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Growth sensitivity to climate varies with soil moisture regime in spruce-fir forests in central British Columbia

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Abstract

Key message Growth sensitivity to climate varies with soil moisture regime in spruce–fir forests in central British Columbia. Stands growing at their dry edaphic limits displayed especially strong and unique climatic sensitivities. Abstract Soil moisture regime is an important influence of productivity, process, and structure in forested ecosystems. In western North America, projected warming trends may result in decreasing available soil moisture; however, the potential effects on forest growth remain unclear. This study aimed to determine the influence of stand-level soil moisture regime on the climatic sensitivity of mature hybrid white spruce (*Picea glauca* (Moensch) Voss x *Picea engelmannii* Parry) and sub-alpine fir (*Abies lasiocarpa* (Hook.) Nutt.) forests in central British Columbia, Canada. We collected and analyzed tree-ring data from 51 stands spanning a range of soil moisture regimes. Dendroecological analyses of climate–growth relationships indicated that warm summer temperatures and drought limit growth for both species across all soil moisture regimes displayed unique climate-growth relationships; growth in populations on wetter sites was more correlated with summer climate from the year prior to growth. Radial growth responses to prior summer temperatures strengthened over the past ca. 80 years in both species and across most sites, suggesting that climate–growth relationships are shifting in this region. This study presents evidence of the importance of considering site-level ecological factors such as soil moisture regime when studying forest growth responses to climate.

Keywords Dendroecology \cdot White spruce \cdot Subalpine fir \cdot British columbia \cdot Forest ecology \cdot Soil moisture regime \cdot Climate change

Introduction

The effects of climate change on forest productivity will not be uniform over space and time. At the stand level, growth responses to climatic variation are modulated by a complex suite of biological factors (e.g., species, stand age, and stand density), local environmental factors (e.g., topography,

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² Ecora Resource Group Ltd., 579 Lawrence Avenue, Kelowna, BC V1Y6L8, Canada aspect, slope position, and soils), and regional climatic patterns (e.g., continentality and aridity). Elucidating future forest responses to climate change using dendroecological approaches can provide important information regarding long-term trends in forest productivity (Charney et al. 2016; Xu et al. 2017), but given the complex factors underlying these responses, dendroecological studies often must consider a wide range of complex and interacting factors (Fritts and Swetnam 1989). The influence of local and regional factors on forest climate-growth relationships can be studied by sampling and characterizing variation in productivity across biological and environmental gradients (Fritts and Swetnam 1989; Fritts 2012). Examples of biological and environmental gradients sampled in previous dendroecology studies include species (Miyamoto et al. 2010), regional climate (Griesbauer et al. 2011), and elevation (Zhang and Hebda 2004).

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The soil moisture regime (SMR) of a site is a measure of typical moisture available for plants over the growing season. Soil moisture regime reflects the balance of moisture inputs (e.g., gains through precipitation) and outputs (e.g., losses through percolation and evapotranspiration), and is controlled by a complex suite of macro- and micro-scale factors that include: regional climate patterns, topography, soil characteristics, and stand factors. In British Columbia (BC), Canada, the identification of soil moisture regime in forested ecosystems commonly uses two methods based on the provincial Biogeoclimatic Ecosystem Classification (BEC) system (Meidinger and Pojar 1991). The BEC system assigns a relative soil moisture regime class (RSMR) to sites within relatively homogenous areas of climate called biogeoclimatic (BGC) units (Meidinger and Pojar 1991). The RSMR is inferred from site factors such as slope position, slope gradient, and aspect, and soil factors such as soil depth, coarse fragment content, and soil texture (B.C. Ministry of Forests and Range 2010), and provides a relative scale that is used to compare SMR between sites within a given BGC unit. The actual soil moisture regime (ASMR) is an alternative method of characterizing site SMR and provides a method of comparing available soil moisture across BGC units. It is defined as the ratio of actual evapotranspiration (AET) and potential evapotranspiration (PET), and can be estimated using site-specific equations that consider climatic and geographic variables (Palutikof et al. 1994; Lu et al. 2005; Bormann 2011). More recently, a drought assessment tool has been developed for use in BC which calculates AET/PET using a modeling approach that considers climate and soil characteristics (Nitschke and Innes 2008; Nitschke et al. 2012; DeLong et al. 2019).

The soil moisture regime of a stand controls many aspects of forest composition and processes, reflecting the dominant influence of available soil moisture on tree growth, reproduction, and responses to disturbances including drought (Kimmins 2004). Tree species and populations show strong adaptation to local conditions (O'Neill et al. 2008). On particularly dry sites, forests may show relatively strong responses to climate (Fritts 2012) or even unique climate-growth relationships compared to other populations within the species range (Griesbauer and Green 2012). For example, Douglas-fir (Pseudotsuga menziesii var. glauca (Beissn.) Franco) and white spruce (Picea glauca (Moensch) Voss) forests growing in semi-arid environments may rely on soil moisture from snowfall prior to the growing season, whereas populations growing on wetter sites do not show this same reliance (Griesbauer and Green 2010, 2012). This phenomenon has been well understood for decades, and dendroclimatologists often target trees growing at their dry tolerance limits to amplify the climatic signal in tree rings, which allows for the reconstruction of historical climates prior to the instrument record (Fritts 2012). When

using dendroecological approaches to elucidate the broader impacts of climate change on forests, it is important to sample populations across a range of representative stand types and conditions, not just at moisture-limited sites where responses might be the strongest (Klesse et al. 2018). However, there are relatively few dendroecological studies that have occurred across a range of stand-level soil moisture regimes within a relatively small geographic area (Anning et al. 2013); this approach can help highlight variation in stand-level growth responses to climate within a relatively homogenous climatic regime.

In central British Columbia, hybrid white spruce (Picea glauca (Moensch) Voss x Picea engelmannii Parry, hereafter, spruce) and subalpine fir (Abies lasiocarpa (Hook.) Nutt., hereafter, fir) commonly co-occur in mid- to late-seral stands across a wide range of elevation, regional climate, and microsite conditions (Meidinger and Pojar 1991). Both species share similar silvics and life strategies; they are both shade-tolerant and able to persist in the understory for decades. Subalpine fir, in particular, is commonly found in the understory of mature stands and is able to capitalize on gap dynamics to capture growing space and canopy position (Klinka et al. 2000). Across a range of environments, radial growth in spruce in western Canada has been found to be controlled by temperatures (Zhang et al. 1999; Wiley et al. 2018) and drought (Miyamoto et al. 2010; Griesbauer and Green 2012; Hogg et al. 2017). Wiley et al. (2018) also found that in central BC, spruce populations on xeric sites were more sensitive to June climate, compared to populations growing on mesic sites. Spruce growth declines associated with warmer temperatures and decreased soil moisture availability have been described in Alaska (McGuire et al. 2010), and Wang and Klinka (1996b) found that the growth potential of spruce varied with actual soil moisture regime. Dendroecological studies of subalpine fir radial growth in central BC have found that summer temperatures and precipitation are a primary climatic influence of radial growth at lower elevations, whereas winter conditions limit growth at higher elevations (Ettl and Peterson 1995; Zhang et al. 1999; Splechtna et al. 2000; Peterson et al. 2002; Miyamoto et al. 2010).

In this study, we used a dendroecological approach to examine radial growth responses to climate in spruce and fir stands across a gradient of soil moisture regimes in central British Columbia, and tested the following hypotheses:

Spruce and fir radial growth respond to different climate drivers in central BC;

Radial growth responses to climate vary with stand-level soil moisture regime, with climate–growth responses being strongest on drier sites; and Radial growth responses to climate have varied historically, possibly associated with climate trends over the past century.

Methods

Site

This study uses a tree-ring dataset collected in summer 2010 from 51 forest stands in central British Columbia, Canada (Fig. 1). Sites were selected randomly from undisturbed, unmanaged mature (>80 years) spruce–fir forest polygons within 500 m of a road, using the British Columbia Vegetation Resources Inventory spatial information (https://www2. gov.bc.ca/gov/content/industry/forestry/managing-our-fores t-resources/forest-inventory). The sites were located across a gradient of relative soil moisture regimes ranging from xeric to subhygric in eight variants of the Sub-Boreal Spruce biogeoclimatic zone (Meidinger and Pojar 1991). The Sub-Boreal Spruce Zone occupies a large portion of the Interior Plateau Region of BC, and is characterized by long, cold, and snowy winters, and relatively short but warm summers. Site mean annual temperatures (based on 1961–1990 climate normal period) ranged from 0.9 to 4.6 °C, and mean annual precipitation ranged from 502 to 797 mm (Appendix Table 3). The elevation of the sites ranged from 590 to 1280 m above sea level.

Stand-level ecological information was collected for each site, including: slope position, slope gradient, aspect, soil texture, coarse fragment content, and soil edaphics, using the protocols described in the BC Ministry of Forest and Range's Field Manual for Describing Terrestrial Ecosystems (B.C. Ministry of Forests and Range 2010). For analysis, soil textures were grouped into three texture classes, as per BC Ministry of Forests and Range (2010), as follows: coarse texture class comprised sandy soil textures with higher coarse fragments; medium texture class comprised very fine sands



Fig. 1 Location of 51 study sites in central British Columbia, Canada

and loamy soils with moderate coarse fragments, and fine texture class comprised silty and clay soils with relatively low coarse fragments. Site data are summarized in Appendix Table 3.

Tree data

Within each stand, trees were sampled that met the following criteria:

- a) Hybrid white spruce or subalpine fir;
- b) Free of disease, insect attack, or other damage that may affect radial growth; and
- c) Occupied a dominant or co-dominant canopy position.

A single core was taken from each tree at 1.3 m height above the point of germination, using a 5.2 mm standard increment borer. Within a site, cores were taken from 8 to 20 trees per species. Low numbers of trees collected on some sites reflect conditions where there were relatively few individuals of a given species. On steep slopes, cores were taken perpendicular to the slope to minimize the effects of tension and compression wood on radial growth. We also recorded diameter of each tree at 1.3 m height. The total height of each tree was measured using a laser hypsometer.

Core processing

Cores were glued to wooden mounts and sanded with progressively finer sandpaper grit to expose the annual rings. Annual rings were then assigned a calendar year by visually crossdating cores within a site (Fritts 2012). Once crossdated, annual rings were measured to 0.001 mm precision using the Velmex ring-measurement system (Velmex Inc. 1992) interfaced with MeasureJ2X (VoorTech Consulting 2004). The COFECHA software (Grissino-Mayer 2001) was used to statistically validate crossdating. Cores that could not be visually or statistically crossdated were removed from further analysis (less than approximately 1% of total cores).

Chronology development

The dplR package (Bunn 2010) for the R statistical software platform (R Core Team 2016) was used to develop an annual ring-width chronology for each species within a site. To remove long-term growth trends potentially associated with age and stand dynamics, a cubic smoothing spline was applied to remove 50% of variation at a length of two-thirds of each tree series. Autocorrelation was then removed from each series using a site-specific autoregressive model, and residuals were averaged among all trees of the same species and site using biweight robust mean to produce a unitless chronology. For each ring-width chronology, we calculated the mean intrasite correlation (mean correlation of each tree with the master chronology; MIC) and the expressed population signal (Wigley et al. 1984, EPS). Both MIC and EPS provide a measure of the strength of the common signal within the chronology, and can be used to assess the climatic signal contained with the annual growth. A minimum EPS value of 0.85 is commonly used to screen chronologies for sufficient signal strength in dendroclimatic analyses; however, this practice may not be appropriate in all cases (Buras 2017).

Climate data

To analyze the relationship between annual growth and climate, we used adjusted monthly precipitation and homogenized temperature records (Vincent et al. 2002, 2012; Mekis and Vincent 2011) from Canada's National Climate Data and Information Archive (climate.weather.gc.ca). We selected data from three climate stations: Prince George Airport, Fort St. James airport, and Quesnel Airport (Fig. 1). To complete the climate–growth analysis, we filled in missing monthly data in each station's record using ClimateBC (version 2.5, Wang et al. 2012) monthly estimates using the climate station's geographic coordinates and elevation (meters above sea level). Climate normals (1961–1990 normal period) were also generated for each site using ClimateBC, using site-specific geographic coordinates and elevation as inputs.

Actual soil moisture regime

We computed mean annual AET/PET ratios for each site using a water balance model developed for use in BC, based on the Tree and Climate Assessment Model (Nitschke and Innes 2008; Nitschke et al. 2012; DeLong et al. 2019). The model uses historical daily climate data and soil characteristics to estimate daily water balance for different soil moisture regimes within a BGC unit; daily water balances are then summarized at annual (i.e., January to December) timescales to assign a mean annual AET/PET ratio. We used each site's AET/PET to assign an actual soil moisture regime class, using the classification regime described in Table 1 (Meidinger and Pojar 1991). Sites in this study spanned three ASMR classes: (i) moderately dry, (ii) slightly dry, and (iii) fresh. To understand the relationship between site variables and modeled AET/PET ratio, we developed linear models with AET/PET as the dependent variable, and the following site variables as independent variables: (i) soil texture class; (ii) slope position; (iii) aspect; (iv) slope grade; and interactions between these variables and modeled 1960-1990 climate normals (mean annual temperatures, precipitation, and mean summer temperatures and precipitation).

 Table 1
 Mean annual AET/PET ratio and corresponding actual soil moisture regime (ASMR) classes used in this study

Months with soil mois- ture deficit	ASMR class
> 1.5 but < = 3	Moderately dry
>0 but $< = 1.5$	Slightly dry
None	Fresh
	Months with soil mois- ture deficit > 1.5 but < = 3 > 0 but < = 1.5 None

AET/PET mean annual actual evapotranspiration/potential evapotranspiration ratio; ASMR actual soil moisture regime (Meidinger and Pojar 1991)

Climate-growth analysis

All climate-growth analyses were completed using the treeclim package (Zang and Biondi 2015) for R. For each chronology, we identified important climatic influences on radial growth by calculating Pearson's correlation coefficients between ring-width and climate variables over the 1959–2009 (n = 60 years) time period common to all chronologies. Climate data were used from the climate station closest to the chronology's location. Four monthly climate variables were included in the analysis: (1) maximum temperatures (TMX); (ii) precipitation (PPT); (iii) Hargreaves reference evaporation (Eref), and (iv) climatic moisture deficit (CMD). Hargreaves reference evaporation provides a temperature-based estimate of potential evapotranspiration (Hargreaves and Allen 2003), and climatic moisture deficit provides an estimate of monthly water balance by considering Hargreaves reference evapotranspiration and precipitation (Wang et al. 2012). Eref and CMD were calculated using monthly station data as per Wang et al (2012). The significance of all computed correlations was tested by computing 95% confidence limits from 1000 bootstrap iterations.

We included climate variables from the year prior to growth, as well as climate from the current growth year. Climate variables were tested using monthly and seasonal variables. Months used in this analysis ranged from the June in the year prior to growth to September of the current growth year. We followed the approach of Meko et al. 2011) to test the influence of 3-, 6-, and 9-month groupings of monthly climate variables on growth. We identified important seasonal climate variables based on the number of chronologies with significant correlations (p < 0.05) and the strength of the correlations.

We tested the temporal stability of correlation coefficients by calculating moving correlation functions [MCFs, Biondi (1997); Zang and Biondi (2015); Biondi (2000)]. This approach entailed calculating correlation coefficients over a sliding window of 31-year length, offset by 1 year (e.g., 1979–2009, 1978–2008, ... 1901–1931). This allowed for correlation coefficients to be compared over consecutive time periods to identify temporal changes in the strength and

possibly direction of the linear relationship between growth and climate. For the MCF analysis, we used the maximum time span that overlapped the climate and ring-width chronology (i.e., we did not limit MCF analysis to the 1950–2009 time period as per other climate–growth analyses).

To evaluate MCFs at the soil moisture class level, we grouped chronologies by species and ASMR class, and extracted the first principal component for each grouping to generate a single composite chronology for each species/ ASMR combination. These composite chronologies were then used as the response variable for the MCF analysis. Because there was only one fir chronology on fresh sites, we could not extract the first component for that species and ASMR combination; rather, we used the chronology itself to compute MCF.

Gradient analysis

We evaluated the influence of soil moisture regime on tree size by developing linear regression models for each species with mean stand height and DBH as dependent variables, and soil moisture regime (AET/PET ratio) and stand age as independent variables. To estimate stand age, we used the first year of the site's chronology, recognizing that this provided a biased estimate of stand age where the cores missed the pith.

To evaluate how climatic sensitivity varied across a gradient of soil moisture regimes, we used two approaches. The first approach was to qualitatively assess climate–growth relationships by actual soil moisture regime class. This was completed by grouping chronologies by species and ASMR class, and comparing climate–growth relationships among ASMR classes. In the second approach, we quantified variation in climatic sensitivity across stand-level soil moisture regime using a method similar to (Miyamoto et al. 2010 and Griesbauer et al. 2011). This approach entailed two steps:

For each ring-width chronology, we quantified sensitivity to climate through a univariate linear regression between growth and a given climate variable over the 1950–2009 time period. Because the β coefficient from the linear regression equation $y=a+\beta x$ quantifies the slope of a linear relationship, we used β from the regression between each chronology and climate variable as a measure of growth sensitivity to that variable. Similar to previous studies (Miyamoto et al. 2010; Griesbauer et al. 2011), we included all coefficients, even if they were not statistically significant (i.e., p > 0.05) to preserve the full range of the response surface across the soil moisture gradient. In a final step, we quantified variation in growth sensitivity to a given climate variable among chronologies by regressing chronology sensitivity (i.e., β for each chronology) across a gradient of soil moisture, represented by AET/PET ratio.

Results

Tree data and chronology development

The dataset for this study consists of 761 cores (558 spruce, 203 fir) collected across 51 sites (Table 2). A total of 55 chronologies were developed (40 spruce, 15 fir), across three actual soil moisture regime classes.

Spruce heights and DBH increased significantly (p < 0.05) with site mean annual AET/PET ratio, but the size of fir trees did not (Fig. 2). Stand age, as estimated from chronology length, was not a significant factor for either species, and was omitted from the final models.

Spruce chronologies ranged in length from 71 to 246 years, with expressed population signal values ranging from 0.810 to 0.947, and mean intrasite correlations ranging from 0.221 to 0.547 (Appendix Table 4). Fir chronology lengths ranged from 87 to 212 years, expressed population signal values ranged from 0.811 to 0.932, and mean intrasite correlations ranged from 0.283 to 0.476. A total of 15 chronologies had EPS below the 0.85 threshold recommended by (Wigley et al. 1984), likely due to relatively few trees available for sampling on some sites, rather than a weak climate signal among trees. All chronologies were included in subsequent analyses.

Actual soil moisture regime

The mean annual AET/PET for the 51 sites ranged from 0.77 to 1 (Appendix Table 3). A linear model with AET/PET as response variable and site-level factors as independent variables showed that slope position and soil texture class were significant (p < 0.001 for both) and together explained 51.8 (adjusted R^2) of the variation in AET/PET (model not shown). Other site factors, including climate normals, coarse

 Table 2
 Number of trees sampled and chronologies developed by species and actual soil moisture regime class (ASMR)

Species	ASMR	Chronologies	Trees
Fir	MD	3	41
	SD	11	147
	F	1	15
Spruce	MD	19	259
	SD	16	220
	F	5	79

ASMR actual soil moisture regime class (Meidinger and Pojar 1991); MD moderately dry; SD slightly dry; F fresh fragments, slope, and aspect, were not found to be significant (i.e., p > 0.05). The model showed that AET/PET increased (i.e., sites had more available soil moisture) on lower slope positions (Fig. 3). The increase in AET/PET was largest between mid- and lower slope positions. Level sites were predicted to have an AET/PET ratio between mid- and lower slope positions (not shown). AET/PET also increased as soil textures became finer (i.e., was lowest on sites with coarse-textured soils and higher on sites with finer textures).

Climate-growth relationships

Correlation coefficients computed between chronologies and maximum temperature, precipitation, climatic moisture deficit, and Hargreaves reference evaporation over sequential groupings of 1-, 3-, 6-, and 9-month seasons from 1950 to 2009 (not shown, see Appendix for an example) indicated that the following monthly groupings had the strongest and most consistent relationships with annual radial growth in both species:

May–July TMX, CMD, PPT, and Eref variables. Hereafter, we refer to this 3-month grouping as "summer".

March–May variables. We refer to this 3-month grouping as "spring".

March–August variables. We refer to this 6-month grouping as "growing season".

Prior June to prior August variables. We refer to this as "prior summer", recognizing that the monthly groupings differ from "summer".

June variables. We simply refer to this 1-month grouping as "June".

Spruce

Spruce chronologies had slightly stronger correlations with temperature and drought-related variables (i.e., Eref and CMD) than precipitation over the 1950–2009 period (Fig. 4 and Appendix Table 5). The seasons with strongest correlations varied with soil moisture regime. Spruce chronologies from the driest sites (moderately dry soil moisture regime class) had strongest correlations with summer and growing season variables; in contrast, spruce growing on fresh sites had stronger and more significant (p < 0.05) correlations with previous summer climate. Spruce growing on slightly dry sites had growth that was correlated equally with previous and current year climate.

Fir

Similar to the spruce chronologies, fir chronologies had stronger correlations with temperature and drought-related variables as opposed to precipitation (Fig. 5 and Appendix



Fig. 2 Relationship between stand mean height (top panel) and diameter at breast height (DBH, bottom panel) and the stand mean annual actual evapotranspiration/potential evapotranspiration ratio (AET/PET)

Table 6). In contrast to spruce, fir across all three soil moisture regimes had the strongest correlations with climate in the same months, summer and June. The strength of the correlations to a given climate variable and season varied with soil moisture regime; they were strongest on moderately dry sites, and weakest on fresh sites. Fir on moderately dry sites also had more significant correlations with climate over spring and summer seasons, whereas moderately dry and fresh sites had radial growth correlated primarily with summer season.

A comparison between spruce and subalpine fir chronologies showed that on moderately and slightly dry sites, subalpine fir had stronger correlations than spruce to summer climate. On fresh sites, the species responded to different climate variables (spruce, previous summer climate, and fir, current June), with similar correlations to these variables.

Climatic sensitivity across soil moisture regime

In both species, stand AET/PET ratio significantly predicted growth sensitivity to summer climate variables (p < 0.05, Fig. 6 and Appendix Table 7). Growth sensitivity to summer climatic moisture deficit was strongest in stands growing on the driest sites (i.e., with lowest AET/PET), and variation in sensitivity varied linearly and significantly with AET/PET ratio (p=0.011 and 0.007 for fir and spruce, respectively). We also fit a linear model with aggregated data from both species, and included species as a fixed effect (not shown). This model indicated that slope and intercept did not vary between species, suggesting that radial growth sensitivity to summer climatic moisture deficit in both spruce and fir varied similarly over a soil moisture gradient. Similar Fig. 3 Predicted mean annual actual evapotranspiration/potential evapotranspiration ratio (AET/PET) and standard errors for different levels of slope position (left) and soil texture class (right) from a linear model (not shown). Both factors were significant (p < 0.001) in a multivariate linear model explaining 51.8% variation in site AET/PET



relationships were found with other summer climate variables (Appendix Table 7). In spruce, sensitivity to June climate varied significantly with soil moisture. For both species, growth sensitivity to climate in other seasons (spring, prior summer, and growing season) did not vary significantly with stand AET/PET ratio.

Temporal stability of climate-growth relationships

First components of the chronologies by species and ASMR class explained between 46.1 and 61.8% of chronology variation (Appendix Table 8). All chronologies were significantly correlated with their respective principal component-derived composite chronology (p < 0.01, not shown).

Moving correlation functions indicated that climate-growth relationships have historically changed over time (Fig. 7). In both species, growth became more negatively correlated with maximum temperatures of the summer prior to growth. Spruce growth was significantly correlated with this climate variable for more consecutive 31-year periods on fresh sites, whereas growth on dry sites became negatively correlated only in recent decades. Correlation coefficients on fresh sites were stronger than - 0.7 for recent 31-year windows.

Fir growth responses to prior summer temperatures have reversed over the past century. In periods ca. 1930–1970, fir growth on moderately and slightly dry sites responded positively to warmer previous summers, with correlation coefficients significant and above 0.5. In recent decades, this relationship reversed and growth was negatively and significantly correlated with warmer summers in the year before growth.

In both species, growth on moderately dry sites was most consistently correlated with CMD over time. Correlations were also strongest on these sites. Spruce growth on slightly dry sites became more correlated with this variable in recent decades. Fir and spruce growth on wetter sites did not have consistent relationships with spring CMD over time.

Similar to spring CMD, growth for both species on moderately dry sites was consistently and positively correlated with summer precipitation. Both species on moderately dry (MD) ASMR class sites had the strongest correlations during the ca. 1945–1975 period, with correlations becoming slightly weaker (although still significant, p < 0.05) in subsequent periods. MCFs indicated that spruce and fir growth on slightly dry and fresh sites were not consistently correlated with summer precipitation over time.

Correlations between growth and summer maximum temperature were consistently negative in both species and all sites over the past ca. 80 years, with the exception of fir on fresh sites. Spruce growth on fresh sites appeared to becoming less influenced by summer temperatures over the past ca. 80 years, with correlations becoming insignificant (p > 0.05) in recent 31-year time periods.

Discussion

Similar to other dendroecological studies in low-elevation environments (Ettl and Peterson 1995; Zhang et al. 1999; Peterson et al. 2002; Miyamoto et al. 2010; Griesbauer and Green 2012; Hogg et al. 2017; Wiley et al. 2018), we found that warm summer temperatures and drought limit radial growth in hybrid white spruce and subalpine fir stands in central BC. In this region, summer temperatures and climatic moisture deficits have increased over the past ca. 70 years (Foord 2016; Hember et al. 2017a, b), and these trends are



Fig.4 Climate–growth relationships for spruce across actual soil moisture regime classes. Bars indicate mean correlation coefficient and whiskers are standard errors. The proportion of chronologies with significant (p < 0.05) correlations between annual growth and sea-

sonal climate is shown near y=0 for each variable. Climate variables: *cmd* climatic moisture deficit; *eref* Hargreaves reference evaporation; *ppt* precipitation; *tmx* maximum temperatures

projected to continue in the future (Foord 2016). This will likely result in a decrease in available soil moisture, largely driven by increased evapotranspiration associated with higher temperatures (Barber et al. 2000; Adams et al. 2009; Williams et al. 2013). Sustained decreases in soil moisture availability during the growing season could have several widespread implications to spruce–fir forests, including a loss of productivity, increasing growth sensitivity to climate, and lower resilience to forest health factors (Barber et al. 2000; Adams et al. 2009; Williams et al. 2013). Common patterns of climate–growth relationships across a range of environment suggest that at broad scales, these species may exhibit relatively uniform responses to synoptic warming trends (Peterson et al. 2002). This also suggests that across their range, spruce and fir populations are adapted to local climate and environmental conditions and may show maladaptation as local climate regimes shift away from historical normals (O'Neill et al. 2008).

Spruce and fir growth responses to summer climate

While our results suggest broad patterns of growth responses to summer climate, dendroecological analyses at finer spatial and temporal scales also suggest that growth responses to climate will vary with site conditions, between species, and over time, similar to other studies in this region and elsewhere (Ettl and Peterson 1995; Peterson et al. 2002; Miyamoto et al. 2010; Griesbauer and Green 2012; Wiley et al. 2018). We note that this phenomenon appears to be better documented in white spruce than subalpine fir. The



Fig. 5 Climate–growth relationships for fir across actual soil moisture regime classes. Bars indicate mean correlation coefficient and whiskers are standard errors. The proportion of chronologies with significant (p < 0.05) correlations between annual growth and seasonal cli-

mate is shown near y=0 for each variable. Climate variables: *cmd* climatic moisture deficit; *eref* Hargreaves reference evaporation; *ppt* precipitation; *tmx* maximum temperatures

sensitivity of radial growth to summer climate of both species varied consistently and similarly across a gradient of soil moisture regime defined by AET/PET ratio. In both species, radial growth sensitivities to summer temperatures and evapotranspiration were strongest in populations growing at the dry extremes of the soil moisture gradient that we sampled, and were weaker in populations growing on wetter sites (Figs. 4 and 5). Wang and Klinka (1996b) found that white spruce productivity varied with actual soil moisture regime, and was lowest in populations growing at the dry and wet extremes of the species soil moisture distribution in central BC. Similar changes in climatic sensitivities have been reported across climatic gradients in spruce and fir populations (Ettl and Peterson 1995; Peterson et al. 2002; Miyamoto et al. 2010; Griesbauer and Green 2012) as well as other species (Griesbauer et al. 2011; Anning et al.

2013). These studies confirm that populations growing at the margins of species distributions tend to display a higher sensitivity to limiting climate variables (Ettl and Peterson 1995; Barber et al. 2000; Peterson et al. 2002; Fritts 2012).

Spruce and fir populations growing at the dry extremes of their soil moisture limits in the region (Wang and Klinka 1996a; b) and province (DeLong et al. 2019, and see Fig. 6) may be especially vulnerable to climate change. Our results show that radial growth responses in these populations are primarily influenced by conditions during the early growing season (especially May–July), which suggests that the tree responds to warm and dry conditions by reducing earlywood growth as drought conditions intensify (Watson and Luckman 2002). Relatively high radial growth sensitivity to summer conditions on dry sites may represent an adaptive trait in these populations (McLane et al. 2011), whereby they are

Spruce

 $R^2=0.19$

1.00



Fig. 6 Variation in radial growth sensitivity to summer Hargreaves reference evapotranspiration across a soil moisture gradient in fir (left) and spruce (right) populations. For each chronology, radial growth sensitivity was quantified using the slope coefficient from a linear regression between chronology radial growth and summer Hargreaves reference evaporation (i.e., the β coefficient from the linear

regression equation $y = a + \beta x$). Both relationships are significant (p < 0.05). AET/PET, site mean annual actual evapotranspiration/ potential evapotranspiration ratio; Eref, Hargreaves reference evaporation (Hargreaves and Allen 2003). Vertical dashed lines represent theoretical species thresholds as per Delong et al. (2019)

able to limit water loss through stomatal conductance, at the expense of producing photosynthates for radial growth. Over the long term, however, this trait could result in prolonged growth declines in these populations, which could lead to decreasing stand health and vigour, with lower resilience to disturbances such as insect attacks and drought (Barber et al. 2000; Williams et al. 2013). For this reason, these populations may be at high risk of drought-induced maladaptation. Spruce and fir populations growing on these sites should be monitored for early indicators of climate-related forest decline in this region.

At the wetter end of the soil moisture spectrum sampled in this study, spruce populations had strong relationships with summer conditions from the year prior to growth, which is unique from populations on drier sites. Summer conditions influence latewood production (Watson and Luckman 2002) as well as the tree's allocation of carbohydrate reserves for next year's growth (Fritts 2012). These populations may have less plasticity to adapt radial growth to current conditions, which can result in high amounts of carbohydrate allocation to earlywood formation even during summer seasons with warmer temperatures or climatic moisture deficit. Given that these sites rarely experience soil moisture deficit, however, it appears that spruce and fir populations growing on wetter sites are at lower short-term risk from drought mortality. What is uncertain, however, are the long-term implications of soil moisture declines over time associated with warmer temperatures and increased evapotranspiration. If a given site changes soil moisture regime classes from fresh to slightly dry, it is not clear if populations will adapt by increasing their radial growth sensitivity to summer conditions, or if they will have lower overall adaptive capacity.

Spruce radial growth dependence on previous year climate may be confounded by the relationship between climate and mast years. Spruce cone crops show strong regional and temporal synchrony, and are controlled by a combination of climatic and endogenous factors (Lamontagne and Boutin 2007). Warm and dry summers can elicit a strong mast year in spruce trees if sufficient growing seasons have passed since the previous mast year. Mast years can result in a strong reduction in radial growth during the same year, likely because the tree allocates the majority of available carbohydrates to cone production, at the expense of wood formation (Selås et al. 2002; Krebs et al. 2017). Norway spruce radial growth was reduced by up to 50% during strong mast years between 1971 and 1999 (Selås et al. 2002). In contrast, a study of white spruce



Fig. 7 Moving correlation functions between the first principal component of chronologies grouped by ASMR class and four climate variables, over consecutive 31-year periods. MD, moderately dry; *SD* slightly dry; *F* fresh; Prior. *Summ:tmx* maximum temperatures of

summer prior to year of growth; *Spring:cmd* spring climatic moisture deficit; *Summer:ppt* summer precipitation; *Summer:tmx* summer maximum temperatures. Teal color indicates significant correlation coefficients (i.e., p value < 0.05)

populations in Yukon Territory, Canada, found inconsistent relationships between mast years and radial growth (Krebs et al. 2017). We recommend further study to elucidate the relationship between mast years and radial growth across site types within a region, as this will improve understanding of climatic influence on spruce radial growth.

In contrast to spruce, radial growth in fir populations growing across the gradient of ASMR classes was consistently responsive to current summer conditions, with the strength of climate–growth relationships increasing with site soil moisture deficit. Within the relatively narrow climatic range of this study, climate variables explaining fir radial growth appear consistent. In the Pacific Northwest region of the US, subalpine fir growth responded to different climate variables along an elevation gradient; growth was more limited by growing season soil moisture deficit at lower elevations, and limited by winter snowpacks and short growing seasons at higher elevations (Ettl and Peterson 1995; Peterson et al. 2002). Across its entire range, fir may respond to warmer temperatures with enhanced growth in cold-limited sites, and growth decreases in moisture-limited sites. The latter appears more likely for fir populations at lower elevations in our study region.

Climate variables important to radial growth

Growth in both species had stronger correlations with temperature and drought variables than precipitation alone. Mean correlation coefficients and number of chronologies with significant correlations were essentially the same between maximum temperatures, reference evapotranspiration, and climatic moisture deficit. Both drought-related variables contain temperatures in their formulae. Changes in soil moisture availability may be especially important to monitor and study, and precipitation may not be a sufficient climate variable to consider alone in understanding potential forest responses to climate change (Adams et al. 2009; Williams et al. 2013) in these two species. Lodgepole pine (Pinus contorta Dougl. ex Loud var. latifolia Engelm.) radial growth in central BC has been found to respond positively to summer temperatures and warmer winter temperatures the year before growth (Miyamoto et al. 2010). In contrast, radial growth in Douglas-fir shows a much stronger dependence on precipitation and very little relationship with temperatures (Griesbauer and Green 2010).

We also found that productivity of spruce appears to vary with available soil moisture, with average tree size, in terms of both diameter and height, increasing with site AET/PET ratio. Wang and Klinka (1996b) also found that spruce productivity in central BC varied with actual soil moisture regime class; spruce growing on fresh ASMR class sites had the highest productivity compared to wetter or drier ASMR classes. In contrast, the size of subalpine fir trees did not appear to vary with soil moisture class in our study. It is important to note that we did not control for potentially confounding factors including stand age and density in our analyses; therefore, the relationship between tree size and soil moisture regime in our study remains inconclusive. More work in this area will help elucidate the broad- and fine-scale controls that should be considered when managing forest adaptation to climate change.

Temporal stability of climate-growth relationships

Our results show that historic climate–growth relationships changed over the past ca. 80 years in both spruce and fir populations. This phenomenon has been recorded in spruce elsewhere (Griesbauer and Green 2012; Chavardès et al. 2013; and c.f. D'Arrigo et al. 2008), but to our knowledge, not in subalpine fir populations. On all sites and in both species, temperatures from the previous summer have become increasingly negatively correlated with growth in recent decades. This phenomenon appears to have occurred earliest on fresh sites, and more recently on moderately dry sites. If this is associated with historic trends of increased summer temperatures and decreasing soil moisture availability (Foord 2016; Hember et al. 2017a; b), radial growth may become increasingly correlated with the amount of carbohydrates allocated to growth from the previous year, in addition to growth responses during the current season. If this trend continues, it may be possible that populations in both species will converge in terms of climate–growth relationships; warm summer temperatures from the year prior to growth may become the dominant control on productivity. Increasing growth sensitivity to climate has been linked to longterm growth declines in interior western portions of North America, including our study region (Charney et al. 2016).

This shift in growth response to prior summer temperatures appears to have been strongest in fir populations growing on moderately and slightly dry sites. In the time period of ca.1930–1970, growth in these populations was positively correlated with summer temperatures from the prior summer; over the ca.1979-2009 period, that relationship had reversed and become significantly negative. Similar trends have been described in white spruce and Douglas-fir populations (Griesbauer and Green 2010, 2012), and may reflect a temperature threshold that has been exceeded with recent climate change (Wilmking et al. 2004). Thresholdcontrolled growth responses in tree populations may lead to sustained growth declines (Wilmking et al. 2004) and unpredictable forest responses. An alternative explanation is that climate-growth relationships may co-vary with decadal trends in synoptic ocean-atmosphere teleconnection indices (Pompa-García and Jurado 2014; Pompa-García et al. 2015). The two periods of positive and negative fir growth correlations with prior summer temperatures coincide approximately with historical cold and warm phases of the Pacific Decadal Oscillation (Mantua and Hare 2002). This oscillation has been linked to radial growth in forests in western North America (Peterson et al. 2002; Griesbauer et al. 2011), likely through controls on local climate; in the region of this study, warm phases of the Pacific Decadal Oscillation result in anomalously warm March-August temperatures (Fleming and Whitfield 2010). Shifts in these teleconnection indices may interact with long-term climate trends to affect forest productivity at varying temporal scales.

Some climate–growth relationships have remained stable over the past ca. 80 years. At the dry extremes sampled in this study, growth responses to summer maximum temperatures have been consistently negative in both species, and are among the strongest correlations in the study (e.g., correlation coefficients close to -0.8 for some 31-year windows in spruce populations. On sites with chronically low soil moisture availability, climate exerts a strong growth limitation that will likely persist in the future.

The use of actual soil moisture regime as a forest drought monitoring tool

Our study showed that soil moisture regime, defined using either AET/PET ratio, actual soil moisture regime class (Meidinger and Pojar 1991; Wang and Klinka 1996b; Klinka et al. 2000), or other indices (e.g., Anning et al. 2013) provide a useful measure for ecological gradient studies. Using AET/ PET and actual soil moisture regime can provide an advantage over the more commonly used relative soil moisture regime, because it allows soil moisture regime to be compared across climatic regimes. In our study, actual soil moisture regime class was significantly predicted by slope position and soil texture class, both of which are linked to soil water holding capacity of a site. Other variables that are known to influence soil moisture regime, such as climate normals, aspect, slope grade, and elevation, did not predict ASMR in our region. This likely reflects the relatively narrow climatic range of our study sites. Further study of ASMR and local site factors across broader climatic gradients could be helpful to develop soil moisture regime prediction models (Anning et al. 2013).

If summer temperature increases continue in this region, it may be possible that mean annual soil moisture availability on some sites will eventually shift to a drier ASMR class, driven by concurrent shifts in evapotranspiration. This could have several implications for spruce and fir populations. On sites with a moderately dry ASMR class, a shift to the next drier ASMR class (i.e., very dry) could result in a soil moisture threshold that exceeds the tolerance of in situ populations, which could increase mortality risk on these sites (Adams et al. 2009; Williams et al. 2013). On slightly or fresh sites, a shift in ASMR class could result in changing climate-growth relationships, and trees may display increased sensitivity to summer temperatures and drought. Our study did not include spruce and fir populations growing on sites with ASMR classes wetter than fresh (i.e., sites with prominent mottling or groundwater present during the growing season). These sites do not experience soil moisture deficit during the year and may serve as climate refugia where trees are temporarily buffered from the effects of climate change (Linares and Tíscar 2011).

Actual soil moisture range limits for British Columbia tree species have been estimated (Klinka et al. 2000). These estimates can be further refined by studies that quantify variation in species productivity (Wang and Klinka 1996b) and tree species distribution (DeLong et al. 2019) across ASMR gradients. These studies show that ASMR can be used to infer productivity and survival optima within a region; further work to compare forest processes, structure, and function across soil moisture regimes can further enhance our understanding of soil moisture's role in controlling forest responses to climate change across biological, spatial, and temporal scales (Anning et al. 2013).

Conclusions

The management of forests in the twenty-first century will require careful consideration of the complexities underlying forest responses to climate change, and the integration of complicated models into management frameworks (Millar et al. 2007). Ecological studies that consider variation in forest responses across multiple scales can help managers anticipate changes in forest structure and processes by identifying forest types at higher risk from climate change, and by identifying potential pathways of change. Our study showed that productivity in spruce-fir forests in central British Columbia may be broadly sensitive to changes in summer temperatures and drought, and that forests growing on dry sites may be especially sensitive. The mechanisms by which summer temperatures influence radial growth may be shifting; in current decades, growth in both species appears to be increasingly influenced by summer conditions in the year before growth. This may indicate shifting adaptive responses to historical trends of increasing summer temperatures and moisture deficit in central BC over the past ca. 80 years.

Author contribution statement HG is the first supervisor of this project and contributed to experimental design, data collection, data validation, analyses, and writing the manuscript. CD is a project co-leader, second supervisor of this project, contributed to data collection, provided input to the manuscript, and co-wrote the project funding proposal. BR provided guidance throughout the project, contributed to data collection, and provided input to the manuscript. VF is a project co-leader, provided guidance on climate-related analyses of this project, provided input to the manuscript, and co-wrote the project funding proposal.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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Appendices

See Tables 3, 4, 5, 6, 7 and 8.

 Table 3
 Ecological and geographic data for 51 study sites

Site	Lat	Long	El	BGC	ASMR	AET/PET	MAT	MAP	Slope	Pos	Aspect	Soil
BL10	53.355	123.087	775	SBSdw2	MD	0.8490	3.7	539	3	Level	Flat	Medium
BL16	53.309	123.046	690	SBSdw2	MD	0.8180	3.9	524	2	Crest	Flat	Medium
BL18	53.295	123.063	750	SBSdw2	MD	0.8180	3.6	524	100	Upper	North	Medium
BL2	53.466	123.461	1270	SBSdw2	MD	0.8180	1.5	615	35	Crest	North	Medium
BL22	53.442	122.945	880	SBSdw2	MD	0.8490	3.4	738	40	Upper	South	Medium
BL24	53.788	122.722	600	SBSmh	SD	0.8580	4.5	574	20	Mid	North	Fine
BL25	53.682	122.799	790	SBSdw3	SD	0.8740	3.5	706	33	Upper	North	
BL28	53.286	122.342	915	SBSdw1	SD	0.8960	3.2	665	20	Upper	North	Medium
BL2M	53.478	123.462	855	SBSdw2	SD	0.8950	3.0	602	5	Mid	North	Medium
BL7	53.362	123.245	810	SBSdw2	F	1.0000	3.4	538	0	Level	Flat	Fine
BL9	53.357	123.081	795	SBSdw2	MD	0.8490	3.6	539	5	Crest	North	Coarse
BL9M	53.359	123.082	780	SBSdw2	F	1.0000	3.7	540	0	Level	Flat	Medium
FSJ0	54.505	124.260	900	SBSdw3	SD	0.8510	2.3	506	5	Crest	North	Coarse
FSJ0M	54.485	124.291	1100	SBSdw3	F	1.0000	1.7	509	10	Lower	North	Medium
FSJ15	54.562	124.460	800	SBSdw3	MD	0.7940	2.7	502	5	Crest	Flat	Coarse
FSJ19	54.526	124.184	1260	SBSdw3	SD	0.8510	1.0	520	100	Mid	South	
FSJ19X	54.527	124.184	1280	SBSdw3	MD	0.7940	0.9	520	110	Mid	North	
FSJ24	54.810	124.058	875	SBSdw3	SD	0.8740	1.8	676	0	Crest	South	Medium
FSJ27	54.730	124.339	960	SBSmk1	SD	0.8640	1.7	619	0	Crest	Flat	Medium
FSJ3	54.393	124.133	920	SBSdw3	MD	0.7940	NA	NA	0	Crest	South	Medium
SUM2	54.476	122.645	730	SBSmk1	SD	0.8640	2.6	752	10	Crest	South	Medium
SUM2M	54.474	122.644	720	SBSmk1	SD	0.9090	2.7	753	3	Lower	South	Medium
SUM3	54,399	122.623	770	SBSmk1	SD	0.8640	2.4	752	5	Crest	North	Coarse
SUM4	54,388	122.658	740	SBSmk1	SD	0.9090	2.4	752	0	Mid	North	Medium
SUM6	54,386	122.628	760	SBSmk1	MD	0.8010	2.4	742	0	Crest	North	Medium
SUM7	54,464	122.737	700	SBSmk1	MD	0.8010	2.8	739	0	Crest	Flat	Coarse
SUM8	54.370	122.654	760	SBSmk1	SD	0.8640	2.3	744	0	Level	Flat	Coarse
SUM8B	54 446	122.631	710	SBSmk1	MD	0.8010	2.3	757	0	Crest	South	Coarse
BUC13	53 392	122.010	630	SBSmw	SD	0.8690	41	596	90	Mid	South	Medium
BUC17	53 165	122.535	600	SBSmh	MD	0.8000	4.6	558	0	Unner	South	Coarse
BUC17M	53 165	122.535	590	SBSmh	F	1.0000	4.6	558	0	Level	South	Fine
BUC8	53 501	122.330	920	SBSmk1	SD.	0.8640	27	733	15	Unper	South	Medium
ESI20	54 524	122.407	930	SBSdw3	MD	0.0040	2.7	513	25	Mid	South	Wiedium
SUM17	54 990	123.048	700	SBSmk1	MD	0.8010	2.2	581	5	Unner	North	Medium
SUM25S	54 966	123.040	710	SBSmk1	MD	0.8010	2.4	565	0	Level	Flat	Medium
SUM11	54 343	122.675	740	SBSmk1	MD	0.8745	2.4	731	0	Crest	North	Coarse
SUM12	54 263	122.031	740	SBSmk1	SD SD	0.8745	2.4	653	0	Upper	South	Medium
SUM14	54 307	122.775	750	SBSmk1	5D F	1.0000	2.0	701	0	Lower	Flat	Fine
SUM07D	51 971	122.392	760	SDSIIKI SBSml-1	SD .	0.8640	2.0	737	10	Mid	South	Medium
SUM2/D	54 242	123.032	750	SDSHIKI SDSmlr1	SD SD	0.0040	2.5	721	0	Loval	Flot	Modium
SUM9	54.545 54 566	122.047	730 810	SDSHKI SDSA2	5D 5D	0.9090	2.4 2.6	731 506	10	Level	Fiat	Coerce
TOJI JIVI VANI 1	52 720	124.437	010 860	SDSUWS	SD MD	0.0910	2.0 2.5	500	10	Crost	Flot	Madium
VANH	55.728	124.790	860	SBSdk	MD	0.8070	2.5	526	U	Crest	Flat	Medium

 Table 3 (continued)

Site	Lat	Long	El	BGC	ASMR	AET/PET	MAT	MAP	Slope	Pos	Aspect	Soil
VAN16	53.810	124.210	1220	SBSmc2	SD	0.9000	1.3	573	0	Crest	Flat	Medium
VAN23	54.137	124.954	820	SBSdw3	SD	0.8740	3.0	579	10	Upper	South	Coarse
VAN28	53.819	124.368	940	SBSdw2	MD	0.8180	2.3	564	0	Crest	Flat	Medium
VAN3M	53.636	124.986	860	SBSdk	SD	0.9040	2.5	507	15	Lower	North	Medium
VAN5	53.936	125.102	940	SBSdk	SD	0.8540	2.8	555	20	Mid	South	Coarse
VAN9B	53.729	124.798	800	SBSdk	MD	0.7730	2.9	545	0	Crest	Flat	Coarse
VAN10	53.728	124.713	740	SBSdk	SD	0.8540	2.8	509	0	Upper	North	Medium
VAN26	53.517	124.038	860	SBSdw2	MD	0.8490	2.6	562	0	Level	Flat	Coarse
VAN7	53.733	125.041	900	SBSdk	MD	0.8070	3.1	606	0	Crest	South	Medium

Lat Degree North; Long Degree West; El Elevation (meters above sea level); BGC biogeoclimatic unit (Meidinger and Pojar 1991); ASMR actual soil moisture regime class (Meidinger and Pojar 1991); AET/PET mean annual actual evapotranspiration/potential evapotranspiration ratio; MAT mean annual temperature (°C); MAP mean annual precipitation (mm); Slope slope grade (%); Pos slope position; Soil soil texture class

Biogeoclimatic unit codes are as follows: the first three letters, SBS, identify the sites within the Sub-Boreal Spruce BGC Zone. The fourth letter denotes the relative precipitation regime within the BGC Zone: d dry; m moist. The fifth letter denotes the relative temperature regime within the BGC Zone: h hot; w warm, k cool, c cold. The last two letters and last number together denote a subzone and variant classification within the larger BGC Zone

Table 4Statistics for 55 radialgrowth chronologies

Site	Species	First	Last	Years	Trees	MIC	EPS
BL25	Fir	1910	2009	100	8	0.440	0.858
FSJ0	Fir	1857	2009	153	15	0.476	0.932
FSJ0M	Fir	1921	2009	89	15	0.343	0.880
FSJ24	Fir	1798	2009	212	18	0.393	0.921
SUM2	Fir	1812	2009	198	10	0.350	0.840
SUM2M	Fir	1823	2009	187	9	0.376	0.844
SUM3	Fir	1887	2009	123	15	0.351	0.886
SUM4	Fir	1878	2009	132	16	0.283	0.862
SUM6	Fir	1911	2009	99	15	0.375	0.899
SUM8	Fir	1917	2009	93	10	0.301	0.811
SUM8B	Fir	1923	2009	87	14	0.299	0.836
FSJ20	Fir	1865	2009	145	12	0.328	0.854
SUM12	Fir	1848	2009	162	16	0.313	0.878
SUM27B	Fir	1886	2009	124	15	0.300	0.865
SUM9	Fir	1820	2009	190	15	0.298	0.861
BL10	Spruce	1895	2009	115	10	0.359	0.846
BL16	Spruce	1885	2009	125	11	0.535	0.926
BL18	Spruce	1894	2009	116	12	0.545	0.933
BL2	Spruce	1886	2009	124	16	0.288	0.865
BL22	Spruce	1929	2009	81	10	0.438	0.878
BL24	Spruce	1931	2009	79	15	0.396	0.895
BL25	Spruce	1883	2009	127	16	0.440	0.924
BL28	Spruce	1816	2009	194	11	0.296	0.822
BL2M	Spruce	1866	2009	144	13	0.273	0.830
BL7	Spruce	1867	2009	143	12	0.381	0.881
BL9	Spruce	1898	2009	112	10	0.532	0.913
BL9M	Spruce	1883	2009	127	16	0.292	0.865
FSJ15	Spruce	1847	2009	163	15	0.547	0.947
FSJ19	Spruce	1885	2009	125	9	0.413	0.861
FSJ19X	Spruce	1840	2009	170	11	0.310	0.831

Table 4 (continued)

Site	Species	First	Last	Years	Trees	MIC	EPS
FSJ27	Spruce	1885	2009	125	15	0.431	0.919
FSJ3	Spruce	1822	2009	188	15	0.379	0.901
SUM7	Spruce	1896	2009	114	15	0.512	0.940
BUC13	Spruce	1876	2009	134	12	0.410	0.889
BUC17	Spruce	1864	2009	146	19	0.349	0.910
BUC17M	Spruce	1895	2009	115	20	0.308	0.889
BUC8	Spruce	1764	2009	246	15	0.277	0.852
SUM17	Spruce	1882	2009	128	15	0.432	0.919
SUM25S	Spruce	1899	2009	111	16	0.355	0.897
SUM11	Spruce	1800	2009	210	14	0.270	0.833
SUM12	Spruce	1833	2009	177	15	0.238	0.824
SUM14	Spruce	1896	2009	114	16	0.292	0.868
SUM27B	Spruce	1889	2009	121	15	0.254	0.836
FSJ15M	Spruce	1901	2009	109	15	0.435	0.919
VAN11	Spruce	1886	2009	124	15	0.449	0.923
VAN16	Spruce	1868	2009	142	13	0.405	0.899
VAN23	Spruce	1880	2009	130	14	0.269	0.837
VAN28	Spruce	1903	2008	106	15	0.266	0.844
VAN3M	Spruce	1892	2009	118	15	0.221	0.810
VAN5	Spruce	1939	2009	71	15	0.319	0.850
VAN9B	Spruce	1886	2009	124	10	0.406	0.866
VAN10	Spruce	1885	2009	125	12	0.428	0.898
VAN26	Spruce	1866	2009	144	15	0.241	0.826
VAN7	Spruce	1895	2009	115	15	0.334	0.876
FSJ0M	Spruce	1920	2009	90	15	0.414	0.914

MIC mean intrasite correlation; EPS expressed population signal (Wigley et al. 1984)

Table 5Mean correlation coefficient and proportion of spruce chronologies with significant correlations (p < 0.05) between radial growth andclimate from 1950 to 2009

ASMR	Climate variable	Prior sum	mer	Spring		Summer		Growing	season	June	
		Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn
MD	cmd	- 0.198	0.32	- 0.227	0.56	- 0.389	0.80	- 0.364	0.80	- 0.305	0.68
MD	eref	- 0.170	0.32	- 0.071	0.08	- 0.375	0.80	- 0.249	0.64	- 0.365	0.84
MD	ppt	0.208	0.36	0.201	0.32	0.335	0.80	0.330	0.80	0.224	0.56
MD	tmx	- 0.145	0.28	- 0.115	0.04	- 0.370	0.84	- 0.246	0.48	- 0.383	0.84
SD	cmd	- 0.306	0.70	- 0.189	0.39	- 0.260	0.52	- 0.253	0.57	- 0.161	0.48
SD	eref	- 0.318	0.78	- 0.091	0.17	- 0.277	0.65	- 0.188	0.48	- 0.256	0.57
SD	ppt	0.278	0.48	0.182	0.43	0.213	0.48	0.238	0.61	0.080	0.35
SD	tmx	- 0.295	0.65	- 0.130	0.35	- 0.288	0.74	- 0.191	0.43	- 0.277	0.57
F	cmd	- 0.349	0.83	- 0.095	0.00	- 0.133	0.50	- 0.131	0.33	- 0.019	0.00
F	eref	- 0.380	0.83	-0.088	0.00	- 0.164	0.50	- 0.109	0.50	- 0.115	0.17
F	ppt	0.321	1.00	0.107	0.00	0.076	0.00	0.129	0.33	- 0.055	0.00
F	tmx	- 0.375	0.83	- 0.106	0.17	- 0.199	0.67	- 0.114	0.33	- 0.161	0.17

ASMR actual soil moisture regime; MD moderately dry; SD slightly dry; F fresh; cmd climatic moisture deficit; eref Hargreaves reference evapotranspiration; ppt precipitation; tmx maximum temperatures; Cr.Cf mean correlation coefficient between ring-width chronology and climate variable; Prp.Crn proportion of chronologies with significant (p < 0.05) correlation with climate variable

ASMR	Climate vari- able	Prior summer		Spring		Summer		Growing seat	son	June	
		Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn	Cr.Cf	Prp.Crn
MD	cmd	- 0.109	0.00	- 0.360	1.00	- 0.512	1.00	- 0.432	1.00	- 0.404	0.75
MD	eref	-0.039	0.00	0.010	0.00	- 0.508	1.00	- 0.261	0.50	-0.430	1.00
MD	ppt	0.133	0.00	0.307	0.75	0.436	0.75	0.350	1.00	0.301	0.75
MD	tmx	0.021	0.00	-0.085	0.00	- 0.485	1.00	-0.270	0.50	-0.420	1.00
SD	cmd	-0.100	0.07	-0.227	0.57	- 0.212	0.57	-0.155	0.29	-0.127	0.21
SD	eref	-0.065	0.07	-0.055	0.00	-0.317	0.71	-0.134	0.21	-0.276	0.50
SD	ppt	0.135	0.14	0.195	0.57	0.116	0.14	0.086	0.14	- 0.002	0.14
SD	tmx	- 0.061	0.07	- 0.099	0.00	- 0.355	0.79	- 0.161	0.43	- 0.319	0.57
ц	cmd	-0.015	0.00	-0.165	0.00	-0.160	0.00	-0.110	0.00	-0.189	0.00
Ц	eref	-0.133	0.00	0.072	0.00	-0.221	0.00	- 0.020	0.00	- 0.319	1.00
ц	ppt	-0.008	0.00	0.133	0.00	0.055	0.00	0.062	0.00	0.030	0.00
Ч	tmx	-0.149	0.00	-0.051	0.00	-0.215	0.00	- 0.066	0.00	- 0.344	1.00
ASMR actual temperatures, variable	soil moisture regin ; <i>Cr.Cf</i> mean corre	me; <i>MD</i> modera lation coefficien	tely dry; SD slig t between ring-w	htly dry; F fresh vidth chronology	t; <i>cmd</i> climatic n and climate var	aoisture deficit; diable; Prp.Crn p	<i>eref</i> Hargreaves proportion of ch	reference evapoti ronologies with s	ranspiration; <i>ppt</i> significant (<i>p</i> < 0.	precipitation; <i>tm</i> . 05) correlation v	<i>x</i> maximum vith climate

Table 6 Mean correlation coefficient and proportion of fir chronologies with significant correlations (p < 0.05) between radial growth and climate from 1950 to 2009

 Table 7
 Model
 output
 from
 linear
 analysis
 of
 climatic
 sensitivity

 across soil
 moisture
 gradient
 defined
 by
 site
 mean
 annual
 AET/PET

 ratio
 ratio<

Species	Season	Clim.Var	Coefficient	P value	R^2
Fir	Prior summer	Cmd	0.0010	0.477	0.040
		Eref	0.0003	0.947	0.000
		Tmx	- 0.0336	0.685	0.013
		Ppt	- 0.0011	0.435	0.047
	Spring	Cmd	0.0073	0.014	0.382
		Eref	0.0004	0.916	0.001
		Tmx	0.0245	0.629	0.018
		Ppt	-0.0067	0.044	0.278
	Summer	Cmd	0.0052	0.011	0.400
		Eref	0.0141	0.006	0.456
		Tmx	0.1886	0.019	0.358
		Ppt	- 0.0060	0.013	0.389
	Growing season	Cmd	0.0038	0.022	0.343
		Eref	0.0059	0.063	0.242
		Tmx	0.1481	0.086	0.210
		Ppt	- 0.0038	0.039	0.288
	June	Cmd	0.0071	0.102	0.192
		Eref	0.0176	0.092	0.203
		Tmx	0.0786	0.143	0.158
		Ppt	- 0.0079	0.092	0.203
Spruce	Prior summer	Cmd	- 0.0009	0.379	0.020
		Eref	- 0.0044	0.112	0.065
		Tmx	-0.0888	0.061	0.089
		Ppt	0.0005	0.645	0.006
	Spring	Cmd	0.0050	0.020	0.135
		Eref	- 0.0018	0.417	0.017
		Tmx	-0.0022	0.943	0.000
		Ppt	-0.0051	0.034	0.113
	Summer	Cmd	0.0044	0.005	0.190
		Eref	0.0101	0.014	0.149
		Tmx	0.1233	0.048	0.099
		Ppt	- 0.0052	0.003	0.208
	Growing season	Cmd	0.0031	0.014	0.149
		Eref	0.0039	0.063	0.088
		Tmx	0.1013	0.075	0.081
		Ppt	- 0.0032	0.023	0.129
	June	Cmd	0.0085	0.002	0.232
		Eref	0.0231	0.001	0.243
		Tmx	0.1118	0.004	0.197
		Ppt	- 0.0086	0.002	0.222

Clim.Var climate variable; *Cmd* climatic moisture deficit; *Eref* Hargreaves reference evapotranspiration (Hargreaves and Allen 2003); *Tmx* maximum temperatures; *Ppt* precipitation

 Table 8 Results from principal components analysis of chronologies and ASMR groupings

Species	ASMR	Var.Exp	Num.Crn	Mean.Corr
Fir	MD	0.618	4	0.78
	SD	0.534	12	0.73
Spruce	MD	0.463	20	0.61
	SD	0.461	17	0.65
	F	0.512	6	0.69

ASMR actual soil moisture regime class (Meidinger and Pojar 1991); MD moderately dry; SD slightly dry; F fresh; Var.exp chronology variance explained by principal component (%); Num.Crn number of chronologies represented by principal component; Mean.Corr mean correlation between chronology and principal component

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