

# Moisture deficits limit growth of white spruce in the west-central boreal forest of North America

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## ABSTRACT

Climate change may cause reduced forest productivity and higher tree mortality due to water deficits that result from increased evapotranspiration. Such limitations may occur in some areas of the North American boreal forest where precipitation is low and warming trends are high. This paper analyzes climatic factors that limit the growth of a commercially important and widespread boreal tree species, white spruce (*Picea glauca* (Moench) Voss), based on a range-wide dendroclimatological analysis of 9795 trees from 227 sample sites across the North American boreal forest. A bootstrapped response function analysis was conducted for monthly temperature and precipitation variables, and a multivariate regression tree analysis was used to group white spruce populations with similar response coefficients where climatic factors explained 46% of the total variance in response coefficients. The results of this study show that white spruce populations in the west-central boreal forest of North America are the most precipitation-limited group and therefore likely to be most susceptible to climate change. Populations both to the north and south of this group appear less vulnerable, and eastern populations generally do not experience growth-limiting moisture deficits. Regional climate change projections suggest that moisture limitations will become more pronounced in the future, especially for southwest and west-central boreal tree populations.

## 1. Introduction

Boreal forest ecosystems play a vital role in carbon sequestration and are a globally important carbon sink (Reinmann et al., 2019). The ability of northern forests to regulate natural cycles for carbon and water, with northern ecosystems potentially driving climatic feedback loops at globally relevant scales, makes boreal forests an important terrestrial ecosystem for preserving the ecological functions and services we rely on. Northern boreal forest regions have also experienced more rapid warming, about twice the rate as the global average (IPCC, 2014), creating the impetus to study how climatic changes might affect northern tree species. Generally, it is expected that climate warming will result in increased evapotranspiration that may be regionally mitigated or amplified by changes to precipitation regimes (IPCC, 2014), potentially leading to water deficits and drought stress.

One way of analyzing how forests have been impacted by climate over time is through the study of tree-rings. Correlations between annual tree ring widths and climate can be used to infer climate conditions of past centuries (e.g., Douglass, 1919; Sheppard, 2010). Conversely, with accurate climate data available for previous decades from

weather station records, climatic effects on past tree growth can also be inferred (e.g., Chen et al., 2017). This field of historical biology has become an important tool for natural resource managers in the context of climate change to predict climate change impacts on natural and managed ecosystems (e.g., Daniels et al., 2017).

For the boreal forest, previous research suggests that eastern North American regions are less vulnerable to climate change than western boreal forest regions. A study of black spruce (*Picea mariana*) tree-rings in northeastern North America indicates that high precipitation can mitigate the negative impacts associated with a warming climate under future climate change projections (D'Orangeville et al., 2016). Mean annual precipitation in the northeastern boreal forest of North America is more than double the amount that is normally received in central and western areas of the continent, creating an east-west gradient for water availability (D'Orangeville et al., 2016). Other studies have shown that the western regions of North America have already experienced growth reductions and tree mortality as a result of regional warming and water stress, primarily in the western and southern fringe of the boreal forest (van Mantgem et al., 2009; Birdsey & Pan, 2011; Peng et al., 2011).

White spruce is a widespread and valuable boreal tree species that

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accounts for approximately 26% of Canada's softwood growing stock (Forintek Canada Corp, 2006). However, this species may be vulnerable to climate change as recent growth reductions have been linked to late-20th century warming (Jacoby and D'Arrigo, 1995; Porter and Pisaric, 2011). Chhin et al. (2004) associated reduced radial growth to historical drought events in the prairies of Canada and the Great Plains of the United States. Similarly, dendroclimatic analyses of spruce in the western Canadian interior concluded that climatic drying and drought conditions over the last 20 years have significantly impacted the growth of white spruce in this region (Chen et al., 2017; Hogg et al., 2017; Hogg and Wein, 2005). Further north, white spruce populations in the interior of Alaska exhibited precipitation-limited growth (Lloyd et al., 2013). Sang et al. (2019) found that western white spruce populations planted in a common garden experiment suffered substantial growth reductions, with similar behaviour of all populations throughout the species range under severe drought conditions in this experiment.

In this paper, we contribute a continental-scale analysis of white spruce response to climate by reanalyzing a comprehensive dataset from the International Tree Ring Data Bank (Grissino-Mayer and Fritts, 1997; Zhao et al., 2018), a sample plot network of the Canadian Forest Service (Hogg et al., 2017), and additional data from scientists who previously published regional dendrochronological studies with white spruce (Girardin et al., 2016; Hogg et al., 2017; Roy et al., 2017; Lemus-Lauzon et al., 2018). The research approach is a dendroclimatological response function analysis, where monthly historical climate data are correlated with interannual variation in radial growth. We then use a constrained cluster analysis to group individual chronologies according to similar response coefficients, with the groups being delineated by long-term climate conditions of the sample sites. Our objective is to compare the climatic limitations of white spruce populations across broad macroclimatic regions of the North American boreal forest, and to identify populations that are most vulnerable to growth reductions or mortality under climate change.

## 2. Methods

### 2.1. Climate data

Climate data for North America were generated using the ClimateNA v5.10 software package based on the methodology described by Wang et al. (2016). These climate data were generated by interpolating historical weather station data using the Parameter-elevation Regressions on Independent Slopes Model (PRISM) methodology (Daly et al., 2008). This software was used to extract climate data for all white spruce chronology locations used in this study, including historical monthly data from 1901 to present to analyze interannual growth response to climate variation. In addition, 30-year (1961–1990) climate normal data were extracted to characterize the general climate conditions of sample sites. Also, future climate projections were generated based on 15 atmospheric-ocean general circulation models (AOGCMs) from the CMIP5 multimodel dataset. The AOGCMs CanESM2, ACCESS1.0, IPSL-CM5A-MR, MIROC5, MPI-ESM-LR, CCSM4, HadGEM2-ES, CNRM-CM5, CSIRO Mk 3.6, GFDL-CM3, INM-CM4, MRI-CGCM3, MIROC-ESM, CESM1-CAM5, GISS-E2R were chosen to represent all major clusters of similar AOGCMs by Knutti et al. (2013). All extractions of data for historical and future climate at chronology sites were carried out with the ClimateNA software package (Wang et al. 2016), available online at <http://tinyurl.com/ClimateNA>.

The following climate variables were used to characterize long term climate conditions: Mean Annual Temperature in units of °C (MAT); Mean Warmest Month Temperature in °C (MWMT); Mean Coldest Month Temperature in °C (MCMT); Mean Annual Precipitation in mm (MAP); Total Difference between MCMT and MWMT in °C (TD); May to September Precipitation in mm (MSP); Annual Heat-Moisture Index (AHM) calculated as  $(MAT + 10)/(MAP/1000)$ ; Summer Heat-Moisture

Index (SHM) calculated as  $MWMT/(MSP/1000)$ ; Hargreaves Climatic Moisture Deficit (CMD) calculated as  $E_{ref}-PPT$ , representing the sum of the monthly difference between reference evaporation ( $E_{ref}$ ) and precipitation (PPT) according to Wang et al. (2012); Degree Days below 0 °C (DD < 0); Degree Days above 5 °C (DD > 5); Frost-Free Period (FFP); Beginning of the Frost-Free Period (bFFP); End of the Frost-Free Period (eFFP); Extreme Minimum Temperature (EMT); Precipitation as Snow (PAS); and Number of Frost-Free Days (NFFD). For further details on the estimation of these climate variables, see Wang et al. (2016).

### 2.2. Tree-ring data

Tree-ring data for white spruce across North America were obtained from the International Tree-Ring Data Bank (ITRDB) (Grissino-Mayer and Fritts, 1997). We use a version of the database prepared by Zhao et al. (2018), where raw tree-ring data were collected and formatting issues were corrected. Additional raw tree-ring data were collected from researchers who previously published dendrochronological research with white spruce (Girardin et al., 2016; Hogg et al., 2017; Roy et al., 2017; Lemus-Lauzon et al., 2018). An additional source used to cross-reference master chronologies was Dendrobox, an interactive and exploratory tool to visualize tree-ring data available from the ITRDB (Zang, 2015). In total, white spruce chronology data were compiled for 9795 trees from 227 sample locations across the North American boreal forest (for details refer to Appendix A Supplementary Data 1).

Trees that experience drought or defoliation from insect pests can produce false or missing tree-rings (Keen, 1937; Evenden, 1940; O'Neill, 1963; Swetnam et al., 1985). Therefore, individual chronologies from the same sample sites were cross-dated to identify and correct for missing and false rings. We then detrended the chronologies by fitting a smoothing spline to each ring-width series using a frequency response of 0.5 and a wavelength of 0.67 for all chronologies, dividing the actual ring-width by each yearly value of the fitted growth curve (Fritts, 1966). Detrending was implemented with the *dplR* package (Bunn, 2008) for the R programming environment (R Core Team, 2018). The resulting dimensionless ring-width indices were then averaged with other trees from the same sample location to build a master chronology for each white spruce site (Cook & Peters, 1997), also implemented with the *dplR* package. This resulted in a total of 227 master chronologies with an average expressed population signal of 0.88 and a mean of 43 trees per chronology that were used for further dendroclimatological analysis (for detailed statistics on interseries correlations and expressed population signal for each chronology, see Appendix A, Supplementary Data 1).

### 2.3. Analysis of climate-growth associations

We tested mean monthly temperature and precipitation variables from June of the previous year to September of the current year as predictor variables for standardized annual growth increments from 1901 to 2001. Climate variables from the previous growing season and winter months can be important to incorporate into the model because legacy growing conditions can influence tree growth the following year (Fritts, 1966; Swetnam et al., 1985). For the response function analysis, indirect regression techniques aim to mitigate predictor multicollinearity by regressing the annual growth measurements against the principal components of the climate data, where the principal components with the smallest variances are discarded (Bondi and Waikul, 2004; Zang and Biondi, 2015). Statistical significance of growth-climate relationships was tested through bootstrapping, generating a distribution of response coefficients through subsampling the chronology data with 1000 iterations. Coefficients that did not include zero within the 95% confidence interval of the distribution were regarded as statistically significant. All the above analysis was implemented with the *treeclim* package (Zang, 2015) for the R Programming Environment (R Core Team, 2018).

### 2.4. Constrained clustering of chronologies

We use a multivariate regression tree (MRT) analysis in order to group chronologies based on the similarity in their response coefficients to monthly climate data, but using long-term average climate conditions of the chronology sites as partitioning criteria to arrive at groups that are interpretable as macroclimatic regions. MRT minimizes the variance in multiple response variables (here, coefficients from the response function analysis described above), using multiple predictor variables as grouping criteria (here, 30-year normal climate variables) in a recursive binary partitioning algorithm (Ouellette et al., 2012). MRT is a constrained clustering method, where splitting the data at the initial node explains most of the variance and maximizes homogeneity of the response variables within groups (De'Ath, 2002).

For the groups of chronologies resulting from the MRT, average monthly climate data for the 1961–1990 normal period were used to generate Walter and Lieth climate diagrams (Walter and Lieth, 1969) with the R package *climatol* (Guijarro, 2018). The diagrams were created for each group of chronologies generated by the multivariate regression tree analysis to interpret monthly response coefficients in light of long-term average climate conditions, i.e. the environment to which tree populations are putatively adapted. These chronology groups were then mapped using ArcGIS Desktop 10.5.1 (ESRI, 2011).

## 3. Results

### 3.1. Grouping of chronology sites

The multivariate regression tree analysis produced six groups that explained 46% of the variance in monthly response function coefficients among chronologies (Fig. 1). According to their approximate geographical location, we label these groups northwest, north-central,

northeast, southwest, west-central, and east-central (Fig. 2). The first split (Node #1), explaining 13% of the variance in response coefficients, created a roughly diagonal separation of the species range into samples comprising of the southwest and west-central populations versus all other groups. This split was based on the number of frost-free days, or alternatively, could also be made using growing degree days, mean annual temperature, or the annual heat moisture index (Table 1). Thus, the primary split describes groups with response functions unique to warmer and drier environments with a longer growing season in the southwestern portion of the species range. The second split explained 10.7% of the variance in response coefficients and created the north-central group based on the mean coldest monthly temperature being below  $-27.1\text{ }^{\circ}\text{C}$ , or alternatively, variables that indicate a short frost-free period (Table 1), i.e., this group is characterized by winter length and severity. The third and fourth split resulted in east-central, northwest, and northeastern groups based on growing degree days and growing season length. Split 5 further partitions the warm and dry portion of the species range created by the first split, accounting for 8.1% of the variance, where the southwest group is distinguished from the west-central group by the warmest mean annual temperatures or the highest growing degree days (Fig. 3, Table 1).

Overall, the regression tree clustering partitioned groups primarily by variables that describe temperature and growing season length conditions. Variables describing drought conditions only occur once as alternative auto-correlated climate variable for the first split (Table 1), which would create the same or near identical groups as number of frost-free days (Fig. 2, Node 1).

### 3.2. Climate of chronology groups

Walter and Lieth climate diagrams (Fig. 3) and additional climate variables (Table 2) for the six groups produced by the multivariate

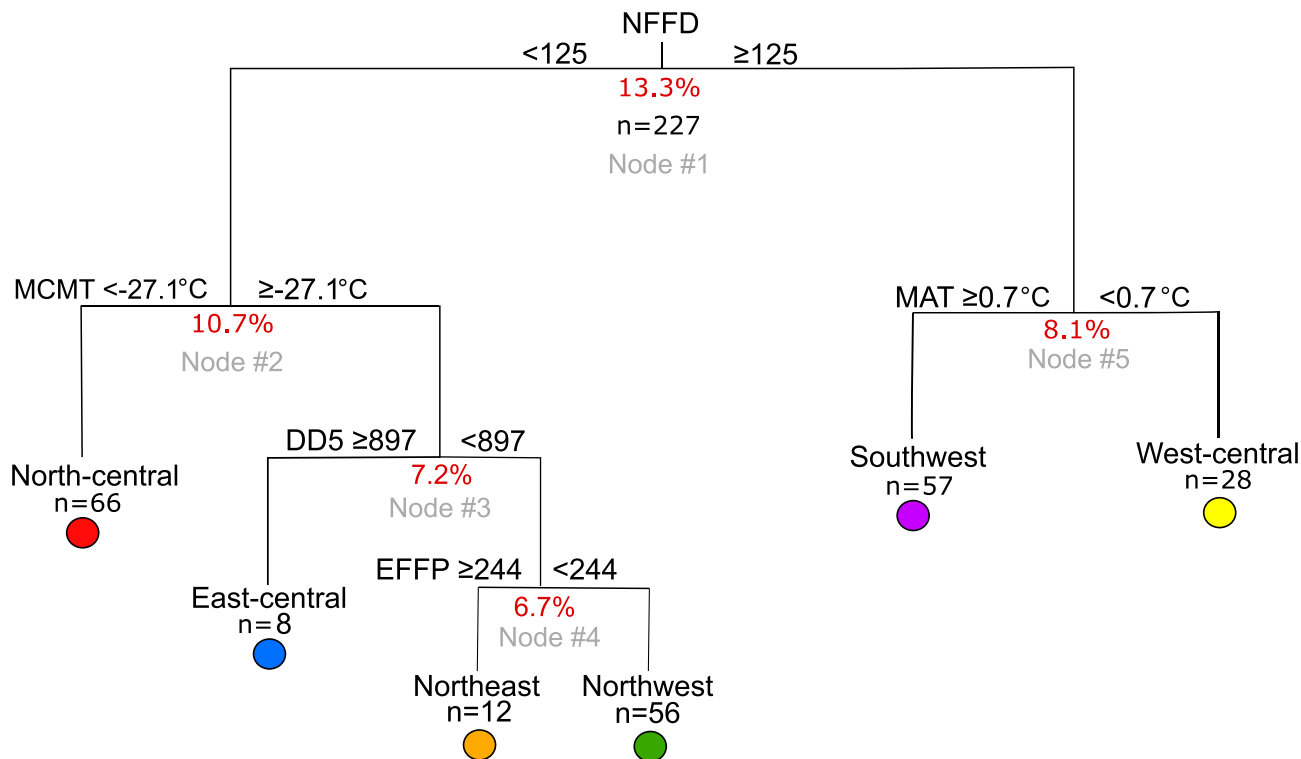
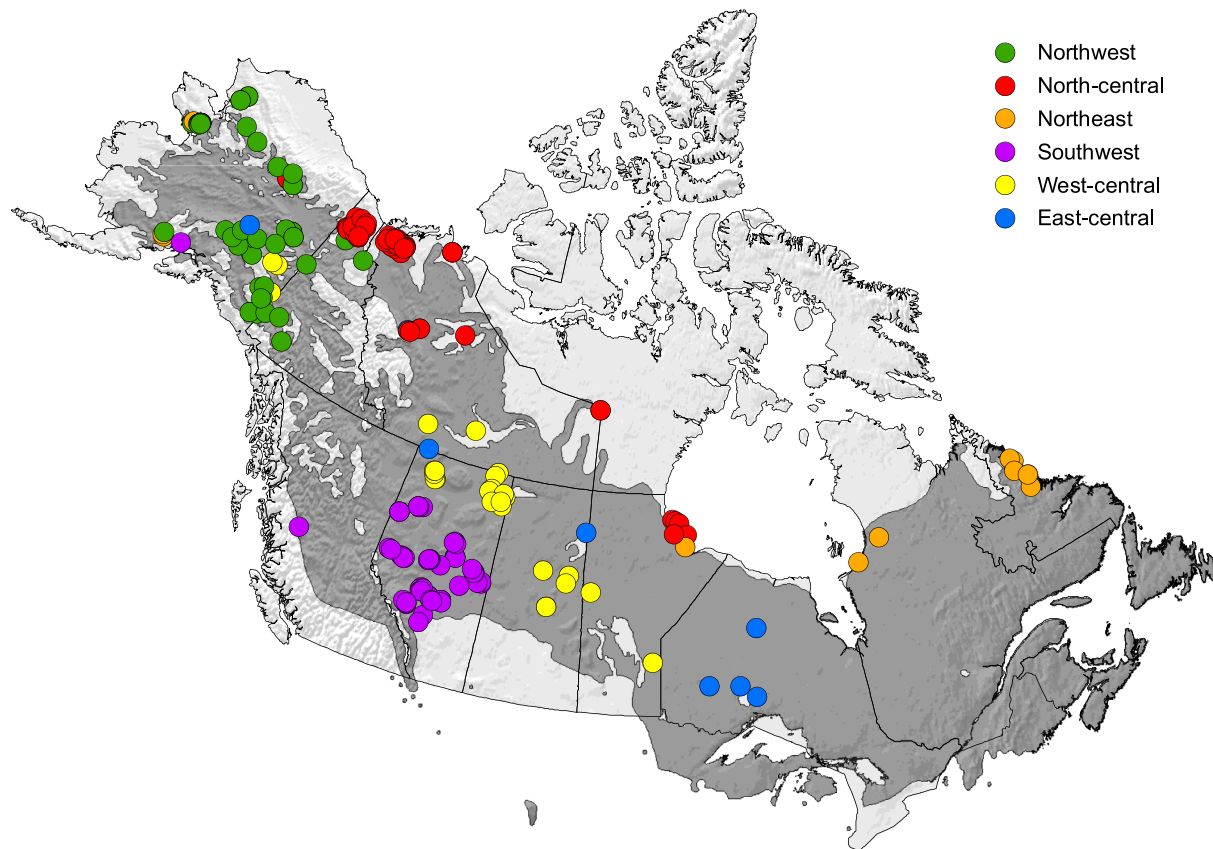


Fig. 1. Multivariate regression tree analysis of 277 chronology sites, where six groups with similar dendochronological response functions are delineated based on climate normal conditions at each site. The climate variables chosen by the MRT algorithm include: NFFD (number of frost-free days); MCMT (mean coldest month temperature); DD > 5 (degree days above 5 °C); EFFP (end of the frost-free period); and MAT (mean annual temperature). Each node shows the percentage of variance in response coefficients explained in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 2.** The location of each white spruce chronology used in this study grouped into regions with similar climate and growth response coefficients by a multivariate regression tree analysis (Fig. 1). The dark grey area represents the species range of white spruce.

**Table 1**  
Alternative auto-correlated climate variables that could be used in the multivariate regression tree analysis in Fig. 2 to delineate regional chronology groups.

Alternative climate variables	Value (right side)
<b>Node #1</b>	
Degree days above 5 °C	≥ 894
Mean annual temperature (°C)	≥ -2.3
Annual heat moisture index	≥ 15
<b>Node #2</b>	
Beginning of frost-free period (day)	< 154
Frost-free period (days)	≥ 103
<b>Node #3</b>	
End of frost-free period (day)	< 245
<b>Node #4</b>	
No alternative variable	
<b>Node #5</b>	
Degree days below 0 °C	≥ 2241

regression tree analysis provide a more comprehensive characterization of seasonal and annual climatic conditions. Overall, average annual temperatures between the six groups varied by approximately 10° C (Table 2). The lowest temperatures occurred in the north-central group, and the highest average annual temperature was in the southwest group, making this region the only one to have a mean annual temperature above freezing (Table 2).

The Walter and Lieth climate diagrams show that the southwest and the west-central groups have the longest and warmest growing seasons for white spruce populations with 5 months above 0 °C (Fig. 3), about 100 days of continuous frost-free period, and more than 1000 growing

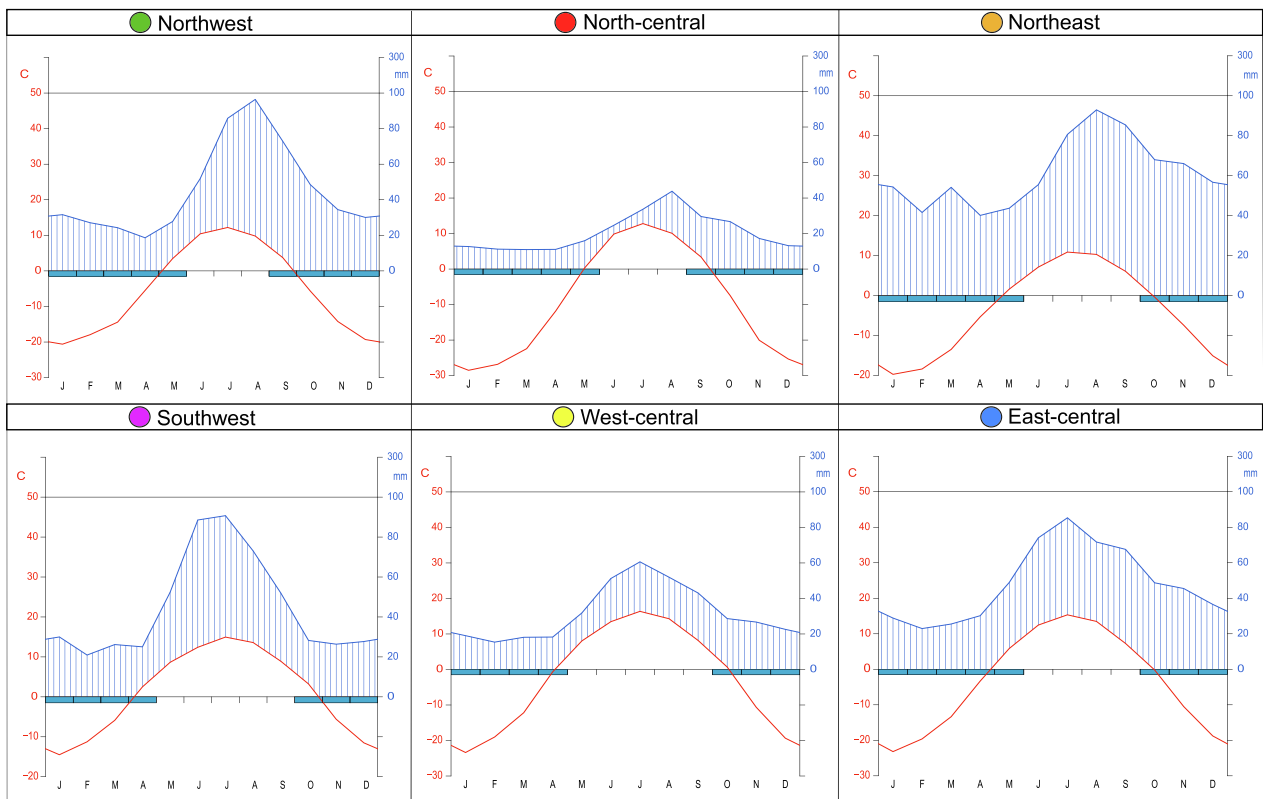
degree days (Table 2), far exceeding the remaining groups. White spruce growing in the northwest and north-central groups have only 3 months above 0 °C (Fig. 3) and only about 70 days of continuous frost-free periods (Table 2). The remaining east-central groups are characterized by relatively high mean annual temperature and precipitation levels, and frost-free periods of 80–90 days (Fig. 3).

Drought conditions arise in areas where the interplay between temperature and precipitation result in moisture deficits. A useful metric to assess drought risk in addition to temperature and precipitation levels is Hargreave’s climate moisture deficit (CMD). Here, evapotranspirative demand relative to precipitation is expressed in mm, where higher CMD values indicate a larger moisture deficit. Our results show the highest moisture deficits were present in the west-central group (Table 2). Moisture deficits were substantially smaller for populations both north and south of the west-central group. Although the north-central group received the least precipitation, temperatures in this region are also low, reducing evapotranspirative demand. The north-central group does have the strongest summer drought condition as indicated by the summer heat moisture index (Table 2, SHM), also visible in Fig. 3. The highest amount of total annual precipitation was received in the northeast group, around 750 mm per year (Fig. 3), likely making this group the least susceptible to drought conditions with a SHM of 31.6 and a CMD of 30 mm.

### 3.3. Drought limited populations

Dendrochronological response coefficients also indicate that white spruce in the west-central group is the most sensitive to drought conditions, as indicated by their response to variations in monthly precipitation and temperature (Fig. 4). Radial tree growth was consistently negatively affected by years with high temperature or low precipitation





**Fig. 3.** Walter and Lieth climate diagrams for each of the six chronology groups. The blue y-axis and related lines represent average precipitation (mm) received in that region from 1901 to 2001. The red y-axis represents the average temperature (°C) recorded over the same 100-year time series. The dark blue horizontal bars indicate months with freezing temperatures. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

across most months with the exception of July of the current year. Temperature increases during the previous growing season in particular caused a negative growth response. The west-central group also showed the highest number of statistically significant relationships between monthly precipitation variables and growth in individual chronologies (Table 3). Response coefficients for temperature were less consistently significant for this group, however.

In addition to the west-central group, the southwest chronology group also appears to be potentially vulnerable to drought. Response coefficients generally show similar magnitude and direction as the west-central group, although to a lesser degree and with fewer percentages of significant response coefficients. This group also deviates from the west-central group by generally preferring warmer temperatures during the current growing season, whereas the west-central group predominately showed a negative response to higher temperatures.

The remaining populations do not generally appear to be drought

limited. Coefficients between growth and precipitation for the north-west and east-central groups are variable, and for the north-central and northeast groups, low precipitation values are generally associated with better growth. This is partially consistent with the climate for these regions. They either receive relatively large amounts of precipitation, or in the case of north-central group, the conditions are presumably too cold and growing seasons are too brief to respond negatively to increases in temperature (Fig. 3, Table 2).

### 3.4. Temperature limited populations

All three northern populations (northwest, north-central and northeast), show a consistent positive response to temperature in June of the current growing season (Fig. 4). This is also the first month with temperatures above freezing for these three populations, indicating that an early start to the growing season due to warm temperatures is an essential condition to above average radial growth. Temperature

**Table 2**

Climate normals (1961–1990) for biologically relevant climate variables for six chronology groups. Climate variables include: MAT, mean annual temperature; MWMT, mean warmest month temperature; MCMT, mean coldest month temperature; MAP, mean annual precipitation; MSP, May to September precipitation; AHM, annual heat moisture index; SHM, summer heat moisture index; CMD, climate moisture deficit; DD > 0, degree-days above 0°C; DD > 5, degree-days above 5 °C; and FFP, frost-free period.

Group	MAT (°C)	MWMT (°C)	MCMT (°C)	MAP (mm)	MSP (mm)	CMD (mm)	AHM (°C/m)	SHM (°C/m)	DD < 0	DD > 5	FFP (days)
Northwest	-4.8	12.4	-20.3	536	333	87	11.7	44.8	3032	6445	83
North-central	-8.9	12.9	-28.8	257	152	133	3.7	90.2	4380	609	71
Northeast	-3.7	10.9	-19.3	747	353	29	8.6	31.6	2524	525	70
Southwest	1.4	14.9	-23.0	551	366	125	21.3	42.2	1572	1158	101
West-central	-1.9	16.3	-23.4	408	254	184	20.2	66.8	2682	1167	99
East-central	-2.6	15.5	-23.3	581	347	108	13.8	47.8	2818	991	88

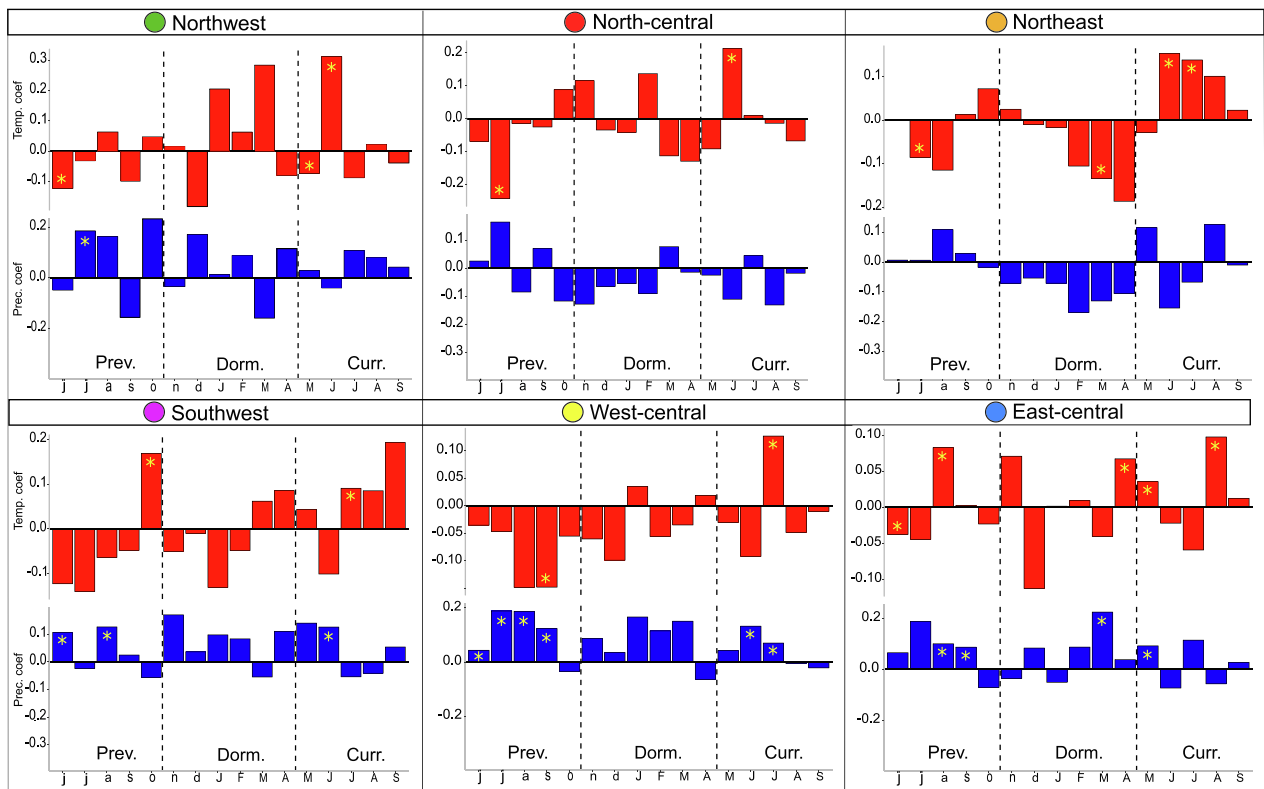


Fig. 4. Average response coefficients for each chronology group, where negative or positive responses to precipitation and temperature are displayed for the previous, dormant, and current growing period. An asterisk denotes where more than 10% of individual chronologies showed a statistically significant growth response. Note that the y-axis scales differ among regions.

**Table 3**  
The percent of significant growth-climate response coefficients in each chronology group. Significance for an individual chronology implies that the 95% confidence interval of the coefficient does not include zero. The gray scale highlights high percentages of significant coefficients in the group.

Group	Month of previous year						Month of current year									
	j	j	a	s	o	n	d	J	F	M	A	M	J	J	A	S
<b>Precipitation</b>																
Northwest	-	11	7.1	5.4	3.6	3.6	5.4	1.8	1.8	-	3.6	1.8	-	1.8	3.6	7.1
North-central	-	4.5	-	-	-	7.6	1.5	-	-	1.5	-	-	-	1.5	-	-
Northeast	8.3	-	-	-	-	8.3	8.3	8.3	-	-	-	-	-	-	-	-
Southwest	11	3.5	12	1.8	5.3	7	1.8	7	1.8	1.8	7	8.8	16	8.8	1.8	-
West-central	11	11	32	11	-	3.5	7.1	7.1	-	-	7.1	3.6	14	11	-	-
East-central	-	-	13	13	-	-	-	-	-	13	-	13	-	-	-	-
<b>Temperature</b>																
Northwest	14	38	-	-	8.9	29	5.4	3.6	3.6	-	8.9	13	66	5.4	-	-
North-central	3	58	-	-	9.1	1.5	-	7.6	1.5	1.5	7.6	4.5	33	6.1	-	-
Northeast	8.3	17	8.3	-	8.3	-	8.3	-	-	17	-	-	33	42	-	-
Southwest	7	-	5.3	-	11	1.8	-	3.5	1.8	1.8	1.8	1.8	3.5	11	1.8	7
West-central	3.4	-	3.4	14	3.4	3.4	-	3.4	-	3.4	3.4	3.4	6.9	10	-	-
East-central	13	-	13	-	-	-	-	-	-	-	13	13	-	-	13	-

response of these three northern populations to the previous dormancy period is variable. In the northwest, response to warm winter temperature was generally positive, in the north-central region neutral, and in the northeast negative. Given that the northeastern group received the most annual precipitation, more precipitation as snow in cold years may prevent an early spring thaw which could benefit growth. The northern populations generally had a large proportion of significant individual response coefficients for temperature variables, with some of the highest proportions of significant within-population responses

found in some months (Table 3).

#### 4. Discussion

##### 4.1. Populations vulnerable to climate change

One important finding was that white spruce populations in the southwest and west-central boreal regions are precipitation-limited, where significant positive growth responses to increased precipitation

**Table 4**

Observed climate change expressed as the difference between the 1961–1990 climate normal period and a recent 15-year climate average (2001–2015), and projected climate change for the 2050s relative to the 1961–1990 normal (mean and range). The future predictions are based on 15 models of the CMIP5 multi-model dataset for the RCP 4.5 scenarios that were chosen for high validation statistics and for representing all major clusters of similar AOGCMs (Knutti et al., 2013). Variables include: MAT, change mean annual temperature (°C); MAP, change in mean annual precipitation (mm); and CMD, change in climate moisture deficit (mm).

Groups	Observed trend			Predicted 2050s mean			Predicted 2050s range		
	MAT	MAP	CMD	MAT	MAP	CMD	MAT	MAP	CMD
Northwest	+1.2	+20	+8.6	+3.6	+89	+6.6	+2.2 to +5.9	+54 to +164	–12 to +29
North-central	+1.2	–9.2	+11	+4.1	+40	+17	+2.0 to +6.6	+15 to +81	–22 to +71
Northeast	+0.8	+14	+5.3	+3.5	+72	+16	+1.7 to +6.3	+21 to +122	–14 to +40
Southwest	+0.7	–12	+3.5	+2.8	+34	+30	+1.5 to +4.5	–24 to +170	–60 to +87
West-central	+1.1	+/-0	+7.7	+3.2	+38	+28	+1.8 to +4.6	+1.3 to +101	–38 to +87
East-central	+0.9	+29	–3	+3.3	+51	+21	+1.8 to +4.7	+16 to +117	–22 to +65

occurred during the previous and current growing season (Fig. 4). Given the longer growing season length, higher temperatures, and low precipitation levels, a moisture-deficit has already limited the radial growth of white spruce over the past century. Regional tree-ring studies have reported reduced productivity under drought conditions in these regions (Hogg and Wein, 2005; Chhin et al., 2004; Sang et al., 2019). Our study suggests that the west-central group, north of the southwest group, is actually the most precipitation-limited group, and therefore likely to be most susceptible to climate change. Although further north and colder than the southwest group, overall climate moisture deficits are highest here due to low precipitation.

In the last several decades, the west-central group has experienced substantial warming, leading to one of the highest increases in climate moisture deficits across the study area (Table 4). Future projections from general circulation models for the 2050s show that the west-central region is also predicted to have the strongest warming, leading to the highest moisture deficit of any region: a CMD value of 212 mm (Table 4 difference added to Table 1 value). This would make the moisture deficit of the west-central group 25% higher than the second driest group in the southwest by the 2050s. The second highest moisture deficits are expected for the southwest group, with CMD values of 155 mm by the 2050s. The southwest group has also experienced the highest increase in climate moisture deficits based on observed climate trends (Table 4).

We should note that we report 2050s projections for a relatively optimistic future climate change scenario RCP 4.5, where global carbon emissions would peak and subsequently reduce over the next 20 years. The projections from 15 general circulation models are fairly consistent for temperature, but show wide variance in precipitation projections. As a consequence, the range of projected changes to moisture deficits are also quite variable, and reductions in climate moisture deficits remain a possibility in all regions (Table 4, CMD range). That said, observed trends over the last decades indicate that all except one region in the east have experienced trends towards higher moisture deficits.

#### 4.2. Positive growth effects from climate warming

While the southern white spruce groups were often precipitation-limited, radial growth at the northern sites were instead primarily limited by cold temperatures and short growing seasons. Extended growing seasons under climate change would likely have beneficial effects on growth. This study has shown a consistent positive growth response to warmer spring temperatures for northern populations. Other studies have also shown that populations in the most northern reach of the boreal forest possess the earliest budbreak as a key adaptation to fully utilize the short growing season (Liepe et al., 2016). Since the northern regions are expected to have the lowest moisture deficits, with CMD values below 100 by the 2050s, an extended growing season should be conducive to increased growth without moisture limitations. For the east-central region, moisture deficits by the 2050s are still

moderate as well with a CMD value of 129 (Tables 1 and 4), where climate warming may have positive growth effects. We should note, however, that our study lacks samples from the southeast of the species range, where moisture limitations may occur under climate change.

Out of the three northern regions, the north-central group appears to be the most susceptible to drought. Though this group historically received the least mean annual precipitation overall, our response coefficients did not exhibit the same temperature-induced drought risk when compared to the southern groups (Fig. 4). This is likely because the north-central group currently experiences relatively cooler annual temperatures and a much shorter growing season (Table 2). However, future increases in temperature could likely intensify the current evapotranspirative demand for this region where warmer, longer growing seasons could prove to be undesirable in the long-term.

#### 4.3. Limitations and applications

The chronologies we analyzed were originally taken for diverse purposes, but most of them were collected by dendroclimatologists who selected trees and sites that were expected to be sensitive to the climate variable of interest. Therefore, we likely have a partial sampling bias toward sites exposed to warm and dry conditions, such as south facing slopes, ridges or rocky microsites. However, it is unlikely that prior sampling objectives are confounded with geographic regions (*i.e.* differences in sampling objectives for different regions) to produce bias relative to our main objective: detecting broad regional differences in climatic factors that limit growth, and inferring regional vulnerability to climate change.

Because of this partial sampling bias, and because we analyze growth response to high frequency climate variability in detrended chronology data, our research does not provide evidence for long-term growth response to directional climate trends. Furthermore, standardized radial increments are not necessarily representative of whole tree growth. For example, moisture-limited trees may shift resource allocation to favor root growth.

Lastly, we should note that our statistical power to detect climate-growth relationships was limited by the choice of statistical technique, which accounts for multicollinearity, as well as time series length of 80–100 years. Nevertheless, climatic factors in the MRT analysis explained 46% of the total variance in response coefficients, with the remainder attributable to other site factors such as soil conditions and ground water access. Biotic factors may also play a role. For example, at forest edges, exposed vegetation is more sensitive to climate fluctuations than under continuous canopy coverage (Helama et al., 2005). Canopy density and early successional competition can also influence growth at a particular site where climatic conditions are otherwise identical (Juday et al., 2003). Our sampling reflects growth on mature stands, and highlights differences among broad macroclimatic regions while smaller scale variation remains unaccounted for in our methodology, but nevertheless accounts for more than half the variation.

Choosing drought-resilient planting stock for reforestation programs in western and central Canada could help mitigate reductions in forest productivity where precipitation-limited populations of white spruce currently exist. However, Sang et al. (2019) showed that white spruce populations that possess the ability to maintain productivity under extended drought conditions may not exist. Assisted migration efforts should therefore focus on moving populations with higher growth potential from the south towards northern planting sites where climate moisture deficits are small (Sang et al., 2019). Regional climate change projections suggest that moisture limitations will become more pronounced in the future, especially for southwest and west-central boreal tree population (Table 4, CMD trends). Given observations of reduced productivity and mortality under drought conditions in the western portion of the species range (Chhin et al., 2004; Peng et al., 2011; Hogg et al., 2017; Sang et al., 2019), our results support the view that moisture limitation may become a dominant limiting factor for radial growth of white spruce populations of the southwest and west-central boreal forest.

### CRedit authorship contribution statement

**Ashley Hynes:** Conceptualization, Methodology, Formal analysis, Writing - original draft. **Andreas Hamann:** Conceptualization, Writing - review & editing, Supervision, Resources, Funding acquisition.

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### Appendix A

**Supplementary Data 1.** List of chronology data with sample identifier (ID), sample location, sample depth, the mean interseries correlation between all series from different trees ( $r_{bar, bt}$ ), the expressed population signal ( $\epsilon_{ps}$ ), the first and last year of the chronology analyzed in this study, data collector, custodian, or author with reference, and group membership according to our multivariate regression tree analysis shown in Fig. 1.

### Appendix B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.117944>.

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