Assessing the climatic sensitivity of Douglas-fir at its northern range margins in British Columbia, Canada

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Abstract Northern hemisphere tree species growing at their northern range margins may be particularly responsive to climate change and could provide important information regarding future broad-scale responses. We analyzed and compared tree-ring data between five Douglas-fir [*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco] populations growing at the species' northernmost distribution in British Columbia, Canada, and five populations located 150 km to the southeast. We quantified climate–growth relationships using uni- and multivariate techniques at different temporal scales. Our data suggest that (1) even at its northernmost distributions, precipitation limits long-term mature Douglas-fir radial growth more than temperatures, (2) northernmost Douglas-fir populations are distinct from populations located further within the species' range in terms of certain key short-term growth responses, and (3) northernmost Douglas-fir growth sensitivities to climate may be increasing over time. In the future, mature Douglas-fir productivity in the northern portion of its range may be primarily limited by precipitation, and responses may be strongest at the species' range margins.

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Introduction

With growing evidence that climate change is substantially affecting forest processes, structure, and function (Parmesan 2006), projecting the potential responses of tree species to future climates has emerged as an important research focus (Aitken et al. 2008). The study of annual tree-rings (dendrochronology) can be useful in this regard due to the strong link between climate and radial growth (Fritts 1976) that allows historical growth responses to climate (hereafter, climate–growth) to be quantified at various temporal scales. Radial growth is a good metric of tree species productivity, resilience, and fitness (Givnish 1995), and therefore it can provide an indication of adaptive capacity and future viability (Littell and Peterson 2005).

Because climate can strongly limit the distribution of tree species (Hamann and Wang 2006), early and strong responses to climate change may be seen in trees growing at climatically controlled distribution limits (Wilmking et al. 2004). Consequently, there is considerable interest in understanding and projecting tree-ring responses to climate change in these areas. Tree-ring studies have focussed on ecotonal boundaries such as forest–grassland, forest–alpine, and forest–tundra transitions (e.g., Daniels and Veblen 2004; Wilmking et al. 2004); however, we know of few studies that have examined growth responses of a tree species at distribution limits located within contiguous forest (e.g., Pederson et al. 2004). This type of distribution limit may be suitable for detecting climate change impacts in temperate forests (Loehle 2000), where intrinsic factors, inter-specific competition, and biotic interactions may play an important role in tree population adaptation to climate change (Aitken et al. 2008).

In this study, we examined the climate–growth relationships of interior Douglas-fir [*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco] at its northern range margins (NRMs; Pederson et al. 2004) in British Columbia (BC), Canada. Interior Douglas-fir (hereafter, Douglas-fir) is a commercially important conifer in western North America (Hermann and Lavender 1990) with wide ecological amplitude reflecting strong local adaptation (Rehfeldt 1991). At its NRM, Douglas-fir is irregularly distributed in both pure and mixed-species stands or as isolated veteran trees in stands dominated by other species (Jull 1999). These unique distribution patterns may partly reflect the influence of short-term extreme climatic events such as frost events or ice storms that limit establishment and juvenile development (Jull 1999; DeLong 1999). Douglas-fir productivity at its northern extremes can exceed that of other co-occurring conifers, creating considerable management interest for this species at its NRM (Jull 1999; Kessler 1999; Rogers 2006). NRM Douglas-fir abundance may be in decline, possibly associated with Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) outbreaks, historical fire suppression, or post-harvest conversion to other species (Daintith and Vyse 1999; Jull 1999). Regardless of abiotic and biotic determinants of Douglas-fir distributions, its fundamental climatic niche may expand northward with climate change (Hamann and Wang 2006), in which case mature in situ populations will provide seed source for range expansion.

Previous studies have established a strong link between Douglas-fir radial growth and precipitation in BC (e.g., Watson and Luckman 2002; Griesbauer and Green 2010) and other regions (e.g., Littell et al. 2008). What remains unclear is the nature of climate–growth relationships at the species' NRM (Griesbauer and Green 2010). In order to address this knowledge gap, we compared long- and short-term growth responses to climate between two clusters of mature Douglas-fir populations: (1) NRM populations and (2) populations in the same geographic region but located approximately 150 km to the southeast of the northern species range margin.

Methods

Sampling sites

Annual tree-ring data were collected from Douglas-fir trees in ten study sites located in the central interior region of BC, Canada (Fig. 1). We located five sample sites at the NRM, near Fort St. James (54°26′N, 124°15′W), and located the other five sample sites approximately 150 km to the southeast, near Prince George (53°55′N, 122°44′W). For the purposes of this study, we report five NRM chronologies as being located in the 'NRM' subregion, and five southern chronologies as being located in the 'WR' (within-range) subregion. The subregions have significantly different mean annual and seasonal climates ($P < 0.001$); the Fort St. James climate station receives an average of 492 mm of precipitation per year and has a mean annual temperature of 2.7°C, whereas the Prince

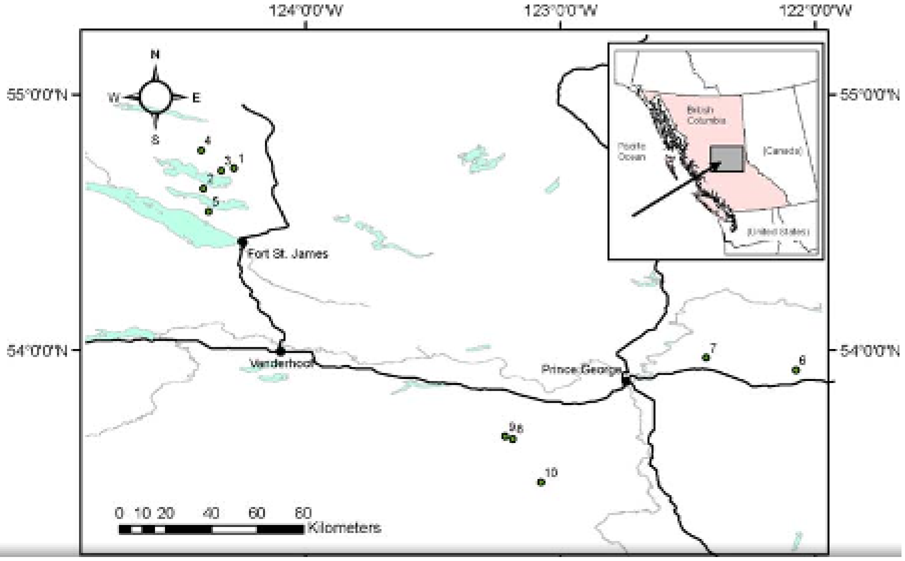


Fig. 1 Sample site locations in BC, Canada. Refer to Table 2 for site codes. Climate stations used for this study are located in Fort St. James and Prince George

Table 1 Climate normals (1961–1990) for Fort St. James and Prince George climate stations

	Season[a]	Fort St. James (el. = 686 m)		Prince George (el. = 691 m)		P^b
		Mean	SD	Mean	SD	
PPT (mm)	Winter	239	54	328	69	0.0000
	Spring	107	33	159	46	0.0000
	Summer	145	44	196	68	0.0012
	Annual	492	69	686	90	0.0000
TAV (°C)	Winter	−5.1	1.8	−3.8	1.8	0.0085
	Spring	8.1	0.8	9.1	0.8	0.0000
	Summer	13.0	1.0	13.2	0.9	0.4149
	Annual	2.7	1.0	3.7	1.0	0.0005

el. elevation (metres above mean sea level), *PPT* precipitation, *TAV* mean temperature, *SD* standard deviation

[a] Refer to Table 5 for season details

[b] *P* values refer to *t* test statistics between means

George climate station receives an average of 686 mm of precipitation and has a mean annual temperature of 3.7°C (Table 1).

In order to isolate the climate signal as much as possible in tree-ring variation, we targeted sites without evidence of edaphic or other limiting factors (e.g., shallow rocky soils, cold air ponding, steep northerly aspects) or recent disturbance (e.g., fire, harvesting, insect attacks). Between 18 and 40 healthy and mature (>100 years old) trees were sampled at each site to match climate record lengths and to build a robust population chronology. Tree-ring variability related to inter-tree competition was minimized by sampling trees with a dominant canopy position. A single increment core was taken from each sample tree at approximately breast height. Where sampling occurred on slopes, increment cores were taken perpendicular to the slope to avoid compression and tension wood (Josza 1988).

Processing and chronology development

Increment cores were mounted and sanded to enhance the contrast of tree-ring boundaries. Cores were visually crossdated to assign calendar years to annual growth rings (Fritts 1976). Ring widths were measured to the nearest 0.01 mm using WinDendro™ image analysis software (Régent Instruments Inc 2005). Crossdating was statistically verified using COFECHA software (Holmes 1983). After checking for measurement errors, cores that did not crossdate with the master chronology were excluded from the final chronology (Cook and Kairiukstis 1990). Generally, very few (less than 3% of the total) cores could not be crossdated, usually due to rot or breaks in the core.

The ARSTAN software (version 4.0c) (Cook 1985) was used to prepare the final chronologies. A cubic smoothing spline with a 50% frequency response cutoff of 60 years was used to remove linear trends and very low-frequency variation from each tree's time series as these often represent non-climatic forcings (e.g., ring widths tend to decrease over time associated with increasing tree age and size) and can mask the climatic signal (Cook 1985). After detrending, autocorrelation was analyzed for all trees within a site and a common autoregressive model was then applied to each tree's time series (Cook and Krusic 2005). Residuals from autoregressive modeling were averaged together using robust mean calculation to produce a residual growth chronology that represented stand growth variation (Cook and Krusic 2005). Removing autocorrelation from growth chronologies is often necessary for climatic analysis (e.g., Littell et al. 2008) because autocorrelation has statistical implications and may reflect non-climatic processes such as stand-level disturbances and morphological influences on growth (Cook 1985).

Data analysis

Chronology analysis

Chronology characteristics were described with the following statistics produced by the ARSTAN software: (1) mean sensitivity (a measure of inter-annual growth variation; Cook and Kairiukstis 1990), (2) standard deviation, (3) average intrasite correlation (average correlation of growth variation of all trees within a site to the final chronology), and (4) expressed population signal (EPS; Wigley et al. 1984). Average intrasite correlation and EPS are commonly used as a measure of the strength of the common (presumably climatic) signal contained in the chronologies (Cook and Kairiukstis 1990; Wigley et al. 1984). Wigley et al. (1984) suggest a minimum EPS of 0.85 for dendroclimatic analysis.

Principal components analysis

To highlight the influence of climate patterns on growth in each subregion, we extracted the leading mode of growth variation with a principal components analysis (PCA) of the five chronologies in each subregion. PCA was restricted to a common time period (1900–2005). Principal components (PCs) with a corresponding eigenvalue greater than one were interpreted to represent significant temporal growth patterns (Tabachnick and Fidell 2001) and were retained for climate–growth relationships analyses (below).

Climate data

We used adjusted monthly precipitation records (Mekis and Hogg 1999) and homogenized monthly average, average maximum, and average minimum temperature records (Vincent and Gullett 1999; Vincent et al. 2002) provided by the Climate Research Division of the Meteorological Service of Canada (http://www.cccma.bc.ec.gc.ca/hccd/) for the Fort St. James and Prince George climate stations. Fort St. James climate data were used to determine climate–growth relationships in the NRM subregion, and Prince George climate data were used for the WR subregion. We limited our analyses to seasonal and annual variables, as preliminary data analyses and other studies (e.g., Watson and Luckman 2002) have shown that integrations of climate over multiple months (i.e., seasons) are more important growth influences than variation at a monthly scale. Seasonal and annual climate variables were derived by averaging monthly values based on a priori knowledge of appropriate climate variables suitable for use in describing Douglas-fir climate–growth relationships (Watson and Luckman 2002; Littell et al. 2008; Griesbauer and Green 2010) and preliminary data analyses. Growth was compared to climate variables from July prior to the growing season through October following the growing season, as climate in the preceding year can affect the current year's growth (Fritts 1976). The monthly inputs for the seasonal and annual climate variables are listed in Table 5. We note that in this study, 'annual' refers to the 12-month period spanning the previous July to current June. Where monthly values were missing in climate station records (only precipitation data were missing), the associated derived seasonal variable was computed as a non-number and omitted pair-wise from analyses.

Long- and short-term climate–growth relationship analyses

We quantified long-term climate–growth relationships by computing correlation and response coefficients between subregional growth chronologies (as represented by the principal component of chronology variation in each subregion) and climate data over a 93-year period common to climate station data in both subregions (1913–2005). We used response function analysis to compute the response coefficients (Fritts 1976; Biondi and Waikul 2004). A response function is a multiple regression technique that eliminates multicollinearity among climate predictor variables by transforming the climate variables into a set of orthogonal principal components using PCA prior to regression (Fritts 1976; Biondi and Waikul 2004). Regression coefficients are then computed for a subset of the principal components and transformed back to the original variables (called 'response coefficients'). The principal component subset was chosen using the PVP criterion, where the eigenvalues were progressively analyzed and their corresponding eigenvector retained until the point where the cumulative product of the eigenvalues fell below one (Guiot 1990). Response coefficients and their 95% confidence intervals were computed with 1,000 iterations of the bootstrapped response function algorithm described in Biondi and Waikul (2004).

Short-term climate–growth relationships were quantified with moving correlation and response functions (Biondi 2000; Biondi and Waikul 2004; Wilson and Elling 2004; Carrer and Urbinati 2006; D'Arrigo et al. 2007), using the 1900–2005 Fort St. James climate record and the 1913–2005 Prince George climate record. A moving correlation function (MCF) computes correlation coefficients between two time series using a fixed time window that is incrementally moved over the full series length; time-dependent variation in the coefficients provides a measure of temporal stability in the linear relationship between the two series (Biondi 2000; Biondi and Waikul 2004). For all correlation analyses, bootstrapped bias-corrected accelerated 95% confidence intervals were calculated for each correlation coefficient using 1,000 iterations (The Mathworks Inc. 2007). Analyses using all climatic variables would have produced too many results for reasonable interpretation and discussion, therefore, we focused on a subset of climatic variables that explained the greatest proportion of growth variation and likely had some physiological basis relevant to Douglas-fir climate–growth relationships (Littell et al. 2008). Specifically, we focused on annual, spring, and prior summer precipitation, and prior summer average, average maximum, and average minimum temperatures.

A moving response function quantifies the growth response to multiple climatic factors over a moving time window, similar to an MCF (Biondi 2000; Biondi and Waikul 2004; Carrer and Urbinati 2006). Response functions were computed using seasonal precipitation and average temperatures. To provide a fine temporal resolution while ensuring sufficient degrees of freedom for the moving response function (Biondi and Waikul 2004), we used a time window of 31 years, offset by 1 year

Table 2 Site descriptions and descriptive statistics for Douglas-fir sample sites

Subregion	Site	Site code	Lat (°N)	Long (°W)	El (m)	Trees (n)	Chronology (years)	MS	SD	AIC	EPS
NRM	Arch	1	54.73	124.30	860	27	2006–1880 (127)	0.174	0.153	0.461	0.958
	Battle	2	54.56	124.40	860	21	2006–1887 (120)	0.156	0.137	0.474	0.950
	Bison	3	54.72	124.35	840	23	2006–1844 (163)	0.198	0.176	0.473	0.954
	Dolphin	4	54.80	124.43	940	21	2006–1799 (208)	0.184	0.185	0.415	0.937
	Pinchi	5	54.65	124.42	880	26	2006–1880 (127)	0.156	0.135	0.450	0.955
WR	Bowron	6	53.94	122.10	780	25	2005–1818 (188)	0.175	0.147	0.406	0.945
	Ferndale	7	53.95	122.46	780	21	2005–1833 (173)	0.203	0.171	0.493	0.953
	Gregg11	8	53.67	123.21	815	18	2005–1860 (146)	0.220	0.184	0.496	0.947
	Gregg24	9	53.68	123.24	840	23	2005–1868 (138)	0.222	0.180	0.592	0.971
	PG1412	10	53.50	123.10	740	31	2005–1865 (141)	0.199	0.168	0.458	0.955

Lat latitude, *Long* longitude, *El* elevation, *MS* mean sensitivity, *SD* standard deviation, *AIC* average intrasite correlation, *EPS* expressed population signal

increments. For each 31-year time window, the significant response coefficients were entered into a multiple regression model to determine the adjusted coefficient of determination between climate and growth.

We also compared long- and short-term growth patterns in both subregions by computing correlation coefficients between the leading principal components, using the same time windows as for the climate–growth relationships (1913–2005 for the long-term and moving 31-year windows over the 1900–2005 period for the short-term).

Results

Chronology analysis

Final chronologies for sampling populations were built using between 18 and 31 trees, and they ranged in length from 120 to 208 years (Table 2). All chronologies had relatively high intrasite correlations (ranging from 0.406 to 0.592) and high expressed population signals (ranging from 0.937 to 0.971), indicating a sufficient population signal for climate analysis (Wigley et al. 1984). Expressed population signals also exceeded 0.85 in all chronologies when assessed using 31-year moving windows over a 1900–2005 period (Fig. 2), indicating temporally stable chronology signals. Mean sensitivity ranged from 0.156 to 0.222 and standard deviation from 0.135 to 0.185.

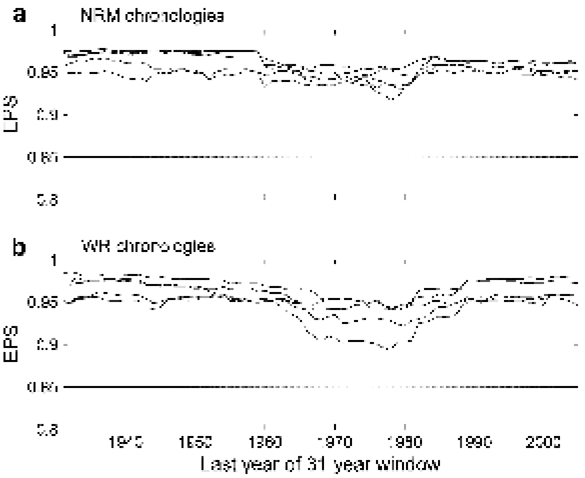


Fig. 2 Chronology expressed population signal (EPS) over successive 31-year windows. *Horizontal line* is minimum EPS recommended by Wigley et al. (1984) for dendroclimatic analysis

Principal components analysis

Chronologies in each subregion showed coherent interannual growth patterns, synchronous pointer years (Fig. 3a, c), and significant correlations between annual growth variation (both intra- and inter-regional) from 1913 to 2005, with intra-regional chronologies generally having the highest correlations (Table 3). A PCA of NRM chronologies extracted one principal component (Fig. 3b) that explained 81.2% of their variance (Table 4), and a PCA of WR chronologies extracted one principal component (Fig. 3d) that explained 76.4% of their variance (Table 4). All other principal components had eigenvalues less than one (not shown). All chronologies were significantly correlated with their corresponding principal component (all $r > 0.8$, $P < 0.0001$, Table 4).

Inter-regional growth patterns

The leading principal components from both subregions were significantly correlated with each other from 1913 to 2005 ($r = 0.70$, $P < 0.0001$). Moving correlation functions revealed that the correlation strength between subregions varied somewhat over the twentieth century; however, correlations were significant ($P < 0.05$) over all windows

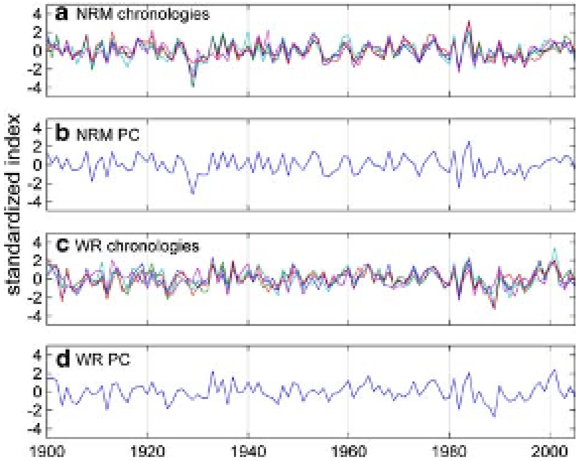


Fig. 3 Residual ring-width and principal components chronologies for Douglas-fir in NRM and WR study subregions

(Fig. 4a). Correlation coefficients were generally above 0.6 until the ~1920–1950 period, when they began to gradually weaken. Correlations were lowest (although still significant) over the middle of the twentieth century (~1944–1974). Growth patterns converged noticeably after the mid-century (e.g., $r > 0.8$ for the 1975–2005 period).

Long-term climate–growth relationships

From 1913 to 2005, Douglas-fir growth in both subregions (as represented by the leading principal components) was positively correlated with annual, prior summer, and spring precipitation and rain, as well as winter temperatures (Table 5). Growth in both subregions was also negatively correlated with spring and prior summer temperatures. Generally, correlations were stronger with precipitation than temperature variables. The principal component representing WR Douglas-fir growth had stronger correlations with climate than the principal component representing NRM Douglas-fir growth during this time period.

Response functions computed for the 1913–2005 period generally supported correlation analysis results (Table 5). Growth in both subregions showed positive responses to prior summer precipitation, spring precipitation, and winter temperatures. Growth in the WR subregion showed negative responses with spring average temperatures. Multiple seasonal variables explained more growth variation over the 93-year period in the WR subregion (34.8%) than the NRM (18.2%). While the correlation analysis indicated that annual precipitation explained more growth variation than seasonal precipitation amounts, this variable could not be used in the response function analysis because it was a perfect linear combination of the seasonal variables, meaning that the inverse of the correlation matrix used in PCA could not be computed (The Mathworks Inc. 2007).

Short-term climate–growth relationships

Moving correlation functions

MCFs revealed that growth responses to annual precipitation (and rain) in WR Douglas-fir were significantly positive over all consecutive 31-year windows over the full climate record (Fig. 4b, c). In contrast, MCFs with NRM Douglas-fir growth and annual precipitation (and rain) showed less stable responses over the past century. Correlations between NRM growth and annual precipitation were significantly positive during the early portion of the twentieth century but gradually decreased after the 1905–1935 MCF window, becoming insignificant over the middle of the twentieth century (e.g., $r < 0.2$, $P > 0.05$ over the 1935–1965 period). Growth gradually became positively associated with annual precipitation again over the last half of the century. Responses to annual rain were similar, except that the strongest correlations occurred over the more recent MCF windows. After the 1956–1986

Table 3 Correlation matrix between five NRM and five WR residual chronologies (1900–2005)

	Arch	Battle	Bison	Dolphin	Pinchi	Bowron	Ferndale	Gregg11	Gregg24
Battle	0.886								
Bison	0.813	0.813							
Dolphin	0.743	0.744	0.690						
Pinchi	0.766	0.807	0.719	0.642					
Bowron	0.473	0.460	0.531	0.515	0.532				
Ferndale	0.551	0.533	0.564	0.505	0.578	0.751			
Gregg11	0.612	0.624	0.629	0.569	0.709	0.644	0.728		
Gregg24	0.558	0.554	0.496	0.525	0.600	0.538	0.668	0.827	
PG1412	0.549	0.512	0.539	0.502	0.595	0.612	0.667	0.786	0.797

All correlations are significant at $P < 0.001$

Table 4 PCA summary (1900–2005)

	NRM		WR
Component	1		1
Eigenvalues	4.06		3.82
Variance (%)	81.2		76.4
Loadings[a]			
Arch	0.94	Bowron	0.81
Battle	0.91	Ferndale	0.88
Bison	0.95	Gregg11	0.92
Dolphin	0.84	Gregg24	0.88
Pinchi	0.87	PG1412	0.89

[a] All loadings are significant at $P < 0.0001$ ($n = 106$)

period, growth associations with annual rain remained positive and relatively stable.

Growth in both subregions became increasingly associated with spring precipitation over the twentieth century (Fig. 4d). A scatterplot analysis showed that a significantly positive relationship between NRM growth and spring precipitation was strongly weakened by a single extreme outlier point (1993, not shown). Spring precipitation in 1993 was the highest on record, but corresponding growth was below average. This outlier was removed for all moving correlation and response function analyses of the NRM subregion.

Similar to annual rain and precipitation, WR Douglas-fir growth was positively correlated with prior summer precipitation over most 31-year windows, with the strongest correlations occurring over periods prior to ~1960 (Fig. 4e). In contrast, NRM Douglas-fir only showed consistent significantly positive growth responses with prior summer precipitation over recent decades.

In both subregions, Douglas-fir growth responses to prior summer average temperatures were unstable over the past century (Fig. 5a). At NRM, this climate–growth relationship changed from weakly negative during the first decades of the twentieth century to significantly positive from ~1946 to 1976 and then back to negative over the

Fig. 4 MCFs for subregional Douglas-fir growth patterns and climate–growth relationships. Significant correlation coefficients ($P < 0.05$) are *shaded*. Due to missing precipitation data in both climate records, time windows may be less than 31 years. Also, 1993 spring PPT data removed from MCF for NRM subregion

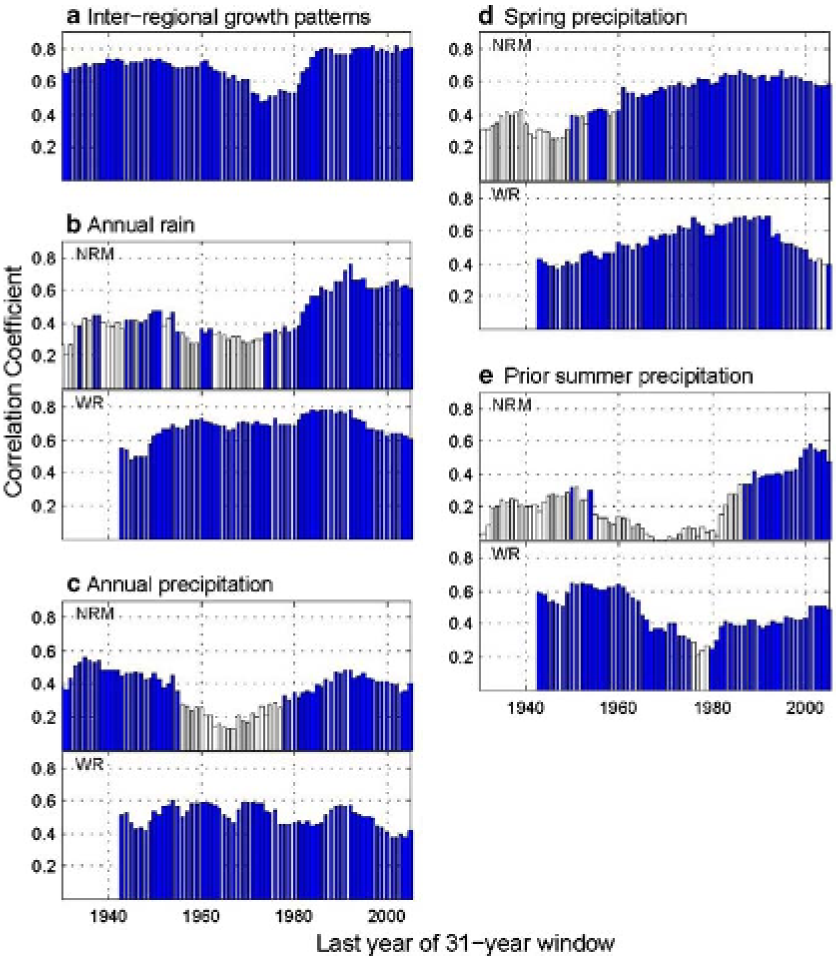


Table 5 Correlation and response coefficients between annual growth variation and seasonal climate variables from 1913 to 2005

Subregion	Season	Correlation coefficients						Response coefficients[a]	
		TMN	TAV	TMX	Rain	Snow	PPT	PPT	TAV
NRM	Prior summer[b]			−0.273	0.229		0.231	0.351	
	Winter[c]		0.207						0.375
	Spring[d]			−0.298	0.411[e]		0.397[e]	0.604	
	Summer[f]								
	Annual[g]				0.444[e]		0.318[e]		
WR	Prior summer[b]			−0.241	0.432[e]		0.437[e]	0.588	
	Winter[c]	0.226	0.220		0.213[h]				0.420
	Spring[d]		−0.304	−0.358	0.413[e]		0.407[e]	0.542	−0.408
	Summer[f]								
	Annual[g]				0.545[i]		0.371[i]		

TMN average minimum temperature, *TAV* average mean temperature, *TMX* average maximum temperature, *PPT* precipitation

All coefficients shown are significant at $P < 0.05$ ($n = 93$ except where shown), based on bootstrapped confidence limits

[a] Adjusted R^2 values from response functions: NRM = 18.2%; WR = 34.8%. Sample size for NRM = 92, WR = 88. Sample sizes reduced due to missing precipitation data

[b] Prior summer variables derived from an average of previous June to September monthly values

[c] Winter variables derived from an average of previous October to current March monthly values

[d] Spring variables derived from an average of April to June monthly values

[e] $n = 92$. Sample sizes reduced due to missing precipitation data

[f] Summer variables derived from an average of current July to September values

[g] Annual variables derived from an average of previous July to current June monthly values

[h] $n = 89$. Sample sizes reduced due to missing precipitation data

[i] $n = 88$. Sample sizes reduced due to missing precipitation data

last three decades. WR growth was not generally significantly correlated with this variable, although the MCFs showed similar temporal patterns as described for the NRM sites. Growth in both subregions became negatively correlated with prior summer maximum temperatures in recent decades (Fig. 5b) and positively correlated with prior summer average minimum temperatures over the 1948–1978 period (Fig. 5c). As well, NRM Douglas-fir growth was negatively correlated with prior summer maximum temperatures during the early portion of the twentieth century (Fig. 5b).

Moving response functions

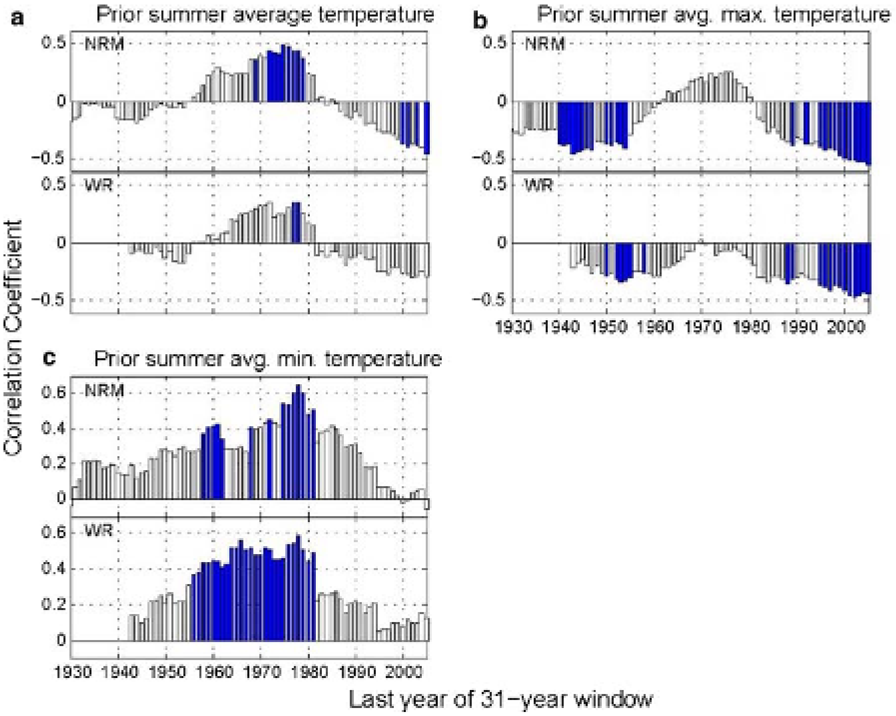
The moving response function computed for the NRM subregion generally supported correlation analysis results (Fig. 6a). Response coefficients for spring precipitation were insignificant over the first portion of the twentieth century, but increased steadily since the 1920–1950 period. Prior summer precipitation and winter temperature became significant variables in recent decades. Adjusted R^2 values computed over each time window using the bootstrapped response coefficients show a steady increase in the strength of the growth responses to climate over the twentieth century, with over 50% of growth variation explained by seasonal precipitation and temperature in recent decades (Fig. 6b).

Response coefficients computed for the WR subregion showed that growth was responsive to prior summer precipitation in the early portion of the climate record (Fig. 7a). Growth became responsive to spring precipitation over the latter portion of the climate record. Similar to the NRM subregion, WR growth became responsive to prior summer precipitation and winter temperatures over recent decades. Adjusted R^2 values for the WR subregion moving response function were generally more stable than in the NRM subregion (Fig. 7b).

Discussion

Our study did not detect a unique long-term climatic limitation in the NRM trees compared to WR trees. In fact, the primary climatic limitations (precipitation) are similar to interior low- to mid-elevation Douglas-fir populations across its range (Watson and Luckman 2002, Griesbauer and Green 2010); cold temperatures do not appear to be a primary growth limitation at the species' northern limits. Similar results were reported for oak species (*Quercus* spp.) in eastern Canada (Tardif et al. 2006). However,

Fig. 5 MCFs between prior summer temperatures and subregional Douglas-fir growth. *Avg* average, *max* maximum, *min* minimum. Significant correlation coefficients ($P < 0.05$) are *shaded*



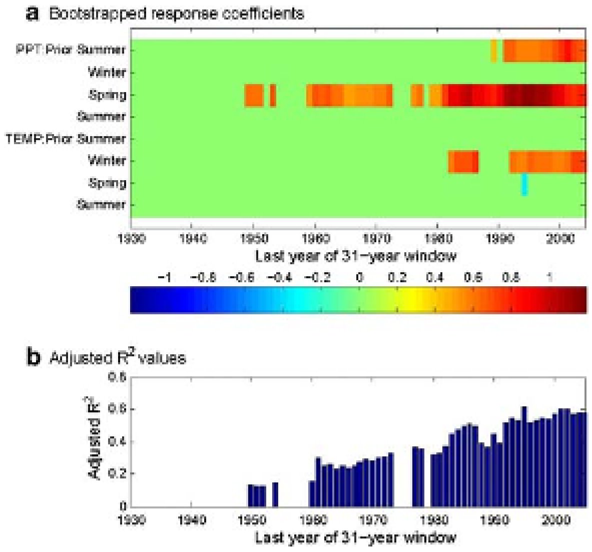


Fig. 6 Moving response functions between seasonal climate and NRM subregion Douglas-fir growth. All coefficients shown are significant ($P < 0.05$), based on bootstrapped confidence intervals. **a** The response coefficients, **b** the adjusted R^2 value for the same time period using the response coefficients to predict growth. Due to missing precipitation data in climate record, some time windows are less than 31 years. Also, 1993 data removed from moving response function. *PPT* precipitation, *TEMP* average temperature

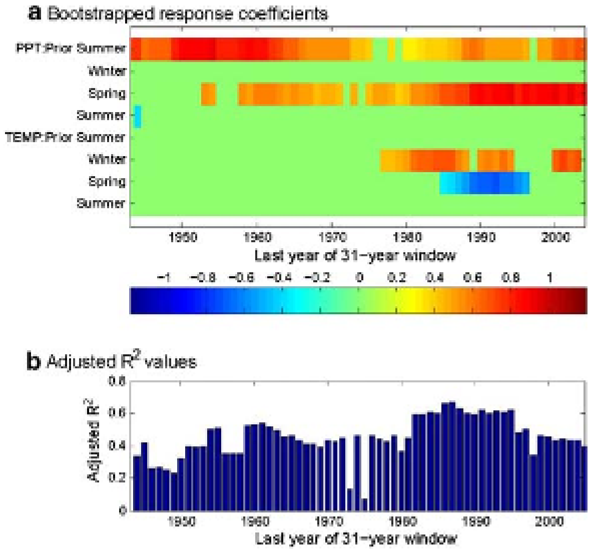


Fig. 7 Moving response functions between seasonal climate and WR subregion Douglas-fir growth. All coefficients shown are significant ($P < 0.05$), based on bootstrapped confidence intervals. **a** The response coefficients; **b** the adjusted R^2 value for the same time period using the response coefficients to predict growth. Due to missing precipitation data in climate record, some time windows are less than 31 years. *PPT* precipitation, *TEMP* average temperature

unique and strong Douglas-fir climate–growth relationships have been described in populations growing in forest-grassland and high-elevation ecotones (e.g., Case and Peterson 2005; Griesbauer and Green 2010). Jull (1999) has suggested that the northern limits of Douglas-fir range are not strictly climatic in nature, and from a mature tree perspective, our results appear to support this. Species' NRM limits could reflect complex interactions between climate and fecundity, habitat availability, competition (Sutton et al. 2002), mycorrhizal associations, or other ecological factors. Elucidating the primary controls on species' northern ranges will be important in projecting future species distributions under climate change scenarios (Sutton et al. 2002); current bioclimate models that assume spatially uniform responses to climate change are likely too simplistic (O'Neill et al. 2008). Tardif et al. (2006) suggest that models need to consider more biologically relevant climatic parameters instead of assuming positive responses to warming temperatures at species' northern limits.

Although NRM and WR Douglas-fir appear generally similar over a long period, we did detect differences by examining climate–growth relationships at shorter temporal scales. Most importantly, NRM Douglas-fir express greater apparent temporal instability in climate–growth relationships compared to WR populations, which has been noted in other species at higher latitudes (c.f. D'Arrigo et al. 2007). Changes in climate–growth relationships over sometimes relatively short periods (decades) may indicate that the climatic limitations to Douglas-fir growth at the NRM fluctuate over time. These sorts of results also suggest that the mechanisms by which climate controls species ranges can be complex in certain environments. Although our study was not designed to detect the mechanistic drivers of these fluctuations, we discuss possible reasons for these unique NRM climate–growth responses below. Regardless of the drivers, the implications of temporally unstable climate–growth relationships is that NRM populations may present greater challenges in predicting responses to environmental change relative to WR populations.

Do the different short-term growth responses highlighted in this study indicate that NRM and WR populations have different adaptive capacities with respect to climate change? Certain Douglas-fir traits such as height growth can vary sharply along temperature gradients at small (e.g., watershed) spatial scales (St. Clair et al. 2005), reflecting genetic adaptation to local selection pressures that can be especially strong at a species' margin (Aitken et al. 2008). The mean annual temperature in Fort St. James is significantly colder (by 1°C, based on 1961–1990 averages) than Prince George ($P = 0.0005$, Table 1). It seems likely the colder climate (and growing-season frost events; Jull 1999) at the NRM has historically selected for individuals with high cold tolerance, presumably at the expense of more competitive growth strategies (Loehle 1998; Green 2005). The recent increase in sensitivity to overall climate observed in NRM populations may indicate these populations are not as adapted to soil moisture deficits as WR populations (discussed below). On the other hand, climate–growth relationships and growth patterns in both subregions have converged in recent decades, which may suggest similar adaptive responses to common limiting factors. Projected sustained temperature increases in the region (Christensen et al. 2007; BC MoE 2007) may create conditions that approach the limits of adaptive plasticity of NRM and WR populations, in which case, there may be broad regional increases in sensitivity to climate. Below, we discuss some of the similarities and differences between NRM and WR populations in terms of growth responses to precipitation and temperatures, and also discuss the potential increase in climatic sensitivity in NRM populations.

Growth responses to precipitation

When examined over the full common time period (93 years), Douglas-fir productivity in both study subregions was primarily associated with annual, prior summer, and spring precipitation. Similar responses have been reported for Douglas-fir across its range in North America (e.g., Zhang and Hebda 2004; Littell et al. 2008; Griesbauer and Green 2010), possibly reflecting a strong growth dependence on available soil moisture during the growing season (Littell et al. 2008). Ample summer precipitation can increase carbohydrate allocation to the subsequent year's formative tissues (Kozlowski and Pallardy 1997). Early growing-season (spring) precipitation may be important to Douglas-fir growth as it tends to initiate photosynthetic activity promptly in response to favorable conditions (Watson and Luckman 2002). Winter precipitation may also be important to tree growth as snowmelt contributes early season soil moisture (Vaganov et al. 1999). Thus, annual (previous summer to current spring) precipitation can represent an especially important growth indicator as it reflects the integration of important seasonal precipitation limits (Littell 2006).

Contrary to expectations, NRM Douglas-fir populations had weaker long-term climate–growth relationships than did WR populations. However, this appears to be related to variable short-term growth responses embedded within the past century. For example, significant correlations between NRM growth and annual precipitation from the 1913–2005 analysis are likely due to two periods of significant relationship that occurred in the early and late decades of the twentieth century. In contrast, the WR Douglas-fir populations show consistently significant growth responses to annual precipitation over the full climate record.

Episodic multiannual to decadal climatic events can strongly influence tree processes (Gray et al. 2006). For example, Daniels and Veblen (2004) document contrasting climate–growth responses during different PDO phases (warm-dry vs. cool-wet) in *Nothofagus pumilio* populations in northern Patagonia. The significant positive correlations between NRM growth and annual precipitation during the

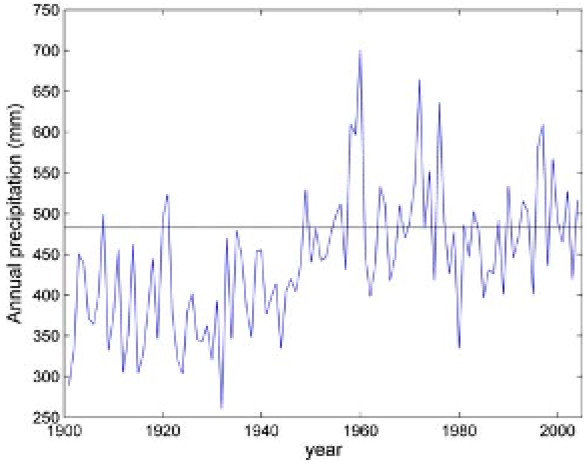


Fig. 8 Fort St. James annual precipitation from 1900 to 2005. *Horizontal line* represents 1961–1990 average

early decades of the twentieth century coincides approximately with a period of anomalously low precipitation values (relative to 1961–1990 normals) in the Fort St. James climate record (Fig. 8). This period of low precipitation may have been associated with a severe drought that has been documented over most of western North America during that time (Watson and Luckman 2004). Reductions in soil moisture resulting from this prolonged drought may have elicited strong growth responses to precipitation in NRM populations, but apparently similar responses were not elicited in WR populations.

After the mid-1940s, Fort St. James annual precipitation increased sharply for several decades (Fig. 8). Perhaps concurrently, NRM Douglas-fir growth became gradually less correlated with annual precipitation, with a period of insignificant ($P > 0.05$) correlations from 1940s to 1970s. Ample amounts of annual precipitation over this period in the cooler Fort St. James environment may have reduced soil moisture deficits, thereby reducing precipitation–growth responses. Although the Prince George annual precipitation data show a similar pattern of low annual precipitation in the early portion of the twentieth century (not shown), a temporally stable response to annual rainfall and precipitation suggests that growth continued to be limited by annual soil moisture balances even after the drought subsided. The significantly warmer temperatures in the Prince George area (Table 1) may increase soil moisture deficits and thus elicit a more stable precipitation–growth response.

Growth patterns in both study subregions show strong common patterns over the past century which have become increasingly correlated in recent decades. This suggests a synchronization of growth responses to common climatic forcing (Zhang and Hebda 2004), as suggested by the development of similar climate–growth relationships in both subregions. Increased NRM sensitivities to annual, prior summer, and spring precipitation over recent decades indicate that seasonal water supply limitations at the species' northern limits are becoming more acute, and perhaps more similar to WR environments. The driver behind this phenomenon may be a strong upward trend in temperatures over the last 50 years (Christensen et al. 2007). Although total precipitation in northern BC has increased over the twentieth century (BC MoE 2007), soil moisture reserves may be decreasing due to greater evapotranspiration at higher temperatures (BC MoE 2007; Pike et al. 2008). As temperature increases are projected to continue and even accelerate in this area (Christensen et al. 2007; BC MoE 2007), soil moisture deficits will likely become even more limiting to Douglas-fir productivity in the north (and across most of its range; Littell et al. 2008; Griesbauer and Green 2010).

We note that some of the fluctuations in NRM climate–growth responses correspond roughly with the two most recent Pacific Decadal Oscillation (PDO) phases. PDO represents a major mode of low-frequency climate variability in western North America as a result of North Pacific sea surface temperature anomalies (Mantua et al. 1997). The positive PDO phase typically bring anomalously warm and dry conditions to western North America, especially in winter (Mantua et al. 1997; Stahl et al. 2006) and spring (Minobe 2000; Cayan et al. 2001); the negative PDO phase has the opposite influence on local climate. However, PDO influences on local climate will be potentially confounded by other climate modes such as the El Niño/Southern Oscillation as well as anthropogenic climate change (Pike et al. 2008). Tree-rings can be correlated with PDO variability, including Douglas-fir at high elevations in coastal (Case and Peterson 2005) and interior (Griesbauer and Green 2010) environments. With respect to NRM Douglas-fir, the period of insignificant correlations with annual and prior summer precipitations appears to roughly correspond with the cool PDO phase lasting from 1947 to 1976 (Mantua et al. 1997). As well, NRM growth was positively correlated with prior summer temperatures roughly over this period. Over the recent warm PDO phase (1977 to at least the late 1990s, Mantua and Hare 2002), these growth responses changed; growth became significantly correlated with precipitation, and the response to prior summer temperatures reversed and became significantly negative. Although our study was not designed to detect changes in climate–growth relationships associated with PDO phases, these patterns represent an area for future research.

A gradual increase in growth sensitivity to spring conditions may be related in part to warming temperatures. Under climate change, warmer springs and/or earlier snowmelt may lead to an earlier start to the growing season in BC (MoE 2007). Douglas-fir may be initiating growth sooner in the year, a phenological change observed in many Northern Hemisphere plant ecosystems (Walther et al. 2002; Walther 2003; Parmesan 2006). As the growing window for Douglas-fir shifts toward an earlier date, the amount of radial growth in a season may become increasingly controlled by snowmelt and spring precipitation. Spring conditions would also become increasingly important if summer droughts effectively shorten the growing season.

Growth responses to temperatures

Growth expressed generally weaker responses to temperatures than to precipitation. In both subregions, winter temperatures appeared to have positively influenced growth in the latter half of the twentieth century. The positive influence of winter temperatures on the growth of other tree species at or near their NRM has been documented in previous studies (e.g., Pederson et al. 2004; Huang et al. 2009). As winters have warmed significantly across BC over the past century (BC MoE 2007), we would not have expected temperature correlations to strengthen if temperatures were the primary limitation. Warmer winter temperatures may be correlated with other limitations. For instance, lower snowpacks and earlier snowmelt under warming winter conditions (Vaganov et al. 1999) could have recently become more important growth influences, as previously discussed.

Links between Douglas-fir growth and prior summer conditions have been reported in previous studies (e.g., Littell et al. 2008). We found a negative long-term growth response to prior summer average temperatures in both subregions. However, the MCFs showed considerable instability in temperature–growth relationships over the past century seen most noticeably in NRM growth responses. In fact, depending on the period examined, growth responded either positively or negatively to prior summer average temperatures (as discussed previously, this may be related to different PDO phases). By also examining growth responses to average minimum and maximum temperatures, a clearer picture of temperature–growth responses emerged. The period of positive growth correlations with prior summer temperatures appears to be largely a result of positive responses to warmer minimum (nighttime) temperatures, whereas the period of negative growth correlations to prior summer temperatures appears to be more related to negative responses to maximum (daytime) temperatures. Examining growth responses to minimum, maximum, and mean temperatures may allow for a mechanistic interpretation of temperature–growth limitations, rather than simply using mean temperatures as a predictor of growth responses (Wilson and Luckman 2002).

Increasing climate sensitivity in marginal populations

The moving response function analyses for NRM Douglas-fir populations showed no complex seasonal temperature and precipitation growth responses prior to the middle of the twentieth century. Sometime after the middle of the century, however, NRM Douglas-fir sensitivity to seasonal climate (as measured by adjusted R^2 values and response coefficients) began an almost year-over-year increase, mostly in response to spring and prior summer precipitation as well as winter temperatures. MCFs also indicated that NRM growth became rapidly sensitive to annual rain amounts in recent decades. Although climate has changed by a roughly similar magnitude in both subregions (BC MoE 2007), NRM populations seem to show a stronger shift in responses than WR populations.

A lack of growth response to seasonal temperature and precipitation in the first half of the twentieth century does not necessarily mean that climate did not limit growth in NRM Douglas-fir over this time. Expressed population signal values above 0.85 over successive 31-year windows indicated a strong (presumably) climate signal in all NRM chronologies during this time (Wigley et al. 1984). These trees were likely responding to other climatic variables (such as annual precipitation) during the early portion of the twentieth century. It is also possible that NRM growth was limited by variables not captured by climate station data such as short-term growing-season frost events (Feliksek and Wilczynski 2003) or that these populations had non-linear or threshold responses to climate (Büntgen et al. 2006), which would not be detected with linear techniques such as regression and correlation analyses.

If increased growth sensitivity to local climate precedes stronger expressions of maladaptation or adaptational lag (Aitken et al. 2008), we may have detected early indications in NRM populations. This may have implications for the long-term health of mature Douglas-fir populations at their NRM, as climatically stressed trees may have lower tolerance to diseases, insect attacks, and drought events (Littell 2006). Further, maladapted NRM Douglas-fir may become less competitive than co-occurring species such as white spruce (*Picea glauca* [Moench] Voss) and lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), both of which are located well within their ranges in central BC.

Recent anecdotal evidence suggests that Douglas-fir abundance along its northern limits is declining, possibly due to Douglas-fir bark beetle infestations (DeLong 1999; Jull 1999; Kessler 1999). Ultimately, increased climate sensitivity and forest health factors may create a future retreat in the margins of mature Douglas-fir populations in central BC. Although Douglas-fir climatic habitat is expected to expand northward under climate change (Hamann and Wang 2006), it is important to recognize that mature in situ populations may not be genetically suited to new environmental conditions and unable to contribute progeny to successfully expand the range. Northward expansion of the species may depend on more drought-tolerant genotypes from within the range or facilitated migration management interventions, however, other adaptive traits, such as frost tolerance, may also be critical to the successful establishment of this species outside its range.

Conclusions

Our study demonstrates the importance of examining climate–growth relationships at the edge of a species' range and at various temporal scales in order to consider spatial and temporal complexities that may challenge assumptions underlying generalized species-level predictions of future responses to climate change. The species studied here demonstrates that not all tree species are primarily limited by cold temperatures at their NRM in the northern hemisphere. This finding further supports suggestions that future species and productivity estimates need to consider specific biological mechanisms (Aitken et al. 2008). Further, it is important to consider the short-term climate–growth responses that could be hidden within longer time frames, as they may be more accurate indications of climatic limitations. Douglas-fir growth responses over recent decades indicate that precipitation will continue to be a limiting factor across this area and may become more critical in the future with warming temperatures. Management of this species at its northern distributions will require thoughtful consideration of the link between genecology, growth, and soil moisture and how these parameters may change over time (Rogers 2006). Although too early to predict the future state of Douglas-fir at its NRM, our results suggest that it may become particularly sensitive to climate in this portion of its range. Long-term monitoring is recommended in forests where climate change may have relatively rapid and strong impacts.

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