



Original article

Growth–climate response of Jack pine on clay soils in northeastern Canada

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ABSTRACT

We used tree-ring data from a major North American boreal tree species, Jack pine (*Pinus banksiana* Lamb.), to decipher spatial and temporal tree-growth responses to climate variability within the area of northwestern Quebec and northeastern Ontario. Fifteen sites with clay soils were selected and grouped into North and South sub-regions at approximately 49°N and 50°N, respectively. Tree-ring chronologies were analyzed through a response function for the years 1951–2000 to identify growth-limiting climate factors. Increased precipitation in June in the previous year and a warm month of April this year favored radial growth whereas higher temperature in September and increased precipitation in October, both of the previous year, and current June precipitation were negatively related to growth. There was a clear difference in climatic response between the southern and northern sub-regions: southern sites were more responsive to temperature dynamics while on northern sites Jack pine growth appeared negatively influenced by an excess of precipitation. Soil conditions, with larger areas covered by less water permeable clay deposits in the northern sub-region, explain this result. If recently observed trends towards warmer springs continue, Jack pine may increase its radial growth in the study area. However, increases in fall precipitation, also predicted under the future climate, may offset the positive effect of previous years weather on clay sites.

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Introduction

The human-induced buildup of atmospheric CO₂ and other greenhouse gases has resulted in an increase of 0.6 ± 0.2 °C in global mean surface temperature from 1861 to 2005 (IPCC, 2007). South of 60°N in Canada, mean annual temperature from 1900 to 1998 has increased between 0.5 and 1.5 °C (Zhang et al., 2000). By 2100, based on seven global climate models forced by various scenarios of greenhouse gas emissions, it is expected that mean annual temperature in the Eastern Canadian boreal forests may be about 5 °C higher than today and 7 °C higher during the winter (Bergeron et al., 2010).

Similarly dramatic changes were observed with respect to precipitation, with an increase in annual total precipitation from 5% to 35% from 1861 to 2005 (Zhang et al., 2000) and it is expected that an increase from ca. 10 mm in monthly precipitation by 2100, during fall, winter and spring seasons (Bergeron et al., 2010).

Climatic variability has been shown to cause changes in community structure, forest growth and productivity (Ritchie, 1986; Kullman, 1996; Hofgaard, 1997; Scott et al., 1997) triggering changes in the disturbance regime (Bergeron and Archambault, 1993; Engelmark et al., 1994) and water regime (Cook and Jacoby, 1977; Tardif and Bergeron, 1997) and affecting vitality and physiology of forest ecosystems (Kullman, 1986; Hofgaard et al., 1991; Lavoie and Payette, 1994). Such changes had already affected boreal areas bordering the North Atlantic throughout the entire Holocene and caused changes in species distribution and abundance (Larsen, 1971; Richard, 1993; Payette and Lavoie, 1994; Ali et al., 2008; Carcaillet et al., 2010). Present-day climate change could have even stronger impacts on boreal forests (Soja et al., 2007). Remote sensing measurements over North America (Zhou et al., 2001) have indicated approximately 12 ± 5 days growing season extension from 1981 to 1999 as a consequence of recent warming. Rapid warming of average annual surface air temperature at northern latitudes has also led to increased soil temperature and soil freeze thaw in both permafrost and non-permafrost regions (Osterkamp and Romanovsky, 1999; Camill, 2005).

Landscape-scale species distribution and abundance patterns are generally controlled by both climate and, indirectly, by

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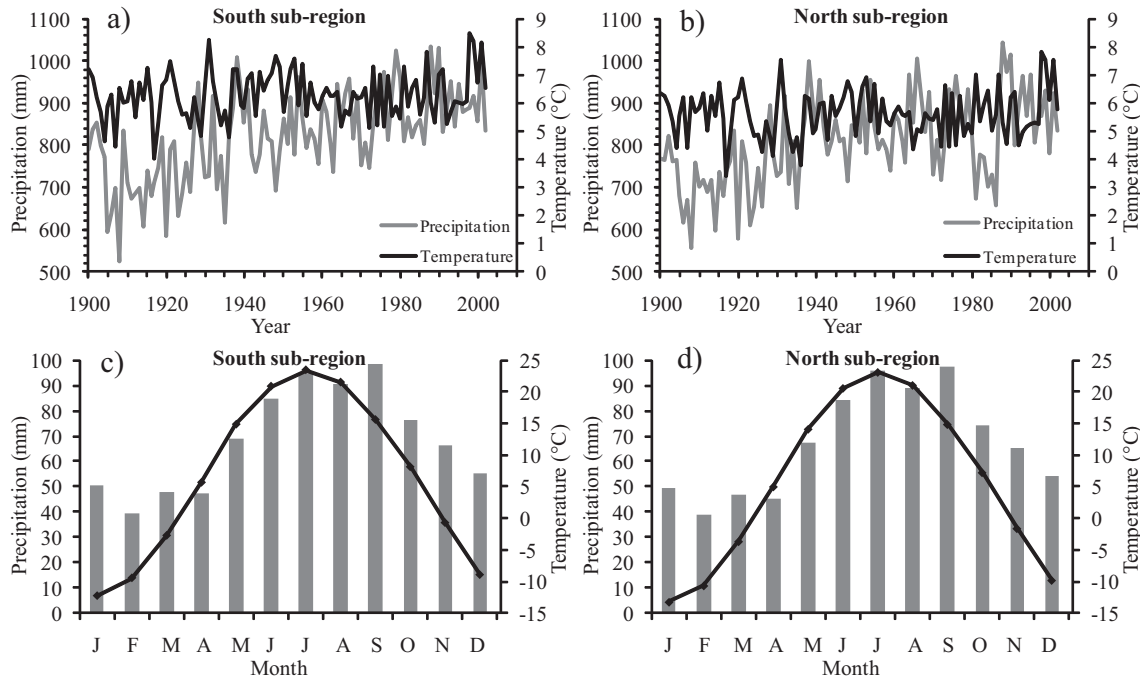


Fig. 1. Annual maximum mean temperature and annual total precipitation for the period 1900–2002 in (a) southern and (b) northern sub-regions. Ombrothermic diagrams for (c) South and (d) North sub-regions, in which the histograms represent mean monthly precipitation and the diamonds maximum monthly temperatures.

disturbance regime (Bergeron and Brisson, 1990; Bekker and Taylor, 2001; Giesecke et al., 2007). Usually, the limiting effect of precipitation decreases and the importance of temperature increases with increasing latitude (Tuhkanen, 1984; Woodward, 1987). In the eastern Canadian boreal forest, dendroclimatic investigation on boreal species along latitudinal gradients indicated that the present vegetation was not in equilibrium with current climate and there is a need for detailed knowledge of species-specific growth responses to environmental changes (Hofgaard et al., 1999; Huang et al., 2010; Drobyshev et al., 2010).

In the Canadian boreal forest, Jack pine (*Pinus banksiana* Lamb.) is a shade-intolerant fire-adapted species, colonizing dry and nutrient-poor habitats, e.g. sand plains or outwash channels of glacial origin, where it is more competitive than other boreal tree species (Bergeron and Brisson, 1990; Gauthier et al., 1993; Lesieur et al., 2002; Bergeron et al., 2004). Nevertheless, even if its density and basal area are higher on well-drained tills than on clay sites, it presents higher productivity on mesic but not waterlogged soils (Béland and Bergeron, 1996). Due to the scarcity of dry and sandy deposits, Jack pine is thus a secondary element of the regional vegetation in boreal Québec (Gérardin, 1980).

Although fall, winter and spring precipitation are predicted to increase during the 21st century in the eastern Canadian boreal forest, the associated increase in temperature may result in overall negative dynamics in water availability and an increase in fire frequency (Bergeron et al., 2010). This could thus prevent expansion of the mixedwoods into the coniferous forest and enhance Jack pine distribution and growth where its development is presently limited by low fire-frequency and high water table. Jack pine is one of the most important commercial species in eastern Canada (OMNR, 2004; Parent, 2010). Within the context of sustainable forest development, it is therefore critical to better understand the responses of all species to climate variability, which should help in predicting changes in forest composition and structure in the eastern boreal forest of North America.

Tree rings have long been used to explore the long-term growth reactions to historical climate variations and to further assess

the impacts of future climate warming on tree growth and forest ecosystems (Fritts, 1976; Tardif et al., 2001; Drobyshev et al., 2010, 2011). In this paper, we present the results of a dendroclimatic study of Jack pine in the boreal zone of Western Quebec and Eastern Ontario. Our primary goal was to evaluate climatic sensitivity of natural Jack pine stands using monthly climatic data. We hypothesized that increase in latitude, resulting in decrease in average growing season temperature, length of the growth season and lower evapotranspiration due to colder and wetter environments would create generally more stressful conditions for pine growth and subsequently lead to its higher climatic sensitivity. Therefore, the objectives of our study were to (1) identify climatic factors correlated with radial growth of *Pinus banksiana* in the boreal forest, (2) evaluate the variation in growth responses in relation to latitude (49 and 50°N) and (3) discuss possible impacts of soil moisture on climate–growth relationships in Jack pine forests.

Materials and methods

Study area

The climate of the study area is continental with cold winters and typically warm dry summers. Average annual maximum temperatures recorded to the North (49°59'N, 78°47'W) and to the South (49°19'N, 79°15'W) of the study area are -5.6 and 6.3 °C, respectively, with an average of 807 and 821 mm of precipitation (Fig. 1). Monthly mean temperatures vary from -9.8 to 23.1 °C to the North, and from -9.0 to 23.4 °C to the South, with a mean of 13.3 and 13.8 °C during the spring months (April–June). January is the coldest month and July the warmest. The amount of precipitation is maximum during the summer months (July–September) and minimum in February, varying from 39 to 97 mm in the North and from 40 to 98 mm in the South. Due to the fact that the northern and southern sub-regions of our study zone only differ by half a degree in latitude, the length of the growing season differs by 5 days between the zones (136 days vs. 141 days).

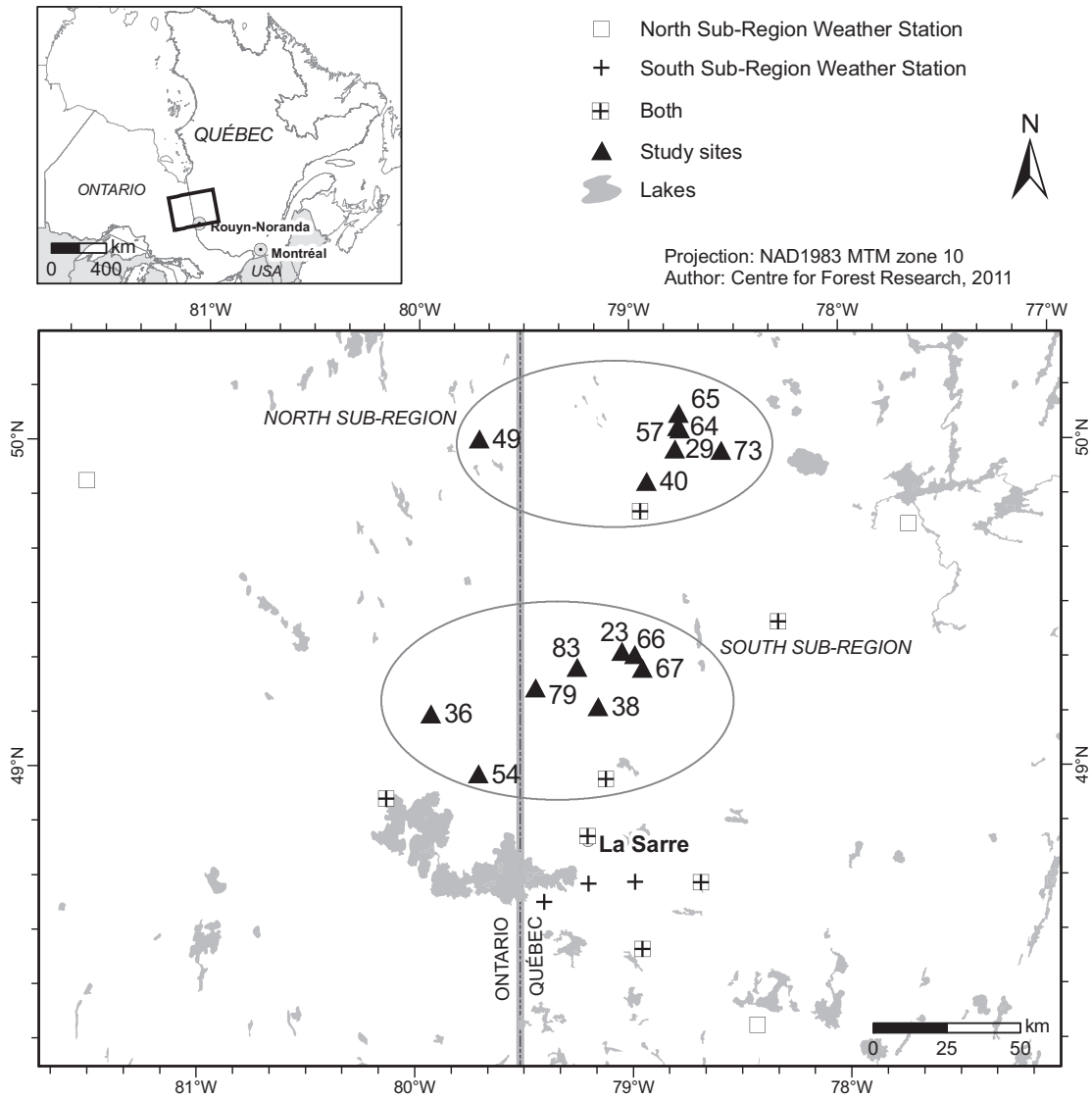


Fig. 2. Location map of the study area in western Quebec and eastern Ontario. The inset shows the position of sites (23–83) within the South and North study sub-regions, main contributing weather stations to climate data, main lakes, and main roads.

The study area (49°–50°06'N; 78°34'–79°57'W) is located in the northwestern Quebec and northeastern Ontario, within the black spruce (*Picea mariana* Mill.)–feathermoss bioclimatic domain (Robitaille and Saucier, 1998), in the Clay Belt region (Fig. 2). The Clay Belt is a large physiographic area created by lacustrine deposits from the proglacial lakes Barlow and Ojibway (Veillette, 1994). The sites in the southern part of our study region are located on quite permeable Ojibway clays, while the sites in the northern part are located on Cochrane tills, more compressed and less permeable clays.

The topography of the landscape is generally flat and uniform with low-elevation hills and rocky outcrops mainly between 300 and 400 m above sea level. Most of the area is dominated by *P. mariana*, which forms monospecific and structurally diverse stands, while sporadic deciduous- and pine-dominated stands are dispersed across the landscape (Boudreault et al., 2002; Harper et al., 2002, 2005). Fire cycle length has increased from 101 years before 1850 to 398 years since 1920, the mean stand age being 148 years (Bergeron et al., 2004). Trembling aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marshall), Jack pine and black spruce (Rowe, 1972) dominate post-fire stands.

Dataset

Site selection and tree sampling

Sampling was performed during the summers of 2000–2002 and included mixed black spruce and Jack pine stands on mesic habitats (Fig. 2). Original data were collected as a part of a study of stand dynamics (Lecomte et al., 2006). Sampled stands were Jack pine dominated and originated from 15 distinct fires of different ages. Selected stands were on fine-textured mineral deposits with a slight slope and free of any sign of anthropogenic disturbance. Sampled sites were grouped into two sub-regions based on the position along North–South gradient: North (above 50°N latitude) and South (between 49° and 49°40'N latitude) (Fig. 2).

Stand age (time since last fire) for the youngest stands (<100 years old) was determined from a stand initiation map (Bergeron et al., 2004) and was validated by counting rings from cross-sections taken at the base of dominant trees. In older stands (>100 years), stand age was obtained by cross-dating (Stokes and Smiley, 1968) cross-sections taken at the base of live and dead dominant trees. Within each sampled area, a plot of 10 m × 10 m was established. All Jack pine trees higher than 2 m were cored, including

Table 1
Site characteristics.

Zone/site number	Latitude, longitude (N, W)	<i>Pinus banksiana</i> (%) basal area ^a	Residual OM ^b (cm)	Stand initiation year ^c	Chronology length (years)	Radii (trees) included
29	49°59', 78°47'	64.6	1.2	1865	132	13 (11)
40	49°53', 78°55'	61.2	1.1	1849	143	6 (6)
49	50°01', 79°43'	48.4	1.2	1847	147	10 (8)
57	50°04', 78°46'	58.4	1.2	1914	92	23 (15)
64	50°03', 78°46'	41.1	1.9	1779	213	3 (2)
65	50°06', 78°46'	57.3	2.1	1797	203	5 (5)
73	49°59', 78°34'	68.4	1.3	1852	150	26 (21)
North	–	–	–	–	214	86 (68)
23	49°22', 79°02'	44.4	1.3	1914	74	40 (24)
36	49°11', 79°56'	59.1	1.6	1924	79	38 (22)
38	49°12', 79°09'	37.2	1.6	1916	78	19 (11)
54	49°00', 79°43'	78.4	1	1951	49	85 (52)
66	49°22', 78°59'	48	1.7	1851	153	13 (13)
67	49°19', 78°57'	22.3	1	1772	174	4 (4)
79	49°16', 79°27'	45.8	1.1	1823	179	6 (6)
83	49°19', 79°15'	56.8	1	1824	171	8 (8)
South	–	–	–	–	224	213 (140)

^a Include both live and dead stems > 2 m in height.

^b Thickness of the residual organic matter, i.e. the organic matter that was not burned by the last fire, located between the mineral horizon and the uppermost charcoal layer.

^c Year of the last fire.

excavated dead trees buried under the organic matter. This resulted in 9–55 Jack pines sampled per plot and the total number of trees for all species varied from 31 to 113 per plot.

Cross-section preparation and analysis

Cross-sections were sanded with up to 400-grit paper and visually cross-dated with the use of pointer years using a dissecting microscope at 40× magnification (Stokes and Smiley, 1968). Each cross-section was scanned and ring widths were measured using CooRecorder 7.2 software (Larsson, Cybis Elektronik & Data AB 2010, <http://www.cybis.se/>). Two radii were measured on each cross-section. When this was not possible because a cross-section was too disintegrated, only one radius was delineated. CDendro 7.2 program (Lars-Åke Larsson, Cybis Elektronik & Data AB 2010, <http://www.cybis.se/>) was then used to cross-date the samples and generate data for the COFECHA computer program (Holmes, 1983) to perform final quality reviews of the data. All cross-sections with potential errors were reevaluated and corrected if possible; otherwise they were omitted from further analyses. Additionally, series that had low correlation with the mean site chronology (below 0.5 for sites < 100 years, and below 0.4 for the sites > 100 years) were excluded. Elimination of trees throughout the cross-dating and validation processes resulted in a total data set of 208 trees (299 radii, Table 1).

Construction of chronologies

The ARSTAN program (Cook, 1985) was used to standardize the raw tree-ring width data and remove individual long-term growth trends (Fritts, 1976; Fritts and Swetnam, 1989; Cook and Kairiukstis, 1990). The series were subjected to robust autoregressive modeling and outlier removal (Cook, 1985). This method removes autocorrelation in tree-ring series, which may obscure climate-growth relationships and a common signal present in a stand chronology. The chronologies resulting from “horizontal line through mean”, “negative exponential” and “cubic-smoothing spline” detrending methods were graphically compared to each other. If low-frequency patterns in the chronologies were climatically induced, they would be expected to be similar within sites while if they were due to a disturbance, they should have differed and be more localized. The first two methods did not

remove much low-frequency variability and age-related growth trends while “cubic-smoothing spline” appeared more effective in removing such variability. Consequently, the detrending method chosen was a 32-year (50% frequency-response function) “cubic-smoothing spline”. Residual detrended chronologies for each site and sub-region were used for all correlation and response function analyses.

Individual radii were averaged to form the site- and sub-region-specific chronologies. To facilitate analyses of the long-term changes throughout the gradient, a ring-width chronology was constructed for 15 sites and two sub-regions: North sub-region and South sub-region.

Expressed population signal (EPS; Wigley et al., 1984), a function of inter-tree correlations, was used to assess the strength of common signals in the developed chronologies.

Climatic data and statistical analyses

Climatic data were obtained through BioSIM simulations using a database of daily weather station data values (Règnière and Bolstad, 1994). BioSIM is a model that allows interpolation of daily weather data from a dataset of weather stations for specified locations. Daily data were obtained by interpolating data from the 10 weather stations closest to the North sub-region and to the South sub-region (Fig. 2) and adjusting for differences in latitude, longitude and elevation between the data sources and the location thus avoiding a heterogeneity problem. One bias could result from the differences in the type of instrument used to collect rainfall. However, it only concerns rainfall traces at a monthly level therefore this bias is weak.

An examination of the availability of weather stations used for interpolation shows fewer weather stations prior to 1930. The mean distance between the meteorological stations and the sites in our study area decreases by an order of two from the beginning to the end of the 20th century (Girardin et al., 2011), implying lower data quality in the earlier period. To address this issue we limited our analyses to 1951–2000, which also corresponds to the common period covered by the climate record and the majority of the site chronologies.

Table 2
Statistical characteristics of residual chronologies for sites and sub-regions.

Zone/site number	Average intercorrelation	Average mean sensitivity	Signal-to-noise ratio	Expressed population signal
29	0.590	0.159	11.111	0.917
40	0.474	0.164	16.028	0.941
49	0.547	0.138	13.578	0.931
57	0.598	0.168	18.754	0.949
64	0.481	0.179	7.900	0.888
65	0.460	0.157	0.655	0.396
73	0.579	0.108	12.801	0.928
North	0.498	0.124	18.161	0.948
23	0.663	0.170	67.236	0.985
36	0.591	0.168	53.385	0.982
38	0.615	0.164	40.637	0.976
54	0.640	0.184	3.610	0.783
66	0.437	0.172	3.036	0.752
67	0.420	0.134	29.710	0.967
79	0.553	0.164	17.467	0.946
83	0.432	0.122	30.924	0.969
South	0.468	0.122	1.443	0.591

The ten most effective weather stations in generating climate data for site locations over the chosen period are represented in Fig. 2. Their average distance to the North sub-region was 129 km and 70 km to the South sub-region (sites 29 and 83 having been chosen as geographical centers of North and South sub-region, respectively).

For dendroclimatic analyses we used a window of 15 months, from previous year June ($t - 1$) to August in the growth year (t). This resulted in 30 climate variables (15 monthly total precipitation and 15 mean monthly maximum temperatures).

Climatic response of *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 program DendroClim 2002 (Biondi and Waikul, 2004). One thousand bootstrap iterations were computed to assess statistical significance of the climate variables (Guiot, 1990).

Expressed population signal (EPS; Wigley et al., 1984) is a function of inter-tree correlations, and is presented in Table 2.

Results

Chronologies and statistics

Jack pine chronologies developed in our study ranged from 49 to 213 years in length (Table 1). The number of included trees varies from 2 to 52 per site, depending on stand age. Due to the rapid decay of Jack pine wood with age, the amount of samples suitable for measurements was limited to old stands (>200 years), i.e. open structured black spruce-dominated stands (Lecomte et al., 2006).

Although we cannot exclude effects of stand density and history, old stand chronologies (>200 years; sites 64, 65 and 67) showed the end of 18th century as a period with generally fast growth, followed by slower growth, with regionally low diameter growth rates (Fig. 3). In the 1800s, two decreasing growth periods can be noticed in both sub-regions, the first one in the 1840s and a longer second one in the 1870s.

Positive growth is particularly apparent in the northern sub-region during the 1950s and 1960s and ends with a sudden decrease peak in 1960. Finally, since the 1970s, growth has shown a net downward trend throughout the latitudinal gradient.

EPS and mean sensitivity values indicated a strong common signal for most sites (0.887 ± 0.039 ; mean \pm SE), except for site 65 (EPS=0.396) (Table 2). Signal-to-noise ratio (SNR; Cook & Kairiukstis, 1990) showed high values for young stands (<100

years) and lower values for older (>100 years) stands (Table 2). Changes in chronology quality was also observed with respect to series average intercorrelations, varying from 0.497 ± 0.020 (mean \pm SE) in old stands (>100 years old) to 0.621 ± 0.035 (mean \pm SE) in younger stands.

Climate–growth relationships

To filter out patterns with low consistency, we only present climatic variables with at least three significant site-level correlations. A warmer September and wetter October during the previous year and wetter current June had a negative effect on radial growth, while increased temperature during the growing month of April and higher amount of precipitation during previous June had a positive effect on growth (Fig. 4). Comparing response functions of North and South chronologies indicated that Jack pine was more affected by temperature in the southern sub-region than in northern the sub-region (3 variables significant vs. none, respectively), while it was more affected by precipitation in the northern sub-region than in the southern sub-region (two significant variables vs. one, respectively; Fig. 4b). Specifically, significant negative growth response to previous year October and current year June precipitation was recorded within the northern sub-region (75 and 100% of responding sites, respectively) and the positive response to previous year June precipitation within the southern sub-region (100% of responding sites).

In the southern sub-region, Jack pine growth was positively correlated with current year April temperature. The October precipitation of the previous year and April temperature of the current year appeared to be the main factors controlling growth. Sites younger than 100 years (23, 36, 38 and 54) within the southern sub-region showed more significant correlations with temperature and precipitation variables when compared to the oldest sites (>100 years, 66, 67, 79 and 83) (Fig. 4a).

Sites in the northern sub-region showed negative effects on growth by October precipitation of the previous year whereas June precipitation of the current growing period was the most pronounced (Fig. 4). Three sites did not respond significantly to any climate variable (Fig. 4a).

Considering sites of both sub-regions, sites of intermediate age (120 years < age < 150 years, sites # 29, 40 and 49) were more climate-sensitive than the youngest (<100 years, 57) and oldest sites (>200 years; 64).

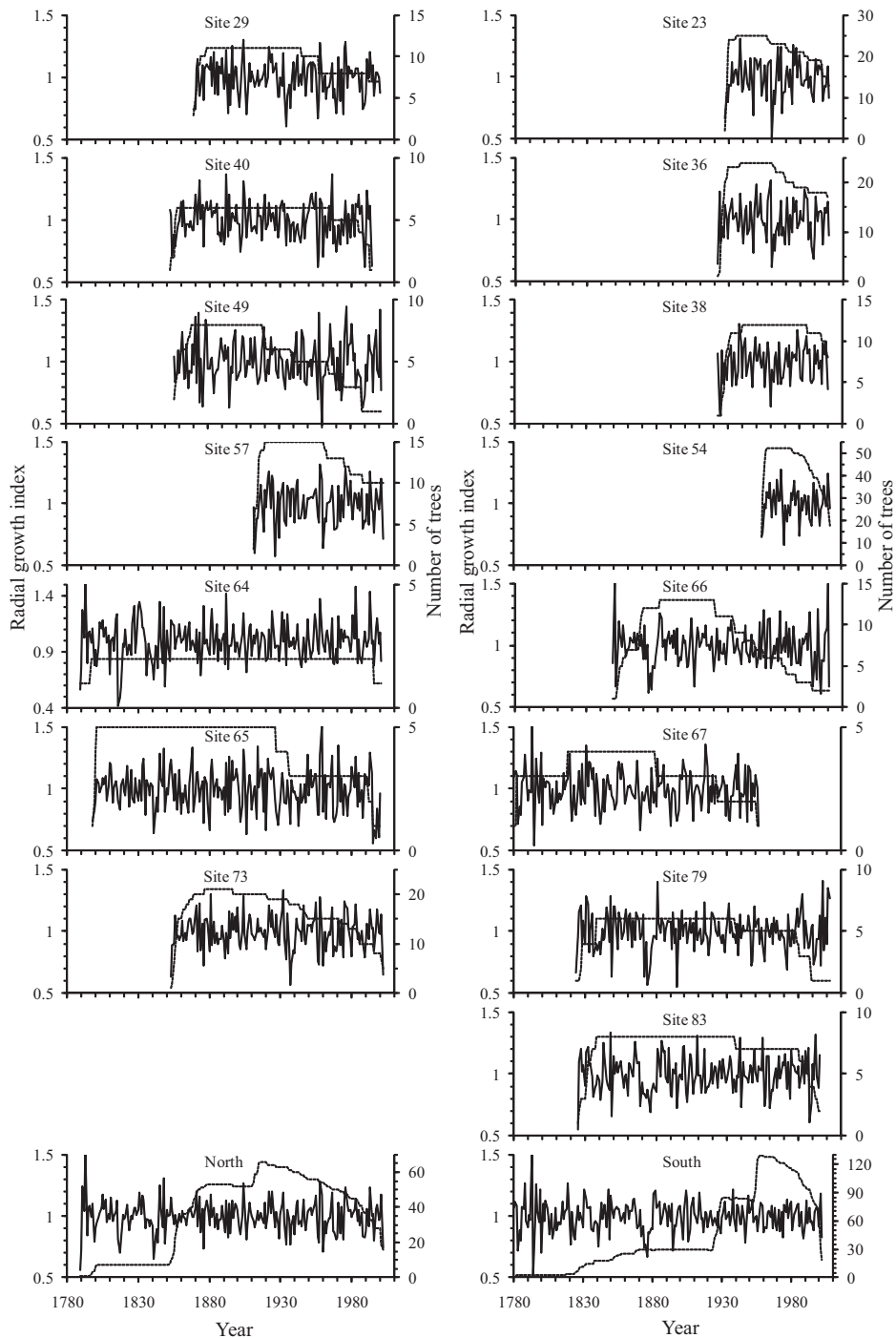


Fig. 3. *Pinus banksiana* residual chronologies, 32-year spline detrended, for all sites along the latitudinal gradient and for northern and southern sub-regions. The dotted lines show the number of trees included in the mean chronology.

Discussion

Radial growth–climate correlations

Positive factors

Jack pine growth responded positively to precipitation in June of the previous year and temperature in April of the current year. Concerning the positive effect of previous June precipitation in the southern sub-region, [Béland and Bergeron \(1996\)](#) showed that moderately dry to moist clays represented favorable conditions for Jack pine high productivity and our southern sites were located

on such soils ([Rowe, 1972](#)). An increase in precipitation at the beginning of the xylem production period, which occurs from mid-May to end of August ([Ko Heinrichs et al., 2007](#)), is likely beneficial for wood production. Further, warm temperatures in spring could favor conifer species owing to their evergreen foliage, which allows them to take advantage of early growing season warmth ([Graumlich, 1993](#)). The importance of air temperature was probably due to its role in triggering the onset of photosynthesis in spring ([Tanja et al., 2003](#)). Higher spring air temperature could also accelerate soil thawing, resulting in the availability of unfrozen soil water that is necessary for overcoming the dormant period

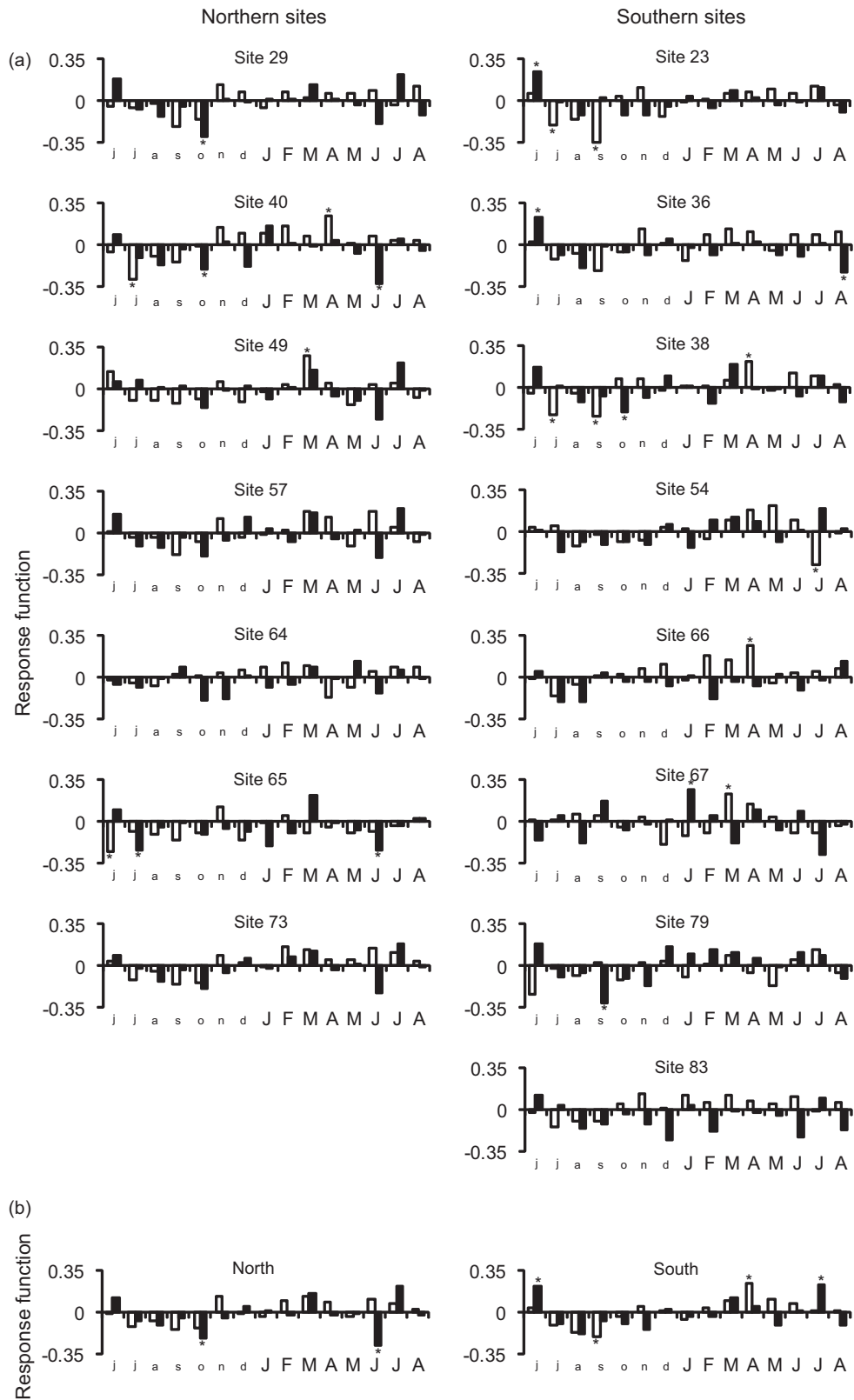


Fig. 4. (a) *Pinus banksiana* growth response function analyses to cumulative precipitation and monthly maximum mean temperature for the period 1951–2000, in the northern and southern sites. Open and solid bars refer to temperature and precipitation, respectively. An asterisk indicates significance of response function coefficient. (b) *Pinus banksiana* growth response function analyses to cumulative precipitation and monthly maximum mean temperature for the period 1951–2000, in the northern and southern sub-regions. Open and solid bars refer to temperature and precipitation, respectively. An asterisk indicates significance of response function coefficient.

(Goodine et al., 2008). Our results thus confirm the positive role of spring temperatures in controlling tree-radial growth in conifer trees of eastern Canadian boreal forest and agree with results from previous studies (Hofgaard et al., 1999; Tardif et al., 2001; Girardin et al., 2006; Huang et al., 2010).

Negative factors

Previous year September temperatures in the southern sub-region generally negatively affected Jack pine growth. We hypothesize that higher late summer temperatures could enhance tree respiration and evapotranspiration thereby resulting in increased water deficit. Climate conditions in late summer influence the bud size (Kozłowski et al., 1991), the size of dormant bud being related to the amount of needle area produced during the first year of bud expansion. Since first year needles are known to be the most photosynthetically efficient (Wang et al., 1995), decreases in their photosynthetic area (which could be expected from decrease in overall bud size) would lower wood production in subsequent years. Our results were consistent with those of Hofgaard et al. (1999) and Huang et al. (2010), who also documented a negative effect of previous summer temperature on radial growth of Jack pine between 49 and 50°N in the mixed boreal forest of western Quebec.

Considering the whole analyzed dataset, our results showed that the previous year moisture condition was one of the most important factors affecting Jack pine growth. In the northern sub-region, Jack pine growth responded negatively to precipitation in June of the current year. The excess of precipitation would be an indicator of less radiation, i.e. less photosynthetic production. Moreover, the northern sub-region is colder than the southern one, thus evapotranspiration is weaker and leads to more humidity in the soils. What is more, the northern sites are located on less permeable clays than are the southern ones (Rowe, 1972), likely amplifying the negative effects of abundant precipitation. We could apply the same logic in explaining the negative effect of previous year October precipitation (Fig. 4). Another hypothesis would relate larger amounts of precipitation with a longer physiologically active periods in the previous year, leaving less time for trees to undergo winter hardening (Pallardy, 2007). Therefore, climatic changes leading to changes in precipitation would likely have the greatest impact on forest growth in this region.

The role of soil conditions

Significant negative growth responses to precipitation during current year June and previous October in the northern sub-region might be related to Jack pine biology and dominant soil conditions of the area. Jack pine is known to quickly occupy areas where mineral soils have been exposed to major disturbances and can grow in a wide range of soil types ranging from dry and sandy soils to clay loams (Bozic, 2010). Moderately dry or moist clays favor productivity of Jack pine (Béland and Bergeron, 1996). It is less competitive than other coniferous species and is typically replaced by black spruce on more humid sites (Gauthier et al., 1993).

Differences in dominant soil conditions might therefore explain the different effect of October precipitation between current and previous studies (Hofgaard et al., 1999; Savva et al., 2008; Huang et al., 2010). In contrast with Huang et al. (2010) and Savva et al. (2008), we found only significant effects of previous June precipitation, but no positive growth responses to March precipitation. Different types of reported coefficients could lead to this result (response coefficients in our paper and correlation coefficients in above-mentioned studies). Our results were non-consistent with those of Hofgaard et al. (1999), who found very limited effects of precipitation on radial growth. As our sites were more humid,

this difference could result from the fact that our study sites can experience waterlogged conditions and increases in precipitation meaning less oxygen available for tree roots.

Changes in the radial-growth climate relation with respect to latitude

The response to climate varied between South and North sub-regions.

When comparing the response functions of sub-regional chronologies (Fig. 4), it appeared that the North sub-region only reacted to precipitation factors and not to temperature. Because they live in colder conditions, a response of northern trees to temperature should have been observed and it should have been more marked than in trees from the South.

The chronology of the southern sub-region was responsive to both temperature and precipitation. However, this result might be an artifact of our dataset. Sites 57 and 73, which did not present responses to any climate variable, contributed 53% of the trees used in the average North chronology (Table 1). The North chronology was therefore less representative of sites of the northern sub-region than was the South chronology for sites of the southern sub-region. The fact that northern sites appeared to be more sensitive to precipitation dynamics suggested that precipitation was an important growth-limiting factor for this species already growing in wet conditions.

During the summer months, southwestern Quebec is affected by warm, moist air originating from the South, whereas the northern area is influenced by cold, dry polar air during winter (Sheridan, 2002). This gradual change in climate factors along a North–South gradient has been suggested in previous studies, which had shown an impact of temperature and precipitation on radial-growth responses (Hofgaard et al., 1999). We thus expected similar differences in climatic response between the southern and the northern sub-regions although our chosen latitudinal gradient was smaller. Our results did not support previously published empirical observations or the outcome of tree growth modeling (Girardin et al., 2008; Huang et al., 2010). Discrepancies in results could not be linked to differences in the thickness of soil organic matter (Table 1) nor to stand age (Table 1 and Fig. 4a). However, the sites studied by Huang et al. (2010) were much more xeric than ours, which are all located on clay. This would confirm that Jack pines present different reaction patterns to climate variables when growing in more humid, growth limiting conditions than when growing on xeric sites.

Conclusion

In the Northern Hemisphere, climate change was associated with warmer winters (IPCC, 2007) and an increase in temperature and precipitation is projected in Canada by 2100 (Plummer et al., 2006; Bergeron et al., 2010). Despite certain limitations of the current study, some patterns of Jack pine growth responding to future climate variability can be suggested.

In the Eastern part of the Canadian boreal forest, Jack pine growth may increase as a result of warmer spring temperatures, which may alleviate the effects of limited growing season warmth though an earlier start of the growing season. It could also limit the effects of cold on soil resource supply, hence leading to enhanced growth of Jack pines, although an earlier start of the growing season would increase the risk for the hydrated trees to be exposed to late spring frosts (Hänninen, 2006).

Our study also showed a one year lag in Jack pine reaction to growing conditions, with a major role of precipitation affecting tree

growth on clay soils, highlighting the modifying effect of soil conditions on eventual large scale precipitation changes. On permeable clays of the southern sub-region, one could expect a positive relation between precipitation and growth, while on less permeable soils of the northern sub-region the opposite effect is expected, primarily due to the increase in soil water logging and decrease in available soil oxygen.

Consequently, with continued climate change and associated predicted increase in fire frequencies (Bergeron et al., 2010), if the amount of water does not increase too much, Jack pine might be able to extend its habitat onto clay soils during the next decades, except where soils are already waterlogged. Further studies should explore the effects of climate change on Jack pine and other boreal species, e.g. by incorporating both direct and indirect impacts of climate change (e.g. insect outbreaks and fires).

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