Taxonomy, together with ontogeny and growing conditions, drives needleleaf species' sensitivity to climate in boreal North America

Running head: DRIVERS OF BOREAL FOREST GROWTH

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Paper type: Primary research article

Abstract

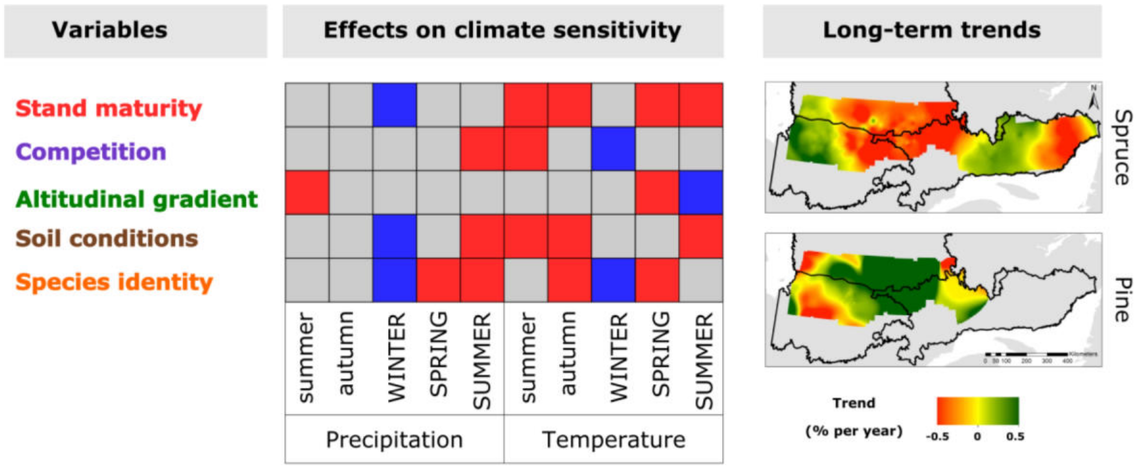
Currently, there is no consensus regarding the way that changes in climate will affect boreal forest growth, where warming is occurring faster than in other biomes. Some studies suggest negative effects due to drought-induced stresses, while others provide evidence of increased growth rates due to a longer growing season. Studies focusing upon the effects of environmental conditions on growth-climate relationships are usually limited to small sampling areas that do not encompass the full range of environmental conditions; therefore, they only provide a limited understanding of the processes at play. Here, we studied how environmental conditions and ontogeny modulated growth trends and growth-climate relationships of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) using an extensive data set from a forest inventory network. We quantified the long-term growth trends at the stand scale, based upon analysis of the absolutely-dated ring-width measurements of 2266 trees. We assessed the relationship between annual growth rates and seasonal climatic variables, and evaluated the effects of various explanatory variables on long-term growth trends and growth-climate relationships. Both growth trends and growth-climate relationships were species-specific and spatially heterogeneous. While the growth of jack pine barely increased during the study period, we observed a growth decline for black spruce which was more pronounced for older stands. This decline was likely due to a negative balance between direct growth gains induced by improved photosynthesis during hotter-than-average growing conditions in early summers and the loss of growth occurring the following year due to the indirect effects of late-summer heatwaves on accumulation of carbon reserves. For stands at the high end of our elevational gradient, frost damage during milder-than-average springs could act as an additional growth stressor.

Competition and soil conditions also modified climate sensitivity, which suggests that effects of climate change will be highly heterogeneous across the boreal biome.

Keywords: boreal forest, Canada, climate change, climate-induced stress, dendroecology, Quebec

Graphical Abstract

The figure displays the effects (red=negative, blue=positive) of explanatory variables on tree sensitivity to climate, and the resulting 1970-2005 growth trends. Old-growth boreal black spruce stands exhibited a more negative response to previous summer temperature, identified as the primary climatic driver of growth trajectories for this species. This finding suggests an exacerbated effect of heat-induced stresses, which resulted in more negative long-term growth trends for old-growth stands, especially when combined with late-frost damage. Other explanatory variables, such as regional climate, competition and soil conditions, modified tree sensitivity to climate.



Variables	Precipitation summer	Precipitation autumn	Precipitation WINTER	Precipitation SPRING	Precipitation SUMMER	Temperature summer	Temperature autumn	Temperature WINTER	Temperature SPRING	Temperature SUMMER
Stand maturity	⬜	⬜	🟦	⬜	⬜	🟥	🟥	⬜	🟥	🟥
Competition	⬜	⬜	⬜	⬜	🟥	🟥	⬜	🟦	⬜	⬜
Altitudinal gradient	🟥	⬜	⬜	⬜	⬜	⬜	⬜	⬜	🟥	🟦
Soil conditions	⬜	⬜	🟦	⬜	🟥	🟥	🟥	⬜	⬜	🟥
Species identity	⬜	⬜	🟦	🟥	🟥	⬜	🟥	🟦	🟥	⬜

1. INTRODUCTION

The boreal biome is warming faster than other regions of the world (IPCC, 2013). As a result of a 35 % increase in atmospheric CO_2 concentrations relative to pre-industrial conditions, mean annual air temperature has risen by 0.5 to 3 °C in boreal North America and an additional increase of 4-5 °C is expected by 2100 (Price et al., 2013). Climate change threatens the ecological, social and economic services that boreal forests provide (Gauthier, Bernier, Kuuluvainen, Shvidenko, & Schepaschenko, 2015). It is also unclear whether boreal forests will continue to act as a carbon sink or will shift to become a carbon source (Kurz et al., 2013), thereby renewing the scientific focus on these ecosystems and on their ability to cope with, and to mitigate, global warming. As a proxy for tree vigour, secondary growth can be used to study the response of trees to a changing climate and, thus, to assess current and future trajectories of the boreal forest.

In the Northern Hemisphere, evidence of increased mortality rates and decreases in tree growth and forest productivity is accumulating, not only for the interior of the boreal forest (Cahoon et al., 2018; Girardin et al., 2016; Hember, Kurz, & Coops, 2016; Zhu et al., 2016), but also at its northern edge (D'Arrigo et al., 2004). These 'negative' trends were linked, amongst other factors, to heat and hydric stresses resulting from rising temperatures and more frequent, longer-lasting, and harsher drought episodes (Barber, Juday, & Finney, 2000; Girardin et al., 2016; Juday & Alix, 2012; Nicklen et al., 2018; Trugman, Medvigy, Anderegg, & Pacala, 2018; Zhang et al., 2008). In contrast, other studies provided strong evidence for increased growth rates and higher stand productivity (Beck et al., 2011; Girardin et al., 2011; Hember, Kurz, & Coops, 2017). These 'positive' trends, which were observed mainly for the northernmost forested area, namely, the taiga, were likely due to higher rates of carbon assimilation and a longer growing season (Gennaretti, Arseneault, Nicault, Perreault, & Bégin, 2014; Ju & Masek, 2016). These contrasting observations demonstrate uncertainties regarding the persistence of the existing structure, composition and function of the boreal biome under future warmer and dryer climatic conditions.

Tree sensitivity to climate is highly variable across the globe and is modulated by environmental drivers that vary at local to global scales (Babst, Poulter, et al., 2012; Girardin et al., 2016). Amongst these drivers, topography creates spatially heterogeneous macroclimatic conditions and can modify the way that trees respond to changes in regional climate (Hasler, Geertsema, Foord, Gruber, & Noetzli, 2015; Matías, Linares, Sánchez-Miranda, & Jump, 2017). For example, in Central Europe, water-limited lowland forests are more sensitive to drought, whereas forests in the upland portion of the elevational gradient are primarily temperature-limited (Altman et al., 2017) and can benefit from stronger and faster warming, which is expected for mountainous areas (Pepin et al., 2015). More specifically, higher mean summer temperatures could improve the growth of trees at the high end of the elevational gradient by increasing the number of wood cells that are produced annually through improved xylogenetic processes and hydraulic performance (Castagneri, Petit, & Carrer, 2015; Dulamsuren, Hauck, Kopp, Ruff, & Leuschner, 2017). In contrast, some studies have observed decreased growth rates, even for trees growing in mountainous sites in both central Europe and North America (Dittmar, Zech, & Elling, 2003; McLaughlin, Downing, Blasing, Cook, & Adams, 1987; Piovesan, Biondi, Filippo, Alessandrini, & Maugeri, 2008), which questions the capacity of high-elevation forested ecosystems to better cope with climate change (Austin & Niel, 2011).

The annual growth performance of a tree is linked to its ability to access optimal amounts of water, light and nutrients (Fritts, 1971), the availability of which is primarily controlled by site-specific abiotic factors, such as soil conditions (e.g., Hember et al., 2017). Soil structure, drainage and thickness of the organic layer determine soil water-holding capacity (Minasny & McBratney, 2017) and drive nutrient cycling (e.g., Cavard, Bergeron, Paré, Nilsson, & Wardle, 2018). In addition to its direct effects on tree growth, soil moisture content alters microclimate and, thus, evapotranspiration rates, which may modulate growth-climate relationships (Manrique-Alba et al., 2017). By modifying resource availability, inter-individual competition can exacerbate tree sensitivity to harsh climatic conditions (e.g. Buechling, Martin, & Canham, 2017; Ford et al., 2016; Gleason et al., 2017; Jiang et al., 2018; Nicklen et al., 2018), or buffer growth gains from favourable periods (Cortini, Comeau, & Bokalo, 2012). Ultimately, the capacity of a tree to efficiently use resources will also dictate its response to climate (e.g., Carrer & Urbinati, 2004). Apart from genotype-driven differences, ontogeny-related changes in a tree's physiological needs and in the efficiency of its hydraulic network (Ryan, Phillips, & Bond, 2006) can modify its sensitivity to climate (e.g., Altman et al., 2017).

The high spatial variability in growing conditions that is encountered in boreal forests, together with the multiplicity of interacting effects and feedbacks of environmental variables that are present, hinder our understanding of the response of boreal forest trees to climate. In regions with geographically limited and sparsely replicated sample networks (Gewehr, Drobyshev, Berninger, & Bergeron, 2014), assessing climate effects on tree growth is very difficult (but see Girardin et al., 2016), given that field-based measurements do not cover the full range of variation in growing conditions. Some studies in western boreal North America and boreal Europe have examined variations in growth-climate relationships along latitudinal and longitudinal gradients (Lloyd, Bunn, & Berner, 2011) or between sites with different slope orientations (i.e. north vs south facing sites; Johnstone, McIntire, Pedersen, King, & Pisaric, 2010; Walker & Johnstone, 2014) and moisture conditions (Walker & Johnstone, 2014; Wilmking & Myers-Smith, 2008). However, studies testing the effect of elevation gradient on the trees sensitivity to climate are lacking, particularly in the eastern boreal North America. Furthermore, most past studies have focused upon the direct effects of abiotic or biotic factors on tree growth, while the feedback effects of environmental conditions on growth-climate relationships are still rarely decribed (But see Nicklen et al., 2018; and Nicklen, Roland, Ruess, Schmidt, & Lloyd, 2016 for the Pacific Coast of North America).

Here, we used an extensive and well-replicated provincial inventory network that provides absolutely dated and annually resolved tree-growth data, as well as site-specific environmental information for unmanaged forests in eastern boreal North America. This network is located at the boundary between the interior boreal forest and the taiga, and includes sample plots characterized by highly contrasting growing conditions. Our overall objective was to examine whether the potential impacts of recent changes in climate varied as functions of explanatory variables with respect to the growth of two needleleaf species that are broadly distributed across North America, black spruce (*Picea mariana* (Miller) B.S.P.) and jack pine (*Pinus banksiana* Lambert). We first quantified the recent growth trends for the two species which, given the high variability in growing conditions, were expected to be heterogeneous across the study zone. Then, we determined the climate sensitivity of the two species, i.e., the relationship between inter-annual variation of secondary growth rates and fluctuations in seasonal values of mean temperature and total precipitation over the period 1970-2005. We hypothesized that the growth of both species would be negatively impacted by higher-than-average temperature during summer and positively affected by higher-than-average temperature during spring and by higher-than-average precipitation during summer. Finally, we assessed how explanatory variables (e.g. climate, competition and soil conditions) affected spatial variability in growth-climate relationships. We hypothesized that the negative effect of hotter- and dryer-than-average summers, as well as the positive effect of high spring temperature on tree growth, would be exacerbated in stands in the upper portion of the elevational gradient. We also hypothesised that old stands, as well as trees growing in a highly competitive environment and in well-drained sites, would respond more negatively to summer heatwaves.

2. MATERIALS AND METHODS

2.1 Sampling area

Our sampling network covered three degrees of latitude (50.25-53.25°N) and nearly extended across the entire Province of Quebec (Canada) from east to west (57.5-78.25°W). It was located in the boreal biome, which is characterised by needleleaf-dominated forests (Robitaille, Saucier, Chabot, Côté, & Boudreault, 2015). Some regional patterns of climatic conditions, dominant vegetation and natural disturbance regimes make it possible to divide this wide biome into bioclimatic domains (Ansseau et al., 1997). In the north portion of the region, the spruce-lichen bioclimatic domain is characterised by a harsh, cold and dry climate, resulting in an open black spruce-dominated forest with a lichen mat, i.e., the taiga vegetation subzone. South of the 52nd parallel, continuous boreal forest that is composed mostly of pure black spruce stands covers the spruce-moss bioclimatic domain. The latter is subdivided into western and eastern zones based on precipitation patterns and fire cycles. The western part is drier and, consequently, more prone to wildfire than the eastern zone (Gouvernement du Québec, 2003). Within these three main bioclimatic domains, hereafter referred to as "Boreal West," "Boreal East" and "Taiga" (Figure 1), lower-level landscape units are defined based upon the recurrent arrangements of the main permanent ecological and vegetation features (48 landscape units are present in our sampling area), which in turn are divided into ecological districts (284 ecological districts within our sampling area) that are based upon their geological and physiographic features (Ansseau et al., 1997). Please refer to the Figure 1 (B) for examples of geographical units mentioned throughout the paper.

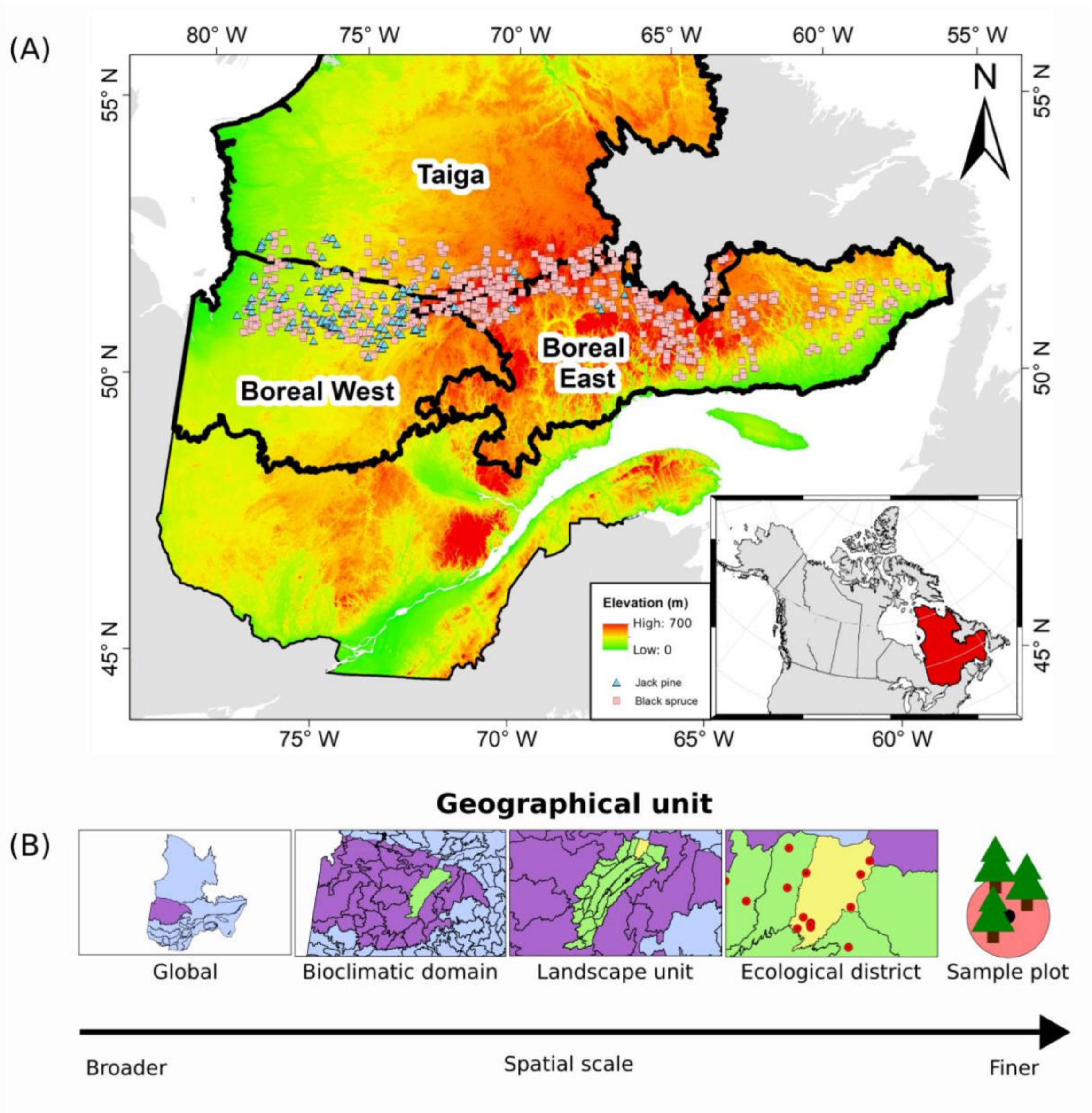


FIGURE 1 (A) Forest inventory plot network. The pink squares and blue triangles represent black spruce and jack pine temporary sample plots, respectively. The three main bioclimatic domains encompassing the sample network are also delineated. The background colour gradient represents the elevation gradient. (B) Geographical units involved in statistical analyses, from the broader global scale of the province of Quebec to the finer scale of the sample plot.

2.2 Tree-ring material

The data that we used for this study were acquired from a sampling program of 400-m^2 randomly distributed temporary circular sample plots (n = 875 plots), which was established by the Ministère des Ressources naturelles et de la Faune du Québec (MRNFQ) from 2005 to 2009 (Programme d'inventaire écoforestier nordique; Létourneau et al., 2008). In each sample plot, the diameter at breast height (DBH, 1.3 m) of all living and dead stems (DBH > 9 cm) was measured and environmental and stand-level conditions were recorded. Disks were collected for stem analysis from one to three dominant or co-dominant trees per species according to the provincial normative sampling protocol (Ministère des Ressources Naturelles du Québec, 2008). We used only black spruce and jack pine data since these species represented most (76 % and 15 %, respectively) of the sampled trees. We selected 1-m-height stem-disks as a trade-off between basal ring distortion and the number of visible rings (DesRochers & Gagnon, 1997). A total of 1914 black spruce and 352 jack pine disks with each having a minimum of 20 visible rings, representing 812 sample plots, were retained for subsequent analyses. Sample disks were processed using standard dendrochronological procedures for acquisition of ring-width measurement series across four radii per disk (Ministère des Ressources Naturelles du Québec, 2008). For each ring-width series, cross-dating and measurements were statistically verified using the program COFECHA (Holmes, 1983). No major anomaly in these tree-ring measurements was observed, and therefore all were retained for subsequent analyses.

2.3 Climate data and explanatory variables

For each plot, daily maximum and minimum temperatures (°C) and total precipitation (mm) were obtained for the period of 1970-2005 using thin plate spline smoothing algorithms (ANUSPLIN), which interpolate site-specific estimates at a 0.08° x 0.08° spatial resolution from historical weather observations, as described in Price et al. (2011). Mean temperatures, which were computed as the average of monthly maximum and minimum temperature values, were averaged and precipitation was summed at a seasonal scale (meteorological seasons according to Trenberth, 1983: spring = March-May, summer = June-August, autumn = September-November, winter = December-February). Readers should refer to Supporting Information S1 for an overview of the trends in seasonal climate in the study area.

Stand and environmental conditions were acquired from the plot survey conducted by the Ministère de la Faune, des Forêts et des Parcs du Québec (Table 1, MFFPQ; Robitaille et al., 2015). We considered the proportion of clay, sand and silt in the mineral soil, organic layer thickness (OLT) and hydrological conditions of the sample plot assessed as drainage classes. Elevation and slope were extracted for our sample plots from the SRTM 90m Digital Elevation Database v4.1 (Jarvis, Reuter, Nelson, & Guevara, 2008). For stand-level demographic features, stand age was defined as the age of the oldest sampled tree in the plot. Stand basal area (BA) was computed as the sum of basal areas of all trees with DBH > 9 cm within the plot, on a per-hectare basis. A tree-level competition index (CI) was computed as the number of trees that were taller than the focal tree, divided by the total number of trees within the plot, to assess assymetric competition (Ford et al., 2016), following Weber et al. (2008). To do so, the height of all trees within a plot was estimated from DBH using the allometric equations of Fortin et al. (2009). Individual CI values were averaged at the plot level to ensure consistency with the working scale of the growth-climate analyses. Temperature and precipitation normals were computed for the

1970-2005 period to account for the west-to-east (continental-to-oceanic) climate gradient. For brevity's sake, these plot-level characteristics will be refered hereafter to as "explanatory variables".

TABLE 1 Plot-level statistics for the studied explanatory variables, by bioclimatic domain

	Boreal West			**Boreal East**			**Taiga**		
	mean	**sd**	**range (min | max)**	**mean**	**sd**	**range (min | max)**	**mean**	**sd**	**range (min | max)**
Clay (%)	6.69	13.32	0 | 79	4.76	2.86	0 | 18	4.96	6.34	0 | 47.9
Sand (%)	63.51	30.71	0 | 99.5	66.77	24.13	0 | 99.5	68.55	23.94	0 | 96.5
Silt (%)	12.11	11.95	0 | 52	18.75	11.31	0 | 53.9	17.93	12.29	0 | 72
OLT (cm)	21.23	25.45	1 | > 100	18.49	17.35	0 | > 100	15.93	19.66	0 | > 100
Drainage (unitless)	3 (median class)	-	1 | 6	3 (median class)	-	1 | 6	3 (median class)	-	1 | 6
Elevation (m a.s.l.)	320.22	89.84	96 | 637	549.55	167.39	100 | 860	522.59	171.4	113 | 912
Slope (degree)	2.28	1.97	0.13 | 13.15	3.55	3.33	0.13 | 19.58	2.32	2.29	0.13 | 12.36
Age (years)	105.23	55.82	28 | 294	163.69	65.81	28 | 331	145.59	63.68	30 | 309
BA (m^2 ha^{-1})	15.89	10.59	0.78 | 49.88	17.27	10.21	0.90 | 55.39	10.57	6.60	0.59 | 35.44
CI (unitless)	0.77	0.19	0.07 | 1.00	0.79	0.16	0.02 | 0.98	0.69	0.21	0.07 | 1
Prec. (mm)	807.11	59.07	685.56 | 927.26	956.09	106.87	775.83 | 1174.67	803.74	75.3	668.60 |955.34
Temp. (°C)	-1.71	0.61	-3.07 | -0.31	-2.21	1.28	-4.02 | 0.49	-2.28	1.03	-4.35 | -0.93

Note: Clay = percentage of clay within the soil; Sand = percentage of sand within the soil; Silt = percentage of silt within the soil; OLT = organic layer thickness; Drainage = drainage classes: from 1: rapid drainage to 6: poor drainage ; Elevation = altitudinal gradient; Slope = terrain's slope, in degrees; Age = stand age (age of the oldest tree in a plot, computed as the number of years between the calendar year of the oldest ring and the calendar year of the most recent ring recorded for a tree); BA = basal area; CI = competition index; Prec. = average annual precipitation over the 1970-2005 period; Temp. = average mean annual temperature over the 1970-2005 period.

2.4 Statistical procedures

To test our working hypotheses, we applied a 3-step statistical procedure involving different spatio-temporal scales (see workflow diagram in Supporting Information S2).

Step 1 : Trend analysis

Ring-width measurements of the four radii were averaged (arithmetic mean statistics, see Supporting Information S3 for descriptive statistics of the raw series), and the mean ring-width series were converted into basal area increments ($BAI_t = \pi R_t^2 - \pi R_{t-1}^2$) using the function bai.out in the R-package dplr (Bunn, 2008). We assumed the cross-sections were perfectly circular in shape, and used these as a proxy for secondary growth to provide an accurate quantification of wood production with ever-increasing tree diameter (Biondi & Qeadan, 2008). Rings that were formed during the first 10 years were then eliminated, given that they usually exhibit an atypical response to environmental drivers compared with more mature rings (Loader, McCarroll, Gagen, Robertson, & Jalkanen, 2007). Next, BAI were detrended using Generalised Additive Mixed Models (GAMM) to remove the remaining ontogeny-induced (i.e., tree age and size) trends. One model was constructed for each species and ecological district (See Supporting Information S4 for information about the BAI chronologies and diagnostic plots of the GAMM models). Organic layer thickness was added as a fixed term to account for the spatially-heterogeneous and mostly time-independent effect of site quality on tree growth (Lavoie, Harper, Paré, & Bergeron, 2007). BAI values were log-transformed to improve the normality of their distributions. The structure of the GAMM model is as follows:

$$\log(BAI_{ijklt}) = \log(BA_{ijklt}) + OLT_{kl} + s(AgeC_{ijkt}) + (TreeID_{ijkl}) + corAR1_{ijkl}$$

where *i* represents the individual tree, *j* represents the species, *k* represents the plot, *l* represents the ecological district, and *t* represents the year. BAI is the basal area increment of tree *i* at specific year *t*, BA is the basal area of tree *i* at specific year *t* (computed as the sum of BAI of previous years), OLT is the organic layer thickness of plot *k*, and AgeC is the cambial age (1-m height ring count) of tree *i* at year *t*. An autoregressive term, AR1 (autoregressive order $p = 1$, moving average order $q = 0$), was added to account for temporal autocorrelation. We tested the significance of a nested random effect (tree nested in plot) by conducting ANOVAs and likelihood ratio tests. Because it did not improve the model's fit and led to the same results (data not shown), we discarded the random term of the plot from the final model and kept only the random effect of the tree (TreeID).

Annual Growth Changes (GC), which were expressed as the percent deviation from predicted values of the GAMM model, were then computed following Girardin et al. (2016). GC values were aggregated by year, plot and species using the median statistics for computation of GC_{median} chronologies (robust statistics; Huber, 2005). Because, for several trees, the 2005 growth-ring was the last whole growth-ring, the upper temporal limit of the analyses was fixed to 2005 to ensure consistency between chronologies. From the GC_{median} chronologies, growth trends were examined over two time periods: 1950-2005 and 1970-2005. These periods were marked by significant increases in mean annual temperatures of the area (Price et al., 2013) and characterized by the highest number of tree rings per calendar year (i.e. the highest sample depth, see Supporting Information S3.2). Linear regressions were applied ($GC_{median} \sim$ year), and the estimated regression slope was used as a proxy for the long-term growth trend. Trend significance was assessed following the statistical procedure described by Yue et al. (2004). This method corrects the p-value of the non-parametric Mann-Kendall trend test with the effective sample size of the time series to reduce the influence of serial correlation (function mkTrend in the R-package fume; Santander Meteorology Group, 2012). Even if there were trend reversals for a few plots (Figure 2), the 1970-2005 and 1950-2005 trends were globally highly correlated (see Supporting Information S5.1). For the purposes of comparison, 1970-2005 GAMM-based trends were compared with trends that were estimated from the application of two other commonly used detrending methods, namely modified negative exponential models and regional curve standardisation (See Supporting Information S5.2).

Step 2 : Growth-climate relationships

Since weather station data availability and, therefore, climate data accuracy, is better for the most recent time periods (Ols, Girardin, Hofgaard, Bergeron, & Drobyshev, 2017), we decided to retain data from the shorter and most recent period, i.e., 1970-2005, for climate-growth analyses. Linear mixed models were fitted by plot and species, which included residuals of GAMM-detrended BAI as response variables, together with the set of seasonally aggregated climatic variables as fixed terms, and tree identity as a random term. Mean seasonal temperature and total precipitation of the year of ring formation were considered as explanatory variables. Since trees can allocate carbohydrates that were acquired in the previous growing season to the biomass production of the year of ring formation (Granda & Camarero, 2017), climate data from summer and autumn of the previous year were also considered as fixed terms, leading to a total of ten climatic variables (please refer to the Supporting Information S6.1 for the list of climate variables used in linear mixed models). The structure of the global model is as follows:

$$Res_{ijkt} = \sum_{n=1}^{10} Clim_{kt} + (TreeID)_{ijk} + corAR1_{ijk}$$

where *i* represents the tree, *j* represents the species, *k* represents the plot and *t* represents the year. (TreeID) is a random term that accounts for the variability between individual trees. An error term with an AR1 ($p = 1$, $q = 0$) correlation structure was added to the model which accounts for the serial correlation. Collinearity amongst climatic variables was low, with the mean of pairwise Pearson correlations between variables below a stringent threshold value of 0.4 (Supporting Information S6.1; maximum value of $|0.37|$; Dormann et al., 2013). Multi-model selection based upon the Akaike information criterion corrected for small sample size (AICc), was performed for this global model using the package MuMIn (Bartoń, 2018). A 95% confidence set of models was selected for multi-model inference as models whose cumulative Akaike weight is below 0.95 (Burnham & Anderson, 2002). Readers can consult Supporting Information S6.3 for AICc values of all of the 1024 evaluated models, along with Akaike weights of the best model and the number of models used for multi-model inferences. Weighted averages of parameter estimates were derived from this set of best approximating models, and Student's t-statistics were computed as the ratio between the average model estimate and its corresponding standard error. These statistics provide both the general direction of the growth-climate relationship (i.e., negative or positive slope), and the strength of this relationship (the farther from zero the t-value is, the stronger is the effect), weighted by the model's predictive capacity and based upon the selected climatic variables. The 95 % adjusted confidence intervals of the t-statistics were also computed, together with Pearson correlations between residuals from the GAMM models and predicted values from the climate models (Supporting Information

S6.2) as an additional means of assessing the model's predictive capacity. Results of growth-climate analyses that were based upon residuals from the two additional detrending methods are provided in Supporting Information S7.

Slopes from the linear regressions and t-statistics from the climate-growth mixed models were interpolated across the whole area using the Empirical Bayesian Kriging algorithm of the Geostatistical Analyst tool in ArcGIS v.10.4 (input options: empirical transformation of the data, semi-variogram model = exponential-type, search radius = 1°, smoothing factor = 0.2). The output raster maps permitted visual examination of geographical patterns in long-term growth trends and climate sensitivity.

Step 3 : Link with explanatory variables

The relationships between explanatory variables (listed in Table 1) and tree sensitivity to climate were assessed by conducting redundancy analyses (RDA) using Canoco software v.4.5 (ter Braak & Smilauer, 2009). Because tree sensitivity to climate and environmental conditions are highly variable from east to west (see Figure 4 and Table 1), site conditions might affect growth-climate relationships depending upon the location of the plot (Wu et al., 2018). If averaged over the whole gradient, the effect of these conditions could cancel each other out. Consequently, one RDA was conducted per bioclimatic domain as a trade-off between data aggregation and ecological relevance, as recommended by Ols et al. (2018). The t-statistics from the climate mixed models were considered as response variables (i.e., the "species" data matrix) and explanatory variables were considered as independent variables (i.e., the "environment" matrix). Climate normals were also included as independent variables, together with a dummy variable accounting for the species identity of the sampled tree, i.e., the difference in sensitivity to climate between jack pine (the reference level) and black spruce. Please refer to Supporting Information S8.3 for the list of independent variables considered in RDA analyses. Latitude, longitude and the average distance to the four nearest weather stations (ranging from 3.8 km to 153.1 km, see Supporting Information S8.1) were added as conditioning variables to remove the effects of spatial non-independence of the plots and the potential lack of accuracy in the climate data set prior to analysis. Independent variables were transformed to improve the normality of their distributions, and then standardised prior to analysis (R package rcompanion; Mangiafico, 2017; Tukey's ladder of powers; Tukey, 1977). Forward selection of independent variables was done using Monte-Carlo permutation tests (n = 9999 permutations under the reduced model; $\alpha = 0.05$). Growth trends were included passively in the RDA in order to examine these in context with climate-environmental relationships (such supplementary 'passive' variables do not influence the ordination). To summarise the information that was displayed by the ordination plots (Supporting Information S8.2), modified t-tests accounting for spatial autocorrelation were conducted between each of the RDA-selected independent variables and response variables (i.e., tree sensitivity to climate). The function modified.ttest of the R package SpatialPack was used (Osorio, Vallejos, Cuevas, & Mancilla, 2018); $\alpha = 0.05$).

Significant variables were grouped into six sets according to the ecological process they represent: stand maturity, competition, altitudinal gradient, soil conditions, regional climate, and species identity (also see Supporting Information S8.3). Variation partitioning was then conducted to identify common and unique contributions to the total percentage of variation in the matrix of response variables (adjusted R^2) explained by the model and better address the question of relative influences of the six sets of independent variables that were considered in the model (Peres-Neto, Legendre, Dray, & Borcard, 2006). The forward selection procedure used in the RDA led to up to five sets of independent variables by bioclimatic domain. The variation partitioning algorithm (varpart) in the R-package vegan was used (9999 permutations, partitions computed from adjusted R^2; Oksanen et al., 2018), which only allows a maximum of four sets of independent variables to be considered in a same analysis. To overcome this limitation, we determined the unique and common contributions of stand maturity, competition, altitudinal gradient, soil conditions and regional climate. Next, we determined the contribution of the taxonomic identity of the tree (selected in each of the three bioclimatic domains) by comparing it to the contribution of all other independent variables grouped together. The dummy species variable in RDAs allowed the quantification of the variability in growth-climate relationships resulting from the difference between the two species without splitting the data by species, which would have lowered the number of sample plot by analysis and consequently the statistical power, i.e. the likelihood to correctly reject the null hypothesis. Analyses by species were also tested and results of these analyses are provided as Supporting Information S8.4.

3. RESULTS

3.1 Growth trends are spatially heterogeneous and species-specific

When averaged over the sample plots, dissimilar long-term growth trends appeared between species (Supporting Information S9). Growth rates of black spruce decreased, with a trend estimated at -0.35 % y^{-1} ± (std) 1.61 % y^{-1} from 1950 to 2005. For the 1970-2005 period, the trend in the annual growth rate was -0.14 % y^{-1} ± 2.44 % y^{-1}. For jack pine, both the 1950-2005 and 1970-2005 periods were characterised by an annual increase in growth of 0.21 % y^{-1} ± 3.31 % y^{-1} and 0.21 % y^{-1} ± 3.37 % y^{-1}, respectively. However, species-specific growth trajectories were not homogeneous across the study region (Figures 2 and 3; Supporting Information S9). Growth of black spruce increased in the western part of the Boreal West and in the central part of the Boreal East between 1970 and 2005, but decreased elsewhere (Figure 2). Growth of jack pine increased regardless of bioclimatic domain between 1950 and 2005, but decreased in the western parts of Boreal West and Taiga between 1970 and 2005 (Figures 2 and 3).

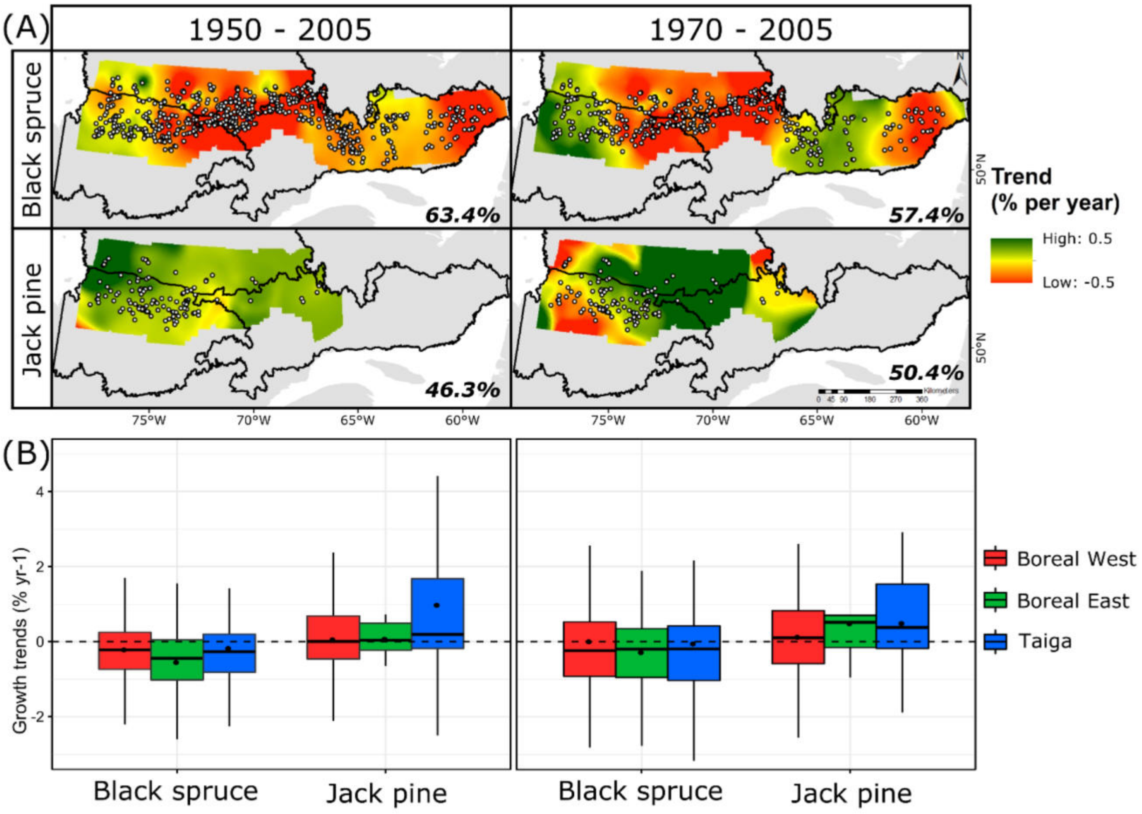


FIGURE 2 (A) Growth trends for black spruce and jack pine, for the 1950-2005 and 1970-2005 periods, shown as slope coefficients of the plot-scaled regression models of detrended BAI values against calendar years. Empirical Bayesian kriging was applied to interpolate plot-based trends across the entire area. Dots highlight significant trends (α = 0.1). The

proportion of significant trends is shown at the bottom of each map. (B) Distributions of growth trend slopes by species and bioclimatic domain (boxplots). Black dots represent the mean value for the specific species and bioclimatic domain. Black lines inside the boxplots are median values, and error bars represent the lower and upper whiskers (representing the variability outside the upper and lower quartiles). The dotted line represents a value of zero, i.e., no trend in long-term growth.

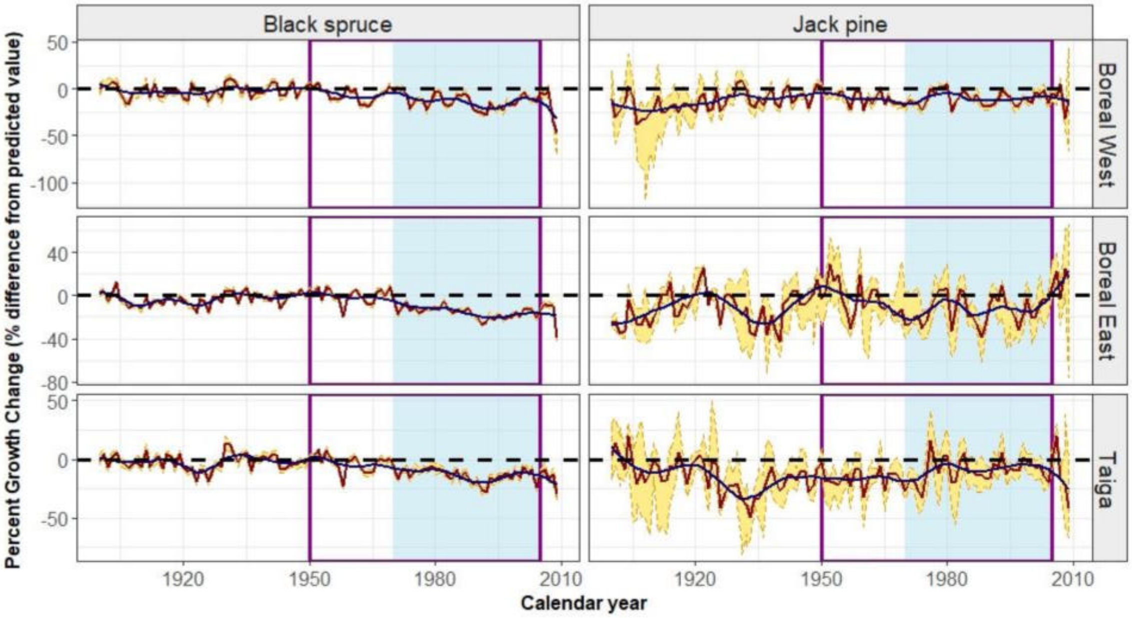


FIGURE 3 Median chronologies (red curves) of black spruce (left panels) and jack pine (right panels) detrended BAI (growth change) per bioclimatic domain (upper row: Boreal West; middle row: Boreal East; lower row: Taiga). Yellow shading and dotted lines delimit the bootstrapped 95 % confidence intervals, with LOESS smoothing shown by the blue lines (span = 0.2). Violet box and blue shading highlight the two time intervals (1950-2005 and 1970-2005, respectively). Black dashed lines denote a zero effect, i.e., no deviation compared to the value predicted by the GAMM model.

3.2 Sensitivity to climate is dissimilar across the landscape

Growth–climate response patterns were estimated for the two tree species to identify the key climate factors that were driving observed variability in growth (Figure 4). Summer temperature of the year preceding growth and spring precipitation in the year of growth had significant negative relationships with black spruce growth, while winter precipitation and winter temperature had a positive influence. The importance of these variables was not limited to particular regions but extended across vast areas (Figure 5). Black spruce tree sensitivity to other climate variables was more spatially heterogeneous (Figures 4 and 5). A high level of precipitation during previous-year summers had a significant positive effect upon the growth of black spruce within the Boreal East and Boreal West; this effect was not statistically significant in the Taiga (Figure 4). Excess-heat and high precipitation during previous-year autumns negatively affected spruce growth in the Boreal West and Taiga but had no significant effect in the Boreal East. Within the Boreal East and Taiga, the growth of black spruce was increased by hotter-than-average summers occurring during the year of ring formation and was decreased by milder-than-average springs. These relationships were mostly the opposite of what was observed within the Boreal West.

The response of jack pine to climate was less statistically significant and often opposite to that of black spruce. Regardless of bioclimatic domain, jack pine growth was increased by previous-year warm autumns and current-year summer warmth, but it was decreased by high winter precipitation (Figures 4 and 5). Current- and previous-year wet summers significantly increased the growth of jack pine within the Boreal East and Boreal West (Figure 4). Jack pine growth was positively correlated with mild and wet springs within the Taiga and with mild winters within the Boreal West, but was negatively impacted by wet springs within the Boreal East (Figure 4).

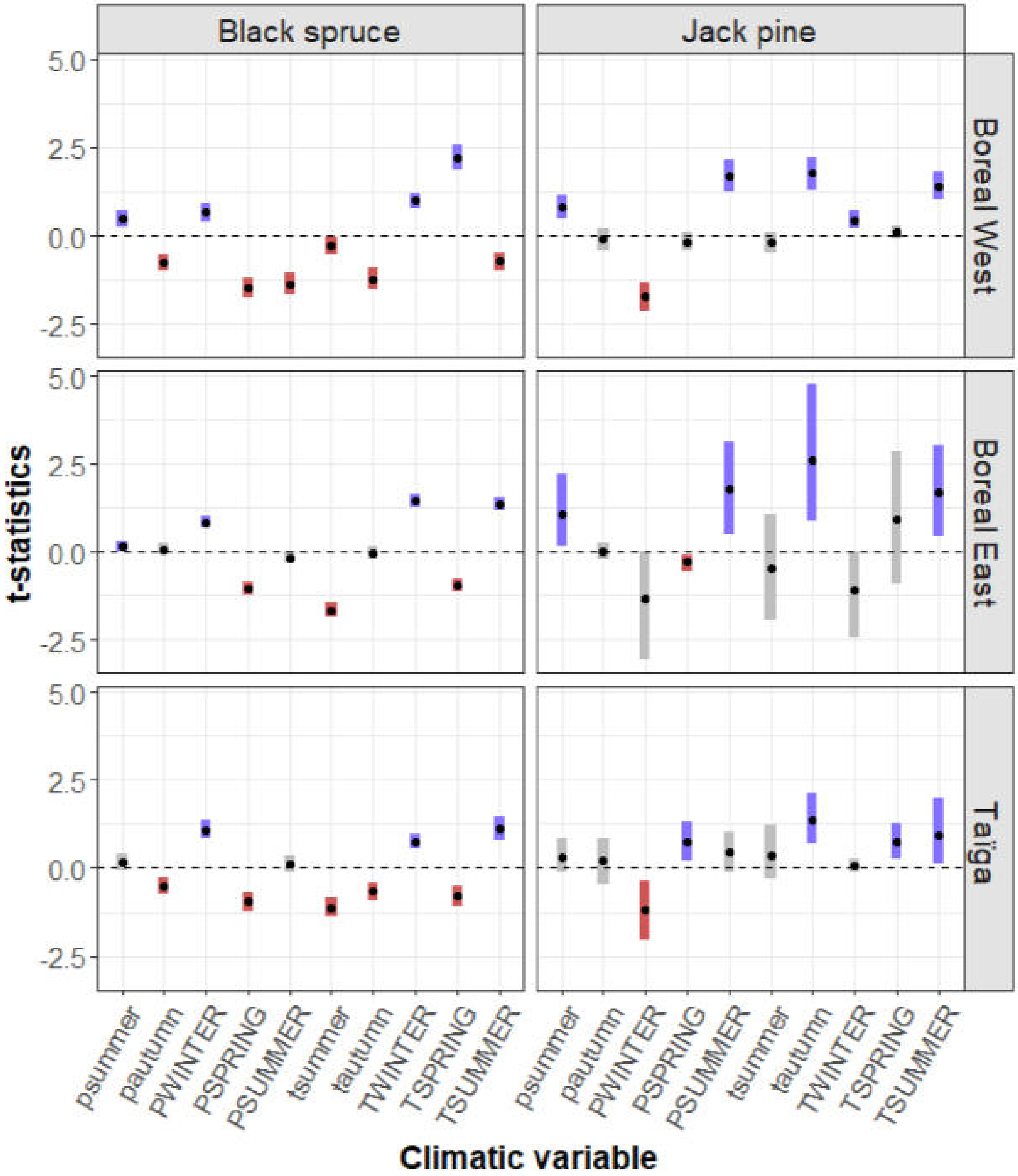


FIGURE 4 Arithmetic means (black dots) and bootstrapped 95 % confidence intervals (rectangles, R=10000 replications) of t-statistic values per bioclimatic domain for black spruce and jack pine, for each of the seasonal climatic variables. “T” and “P” at the beginning of a variable’s name denote temperature and precipitation, respectively. Uppercase letters denote climatic variables for the current growing season (winter, spring,

summer), and lowercase letters denote climatic variables of the previous growing season (previous summer, previous autumn). Blue and red rectangles indicate a significant (95 % confidence interval excluding zeroes) positive and negative effect, respectively, of the climatic variable at the scale of the bioclimatic domain, and grey rectangles are for non-significant values.

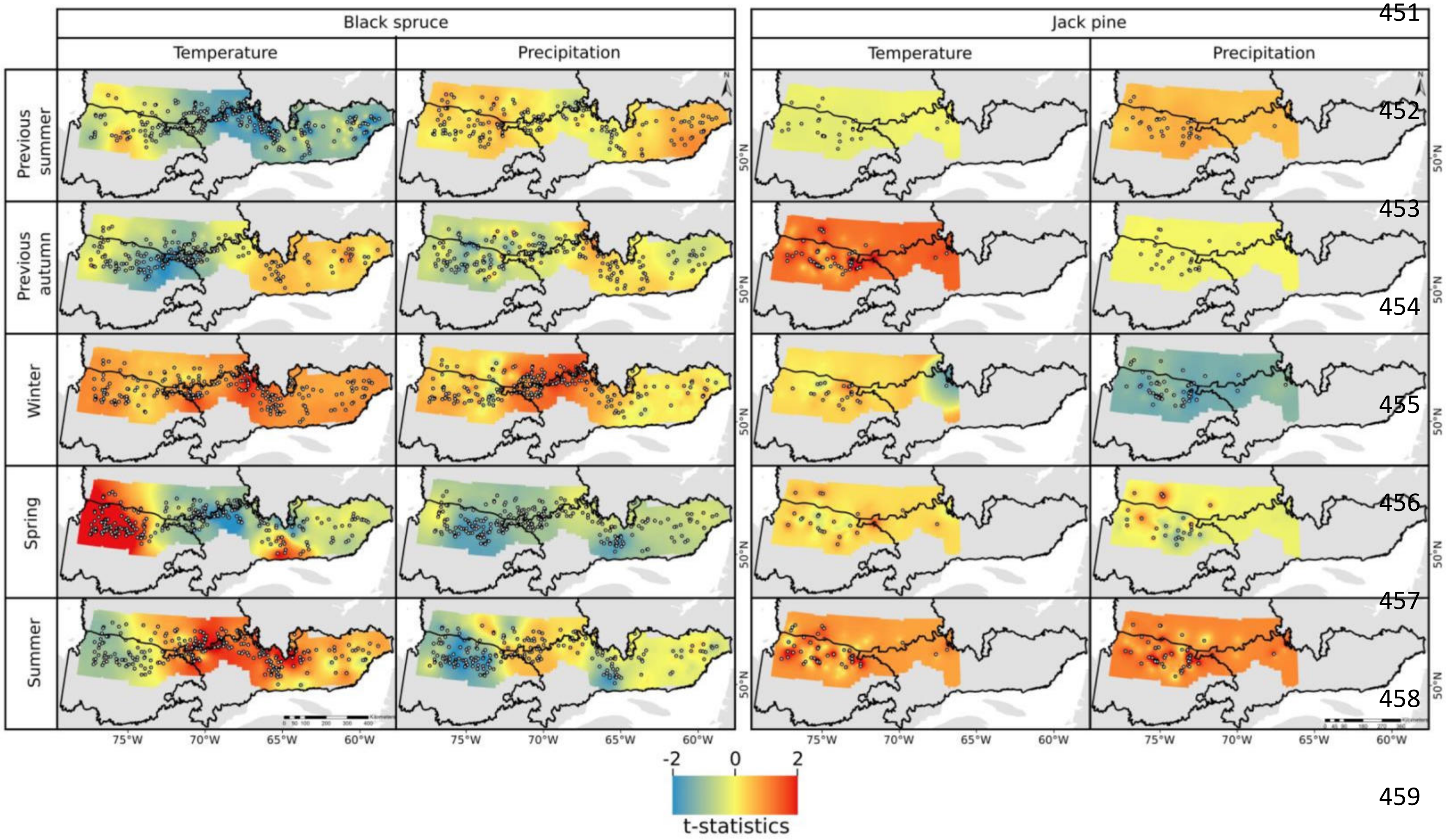


FIGURE 5 Kriging-interpolated growth response significance (based on t-statistics, 1970-2005) to seasonal climatic variable (left: temperature, right: precipitation) for black spruce (left panel) and jack pine (right panel). Green-to-blue colours denote a negative effect of the climate variable on tree growth, yellow colour means no impact of the climate variable on tree growth, and orange-to-red colours

denote a positive effect. Dots display significant values, i.e., plots for which the 95 % confidence interval of the t-statistics excludes zero.

3.3 Plot-level features had low but significant effects on growth-climate relationships

Sensitivity to climate differed between the two species, especially within the Boreal West, where species identity of the sampled trees alone accounted for 15 % of variation in growth-climate relationships (Figure 6). Such taxononomic variability in growth sensitivity to climate can be readily noted in Figures 4 and 5. Contributions of the sets of explanatory variables stand maturity, competition, altitudinal gradient, soil conditions, and regional climate to the climate sensitivity variance were much lower. The elevational gradient explained the highest proportion of variation in tree response to climate within the Boreal East and Taiga (5 % and 9 %, respectively; Figure 6). Stand maturity, alone or in combination with other explanatory variables, accounted for 7 %, 1 % and 5 % of the variation in growth-climate relationships within the Boreal West, Boreal East and Taiga, respectively. For competition, these values were respectively 3 %, 2 % and 2 %.

Stands that were composed mainly of old black spruce trees exhibited growth that was more negatively correlated with previous-year summer and autumn temperatures, but more positively correlated with winter precipitation compared to recently regenerated stands (Figures 6 and 7, and Supporting Information S10.1). These old-grown black spruce stands also exhibited the steepest declines in growth rates during 1970-2005 (Supporting Information S11). The positive effect of warmer-than-average autumns, winter and springs on the growth of jack pine was lower for stands that were composed of old trees in comparison with more recently regenerated stands (Supporting Information S8.4). Snowy and mild winters increased the growth of black spruce more than that of jack pine, but black spruce growth was more negatively correlated with wet and warm springs and with excess-heat during autumns of the previous years than that of jack pine. Previous-year wet summers and current-year mild springs decreased the growth of stands in the upper portion of the elevational gradient (i.e., above 500 m a.s.l.), while excessively high temperatures during current-year summers increased their growth more strongly than for stands at lower elevations (Figures 6 and 7, and Supporting Information S10.1 and S10.2). Similarly, growth in stands that were composed of taller trees (higher CI) was more negatively affected by excess-heat during previous-year summers than those stands that were composed of smaller-sized trees. Tree growth in more densely populated stands (higher BA) was also more positively correlated with winter temperature, but less positively correlated (within Boreal East and Taiga) or more negatively correlated (within Boreal West) with current-year summer precipitation than stands of lower densities (Figures 6 and 7 and Supporting Information S9.1).

The effect of other explanatory variables on tree sensitivity to climate was restricted to a specific region, such as soil conditions within the Boreal West and the continental-to-oceanic climate gradient within the Boreal East, which accounted for 3 % and 5 % of the variation in growth-climate relationships, respectively (Figure 6).

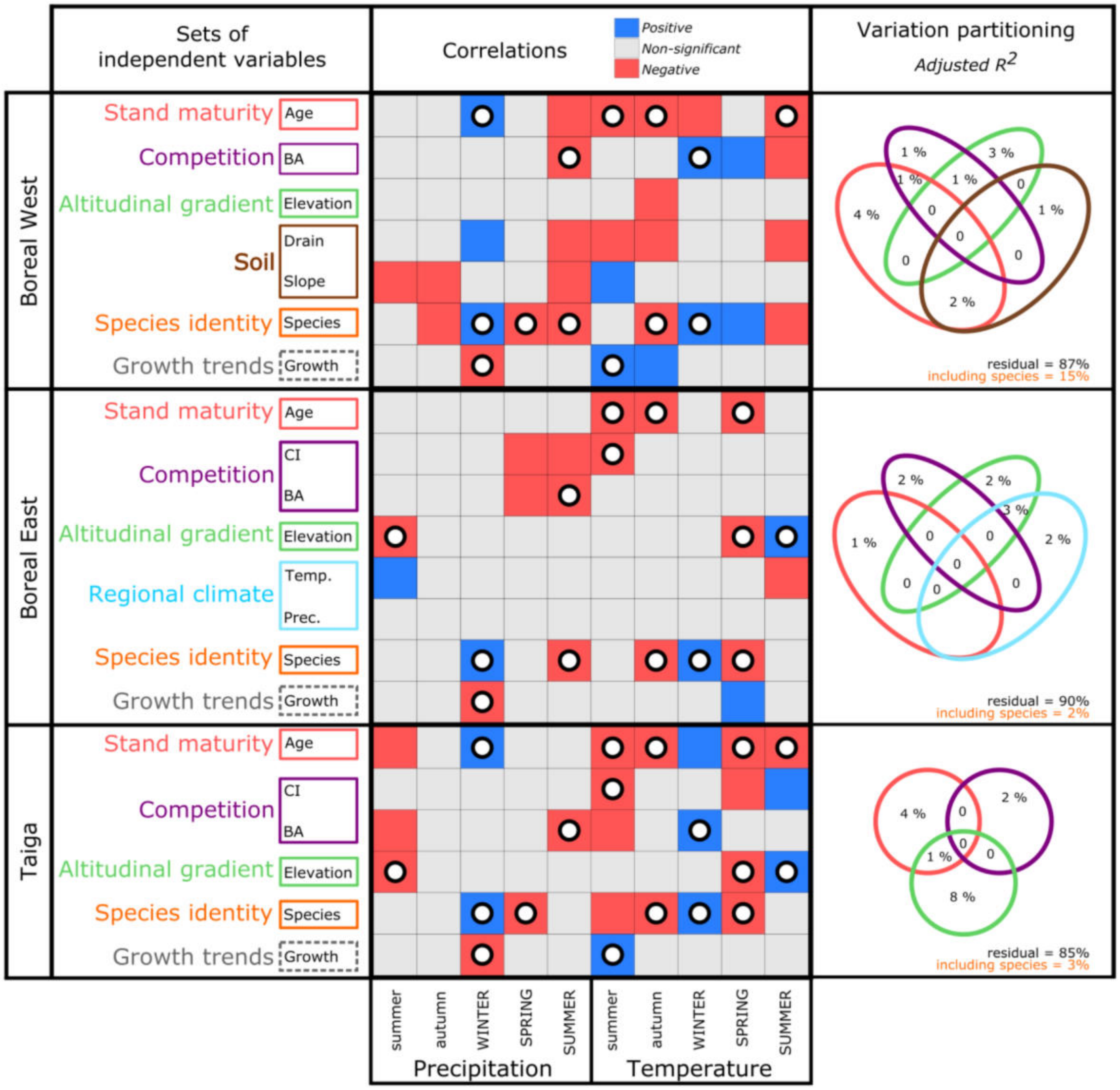


FIGURE 6 Left: The sets of independent variables used in variation partitioning (Please refer to Table 1 for variable ranges). Middle: Effect of each explanatory variable on tree sensitivity to climate, based on autocorrelation-corrected Pearson correlations. The relationship between long-term growth trends and climatic variables is also shown (uppercase letters: current year; lowercase letters: previous year). Red and blue shadings are for negative and positive relationships, respectively, that are significant at α = 0.05. Gray shadings denote non-significant relationships. Significant relationships common to at least two bioclimatic domains are emphasised with a dot. Right: Proportion of variance

explained by each set of independent variables, alone or in combination with other sets (Venn diagrams), by bioclimatic domain. The proportion of variance explained only by the species (pine or spruce) and the proportion of variance unexplained by the selected variables are shown below the diagrams.

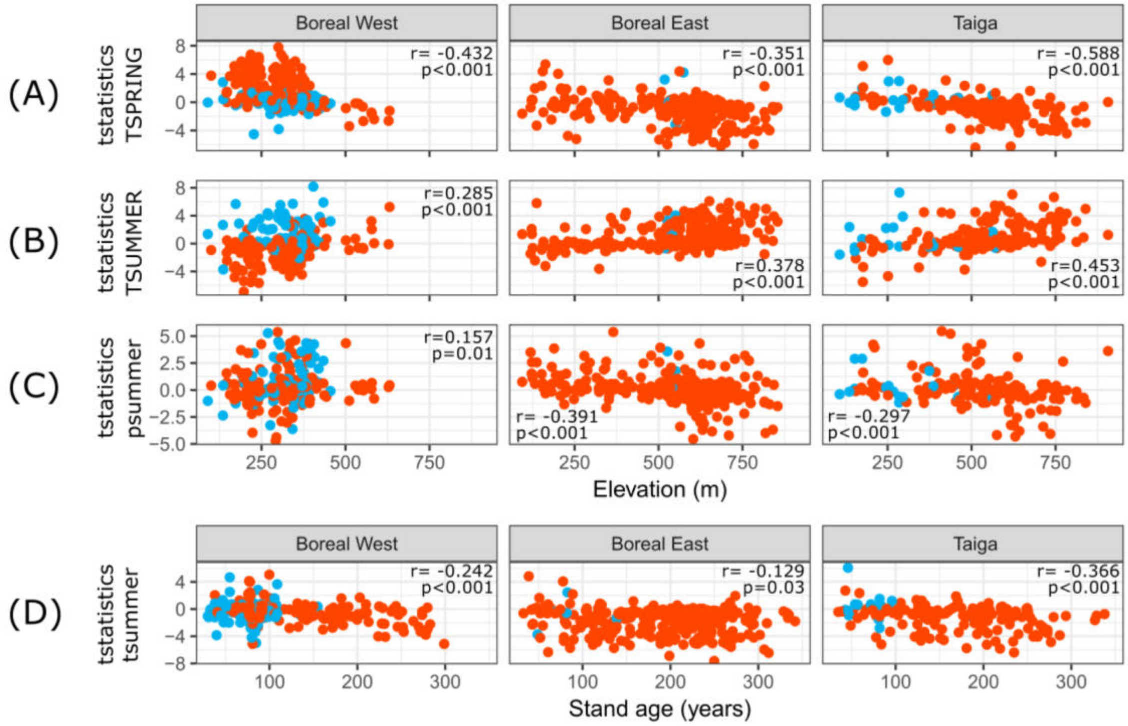


FIGURE 7 Effect of topographic position on sensitivity to (A) spring temperature, (B) summer temperature, (C) previous sumer precipitation, and (D) effect of the age of the stand on the sensitivity to previous summer temperature. Blue and orange dots are observed values for jack pine and black spruce, respectively. Also shown are the Spearman's rho coefficient (r) and p-value of the modified t-test corrected for the effect of spatial correlation.

4. DISCUSSION

Using a dendroecological dataset from a randomly distributed forest inventory network that consisted of 812 plots and 2266 trees, we provided an overview of the response of two major boreal needleleaf species to recent climate change, across explanatory variables that include stand maturity, competition, elevational gradient, soil conditions, and regional climate within eastern boreal North America. Our results highlighted spatial heterogeneity in long-term growth trends across the studied forest: in some areas growth rates decreased, while in others growth increased over the last few decades. Tree sensitivity to climate was also highly spatially heterogeneous. Our study underscores the utility of employing broadly distributed datasets for assessing the complexity of climate change effects on a forest ecosystem (Klesse et al., 2018; Nicklen et al., 2018).

The species identity of the tree explained a greater proportion of variation in growth-climate relationships than did all other explanatory variables in the Boreal West. Further, we observed contrasting growth trends between the two species. Our analyses suggest that sensitivity to climate is determined primarily by a species-specific set of functional traits. Black spruce and jack pine usually occupy sites with different soil structures (Balland, Bhatti, Errington, Castonguay, & Arp, 2006) and have very different root system architectures and physiological efficiencies (Blake & Li, 2003; Strong & La Roi, 1983), which could explain differences in climate sensitivity.

We identified previous-year summer temperature and, to a lesser extent, previous-autumn temperature as two of the climatic factors with the greatest negative effects on annual growth rates of black spruce trees. Excess-heat during late summer and autumn may lead to declines in carbohydrate reserve accumulation at the end of the growing season, thereby negatively affecting spring growth, as was previously observed in both boreal

North America and northern Europe (Girardin et al., 2016; Ols et al., 2018). Decreased reserve formation of heat-stressed trees can result from accelerated respiration, which leads to higher and more rapid use of photosynthates that otherwise would be available for storage (Anderegg & Anderegg, 2013; Granda & Camarero, 2017; Sala, Woodruff, & Meinzer, 2012). The steepest declines in observed growth for individuals that were the most greatly affected by above-average temperature during summer of the year prior to ring formation suggest that hot extremes are one of the primary determinants of growth trajectories for boreal black spruce forests, as has been observed for white spruce seedlings in plantations by Benomar et al. (2018). The deeper root system of jack pine trees could have allowed them to access additional water resource in deeper soil layers, and their greater resource use efficiency could have prevented them from an overuse of carbon reserves during heatwaves, potentially leading to an uninterrupted carbohydrates storage during hotter-than-average late growing seasons. The resulting higher amount of photosynthates available the following spring could explain the positive correlation between jack pine growth and previous autumn temperature. Our results also suggest that in addition to the effect of species-specific traits, some variation originated from spatially varying site features like stand maturity, position along the elevational gradient, regional climate and soil conditions. Yet, these site-level features explained a lower proportion of the variance in patterns of growth-climate relationships within bioclimatic domains.

As predicted from our main working hypothesis, position along the elevational gradient explained a low but significant proportion of the variation in tree response to spring and summer temperature and to previous summer precipitation. This finding illustrates diverging climatic constraints, from water-limited trees at low elevation to trees constrained by cold temperatures during the growing season at the high end of the elevational gradient. Contrary to our expectations, growth of black spruce was more negatively affected by mild springs when located in the upper portion of our elevational gradient. This counter-intuitive effect of mild springs was recently observed elsewhere (Babst, Carrer, et al., 2012; Ols et al., 2017) and could result from earlier onset of physiological activity and growth in response to warming (Gu et al., 2008; Richardson et al., 2018; Vitasse, Signarbieux, & Fu, 2017). Late-frost events generally occur more frequently at higher elevations and in cold regions such as the Boreal East and Taiga than at lower elevation or in relatively warmer regions such as the Boreal West. These events can damage early formed shoots and roots, thereby reducing total seasonal growth (Kidd, Copenheaver, & Zink-Sharp, 2014; Montwé, Isaac-Renton, Hamann, & Spiecker, 2018).

Summer warmth had a contrasting effect on tree growth, depending upon its occurrence. While previous-year high temperatures had negative effects on growth during the following growing season, hotter-than-average summers had an immediate and positive effect on growth rates in the year of occurrence. The latter relationship, which had been observed in the Boreal East and Taiga, was more pronounced for stands at upper elevation sites than at lower elevations and could be linked to a decrease in the risk of late-frost damage and faster snowmelt in early summer (Vitasse et al., 2017). Hot summers are also correlated with high solar radiation and, consequently, with higher rates of photosynthesis, especially in sites where water is not a factor limiting to tree growth, such as stands at the high end of our elevational gradient in the Boreal East and Taiga. Temperature generally decreases with elevation, so an increase in summer temperature can lead to a greater net beneficial effect on tree growth at higher elevations (see Supporting Information S12).

However, the resulting growth gain would have been outweighted by the growth decline due to late frost damage, which could explain that growth trends in stands within the central hilly area were more negative than in the westernmost stands.

Effects of other variables on climate sensitivity, such as stand maturity and competition, were generally consistent accross regions. Excess-heat during previous-year summers and autumns had a significantly greater negative impact on black spruce growth in older stands compared to more recently regenerated stands. The increase in climate sensitivity with age has been extensively documented (e.g., Altman et al., 2017; Schuster & Oberhuber, 2013), and was linked to ontogeny-related morphophysiological changes (Ryan et al., 2006) leading to a decrease in hydraulic conductance (Magnani, Mencuccini, & Grace, 2000). During drought, hydraulic conductance may decrease more strongly in old and tall trees because of greater path resistance (Ryan & Yoder, 1997); the resulting decreases in stomatal conductance and photosynthesis may entail, along with greater metabolic demand in tall trees (Hartmann, 2011), depletion of carbohydrate reserves in older stands. This response is a potential explanation for the negative relationship between 1970-2005 growth trends and stand age (Supporting Information S11; see also Chen et al. (2016); Girardin et al. (2014)).

Competition pressure also significantly modulated the growth-climate relationships. Growth of trees in densely vegetated (high BA) stands that were composed of taller individuals (high CI) was more negatively correlated with excess-heat during previous-year summers and less positively correlated to current-year wet summers than in a less competitive environment. These relationships could have originated from lower carbon assimilation and carbohydrate reserve formation originating from reduced water availability (Gleason et al., 2017). In contrast, black spruce trees responded more positively to mild winters in densely vegetated compared to more sparsely populated stands, which may be due to the stabilizing effect of a dense canopy on local-scale hydrothermal properties (Gu et al., 2008; Vaganov, Hughes, Kirdyanov, Schweingruber, & Silkin, 1999), similar to the effect of high structural diversity (Aussenac et al., 2017).

Soil conditions accounted for a significant proportion of the variation in growth-climate relationships, but this was true only for black spruce in the Boreal West. This region is characterised by a contrasting physiography spanning comparatively flat landcapes with a high proportion of peatlands in the west to hilly terrain with sandy-loam soils in the east (Robitaille et al., 2015; also see Figure 1 and Table 1), together with resulting differences in soil hydrology. During hot summers, the water table of soils with a high proportion of organic material is lowered, and in combination with the high degree of dessication of the peat substrate (Gewehr et al., 2014; Voortman et al., 2013), may have reduced water availability and exacerbated summer heat stress, particularly for trees with shallow rooting systems such as black spruce. Paradoxically, an excess of water during consecutive wet springs and summers also reduced growth of black spruce in Boreal West (Figure 5), most likely because of hypoxic stresses resulting from elevation of the water table in poorly drained sites (Zobel, 1990). A positive correlation between growth of western black spruce trees and the annual area burned, which is a proxy for litter and deep organic layer dryness (Molinari et al., 2018), adds credibility to the assumption that tree sensitivity to precipitation was strongly modulated by soil hydrology in the Boreal West (Supporting Information S13).

Overall, we identified mostly negative growth trends for black spruce and only barely positive trends for jack pine during the 1970-2005 period, which confirms the absence of climatically-induced stimulation of tree vigour that was previously observed for the boreal forest (Girardin et al., 2016; Hember et al., 2016; Ju & Masek, 2016; Zhu et al., 2016). However, forest growth trends were spatially heterogeneous, and the productivity of some areas increased over the last few decades. Variability in growth-climate relationships that was explained by the set of variables considered in our analysis remained low (< 25 %), as is the case in many studies focusing on ecological processes. Our random sampling strategy implies that many factors, which are potentially involved in growth-climate relationships, were not considered and could not be controlled for, such as the effect of non-tree vegetation, insect epidemics, or nutrient cycling. In addition, the genetic diversity of the species under study surely induced different responses to climate between populations (Housset et al., 2016; but see Avanzi et al., 2019). Based upon our results, we suggest that the warming threshold beyond which the productivity of the boreal forest will shift from positive to negative (~ +2 °C; D'Orangeville et al., 2018) is likely very heterogeneous across the boreal biome, but may already have been reached in many of our black spruce stands.

ACKNOWLEDGEMENTS

This research was conducted as part of the International Research Group on Cold Forests. This study was made possible thanks to the financial support that was provided by the Strategic and Discovery programs of NSERC (Natural Sciences and Engineering Research Council of Canada), and a MITACS scholarship co-funded by NSERC and Ouranos. Additional financial support was provided by the Canadian Forest Service and the UQAM

Foundation (De Sève Foundation fellowship and TEMBEC forest ecology fellowship). We thank Dan McKenney and Pia Papadopol (Canadian Forest Service) for providing the ANUSPLIN climate data. Many thanks to XiaoJing Guo (Canadian Forest Service) for the initial version of the R-scripts and helpful advice during statistical analyses, to Claire Depardieu for relevant comments on the manuscript, and to Isabelle Lamarre and W. F. J. Parsons for language editing.

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