

were from ca. 1570 to ca. 1730 and during most of the 1800s (Bradley and Jones 1993), followed by a circumpolar warming, and a climatic transition into the present century. Several boreal tree species have shown significant growth increases since late 1800s (Jacoby and Cook 1981; Payette and Filion 1985; Payette et al. 1985; Scott et al. 1988; Hofgaard et al. 1991; Archambault and Bergeron 1992; D'Arrigo and Jacoby 1993; Kelly et al. 1994). Pronounced impacts of climate on tree-ring growth are generally seen along latitudinal distribution limits of the species, e.g., the southern part of the boreal forest. Both high- and low-frequency changes in precipitation and temperature pattern are emphasized (Emanuel et al. 1985; Bonan et al. 1990). These spatial and temporal gradients offer possibilities to test the hypothesis of the stability of a climatic boundary over time. Additionally, detailed analyses of species specific growth responses, to a broad range of climate variables, during the climatic transition from the LIA into the present century are useful tools in assessing responses to future warming.

In this paper we use tree ring analyses (Fritts 1976; Fritts and Swetnam 1989; Schweingruber 1996) to (i) evaluate climatic factors correlated with radial growth of *Picea mariana* and *Pinus banksiana* in the southern part of the boreal forest, (ii) evaluate the variation in species responses in relation to a latitudinal gradient from 48 to 50°N along the Quebec–Ontario border, (iii) evaluate species-specific response to the recent warming since the mid-nineteenth century, and (iv) investigate possible climatic evidence of the shift in dominant species at latitude 49°N.

Material and methods

Latitudinal gradient and sample sites

Ring-width chronologies were developed from five sites along a latitudinal gradient in western Quebec, from 48 to 50°N, with a 0.5° latitudinal interval (Fig. 1). The region surrounding the study area is known as the northern clay belt of Quebec and Ontario, a large physiographic region created by lacustrine deposits from the proglacial lakes Barlow and Ojibway (Veillette 1994). The main part of the study area drains northwards to James Bay, but the southernmost part of the latitudinal gradient drains southwards through the Ottawa River. The topography of the landscape is generally flat and uniform with low-elevation hills and rock outcrops, mainly between 300 and 400 m above sea level (a.s.l.).

The area is characterized by two bioclimatic vegetation zones (Grondin et al. 1996). The southern part of the area is characterized by late-successional stands dominated by balsam fir with paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* Moench), and black spruce. In the northern part, black spruce becomes the main dominating species. Post-fire stands dominated by trembling aspen (*Populus tremuloides* Michx.), paper birch, and jack pine are abundant in both zones (Rowe 1972).

The sampling (in July and September 1994) included *Picea mariana* and *Pinus banksiana*, growing in xeric habitats along the latitudinal gradient. Xeric habitats were chosen to maximize individual tree age. All sampling sites along the gradient were rock outcrops except for the northernmost site, where a well-drained sandy hill was chosen. At each site one or two locations with old stands were sampled (Table 1).

Although xeric sites were chosen throughout the gradient, the moss cover and thus the potential soil moisture varied because of individual differences in time since stand initiation (Table 1).

Table 1. Site characteristics.

Site	Name	Species	Latitude, longitude (N, W)	Stand age (years) ^a	Chronology length	Cores (trees) included	No. of cores at 1913 ^b	Absent rings (%)	No. of false rings
A	Opasatica Lake	<i>Picea mariana</i>	48°06', 79°18'	>300	298	61 (31)	59	0	20
B	Hébécourt Lake	<i>Picea mariana</i>	48°29', 79°27'	234	206	59 (31)	57	0	59
B	Hébécourt Lake	<i>Pinus banksiana</i>	48°29', 79°27'	234	219	49 (33)	44	0.17	139
B	Duparquet Lake	<i>Pinus banksiana</i>	48°28', 79°19'	197					
C	Chicobi Hills	<i>Picea mariana</i>	48°51', 78°38'	>180	177	61 (32)	60	0.01	29
C	Chicobi Hills	<i>Pinus banksiana</i>	48°51', 78°38'	>180	182	57 (31)	56	0.11	13
D	Hedge Hills	<i>Picea mariana</i>	49°16', 78°24'	ca. 144	181	67 (34)	67	0.01	26
D	Joutel W	<i>Picea mariana</i>	49°26', 78°27'	>180					
D	Hedge Hills	<i>Pinus banksiana</i>	49°16', 78°24'	ca. 144	185	67 (35)	66	0.04	49
D	Joutel W	<i>Pinus banksiana</i>	49°26', 78°27'	>190					
E	Joutel N	<i>Picea mariana</i>	49°47', 78°32'	>280	218	57 (29)	57	0.02	2
E	Joutel N	<i>Pinus banksiana</i>	49°47', 78°32'	>280 ^c	282	51 (26)	6 ^d	0.07	6
E	Joutel N	<i>Pinus banksiana</i>	49°47', 78°32'	ca. 85					

Note: For sites where two sample sets were taken for a species, values for the chronology length, cores (trees) included, number of cores at 1913, absent rings, and number of false rings are combined totals.

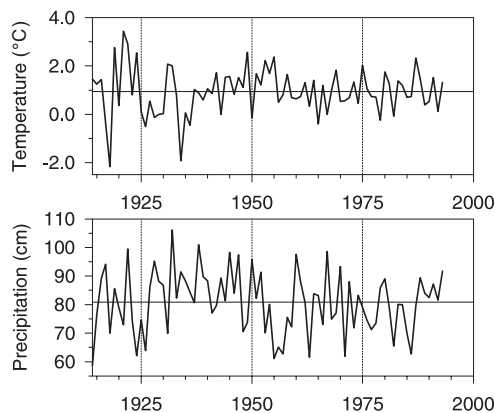
^aTime since last fire or approximate time since stand initiation.

^bFirst year of climatic record from Iroquois Falls.

^cSnags.

^dMore than 30 cores were used from 1920 onwards.

Fig. 2. Annual mean temperature and annual total precipitation calculated for the period September to August (1914–1993) at the Iroquois Falls meteorological station (Environment Canada 1993).



Within these xeric habitats the fine-scale distribution of the sampled species differed somewhat, with predominantly jack pine growing in the most xeric positions.

The stand at site A (Fig. 1) had an old-growth character, i.e., trees in a broad range of age classes and dead trees in different degrees of decomposition. The tree layer consisted of the above-mentioned species, except jack pine, but additionally eastern white cedar (*Thuja occidentalis* L.) and white pine (*Pinus strobus* L.) were important components. Sites B and D were the two most xeric sites. The tree layers of both sites were dominated by black spruce and jack pine cohorts that regenerated after the last fire. The tree layer of site C had an old-growth character, and *Picea mariana*, *Picea glauca*, *Pinus banksiana*, *Abies balsamea*, and *Betula papyrifera* codominated the stand. At site E, two stands were sampled, one old-growth stand lacking living jack pine and one younger post-fire stand dominated by the jack pine cohort that regenerated after the last fire in the beginning of present century (Table 1). The tree layer of the old-growth stand was dominated by *Picea mariana* but included also *Abies balsamea* and *Betula*

papyrifera and standing and prostrate dead *Pinus banksiana*. This site was the only one where dead trees were included to build the chronology.

Climate

In general, and on the regional scale, the area is influenced by cold and dry arctic air during winter, and by warm and moist air originating from the south during summer. 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 shaping through time (Bryson 1966; Gates 1993). The climate of the transect is continental with cold winters and warm summers. The mean annual temperature ranges from just over 1°C in the southern sections of the transect to near 0°C in the northern sections. A cold arctic air mass dominates the transect during the winter with the mean temperature in January ranging from -17°C in the south to -20°C in the north. In the summer, a relatively moist tropical airmass and a typically dry polar airmass alternately influence the transect. July mean temperature ranges from 17°C in the south to about 16°C in the north. Growing degree-days above 5°C are about 1300–1400 across the transect. The mean annual precipitation ranges from over 900 mm in the southeast to about 850 mm in the north. Snowfall averages around 300 mm across the transect (Environment Canada 1986a, 1986b, 1993). Iroquois Falls meteorological station (48°45'N, 80°40'W, 259 m a.s.l.), located close to the center of the gradient (Fig. 1), exemplifies the local climate (Fig. 2). The mean annual temperature is 0.8°C; the mean of the coldest month, January, is -17.6°C; and mean of warmest month, July, is 17.1°C. On average, the area has 5 months with mean temperatures $\geq 5^\circ\text{C}$, May through September, which approximates the length of the growing season. Precipitation data show a maximum in July–September and a minimum in February (Environment Canada 1993).

Core sampling and preparation

A mean of 33 trees per species (range 30–35 spruce and 26–38 pine) were cored at each of the five latitudinal sites (A–E). Two samples from each tree were collected at breast height in opposite directions. Only living trees were used throughout the gradient

Table 2. Chronology statistics.

	<i>Picea mariana</i> sites					<i>Pinus banksiana</i> sites				
	A	B	C	D	E	B	C	D	E	
Autocorrelation*	0.55	0.32	0.33	0.37	0.36	0.42	0.29	0.54	0.40	
AR model*	6	1	1	3	1	1	1	2	1	
Signal-to-noise ratio	13.9	13.7	18.0	18.6	14.8	12.0	12.7	18.3	7.8	
Variation in PC1 (%)	38.3	36.8	40.5	39.6	38.9	36.1	34.8	37.3	38.8	
Mean sensitivity	0.17	0.17	0.16	0.17	0.18	0.22	0.19	0.22	0.19	
SD	0.16	0.15	0.14	0.15	0.15	0.19	0.16	0.21	0.16	
Mean correlation										
Among all cores	0.36	0.35	0.39	0.38	0.37	0.34	0.32	0.35	0.35	
Among trees	0.36	0.35	0.38	0.38	0.36	0.33	0.32	0.35	0.34	
Within trees	0.57	0.52	0.61	0.59	0.54	0.55	0.54	0.62	0.62	

Note: The years 1914–1993 were used as common interval for all chronologies except *Pinus banksiana* site E, where 1924–1993 were used because of the small number of old trees.

*Statistics refer to variation in the standard chronology.

except for the northernmost site, where the data set was increased with 10 old pine snags. All cores were mounted, planed, and visually cross-dated by the use of pointer years. The ring widths were measured with an accuracy of 0.01 mm, using a Velmex Uni Slide traversing table connected to an Acu Rite III digital computer. The COFECHA computer program (Holmes 1983) was used to test for possible dating or measurement errors. All cores with potential errors were rechecked and corrected if possible; otherwise, they were omitted from further analyses. Additionally, series that had low correlation with the mean site chronology ($r < 0.5$) were excluded. Elimination of cores and (or) trees throughout the cross-dating and validation procedures resulted in a total data set of 529 cores (Table 1).

Construction of chronologies

The Dendrochronology Program Library software package was used for all the statistical analyses (Holmes 1992). Raw ring-width series were standardized to remove individual long-term growth trends (Fritts 1976; Fritts and Swetnam 1989; Cook and Kairiukstis 1990). These individual index series were used to construct master chronologies for each site and species.

High-frequency chronology

Procedures in ARSTAN (Cook 1985; Holmes 1992) designed to eliminate nonclimatic variation were applied on the ring-width series. The following steps were followed.

- (i) Each individual raw ring width chronology was detrended by using a spline function (Cook and Peters 1981) and the degree of smoothing was fixed at 50% frequency response of 60 years. A 60-year spline preserves about 99% of the variation within individual series at a wavelength of 19 years. This means that common trends (1–20 years) between trees are conserved.
- (ii) Long-term variation in ring-width series were removed by dividing observed values by predicted values, thereby obtaining standardized ring-width indices.
- (iii) To further remove effects of endogenous stand disturbances, the indices for individual cores were averaged together by applying a robust estimation of the mean value function (Cook 1985).
- (iv) Finally, the series were prewhitened by autoregressive modeling (Cook 1985; Cook and Kairiukstis 1990). This procedure removes lower frequency variation and enhances the common signal, which normally has a better correlation to yearly climatic fluctuations. These residual chronologies (detrended and prewhitened) for each site and species were used for all

correlation analyses and principal component analyses (see below).

Low-frequency chronology

To facilitate analyses of the long-term changes throughout the gradient, a ring-width chronology including the low-frequency signal was constructed for each site and each species. These low-frequency chronologies were constructed by dividing each individual tree-ring series by its mean, using procedures in the ARSTAN program (Cook 1985; Holmes et al. 1986). This straight-line standardization approach gives an equal weight to slow- and fast-growing trees without altering each series' low-frequency trends (Fritts 1976). Individual cores were then averaged together to form the site- and species-specific low-frequency chronologies.

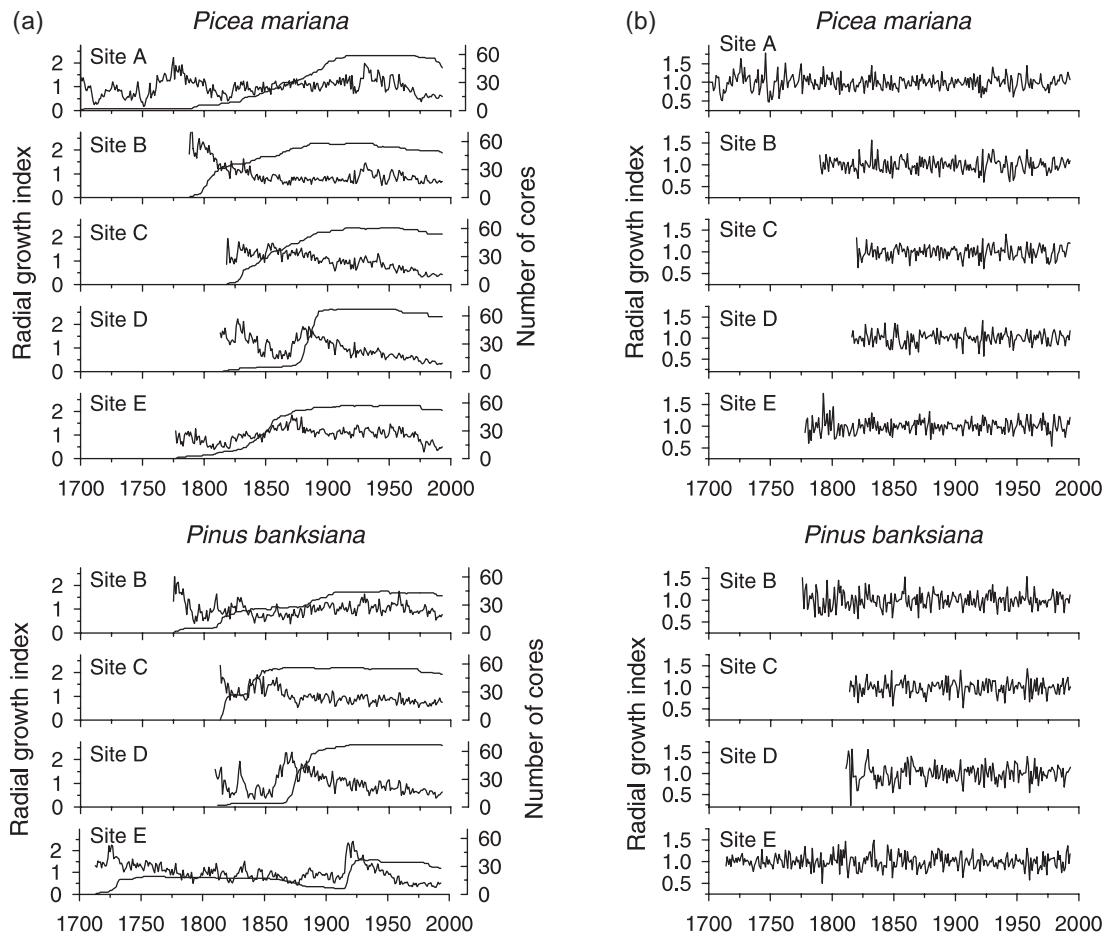
Relationships between sites and between species

Correlation patterns along the gradient, among sites, among species, and through time were examined by using Pearson's correlation and principal component analyses (PCA) (Peters et al. 1981; Blasing et al. 1984). Six 51-year intervals, held in common by all chronologies, from 1825 to 1993 were used for these analyses. (Additionally, a seventh interval, 1800–1850, was used for the longest chronologies.) All intervals were shifted by 25 years except for the last one, where the shift was 17 years to create a complete 51-year interval up to 1993. Through standard PCA techniques (program CANOCO, version 3.1; Ter Braak 1988) the nine residual chronologies were transformed into principal components (PCs). We used a correlation matrix where the years were considered as variables and the nine site chronologies as observations. The loadings of the PCs were used for analyses of species-specific and latitudinal dependent patterns through time.

Growth–climate relationship

Climatic response of *Picea mariana* and *Pinus banksiana* radial growth was analyzed with correlation and response-function analyses (Fritts 1976; Blasing et al. 1984; Briffa and Cook 1990) by using standard procedures in the software program PRECON, version 4.0 (Fritts et al. 1991). Fifty bootstrap iterations were computed to assess statistical significance of the climate variables (Guiot 1990). The analyses were performed to test two different relationships: (i) the relation between ring-width indices and climate variables and (ii) the relation between main principal components scores and climate variables. The analyzed relationships were computed for 32 climate variables consisting of monthly mean temperature and total precipitation values from Iroquois Falls meteorological station. A sequence of 16 months, from May in the year prior to

Fig. 3. *Picea mariana* and *Pinus banksiana* chronologies for all sites along the latitudinal gradient. (a) Standard chronologies. The thin lines show number of cores included in the mean. (b) Residual chronologies.



growth ($t - 1$) to August in the year of growth (t), were used. Missing data, only 1.8% since the start in 1913, have been estimated from the nearby Cochrane station, 40 km northwest of Iroquois Falls (Archambault and Bergeron 1992). The analyzed period was 1914–1993, which was the length in common between the climate record and the chronologies. Additionally, two sub-periods, 1925–1975 and 1943–1993, were analyzed.

Results and interpretation

Chronology statistics, long-term trends along the gradient and characteristic periods

Spruce chronologies might be somewhat more informative than the pine chronologies, as spruce has a slightly stronger signal-to-noise ratio and more variance in the first eigenvector. Variation within trees and among trees is similar for both species along the gradient (Table 2). The low-frequency variation in ring width visualized by the low-frequency chronologies (Fig. 3a) give insights into long-term environmental trends in this southern boreal forest region. At the local scale these trends are affected by climate, disturbance, tree recruitment, and aging processes within the individual stands. At the regional scale, when focusing on the oldest stands, these trends may disclose spatiotemporal changes in the climate. The youngest stands (sites C and D and the young pine group in site E) show clear age-related growth trends. No such trend was shown by the oldest stands during

the last 150–200 years, apart from during recent decades. All sudden growth releases in the pine sites and in spruce site D are related to increase in the number of cores included (Fig. 3a) (i.e., large ring widths near the center on young trees; this effect is preserved in straight-line standardization). Taking this into consideration, the longest chronologies (A, B, and E) show that the 1800s and the early 1900s was a period with slow growth, succeeded by a period with slightly faster diameter growth. Positive growth response to improvement of the climate during the 1930s to 1950s is best shown by spruce along the gradient, and then most evident in the southernmost site. Furthermore, since the 1950s, growth of both spruce and pine has shown a net downward trend.

Pine shows more year-to-year variation (mean sensitivity) than spruce (Table 2), a pattern that remained consistent during the six analyzed successive 51-year intervals between 1825 and 1993 (Table 3). During the interval 1850–1900, the mean sensitivity of both species decreased. Additionally, both species show a slight decrease in year-to-year variation during the last 51 years, but the decrease in spruce is more pronounced than in pine.

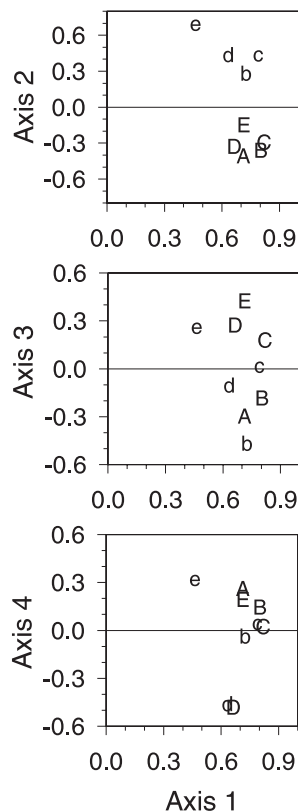
Altogether, 343 false rings were noted. Their appearance and distribution were site and species specific (Table 1) and temporarily uneven. This pattern indicates that the production of false rings in the area is related to ground moisture

Table 3. Mean sensitivity for successive 50-year intervals (overlapping by 25 years).

Sites	1825–1875	1850–1900	1875–1925	1900–1950	1925–1975	1944–1993
<i>Picea mariana</i>						
A	0.19	0.14	0.18	0.20	0.16	0.15
B	0.19	0.16	0.18	0.18	0.15	0.15
C	0.15	0.14	0.18	0.18	0.16	0.15
D	0.22	0.16	0.17	0.20	0.15	0.14
E	0.17	0.14	0.16	0.15	0.16	0.19
Mean	0.18	0.15	0.17	0.18	0.16	0.16
<i>Pinus banksiana</i>						
B	0.21	0.20	0.18	0.20	0.20	0.18
C	0.18	0.15	0.18	0.19	0.22	0.19
D	0.21	0.20	0.22	0.23	0.23	0.20
E	0.20	0.18	0.18	0.15	0.18	0.21
Mean	0.20	0.18	0.19	0.19	0.21	0.20

Note: For each site, the lowest value is given in boldface.

Fig. 4. Principal components score positions of all *Picea mariana* (A–E) and *Pinus banksiana* (b–e) residual chronologies, 1825–1993.



conditions (cf. Material and methods). For both species and at all sites, most of these false rings (56%) occurred in the period 1880s to 1920s, which could be interpreted as a period with increased drought stress (Fritts 1976).

Relations between sites and between species

Principal component analyses

Principal component analyses were run for all the chronologies (1825–1993; Fig. 3b) with the purpose of discriminating the major environmental factors responsible for the

position of each individual chronology through time. Cumulatively, the first four PCs accounted for 85% of the total variance. The loadings for PC1 describe the environmental signals that were held in common by both spruce and pine (Fig. 4). The second axis (PC2) encompasses variables specific to differences between the species. All spruce chronologies had low component loadings and pine chronologies had high values that clearly separated them into two groups. PC3 shows the sum of variables discriminating a north–south gradient, where the southernmost site had the lowest loadings and the northernmost had the highest loadings for each species separately. Along the fourth axis (PC4), spruce and pine appear more or less in pairs per site. This indicates that there might still be some site-specific and (or) stand-dynamic signal left in the chronologies (6% of the variation). Analyses of relative chronology positions through time showed that these patterns were consistent throughout all six analyzed intervals (Fig. 5).

Ordinations based on the six intervals identify the temporal pattern in chronology positions. Along the common environmental axis (PC1) the correlation between each chronology and the axis increases continuously from the mid-1800s up to the mid-1900s (Fig. 5). Thus, some growth-related variables explained increasingly more of the variance in both species at all sites up to the middle of the current century. This indicates that the climatic forcing of growth of both species along the entire latitudinal gradient changed towards homogeneity. During the last 51 years this homogeneity has slightly decreased. The least homogeneous 51-year intervals for spruce and pine were 1850–1900 and 1825–1875, respectively (Fig. 5). The most homogeneous interval for both species was 1925–1975. Additionally, for the period 1850–1900, axis one explained 20% less common variation than for 1925–1975 (Table 4). This indicates a more site-specific response during that period compared with the other analysed periods. The correlation between each chronology and the second axis, where the differences in species appear, were more or less constant for the analyzed time intervals, when both species were taken together (Fig. 5a). However, individual sites did change position within each species group, and the density of the groups were changed. Along this axis, spruce sites had the least in common during 1875–1925, and pine sites, during 1850–1900. Both spruce and

Fig. 5. Principal components score positions of all *Picea mariana* (A–E) and *Pinus banksiana* (b–e) residual chronologies for six successive 51-year intervals from 1825 to 1993. (a) PC 1 versus PC 2. (b) PC 1 versus PC 3.

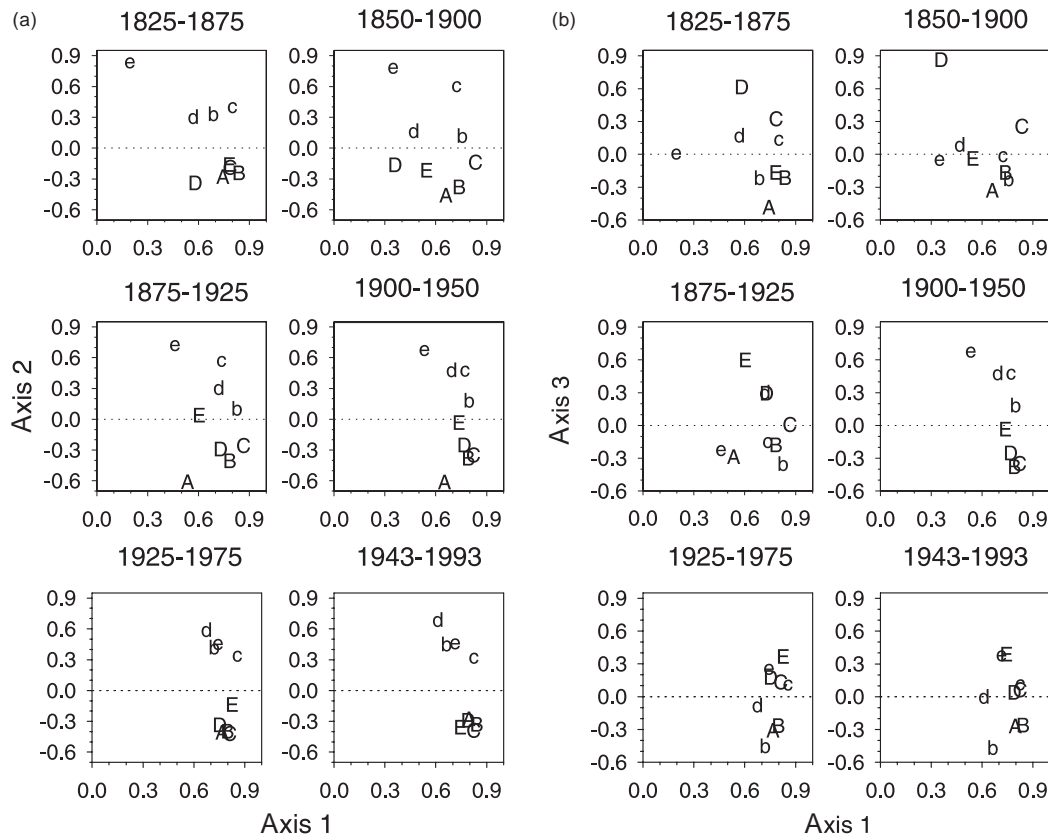


Table 4. Percentage of variance explained by the first four axes of each PCA.

Period	Axis 1	Axis 2	Axis 3	Axis 4
1825–1875	47.7	15.6	9.9	8.5
1850–1900	39.3	16.7	11.2	10.5
1875–1925	49.9	18.6	9.3	7.2
1900–1950	53.9	18.7	7.7	5.9
1925–1975	59.8	16.7	7.1	5.4
1943–1993	57.7	17.4	7.5	5.4

pine chronologies had the most condensed distribution during the later half of the current century. This pattern suggests that the concordance between species-specific environmental variables along the latitudinal gradient was destabilized for spruce around the turn of the century, and for pine somewhat earlier, and again stabilized during the later half of the current century. Along the third axis, where the south–north gradient is presented, the total range between sites is more or less constant (Fig. 5b). Correlation between individual chronologies and this axis change only slightly through time except for the northernmost site (site E). During the 1800s, these chronologies did not “fit” into the north–south pattern of the axis. However, during the 1900s they moved, in relation to the other chronologies, to a position at the northernmost end of the environmental gradient. This might be interpreted as a consolidation of the north–south climatic gradient during the later half of the current century.

Correlation analyses

Analyses of spatiotemporal similarities between the sites showed that for both black spruce and jack pine the correlation between sites, irrespective of distance between the sites, was lowest during the 51-year interval centered around 1875 (Table 5). Low correlations for both species, and at both long and short distances, are indicative of variable environmental conditions on a regional scale. As the residual chronologies (Fig. 3b) were produced to reduce magnitude of the effects of site-specific and age-related environmental factors, these correlation analyses give insight into spatiotemporal changes in the climate environment.

For spruce at the greatest distance between sites (i.e., 2° latitude) the weakest correlation occurred around the turn of the century. This is somewhat later than at all other distances for both species (Fig. 6). At the same time, sites at 0.5–1° latitude distance were correlated more strongly. Strong correlations between close sites suggest that climatic conditions (to diameter growth) included low spatial variability throughout the region during the time period. Weak correlations at longer distances indicate the presence of a long environmental (climatic) gradient along the spatial gradient. Similar and strong correlations between all possible site combinations are indicative of homogeneous climatic conditions throughout the whole latitudinal gradient. One such period, centered around 1950, was present in the spruce data (Fig. 6a). This means that the diameter growth of spruce during the mid-20th century was controlled by a similar climate pattern along the whole spatial gradient. The mid-19th

Table 5. Correlations between sites, based on the residual chronologies, during successive 51-year intervals (overlapping by 25 years), and for 1825–1993.

Sites	Latitudinal distance (°)	1800–1850	1825–1875	1850–1900	1875–1925	1900–1950	1925–1975	1950–1990	1825–1993
<i>Picea mariana</i>									
A–B	0.5	0.61	0.76	0.68	0.58	0.69	<u>0.80</u>	0.74	0.72
A–C	1	—	0.46	0.48	0.58	<u>0.70</u>	<u>0.70</u>	0.67	0.62
A–D	1.5	—	0.26*	0.10 ns	0.39	0.53	<u>0.63</u>	0.51	0.41
A–E	2	<u>0.64</u>	0.62	0.29*	0.22 *	0.47	0.58	0.50	0.49
B–C	0.5	—	0.63	0.57	0.74	0.73	0.75	<u>0.80</u>	0.70
B–D	1	—	0.45	0.24 *	<u>0.68</u>	0.65	0.60	0.67	0.55
B–E	1.5	0.41	0.64	0.33	0.33	0.47	<u>0.65</u>	0.59	0.52
C–D	0.5	—	0.57	0.43	0.64	0.71	<u>0.76</u>	0.73	0.62
C–E	1	—	0.61	0.51	0.54	0.56	<u>0.71</u>	0.70	0.60
D–E	0.5	—	0.39	0.08 ns	0.40	0.57	0.61	<u>0.67</u>	0.45
Mean		0.55	0.54	0.37	0.51	0.61	<u>0.68</u>	0.66	0.57
<i>Pinus banksiana</i>									
B–C	0.5	—	0.62	0.62	0.70	<u>0.72</u>	0.71	0.59	0.64
B–D	1	—	0.43	0.25 *	0.53	0.60	0.69	<u>0.72</u>	0.54
B–E	1.5	0.36	0.25 *	0.25 *	0.42	0.46	<u>0.59</u>	0.51	0.38
C–D	0.5	—	0.51	0.40	0.64	0.66	<u>0.71</u>	<u>0.71</u>	0.60
C–E	1	—	0.45	0.64	0.72	0.69	<u>0.77</u>	<u>0.77</u>	0.62
D–E	0.5	—	0.15ns	0.11 ns	0.39	0.56	0.69	<u>0.74</u>	0.39
Mean		—	0.40	0.38	0.57	0.61	<u>0.69</u>	0.67	0.53

Note: For each pair of sites the weakest (bold) and strongest (underlined) correlations are indicated along with their latitudinal distance. For the 51-year intervals, correlations >0.23 ($p < 0.05$) and >0.33 ($p < 0.01$) are significant. For 1950–1990, correlations >0.26 ($p < 0.05$) and >0.37 ($p < 0.01$) are significant. *, $0.05 > p > 0.01$; ns, nonsignificant ($p > 0.05$).

century also reflects impact of a short environmental gradient but with somewhat more climatic variability. During recent decades, the homogeneous climatic growth conditions has changed to still low climatic variability but with a longer environmental gradient present along the spatial gradient.

Pine shows a similar pattern to spruce, with the strongest common signal during the mid-20th century (Fig. 6b), but the interval with the weakest correlation (Table 5) is not as emphasized as in spruce. Instead, the entire analyzed part of the 19th century seems to have unstable climatic conditions for pine. Furthermore, the correlation data for pine throughout all analyzed time sequences reflects an overall stabilization of the climatic conditions. The spatial gradient for pine data is shorter and, thereby, shows less clear changes in the environmental gradient, but it is evident that there has been a decline in growth pattern similarities along the latitudinal gradient during recent decades (Fig. 6b). Analyses involving both species at all sites also pointed out the interval around 1875 as the period when the growth pattern of these stands had the least in common (Fig. 6c). This indicates that the environmental (climate) forcing differed the most between the species during that time interval. They were most closely related during 1925–1975 and showed decreasing growth pattern similarities during recent decades.

Correlation with climate

Species-specific responses to climate

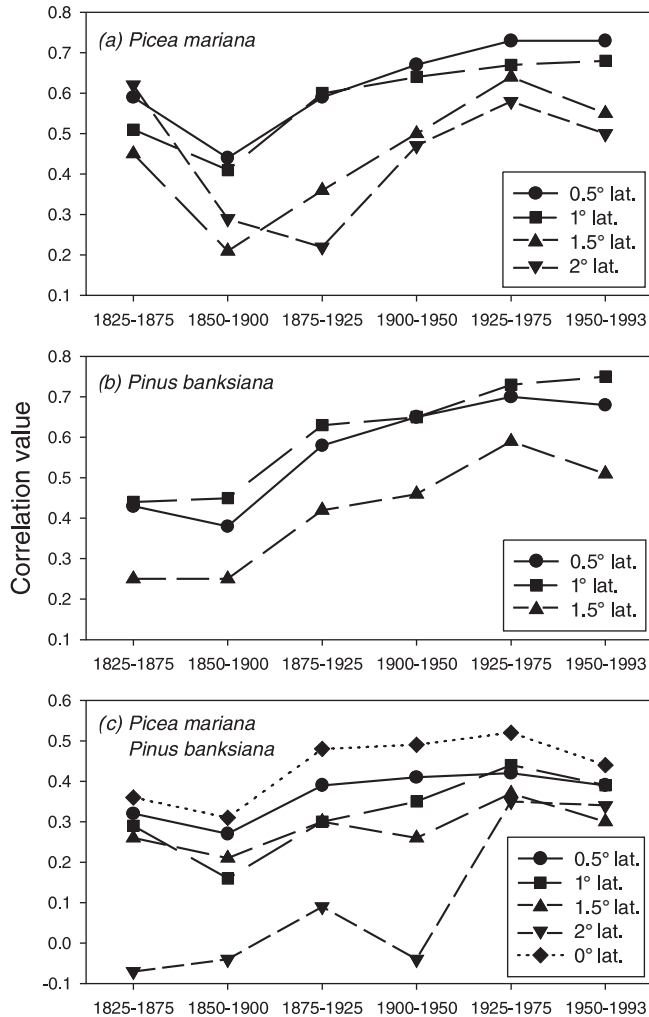
The main pattern to both *Picea mariana* and *Pinus banksiana* throughout the latitudinal gradient is a negative radial growth effect by late-summer temperatures above the mean in the year $t - 1$ and a positive effect by an early start

of the current growth period. This pattern is consistent for both the correlation function and the response function, but the central points differ slightly between the species (Fig. 7).

For spruce during the year t , a dominating positive temperature effect in spring in the north decreases to the south and changes gradually into negative temperature impact during the summer months. During the year $t - 1$, a warm August has a negative effect throughout the gradient except for the northernmost site. These negative temperature impacts point towards an increasing influence of precipitation toward the south along the latitudinal gradient. Precipitation above average in June in both the year $t - 1$ and in the year t had a significantly positive effect on radial growth. The importance of this precipitation effect was enhanced in the south and was most strongly indicated by significant response function elements. The negative effect of high temperatures in October in the year $t - 1$ at the southernmost site is probably also a precipitation signal (rain and snow; cf. Fig. 2). During above-average temperatures, less water would be available to saturate the soil and persist into the next year. Additionally, less snow would be available to add to ground moisture conditions during early summer. Taken together, this indicates that the most important climatic factors for radial growth of spruce along the entire gradient is an early start of the growing season and above-average precipitation during early summer in the south.

As for spruce, pine was negatively affected by late summer above-average temperatures during the year $t - 1$. In contrast to spruce, pine was positively affected by a prolongation of that growing season and negatively affected by precipitation in October (Fig. 7). This probably indicates a negative impact of early snowfall, terminating the growth

Fig. 6. Correlation through time by latitudinal distance between sites (i.e., mean correlation for all sites that are 0.5, 1, 1.5, 2, and 0° of latitude distant from the other site: (a) correlation between *Picea mariana* chronologies; (b) correlation between *Pinus banksiana* chronologies; and (c) correlation between *Picea mariana* and *Pinus banksiana* chronologies. See Table 5 for the number of correlations included in each mean.



period. During year t , pine was positively affected by an early start of the growing season throughout the gradient (not significant at site B). Additionally, the results for the current growing season point towards a positive effect of warm summers in the north and a negative effect in the south. Response-function analyses give more or less the same signal as correlation function analyses but place more emphasis on the positive effect of above-average temperatures in early spring (March) of the year t .

Climatic signals along environmental gradients

Changes in climatic signals along environmental gradients through time were revealed by the use of correlation and response function analyses. Loadings for the three first PCs (cf. above) were run with temperature and precipitation data (Fig. 8). Along the first axis (PC1), representing the common environmental signal at all sites and in both species, an above-average temperature during spring in the year t is a

pervasive pattern (Fig. 8). However, a slight shift in the central point from March to April occurred between 1925–1975 and 1943–1993 (response function). Additionally, site positions along this environmental gradient through time were significantly correlated with below-average temperature in the August prior to growth. During the last 51 years this negative temperature impact was prolonged to also include July and, to some degree, June (positive relationship with above-average precipitation).

Along the axis that differentiates the species from each other (PC2) the most important climate variables are those connected with a prolonged growing season in the autumn prior to growth (Fig. 8). This is indicative of species-specific differences in ability to stay active throughout long growing seasons. During the mid-20th century above-average temperature and below-average precipitation during both October and November increased the environmental distance between spruce and pine. This pattern was slightly changed during the last 51-year interval, when only October had a significant separating effect. However, the effect of a dry July in the year $t - 1$ increased. During year t there was no significant effect when divided into 51-year periods. For the whole period since 1914, however, a dry April and above-average temperature in June significantly added to the environmental distance among the species.

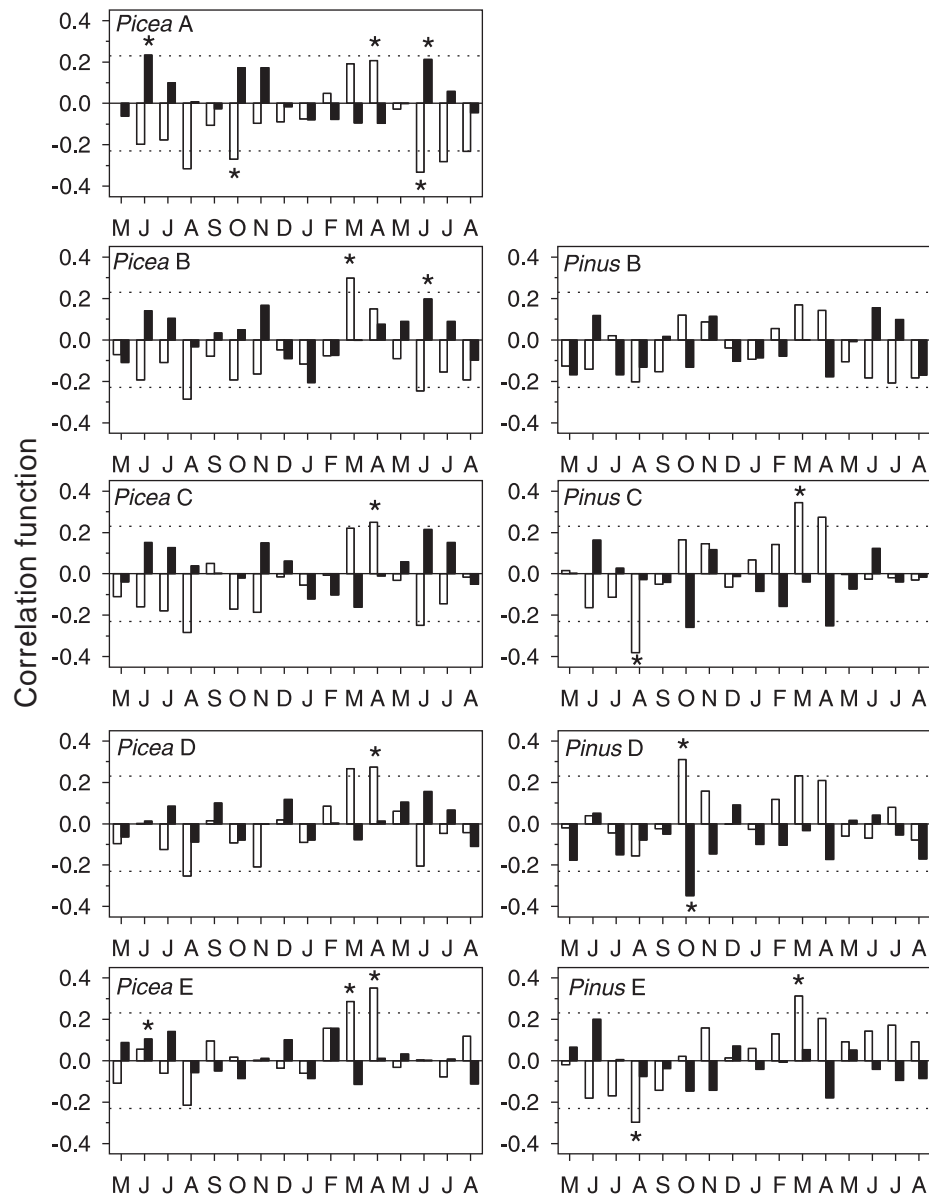
The main climatic variable responsible for the chronology position along the north–south environmental gradient (PC3) during the whole period 1914–1990 was summer temperature during the year t and precipitation in May of the year $t - 1$ (Fig. 8). The positive effect of above-average summer temperatures was not significant during 1925–1975. During the last 51-year interval it turned significant for June and August (with the central point in August). A positive relationship with May precipitation in year $t - 1$ remained more or less stable between the intervals, but an increasingly positive impact of precipitation in July prior to growth was shown during the last 51 years.

Discussion

Growth–climate relationships

The studied gradient crosses the southern boreal forest region where both *Picea mariana* and *Pinus banksiana* approach their southern distribution limit of regional dominance (Burns and Honkala 1990). Given that the limiting effect of precipitation increases towards the south (Woodward 1987) and the fact that xeric sites were chosen (that would amplify the moisture signal), it is somewhat surprising that we did not find a stronger effect of precipitation on growth. Only one fifth of the significant correlation-function and response-function values between growth and climate variables considered precipitation. However, all significant temperature and precipitation values indicate crucial periods, during the years of ring production, when the importance of the temperature–moisture balance is pronounced. Through time, the main climatic variable favoring growth of both spruce and pine has been a moist summer prior to growth and an early start of the growing season in the year t (Figs. 7 and 8). Additionally, a prolongation of the growing season into late fall favors pine and is thus the most separating factor between the species (Fig. 8). Therefore, climatic changes

Fig. 7. Correlation functions, based on residual chronologies from all sites (A–E), showing the effect of temperature (open bars) and precipitation (solid bars) on ring width indices of *Picea mariana* and *Pinus banksiana*. Sign of correlation function coefficients are shown for monthly temperature and precipitation, for May ($t - 1$) to August (t), during the period 1914–1993. Broken lines show statistically significant ($p < 0.05$) correlation function values. An asterisk above or below a bar indicates significant response function elements.



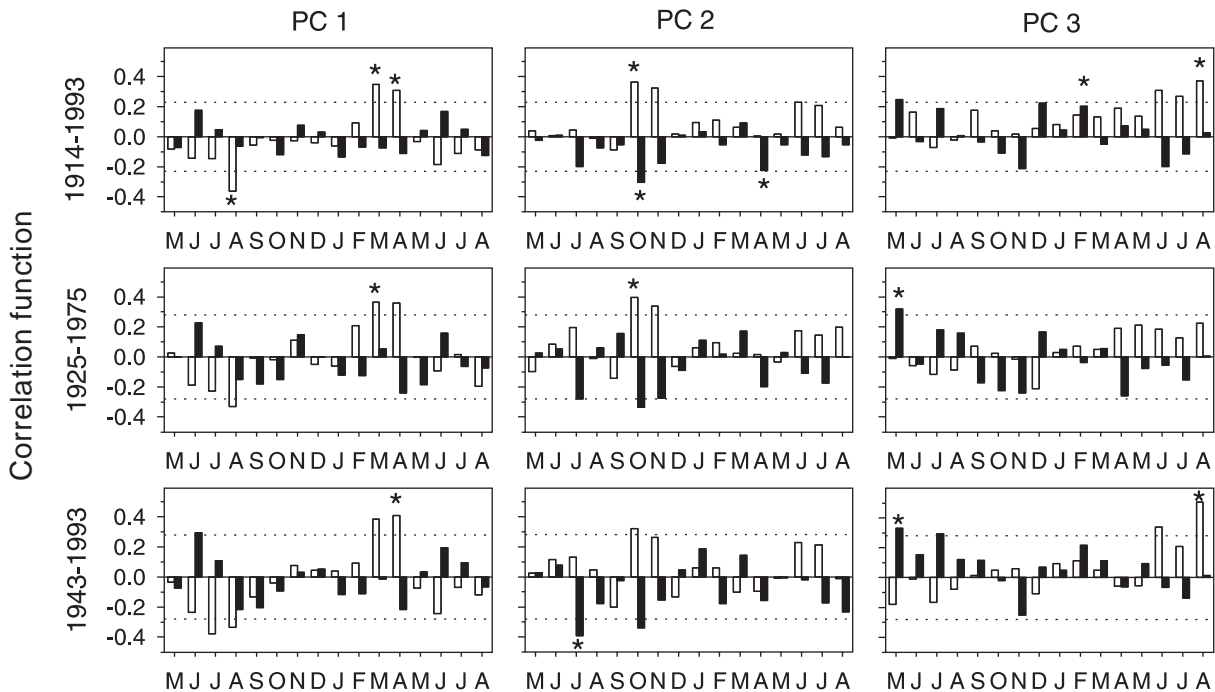
leading to changes in these variables, in particular, would have the greatest impact on forest growth in this region.

Spatiotemporal patterns

The entire Holocene might appear to have been characterized by remarkably stable climate when compared with other interglacial periods (Dansgaard et al. 1993; GRIP Members 1993). When shorter time scales are considered, important climatic changes have occurred during the Holocene, including the Hypsithermal and the LIA (Grove 1988; Gates 1993). The climatic transition from the LIA to the present, visualized in this study by growth responses of *Picea mariana* and *Pinus banksiana* between 48 and 50°N,

encompassed changes in most analyzed climate variables. However, the main pattern seems to have been a shift from a long common environmental gradient to a short gradient (Fig. 5). This was possibly due to increased length of the growing season during the year t and increased moisture availability in the year $t - 1$. This pattern was consistent with a shift in dominant air mass from arctic air to temperate air (Bryson 1966). The studied time period can be divided into three distinct periods, when important changes in the climate regime of the region occurred. First, a stable situation during the mid-19th century changed to more spatio-temporal variability in the period centered around 1875. Following that period, which disrupted the similarities

Fig. 8. Correlation functions, based on principal component scores, for monthly temperature (open bars) and precipitation (solid bars) for the intervals 1914–1993, 1925–1975, and 1943–1993, respectively. The PC1–PC3 are based on the residual chronologies for *Picea mariana* and *Pinus banksiana* from all sites (cf. Fig. 5). Signs of correlation function coefficients are shown for May ($t - 1$) to August (t). Broken lines show statistically significant ($p < 0.05$) correlation function values. An asterisk above or below a bar indicates significant response function elements.



between all sites, the region was influenced by a gradually less variable climate during the first half of the current century. The third main period identified is the mid-20th century, which was characterized by more “stable” growing conditions (probably due to low spatiotemporal climatic variability).

During the mid-19th century the results show a fairly stable climate situation along the entire gradient. The sites were well correlated with each other (Table 5, Figs. 6a and 6b), the species were well separated in their environmental space (Fig. 5a), and the trees were sensitively reflecting year-to-year variations in their environment but were growing slowly. This pattern indicates that the climate was less favorable, possibly because of colder conditions, but that the trees were not subjected to severe stress. Instead, such a pattern reflects some kind of balance with the climatic environment; it points towards fairly dry conditions during both spring and autumn but probably no extreme drought stress during summer.

During the period around 1875 the results suggest a changing climatic period when the north–south gradient was disrupted, and the common variance between the species decreased as also shown by the decrease in correlation. Additionally, the trees were no longer responding sensitively to year-to-year variations (Table 3). This decrease in mean sensitivity around 1875 shows that it was possibly not only the environmental conditions that changed during that interval but also the vitality of the stands. Low-vitality trees (e.g., senescent, old, or dying trees) are shown to have low ability to respond to year-to-year variations in their environment (Jacoby and D’Arrigo 1995; Kullman 1996b). However, dur-

ing the time interval 1850–1900, when the mean sensitivity decreased throughout the gradient, most trees were young. Since then they have lived another 100–150 years and have apparently gained in vitality, which is paralleled in other boreal forest ecosystems (Kullman 1986; Payette et al. 1985; Hofgaard et al. 1991). Consequently, the spatially consistent decrease in mean sensitivity can not be explained by old age. It probably indicates that the stands along the entire gradient were suffering from climatic stress during the period around 1875. This stress was uniform in its temporal occurrence along the gradient but not uniform in the climatic variables causing the stress from site to site, as correlation between sites decreased. Three main changes in climate pattern can be deciphered. The north–south gradient was weakened, which indicates a change towards decreased moisture availability during early summer in the year $t - 1$ and a cold summer in the year t (Fig. 8, PC 3). The similarity between spruce and pine chronologies increased, pointing towards a cold and moist autumn (Fig. 8, PC2). Finally, the overall decreased correlation among sites indicates that August in the year $t - 1$ was dry, and spring in the year t was cold (Fig. 8, PC1). Pine was less affected than spruce to the changes during 1850–1900 possibly because of better drought resistance. This greater sensitivity of spruce to moisture limitation is consistent with the physiological differences between the species (Burns and Honkala 1990). Further, the presence and distribution pattern of false rings points towards a period of drought stress.

The continuous change towards more favorable growth conditions for both species, up to the mid-20th century, is indicative of a moist and warm climate with long growing

seasons. This increased moisture availability in the studied area is also verified by a substantial decrease in the fire frequency (Bergeron and Archambault 1993), and an increase in major floods (Tardif and Bergeron 1997b), after the end of the LIA. Furthermore, the north-south gradient was established during the first half of the current century, with summer temperatures in the year t and summer precipitation in the year $t - 1$ being the most determining variables (Figs. 7 and 8). The similarity between spruce and pine decreased, pointing to a prolonged growing season for pine into October. Since the mid-20th century this climate pattern has been somewhat weakened as seen from decreased correlation between sites. This indicates an increasing importance of moisture availability during summer in the year $t - 1$.

Several lines of evidence presented here suggest that a shift in the climate pattern occurred during the end of the 1800s. Small but important changes of a wide range of temperature and precipitation variables mediated growth response changes throughout the transition zone between mixedwood and boreal coniferous forest. These apparent climate changes and responses did not show any evidence of temporal differences along the studied gradient. No distinct spatial position separating different climatic patterns along the gradient was found during any time interval. Lack of such a spatial position indicates that the changes were synchronous in time along the entire gradient.

In terms of changing positions of air masses, it can be inferred that during the LIA the arctic air had its summer mean position south of 48°N. Consequently, the growth of the forests along the whole gradient was controlled by a cold and dry climate. Around 1875 the gradient from 48 to 50°N was encompassed by a transition zone between the two dominating air masses, dry arctic air and moist air of southern origin. Additionally, it can be inferred that during the mid 20th century the arctic air had its mean position north of 50°N. Consequently, the gradient was dominated by moist and warm air masses with a southern origin. A similar temporal pattern in the mean summer position of the Arctic Front has been shown at the Arctic tree line, 10° of latitude to the north (Scott et al. 1988). In that area, arctic conditions dominated during most of the 19th century, a consistent warming trend after 1880 led to dominance of temperate conditions during the mid-20th century, and arctic conditions have dominated after 1970 (Scott et al. 1988). Together, these data visualize the large-scale sudden shift of the mean position of the Arctic Front that occurred at the end of the 19th century. Additionally, such shifts are influenced by changes in the North Atlantic Oscillation (NAO) (Hurrell 1995). The largest changes in NAO between single years occurred during the 1880s to 1890s (Hurrell 1995), which is indicative of a period with increased climatic variability.

Vegetation zonation

The present data has not provided any evidence that a distinct position between the two dominating air masses was formed at 49°N during any part of the studied time period, as could be inferred from the shift in forest composition at that position (Grondin et al. 1996). Instead, the climatic transition from the LIA into the present climate apparently acted as a wave on a large regional scale. On a finer spatial scale

the change appeared as a sudden change without leaving any evidence of temporal transition along the gradient. Thus, the present regional vegetation pattern, with *Picea mariana* dominating north of 49°N and *Abies balsamea* dominating south of 49°N, cannot be explained by the present climate condition or by the shift in climate conditions since the LIA. It is essential to be aware of this nonequilibrium relation between climate and species distribution when assessing vegetation responses to future climate change (Sykes and Prentice 1996; Hofgaard 1997). The present situation is not in equilibrium and consequently cannot be used as such in models of future vegetation pattern and species distributions. However, detailed knowledge of species-specific growth responses to changes in a wide range of climate variables is a fundamental prerequisite for reliable predictions of future boreal forest development.

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