

Spatial analysis of black spruce (*Picea mariana* (Mill.) B.S.P.) radial growth response to climate in northern Québec – Labrador Peninsula, Canada

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Abstract: The aim of this study is to analyze the relationships between black spruce (*Picea mariana* (Mill.) B.S.P.) growth and climate at a large spatial scale in North America's northeastern boreal forest. The study area (approximately 700 000 km²) is located in the taiga zone of the Quebec – Labrador Peninsula. A network of tree-ring chronologies from 93 black spruce populations was developed. A hierarchical cluster analysis was conducted to analyze tree-ring series affinities, and response functions were calculated to analyze relationships between tree rings and climate. The cluster analysis results showed well-marked spatial affinities among the tree-ring series. These affinities were strongly linked with the spatial variability of the relationships between tree rings and climate. The interannual growth variations were governed mainly by the temperature variables that preceded the growing season (November (negative influence), December–January (positive influence), and April (positive influence)). The growing-season temperature (July temperature) mainly influenced the northernmost populations. Relationships between tree rings and climate in the northeastern boreal forest varied at a large spatial scale. This variability was expressed by a north–south contrast, which appears to be related to a temperature gradient, and an east–west contrast linked to a humidity gradient, which favors winter snow cover.

Key words: dendroecology, relationships between tree rings and climate, taiga, black spruce, Quebec – Labrador peninsula, spatial variability.

Résumé : Le but de cette étude est d'analyser la variabilité spatiale des relations entre la croissance de l'épinette noire (*Picea mariana* (Mill.) B.S.P.) et le climat dans la forêt boréale Nord-Américaine. La zone d'étude (environ 700 000 km²) se trouve dans la région de la taïga de la péninsule Québec–Labrador. Un réseau de dendrochronologies provenant de 93 peuplements d'épinette noire a été construit. Une analyse de regroupement hiérarchique a été réalisée pour analyser les affinités entre les séries et des régressions linéaires multiples associées à la technique « bootstrap » ont été utilisées pour calculer les fonctions de réponse des arbres au climat. Les variations interannuelles de la croissance sont régies principalement par des variables de température qui précèdent la saison de croissance (température des mois de novembre (influence négative), décembre–janvier (influence positif) et avril (influence positif)). Les températures ayant une influence durant la période de végétation (température de juillet) ne s'exerce que sur les peuplements les plus septentrionaux. Les relations cerne-climat dans le nord de la forêt boréale varie fortement sur la zone étudiée. Cette variabilité est exprimée par un contraste nord–sud qui semble être reliée à un gradient de température et par un contraste est–ouest lié à un gradient d'humidité qui favorise la couverture de neige en hiver.

Mots-clés : dendroécologie, relations cerne–climat, taïga, épinette noire, péninsule Québec – Labrador, analyse spatiale.

Introduction

North America's boreal forest is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.), a species indigenous to North America (Farrar 1995). Black spruce forests can be divided into three major forest zones (from south to north): closed spruce–moss forests, spruce–lichen woodlands, and forest tundra (Payette 1983, 1993).

The climate, along with the frequency of disturbance (Payette 2007; Girard et al. 2009), determines both the distribution limits of black spruce and the structure of black spruce forests (Beuker 1994; Lavoie and Payette 1994; Kullman 1996; Hofgaard et al. 1999; Bradshaw et al. 2000; Hänninen et al. 2001; Bertrand and Castonguay 2003). These two factors also influence the physiological and phenological

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processes of this generalist species (Kramer et al. 2000; Kozlowski 2002). In the Quebec – Labrador peninsula, which is located north of the 52nd parallel, black spruce grows over a wide range of environmental conditions from outcrops to peat bogs. Fire occurrences are relatively high in the western region of the peninsula close to James Bay and diminish to become low in the eastern region (Boulanger et al. 2013). In this region, north of the 52nd parallel, black spruce budworm becomes nonexistent or very rare.

The relationships between tree growth and climate can vary spatially due to natural environmental gradients (Briffa et al. 1998; Mäkinen et al. 2002; Pederson et al. 2004; Carrer et al. 2007; Miyamoto et al. 2010). In Québec and Labrador, a number of studies have analyzed the relationship between tree rings and climate in several species (D'Arrigo et al. 1996, 2003; Payette 2007) along latitudinal (Huang et al. 2010; Hofgaard et al. 1999; Girard et al. 2011) and longitudinal (Trindade et al. 2011a, 2011b) transects. Significant variations were observed in the relationship between tree rings and climate for all species and study areas. However, most of these studies have focused on closed-crown boreal spruce and on the influence of environmental variables. Very few studies have addressed the large-scale spatial variability of the relationships between tree rings and climate north of 51°N in the spruce–lichen woodlands and in the forest tundra. The origin of such spatial variation remains unclear (Miyamoto et al. 2010).

The objective of this study is to analyze the relationship between black spruce growth and climate at a large spatial scale in open-crown boreal forests of northeastern North America. Our study area covers the entire Quebec – Labrador Peninsula. It extends from James Bay to the Atlantic Coast (from 49°3'N to 57°72'N and from 58°5'W to 79°1'W). Thus, our study provides a geographical link between studies conducted on the Labrador Peninsula (Trindade et al. 2011a, 2011b; Nishimura and Laroque 2011; Dumaresq 2011), around James Bay (Huang et al. 2010; Hofgaard et al. 1999), and in central Quebec (Girard et al. 2011). Our objectives are (i) to determine the climatic parameters that control tree growth over the entire study area and (ii) to analyze the spatial variability of relationships between tree rings and climate. This study will shed new light on the response of black spruce to climate and will help anticipate future impacts of climate change on the productivity of the most important boreal conifer in northeastern North America.

Materials and methods

Tree-ring data

We created a network of 93 tree-ring chronologies distributed across the Quebec – Labrador Peninsula (Fig. 1; Supplementary Table S1¹). These sites ranged in altitude from sea level to more than 900 m in central Quebec. There was a strong continental gradient including maritime sites situated only a few kilometres from the sea, whereas most of the continental sites were located approximately 480 km from the coast. Black spruce stands sampled in this study (Fig. 1) originate from three major forest formations or bioclimatic zones, as defined in the literature (Payette et al. 2001): forest tundra; spruce–lichen woodlands, which constitute the most widely distributed forest structure in Quebec's high boreal zone (Payette 1992; Girard et al. 2008); and spruce–moss forests. Trees growing in wetlands or peat bogs were not sampled.

A majority of the studied stands were located in the eastern taiga shield (ETS) ecozone (Fig. 1), defined by the Ecological Stratification Working Group (1996). The western part of the ETS consists of three wide ecoregions. The eastern part of the ETS, centered on Labrador, appears to be geographically more complex and is composed of 14 ecoregions. Only four stands were located in

the eastern boreal shield (EBS) ecozone, one in ecoregion 101 and three in ecoregion 105 (Lake Melville).

Stands in the selected sampling area were as homogeneous as possible regarding the topography, soil, and stand structure. A minimum of 12 trees was sampled at each site. Only dominant trees with a straight main stem and free from major anomalies (scars, breaks, etc.) were selected. The sampled stands showed high variability with respect to tree age and density (Supplementary Table S1¹). The youngest sites generally originated from fire and presented an even-aged structure, whereas the oldest sites tended to possess an uneven-aged structure, with the majority of individuals originating through vegetative multiplication. The sites also differed in terms of tree density. Spruce–lichen woodlands are characterized by well-drained, open stands with a sparse shrub layer. By contrast, spruce–moss forests are generally less well drained and possess a denser shrub layer. Our drainage data (Supplementary Table S1¹) shows that 90% of our stands were sampled in drainage categories between 2 and 4 (between well-drained and moderately well-drained terrains, respectively), a percentage that reflects the homogeneity of drainage categories found north of 50°N, in eastern Canada's boreal forest. The sampled stands were generally monospecific, although sporadic occurrences of jack pine (*Pinus banksiana* Lamb.) and larch (*Larix laricina* (Du Roi) K. Koch) were observed in the westernmost stands, whereas balsam fir (*Abies balsamea* (L.) Mill.) and (or) larch were occasionally observed in the easternmost stands.

Climate data and climatic characteristics of the study area

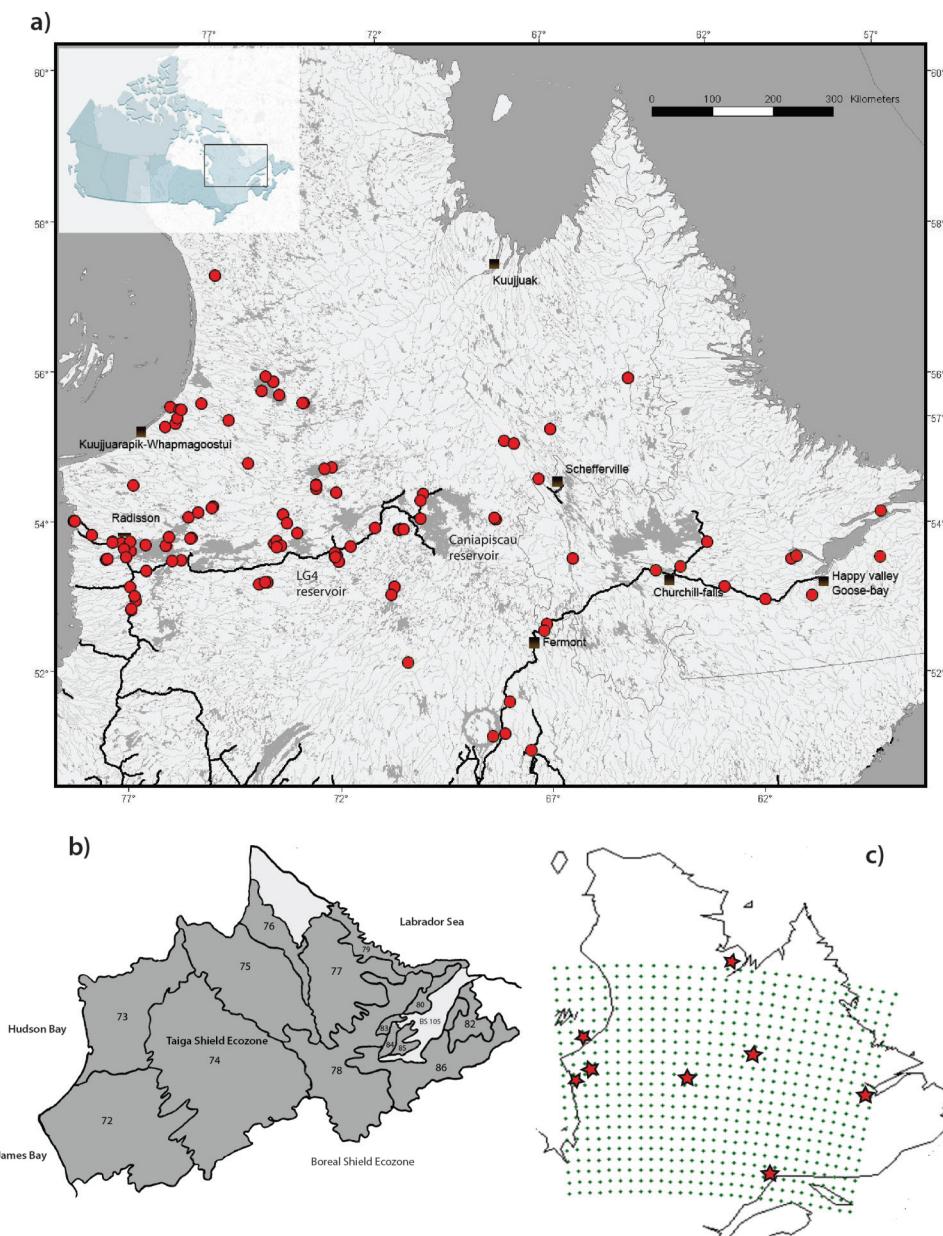
Weather stations are rare and scattered across the study area. Their temporal coverage is often short term and incomplete. For the sake of consistency, we chose a meteorological data grid (0.5° × 0.5°) developed by Hydro-Québec for the province of Quebec and for parts of the adjacent provinces using datasets from weather stations obtained from Environment Canada, the provincial government of Quebec, and private agencies. Available climatic information was kriged using topography as an external drift (Wackernagel 1998; Tapsoba et al. 2005; Jeannée and Tapsoba 2010). The gridded dataset spanned the 1961–2000 period and has been used in a number of recent studies (e.g., Brown 2010; Monette et al. 2012; Poulin et al. 2011). From this gridded dataset, we calculated the sum of monthly precipitation and the mean monthly temperatures for the 1961–2004 period. Temperatures vary along two gradients: a south–north gradient for the western part of the study area and a west–east gradient for the Labrador area. Within the study area, mean annual temperatures range from -6 °C in the northernmost sites to -2 °C in the easternmost sites. In the northernmost sites, mean winter (December–March) and summer temperatures (June–September) are -22 °C and 10 °C, respectively. The easternmost sites present mean winter and summer temperatures of -15 °C and 14 °C, respectively. Summer precipitation within the study area varies along a south–north gradient, with more precipitation falling in the center of Québec. In summer, the mean precipitation is less than 300 mm at the northern sites and more than 450 mm at the southern and central sites. In winter, snowfall varies along a west–east gradient, with the eastern section of the study area receiving approximately 1300 mm of snow, which is nearly twice as much as the 700 mm of snowfall recorded in the western section.

Construction of tree-ring chronologies

The samples were carefully sanded, visually cross-dated under a binocular magnifier, and measured (accuracy of 1/1000 mm) along two radii. Dating of each tree ring was then verified with the program COFECHA (Holmes 1992). The tree-ring width series were subsequently standardized to remove age-related trends and to

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0080>.

Fig. 1. (a) Location of study sites (circles); inset shows location of study area in Canada. (b) Ecozones in the study area. (c) Meteorological grid and main meteorological stations (stars). Figure is provided in colour online.



construct series with comparable dimensions (Fritts 1976). Standardized series were calculated by dividing the tree-ring widths with a theoretical growth curve. This growth curve was calculated using a LOESS fit (Cleveland and Delvin 1988; Nicault et al. 2010) with a smoothing parameter of 0.4, which corresponds to a bandwidth of 40% of the dendrochronological series length. The series was standardized through a function of the R bioindict software package (www.eccorev.fr/spip.php?article389) (R Core Team 2007). Finally, a master chronology for each site was constructed by calculating the mean of all of the standardized mean tree chronologies.

The length of master chronologies ranged from 86 to 358 years (Supplementary Table S2¹). Additional statistics such as expressed population signal (EPS) and mean sensitivity were computed on the entire chronology time period to assess the quality of the master chronology.

Cluster analysis

A hierarchical cluster analysis (Everitt 1974; Gordon 1999) was conducted to analyze the affinities between sites. A measure of similarity was calculated using a matrix of Euclidean distance for each year between all of the mean chronologies for the common period of 1920–1987. Then, Ward's agglomeration algorithm (Ward 1963; Mirkin 2005) partitioned the set of objects. This technique minimizes the interior variance of groups and tends to produce compact, equal-sized dendograms. To evaluate the cluster robustness, we calculated the p values for each cluster via multiscale bootstrap resampling (10 000 iterations). These values, associated with standard error, are expressed in percentage in the dendrogram. Calculations were conducted using the R *pvclust* package (R Core Team 2007).

Analysis of relationships between tree rings and climate

A response function in dendroclimatology is defined as a linear function that links annual tree growth to climate. This linear

function allows climatic parameters that influence tree growth to be identified (Tessier 1986; Guiot 1991; Guiot and Nicault 2010). The goal is not only to determine which climatic parameters influence tree growth but also to identify the nature and strength of the relationships between tree growth and monthly climatic variables. Response functions are linear multiple regressions applied to the principal components of the climatic variables to avoid collinearity. Then, back transformation into the original regressors is applied. The regression is performed 500 times on subsets of data that are randomly selected using the bootstrap method (Efron 1979; Till and Guiot 1990). The coefficients of the response function and the confidence intervals are given by the medians of these iterations at the 2.5th and 97.5th percentiles. Response functions were calculated over three time periods according to the stand sampling date: 1961–1987 (one stand), 1961–1993 (21 stands), and 1961–2001 (68 stands). The explanatory variables consisted of 12 months of temperature data and 12 months of precipitation data, which were integrated separately in the calculation. Temperature and precipitation series were chosen from the grid points closest to the analyzed sites. As ring formation ceases after the end of August – early September, monthly data were applied according to biological years, i.e., from October of the previous year to September of the current year. These calculations were performed using a function of the R *bioindic* package.

The overall reliability of response functions was evaluated based on the determination coefficient (R^2), which expresses the percentage of variance explained by the model, statistical significance according to the *F* test and based on the standard error (root mean squared error (RMSE)), which expresses the model's robustness. The weight of each climatic variable in the regression is evaluated according to its *p* value and to the ratio between each partial regression coefficient (associated with each climatic variable) and its 1/2 95% confidence interval (*S*) (when partial regression coefficient are significant at a 95% level, the *S* value equals one). The sign of the partial regression coefficient also specifies the nature of the relationship (positive or negative) between tree growth and the climatic variables considered.

To analyze the spatial variability of relationships between tree rings and climate, results of the response functions were interpolated over the study area. We used a kriging with external drift (KED) technique that represents a special case of universal kriging, which has been proven to yield higher predictive accuracies in other contexts (Hudson and Wackernagel 2006; Minasny and McBratney 2007; Tapsoba et al. 2005; Hernández-Stefanoni et al. 2011). In addition to the interpolated variable (the results of the response function), KED requires a secondary term (an external drift) that is strongly correlated with the results of the response function and captures the strength and direction of the response function coefficients. The external drift must be available at every estimation point. In the present study, we retained the total amount of snow and latitude as external drifts. Both variables were strongly correlated with the results of the response function (presented below) that we wished to interpolate over the entire study area (the total amounts of snow correlated with November ($r = 0.67$) and April ($r = 0.78$) temperatures; the latitudes correlated with January–December ($r = 0.68$) and July ($r = 0.58$) temperatures). It is important to note that the inclusion of an external drift in the kriging process did not change the results of the response function at the sites where it was calculated but aided in interpolating results where no tree-ring chronologies existed.

Finally, a redundancy analysis was performed to define the main environmental variables associated with the spatial variation of tree-ring responses to the climate. The retained environmental variables were the distance to the sea (DIST), elevation (ELE), longitude (LONG), latitude (LAT), total amount of snow (SNOW), total precipitation (PTOT), minimum temperature of the coldest month (TMIN), and summer mean temperature (TJJA).

Results

Cluster analysis

The hierarchical analysis (Fig. 2) of the growth curves showed that black spruce stands could be divided into four main groups. These groups are discriminated more by regional constraint than by site environmental characteristics. Actually, a few neighboring sites were sampled in very contrasting site conditions from very well-drained soil (xeric condition on outcrop) to less well-drained soil and then to humid soil (peat–bog were avoided). Despite of contrasting soil conditions, these neighboring sites were grouped in the same, very significant small clusters: ROZM, ROZX, ROZI, ROZW (96%), RH, RM, RX (98%), and DA1M, DA1X, DA1R (97%).

The four main groups were named according to the regions where they clustered (Fig. 3). Group 1 (CLSUB) was clearly dissociated from the other three and was composed almost exclusively of subarctic stands located to the northwest of the study area in the Hudson Bay region. Group 3 (CLJAM) was located immediately to the east of the James Bay region. Group 4 (CLLAB) included the easternmost stands. Group 2 (CLCAN) was geographically coherent but overlapped with the other three groups in the central part of the study area, i.e., in the region of La Grande 4 (LG4) and Caniapiscau reservoirs. Two of these groups were highly significant with more than 95% confidence (CLSUB (95%), CLLAB (97%)), one was significant at 92% (CLLAB), and one was significant below 90% (CLJAM, 88%). These results suggest that the existence of these clusters was strongly supported by the data.

Response function

Radial growth appeared to be much more sensitive to temperature (Fig. 4; Supplementary Table S3¹) than to precipitation (Fig. 5; Supplementary Table S4¹). However, the relationship between tree growth and temperature was more complex than the relationship between tree growth and precipitation. Variance explained by temperature differed greatly among stands assessed in this study. The obtained r^2 values ranged from 0.2 to 0.6. Only one-third of r^2 values are significant according *F* test *p* values; however, the intersite coherency of response functions profiles provided an extra measure of confidence in the observed results (Supplementary Table S3¹). The most significant response functions concerned mainly subarctic tree sites (CLSUB). Populations in the northern, western, and eastern sections of the study area (CLSUB, CLJAM, and CLLAB, respectively) were generally found to be more sensitive to interannual climate variations than those located in the central area (CLCAN).

Relationship with temperature

Summer temperatures

Summer temperatures (June, July, and August) showed a strong positive influence on tree growth at only one-third of the analyzed sites (Fig. 4). The CLSUB group and the easternmost CLLAB group presented strong and coherent relationships with July temperatures, whereas the other groups exhibited no relationship at all with summer temperatures. A strong south–north gradient became clearly visible after kriging of July temperature response function coefficients (with latitude as an external drift), depicting a strengthening response to summer conditions toward the tree line (Fig. 6). A west–east gradient could also be distinguished in the response map of July temperatures, with low responses being observed in the CLJAM and CLCAN groups and a strengthening of the coefficients over the easternmost part of the CLLAB group.

Early winter temperatures

November temperatures had a significant influence on 30 of the examined black spruce populations, which again represented approximately one-third of the study sites (Fig. 4). Cool, early winters (mainly in November) were associated with enhanced growth in the CLSUB, CLCAN (western portion), and CLJAM groups

Fig. 2. Results of the hierarchical analysis: affinities between mean tree-ring chronologies calculated in the 1920–1990 period. Significance level and standard error (%) and decimal, respectively) were performed for the four main clusters (dashed rectangles).

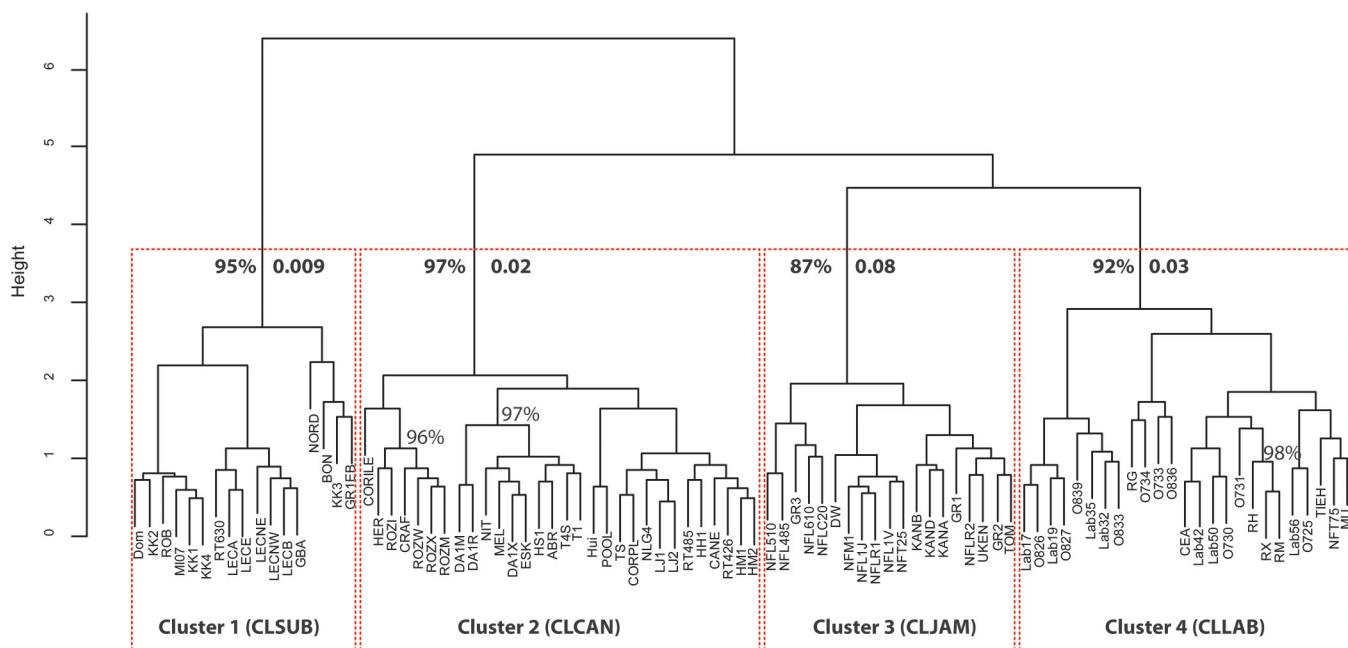
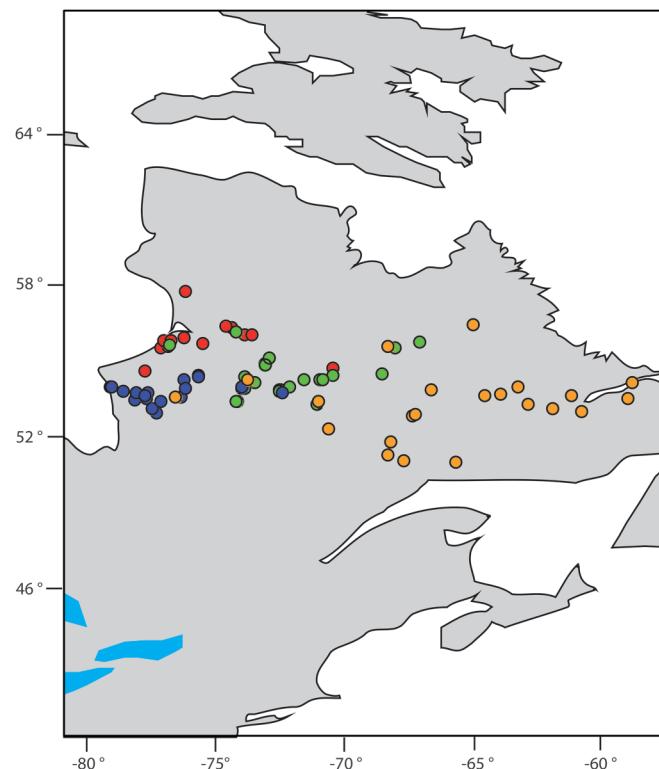


Fig. 3. Mapping of the hierarchical analysis results in study area. Group 1 (CLSUB), red points; group 2 (CLCAN), green points; group 3 (CLJAM), blue points; group 4 (CLLAB), orange points.



during the subsequent season. The KED map of the influence of November conditions on tree growth obtained using the total amount of snow as an external drift (Fig. 6) showed that a negative influence was important in the westernmost portion of the study area, whereas in the easternmost section, no significant relationships with early winter conditions could be found.

Winter temperatures

December and January conditions positively influenced the growth of approximately one-third of the sites (Fig. 4). Mild winters were associated with enhanced growth during the following growing season. The strongest relationships were observed in the CLJAM group and in the westernmost portion of the CLLAB group, whereas the northernmost populations did not show a strong influence of winter temperatures. The KED map (Fig. 6) of the interpolated responses to winter conditions (using latitude as an external drift) demonstrated the existence of a decreasing south-north gradient in the influence of winter temperatures over the study area, with a weaker influence observed near the tree line and a dominant influence observed in the spruce–lichen open forest to the south of the study area.

Early spring temperatures

Mild April temperatures positively influenced tree growth in the CLSUB, CLCAN (western portion), and CLJAM groups, whereas no such effect was found in the CLLAB group. The KED-interpolated response to early spring temperatures (using the total amount of snow as a covariate) showed a strong west–east gradient. Stands located in western Quebec were strongly influenced by April temperatures, whereas those located in central and eastern Quebec did not appear to be significantly influenced by April temperatures.

Influence of environmental variables on the response to temperature

The repartitioning of the stands along axes 1 and 2 (Fig. 7) demonstrated that the relationships between tree rings and climate of groups CLSUB (red), CLJAM (blue), and CLLAB (orange) (defined by the clustering of the chronologies) were distinct from each other. Stands in the CLCAN group (green), which overlapped the other three groups, were dispatched in a coherent geographical group. Indeed, relationships between tree rings and climate exhibited stronger spatial coherence than the results of the clustering analysis conducted on mean chronologies.

The main environmental variables associated with the spatial variation of the relationships between tree rings and climate were LAT (related to a mean summer temperature), LONG (related to

Fig. 4. Results of the response functions of growth to temperature. Histogram, R^2 values at each site; surface chart, degree of significance for each monthly temperature variable. Direct relationships are illustrated in blue, and indirect relationships are illustrated in orange. Populations are grouped by cluster and then classified according to their longitude.

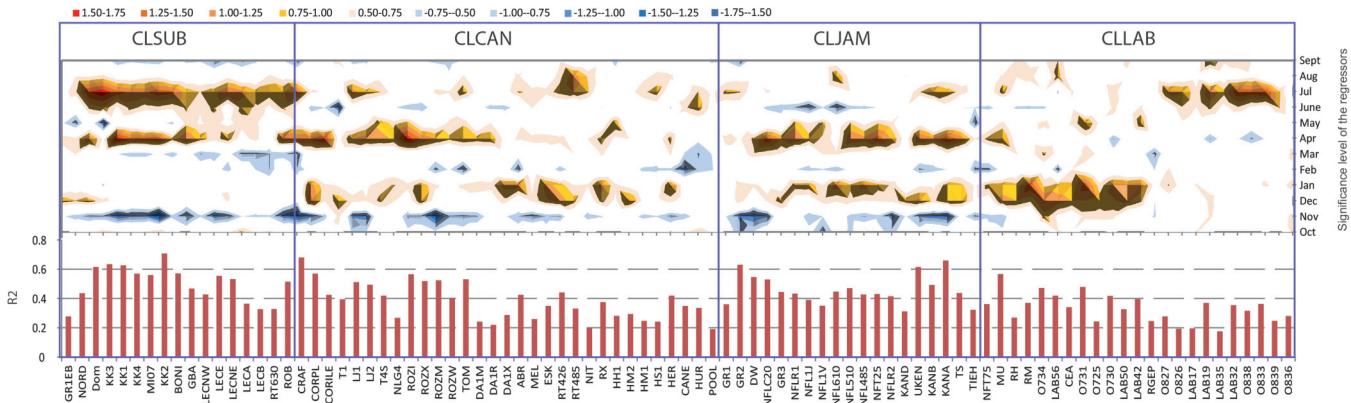
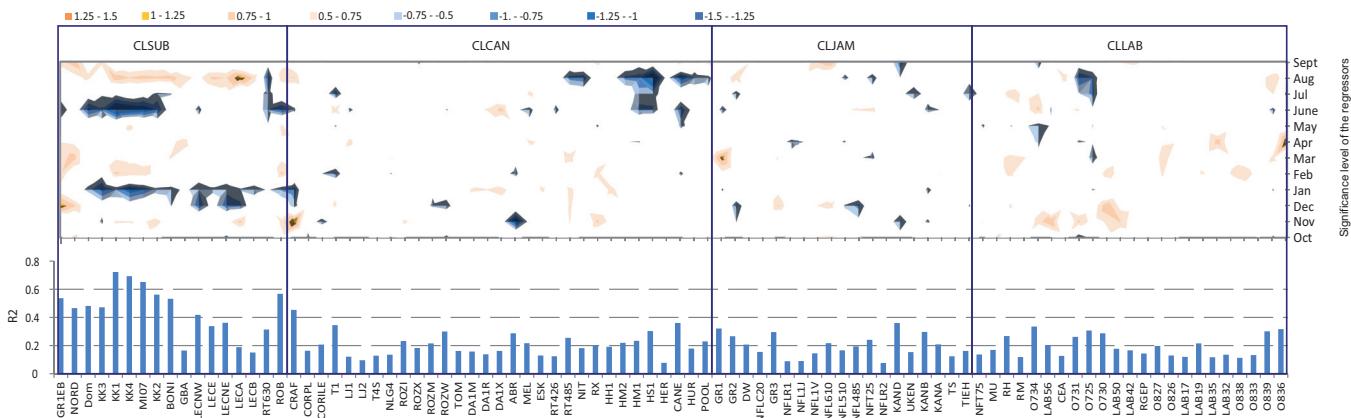


Fig. 5. Results of the response functions of growth to precipitation. Histogram, R^2 values at each site; surface chart, degree of significance for each monthly precipitation variable. Direct relationships are illustrated in blue, and indirect relationships are illustrated in orange. Populations are grouped by cluster and then classified according to their longitude.



snow cover), PTOT, and TMIN. LAT discriminated stands sensitive to winter temperatures from those sensitive to July temperatures. LONG, PTOT, and TMIN discriminated stands sensitive to April and November temperatures from the rest of the stands (Fig. 7). ELE and DIST played a minor role in the relationships between tree rings and climate.

Relationships with precipitation

The values of the coefficient of determination (R^2) associated with the response function were generally lower for precipitation than for temperature and fluctuated between 0.1 and 0.3 (Fig. 5; Supplementary Table S4¹). In addition, regression coefficients associated with these response functions were not significant and confirmed the weak relationship with precipitation. However, the CLSUB group clearly represented an exception, showing a significant negative response to January and June–August precipitation and had R^2 values ranging from 0.4 to 0.7. In other words, dry winters and dry summers were associated with enhanced growth in the subarctic stands and, to a lesser extent, near the Caniapiscau reservoir (eastern CLCAN).

Discussion

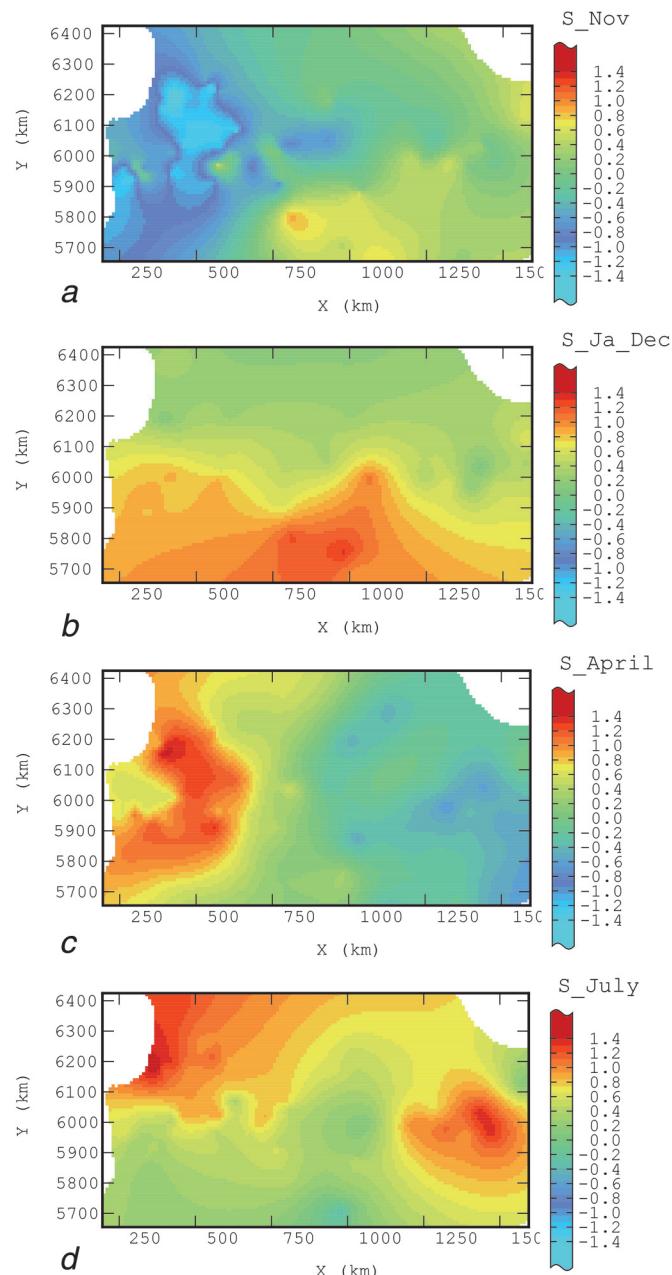
This study provides evidence that different combinations of meteorological conditions can affect black spruce productivity depending on the location of tree stands and regional climatological characteristics. In this context, this work aimed to spatialize

the growth response of black spruce to monthly climatic variations in North America's eastern boreal forest. In particular, our study emphasizes two distinct spatial gradients: a south–north gradient reflecting the strengthening influence of summer temperatures on black spruce growth and a west–east gradient reflecting the longitudinally decreasing influence of November and April temperatures (Fig. 6) on black spruce growth.

South–north gradient

The latitudinal gradient described through our tree-ring network suggests that between 47°N and 54°N, temperatures of the preceding winter have a dominant influence on tree growth. However, north of 54°N and up to the tree line, summer temperatures become the leading factor controlling black spruce growth. This transition between influential variables likely reflects regional climatic gradients. The relatively abrupt transition between the winter-dominated and summer-dominated zones occurs at approximately 54°N. At this latitude, summer temperatures drop from a mean of 14 °C to less than 10 °C within less than one degree of latitude. This decrease represents a significant reduction in the amount of heat available for tree growth and might be sufficient to impose an important stress on tree productivity during the summer period. This transition also roughly corresponds to a shift between discontinuous and continuous permafrost, as well as corresponds to an important ecological transition from open lichen-spruce forest to forest tundra (Payette 1992). All these changes

Fig. 6. Spatialization (krigeage with external drift (ED)) of relationships between tree rings and climate. (a) Spatial representation of the degree of significance for November temperatures (S_{Nov}) to radial growth relationships; chosen ED is mean total amount of snow; (b) spatial representation of the degree of significance for the relationship between December and January temperatures ($S_{\text{Ja-Dec}}$) and radial growth, chosen ED is latitude; (c) spatial representation of the degree of significance for the relationship between April temperatures (S_{April}) and radial growth, chosen ED is mean total amount of snow; (d) spatial representation of the degree of significance for the relationship between July temperatures (S_{July}) and radial growth, chosen ED is latitude.



highlight the existence of a strong latitudinal control on the ecosystems and geosystems of the subarctic area exerted via summer temperatures.

North of 54°N , warm summers increase photosynthetic efficiency and thus tree growth. The growing season in the north is

quite short, and the energy input (from temperature and sunlight) determines the synthesis of carbonaceous materials and the allocation of these resources within the tree trunk (Körner 1998; St George and Luckman 2001). Positive relationships between summer temperatures and growth have been demonstrated for many species at both high latitudes and high elevations (Wilson and Luckman 2003; Carrer et al. 2007; Miyamoto et al. 2010; Trindade et al. 2011a, 2011b; Nishamura and Laroque 2011).

However, south of 54°N , mild winters were found to be favorable for black spruce growth at a number of sites. Such a positive effect of winter temperatures (generally in the months of December and January) has also been described elsewhere (Brubaker 1980; Pederson et al. 2004; Carrer et al. 2007; Miller-Rushing and Primack 2008; Huang et al. 2010; Miyamoto et al. 2010; Tardif et al. 2001), and several hypotheses were formulated to explain this phenomenon. First, mild winter temperatures can minimize tissue damage to the cambium, buds, and leaves caused by severe frost (Grier 1988; Huang et al. 2010). In addition, as forests become more open toward the northern tree line, the wind strengthens the effects of temperature, particularly during cold winters. Indeed, ice crystals carried by the wind augment the effects of cold temperatures by eroding and damaging foliage (Payette et al. 1996; Kajimoto et al. 2002), which reduces the photosynthetic potential of the trees in the following summer. Cold winters may also damage roots when the snow cover is not sufficiently thick (Cox and Zhu 2003; Huang et al. 2010). In the study area, mild winters are also more humid and may contribute to the maintenance of a significant snow cover that protects roots from frost events.

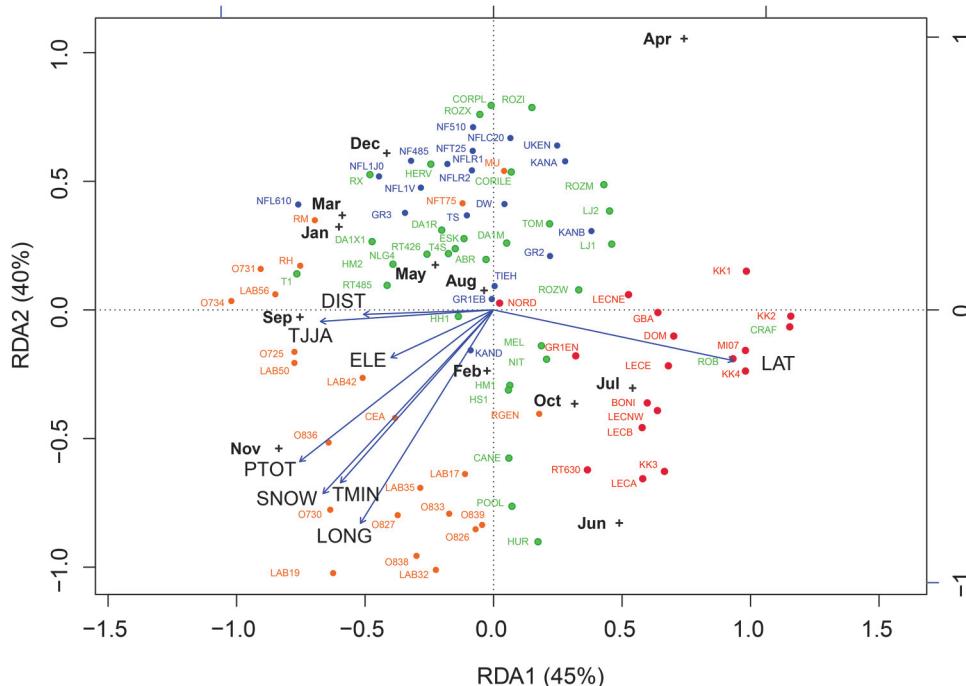
However, subarctic stands (CLSUB group) and those located around the Caniapiscau reservoir also showed a negative influence of summer precipitation on tree growth, which is an indication that black spruce is not limited by water availability in the study area. On the contrary, it implies that this species grows well when precipitation is relatively low during summer. However, this result may not be directly related to precipitation itself but may instead reflect an indirect relationship with cloud cover and temperatures. When a cool summer occurs in these high-latitude areas, climatic conditions are quite humid and cloudy. Under such conditions, less light is available, and colder temperatures result in less efficient photosynthetic activity, particularly near the northern tree line, where summer conditions have a determinant influence.

West-east gradient

The strong west-east contrast in the sensitivity of trees to November and April temperatures can be related to the snow precipitation gradient and thus to the corresponding gradient in the soil insulation potential. The abrupt transition between these two regions occurs at approximately 70°W . On the western side of this transition (in the James Bay – Hudson Bay region), snow precipitation represents approximately half of the precipitation falling over the Labrador region due to the increasing altitude and to a strengthening maritime influence in the easternmost area (Banfields and Jacobs 1998; Sheridan 2002; Trindade et al. 2011b).

In the James Bay – Hudson Bay region, dry winters are associated with a thinner snow cover, which has a less effective insulating effect. Thus, cool, early winters may allow an early snow cover to develop that protects the soil surface from frost penetration during winter months of December and January. According to Geiger (1957), a snow cover of only 7.5 cm can reduce the difference in soil temperatures by approximately 50%. Therefore, a thicker snow cover at the beginning of the winter season may limit soil freezing and reduce root and rootlet mortality. A similar relationship was found for white birch (*Betula papyrifera* Marsh.) in the same area (Huang et al. 2010). Although the species investigated in these works were different, our study reinforces the finding that early winter conditions can be a determinant for tree

Fig. 7. Factorial experiment of the redundancy analysis results. Environmental variables are as follows: distance to the sea (DIST), elevation (ELE), longitude (LONG), latitude (LAT), total amount of snow (SNOW), total precipitation (PTOT), minimum temperature of the coldest month (TMIN), and summer mean temperature (TJJA). Figure is provided in colour online.



growth. However, east of 70°W, thicker snow accumulation likely already provides the necessary insulating effect so that winter temperatures are less effective in damaging roots and rootlets. It is important to note that in more southerly regions, a positive influence of November temperatures has been found to be associated with an extended photosynthetic period (Brubaker 1980). This cannot be the case in the high-latitude ecosystem investigated in this study, because the photosynthetic period of black spruce ends in late October at most sites.

In contrast, high April temperatures may trigger an earlier than usual initiation of photosynthesis (Guehl 1985; Strand and Öquist 1988; Suni et al. 2003). Cold late-winter conditions (associated with a thick snow cover) can have a negative effect on future growth by delaying both soil thawing and the initiation of cambial activity (Graumlich and Brubaker 1986; Peterson et al. 2002; Kirdyanov et al. 2003; Pederson et al. 2004; Miyamoto et al. 2010). However, mild April temperatures can help reduce the thickness of the snow cover, which might trigger earlier growth. In the eastern portion of the study area, however, snow precipitation is always abundant throughout the winter, and the snow cover lasts until late April, regardless of spring conditions. Therefore, it is clear that the easternmost stands that benefit from efficient snow cover protection, even in late April, are less sensitive to late winter meteorological conditions and more responsive to summer temperatures.

Moreover, in the eastern part of the study area, we observed an east–west gradient in which the easternmost sites were highly sensitive to July temperatures and the more continental sites were sensitive to winter temperatures. Sites near the Labrador Sea are located at approximately 54°N and benefit from temperatures equivalent to those found at 52°N on the west coast (Fig. 2). This gradient has previously been observed in the same region by other authors (Nishimura and Laroque 2011; Dumaresq 2011; Trindade et al. 2011a, 2011b), who explained these varying relationships based on a continental gradient. Our observations tend to indicate that this gradient is more influenced by cold Labrador Sea temperatures than by an actual continental effect.

Anticipated climate change

The response to climate is clearly not univariate and uniform on the Quebec – Labrador Peninsula. Instead, it constitutes a rather complex multivariate phenomenon, showing significant spatial heterogeneity and gradients. In this context, the anticipated climate change may have different effects on tree productivity and growth, and these effects may vary depending on the area investigated (Plummer et al. 2006). A uniform warming of winter conditions would favor growth in the southernmost portion of the study area, as such sites are sensitive to winter temperatures. By contrast, the subarctic stands would not necessarily benefit from milder winters, as stands living near the tree line are more sensitive to summer temperatures. However, warmer summers and longer growing seasons would be associated with enhanced growth rates near the tree line but would not be beneficial to the southernmost sites. Ultimately, subarctic sites might also become less sensitive to summer temperatures, as the limitations imposed by the short growing season would presumably be considerably reduced. These projections would likely be modulated by changes in precipitation, as the nonstationary interactions between temperature, precipitation, and tree growth remain incompletely understood in our study area. For example, as observed in the southern part of the Quebec boreal forest (Huang et al. 2010; Tardif et al. 2001), more severe and frequent drought events could occur under a warmer climate. However, the consequences for the growth of black spruce remain undefined, and additional research will be required to elucidate the processes involved, perhaps through higher resolution tree-growth monitoring systems. Moreover, all these projections must also be modulated by the influence of climate warming on forest fire and black spruce budworm infestation, which could also influence forest dynamics and ecology.

Conclusions

The analysis of the relationships between tree rings and climate in the northern Quebec – Labrador Peninsula region revealed high

spatial variability. This variability was expressed spatially by a south–north contrast that appears to be related to a winter–summer temperature gradient and a west–east contrast that is linked to a precipitation gradient and winter snow cover. Tree growth in the majority of the stands depends on winter conditions (the temperatures in November, December–January, and April). Furthermore, only the northernmost stands were mainly influenced by summer temperatures.

Relationships between tree growth and climate are variable in space, and the impact of climate change on tree growth will likely vary according to the region considered. As warmer winter temperatures are predicted (Intergovernmental Panel on Climatic Change 2007), black spruce, whose growth is principally governed by winter and spring conditions, may experience increased growth.

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