

Regional and ecological patterns in interior Douglas-fir climate–growth relationships in British Columbia, Canada

Hardy P. Griesbauer and D. Scott Green

Abstract: How climate change will affect tree growth across species' geographic and climatic ranges remains a critical knowledge gap. Tree-ring data were analyzed from 33 interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) stands spanning wide geographic and climatic conditions in the interior of British Columbia to gain insights into how within-species growth responses to climate can vary based on local environmental conditions over a broad climatic and geographic range, including populations growing at the species' range and climatic margins. Populations growing in relatively warm and dry climates had growth patterns correlated mostly with annual precipitation, whereas populations growing in high-elevation wet and cold climates had growth patterns correlated with snowfall, winter and annual temperatures, and ocean–atmosphere climate systems. Populations growing at climatic extremes (e.g., coldest, driest, warmest) in each study region had the strongest responses to climate. Projected climate change may negatively influence Douglas-fir productivity across most of its range, and populations growing near the species' climatic limits may provide early and strong indications of future responses.

Résumé : Il y a un manque crucial de connaissances concernant la façon dont les changements climatiques vont influencer la croissance des arbres partout dans l'aire de répartition climatique et géographique des espèces. Des données dendrochronologiques provenant de 33 peuplements de douglas bleu (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) soumis à une grande variété de conditions climatiques et géographiques dans la zone intérieure de la Colombie-Britannique ont été analysées dans le but d'avoir une idée de la façon dont la réponse en croissance au climat peut varier au sein de l'espèce sur la base des conditions environnementales locales couvrant un large spectre climatique et géographique, incluant des populations qui croissent à la limite de l'aire de répartition et des exigences climatiques de l'espèce. Les populations croissant sous un climat relativement chaud et sec avaient des patrons de croissance corrélés avec la précipitation annuelle tandis que les populations croissant à haute altitude sous un climat froid et humide avaient des patrons de croissance corrélés avec la précipitation nivale, les températures hivernale et annuelle et les systèmes climatiques océan–atmosphère. Les populations soumises à des extrêmes climatiques (p. ex. climat le plus froid, le plus sec, le plus chaud) dans chaque région étudiée avaient la plus forte réponse au climat. Les changements climatiques anticipés pourraient influencer négativement la productivité du douglas bleu presque partout dans son aire de répartition et les populations qui croissent près des limites climatiques de l'espèce peuvent fournir des indications sérieuses et précoces des réponses futures.

[Traduit par la Rédaction]

Introduction

Climate change is expected to cause substantial changes in tree growth by altering growing season length, growing degree-days, soil moisture availability, and other climate-related factors important to plant life cycles (Davis and Shaw 2001). It is important to gain a better understanding of potential growth responses to climate change, as growth is often a good metric of resilience, reproductive abilities, productivity, and health (Givnish 1995; Littell and Peterson 2005) and can therefore provide information important to future forest management (Littell and Peterson 2005). Further, the successful adaptation of forest management to climate

change will rely in part on a greater understanding of how tree species responses to climate change may vary within a population and over space and time (O'Neill et al. 2008).

The field of dendroecology (the study of ecological processes using tree-ring records; Fritts and Swetnam 1989) has provided a rich body of studies describing climate–growth relationships in temperate tree species at various temporal and spatial scales (e.g., Zhang and Hebda 2004; Littell et al. 2008). Within-species variation in climate–growth relationships has been examined along ecological gradients such as elevation (e.g., Zhang and Hebda 2004) and latitude (e.g., Hofgaard et al. 1999). The recent development of spatiotemporal climate models has further allowed for climate–

Received 19 March 2009. Accepted 28 November 2009. Published on the NRC Research Press Web site at cjfr.nrc.ca on 3 February 2010.

H.P. Griesbauer^{1,2} and D.S. Green. Ecosystem Science and Management, University of Northern British Columbia, Prince George, BC V2N 4Z9, Canada.

¹Corresponding author (e-mail: hardy.griesbauer@gov.bc.ca).

²Present address: Ministry of Forests and Range, 1011-4th Avenue, 5th Floor, Prince George, BC V2L 3H9, Canada.

growth relationships to be analyzed along predefined climatic gradients (Peterson and Peterson 2001). Further, dendroecological examinations of populations growing at the species' range margins, particularly where the range margins represent a species' climatic tolerance limit, can provide early and (or) unique indications of species responses to climate change (e.g., Pederson et al. 2004). Our study aimed to integrate these concepts to gain insights into how within-species growth responses to climate can vary based on local environmental conditions over a broad climatic and geographic range and to extend this concept to include populations growing at the species' range and climatic margins.

Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco) (hereafter referred to as "Douglas-fir") is a commercially important conifer that grows over a wide range of ecological conditions from British Columbia to Mexico (Hermann and Lavender 1990). The distribution of Douglas-fir in the interior (east of the Coast Mountains) of British Columbia represents its northernmost latitudinal range (presumably associated with cold temperatures; Jull 1999) in North America, although range limits associated with high-elevation and forest–grassland transitions are also found in the province. Studies have shown that this species can have a strong growth response to precipitation (e.g., Watson and Luckman 2002; Littell et al. 2008) but may also become increasingly limited by temperatures and snow at high elevations (Adams and Kolb 2005; Case and Peterson 2005). The wide geographic range and ecological amplitude of Douglas-fir distribution in British Columbia, along with three potentially climatically defined range limits within the province, made this species a suitable choice for study. The specific objectives of the study were to combine standard dendroecological techniques with spatiotemporal climate model data to (i) identify spatial patterns (geographic and climatic) of Douglas-fir growth variation and climate-growth relationships across its climatic and geographic range in the interior of British Columbia and (ii) identify climate variables correlated with Douglas-fir radial growth across the study region.

Methods

Sampling

We collected annual radial growth data in 33 mature stands of Douglas-fir in three geographic regions in the British Columbia interior: (i) Northern Interior, (ii) Chilcotin Plateau, and (iii) Southern Interior (Fig. 1). The sample sites were chosen to encompass a wide range of ecosystems (Meidinger and Pojar 1991) and climatic regimes, including sites located at the margins of Douglas-fir distribution in each region. Potential sampling sites were identified by overlaying interpolated spatial mean annual temperature (MAT) and mean annual precipitation (MAP) data (1961–1990 climate normal period) obtained from the ClimateBC model (version 3.1) (Wang et al. 2006) onto mature Douglas-fir coverage obtained from the BC Ministry of Forest and Range's Vegetation Resource Inventory. Sites were then chosen as uniformly as possible across the full MAT and MAP gradients. ClimateBC combines bilinear interpolation and elevation adjustment techniques to downscale gridded climate data from the PRISM model (Daly et al. 2002) and produce scale-free

spatiotemporal climate data covering western Canada (Wang et al. 2006). The study sites ranged in elevation from 370 to 1540 m (Table 1), in MAT from 1.5 to 7.4 °C, and in MAP from 335 to 2077 mm (Table 2).

Sample sites and trees were chosen to maximize the climate signal in growth variation. Sites of average productivity without evidence of abiotic or biotic disturbance were selected to minimize the growth impacts of nonclimatic factors. As well, we avoided sampling trees with obvious growth defects or evidence of disease, fire scarring, or insect attacks as much as possible. At each site, a single increment core per tree was taken at approximately breast height from between 18 and 40 dominant canopy trees greater than 100 years old. Where sampling occurred on slopes, increment cores were taken perpendicular to the slope direction 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 (Cook and Kairiukstis 1990), and ring widths were measured to the nearest 0.01 mm using WinDendro image analysis software (Régent Instruments Inc. 2005). Crossdating was 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, less than 5% of the cores per site could not be crossdated, usually due to either rot or breaks in the core. In rare and isolated cases, individual tree-ring patterns did not match the ring patterns of other trees in the stand (possibly due to tree-level disturbances); these cores were also excluded from the final chronology (Fritts 1976).

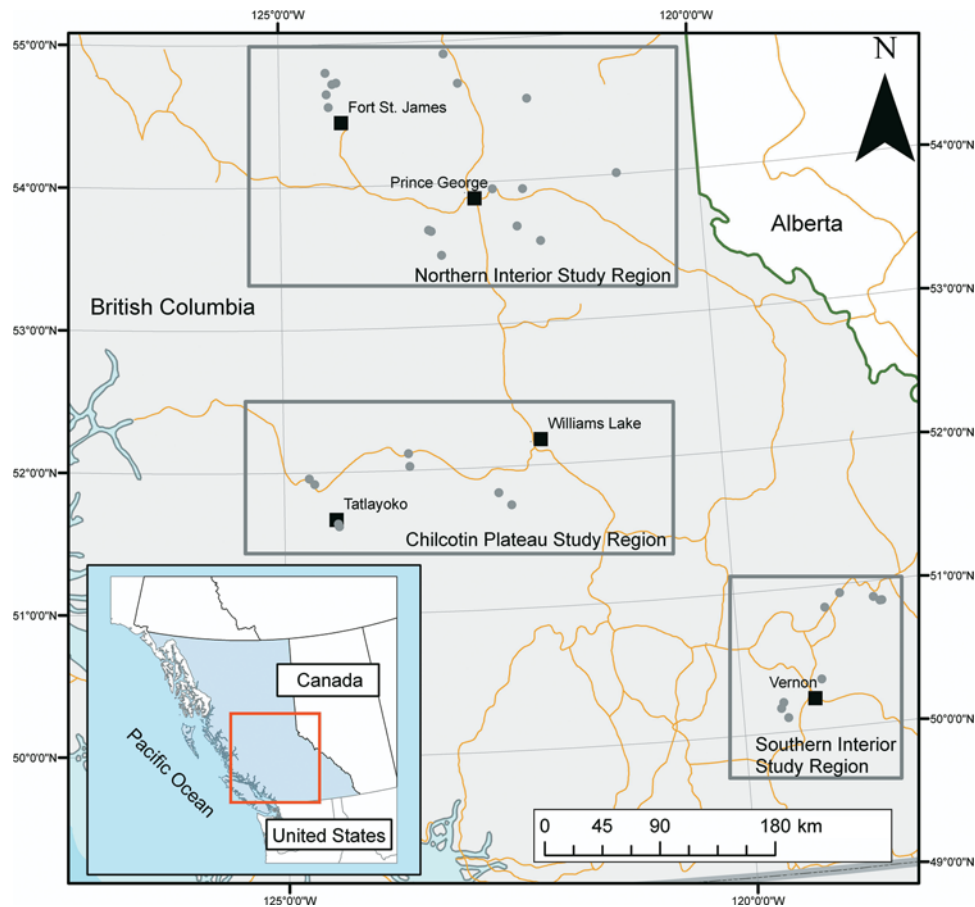
The ARSTAN software (Cook and Krusic 2005) was used to prepare the final chronologies. A cubic smoothing spline with a 50% frequency response cutoff of 60 years was used to remove linear trends and very low-frequency variation from each tree's time series, as these may represent nonclimatic forcings (e.g., ring widths tend to decrease over time associated with increasing tree age and size) and can mask the climatic signal (Cook 1985). This detrending method was based on a preliminary data analysis; we found that a cubic spline at this frequency cutoff best fit the estimated age-related growth trend in most of the chronologies. 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 a common procedure (e.g., Littell et al. 2008) because autocorrelation has statistical implications and may be a function of nonclimatic processes such as stand-level disturbances and morphological influences on growth (Cook 1985).

Data analysis

Chronology analysis

Key chronology statistics were generated using the ARSTAN software including (i) mean sensitivity (a measure of

Fig. 1. Map of the three study regions in British Columbia, Canada. Chronology locations are depicted by circles and climate stations are depicted by squares. **Note:** the Vernon climate station location pertains to both the Vernon Coldstream Ranch and Vernon Bella Vista climate stations.



interannual growth variation; Cook and Kairiukstis 1990), (ii) average intrasite correlation (average correlation of growth variation of all trees within a site to the final chronology), and (iii) expressed population signal. Average intrasite correlation and expressed population signal are commonly used as a measure of the strength of the common (presumably climatic) signal contained in the chronologies (Wigley et al. 1984; Cook and Kairiukstis 1990).

Principal components analysis

Spatially coherent temporal growth patterns were identified for each study region using principal components analysis (PCA) of the chronologies over a common time period (1900–2005). Varimax-rotated principal components (PCs) representing a significant proportion of the original variation (i.e., with a corresponding eigenvalue greater than 1) were retained as composite growth chronologies representing regional patterns of growth variation and used in the climate–growth relationships analysis (below). A preliminary PCA on the entire domain (i.e., using all chronologies) revealed that growth patterns were dominated by regional variation that potentially masked finer-scale (i.e., intraregional) climate-related growth patterns potentially related to site climate and geography (i.e., latitude, longitude, and elevation). To control for regional variation, we treated each study re-

gion (i.e., Northern Interior, Southern Interior, and Chilcotin Plateau) as a separate group for PCA (i.e., a separate PCA was completed for each region) (cf. Rising and Somers 1989). The underlying conditions associated with each PC were identified by plotting the correlation coefficients (also referred to as “loadings”; Tabachnick and Fidell 2001) computed between the original chronologies and the PCs against site-specific climatic normals from ClimateBC (e.g., MAT and MAP, see Table 2) and geographic variables; patterns were then visually assessed and described for each PC (e.g., Zhang and Hebda 2004).

Climate–growth relationships

Associations between climate and annual radial growth were quantified using Pearson simple correlation coefficients computed between local climate station data and regional PCs over a time period common to all climate stations (1939–2004). Bootstrapped bias-corrected accelerated 95% confidence intervals were computed for each correlation coefficient using 1000 iterations (The Mathworks Inc. 2007).

Climate stations were chosen based on spatial interpretations of PCA results, proximity to sample sites, and sufficient time series length (Table 3). Climate data were obtained from adjusted monthly precipitation records (Mekis and Hogg 1999) and homogenized monthly temperature

Table 1. Site descriptions and chronology statistics.

Site	Region	Latitude (°N)	Longitude (°W)	Elevation (m)	Trees (<i>n</i>)	Chronology (years)	Mean sensitivity	AIC	EPS
Alexis	CH	52.12	123.57	1020	24	2006–1750 (257)	0.283	0.616	0.975
Gang	CH	51.73	122.42	680	21	2006–1768 (239)	0.375	0.602	0.969
Hoodoo	CH	51.82	122.56	700	15	2006–1829 (178)	0.448	0.641	0.964
Martin	CH	51.92	124.65	1040	21	2006–1794 (213)	0.244	0.546	0.962
Martin2	CH	51.96	124.71	1240	20	2006–1824 (183)	0.281	0.644	0.973
Newton	CH	52.03	123.56	1050	24	2006–1678 (329)	0.341	0.695	0.982
Tat	CH	51.62	124.38	920	22	2006–1832 (175)	0.231	0.503	0.957
Tat2	CH	51.64	124.39	860	23	2006–1762 (245)	0.289	0.617	0.974
Arch	NI	54.73	124.30	860	27	2006–1880 (127)	0.174	0.461	0.958
Battleship	NI	54.56	124.40	860	21	2006–1887 (120)	0.156	0.474	0.950
Bison	NI	54.72	124.35	840	23	2006–1844 (163)	0.198	0.473	0.954
Bowron	NI	53.94	122.10	780	25	2005–1818 (188)	0.175	0.406	0.945
Dolphin	NI	54.80	124.43	940	21	2006–1799 (208)	0.184	0.415	0.937
Ferndale	NI	53.95	122.46	780	21	2005–1833 (173)	0.203	0.493	0.953
Gregg11	NI	53.67	123.21	815	18	2005–1860 (146)	0.220	0.496	0.947
Gregg24	NI	53.68	123.24	840	23	2005–1868 (138)	0.222	0.592	0.971
Hedrick	NI	54.01	120.97	1250	23	2005–1754 (252)	0.148	0.414	0.942
Ispah	NI	53.68	122.19	840	25	2005–1861 (145)	0.157	0.460	0.955
Kerry	NI	54.70	122.82	800	23	2005–1837 (169)	0.171	0.436	0.947
Mcleod	NI	54.91	122.98	740	26	2005–1884 (122)	0.150	0.433	0.952
Narrow	NI	53.57	121.92	1300	22	2005–1853 (153)	0.157	0.376	0.930
Parsnip	NI	54.57	121.99	1200	20	2005–1633 (373)	0.155	0.381	0.925
PG1412	NI	53.50	123.10	740	31	2005–1865 (141)	0.199	0.458	0.963
Pinchi	NI	54.65	124.42	880	26	2006–1880 (127)	0.156	0.450	0.955
LaCasa	SI	50.10	119.51	425	27	2005–1863 (143)	0.268	0.445	0.956
Queest	SI	50.94	118.82	520	24	2005–1883 (123)	0.181	0.435	0.949
Shorts	SI	50.17	119.58	1340	26	2005–1739 (267)	0.211	0.440	0.953
Sicamous	SI	50.85	119.00	370	25	2005–1889 (117)	0.203	0.376	0.938
Star	SI	50.35	119.11	1540	25	2005–1893 (113)	0.153	0.428	0.949
Wap1	SI	50.86	118.36	1320	20	2005–1880 (126)	0.138	0.352	0.916
Wap2	SI	50.86	118.38	1340	19	2005–1869 (137)	0.136	0.367	0.917
Wap3	SI	50.89	118.45	920	24	2005–1855 (151)	0.187	0.447	0.951
Whiteman	SI	50.21	119.55	700	25	2005–1840 (166)	0.210	0.493	0.960

Note: CH, Chilcotin Plateau; NI, Northern Interior; SI, Southern Interior; AIC, average intrasite correlation; EPS, expressed population signal.

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/>).

We made further adjustments to two climate data records (Table 3). The Williams Lake temperature record was not homogenized at the time of this study; therefore, we used the observed data. However, the station was relocated (and repositioned over 300 m higher) in 1961, which likely introduced inhomogeneities into the climate record. We accounted for this by using ClimateBC elevation-adjusted and interpolated (Wang et al. 2006) homogenized historical temperature data (Mitchell and Jones 2005) from 1939 to 1960. For analysis of the Southern Interior study region, we combined observed 1998–2004 precipitation data from the Vernon Bella Vista climate station with adjusted precipitation data from the Vernon Coldstream Ranch station (Mekis and Hogg 1999) to create a climate time series that matched the length of the other records used in the analysis. Missing data (only precipitation data were missing, see Table 4) were not replaced due to a high potential for errors in estimating missing values (Mekis and Hogg 1999) and were omitted pairwise from analysis.

We also correlated annual growth with three indices describing major modes of climate variability in the Pacific Ocean and North American climate: (i) Smith and Sardeshmukh's (2000) 1900–2003 ENSO (El Niño/Southern Oscillation) index time series of mean standardized monthly sea surface temperature and air pressure anomalies (<http://www.cdc.noaa.gov/people/cathy.smith/best/enso.ts.1mn.txt>), (ii) monthly 1901–2005 PDO (Pacific Decadal Oscillation) indices derived from the leading PC of sea surface temperature anomalies in the North Pacific Ocean (<http://jisao.washington.edu/pdo/PDO.latest>), and (iii) monthly 1951–2000 PNA (Pacific/North American) teleconnection indices derived from a Varimax-rotated PCA of standardized monthly mean 500-millibar height anomalies over the Northern Hemisphere (<http://www.cdc.noaa.gov/Correlation/pna.data>).

Seasonal and annual climate variables (for both climate station records and ocean–atmosphere indices) were derived by averaging monthly values (see Table 4) based on preliminary data analysis as well as a priori information pertaining to Douglas-fir climate–growth relationships (e.g., Watson and Luckman 2002). Where monthly values were missing

Table 2. Sample site climate normals (1961–1990).

Site	MAT (°C)	MWMT (°C)	MCMT (°C)	TD (°C)	MAP (mm)	MSP (mm)	AHM	SHM	PAS (cm)
Alexis	2.3	13.7	−9.9	23.6	335	201	36.8	68.2	106
Arch	1.8	13.7	−11.2	24.9	604	255	19.6	53.6	266
Battleship	2.1	13.9	−11.2	25.1	512	229	23.7	60.6	213
Bison	1.9	13.7	−11.1	24.8	603	255	19.7	53.7	264
Bowron	3.1	14.6	−9.9	24.5	804	346	16.2	42.1	304
Dolphin	1.5	13.3	−11.3	24.6	663	270	17.3	49.2	307
Ferndale	3.5	14.8	−8.9	23.7	861	389	15.7	38.1	298
Gang	4.7	16.4	−8.7	25.1	372	211	39.5	77.9	105
Gregg11	3	14.6	−10.1	24.7	582	255	22.4	57.3	226
Gregg24	2.8	14.3	−10.1	24.4	593	260	21.6	55	235
Hedrick	1.7	12.7	−9.8	22.6	1386	525	8.4	24.3	637
Hoodoo	4.2	15.9	−8.9	24.7	341	202	41.8	78.4	94
Ispah	2.9	14.1	−9.5	23.6	733	332	17.6	42.3	273
Kerry	2.2	14	−11.2	25.3	755	279	16.1	50.3	339
LaCasa	7.3	18.7	−4.5	23.2	394	173	43.9	108.3	92
Martin	2	12.9	−10	23	421	178	28.6	72.6	185
Martin2	1.5	12.3	−10.3	22.7	493	202	23.4	61	226
Mcleod	2.1	14.3	−12	26.3	713	252	17	56.8	331
Narrow	1.9	12.6	−9.6	22.2	992	443	12	28.4	400
Newton	2.4	13.7	−9.7	23.4	338	192	36.8	71.3	113
Parsnip	1.8	13.5	−10.4	23.9	1064	386	11.1	35	477
PG1412	3.5	14.6	−9.1	23.7	680	309	19.8	47.2	242
Pinchi	2	13.7	−11.2	24.9	549	240	21.8	57.2	235
Queest	5.6	17	−6.6	23.6	917	368	17	46.2	273
Shorts	3.8	14.8	−7.3	22.1	615	255	22.4	58	236
Sicamous	7.4	18.9	−5	24	848	379	20.5	50	169
Star	2.4	13.5	−8.5	22	867	325	14.3	41.5	410
Tat	2.8	12.4	−8	20.4	461	183	27.6	68	185
Tat2	3	12.9	−7.8	20.7	452	174	28.9	74.2	179
Wap1	2.5	13.9	−9.4	23.3	2077	676	6	20.5	983
Wap2	2.7	14.1	−9.3	23.4	2062	680	6.1	20.7	952
Wap3	3.6	15	−8.3	23.3	1255	483	10.8	30.9	488
Whiteman	5.8	17	−5.9	22.9	499	217	31.6	78.4	145

Note: MAT, mean annual temperature; MWMT, mean warmest month temperature; MCMT, mean coldest month temperature; TD, continentality (MWMT−MCMT); MAP, mean annual precipitation; MSP, mean summer precipitation; AHM, annual heat–moisture index; SHM, summer heat–moisture index; PAS, precipitation as snow. Refer to Wang et al. (2006) for annual and summer heat–moisture index formulae.

Table 3. Environment Canada climate stations used in climate–growth relationships analysis.

Station name	Latitude (°N)	Longitude (°W)	Elevation (m)	Data length (years) ^a	Corresponding PC ^b
Northern Interior					
Fort St. James	54.45	124.25	686	110 (1895–2004)	N1
Prince George	53.89	122.68	691	94 (1913–2006)	N2, N3
Southern Interior					
Vernon Coldstream Ranch	50.22	119.2	482	98 (1900–1997)	S1, S2
Vernon Bella Vista ^c	50.26	119.31	427	21 (1985–2005)	
Chilcotin Plateau					
Williams Lake ^d	52.18	122.05	940	69 (1939–2007)	C1
Tatlayoko	51.67	124.41	870	76 (1930–2005)	C2

^aClimate data were analyzed over a time period common to all stations (1939–2004).

^bClimate stations corresponding to regional PCs were chosen based on spatial patterns of the PCA loadings, proximity to sample sites, and sufficient time series length.

^cVernon Bella Vista rain, snow, and precipitation data from April 1997 to December 2005 added to Vernon Coldstream Ranch data to extend the time series.

^dClimateBC elevation-adjusted and interpolated (Wang et al. 2006) homogenized historical temperature data (Mitchell and Jones 2005) from 1939–1960 used to account for possible inhomogeneities in Williams Lake observed data.

Table 4. Correlation coefficients computed between climate variables and PCs (N, S, and C) representing regional patterns of Douglas-fir annual growth variation.

	Northern Interior			Southern Interior		Chilcotin Plateau	
	N1	N2	N3	S1	S2	C1	C2
Annual^a							
Precipitation		0.557		0.387 ^e		0.534 ^f	0.589 ^g
Mean temperature			0.352		0.429		0.261
HM		−0.498		−0.387 ^e		−0.467 ^f	−0.585 ^g
PDO					0.456		
ENSO					0.349		
PNA	0.274				0.466		
Prior winter^b							
Snow			−0.432		−0.523 ^e		
Mean temperature			0.397		0.530		0.283
PDO					0.476		
ENSO					0.342		
PNA			0.400		0.593		
Prior summer^c							
Rain		0.324			0.272 ^e	0.324 ^f	
HM		−0.271		−0.251 ^e			
Maximum temperature				−0.403	−0.257		
PDO					0.324		
ENSO					0.390		
PNA							
Spring^d							
Rain	0.365	0.437		0.327 ^e		0.328 ^f	
HM	−0.406	−0.463		−0.317 ^e			
Maximum temperature		−0.304		−0.317			
PDO					0.337		
ENSO							
PNA							

Note: All relationships shown are significant at $P < 0.05$ based on bootstrapped confidence limits. Relationships calculated from 1939 to 2004 ($n = 65$, except where denoted, sample size is reduced by 1 because some of the derived seasonal and annual variables include months from the year preceding the growth year.), except PDO (1901–2005, $n = 105$), ENSO (1900–2003, $n = 104$), and PNA (1951–2005, $n = 55$). HM, heat–moisture index; PDO, Pacific Decadal Oscillation; ENSO, El Niño/Southern Oscillation; PNA, Pacific/North American teleconnection index.

^aAnnual variables derived from an average of previous July to current June monthly values.

^bPrior winter variables derived from an average of previous October to current March monthly values.

^cPrior summer variables derived from an average of previous June to September monthly values.

^dSpring variables derived from an average of April to June monthly values.

^e $n = 64$. Sample size reduced due to missing precipitation data.

^f $n = 62$. Sample size reduced due to missing precipitation data.

^g $n = 61$. Sample size reduced due to missing precipitation data.

in the climate station record, the associated derived seasonal variable was computed as a nonnumber and omitted pairwise from analysis. Growth was compared with climate variables from the previous year's July to the current year's October because climate in the preceding year can affect the current year's growth (Fritts 1976). With respect to climate variables, we use the term “annual” to refer to a 12-month period spanning the previous June to current July (Watson and Luckman 2002). To examine growth responses to interactions between temperature and precipitation, we also created seasonal and annual heat–moisture indices (a ratio of temperature to precipitation as a measure of “dryness”) from derived seasonal and annual temperature and precipitation data using the formula in Wang et al. (2006).

Results

Chronologies

Final chronologies were calculated using from 15 to 31 trees ranging in length from 113 to 373 years (Table 1). All sites had relatively high average intrasite correlations ranging from 0.352 to 0.695, and expressed population signal values were all above 0.85 (Table 1), indicating a sufficient population signal for climate analysis (Wigley et al. 1984). Mean sensitivity ranged from 0.136 to 0.448.

PCA

Northern Interior

PCA of Northern Interior chronologies extracted three

Table 5. PC (N, S, and C) analysis summary.

	Northern Interior			Southern Interior			Chilcotin Plateau		
	N1	N2	N3		S1	S2		C1	C2
Eigenvalue	4.93	4.14	2.99		3.18	2.91		3.46	2.9
% variance (cumulative)	30.8	25.9	18.7		35.3	32.3		43.2	36.3
	30.8	56.7	75.4		35.3	67.6		43.2	79.5
Loading									
Arch	0.868	0.272	0.199	Lacasa	0.773	−0.188	Alexis	0.846	0.309
Battle	0.797	0.302	0.213	Queest	0.661	0.379	Gang	0.858	0.16
Bison	0.899	0.254	0.149	Shorts	0.676	0.562	Hoodoo	0.874	0.15
Bowron	0.261	0.645	0.484	Sicamous	0.813	0.063	Martin	0.482	0.687
Dolphin	0.747	0.285	0.239	Star	0.059	0.743	Martin2	0.468	0.717
Ferndale	0.327	0.763	0.216	Wap1	−0.002	0.889	Newton	0.867	0.325
Gregg11	0.47	0.78	0.129	Wap2	0.036	0.876	Tat	0.095	0.919
Gregg24	0.391	0.806	0.036	Wap3	0.588	0.543	Tat2	0.172	0.906
Hedrick	0.186	−0.03	0.823	Whiteman	0.823	−0.002			
Ispah	0.126	0.517	0.673						
Kerry	0.551	0.306	0.503						
McLeod	0.597	0.227	0.423						
Narrow	0.109	0.548	0.691						
Parsnip	0.487	0.19	0.636						
PG1412	0.299	0.802	0.273						
Pinchi	0.758	0.421	0.100						

Note: Loading (correlation coefficient) significance levels ($n = 106$): 0.191 (95%), 0.249 (99%), and 0.315 (99.9%). Bolded values refer to the highest loadings.

PCs that represented 75.4% (30.8%, 25.9%, and 18.7%, respectively) of the total chronology variance (Table 5). An analysis of the PC chronology loadings revealed that the first PC (hereafter referred to as “N1”) had the strongest correlations with sites north of approximately 54°N and west of approximately 123.5°W with lower values in MAT, mean coldest month temperature, and precipitation as well as high heat-moisture indices (Fig. 2). Based on these observations, N1 was interpreted to represent growth variation in northernmost and westernmost sites that are characterized by relatively cold and dry conditions relative to other sites in the region; these sites are located near the northern margins of the species’ range in the province. The second PC (N2) had a stronger correlation with chronologies from the southernmost sites of the study region with the following characteristics: lower values in MAP and precipitation as snow and higher values in MAT and mean warmest month temperature. This PC was interpreted to represent the warmer and drier (southernmost) sites in the Northern Interior study region. The third PC (N3) had the highest loadings on the easternmost, high-elevation sites located on the western slopes of the Rocky and Cariboo Mountains east of Prince George. This PC was correlated with sites with lower MAT and higher precipitation and snowfall (Fig. 2). N3 was interpreted to represent radial growth variation for high-elevation sites that are at the wet and snowy extremes for Douglas-fir in this region.

Southern Interior

The Southern Interior chronologies had two modes of variability that represented 67.6% (35.3% and 32.3%, respectively) of the total variance (Table 5). The first PC (hereafter “S1”) had the strongest loadings on chronologies from lower-elevation sites in the study area (Fig. 3) with

higher average temperatures and lower precipitation. This PC was interpreted to represent Douglas-fir growing at its warm and dry margins in the region. The second PC (S2) had stronger loadings on higher-elevation sites with lower temperatures and higher precipitation (including snow; Fig. 3). This PC seemed to represent similar ecological conditions as N3 from the Northern Interior study region and was interpreted to represent Douglas-fir at its upper elevation and precipitation extremes in this region.

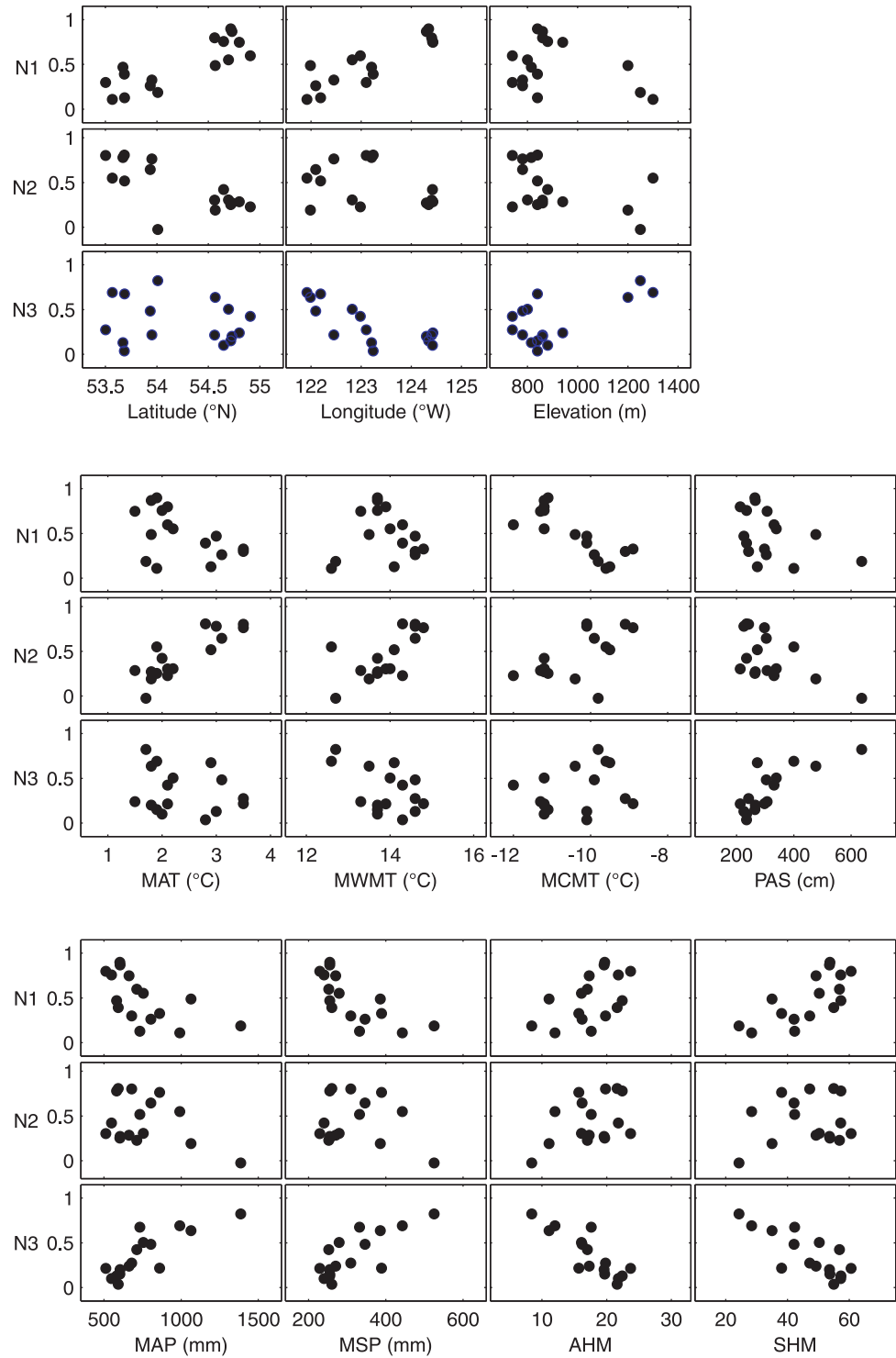
Chilcotin Plateau

The Chilcotin chronologies had two modes of variability that represented 79.5% (43.2% and 36.2%, respectively) of the total variance (Table 5). The first PC (hereafter “C1”) had the strongest correlations with the easternmost sites in the region (Fig. 4), which were also the driest sites of the region (and entire study; Table 2). Growth variation represented by this PC was interpreted to represent Douglas-fir growing at the dry extremes in the region. The second PC (C2) best represented the four westernmost sites with higher values in annual precipitation and snowfall and lower annual heat-moisture index than sites represented by C1.

Climate-growth relationships

Correlation coefficients were computed between annual growth variation and annual, seasonal, and monthly climate variables; however, only results involving annual and seasonal variables are presented because (i) they more consistently explained growth variation across the three regions, (ii) they had higher correlation coefficients than monthly variables, and (iii) they may be more relevant physiologically than monthly variables (e.g., Watson and Luckman 2002). Further, rather than present results for all seasonal and annual variables, we focused our results and discussion

Fig. 2. Northern Interior PC loads against geographic variables and climatic normals. MAT, mean annual temperature; MWMT, mean warmest month temperature; MCMT, mean coldest month temperature; PAS, precipitation as snow; MAP, mean annual precipitation; MSP, mean summer precipitation; AHM, annual heat–moisture index; SHM, summer heat–moisture index. Refer to Wang et al. (2006) for annual and summer heat–moisture index formulae.

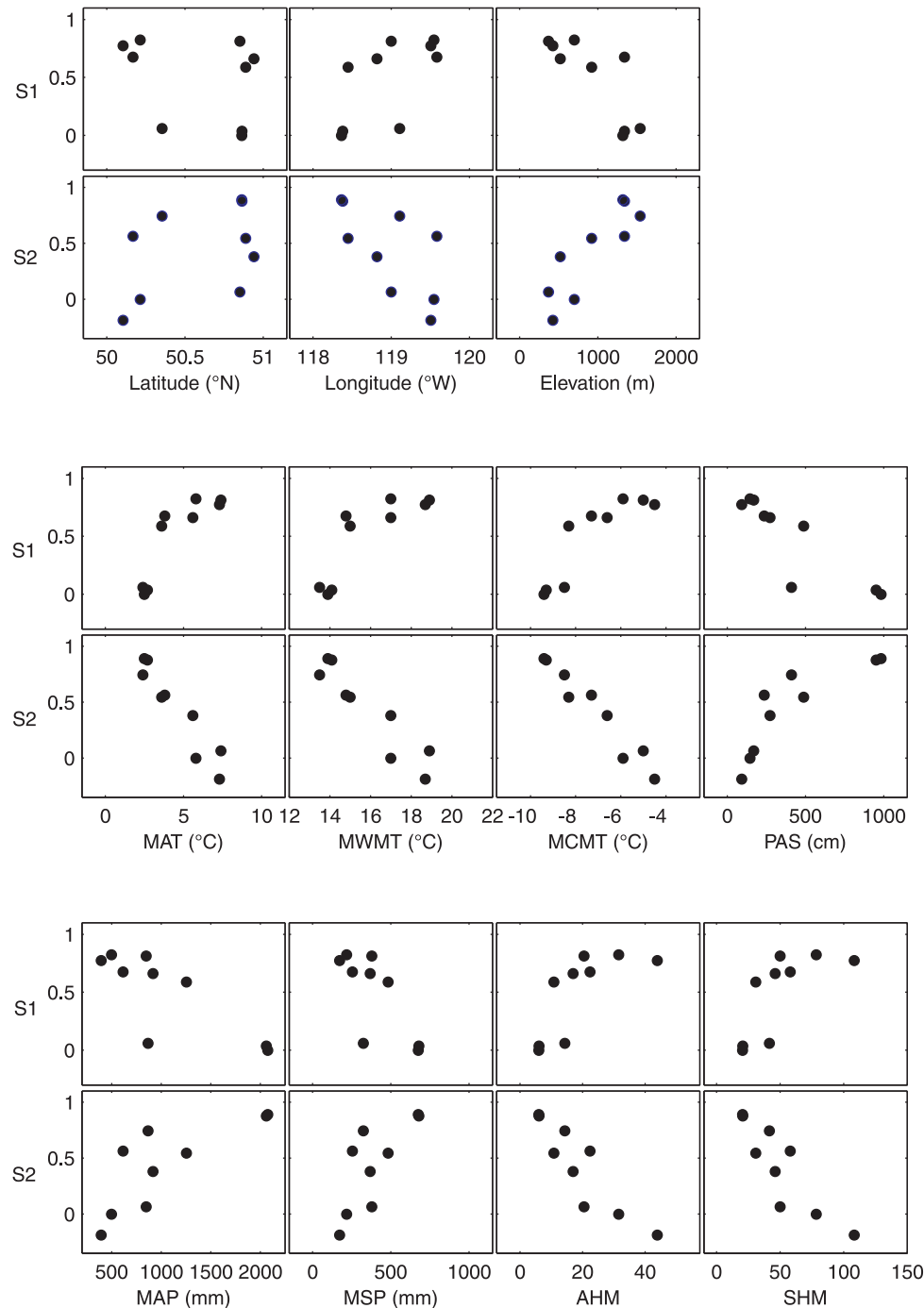


on those variables that appeared to be important in explaining growth variation.

Growth variation represented by PCs describing relatively warm and dry sites in each region (N2, S1, and C1) was positively correlated with annual (previous summer to cur-

rent spring) precipitation and negatively correlated with annual heat–moisture index (Table 4). Growth at these sites was also positively correlated with rain and negatively correlated with heat–moisture index and (or) maximum temperatures during the previous summer and current spring. The

Fig. 3. Southern Interior PC loads against geographic variables and climate normals. Refer to Fig. 2 for codes.



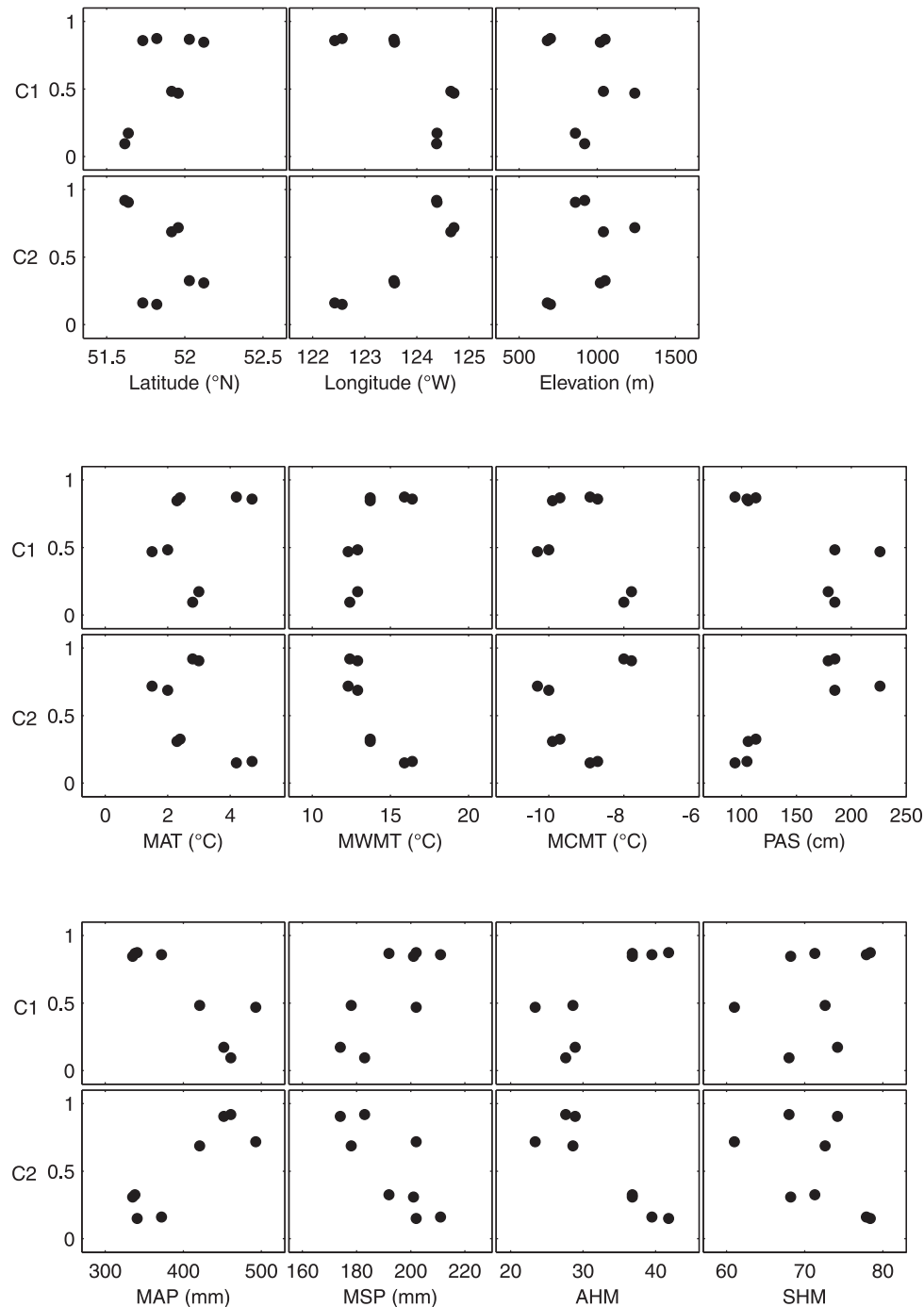
second PC in the Chilcotin study region (C2) had a similar growth association with annual precipitation and heat–moisture index. No PCs had significant correlations between growth and current summer conditions (not shown).

PCs representing high-elevation wet and cold sites in the Northern and Southern Interior study regions (N3 and S2) had positive growth correlations with annual and winter temperatures, winter PNA index, and negative correlations with winter snowfall. Variation in S2 was also positively correlated with annual and winter PDO, PNA, and ENSO indices as well as prior summer PDO and ENSO indices and spring PDO index.

Growth variation in the northernmost Douglas-fir populations in the province (as represented by N1) had positive correlations with annual PNA and spring rain and negative correlations with spring heat–moisture index.

Discussion

Our results add to similar studies of Douglas-fir in other portions of its range (e.g., Zhang and Hebda 2004; Littell et al. 2008) and suggest that Douglas-fir interannual growth patterns are coherent over relatively large distances and likely reflect the influence of regional climate on productiv-

Fig. 4. Chilcotin Plateau PC loads against geographic variables and climate normals. Refer to Fig. 2 for codes.

ity (Zhang and Hebda 2004). Further, the primary climatic limitation to growth appears to be similar over most of the species' range and is especially strong in marginal populations. Thus, there may be widespread similar growth responses to climate change, and populations growing near the climatic limits of the species' range may provide strong and early indications of those responses. Our results support bioclimate models that generally project Northern Hemisphere tree species will lose suitable habitat along their southern margins associated with increasing drought (Hamann and Wang 2006). However, our results also suggest that soil moisture availability will be a critical limita-

tion to some species at their northern limits (Tardif et al. 2006). This supports suggestions that biologically based climate change models must consider relevant climatic parameters and within-species variation (O'Neill et al. 2008); positive responses to increasing temperatures in northern populations should not be assumed (Tardif et al. 2006). While climate change impacts on Douglas-fir productivity could be negative over much of its range, our results also show that climatic growth limitations may be unique in high-elevation Douglas-fir populations; projected climate change scenarios may actually result in increased productivity in these environments.

Regional growth patterns

Our results identify spatially coherent regional patterns in Douglas-fir radial growth that likely reflect common responses to large-scale climate forcings (Zhang and Hebda 2004). Regional growth patterns differentiated primarily by climatic and site conditions. For instance, mid- to low-elevation warm and dry sites in different regions shared similar temporal growth patterns that were distinct from common temporal growth patterns found in the high-elevation wetter and colder sites across regions. In the Northern and Southern Interior regions, differentiation in climate–growth trends along precipitation and temperature gradients could be associated with elevation, similar to findings for Douglas-fir in coastal environments at smaller spatial scales (Case and Peterson 2005).

Similar to other studies (cf. Fritts 1976), growth responses to climate appear to be strongest in populations growing at the climatic extremes (e.g., hottest, driest) in each region. This is supported by the pattern of loadings between each PC and the chronologies, which consistently showed the strongest loadings with sites located at the climatic extremes. However, the PCs in each region were also significantly correlated, although to a lesser degree, with growth from populations growing in more moderate climatic conditions. Therefore, although the relationships quantified between climate and the regional PCs pertain mostly to populations growing at the climatic extremes in each region, they also describe a broader regional response (Littell 2006). PC chronology loading patterns also suggest that under current climate change scenarios (Christensen et al. 2007; Pike et al. 2008a), Douglas-fir climate–growth responses could become stronger and more widespread. It is important to note that the range of climate normals sampled in this study likely does not bracket the full climatic spectrum occupied by Douglas-fir in North America; a “moderate” site in one of our study regions may be situated more at a climatic extreme when considered within the larger context of Douglas-fir’s range from British Columbia to Mexico.

Climate–growth relationships

Low- to mid-elevation sites

PCs explaining the majority of variation in all three regions were generally most correlated with precipitation and integrated precipitation–temperature (heat–moisture index) variables. This finding supports similar relationships described for Douglas-fir in other regions (e.g., Watson and Luckman 2002; Zhang and Hebda 2004; Littell et al. 2008) and suggests that moisture may be a primary limiting environmental factor to Douglas-fir growth across most of its range, including its northern distribution limits. Zweifel et al. (2006) suggested that precipitation may influence radial growth by (i) affecting bud formation and photosynthesis, as well as and water conduction in the subsequent year, and (ii) affecting tree–water relationships, which in turn affect cell division and enlargement, carbon assimilation, and long-term carbon storage. Growing season water deficits suppress Douglas-fir photosynthesis, gas exchange, and transpiration (Lassoie and Salo 1981), which may contribute to reduced radial growth (possibly at the expense of root growth; Waring 1991). Water stress thresholds (and other

climate–growth limitations) may vary with age, microsite conditions, and genetics (Littell 2006).

Annual (previous July to current June) precipitation generally explained more variation in growth than seasonal and monthly precipitation, likely reflecting the integrated influence on growth of precipitation during the late portion of the previous growing season and soil moisture availability during the early portion of the current growing season (Watson and Luckman 2002). Several physiological mechanisms may explain this phenomenon. For example, primordial tissues are formed during the end of the growing season, and water availability during the late summer influences carbohydrate allocation to the following year’s formative tissues (Kozłowski and Pallardy 1997). Trees may allocate more carbohydrates to root systems during the growing season after a dry summer to compensate for drought-reduced root growth (Lassoie and Salo 1981), which could potentially result in a smaller ring. Winter snow and spring precipitation can be important because they provide early-season soil moisture (Carrer and Urbinati 2006), which will be especially important for Douglas-fir, as its needles tend to be fully grown and photosynthesizing relatively early in the year (Watson and Luckman 2002).

Although winter precipitation appears to influence growth (as part of annual precipitation) in the low- to mid-elevation sites in this study, we note that there were no significant correlations between growth in these sites and winter season precipitation alone. A lack of correlation with winter precipitation may suggest that the relationship between winter precipitation and growth is complicated; for example, winter precipitation may only be important during years with dry springs or previous summers. The contribution of snow to growth may also be related to spring temperatures and the rate of spring snowmelt. Such complicated relationships would likely not be captured through linear correlation analysis with seasonal precipitation amounts.

Only the hottest sites in the study (Southern Interior, S1) had negative relationships to temperatures (with exception of N2, which was negatively correlated with spring maximum temperatures). As negative temperature–growth relationships have been previously documented in Douglas-fir (e.g., Zhang and Hebda 2004; Case and Peterson 2005), we expected a somewhat broader temperature response. For the particularly hot S1 sites, summer and spring temperatures may exceed species-specific photosynthesis threshold limits (Brubaker 1980), which can be as low as approximately 20–25 °C for Douglas-fir (Salo 1974; Doehlert and Walker 1981). Additionally, excessively high temperatures could cause unfavorable carbon balance in trees (e.g., ratios of photosynthesis to respiration), and it can lead to increased water loss, reduced nutrient storage, and decreased foliage efficiency (Kimmins 1997).

The eight sites sampled in the Chilcotin Plateau were the driest among all study sites, and all appear to be strongly limited by annual precipitation and heat–moisture index. Although the PCA indicated two significantly different growth patterns in this study region, these growth patterns may simply reflect geographic (longitudinal) differences in temporal precipitation patterns and not distinct climate–growth relationships. Geographic differences in temporal precipitation patterns may also explain a PCA distinction be-

tween N1 and N2 in the Northern Interior yet a similar primary growth response to precipitation.

High-elevation sites

High-elevation Douglas-fir populations in the Northern and Southern Interior regions had climate–growth relationships similar to those in high-elevation sites reported for coastal British Columbia (Zhang and Hebda 2004) and the United States (Case and Peterson 2005), which appear to differ from mid- to low-elevation populations in that low annual temperatures and winter snowfall are primary limiting factors. In cold environments with ample moisture, low temperatures are often assumed to be primary climatic growth limitations (Littell 2006), as they reduce glucose utilization, CO₂ uptake, and photosynthesis (Körner 1998), can damage tree tissues (Körner 1998), and may be associated with shorter growing seasons (Zhang and Hebda 2004). Colder winter temperatures may also be associated with higher snowfall (winter temperatures and snowfall were negatively correlated in both Prince George and Vernon climate station data over their full respective lengths, $P < 0.0001$, data not shown), which was negatively correlated with growth in both the Northern and Southern Interior regions (PCs N3 and S2). Higher snowfall and corresponding snowpacks can limit growth by delaying the start of the growing season, as cambial and root growth generally only begins when the upper soil layers have thawed after snowmelt (Vaganov et al. 1999).

The winter PNA index was correlated with high-elevation growth in both the Northern and Southern Interior regions. PNA is generally positively correlated with surface winter and early spring temperatures and negatively correlated with winter precipitation in British Columbia and western North America (Leathers et al. 1991; Stahl et al. 2006) and tends to be positive during combined positive PDO and ENSO events (Hsieh and Tang 2001). The PNA index may capture variability in climate factors critical to high-elevation Douglas-fir growth over a large spatial range.

Annual and seasonal PDO and ENSO indices were positively correlated with Douglas-fir growth at high elevations in the Southern Interior, similar to growth relationships reported in the US Pacific Northwest (Case and Peterson 2005). PDO and ENSO signals did not appear in high-elevation sites in the Northern Interior; these processes may be regional in their influence of growth-limiting climatic factors in the British Columbia interior. High PDO and ENSO index values generally result in anomalously warm and dry winter conditions in British Columbia and western North America (Moore and McKendry 1996; Stahl et al. 2006), which may result in longer growing seasons through lower snowpack depths and warmer soils (Case and Peterson 2005).

Conclusions

As forest managers prepare for climate change, a better understanding of species-specific responses to climate change across large regions and climatic gradients is required (Peterson and Peterson 2001). We addressed this question by sampling Douglas-fir populations across a wide geographic and climatic range and by linking specific growth responses to local climatic conditions using high-resolution spatiotemporal climate data from the ClimateBC

model (Wang et al. 2006). Our results add to the body of studies that have examined Douglas-fir climate–growth relationships across ecological gradients in other regions (e.g., Zhang and Hebda 2004; Case and Peterson 2005; Littell et al. 2008) but also provide a greater understanding of climate–growth relationships along predefined climatic gradients in a portion of a species' range that contains several range margins presumably associated with climatic limitations. As responses in marginal populations may be early indicators of climate change (Pederson et al. 2004), these populations warrant further research. We recommend that a similar approach be applied to other tree species.

At low- to mid-elevations across most of its range, Douglas-fir annual growth appears to be most widely limited by precipitation totals from the previous July to current June, with the strongest sensitivity in population growth at the dry margins. Even at the northern margins of the species' range, Douglas-fir growth appears to be limited by precipitation (see also Griesbauer and Green 2010). Future decreases in soil moisture availability as a result of increasing temperatures (Christensen et al. 2007; Pike et al. 2008b) may result in widespread increases in precipitation sensitivities and consequent growth declines, with initial and strongest changes in drier areas. At high-elevation margins of its range, Douglas-fir growth appears to be more limited by annual and winter temperatures and snowfall, and associations with PDO, ENSO, and PNA indices in the Southern Interior may reflect the influence of Pacific Ocean – atmosphere climate systems on winter conditions in mountainous environments. Warmer temperatures, less snow accumulation, and earlier snowmelt in the future (Pike et al. 2008b) may increase Douglas-fir productivity in these environments.

Acknowledgements

We thank Kasia Caputa, Yumiko Miyamoto, Emily Müller, and Kara Przeczek for their assistance in the field and laboratory. We also thank Dr. Stephen Déry and Dr. Greg O'Neill for advice and constructive comments through all components of this study, Chris Steeves for GIS analysis, and Gretchen Prystawik for review of this manuscript. This work was funded through the Natural Sciences and Engineering Research Council of Canada, the BC Forest Science Program, and the province of British Columbia.

References

- Adams, H.D., and Kolb, T.E. 2005. Tree growth response to drought and temperature in a mountain landscape in northern Arizona, USA. *J. Biogeogr.* **32**(9): 1629–1640. doi:10.1111/j.1365-2699.2005.01292.x.
- Brubaker, L.B. 1980. Spatial patterns of tree growth anomalies in the Pacific Northwest. *Ecology*, **61**(4): 798–807. doi:10.2307/1936750.
- Carrer, M., and Urbinati, C. 2006. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. *New Phytol.* **170**(4): 861–871. doi:10.1111/j.1469-8137.2006.01703.x. PMID:16684244.
- Case, M.J., and Peterson, D.L. 2005. Fine-scale variability in growth-climate relationships of Douglas-fir, North Cascade Range, Washington. *Can. J. For. Res.* **35**(11): 2743–2755. doi:10.1139/x05-191.
- Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X.,

- Held, I., Jones, R., Kolli, R.K., Kwon, W.T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A., and Whetton, P. 2007. Regional climate projections. In *The physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, New York. pp. 848–940.
- Cook, E. 1985. A time series analysis approach to tree-ring standardization. Ph.D. dissertation, University of Arizona, Tucson, Az.
- Cook, E., and Kairiukstis, L. 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Cook, E.R., and Krusic, P. 2005. Users manual for program ARSTAN [online]. Tree-Ring Lab, Lamont-Doherty Earth Observatory, Columbia University, New York. Available from <http://www.ldeo.columbia.edu/res/fac/trl/public/publicSoftware.html> [accessed 14 October 2006].
- Daly, C., Gibson, W.P., Taylor, G.H., Johnson, G.L., and Pasteris, P. 2002. A knowledge-based approach to the statistical mapping of climate. *Clim. Res.* **22**: 99–113. doi:10.3354/cr022099.
- Davis, M.B., and Shaw, R.G. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science*, **292**(5517): 673–679. doi:10.1126/science.292.5517.673. PMID:11326089.
- Doehlert, D.C., and Walker, R.B. 1981. Photosynthesis and photorespiration in Douglas-fir as influenced by irradiance, CO₂ concentration, and temperature. *For. Sci.* **27**: 641–650.
- Fritts, H.C. 1976. *Tree rings and climate*. The Blackburn Press, Caldwell, N.J.
- Fritts, H.C., and Swetnam, T.W. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. In *Advances in ecological research*. Vol. 19. Academic Press Inc., San Diego, Calif. pp. 111–188.
- Givnish, T.J. 1995. Plant stems: biomechanical adaptation for energy capture and influence on species distributions. In *Plant stems: physiology and functional morphology*. Academic Press, San Diego, Calif. pp. 3–49.
- Griesbauer, H. and Green, D.S. 2010. Assessing the climatic sensitivity of Douglas-fir at its northern range margins in British Columbia, Canada. *Trees*. doi:10.1007/s00468-009-0407-z.
- Hamann, A., and Wang, T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology*, **87**(11): 2773–2786. doi:10.1890/0012-9658(2006)87[2773:PEOCCO]2.0.CO;2. PMID:17168022.
- Hermann, R.K., and Lavender, D.P. 1990. Douglas-fir [online]. U.S. Department of Agriculture. Available from http://www.na.fs.fed.us/spfo/pubs/silvics_manual/Volume_1/pseudotsugamenziesii.htm [accessed 15 July 2006].
- Hofgaard, A., Tardif, J., and Bergeron, Y. 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. *Can. J. For. Res.* **29**(9): 1333–1346. doi:10.1139/cjfr-29-9-1333.
- Holmes, R. 1983. Computer-assisted quality control in tree-ring dating and measuring. *Tree-Ring Bull.* **43**: 69–78.
- Hsieh, W.W., and Tang, B. 2001. Interannual variability of accumulated snow in the Columbia basin, British Columbia. *Water Resour. Res.* **37**(6): 1753–1759. doi:10.1029/2000WR900410.
- Josza, L. 1988. Increment core sampling techniques for high quality cores. Rep. Spec. Publ. SP-30. Forintek Canada Corp., Vancouver, B.C.
- Jull, M.J. 1999. Douglas-fir silviculture “on the edge”: silvicultural systems at the northern range of the species. In *Ecology and management of interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) at the northern extreme of its range*. Proceedings of a Workshop held 7–9 October 1996 in Fort St. James, British Columbia. Edited by J.D. Lousier, and W.B. Kessler. University of Northern British Columbia, Prince George, B.C. pp. 34–44.
- Kimmins, J.P. 1997. *Forest Ecology*. 2nd ed. Prentice-Hall Inc, Upper Saddle River, N.J.
- Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia (Berl.)*, **155**: 445–459.
- Kozlowski, T.T., and Pallardy, S.G. 1997. *Growth control in woody plants*. Academic Press, San Diego, Calif.
- Lassoie, J.P., and Salo, D.J. 1981. Physiological response of large Douglas-fir to natural and induced soil water deficits. *Plant Physiol. Biochem.* **11**: 139–144.
- Leathers, D.J., Yarnal, B., and Palecki, M.A. 1991. The Pacific/North American teleconnection pattern and United States climate. part I: regional temperature and precipitation associations. *J. Clim.* **4**(5): 517–528. doi:10.1175/1520-0442(1991)004<0517:TPATPA>2.0.CO;2.
- Littell, J.S. 2006. Climate impacts to forest ecosystem processes: Douglas-fir growth in north-western U.S. mountain landscapes and area burned by wildfire in western U.S. eco-provinces. Ph.D. dissertation, University of Washington, Seattle, Wash.
- Littell, J.S., and Peterson, D.L. 2005. A method for estimating vulnerability of Douglas-fir growth to climate change in the north-western U.S. *For. Chron.* **81**: 369–374.
- Littell, J.S., Peterson, D.L., and Tjoelker, M. 2008. Douglas-fir growth in mountain ecosystems: water limits tree growth from stand to region. *Ecol. Monogr.* **78**(3): 349–368. doi:10.1890/07-0712.1.
- Meidinger, D., and Pojar, J. 1991. *Ecosystems of British Columbia*. B.C. Ministry of Forests, Victoria, B.C.
- Mekis, É., and Hogg, W.D. 1999. Rehabilitation and analysis of Canadian daily precipitation time series. *Atmos.–Ocean*, **37**: 53–85.
- Mitchell, T.D., and Jones, P.D. 2005. An improved method of constructing a database of monthly climate observations and associated high-resolution grids. *Int. J. Climatol.* **25**(6): 693–712. doi:10.1002/joc.1181.
- Moore, R.D., and McKendry, I.G. 1996. Spring snowpack anomaly patterns and winter climatic variability in British Columbia, Canada. *Water Resour. Res.* **32**(3): 623–632. doi:10.1029/95WR03640.
- O'Neill, G.A., Hamann, A., and Wang, T. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *J. Appl. Ecol.* **45**(4): 1040–1049. doi:10.1111/j.1365-2664.2008.01472.x.
- Pederson, N., Cook, E.R., Jacoby, G.C., Peteet, D.M., and Griffin, K.L. 2004. The influence of winter temperatures on the annual radial growth of six northern range margin tree species. *Dendrochronologia*, **22**(1): 7–29. doi:10.1016/j.dendro.2004.09.005.
- Peterson, D.W., and Peterson, D.L. 2001. Mountain hemlock growth responds to climatic variability at annual and decadal time scales. *Ecology*, **82**: 3330–3345.
- Pike, R.G., Spittlehouse, D.L., Bennett, K.E., Egginton, V.N., Tschaplinski, P.J., Murdock, T.Q., and Werner, A.T. 2008a. Climate change and watershed hydrology: part I — recent and projected changes in British Columbia. *Streamline Watershed Manag. Bull.* **11**: 1–6.
- Pike, R.G., Spittlehouse, D.L., Bennett, K.E., Egginton, V.N., Tschaplinski, P.J., Murdock, T.Q., and Werner, A.T. 2008b. Climate change and watershed hydrology: part II — hydrologic implications for British Columbia. *Streamline Watershed Manag. Bull.* **11**: 8–13.
- Régent Instruments Inc. 2005. WinDENDRO™. An image analysis system for tree-rings analysis. Régent Instruments Inc., Quebec, Que.

- Rising, J.D., and Somers, K.M. 1989. The measurement of overall body size in birds. *Auk*, **106**: 666–674.
- Salo, D.J. 1974. Factors affecting photosynthesis in Douglas-fir. Ph.D. dissertation, University of Washington, Seattle, Wash.
- Smith, C.A., and Sardeshmukh, P. 2000. The effect of ENSO on the intraseasonal variance of surface temperature in winter. *Int. J. Climatol.* **20**(13): 1543–1557. doi:10.1002/1097-0088(20001115)20:13<1543::AID-JOC579>3.0.CO;2-A.
- Stahl, K., Moore, R.D., and McKendry, I.G. 2006. The role of synoptic-scale circulation in the linkage between large-scale ocean–atmosphere indices and winter surface climate in British Columbia, Canada. *Int. J. Climatol.* **26**(4): 541–560. doi:10.1002/joc.1268.
- Tabachnick, B.G., and Fidell, L.S. 2001. Using multivariate statistics. 4th ed. Allyn and Bacon, Boston, Mass.
- Tardif, J.C., Conciatori, F., Nantel, P., and Gagnon, D. 2006. Radial growth and climate responses of white oak (*Quercus alba*) and northern red oak (*Quercus rubra*) at the northern distribution limit of white oak in Quebec, Canada. *J. Biogeogr.* **33**(9): 1657–1669. doi:10.1111/j.1365-2699.2006.01541.x.
- The Mathworks Inc. 2007. Matlab 2007 [online]. The Mathworks Inc., Natick, Mass. Available from <http://www.mathworks.com> [accessed 5 January 2008].
- Vaganov, E.A., Hughes, M.K., Kirilyanov, A.V., Schweingruber, F.H., and Silkin, P.P. 1999. Influence of snowfall and melt timing on tree growth in subarctic Eurasia. *Nature*, **400**(6740): 149–151. doi:10.1038/22087.
- Vincent, L.A., and Gullett, D.W. 1999. Canadian historical and homogenous temperature datasets for climate change analyses. *Int. J. Climatol.* **19**(12): 1375–1388. doi:10.1002/(SICI)1097-0088(199910)19:12<1375::AID-JOC427>3.0.CO;2-0.
- Vincent, L.A., Zhang, X., Bonsal, B.R., and Hogg, W.D. 2002. Homogenization of daily temperatures over Canada. *J. Clim.* **15**(11): 1322–1334. doi:10.1175/1520-0442(2002)015<1322:HODTOC>2.0.CO;2.
- Wang, T., Hamann, A., Spittlehouse, D.L., and Aitken, S.N. 2006. Development of scale-free climate data for western Canada for use in resource management. *Int. J. Climatol.* **26**(3): 383–397. doi:10.1002/joc.1247.
- Waring, R.H. 1991. Responses of evergreen trees to multiple stresses. In *Response of plants to multiple stresses*. Academic Press, San Diego, Calif. pp. 371–390.
- Watson, E., and Luckman, B.H. 2002. The dendroclimatic signal in Douglas-fir and ponderosa pine tree-ring chronologies from the southern Canadian Cordillera. *Can. J. For. Res.* **32**(10): 1858–1874. doi:10.1139/x02-096.
- Wigley, T.M.L., Briffa, K.R., and Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J. Appl. Meteorol.* **23**(2): 201–213. doi:10.1175/1520-0450(1984)023<0201:OTAVOC>2.0.CO;2.
- Zhang, Q.B., and Hebda, R.J. 2004. Variation in radial growth patterns of *Pseudotsuga menziesii* on the central coast of British Columbia, Canada. *Can. J. For. Res.* **34**(9): 1946–1954. doi:10.1139/x04-078.
- Zweifel, R., Zimmermann, L., Zeugin, F., and Newbery, D.M. 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *J. Exp. Bot.* **57**(6): 1445–1459. doi:10.1093/jxb/erj125. PMID:16556628.