Growth responses of three coexisting conifer species to climate across wide geographic and climate ranges in Yukon and British Columbia

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A R T I C L E   I N F O

A B S T R A C T

This work aimed to compare radial growth–climate relationships among three coexisting coniferous tree species across a wide geographic and climate range from southern British Columbia (BC) to central Yukon, Canada. Tree-ring data were collected from 20 mature stands of white spruce (*Picea glauca*), lodgepole pine (*Pinus contorta* var. *latifolia*), and subalpine fir (*Abies lasiocarpa*). Linear relationships between annual growth variation and monthly and seasonal climate were quantified with correlation and regression analyses, and variation in climate–growth responses over a climatic gradient were quantified by regressing growth responses against local mean climatic conditions. Temperatures had more consistent and stronger correlations with growth for all three species than precipitation, but growth–climate responses varied among species and among sites. In particular, pine and fir populations showed different responses between BC and Yukon, whereas spruce showed a more consistent response across the study domain. Results indicate that (1) the response and sensitivity of trees to seasonal climate variables vary among species and sites and (2) winter temperatures prior to growth may have significant impacts on pine and fir growth at some sites. The capacity to adapt to climate change will likely vary among the study species and across climatic gradients, which will have implications for the future management of mixed-species forests in Yukon and BC.

1. Introduction

Climate influences important physiological and phenological processes in trees (Kramer et al., 2000; Kozlowski, 2002; Walther, 2003). Climate change may alter these processes, leading to altered species distributions, forest compositions, resiliences, and productivities (Kramer et al., 2000; Hänninen et al., 2001; Bertrand and Castonguay, 2003). A better understanding of tree growth–climate relationships may help in predicting the potential impacts of climate change on forest ecosystems (Cook and Cole, 1991; Hamrick, 2004; Spittlehouse, 2005).

Tree-ring studies can describe long-term relationships between radial growth and climate (Fritts, 1976). A large body of tree-ring literature suggests that species often express unique radial growth responses to climate (e.g., Mäkinen et al., 2002; Pederson et al., 2004; Goldblum and Rigg, 2005), which may reflect tree species optimal growing conditions and distinct growth–climate mechanisms (May, 1974; Bazzaz, 1987; He et al., 2005). Tree species

climate responses can also vary with site conditions. For example, many northern conifers show clinal patterns in growth–climate relationships along environmental gradients, such as elevation (Splechtna et al., 2000), latitude (e.g., Hofgaard et al., 1999; Mäkinen et al., 2002) and moisture conditions (Linderholm, 2001). The nature of these relationships within and among coexisting species across wide geographic and climatic ranges remains unclear.

Lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.), white spruce (*Picea glauca* [Moench] Voss), and subalpine fir (*Abies lasiocarpa* [Hooker] Nuttall) frequently coexist across wide geographic and climatic ranges in western North America (Burns and Honkala, 1990). Lodgepole pine (hereafter referred to as 'pine') is a shade-intolerant, early-successional species that colonizes quickly after large disturbances (Burns and Honkala, 1990). White spruce (hereafter referred to as 'spruce') is an intermediate-shade-tolerant, mid-successional species, and subalpine fir (hereafter referred to as 'fir') is a shade-tolerant, late-successional species that increases in abundance and dominance through time in the absence of large disturbances (Burns and Honkala, 1990).

Specific study objectives were: (1) to identify and compare climate variables most strongly correlated with radial tree growth within and among coexisting pine, spruce and fir populations across wide geographic and climatic conditions, and (2) to

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characterize and compare growth patterns of study populations to common predictor climate variables across wide geographic and climate conditions for each species.

2. Methods

2.1. Study sites

We collected tree-ring data from 20 sample sites ranging from southern British Columbia (BC) to central Yukon, Canada (Fig. 1), and covering a wide range in mean annual temperatures (−4.0 to 4.3 °C) and precipitations (323–1342 mm) (Table 1). Mean annual temperature and precipitation data (1961–1990 climate normal period) were generated for each site using the ClimateBC model (Wang et al., 2006, see below for model description). Sample sites in BC ranged from 650 m above mean sea level to the elevational treeline at about 1800 m above mean sea level. Low- to mid-elevation stands (≤1400 m) in BC were typically dense, closed-canopy forests comprised of mixed deciduous-conifer stands with wet/cool to dry/warm climates, whereas higher-elevation stands (>1400 m) were typically less dense, open-canopy forests comprised of conifer-dominated stands with a cold and snowy climate. Sample sites in central and southern Yukon ranged from 520 m above mean sea level to the elevational treeline at 1300 m above mean sea level. All sample sites in Yukon were conifer-dominated and characterized by subarctic climates with very cold and long winters, short warm summers, and relatively low precipitation.

Mature (older than 60 years), naturally regenerated stands were targeted for study sampling. To minimize non-climatic influences on tree radial growth, healthy stands with minimal evidence of disturbance and edaphic limitations were selected. Stands with all three study species co-occurring were not available at all study locations. In these cases, individual species were sampled as close to each other as possible. At the time of study, many lodgepole pine stands in central BC were infested with mountain pine beetle (*Dendroctonus ponderosae*), however, we were able to locate and sample unattacked stands.

2.2. Sampling and chronology development

To minimize non-climatic variation in ring-widths for sample trees, healthy, dominant trees with little observable damage were selected for coring. A single increment core per tree was extracted parallel to the slope at approximately breast height (∼1.3 m) from a minimum of 20 trees per species per sampling-site during summers of 2005 and 2006. Standard dendrochronology techniques were used to develop annual growth chronologies (Fritts, 1976). Cores were mounted and sanded to improve annual-ring contrast. Within each population (i.e., study site and species), cores were visually crossdated to identify the precise year of ring formation and to detect missing or false rings (Yamaguchi, 1991). Ring-widths were measured using the Velmex ring-measurement system (Velmex Inc, 1992) interfaced with MeasureJ2X (VoorTech Consulting, 2004). The computer program COFECHA (Grissino-Mayer, 2001) was used to statistically validate visual crossdating. Cores that did not crossdate (based on a critical threshold intercorrelation value of 0.36 based on 40-year segment with 20-year lag) were re-examined under microscope and remeasured using MeasureJ2X. Any cores that did not crossdate after re-examination were removed from the final chronology development.

Dimensionless ring-width chronologies were developed for each species at each sample site using the ARSTAN software (Cook and Holmes, 1986). Growth trends and low-frequency variation possibly associated with non-climatic factors were removed from each tree time series by fitting a cubic smoothing spline with a 50% frequency response cutoff of either 20 or 40 years. Different spline lengths were applied in order to maximize common signals from forests with different stand histories and characteristics (c.f. Szeicz, 1997). A preliminary visual assessment of growth series indicated that the 40-year smoothing spline reduced unwanted low-frequency
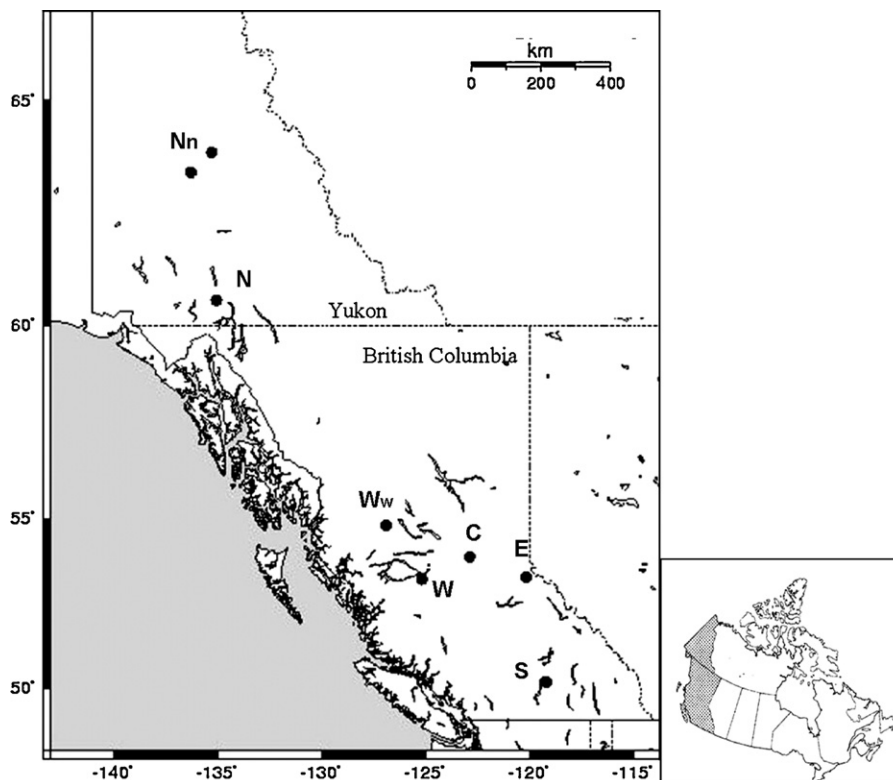

Fig. 1. Study locations in Yukon and British Columbia, Canada. Site codes were assigned based on relative cardinal direction from Prince George (Central).

Table 1
Site descriptions.

Site	Species	Elevation (m asl)	Latitude (N)	Longitude (W)	MAT (°C)	MAP (mm)	Aspect	Site codes
British Columbia								
Vernon								
Silver Star	Pl	1000	50°19′	119°08′	4.3	749	S	S
King Eddy	Sw	1165	50°10′	119°11′	4.5	643	SE	S
King Eddy	Bl	1200	50°10′	119°11′	4.0	749	SE	S
Prince George								
Cranbrook Hill	Pl/Sw/Bl	750	53°55′	122°53′	3.5	585	Flat	C1
Domano Blvd.	Pl/Sw	650	53°48′	122°44′	4.0	577	Flat	C2
McBride								
McBride Peak	Pl/Sw/Bl	1200	53°19′	120°09′	2.2	1031	SW	E1
McBride Peak	Pl/Sw/Bl	1400	53°19′	120°08′	1.6	1137	SW	E2
McBride Peak	Pl/Sw/Bl	1600	53°19′	120°07′	1.0	1241	SW	E3
McBride Peak[a]	Pl/Sw/Bl	1800	53°20′	120°07′	0.4	1342	SW	E4[a]
Smithers								
Onion Mnt.[a]	Pl/Sw/Bl	1550	54°48′	126°52′	0.2	669	SW	Ww1[a]
Onion Mnt.	Sw/Bl	1360	54°48′	126°53′	0.9	642	SW	Ww2
Hudson Bay Mnt.	Pl	1400	54°45′	127°15′	0.4	749	S	Ww2
South of Fraser Lake								
Top Lake[a]	Pl/Sw/Bl	1640	53°16′	125°10′	0.2	712	SW	W[a]
Yukon								
Whitehorse								
Wolf Creek	Pl/Sw/Bl	950	60°35′	135°03′	−1.5	368	SW	N1
Grey Mountain	Pl/Sw/Bl	1150	60°39′	134°53′	−2.0	374	E	N2
Grey Mountain	Pl	820	60°41′	134°58′	−1.3	341	E	N3
Grey Mountain	Sw	845	60°41′	134°57′	−1.2	346	E	N3
Mayo, Keno								
Mayo	Sw	520	63°37′	135°53′	−3.7	324	SW	Nn
Mayo	Pl	510	63°29′	136°16′	−3.9	364	Flat	Nn
Keno Hill	Bl	1300	63°55′	135°15′	−4.0	530	S	Nn

asl: above mean sea level; MAT: mean annual temperatures (1961–1990); MAP: mean annual precipitation (1961–1990); Pl: lodgepolepine; Sw: white spruce; Bl: subalpine fir.
[a] Altitudinal treeline site.

variation while maintaining strong common signals for most populations. A 20-year smoothing spline was used for dense, closed-canopy stands at lower elevations in order to minimize noise from possible stand dynamics.

Autoregressive modeling was used to produce chronologies with a strong climatic signal (Cook and Holmes, 1986). Residuals from autoregressive modeling of the detrended series were averaged together to form a residual chronology. The pooled autoregression model was then reincorporated into the residual chronology to form the ARSTAN chronology, which was used for growth–climate analyses.

Chronology statistics were computed using the ARSTAN software (Cook and Holmes, 1986). Mean interseries correlation measures the average series correlation with the master chronology and provides an indication of the common population growth signal. First-order autocorrelation measures persistence in the final chronology and indicates the presence of low-frequency variation. Mean sensitivity and standard deviation were calculated to characterize growth variation (Fritts, 1976; Villalba et al., 1994). Mean sensitivity is calculated as the mean absolute difference between adjacent ring-widths divided by the mean of the two ring-widths (Cook and Kairiukstis, 1990), and previous studies suggest that a mean sensitivity above 0.09 is sufficient for growth–climate analysis (Villalba et al., 1994; Ettl and Peterson, 1995).

2.3. Climate data

Site-specific historical climate data were generated using ClimateBC version 3.2 (Wang et al., 2006). ClimateBC combines bi-linear interpolation and elevation adjustment techniques to downscale gridded climate data from the PRISM model (Daly et al., 2002) and historical climate series (Mitchell and Jones, 2005) to produce scale-free spatial climate time series and normals covering western Canada, based on user-provided latitude, longitude, and elevation inputs. Model outputs include monthly temperature and precipitation variables, as well as annual derived variables such as frost-free period, continentality, growing-degree days, and heat-moisture index.

2.4. Growth–climate relationship analyses

2.4.1. Correlation analysis

Relationships between site-specific climate data and tree growth from 1953 to 2002 (50 years) were quantified using Pearson simple correlation coefficients, computed using Matlab 2007b (The Mathworks Inc, 2007). The 1953–2002 period was chosen due to the reliability of the climate records and the increased number of climate stations in North America after 1950 (Wang et al., 2006). We selected monthly climate variables for 17 months extending from May of the previous growth year to September of the current growth year, as climate conditions prior to the growing season can influence growth (Fritts, 1976; Larsen and MacDonald, 1995; Brooks et al., 1998). Monthly average temperatures and total precipitation were used as independent variables in the correlation analyses.

2.4.2. Gradient analysis

Within- and between-species climate–growth relationships were examined along a climatic gradient across all sites, which was done in two steps. First, based on correlation analysis results, primary climatic variables explaining growth variation for the three species were identified (i.e., mean growing season and mean winter temperatures). Mean growing season temperatures were derived by averaging consecutive months between May and July

that showed a consistent pattern of significant correlations with species growth variation. For spruce, mean temperatures from June and July were used to derive mean growing season temperatures. Pine mean growing season temperatures were derived from July and August (BC) and June (Yukon) temperature averages. Fir mean growing season temperatures were derived from May and June temperature averages. Mean winter temperatures for all three species were derived by averaging mean monthly temperatures from October to March prior to the growing season.

In the second step of this analysis, linear regression coefficients were calculated between standardized annual ring-widths of the chronologies and their corresponding site-specific mean growing season and mean winter temperatures for the period 1953–2002. Regression slope coefficients (b_1), representing growth response to climate, were then regressed against site-specific climate normals (1961–1990 period) such as annual and summer temperature and precipitation, also produced by the ClimateBC model. In this way, it was possible to determine if a site's climatic conditions could predict growth sensitivity (represented by the regression coefficient) to local climate variability.

Where b_1 was nonsignificant (i.e., $P > 0.05$), we used the coefficient value rather than transforming it to zero prior to analysis. This was done for two reasons: (a) using the original coefficients would the best way to represent how growth responses vary over the full climatic gradient (e.g., linear or nonlinear, which could be lost by transforming nonsignificant coefficients to zero before analysis), and (b) a preliminary data analysis revealed that in all cases, transforming the nonsignificant coefficients to zero did not significantly change the slope or R^2 value in the climatic gradient analysis.

3. Results

3.1. Chronology statistics

All 40 ring-width chronologies had average series intercorrelations greater than 0.5, indicating strong common signals (Table 2). Most chronologies had significant first-order autocorrelations, indicating the presence of low-frequency variation. Average mean sensitivities were 0.16 ± 0.03, 0.14 ± 0.04 and 0.12 ± 0.02 for pine, spruce and fir, respectively. Standard deviations were 0.77 ± 0.25, 0.58 ± 0.22 and 0.57 ± 0.18 for pine, spruce and fir, respectively.

3.2. Correlation analysis

Ring-width chronologies generally had stronger correlations with mean monthly temperatures than with monthly precipitations (Tables 3 and 4). Consequently, study results and interpretation focus on growth–temperature relationships to assess intra- and inter-species differences in regards to common climate variables. Significant correlations between monthly

Table 2
Summary characteristics of the ARSTAN chronology of each population.

Species	Site	Site code	No. trees	Start–end	Mean no. years	Mean sensitivity	Standard deviation	Series intercorrelation	AC(1)	Spline
Pine	Silver Star	S	23	1917–2005	79.1	0.150	0.168	0.614	0.318	20
	Cranbrook Hill	C1	16	1901–2004	82.3	0.131	0.120	0.533	0.338	40
	Domano Blvd.	C2	20	1904–2004	76.3	0.133	0.149	0.581	0.251	20
	McBride Peak 1200 m	E1	20	1901–2004	89.6	0.123	0.121	0.556	0.149	20
	McBride Peak 1400 m	E2	21	1928–2004	69.5	0.142	0.111	0.562	−0.244	20
	McBride Peak 1600 m	E3	20	1911–2004	79.3	0.131	0.121	0.552	–	40
	McBride Peak 1800 m	E4	20	1904–2004	79.6	0.163	0.194	0.615	0.349	40
	Onion Mountain 1550 m	Ww1	16	1899–2005	84	0.201	0.226	0.635	0.174	40
	Hudson Bay Mnt.	Ww2	20	1858–2005	94.9	0.157	0.151	0.588	0.143	40
	Top Lake	W	18	1870–2005	86.6	0.241	0.256	0.685	0.254	40
	Wolf Creek	N1	15	1937–2004	63.3	0.160	0.177	0.693	0.407	40
	Grey Mountain 1150 m	N2	13	1919–2004	65.7	0.157	0.152	0.595	0.173	40
	Grey Mountain 820 m	N3	20	1887–2004	109.7	0.140	0.165	0.674	0.453	40
	Mayo	Nn	14	1905–2004	61.7	0.176	0.183	0.596	0.333	40
Spruce	King Eddy	S	21	1876–2005	107.1	0.146	0.154	0.664	0.332	20
	Cranbrook Hill	C1	18	1868–2004	85.2	0.107	0.121	0.525	0.289	40
	Domano Blvd.	C2	22	1912–2004	71.2	0.133	0.136	0.613	0.224	20
	McBride Peak 1200 m	E1	17	1910–2004	79.1	0.099	0.098	0.590	0.212	20
	McBride Peak 1400 m	E2	12	1927–2004	69.1	0.083	0.094	0.547	0.368	40
	McBride Peak 1600 m	E3	22	1920–2004	74.6	0.106	0.107	0.539	0.252	40
	McBride Peak 1800 m	E4	23	1920–2004	73	0.104	0.099	0.547	0.191	40
	Onion Mountain 1550 m	Ww1	17	1907–2005	81.4	0.151	0.152	0.582	0.182	40
	Onion Mountain 1360 m	Ww2	18	1810–2005	154	0.142	0.147	0.640	0.123	40
	Top Lake	W	22	1843–2005	96.9	0.160	0.160	0.634	0.147	40
	Wolf Creek	N1	14	1919–2004	72.5	0.130	0.137	0.691	0.328	40
	Grey Mountain 1150 m	N2	24	1888–2004	88.3	0.147	0.132	0.671	–	40
	Grey Mountain 845 m	N3	15	1795–2004	114.6	0.186	0.206	0.754	0.285	40
	Mayo	Nn	21	1895–2004	107.4	0.233	0.270	0.786	0.365	40
Fir	King Eddy	S	18	1880–2005	99.5	0.119	0.115	0.573	0.181	20
	Cranbrook Hill	C1	20	1882–2004	82.6	0.117	0.138	0.596	0.365	40
	McBride Peak 1200 m	E1	20	1914–2004	68.6	0.129	0.135	0.558	0.339	40
	McBride Peak 1400 m	E2	20	1927–2004	65.6	0.112	0.101	0.610	–	40
	McBride Peak 1600 m	E3	25	1920–2004	74.7	0.090	0.096	0.593	–	40
	McBride Peak 1800 m	E4	18	1923–2004	72.8	0.106	0.108	0.597	–	40
	Onion Mountain 1550 m	Ww1	17	1870–2005	82.6	0.175	0.168	0.673	0.207	40
	Onion Mountain 1360 m	Ww2	15	1811–2005	138.8	0.102	0.115	0.577	0.210	40
	Top Lake	W	20	1888–2005	90.7	0.144	0.170	0.666	0.182	40
	Wolf Creek	N1	19	1928–2004	66.9	0.123	0.128	0.668	0.343	40
	Grey Mountain 1150 m	N2	14	1926–2004	69.5	0.116	0.140	0.658	0.453	40
	Keno Hill	Nn	40	1890–2004	81.8	0.136	0.136	0.627	0.248	40

AC(1): first-order autocorrelation.

temperatures and ring-width chronologies varied among the three species (Table 3).

3.2.1. White spruce

Eleven of the 14 spruce populations had significant correlations between growth and June and/or July mean temperatures during the growing seasons (Table 3). Spruce populations at low-elevation and warmer sites in BC (S, C1, C2, E1, E2—see Fig. 1) and northern most sites in Yukon (Nn) showed either negative or no growth correlations with June mean temperatures of the current growth years, whereas growth in high-elevation and western populations in BC (E3, E4, W, Ww) and two Yukon populations (N1, N2) was positively correlated with June and July mean temperatures during the growing seasons.

Table 3

Significant correlation coefficients computed between annual growth and mean monthly temperatures from May of the previous growth year to September of the current growth year for the period 1953–2002.

Site[a]	Previous year								Current year								
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
A) Spruce																	
S	−				−												
C1	−												−				
C2													−				
E1	−	−															
E2													−				
E3						−								+	+		
E4			−											+	+		
W														+	+		
Ww1							+						+	+	+		
Ww2				+									+	+	+		
N1								−	−					+	+		
N2	−								−					+	+		
N3										+							
Nn	−	−	−											−	−		
Total	5	3	2	1	1	1			2	2			4	11	7		
B) Pine																	
C1							+			+						−	
C2							+		+	+	+						
E1							+		+	+	+			+	+		
E2				−	+		+			+	+			+	+		
E3				−			+		+	+	+				+		
E4			−	−		+	+		+	+							
W		−				+	+		+		+			+	+		
Ww1		+					+		+	+	+			+		−	
Ww2	+	+	+			+	+		+		+			+		−	
N1				−										−			
N2		−	−	−										−			
N3			−	−										−			
Nn			−											−	+		
Total	1	3	4	6	2	5	8	1	7	7	7		4	5	5	3	
C) Fir																	
S			−										−		+		
C1													−	−			
E1		−	−			+							−	−			
E2		−	−		+									−			
E3		−											−				
E4		−		+	+	+	+										
W					+	+	+	+		+					+		
Ww1	+	+	+		+	+	+	+	+	+			+	+		−	
Ww2						+	+		+	+		−		+			
N1		−	−														
N2		−	−										−				
													−	+			
Total	1	2	5	4	2	5	5	3	3	1	2	1	4	5	5	1	1

Note: (■) $P < 0.001$; (▨) $P < 0.01$; (▢) $P < 0.05$. +/− denote direction of relationship (positive/negative).
[a] See Table 1 for site codes.

Table 4
Significant correlation coefficients computed between annual growth and mean monthly precipitation from May of the previous growth year to September of the current growth year for the period 1953–2002.

Site[a]	Previous year								Current year								
	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S
A) Spruce																	
S			+		+											−	
C1													+			+	
C2													+				
E1			+	+													
E2			+				−										
E3												−					
E4						−						−					
W	+			+										−	−		
Ww1	+			+									−	−	−		
Ww2	+												−	−	−		
N1							+				+						
N2					+		+					+					
N3					+		+	+		+		+					
Nn	−	+	+	+		+			+			+		+	+		
Total	4	1	4	4	3	2	4	1	1	1	1	5	4	4	4	2	
B) Pine																	
S																+	
C1						−		−			+						
C2				+				−			+						
E1			+	+	+	+											
E2			+	+		+						+		+			
E3				+		+						+					
E4	+		+	+		+						+					
W						−				−	+	+		+			
Ww1			+									+					
Ww2			+									+					
N1													+				
N2													+			+	
N3				+												+	
Nn			+	+									+				
Total	1		6	7	1	6		2		1	3	6	3	2		3	
C) Fir																	
S			+						−								
C1													+				
E1				+		−							+			+	
E2			+			−	+										
E3												+					
E4	−		+			−											
W				+							−	+	+				
Ww1			+								−			−			
Ww2			+											−	−		
N1			+														+
N2								+				+					+
Nn																	
Total	1		6	2		3	1	1	1		2	3	3	2	1	1	2

Note: (■) $P < 0.001$; (▨) $P < 0.01$; (▧) $P < 0.05$. +/− denote direction of relationship (positive/negative).
[a]See Table 1 for site codes.

3.2.2. Lodgepole pine

Monthly temperature variables that were correlated with pine ring-width chronologies varied among sites, most notably between BC and Yukon. Growth in BC populations except for the southernmost site (S) was predominantly positively correlated with mean temperatures from October to March prior to growth (Table 3). Seven of the 10 BC populations also showed positive growth correlations with July and August mean temperatures during the growing season. Conversely, growth in Yukon populations was negatively correlated with both mean June temperatures during the growing season and summer mean temperatures during the previous growth year.

3.2.3. Subalpine fir

Monthly temperature variables correlated with fir growth varied considerably among sample sites (Table 3). Within BC,
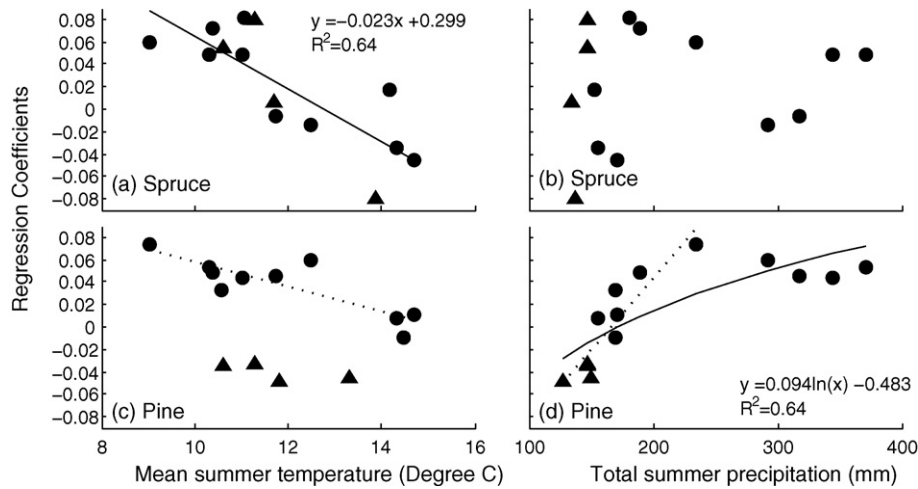
Fig. 2. Growth responses (regression coefficients) of white spruce to the current growing season temperatures (June -July) along a) summer temperature and c) precipitation gradients. Figure parts b) and d) show the growth responses of lodgepole pine to the current growing season temperatures (June for Yukon populations, July -August for BC populations) along summer temperature and precipitation gradients, respectively. The following symbols (● and ▲) represent BC and Yukon chronologies, respectively. Solid lines represent the broad trends across the sample sites ($P < 0.05$). The dotted lines represent (c) the regional trend in BC ($y = -0.011x + 0.168$, $R^2 = 0.73$), and (d) the trend across the sites below a precipitation threshold of 250 mm ($y = 0.0013x - 0.212$, $R^2 = 0.82$). Site summer temperature and precipitation were the 1961–1990 normal.

growth in high-elevation and western populations (E4, W, Ww) was positively correlated with mean temperatures from October to March prior to growth. Western BC fir populations (W, Ww) had positive growth correlations with mean July temperatures during the growing seasons, while growth in low- to mid-elevation populations in BC (E1-3, C1, S) was negatively correlated with May and/or June mean temperatures during the growing seasons and July and/or August mean temperatures during the previous growth years. Growth in Yukon populations was negatively correlated with mean temperatures during the previous or current growing seasons.

3.3. Gradient analysis—growing season temperatures

3.3.1. White spruce

Regression coefficients (b_1) calculated between spruce growth and mean growing season temperatures decreased linearly with sampling-site mean summer temperature ($P < 0.0004$, Fig. 2a). Additionally, regression coefficients switched from positive to negative at a sampling-site mean summer temperature of about 12.4 °C. Regression coefficients were not significantly related to sampling-site total summer precipitation ($P = 0.51$, Fig. 2b).

3.3.2. Lodgepole pine

Across the entire study region (i.e., BC and Yukon), no significant correlation was found between the regression coefficients (b_1 for radial growth-growing season temperature) and sampling-site mean summer temperatures (Fig. 2c, $P = 0.09$). Among BC populations, regression coefficients decreased with sampling-site mean summer temperatures ($P = 0.02$) (Fig. 2c). All Yukon populations had negative regression coefficients (though not related to sampling-site mean summer temperatures). Across all populations, regression coefficients were positively and non-linearly related to sampling-site total summer precipitation ($P < 0.0004$, Fig. 2d). The regression coefficients increased linearly with sampling-site summer precipitation up to about 250 mm ($P < 0.0004$), after which no further increases were observed. The threshold precipitation (x-intercept) where significant relationships changed from negative to positive was about 167 mm.

3.3.3. Subalpine fir

Although eight of the 12 fir ring-width chronologies were significantly correlated with mean growing season temperatures

(either positively to July or negatively to May–June, Table 3), the regression coefficients (b_1) were not correlated with sampling-site mean summer temperatures ($P = 0.07$, not shown), sampling-site total summer precipitation ($P = 0.80$, not shown), or any other climate normals (not shown).

3.4. Gradient analysis—winter temperatures

Spruce growth was generally not correlated with winter temperatures (Table 3), therefore no gradient analysis was computed for this climate variable in spruce populations. Among BC populations, nine of the 10 pine and five of the nine fir ring-width chronologies had positive correlations with October–March mean temperatures prior to growth (Table 3), whereas pine and fir growth in Yukon populations was not significantly correlated with winter temperatures. Among BC populations, regression coefficients (b_1) computed between radial growth
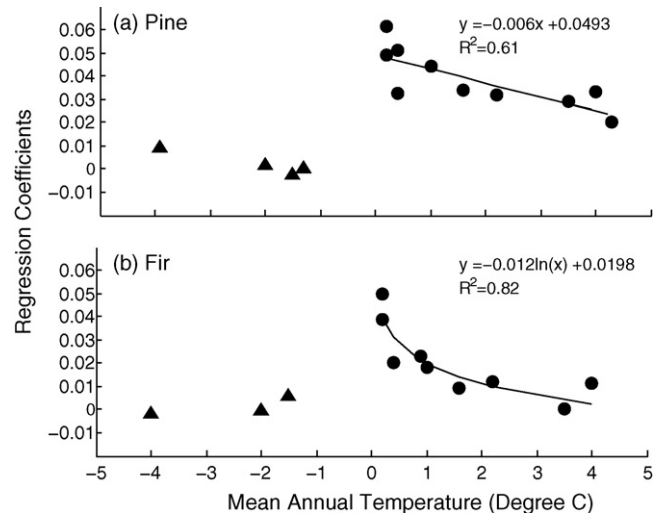

Fig. 3. Growth responses (regression coefficients) of lodgepole pine (a) and subalpine fir (b) to October–March temperatures prior to growth along the mean annual temperature (°C) gradient. The following symbols (● and ▲) represent BC and Yukon chronologies, respectively. Linear and natural logarithmic regressions were only applied for BC sites. The mean annual temperature of each site was the 1961–1990 normal.

and winter temperatures decreased linearly with sampling-site mean annual temperatures for pine ($P < 0.0004$, Fig. 3a) and fir ($P = 0.009$, Fig. 3b). There was no significant relationship between regression coefficients across the entire study region or among Yukon populations. Regression coefficients were not related to sampling-site mean annual precipitation (not shown).

4. Discussion

Our findings suggest that (1) growth response to growing season temperatures varies among study species and sites across the wide geographic and climate ranges sampled in British Columbia and Yukon, and (2) winter temperatures prior to active growth may be important in assessing the potential impacts of climate change on pine and fir growth. Our results concur with other studies that have suggested species responses to climate are not uniform over space (e.g., Mäkinen et al., 2002) and also indicate how these responses can vary over a gradient of local climatic conditions. Our study approach was made possible by the recent development of spatiotemporal climate models that now allow for species responses to be analyzed along pre-defined climatic gradients (Peterson and Peterson, 2001). As forest managers prepare for climate change, this information can provide important guidance in developing local and landscape strategies for managing complex forests. Our results support suggestions that effective adaptation of forest management to climate change will require site-specific solutions; large-scale measures that assume uniform species responses over space may be overly simplistic (Millar et al., 2007; O'Neill et al., 2008).

4.1. Species growth responses to growing season temperatures

The three study species showed different patterns in growth responses to growing season temperatures across the sample sites in BC and Yukon. Study findings suggest that white spruce growth is broadly influenced by summer temperatures (i.e., across all sites), with unique growth responses between warmer sites and cooler sites. Warm June–July temperatures may enhance tree radial growth on cooler sites for several possible reasons. Warmer mean growing season temperatures may enhance photosynthesis and carbohydrate allocation to the stem (Körner, 1998), may reflect the associated result of increased sunshine and correspondingly higher photosynthesis activity (Goldblum and Rigg, 2005), and may be correlated with a longer growing season (Danby and Hik, 2007). Savva et al. (2006) found that the positive correlation coefficients between the radial growth of Norway spruce (Picea abies [Linnaeus] Karsten) and June–July temperatures increased linearly with elevation. They suggested that warm summer temperatures could favour the growth of populations at high-elevation sites, where the growing season is generally short. St George and Luckman (2001) and Wilson and Luckman (2003) reported similar results for high-elevation Engelmann spruce in BC.

For spruce on warm sites, warm temperatures during the growing season may induce moisture stress and decrease growth (Barber et al., 2000; D'Arrigo et al., 2004, 2005; Wilmking et al., 2004). Warm temperatures often increase evapotranspiration from soils and plant tissues (Brooks et al., 1991), inducing stomatal closure and decreased net photosynthesis to minimize water losses in response to increasing moisture stress (Kozlowski, 2002). Barber et al. (2000) reported that the ring-width chronologies of low-elevation white spruce were negatively correlated with summer temperatures in the semi-arid interior of Alaska, where evapotranspiration potentially equals annual precipitation. The negative relationship was associated with reduced CO_2 uptake and higher water loss during photosynthesis.

In contrast with spruce, average site precipitation (based on the 1961–1990 climate normals) may be more important than temperature in predicting growth sensitivities of lodgepole pine to growing season temperatures. Total summer precipitation at all Yukon sites was less than 150 mm, thus, warm temperatures at those sites might have induced moisture stress on tree radial growth as suggested for spruce (Barber et al., 2000; D'Arrigo et al., 2004, 2005; Wilmking et al., 2004). Among BC populations, temperature-induced moisture stress was less likely for lodgepole pine because they occurred at sites receiving more than 155 mm of precipitation per summer (in most cases considerably more), and they had positive correlations with growing season temperatures. Distinct BC-Yukon growth–climate relationships in pine may also reflect intra-specific genetic differentiation, establishing unique biogeographical trends. Wheeler and Guries (1982) suggested the existence of two distinct lodgepole pine subgroups in western Canada, associated with populations originating from different ice-free refugia (central Yukon and southwestern United States) after the last ice age. This suggestion was supported by Xie and Ying (1995), who found that lodgepole pine populations north and south of approximately 57°N showed disparate growth traits.

In subalpine fir, findings from this study and previous studies suggest that the growth–climate relationships may be spatially variable in response to local site conditions (Villalba et al., 1994; Peterson et al., 2002) and elevation (Splechtna et al., 2000). For example, Peterson et al. (2002) reported that the growth responses of subalpine fir varied between wet and cool versus dry and warm sites within a 370-km sample region in western Oregon and Washington. Our findings supported other studies that found low-elevation subalpine fir populations were negatively correlated with spring temperatures while high-elevation populations were positively correlated with summer temperatures in the southern and central interior of BC (Splechtna et al., 2000) and in the Pacific Northwest United States (Ettl and Peterson, 1995; Peterson et al., 2002), however, our findings also showed that these relationships did not vary linearly over a climatic gradient, as was found in spruce populations.

Other studies have suggested that white spruce and subalpine fir might exhibit similar growth responses to climate because they often co-dominate cool and wet habitats and show more shade-tolerance and late-successional positions than lodgepole pine (Burns and Honkala, 1990; Green, 2005, 2007). However, in this study, the growth–climate responses of white spruce differed considerably from subalpine fir. Different growth–climate relationships between mature spruce and fir may be related to the biogeography, genecology, and evolutionary histories of each species. Previous studies have suggested that subalpine fir persisted during the last glacial period in refugia in the Pacific Northwest US (Ettl and Peterson, 2001) and migrated into the Yukon via British Columbia (Spear and Cwynar, 1997). White spruce, on the other hand, existed during the last glacial period in refugia in Yukon and Alaska (Cwynar and Spear, 1991). Consequently, the unique growth–climate relationships between these two species in this study could reflect the adaptive result of different selection pressures during their migrations into the current ranges in BC and Yukon from different routes, which may have made white spruce better suited to cold continental climates than subalpine fir (Cwynar and Spear, 1991).

4.2. Lodgepole pine and subalpine fir growth responses to winter temperatures

Findings from this study suggest that temperatures prior to the growing season may influence the radial growth of lodgepole pine and subalpine fir in BC. Previous studies have suggested that a prolonged growing season, associated with early snowmelt and

late snowfall, could explain the positive effects of warm winter temperatures on tree radial growth at colder sites (Graumlich and Brubaker, 1986; Splechtna et al., 2000; Peterson and Peterson, 2001; Kirdyanov et al., 2003; Pederson et al., 2004; Pfeifer et al., 2005). Peterson and Peterson (2001) and Peterson et al. (2002) suggested that the timing of snowmelt in the spring could determine the date of growth initiation of subalpine fir at high-elevations. Several studies showed that snowpack in early spring (April–May) was negatively correlated with the radial growth of subalpine fir (Peterson and Peterson, 1994; Peterson et al., 2002; Larocque and Smith, 2005) and lodgepole pine (Case and Peterson, 2007) at high-elevations in other regions of western North America.

Additionally, preconditioning of warm early winter temperatures may be associated with increased tree growth in the following growing season (Lebourgeois, 2000). Carbohydrates produced during warm fall conditions can increase storage of reserves in plant tissues (i.e., roots, twigs, old leaves), which can be expressed in enhanced stem growth in the following spring (Kramer and Kozlowski, 1979; Pfeifer et al., 2005). Previous studies, for example, showed that previous fall temperatures were positively correlated with the radial growth of Jack pine (*Pinus banksiana* [Lamb.]) in western Quebec (Hofgaard et al., 1999) and stone pine (*Pinus cembra* L.) in the central and southern European Alps (Oberhuber, 2004; Pfeifer et al., 2005; Carrer et al., 2007).

The potential negative impacts of high snowfall on tree growth (Peterson and Peterson, 2001; Larocque and Smith, 2005) were unclear in this study, and our data did not show significant relationships between winter precipitation and the ring-width chronologies of lodgepole pine or subalpine fir. However, Knowles et al. (2006) showed that reduced snowfall in the western United States in the past 55 years was unrelated to changes in the total precipitation. Holding precipitation constant, warm winter temperatures decrease the percentage of precipitation that falls as snow and increases dense, wet snow that is close to melting point (MWLAP, 2002; Wang et al., 2006). Therefore, variation in temperature may impact snow accumulation during winter and consequently the timing of snowmelt in spring (Knowles et al., 2006). Actual snow data may help in examining the potential influences of snow on tree radial growth.

4.3. Conclusions

Effective forest management responses to climate change will rely on a better understanding of biological responses among coexisting tree species across wide climatic and geographic conditions (Littell et al., 2008; Aitken et al., 2008; O'Neill et al., 2008). Different growth responses to seasonal climate among coexisting species in this study suggest that in a given environment, future climate change may differentially alter the fitness and competitive interactions of coexisting *in situ* species, presumably altering the biogeography of mixed-species forests. For example, findings from this study suggest that on cooler sites in both BC and Yukon, higher growing season temperatures may increase spruce growth, whereas on warmer sites, spruce growth may be negatively affected. The response of pine to increased growing season temperatures across BC and Yukon appears to be more inter-connected to moisture availability; pine growth responses to warmer temperatures may be negative on drier sites, and positive on wetter sites. As well, future warmer winter temperatures may increase pine and subalpine fir growth in BC, particularly on cooler sites (for example, at higher elevations). Such species-specific trends will likely translate into high spatial variability in future changes in interactions among coexisting tree species in a changing climate. In the long term, changes in growth–climate relationships among coexisting tree species could be eventually

expressed through shifts in forest composition and species distributions across multiple spatial and temporal scales, as growth is often a good predictor of species resilience, health, competitiveness, and survival (Stohlgren and Bachand, 1997; Zolbrod and Peterson, 1999; Millar et al., 2004).

References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evol. Appl. 1, 95–111.

Barber, V.A., Juday, G.P., Finney, B.P., 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. Nature 405, 668–673.

Bazzaz, F.A., 1987. Experimental studies on the evolution of niche in successional plant populations. In: Gray, A.J., Crawley, M.J., Edwards, P.J. (Eds.), Colonization, Succession and Stability. Blackwell Scientific Publications, Oxford, pp. 245–271.

Bertrand, A., Castonguay, Y., 2003. Plant adaptations to overwintering stresses and implications of climate change. Can. J. Bot. 81, 1145–1152.

Brooks, K.N., Ffolliott, P.F., Gregersen, H.M., Thames, J.L., 1991. Hydrology and the Management of Watersheds. Iowa State University Press, Iowa.

Brooks, J.R., Flanagan, B., Ehleringer, J.R., 1998. Responses of boreal conifers to climate fluctuations: indications from tree-ring widths and carbon isotope analyses. Can. J. Forest Res. 28, 524–533.

Burns, R.M., Honkala, B.H., 1990. Silvics of North America: 1. Conifers. Agriculture Handbook 654. U.S. Department of Agriculture, Forest Service, Washington, DC.

Carrer, M., Nola, P., Louis, E., Motta, R., Urbinati, C., 2007. Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. J. Ecol. 95, 1072–1083.

Case, M.J., Peterson, D.L., 2007. Growth–climate relationships of lodgepole pine in the North Cascade National Park, Washington. Northwest Sci. 81, 62–75.

Cook, E.R., Holmes, R.L., 1986. Users Manual for Program ARSTAN. Laboratory of Tree-ring Research. University of Arizona, Tucson, USA.

Cook, E.R., Cole, J., 1991. On predicting the response of forests in eastern North America to future climatic change. Climate Change 19, 271–282.

Cook, E., Kairiukstis, L., 1990. Methods of Dendrochronology: Applications in the Environmental Sciences. Kluwer Academic Publishers, Dordrecht, Netherlands.

Cwynar, L.C., Spear, R.W., 1991. Reversion of forest to tundra in the central Yukon. Ecology 71, 202–212.

D'Arrigo, R.D., Kaufmann, R.K., Davi, N., Jacoby, G.C., Laskowski, C., Myneni, R.B., Cherubini, P., 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. Global Biogeochem. Cycles GB3021, doi:10.1029/2004GB002249.

D'Arrigo, R.D., Mashig, E., Frank, D., Wilson, R., Jacoby, G., 2005. Temperature variability over the past millennium inferred from Northwestern Alaska tree rings. Climate Dyn. 24, 227–236.

Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L., Pasteris, P., 2002. A knowledge-based approach to the statistical mapping of climate. Climate Res. 22, 99–113.

Danby, R.K., Hik, D.S., 2007. Responses of white spruce (*Picea glauca*) to experimental warming at a subarctic alpine treeline. Global Change Biol. 13, 437–451.

Ettl, G.J., Peterson, D.L., 1995. Growth-response of sub-alpine fir (*Abies lasiocarpa*) to climate in the Olympic Mountains, Washington, USA. Global Change Biol. 1, 213–230.

Ettl, G.J., Peterson, D.L., 2001. Genetic variation of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in the Olympic Mountains, WA, USA. Silvae Genetica 50, 145–153.

Fritts, H.C., 1976. Tree Rings and Climate. The Blackburn Press, Caldwell, NJ.

Goldblum, D., Rigg, L.S., 2005. Tree growth response to climate change at the deciduous-boreal forest ecotone, Ontario, Canada. Can. J. Forest Res. 35, 2709–2718.

Graumlich, L.J., Brubaker, L.B., 1986. Reconstruction of annual temperature (1590–1979) for Longmire, Washington, derived from tree rings. Quat. Res. 25, 223–234.

Green, D.S., 2005. Adaptive strategies in seedlings of three co-occurring, ecologically distinct northern coniferous tree species across an elevational gradient. Can. J. Forest Res. 35, 910–917.

Green, D.S., 2007. Controls of growth phenology vary in seedlings of three, co-occurring ecologically distinct northern conifers. Tree Physiol. 27, 1197–1205.

Grissino-Mayer, H.D., 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Res. 57, 205–221.

Hamrick, J.L., 2004. Response of forest trees to global environmental changes. Forest Ecol. Manage. 197, 323–335.

Hänninen, H., Beuker, E., Johnsen, Ø., Leinonen, I., Murray, M., Sheppard, L., Skrøppa, T., 2001. Impacts of climate change on cold hardiness of conifers. In: Bigras, F.J., Colombo, S.J. (Eds.), Conifer Cold Hardiness. Kluwer Academic Publishers, Dordrecht, Netherlands.

He, J.-S., Zhange, Q.-B., Bazzaz, F.A., 2005. Differential drought responses between saplings and adult trees in four co-occurring species of New England. Trees 19, 442–450.

Hofgaard, A., Tardif, J., Bergeron, Y., 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. Can. J. Forest Res. 29, 1333–1346.

Kirdyanov, A., Hughes, M., Vaganov, E., Schweingruber, F., Silkin, P., 2003. The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic. Trees 17, 61–69.

Knowles, N., Dettinger, M.D., Cayan, D.R., 2006. Trends in snowfall versus rainfall in the Western United States. J. Climate 19, 4545–4559.

Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115, 445–459.

Kozlowski, T.T., 2002. Acclimation and adaptive responses of woody plants to environmental stresses. Bot. Rev. 68, 270–334.

Kramer, K., Leinonen, I., Loustau, D., 2000. The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. Int. J. Biometeorol. 44, 67–75.

Kramer, P.J., Kozlowski, T.T., 1979. Physiology of Woody Plants. Academic Press, New York.

Larocque, S.J., Smith, D.J., 2005. A dendroclimatological reconstruction of climate since AD 1700 in the Mt. Waddington area, British Columbia Coast Mountains, Canada. Dendrochronologia 22, 93–106.

Larsen, C.P.S., MacDonald, G.M., 1995. Relations between tree-ring widths, climate, and annual area burned in the boreal forest of Alberta. Can. J. Forest Res. 25, 1746–1755.

Lebourgeois, F., 2000. Climatic signals in early wood, latewood and total ring width of Corsican pine from western France. Ann. Forest Sci. 57, 155–164.

Linderholm, H.W., 2001. Climatic influence on scots pine growth on dry and wet soils in the central Scandinavian mountains, interpreted from tree-ring widths. Silva Fennica 35, 415–424.

Littell, J.S., Peterson, D.L., Tjoelker, M., 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. Ecol. Monogr. 78, 349–368.

Mäkinen, H., Nöjd, P., Kahle, H.P., Neumann, U., Tveite, B., Mielikäinen, K., Röhle, H., Spiecker, H., 2002. Radial growth variation of Norway spruce (*Picea abies* (L.) Karst.) across latitudinal and altitudinal gradients in central and northern Europe. Forest Ecol. Manage. 171, 243–259.

May, R.M., 1974. On the theory of niche overlap. Theor. Popul. Biol. 5, 297–332.

Millar, C.I., Westfall, R.D., Delany, D.L., King, J.C., Graumlich, L.J., 2004. Response of subalpine conifers in the Sierra Nevada, California, U.S.A., to 20th-century warming and decadal climate variability. Arct. Antarct. Alp. Res. 36, 181–200.

Millar, C.I., Stephenson, N.L., Stephens, S.L., 2007. Climate change and forests of the future: managing in the face of uncertainty. Ecol. Appl. 17, 2145–2151.

Mitchell, T.D., Jones, P.D., 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int. J. Climate 25, 693–712.

MWLAP, Ministry of Water, Land, and Air Protection, British Columbia, 2002. Indicators of Climate Change for British Columbia. MWLAP, Victoria, BC.

Oberhuber, W., 2004. Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. Tree Physiol. 24, 291–301.

O'Neill, G.A., Hamann, A., Wang, T., 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. J. Appl. Ecol. 45, 1040–1049.

Pederson, N., Cook, E.R., Jacoby, G.C., Peteer, D.M., Griffin, K.L., 2004. The influence of winter temperatures on the annual radial growth of six northern range margin tree species. Dendrochronologia 22, 7–29.

Peterson, D.W., Peterson, D.L., 1994. Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. Can. J. Forest Res. 24, 1921–1932.

Peterson, D.W., Peterson, D.L., 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. Ecology 82, 3330–3345.

Peterson, D.W., Peterson, D.L., Ettl, G.J., 2002. Growth responses of subalpine fir to climatic variability in the pacific Northwest. Can. J. Forest Res. 32, 1503–1517.

Pfeifer, K., Kofler, W., Oberhuber, W., 2005. Climate related causes of distinct radial growth reductions in *Pinus cembra* during the last 200 years. Veg. Hist. Archaeobot. 14, 211–220.

Savva, Y., Oleksyn, J., Reich, P.B., Tjoelker, M.G., Vaganov, E.A., Modrzynski, J., 2006. Interannual growth response of Norway spruce to climate along an altitudinal gradient in the Tatra Mountains, Poland. Trees 20, 735–746.

Spear, R.W., Cwynar, L.C., 1997. Late quaternary vegetation history of White Pass, Northern British Columbia, Canada. Arct. Antart. Alp. Res. 29, 45–52.

Spittlehouse, D.L., 2005. Integrating climate change adaptation into forest management. Forest Chron. 81, 691–695.

Splechtna, B.E., Dobry, J., Klinka, K., 2000. Tree-ring characteristics of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) in relation to elevation and climatic fluctuations. Ann. Forest Sci. 57, 89–100.

St George, S., Luckman, B.H., 2001. Extracting a paleotemperature record from Picea engelmannii tree-line sites in the central Canadian Rockies. Can. J. Forest Res. 31, 457–470.

Stohlgren, T.J., Bachand, R.R., 1997. Lodgepole pine (*Pinus contorta*) ecotones in Rocky Mountain National Park, Colorado, USA. Ecology 78, 632–641.

Szeicz, J.M., 1997. Growth trends and climatic sensitivity of trees in the North Patagonian rain forest of Chile. Can. J. Forest Res. 27, 1003–1014.

The Mathworks Inc., 2007. Matlab Version 2007b. The Mathworks Inc., http://www.mathworks.com.

Velmex Inc., 1992. The Velmex "TA" System for Research and Non-contact Measurement Analysis. Velmex Inc., Bloomfield, NY.

Villalba, R., Veblen, T.T., Ogden, J., 1994. Climatic influences on the growth of subalpine trees in the Colorado Front Range. Ecology 75, 1450–1462.

VoorTech Consulting, 2004. MeasureJ2X. VoorTech Consulting, Holderness, New Hampshire.

Walther, G.-R., 2003. Plants in a warmer world. Perspect. Plant Ecol. Evol. Syst. 6, 169–185.

Wang, T., Hanann, A., Spittlehouse, D.L., Aitken, S.N., 2006. Development of scale-free climate data for western Canada for use in resource management. Int. J. Climate 26, 383–397.

Wheeler, N.C., Guries, R.P., 1982. Biogeography of lodgepole pine. Can. J. Bot. 60, 1805–1814.

Wilmking, M., Juday, G.P., Barber, V.A., Zald, H.J., 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. Global Change Biol. 10, 1724–1736.

Wilson, R.J.S., Luckman, B.H., 2003. Dendroclimatic reconstruction of maximum summer temperatures from upper treeline sites in Interior British Columbia, Canada. Holocene 13, 851–861.

Xie, C.-Y., Ying, C.C., 1995. Genetic architechture and adaptive landscape of interior lodgepole pine (*Pinus contorta* ssp. latifolia) in Canada. Can. J. Forest Res. 25, 2010–2021.

Yamaguchi, D.K., 1991. A simple method for crossdating increment cores from living tree. Can. J. Forest Res. 21, 414–416.

Zolbrod, A.N., Peterson, D.L., 1999. Response of high-elevation forests in the Olympic Mountains to climate change. Can. J. Forest Res. 29, 1966–1978.